

THE ENALIARCTINAE
A NEW GROUP OF EXTINCT
AQUATIC CARNIVORA AND A
CONSIDERATION OF THE ORIGIN
OF THE OTARIIDAE

EDWARD MITCHELL AND RICHARD H. TEDFORD

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 151 : ARTICLE 3 NEW YORK : 1973

THE ENALIARCTINAE
A NEW GROUP OF EXTINCT AQUATIC
CARNIVORA AND A CONSIDERATION OF
THE ORIGIN OF THE OTARIIDAE

EDWARD MITCHELL
Arctic Biological Station
Fisheries Research Board of Canada

RICHARD H. TEDFORD
Curator
Department of Vertebrate Paleontology
The American Museum of Natural History

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 151 : ARTICLE 3 NEW YORK : 1973

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 151, article 3, pages 201-284, figures 1-27, tables 1-4

Issued June 27, 1973

Price: \$3.55 a copy

CONTENTS

ABSTRACT	205
INTRODUCTION	208
Acknowledgments	209
Abbreviations	210
Materials	210
Measurements	210
STRATIGRAPHY	211
Lithostratigraphy	211
Biostratigraphy	214
SYSTEMATICS	218
Order Carnivora Bowditch, 1821	218
Superfamily Canoidea Simpson, 1931	218
Family Otariidae Gray, 1825	218
Enaliarctinae, New Subfamily	218
<i>Enaliarctos</i> , New Genus	218
<i>Enaliarctos mealsi</i> , New Species	220
Description	220
Ontogenetic Age and Sex	243
Comparison with Fissipeds	243
Comparison with Pinnipeds	252
MORPHOLOGIC EVIDENCE FOR AQUATIC ADAPTATION	261
PHYLETIC RELATIONSHIPS	263
OTHER SUPPOSED AQUATIC CARNIVORES IN THE NORTH PACIFIC	265
ASSOCIATED FAUNA	268
Pyramid Hill Local Fauna	268
Woody Local Fauna	272
PALEOECOLOGY	275
SUMMARY AND CONCLUSIONS	276
LITERATURE CITED	280

ABSTRACT

THE NEW GENUS and species *Enaliarctos mealsi* is based on two partial skulls and two natural endocranial casts discovered in the early Miocene Pyramid Hill Sand Member of the Jewett Sand at Pyramid Hill, Kern County, south-central California. The new mammalian subfamily Enaliarctinae is based on *Enaliarctos mealsi*.

Enaliarctos mealsi was a medium-sized arctoid carnivore, a transitional species that departed in structure from terrestrial ursids (Hemicyoninae) and evolved in the direction of aquatic pinnipeds (Otariinae). Ursid features include presence and structure of upper and lower fourth premolars and of two molariform, quadrate-shaped upper molars; the development of sulcus cruciatus and the presence of an "ursid lozenge"; and the morphology of the basicranium and middle ear. Features associated with aquatic adaptation include an enlarged narial chamber, reduced olfactory bulbs, wide snout, long and transversely arched palate, tendencies toward premolarization of the molars, narrow interorbital region, and enhanced brain circulation.

A family Ursidae is recognized that includes primitive terrestrial ursids such as *Cephalogale*, *Hemicyon*, and *Dinocyon* in the subfamily Hemicyoninae. The Enaliarctinae is placed in Carnivora among the Otariidae near the Desmatophocinae. The Otariinae, specifically the Arctocephalini, might be descended from the Enaliarctinae.

The phyletic lineage Hemicyoninae – Enaliarc-

tiniae – Otariinae emphasizes that the pinniped diphyly problem should be redefined to focus on the relationship of the Phocidae to even earlier Arctoidea. The Desmatophocinae might represent a third group independently derived from the middle-Tertiary adaptive radiation of Arctoidea.

A lectotype for *Neotherium mirum* Kellogg, 1931 is chosen, and the species is included in the Enaliarctinae.

The Pyramid Hill local fauna is named and characterized. The fauna comprises invertebrates and more than 39 species of Elasmobranchii, Teleostei, Chelonia, Aves, Squalodontidae (with a summary of northeast Pacific records), Delphinoidea, Mysticeti, Carnivora, Equidae (*Anchitherium* cf. *A. agatensis*), and Tayassuidae (*Desmathyus* sp.). The composition of the fauna indicates a warm-water, near-shore environment at the site of deposition.

The Woody local fauna is named, characterized, and discussed. It is slightly higher stratigraphically in the same rock unit, 14 miles north of Pyramid Hill. We question Wilson's (1935) identifications of otariid pinnipeds from these rocks and doubt the validity of the "phocid" record.

The Pyramid Hill Sand can be assigned to the later Arikareean Land Mammal Age and to the Vaqueros Molluscan Stage, and it lies close to or includes the boundary between the Zemorrian and Saucesian Foraminiferal stages.

Enaliarctinae—новая группа вымерших плотоядных животных и соображения о происхождении

РЕЗЮМЕ

Новый род и вид *Enaliarctos mealsi* выделен по двум частично сохранившимся черепам и двум естественным внутрочерепным ядрам, обнаруженным в миоцене песчаной толщи Джукст Пирамидного Холма, район Керн, юг центральной Калифорнии. Новое подсемейство млекопитающих Enaliarctinae основано на *Enaliarctos mealsi*.

Enaliarctos mealsi был плотоядным животным полярного типа средних размеров. Это промежуточный вид, отклонившийся по строению от земных Ursidae (Hemicyoninae) и развившийся в направлении водных ластоногих (Otariinae). Признаки, унаследованные от Ursidae, включают наличие и строение верхних и нижних четвертых ложнокоренных зубов и двух квадратных верхних коренных зубов, развитие крестовидной борозды (sulcus cruciatus) и наличие

«пластинки Ursidae», а также морфологию основы черепа и среднего уха. Признаки, связанные с приспособлением к водной среде, состоят из увеличенной носовой полости, редуцированных обонятельных луковиц, широкого рыла, длинного поперечно-дугообразного нёба, в склонности к развитию ложно-коренных зубов, узкой области между орбитами и усиленном кровообращении мозга.

Признано, что семейство Ursidae включает примитивных земных млекопитающих типа *Cephalogale*, *Hemicyon* и *Dinocyon* в составе подсемейства Hemicyoninae. Относим Enaliarctinae к Carnivora и помещаем их среди Otariidae, недалеко от Desmatophocinae. Возможно, что Otariinae, в особенности Arctocephalini, произошли от Enaliarctinae.

Происхождение типа и расы по линии Hemicyoninae - Enaliarctinae - Otariinae подчеркивает необходимость пересмотра вопроса эволюционной раздвоенности ластоногих, в процессе которого особое внимание должно быть уделено связи Phocidae с еще более древними Arctoidea. Возможно, что Desmatophocinae являются третьей группой, возникшей самостоятельно вследствие среднетретичного приспособительного расселения Arctoidea.

Избран лейкотип вида *Neotherium mirum* Kellogg, 1931, и вид включен в состав Enaliarctinae. Дается список и описание местной фауны Пирамидного Холма, состоящей из беспозвоночных и из более 39 видов Elasmobranchii, Teleostei, Chelonia, Aves, Squalodontidae (с обобщением сведений о северо-восточной части Тихого океана), Delphinoidea, Mysticeti, Carnivora, Equidae (*Anchitherium* cf. *A. agatensis*), и Tayasuidae (*Desmathys* sp.). Состав фауны указывает на существование тепловодной прибрежной среды в месте отложения.

Дается список и характеристика местной фауны Вууда, а также соображения по поводу этой фауны, находящейся стратиграфически выше в той же толще пород, в 14 милях от Пирамидного Холма. Мы ставим под сомнение определение Уилсона (1935) ластоногих типа ушастых тюленей из этих пород и достоверность сведений о «тюленевых.»

Песок Пирамидного Холма можно отнести к поздне-арикарскому веку земных млекопитающих и к вакверскому ярусу моллюсков. Пески залегают недалеко от границы или на границе земорийского и сосесского ярусов фораминифер.

エナリアークテイニ Enaliarctinae : 水生絶滅食肉目の一新種群とアシカ科 Otariidae の起原についての一考察

概括

新しい属であり種であるエナリアクトス・ミールシ *Enaliarctos mealsi* はカリフォルニア州中南部カーン Kern 郡ピラミッド・ヒル Pyramid Hill にあるジュエツト Jewett 砂岩の第三紀中新世代初めに属するピラミッドヒル砂岩層の中で発見された二つの頭蓋骨の断片と二つの頭蓋内面の自然に形成されたキャストにその根拠をおいている。新しい哺乳動物の亞科であるエナリアークテイニ Enaliarctinae は、エナリアークトス ミールシ *Enaliarctos mealsi* がその根拠である。

Enaliarctos mealsi は、中形のアークトイド arctoid 食肉動物であつた。構造的には、陸生くま類 (Hemicyoninae) から別れて、水生鯨脚動物 (otariinae) の方向に進化した過渡期の種である。くまとしての特徴は、上下部にある四つめの小臼歯、二つの臼歯型四方形をした上部臼歯の存在と構造、十字形のみぞの發達、‘ursid lozenge’ の存在、形態的には、頭蓋基部にある中耳があげられる。水生動物からの適應と考えられる特色としては、廣い鼻孔室、減少した嗅官球根、廣い口部、長く横にアーチ型になつた口蓋、臼歯の小臼歯化への傾向、せまい内部眼窩部、發達した頭腦のじゆんかんなどである。

くま科 Ursidae は亞科である陸生くま科 Hemicyoninae に属するセファロゲール *Cephalogale* ヘルミサイオン *Hemicyon*、ディノサイオン *Dinocyon* のような原始陸生くまを含むと理解されている。この Enaliarctinae は、食肉目 Carnivora の中のデスマトフォシニ Desmatophocinae に近いあしか科 Otariidae に分類される。Otariinae 特にアークトセファリニ Arctocephalini は、この Enaliarctinae から派生したと考えられる。

系統發生的にみると、Hemicyoninae - Enaliarctinae - Otariinae を結ぶ系統は、鯨脚動物の歯の交換の問題を、あざらし科 Phocidae との関係より更にそれ以前のアークトイデ Arctoidea との關聯において再定義されるべきであることを示している。Desmatophocinae は Arctoidea の第三紀中期の適應放散から獨立して派生した第三グループを代表するものと考えられる。

さて、ネオセリウム・ミルウム・ケログ *Neotherium mirum* Kellogg (1931 年) のレクトタイプがえらばれ、その種は、Enaliarctinae に含まれた。

ピラミッド・ヒル地域動物相が命名され特徴づけられた。それは、無脊つゝい動

物 invertebrates と、板鰓類 Elasmobranchii, 硬骨類 Teleostei, かめ類 Chelonia, 鳥類 Aves (北東太平洋記録の概略として), 有鱗類 Squalodontidae, いるか類 Delphinoidea, ミステイセテイ Mysticeti, 食肉類 Carnivora, 馬類 Equidae (中新生及び漸新生代の馬の化石種 *Anchitherium*, *A. agatensis* 参照), いのしし類 Tayassuidae (*Desmathyus* 種) など 39 以上の種から構成されている。この動物相は、暖水の、沈積物のある岸に近い環境に生育していたことを物語っている。

更にウーディ Woody 地域動物相と名づけられ、特色づけられ、そして論じられている。即ち、ピラミッドヒルから 14 マイル北方の層位的には、同じ岩質の

やや高い層から発見されたものに関してである。我々は、Wilson が (1935 年) この岩層から発見したものを、あしか鱗脚動物 otariid pinnipeds であると結論したことに疑問をもつのみならず、あざらし属 "phocid" の記録の妥当性をうたがうものである。

ピラミッドヒル砂岩層は、アリカリアン陸生哺乳動物時代 Arikareean Land Mammal Age の後期とバクエロシアン軟体動物期 Vaquerosian molluscan Stage に属すると分類できる。それはゼモリアンとソーセシアン有孔虫類微小動物期 Zemorrian and Saucesian foraminiferal stages の境界に近い時期か、または、それを含む時期である。

INTRODUCTION

THE INVASION of a radically new adaptive zone by any group of organisms is a phenomenon of great interest to evolutionists, yet it is rare that such major changes can be followed clearly in the fossil record. The adaptation to life in the open seas by terrestrial mammals such as were involved in the origin of the whales (Order Cetacea) and seals, sea lions, and walruses (Order Carnivora, usually grouped as a Suborder Pinnipedia) has so far lacked documentation in the fossil record. In the case of the whales many hypotheses have been advanced as to the nature of their terrestrial progenitor and the evolutionary steps that led from that ancestor to the highly modified pelagic animals that are the first fossil record of the group in the Eocene (see Van Valen, 1968, for recent discussion). The pinnipeds, on the other hand, have long been suspected of originating within the fissiped Carnivora and thus cannot have invaded the seas earlier than the beginning of the Oligocene when their closest fissiped relatives appear. The larger steps involved in the adaptation of the ancestral pinnipeds to pelagic life can be deduced by comparing them with their nearest relatives, the arctoid carnivores. Considerable speculation has been offered over the years regarding these evolutionary steps, their origin and course, but the actual history has so far been unknown. Recent opinion has been ably summarized by McLaren (1960).

The discovery of an early Miocene aquatic carnivore whose skull and dentition is morphologically intermediate between terrestrial canoid carnivores and the aquatic otariid pinnipeds is announced herein. Geochronologically this discovery represents the oldest pinniped-like carnivore reported from the Pacific Coast of North America and as such deserves consideration as a potential otariid ancestor. In the lower Miocene rocks of California and Oregon there are additional traces of highly adapted pinniped-like creatures which may also be otariids. The confirmation of the exact phylogenetic significance of the aquatic carnivore described in the present report to the history of the Otariidae will have to await further discoveries in the lower Miocene and Oligocene near-shore marine beds of the Pacific Coast.

The marine Miocene succession exposed along the western flank of the Sierra Nevada northeast of Bakersfield and north of the Kern River has been famous since the last century as a rich repository of marine mollusks and vertebrates (see fig. 1). Anderson's (1911) pioneer study of the stratigraphy reviewed the earlier work and mentioned the discovery of marine vertebrates, especially shark teeth, by previous workers. Anderson gave notice of the remarkable concentration of marine mammal bones and shark teeth within the upper part of the Miocene section (Anderson's faunal Zone C) at a place later known as "Sharktooth Hill" (sect. 25, T. 28 S, R. 28 E, M.D.B. & M.). This locality yielded a great quantity of fossil vertebrate remains which were described over the ensuing years by Remington Kellogg (mammals, see especially 1931), Alexander Wetmore (birds, 1930), Loye H. Miller (birds, 1961, 1962). Mitchell (1965) has prepared a historical summary of the work at Sharktooth Hill. This single locality has provided an important part of existing knowledge of the Miocene pinnipeds and cetaceans on the Pacific Coast.

The association of marine vertebrate remains and mollusks at the base of the Miocene section was also noted by Anderson (his faunal Zone A) and later in passing by Loel and Corey (1932) in their study of the paleontology of the Vaqueros Formation. The exposures at Pyramid Hill (sect. 14, T. 28 S, R. 29 E, M.D.B. & M.) were particularly mentioned as prolific sources of vertebrate remains and mollusks. No systematic attempt was made to collect fossil mammals from the Pyramid Hill outcrops, but Kellogg (1932) described a porpoise skull (*Argyrocetus joaquinensis*) from these exposures donated by G. M. Cunningham of the Standard Oil Company of California.

In 1928 Leslie E. Wilson, then with Bakersfield Junior College, began systematic prospecting of the basal part of the Miocene section north of Poso Creek in the Woody Quadrangle. Numerous fossil cetacean remains and some limb and axial elements of "pinnipeds" were collected from exposures of the basal Miocene sandstones which Wilson correlated with Anderson's faunal Zone A along Willow Spring Creek

in sects. 12 and 13, T. 26 S, R. 28 E. Six genera (four new) and six species of odontocete whales were described by Wilson (1935) from these localities. Curiously Kellogg's *Argyrocetus joaquiniensis* was not identified among Wilson's collections. The "pinniped" remains were allocated to the families Phocidae, Otariidae, and "Alloidesmidae." All the pinniped records are suspect, as indicated in this study.

No additional work was done in these deposits until 1950 when Chester Stock visited Pyramid Hill and collected fragmentary porpoise crania and two cranial fragments referred to the aquatic carnivore described in this report. Stock concluded that the fragments were pinnipeds and compared them with the living harbor seal (*Phoca* Linnaeus) and the monk seal (*Monachus* Fleming). He intended to describe these remains and had accumulated some notes for this purpose at the time of his death in 1950.

Late in 1960 the present authors decided to report on Stock's material and had begun to prepare the fossils so that they could be fully described. On January 8 of the following year Harold S. Meals discovered a fine skull of the same animal at Pyramid Hill. This specimen showed us clearly that we were dealing with a truly remarkable aquatic carnivore that possessed many of the features expected of an intermediate between terrestrial fissipeds and pelagic pinnipeds. Isolated teeth of the same form were later found at Pyramid Hill by Meals and Richard C. Bishop. The assembled collection enables us now to describe more fully this interesting animal.

In a joint study it seems advisable to point out the division of responsibility. The study broke naturally into two parts along lines dictated by our respective interests and backgrounds. Mitchell concentrated on the overall description of the skull and on comparisons of cranial structures to assess age, sex, aquatic adaptations, and ecology of *Enaliarctos* and its relationship to known fossil and living pinnipeds and other North Pacific aquatic carnivores. Tedford was responsible for the stratigraphy, the description of dentition, and most of the comparisons of dental structures to determine the relationship of *Enaliarctos* to known fossil and living fissipeds. We collaborated on the description of the auditory region and endocast and comparisons with living and extinct pinnipeds and fissipeds. The section on associated fauna was also a joint effort.

ACKNOWLEDGMENTS

We gratefully acknowledge the critical review received from the following colleagues: Mr. C. A. Repenning (U.S. Geological Survey, Menlo Park, California); Dr. Francis H. Fay (U.S. Department of Health, Education and Welfare, College, Alaska); Dr. Jere H. Lipps (University of California, Davis); Mr. Lawrence G. Barnes (University of California, Berkeley); and Miss Barbara Mason (Fisheries Research Board of Canada). We have benefited greatly from their comments, but must take full responsibility for the views expressed herein.

We are grateful to Drs. Theodore Downs and James R. Macdonald of the Los Angeles County Museum for permission to study the materials in their care and for aiding our research in many ways. Through their kindness, the museum records and comparative osteological materials were made available to us, and space was provided for our work at the museum. Important comparative material was lent us by the late Dr. Remington Kellogg, and Dr. David H. Johnson of the National Museum of Natural History, Smithsonian Institution; Dr. Johannes Hürzeler of the Naturhistorisches Museum, Basel; Dr. Victor B. Scheffer of the United States Fish and Wildlife Service, Seattle; Dr. J. Arnold Shotwell, University of Oregon; Dr. Elwyn L. Simons, Yale University; and the late Dr. R. A. Stirton of the Museum of Paleontology University of California, Berkeley. Professor Viret of the Museum des Sciences Naturelles, Lyon, contributed a valuable cast of the skull of *Cephalogale gracile*. Dr. F. Bachmayer lent the Vienna skull of *Cephalogale minor* and generously permitted us to fully prepare it.

Our thanks are also extended to the late Dr. R. A. Stirton, Dr. Shelton P. Applegate of the Los Angeles County Museum, and Mr. John Fitch of the California Department of Fish and Game, for identifying fossil vertebrates from Pyramid Hill rocks. Dr. D. E. Savage contributed important notes on the auditory region of *Cephalogale*. Dr. Warren O. Addicott of the United States Geological Survey advised us on certain stratigraphic matters and permitted free use of his important unpublished study of the Miocene strata of the Kern River district. Dr. L. Radinsky of the University of Chicago gave valuable advice in the interpretation of the endocasts. Messrs. Richard C. Bishop, Joseph Arndt, Harold Meals, and other accomplished

collectors contributed important vertebrate remains from the Pyramid Hill Sand. Dr. Jere H. Lipps also rendered assistance in the field.

Mr. Chester Tarka of the American Museum of Natural History prepared some of the figures and organized most of the illustrative material for this paper. The photographs for other figures are the work of Mr. Armando Solis of the Los Angeles County Museum. The drawings are by Mr. Karoly Fogassy of the University of California at Riverside, except where credited to others in the legends.

ABBREVIATIONS

AMNH, the American Museum of Natural History
 AMNH CA, the American Museum of Natural History, comparative anatomy collection
 AMNH(M), the American Museum of Natural History, Department of Mammalogy collection
 Basel, Natural History Museum, Basel
 BM(NH), British Museum (Natural History)
 CAS, California Academy of Sciences, San Francisco
 LACM, Los Angeles County Museum
 LACM (CIT), California Institute of Technology collection now in the Los Angeles County Museum
 Lyon, University of Lyon
 UCMP, Museum of Paleontology, University of California, Berkeley
 UOMNH, University of Oregon Museum of Natural History
 USNM, National Museum of Natural History, Smithsonian Institution
 USFWS, United States Fish and Wildlife Service, Seattle
 Vienna, Natural History Museum, Vienna
 YPM, Peabody Museum of Natural History, Yale University

MATERIALS

The following specimens were examined in the course of this study: Mustelidae: *Paleogale lagophaga* (Cope), AMNH 9311, 38825; *Potamotherium vallentoni* Geoffroy, AMNH 22520; *Lutra canadensis* (Schreber), LACM M109, M980, M1723; *Enhydra lutris* (Linnaeus), LACM M1572, M1602, M1737. Procyonidae: *Plesictis gennettoides* Pomel, AMNH 11001. Ursidae: *Cephalogale gracile* (Pomel), AMNH 39298 (cast of Lyon St. G. 795), Basel S. G. 2158; *C. minor* Filhol, Vienna A 4445; *Kolponomos clallamensis* Stirton, UCMP 55056 (cast). Otariidae: *Desmatophoca oregonensis* Condon, UOMNH F735;

Allodesmus kelloggi Mitchell, LACM 4320, 4565; *Allodesmus (Atopotarus) courseni* (Downs), LACM 1376; *Dusignathus santacruzensis* Kellogg, UCMP 27121; *Pontolis magnus* True, cast of USNM 3792; *Otaria byronia* (Blainville), LACM M1610, M1715; *Eumetopias jubata* (Schreber), LACM M418, M765, M1692, M1774; *Zalophus californianus* (Lesson), LACM M419, M1694, M1696, M1700, M1707, M1788, 9337, AMNH CA1339; *Arctocephalus australis gracilis* Nehring, USNM 23331, AMNH CA2440; *Arctocephalus australis galapagoensis* Heller, LACM M1656, M1657; *Arctocephalus philippii townsendi* Merriam, LACM 1109, M1735; *Callorhinus ursinus* (Linnaeus), LACM M1699; *Odobenus rosmarus* (Linnaeus), LACM M702, AMNH M35159. Phocidae: *Phoca vitulina* Linnaeus, LACM M484, M485, M486, M1733, 9338; *Erignathus barbatus* (Erxleben), LACM specimen; *Cystophora cristata* (Erxleben), USNM 188962; *Mirounga leonina* (Linnaeus), USNM 241199; *Mirounga angustirostris* (Gill), LACM M1726, M1727.

MEASUREMENTS

For ease in comparing the specimens of *Enaliarctos* with other species we will use a base measurement, the width of the snout across the median borders of the infraorbital canal, and divide this into other measurements to arrive at a ratio that can be used to compare different skulls. This measurement was chosen because it is one of the few that can be taken on both LACM 4321 and LACM (CIT) 5303, and because it reflects one of the major parameters of the skull. The measurement, as we use it, does not include any ventrolateral flaring of the edge of the palate below the infraorbital canals or inflation of the snout above the canals, as the breadth is taken as seen in an anterior view of the skull and is the minimum width between the infraorbital canals. We shall refer to this infraorbital canal minimum width as our basal dimension (BD). The BD for LACM 4321, the holotype, is 54 mm., and that for LACM (CIT) 5303 is 50 mm.

Unless otherwise stated, it is to be understood that all measurements are given in millimeters. The methods of mensuration are explained in the text or tables.

STRATIGRAPHY

IN THE YEARS since the Miocene rocks of the Kern River district were first described there has been considerable refinement of the detailed stratigraphy of these deposits. The early discovery of oil in the district and the exploitation of this resource focused attention on the physical stratigraphy and biostratigraphy. However, little detailed information was published on the areal extent and lithology of the Miocene rocks until the appearance of Addicott's (1970a) monograph on the Kern River Miocene gastropods. The best maps available are the generalized small scale maps produced by the California State Division of Mines (Jahns, 1954) and, recently, in connection with the state mapping program (Smith, 1965). Donald G. Birch (*In* Keen, 1943, fig. 1) and Hackel and Krammes (1958) mapped smaller areas including the paleontologically important region between Sharktooth Hill and Pyramid Hill, and more recently Dibblee et al. (1965) have mapped the same area at a scale of 1:48,000.

LITHOSTRATIGRAPHY

Anderson's (1911) study was the first attempt at subdivision of the Miocene section into lithologic units. He applied the name "Temblor Group" to these rocks thus extending to the Kern River district the term he had first used in 1905 for part of the thick sequence of later Cenozoic rocks exposed in the Mount Diablo Range. In the Kern River district the "Temblor Group" was subdivided into two "members," a "basal member," which Anderson described as "sands, sandy ash-beds, pumiceous ash-beds, and conglomerate with marine fossils," and an upper member of "clays, ashy beds, shales, white and yellow sands with marine fossils." These deposits rest on the plutonic rocks of the Sierra Nevada and are in turn overlapped unconformably by the Kern River "Group" (Anderson, 1911).

Subsequent work by many geologists has resulted in further subdivision of Anderson's "Temblor Group" (fig. 2). The "basal member" became, in ascending order of outcrop units, the Walker Formation, Vedder Sand, Pyramid Hill Sand, and part if not all of the Jewett Sand. The "upper member" comprised the succeeding

Freeman Silt, Olcese Sand, and Round Mountain Silt. These units have assumed formational status over the years and are now widely recognized in surface and subsurface within the district (see fig. 3). Anderson's designation of the whole sequence as "Temblor Group" has been abandoned. Ferguson (*In* Weaver et al., 1944) presented a summary of the stratigraphic column which has not been seriously modified by subsequent published work. Recently Warren O. Addicott has extensively reviewed the Miocene physical stratigraphy and paleontology in the Kern River district (1956, summarized in 1965). He has kindly allowed us free use of his unpublished work and we have drawn heavily from it.

The fossil vertebrate remains from Pyramid Hill discussed herein come from the base of the Jewett Sand within the interval originally designated the "Pyramid Hills Sand" by Wilson in 1935. Wilson described the "Pyramid Hills Sand" (emended to Pyramid Hill Sand in later usage) from outcrops along Willow Spring Creek north of the Woody road in sect. 12, T. 26 S, R. 28 E, as a "hard, white-to-brown sandstone which reaches a thickness in excess of 60 feet locally, the whole member attaining a thickness of 160 feet." At this locality the Pyramid Hill Sand overlies the nonmarine Walker Formation. No type locality was designated, but the name of the unit and subsequent usage indicate that Pyramid Hill in sect. 14, T. 28 S, R. 29 E is the type. Wilson did not discuss the relationship between the Pyramid Hill Sand and the overlying Jewett Sand. These units are gradational both vertically and along the strike. The basal part of the Pyramid Hill Sand is a coarse angular sandstone containing local conglomerate bodies along the contact with underlying units. This basal coarse sand, often called the "grit zone," is widespread and can be traced from the Pyramid Hill area northwest to the Woody road, a distance of about 14 miles. Above the "grit zone" the Pyramid Hill Sand becomes a fine-grained sand with coarser sand lenses and finally passes to silty sand and sandy silt of the typical Jewett Sand (see fig. 2). Subsequently Addicott (1970a) reduced the Pyramid Hill Sand to member status within the

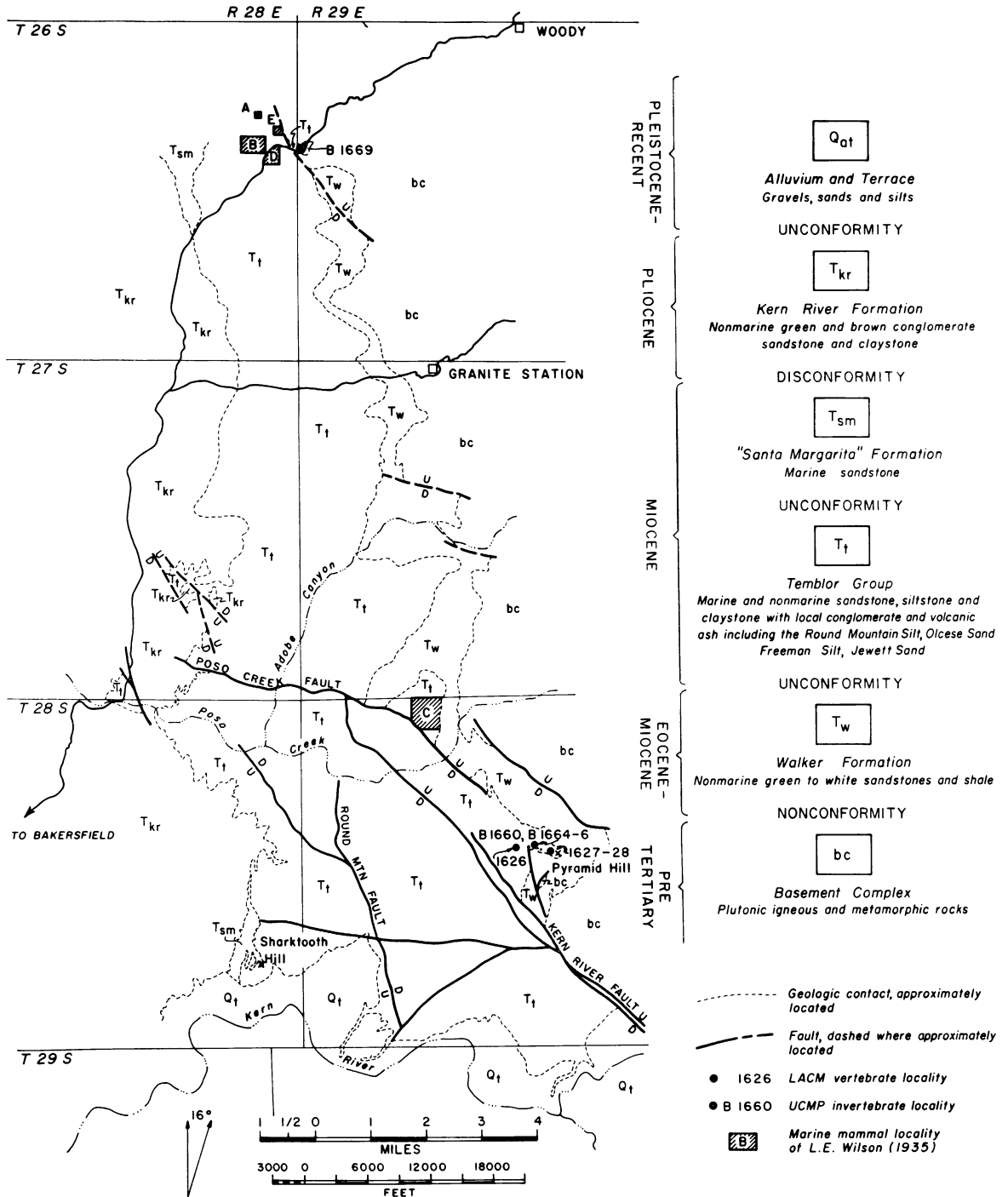


FIG. 1. Geological sketch map showing major Cenozoic rock units of Kern River district north of Kern River. Invertebrate and vertebrate fossil localities indicated are those discussed in text. Geology compiled from various sources, including Addicott (ms, 1956) and Hackel and Krammes (1958). Marine mammal localities of Wilson (1935) include: A. *Allodelphis pratti* (type locality); *Macrodelphis kelloggi* (type locality); *Acrodelphis bakersfieldensis* (type locality); *Miodelphis californicus* (type locality); cetothere; "phocid"; "otariid." B. *Miodelphis californicus*; ?*Macrodelphis californicus*. C. *Acrodelphis bakersfieldensis*. D. *Doliodelphis littlei* (type locality). E. *Eurhinodelphis extensus* (type locality).

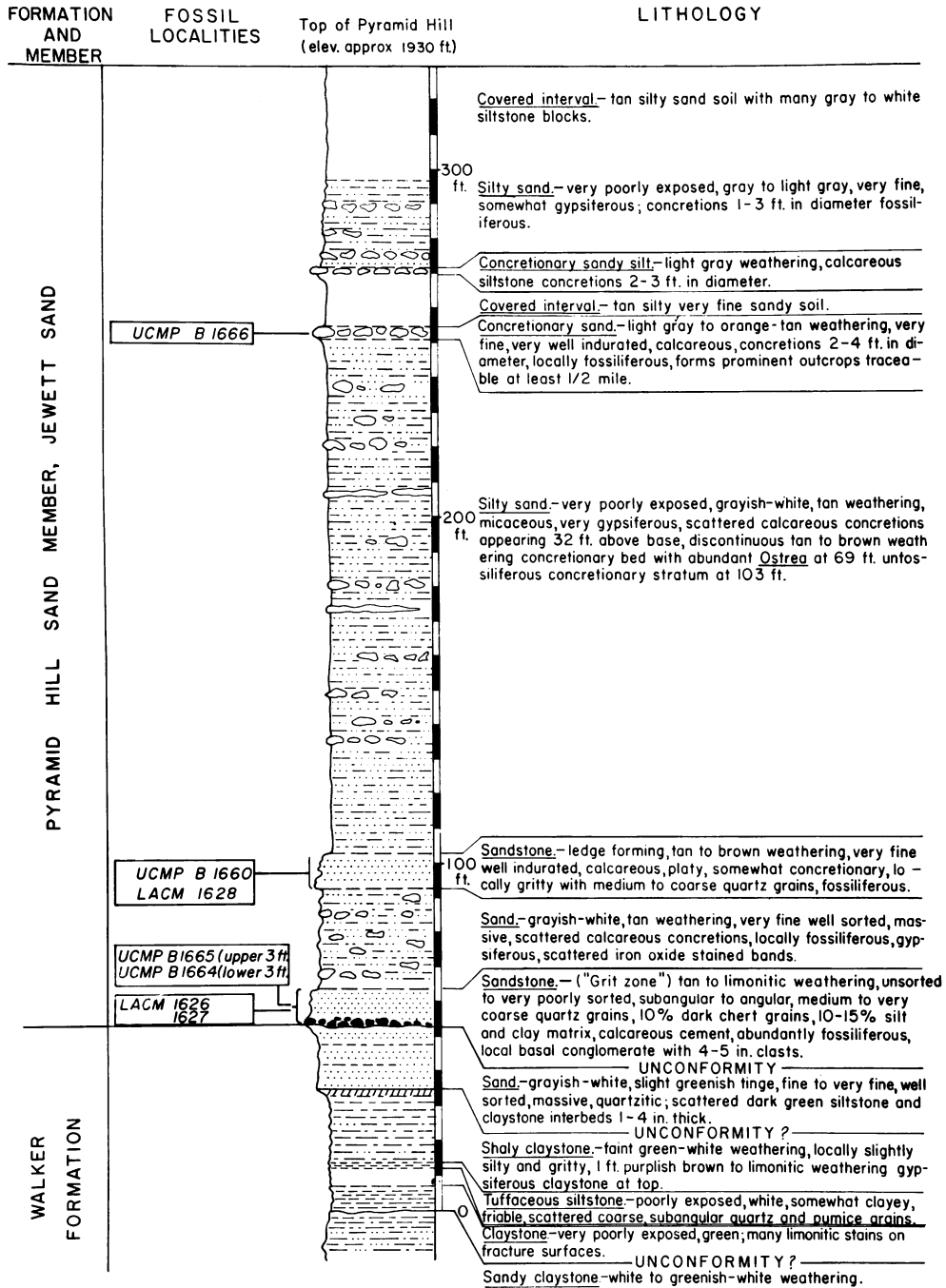


FIG. 2. Columnar section on southwestern slope of Pyramid Hill, north side of a major east-west draining canyon. Bottom of section begins just west of north-south tributary of canyon, east of section-line fence, NW 1/4 SW 1/4 sect. 14, T. 28 S, R. 29 E, M.D.B. & M. Measured by Addicott (ms, 1956). The stratigraphic positions of critical invertebrate and vertebrate localities are shown (tables 1 and 4). Holotype and referred cranial material of *Enaliarctos mealsi* came from base of Pyramid Hill Sand, most likely from basal "grit zone." Referred teeth and land mammal remains are from LACM Loc. 1626, here projected into line of section.

Jewett Sand because of the conformable, gradational relationship between these units in outcrop. He chose a subsurface type section (Shell Oil "Jewett" 1, sect. 29, T. 28 S, R. 29 E) where electric logs permit easier recognition of the top of the unit.

The cranial remains of the aquatic carnivore described in this report were obtained from concretionary sandstone blocks lying on the southern slope of Pyramid Hill in the NE $\frac{1}{4}$ SW $\frac{1}{4}$ NE $\frac{1}{4}$ SW $\frac{1}{4}$ sect. 14, T. 28 S, R. 29 E [LACM (CIT) Loc. 481, LACM Locs. 1627 and 1628]. These blocks had broken off the indurated sandstone ledges which project from the otherwise smooth contour of the hill and tumbled downslope (see fig. 4). The fossil remains are thus from somewhere within the lower 40 feet of the Pyramid Hill Sand Member as exposed at that locality. There is a great likelihood that all are from the basal coarse sand and shell beds (i.e. the "grit zone") that project from the hill, particularly the holotype skull fragment which had such a matrix adhering to it. There were no other prominent sandstone beds of similar character directly up-slope from the spot where it was found (fig. 4).

The isolated teeth referred to the aquatic carnivore come from a different locality within the same stratigraphic interval on the southwestern slope of Pyramid Hill in the SE $\frac{1}{4}$ NW $\frac{1}{4}$ SE $\frac{1}{4}$ sect. 15, T. 28 S, R. 29 E (LACM Loc. 1626). These specimens were sieved from the loose, coarse sand of the "grit zone."

Figure 2 presents a columnar section measured by Addicott on the southern slope of Pyramid Hill. This diagram has been annotated to show the actual or inferred stratigraphic position of the various vertebrate remains reported herein. In addition the stratigraphic positions of critical invertebrate assemblages are shown, and faunal lists provided in table 1.

BIOSTRATIGRAPHY

Anderson (1911) was the first geologist to attempt a biostratigraphic subdivision of the Miocene sequence in the Kern River district. He described three faunal zones, designated from oldest to youngest, A, B, and C, and gave a faunal list of the mollusks from each unit. The lowest faunal zone includes the abundant molluscan remains at Pyramid Hill from the base of the Jewett Sand of later authors (see also Loel and Corey, 1932, for a revised faunal list).

Faunal Zone B includes the Barker's Ranch "horizon" at the top of the Olcese Sand and base of the Round Mountain Silt (see Anderson, 1905; Anderson and Martin, 1914; and Keen, 1943, for lists and descriptions of the fauna). Anderson's faunal Zone C includes the Sharktooth Hill bone bed and the sparse molluscan fauna from the overlying silty sands directly below the unconformity with the Kern River Formation. Addicott (1965, 1970a) has recently summarized and extended knowledge of the biostratigraphy of the Miocene deposits in this region.

The marine mammal remains described in this report come from strata which yield the molluscan fauna characteristic of Anderson's Zone A. Loel and Corey (1932) studied the molluscan faunal sequence from Zone A in greater detail and pointed out that the assemblage from the basal conglomerate (the "grit zone") includes such typical Vaquerosian mollusks as *Lyropecten magnolia* (Conrad) and *Crasostrea vaquerosensis* (Loel and Corey). This assemblage was regarded as being characteristic of the upper part of the "Vaqueros horizon." In the sense in which Loel and Corey used the terms Vaqueros "formation" or "horizon" they are time-stratigraphic units of stage-age magnitude. Loel and Corey's work has been accepted by most stratigraphers as the biostratigraphic basis for the Vaqueros Stage. The molluscan fauna from the finer-grained sands (incorrectly called "Vedder sands" by Loel and Corey) overlying the "grit zone" was regarded as transitional between the Vaqueros and the succeeding Temblor stages. Recently Addicott (1965, and see our table 1) has shown that although this fauna is not so rich as that from the "grit zone" it does contain such typical Vaqueros Stage mollusks as *Ostrea eldridgei yneziana* Loel and Corey and various pectinids including *Vertipecten nevadanus* (Conrad) and *Chlamys hertleini* (Loel and Corey). The association of abundant carbonized wood and fossil cones of conifers with this assemblage suggests shallow-water, near-shore, or perhaps even lagoonal conditions. Such a fauna occurs throughout the Jewett Sand. The overlying Freeman Silt is sparsely fossiliferous, but does not contain the typical Temblor stage assemblage of the Barker's Ranch "horizon." These do not appear until the succeeding Olcese Sand. Thus the scanty molluscan fauna of the Freeman Silt belongs to the transition between

TABLE 1
MOLLUSCA FROM THE PYRAMID HILL SAND MEMBER, JEWETT SAND, PYRAMID HILL,
KERN COUNTY, CALIFORNIA

	Localities ^a			
	"Grit Zone"			Above
	B1664	B1665	B1660	"Grit Zone" B1666
Gastropoda				
<i>Argobuccinum</i> sp. indet.	—	X	X	—
<i>Bruclarkia barkeriana santacruzana</i> (Arnold), 1908	—	X	X	X
<i>B. yaquinana</i> (Anderson and Martin), 1914	—	X	—	—
<i>Calyptrea</i> aff. <i>C. inornata</i> (Gabb), 1866	—	X	—	—
<i>Calyptrea</i> sp. indet.	—	—	X	—
cf. <i>Cancellaria condoni</i> Anderson, 1905	—	—	X	—
<i>Crepidula princeps</i> Conrad, 1856	—	X	—	—
<i>Epitonium</i> sp.	—	X	—	—
<i>Ficus ocoyana</i> (Conrad)	X	X	X	—
<i>Kelletia</i> sp.	—	X	—	—
<i>Megasurcula howei</i> Hanna and Hertlein, 1938	—	X	?	X
<i>Oliva californica</i> Anderson, 1904	—	—	?	—
<i>Polinices reclusianus andersoni</i> (Clark), 1918	?	X	X	?
aff. <i>Thais carrizoensis</i> Loel and Corey, 1932	—	X	—	—
<i>T. trophonoides</i> Anderson and Martin, 1914	—	X	—	—
<i>Trophon kernensis</i> Anderson, 1905	—	X	—	—
Pelecypoda				
<i>Acilia conradi</i> var. Schenk, 1936	—	X	—	—
<i>Amiantis</i> sp. indet.	—	—	X	—
<i>Anadara</i> sp. indet.	—	—	X	—
<i>Atrina alamedensis</i> (Yates in Cooper), 1888	—	X	cf.	—
<i>Chione</i> cf. <i>C. temblorensis subtemblorensis</i> Loel and Corey, 1932	—	—	X	—
<i>Crassatella granti</i> (Wiedey), 1928	—	X	—	—
<i>Dosinia margaritana</i> Wiedey, 1928	—	—	X	—
<i>D. m. projecta</i> Loel and Corey, 1932	—	X	X	—
<i>Dosinia</i> sp. indet.	—	X	—	—
<i>Glycymeris tenuimbricata</i> Clark, 1918	—	X	X	—
<i>Lucinoma acutilineata</i> (Conrad), 1849	—	X	—	X
<i>Lyropecten magnolia</i> (Conrad), 1857	X	—	—	—
<i>Macoma</i> sp. indet.	X	—	—	—
<i>Milthia sanctaerucis</i> (Arnold), 1910	—	X	X	—
<i>Mytilus middendorfi</i> Grewingk, 1848	—	X	—	—
<i>Ostrea</i> sp. indet.	—	X	X	—
"Pecten" sp. indet.	—	X	—	—
<i>Securella panzana</i> (Anderson and Martin), 1914	—	X	cf.	—
<i>S. valentinei</i> (Wiedey), 1929	—	—	X	—
<i>Solen</i> sp. indet.	—	X	X	—
<i>Spisula albaria</i> (Conrad), 1848	—	—	X	—
<i>Spisula</i> sp. indet.	—	X	X	—
<i>Tellina nevadensis</i> Anderson and Martin, 1914	—	—	?	—
<i>Trachycardium vaquerosensis</i> (Arnold), 1908	—	—	X	—
<i>Vertipecten fucanus kernensis</i> (Hertlein), 1925	X	X	—	—
Scaphopoda				
<i>Dentalium petricola</i> Dall, 1909	—	X	—	—
Cirripedia				
Barnacle plates	—	X	—	—

^a See figure 2 for relative stratigraphic positions of the UCMP localities listed. The identifications are those of W. O. Addicott (ms), slightly modified (Addicott, 1968, personal commun.).

the Vaqueros and Temblor stages in this district. We consider the Freeman Silt to represent sediments deposited within the latest part of Vaqueros time. Accordingly the age of the marine carnivore remains discussed here would fall well within the span of Vaqueros time but probably toward the later part of this interval.

It is well demonstrated that the deposits of transgressive seaways are notoriously diachronous, a consideration which raises the question

of the contemporaneity of the various outcrops of the Pyramid Hill Sand. One cannot be certain, for instance, that the fossil mammal remains described here from the outcrops at Pyramid Hill (Pyramid Hill local fauna) are contemporaneous with those from the Pyramid Hill Sand in Wilson's (1935) area along Willow Spring Creek, 14 miles to the northwest (Woody local fauna). Diagnostic molluscan faunas, which would serve as a check, were not found

EPOCHS	STAGES—AGES			FORMATIONS	Marine Mammal Faunas
	Mammalia	Mollusca	Foraminifera		
PLIOCENE	Hemphillian			Kern River Formation	
	Clarendonian	Santa Margarita	Delmontian ?—?—?—?—? Mohnian	"Santa Margarita" Formation	
MIOCENE	Barstovian	Temblor	Luisian	Round Mountain Silt	← Sharktooth Hill l.f.
	? — ? — ?		Relizian	Upper Olcese Sand	
	Hemingfordian			Middle Lower	
		Vaqueros	Saucesian	Freeman Silt	
				Jewett Sand	
	Arikareean			Pyramid Hill Sand	← Woody l.f. ← Pyramid Hill l.f.
		Zemorrian	Vedder Sand Walker Formation		

FIG. 3. Time-stratigraphic subdivision of rock column in Kern River district according to various biostratigraphic disciplines. Rock column (formations) is slightly modified from Ferguson (in Weaver et al., 1944). Foraminiferal stage boundaries follow Weaver et al. (1944) except for position of Zemorrian-Saucesian boundary in local column. Exact position of upper boundary of Arikareean Age and Vaqueros Stage in terms of Kern River column is conjectural, but no higher than lower member of Olcese Sand which bears a Temblor fauna (Addicott, ms). Evidence from Caliente Mountain (Repenning and Vedder, 1961) suggests approximate equivalence of upper boundary of Vaqueros Stage and Arikareean Age. Freeman Silt above Jewett Sand contains limited molluscan fauna without typical Temblor species. Faunas of this stratigraphic position and composition are usually referred to as transitional Vaqueros-Temblor assemblages. We have placed Vaqueros-Temblor stage boundary above the Freeman Silt to correspond with first appearance of Temblor species as suggested by Addicott (1965). Arikareean Age, Vaqueros Stage, and Zemorrian Stage are assigned to Miocene Series-Epoch following established usage in North America (Weaver et al., 1944; Wood et al., 1941) although current correlations based on planktonic foraminifera suggest that all or part of these units may belong to Oligocene (see text). Part of Mohnian and all Delmontian stages are assigned to Pliocene because they are known to equate with mammalian Clarendonian Age (Evernden et al., 1964) traditionally assigned to that epoch by vertebrate paleontologists.

with the marine mammal remains in the latter area. This is an important consideration in view of the occurrence of pinniped-like remains at both localities. Some evidence suggesting that these occurrences are not contemporaneous is indicated by Addicott's discovery that Wilson's marine mammal localities in sects. 12 and 13, T. 26 S, R. 28 E are downthrown along a fault trending along the floor of Willow Springs Creek which brings them into juxtaposition with the Pyramid Hill-basement contact to the east. The stratigraphic position of Wilson's material is not exactly known but projecting subsurface control to the west (Addicott, ms, sect. D-D') suggests that they lie at horizons 100–500 ft. above the Pyramid Hill-basement contact. Poorly preserved Mollusca from greenish white, tuffaceous sandy siltstones at the base of the Pyramid Hill Sand east of this fault (UCMP B1669, road cut in NW $\frac{1}{4}$ sect. 18, T. 26 S, R. 29 E) yielded *Hinnites* and *Lyropecten magnolia* indicating time equivalence with the "grit zone."

The many well cores available from the Kern River district oil fields have provided information on the benthonic foraminiferal assemblages from down-dip equivalents of the surface units in this area. According to R. M. Kleinpell (1938, fig. 14) and Kleinpell and Weaver (1963, fig. 5) the "grit zone" with *Lyropecten magnolia* is equivalent to the upper part of the Zemorrian Foraminiferal Stage. The overlying Jewett Sand contains foraminifera characteristic of the lower part of the succeeding Saucesian Stage. Ferguson (*In* Weaver et al., 1944) and Rudel (1965), however, assign all the Pyramid Hill Sand to the Saucesian Stage. Thus the Pyramid Hill Sand lies close to the boundary between the Zemorrian and Saucesian stages.

The discovery of isolated teeth of land mammals at LACM Loc. 1626 by Harold S. Meals provides evidence for the age of the "grit

zone" in terms of the North American mammal ages. As discussed below, cheek teeth of species of the horse *Anchitherium* Meyer and a peccary (cf. *Desmathyus* Matthew) are comparable in stage of evolution with forms from the Harrison Formation of the Great Plains. A later Arikareean Mammal Age for the "grit zone" of the Pyramid Hill Sand and the contained fossils is thus indicated.

In summary, the fossil invertebrates (table 1) and vertebrates from the Pyramid Hill Sand Member of the Jewett Sand provide evidence for assignment of these strata to the Pacific Coast megafossil and microfossil stages, and to the North American mammal ages. The fortunate occurrence of near-shore marine deposits containing remains of land mammals as well as mollusks plus the evidence from the deeper water facies with benthonic foraminifera provide a direct means of interrelating the geochronologies of the various biostratigraphic disciplines. The Kern River district is one of the important localities in southern California in which these relationships can be studied (see Durham, Jahns, and Savage, 1954; Repenning and Vedder, 1961). Our figure 3 shows the succession of rock, time-rock, and time units within the Miocene of the Kern River district as these are currently understood.

In the present paper we adopt the long-held convention that the Vaqueros and Zemorrian stages and the Arikareean Age represent early Miocene time in western North America (Weaver et al., 1944; Wood et al., 1941). Recent investigations of planktonic foraminifera from the California Tertiary column (Lipps, 1967) suggested that these stages-ages may correspond with part of or all the Oligocene series-epochs as previously intimated by Eames et al. (1962, pp. 35, 91). Evaluation of these data is outside the scope of this report.

SYSTEMATICS

ORDER CARNIVORA BOWDICH, 1821

SUPERFAMILY CANOIDEA SIMPSON, 1931

FAMILY OTARIIDAE GRAY, 1825

ENALIARCTINAE, NEW SUBFAMILY

ENALIARCTOS, NEW GENUS

ETYMOLOGY: Greek *Enalios*, of the sea; *arktos*, bear, referring to the arctoid, including ursid, Carnivora.

TYPE: *Enaliarctos mealsi*, new species.

DIAGNOSIS: A line of aquatic canoids, departing in structure from the terrestrial hemicyonine ursids in those features related to the adaptation of these animals to life in the sea. The subfamily diagnosis follows that of the genus. Skull with no major adventitious vacuities or regions of poor ossification; muzzle short and broad; nasal bones short; bony external nares facing anterodorsally; nasolabialis fossa present; squamosal-jugal contact simple squamous type; cross section of interorbital region in form of I-beam for structural rigidity, with alisphenoid and palatine bones inflated into struts; pterygoid hamulus reduced; supraorbital processes small or absent; interorbital region long, parallel-sided; lacrimal bone present; lacrimal foramen present; orbit relatively large; anterior margin of orbit lying over P⁴; infraorbital foramen large, wider than high; palate slightly arched, with prominent posterior palatine foramina; choanal tube ending at internal nares near level of front of braincase, far behind last cheek tooth; complete vertical choanal septum not extending far behind M²; cheek tooth row slanting toward medial line; dental formula: I[?] C¹ P¹⁻⁴ M¹⁻²; P¹⁻³ large relative to P⁴; P⁴ without parastyle, protocone a broad shelf on lingual side of paracone, its root somewhat posterior to paracone root; molars greatly reduced; M¹ three rooted, of quadrate, cynoid form, smaller than P⁴; M² with single-rooted, tiny alveolus; M₁ with greatly reduced metaconid, talonid unicuspid (hypoconid); foramen rotundum opening into alisphenoid canal; posterior lacerate foramina large and anteroposteriorly ovate; postglenoid foramen small; basicranium wide between bullae; bullae slightly inflated, smooth and flask-

shaped with long auditory tube of small caliber directed slightly anteriorly; stylomastoid foramen surrounded by bulla and mastoid; apical bullar spur and fossa absent; posterior bullar projection absent; tympanohyal posteromedial to stylomastoid foramen; vagina processus styloidei present, separated from foramen stylo-mastoidem by weak projection of bulla; posterior carotid foramen large, well separated from posterior lacerate foramen but near posteromedian corner of bulla; internal carotid artery enclosed within wall of bulla anteriorly, between bulla and basioccipital posteriorly; tympanic cavity narrow, deep, and not extended into surrounding elements; crista tympani produced into tympanic cavity, with free ventral edge; sulcus tympanicus ovate, longest diameter anteroposteriorly; low septum across anterior end of bulla; fossa for muscularis major (tensor tympani) shallow; eminentia vagina processus styloidei absent; no suprameatal fossa; sagittal crest present; lambdoid crest present; occipital shield with much surface relief; skull almost as dorsoventrally deep at level of infraorbital foramina as at auditory bullae; preglenoid and postglenoid processes tightly wrapping around mandibular condyle about 180 degrees; paroccipital and mastoid processes stout and united by ridge of bone; mastoid process directed ventrolaterally; braincase squared off in front, with discrete corners; major crease in wall of braincase corresponding to position of pseudosylvian fissure; cerebral hemispheres cover most of cerebellum; optic chiasma at level of sulcus coronalis; back edge of hypophysis at level of front edge of foramen ovale; olfactory bulbs reduced in size, narrow; gyrus frontalis tiny; gyrus sigmoideus making up major portion of anterior surface of cortex; gyrus lateralis greatly overlapped by expanded gyrus suprasylvius posterior; sulcus coronalis and sulcus lateralis broadly continuous; gyrus coronalis greatly expanded anteroposteriorly; opercularization of gyrus ectosylvius anterior partly accomplished by expanded gyrus coronalis; arterial supply and venous drainage of brain rich; minimum of three major left dorsal cerebral veins branching off left dorsal sagittal sinus; fossa cerebellaris very wide, entrance shaped like figure eight.

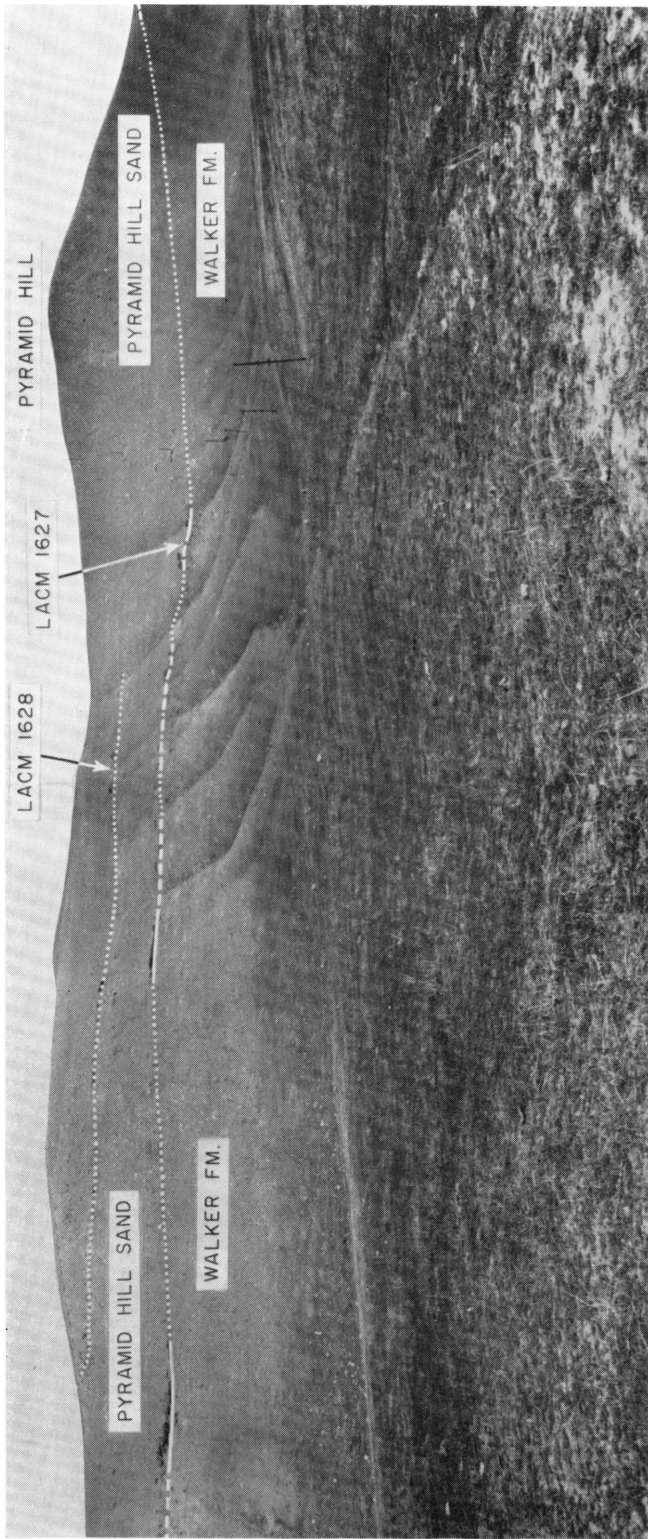


FIG. 4. Looking northeast at southern face of Pyramid Hill (Hill 2098) which surmounts the eastern (right) end of the ridge (middle of S $\frac{1}{2}$ sect. 14, T. 28 S, R. 29 E). Walker Formation-Pyramid Hill Sand contact is sketched, and position of more important fossil marine mammal producing horizons of Los Angeles County Museum, LACM Locs. 1627, 1628, are shown. Holotype and referred crania of *Enaliarctos medsi* were obtained from the float boulders of cemented coarse sandstone from "grit zone" of Pyramid Hill Sand, seen lying on lower slopes of hill below Walker Formation-Pyramid Hill Sand contact. Photos taken by Chester Stock, January 21, 1950 (negatives 1409, 1410, on file in Los Angeles County Museum; both photos labeled "locality LACM (GIT) 481").

Enaliarctos mealsi, new species

Figures 5-18; tables 2, 3

ETYMOLOGY: The patronym is given in honor of Mr. Harold S. Meals, who discovered the holotype and other remains of this marine carnivore and who has materially contributed to research collections from the Pyramid Hill and Sharktooth Hill regions.

HOLOTYPE: Cranial fragment lacking the snout, right zygoma, much of the lambdoidal crest, left mastoid and paroccipital processes, much of both right and left P⁴, right M¹, and both right and left M², LACM 4321.

TYPE LOCALITY: Holotype found in a concretion lying on the surface directly below LACM Locs. 1627 and 1628 (fig. 4). LACM Loc. 1627 is in the lowest fossiliferous, resistant sandstone bed exposed on the southwest flank of Pyramid Hill, Kern County, California, and LACM Loc. 1628 is in a fossiliferous concretionary sandstone bed about 50 ft. stratigraphically above LACM Loc. 1627. Both localities are approximately 1750 ft. north and 1850 ft. east of the southwest corner of sect. 14, T. 28 S, R. 29 E, Rio Bravo Ranch Quadrangle (USGS 1954, 1:24,000). Pyramid Hill is also shown on photo ABL-39R-144, Kern County Index 6, United States Department of Agriculture. LACM (CIT) Loc. 481, the locality of the referred specimens LACM (CIT) 5302 and 5303, was less specifically characterized as the southwest flank of Pyramid Hill, in ledges of fossiliferous concretionary sandstone. LACM (CIT) Locs. 481 and 1627 may be synonymous.

FORMATION: "Grit zone," base of the Pyramid Hill Sand Member of the Jewett Sand. LACM Loc. 1627 is in the basal part of the "grit zone," LACM Loc. 1628 is near the top of this unit as locally recognized at Pyramid Hill (see fig. 2).

AGE: Early Miocene, late Arikareean Land Mammal Age, late Vaqueros Molluscan Stage, latest Zemorrian Foraminiferal Stage.

DESCRIPTION

The skull (figs. 5-7, table 2) lacks the snout from the anterior border of the orbits forward, the right zygomatic arch, and smaller portions of the right occipital condyle and braincase. The specimen was found encased in a small concretion, but those parts exposed to weathering are preserved almost as well as the areas exposed by preparation.

The interorbital area is broad anteriorly and tapers slightly inward posteriorly. Supra-orbital processes are almost absent, being represented only by parallel ridges about 17 mm. long. The supraorbital ridges are slightly more pronounced at the anterior end than at the posterior. About 8 mm. anterior to the supra-orbital ridges are indications of a rather deep fossa for the quadratus labii superioris muscle that evidently lay on the anterolateral surface of the snout, lateral to the nasal bones and anterior to the orbits. The dorsal margin of this fossa is produced into a ridge on the left side and not on the right side. Subdued ridges run from the anterior end of the supraorbital ridges posteromedially to the beginning of the sagittal crest, enclosing a very shallow depression for the origin of muscles. The sagittal crest begins just a few millimeters behind the posterior end of the supraorbital ridges, and runs at a consistent height of about 5 to 6 mm. back to the lambdoid crest. The dorsal surface of the interorbital area of the skull slopes laterally at an angle of about 20 degrees, then ventromedially at an angle of about 60 degrees to form the dorsomedial wall of the orbit. The width of the dorsal surface of the interorbital area 17 mm. behind the supra-orbital ridges is 33 mm., and just below this point the least width of the interorbital septum is less than 20 mm.

The medial wall of the orbit (fig. 5) is a broadly concave plate of bone, channeling back into the orbital fissure. Sutures in this area of the skull, as in other areas, are sometimes quite hard to make out, but it is certain that most of the dorsal half of the medial wall is composed of the frontal bone. We cannot pick out the surrounding sutures, but we assume that a lacrimal bone is present around the 2 mm. by 4 mm. diameter lacrimal foramen. The lacrimal foramen lies inside the orbit, slightly medial to the infra-orbital canal and 9 mm. dorsal to it. The infra-orbital canals are ovate, 8 mm. by 13 mm., with the long axis tilted about 30 degrees dorsolaterally. There are indications of a foramen 2 mm. in diameter in the medial wall of the infraorbital canal, leading perhaps into the nasal chamber. The ventral floor of the infraorbital canal is continued within the orbital area by the horizontal plate of maxillary that forms the base of the maxillary portion of the zygomatic arch laterally, whereas the medial wall of the infraorbital canal is continued posteriorly by the vertical

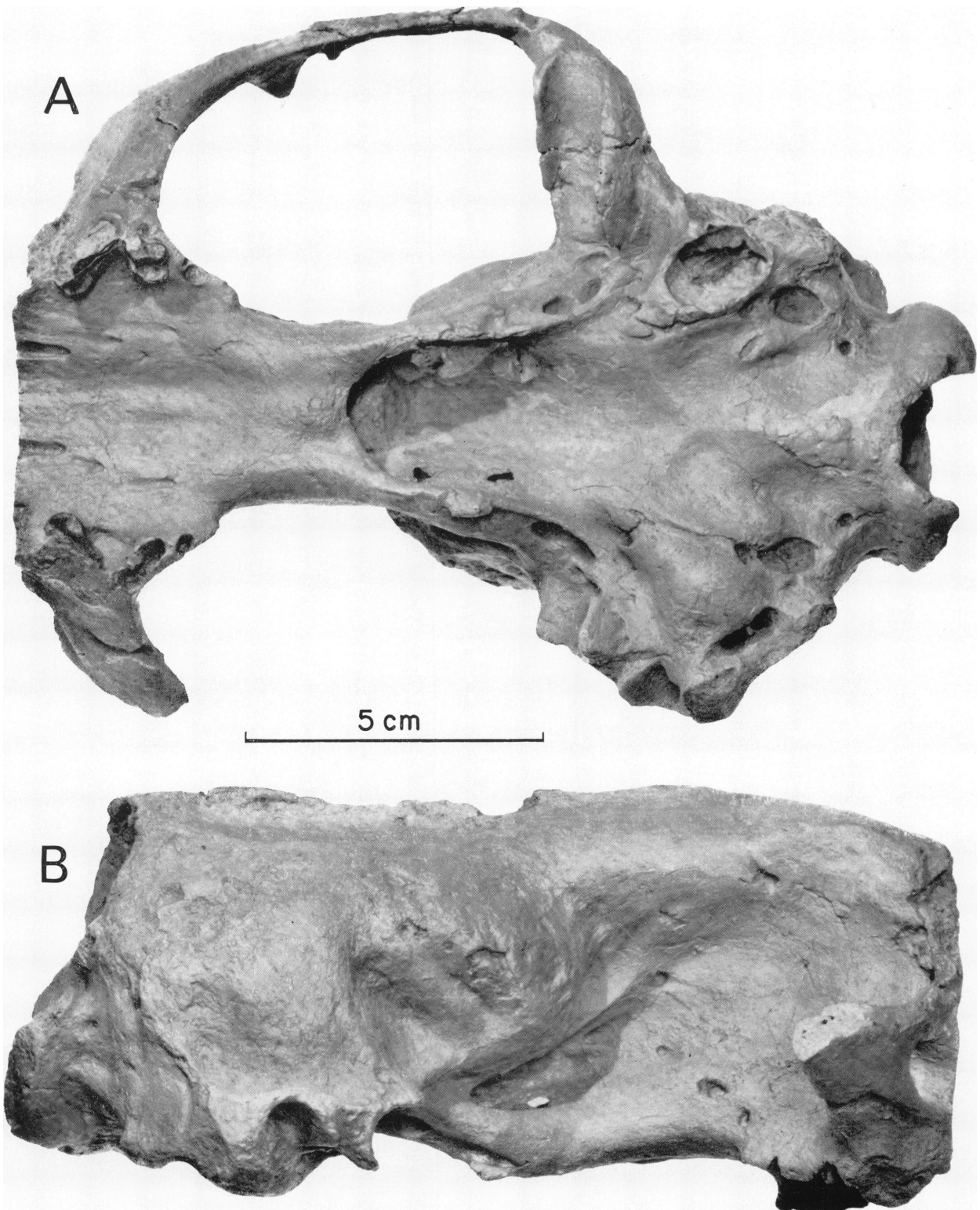


FIG. 5. Holotype skull of *Enaliarctos mealsi*, LACM 4321, from LACM Loc. 1627, Pyramid Hill Sand Member, Jewett Sand, early Miocene, at Pyramid Hill, Kern County, California. A. Ventral view. B. Right lateral view.

TABLE 2
MEASUREMENTS (IN MILLIMETERS) OF THE SKULL OF *Enaliarctos mealsi*

	Holotype LACM 4321	Referred LACM(CIT) 5303
Postpalatal length (palatal notch-basion)	92.5	—
Basion to anterior edge of zygomatic root (18) ^a	150	—
Basion to anterior edge of glenoid fossa (21, "bend of pterygoid")	67.5	—
Breadth of zygomatic root of maxilla	22.0	18.5
Breadth of skull across anterior root of P ²	—	44.3
Breadth of skull across anterior root of P ⁴	—	56.0
Breadth of palate between protocone roots of P ⁴ (15)	38.0	33.5
Breadth of palate behind posterior end of maxillaries	32.0	ca.29
Zygomatic breadth (17)	ca.140	—
Auditory breadth (19)	ca. 94	—
Mastoid breadth (20)	ca.100	—
Paroccipital breadth	65.7	—
Greatest width of anterior nares (3)	—	31.4
Greatest breadth of nasals	—	ca.22
Greatest length of nasals (4)	—	ca.35
Greatest interorbital constriction (6)	—	44.0
Breadth of skull across supraorbital processes (7)	37.7	31.4
Greatest intertemporal constriction	31.0	26.2
Breadth of braincase at anterior edge of glenoid fossa (8)	59.6	—

^aNumbers in parentheses indicate correspondence with the same dimension used by Sivertsen (1954, pp. 18–20) in his craniometry of the Otariidae.

interorbital plate. A ridge runs from the dorsal part of the maxillary portion of the zygomatic arch posteriorly on the interorbital plate and merges with a longitudinal inflation of the palatines leading to the bridge across the alisphenoid canal. Immediately dorsal to this ridge, 3 mm. behind and 5 mm. below the lacrimal foramen, lies an oval depression 1 to 2 mm. deep with well-defined borders. On the left side of LACM 4321 this depression is blind, but on the right side two small foramina seem to open into the depression, one in the anterodorsal and one in the posterodorsal margin. Forty-two mm. posterior to the infraorbital canal, and lying just below the ridge running along its dorsal margin, is a large sphenopalatine foramen 5 mm. long and 3 mm. wide. Six mm. anteroventral to the sphenopalatine foramen lies a smaller posterior palatine foramen 2 mm. in diameter. The posterior palatine foramen is situated just dorsal to the end of the horizontal flange of the maxillary bone that supports the cheek tooth row.

The area of the vertical medial wall of the orbit dorsal to the ridge bordering the dorsal margin of the infraorbital canal is slightly

irregular, being covered with gentle depressions and raised areas. In the dorsoposterior part of this vertical plate are some small ridges slanting ventroposteriorly and abutting into the braincase. The ventralmost and most prominent of these ridges, which is continuous posteriorly with the ventral margin of the braincase at this point, forms the dorsal margin of a small foramen, about 3 mm. in diameter, which can only be the optic foramen. An ethmoidal foramen 3 mm. in diameter lies 15 mm. anterodorsal to the optic foramen, at the tip of the ridge (the pterygoideus-frontal ridge) forming the dorsal border of the optic foramen.

A large fossa lies between the ventral floor of the braincase and the dorsal surface of the expanded palatine bones, leading posteriorly into the anterior lacerate foramen (or orbital fissure), foramen rotundum, and the anterior opening of the alisphenoid canal. These foramina cannot be seen in a lateral view of the skull; it is necessary to look into this large fossa (more correctly termed the orbital fissure) from an anterodorsal viewpoint. In the external wall of the orbital fissure can be found a small triangular

hole that might be the exit of the pterygoid canal. The alisphenoid canal opens via a foramen of 4 mm. diameter on the ventrolateral side of the strut between basicranium and palate, within the alisphenoid bone. Immediately posterolateral to it is a 2.5 mm. diameter foramen ovale. In the dorsal roof of the foramen ovale on the right side (but not on the left) is a small ridge, possibly lying between the areas of the foramen through which pass the mandibular nerve and the accessory meningeal artery. Two other structures lie lateral to the foramen ovale and medial to the glenoid fossa: a small nutrient foramen tucked behind the median posteroventral margin of the glenoid (or condyloid) fossa, and a larger fossa between the median border of the glenoid fossa and the foramen ovale. This latter fossa is 2 mm. in diameter on the right side and twice as large on the left side. It may have served as part of the origin of the external pterygoid musculature. Between the nutrient foramen and the more medial and larger fossa is a line of five or six very small nutrient foramina.

The palate of the holotype (fig. 5), at the level of P³ where the specimen is broken, is arched dorsally to a relatively high degree. At this point it is about 47 mm. wide and 11 mm. high, measuring from the level of the alveoli. This arching diminishes rapidly posteriorly, however, being only 5 mm. high at the level of M², which is 45 mm. wide, center of alveolus to alveolus. Posterior to the level of M² there are a pair of subdued bumps on the palate on either side of a slight ridge, which runs down the center of the palate from about the level of M¹ back to the posteromedial margin of the palate, ending in a third small bump.

There are three prominent pairs of posterior palatine foramina on the palate, opening between the levels of P⁴ and M¹. The anterior pair is the largest (about 2 mm. diameter) with deep furrows 1 mm. deep leading anteriorly, the center pair is smallest in size without pronounced furrows, and the third pair is of medium size with long and shallow furrows running anteriorly. The anterior pair are 14 mm. apart, the posterior pair 23 mm. apart, and the central pair 20 mm. apart. Another, yet smaller, pair lie between the central and posterior pair of posterior palatines and probably should be termed nutrient foramina.

The fossa for reception of the lower carnassial

tooth is a prominent feature in the palate. It is about 8 mm. in diameter and 3 mm. deep, lying in the opening formed by the upper carnassial, which is oriented 45 degrees posterolaterally, and the molar row, which is oriented 55 degrees posteromedially.

The posterior border of the palate is lunate in outline; there is no posterior median palatal spine. The posterior border of the horizontal palate is sharp-edged, but laterally abuts into the vertical portion of the palatine bone, which is inflated to a high degree. The posterior end of the cheek tooth row ends about 4 mm. anterior to the end of the palatine tuberosity of the maxillary, which is effectively the posterior end of the horizontal portion of the maxillary bone. Posterior to this point the ventrolateral border of the palate is rounded and no discrete separation may be made between the ventral and lateral surfaces of the palatine bones. This roundness externally is accompanied by a hollowing out of the vertical part of palatines within the internal choana, effectively forming a strut between the bottom of the palate and the bottom of the braincase. This strut is thin, about 4 mm. thick anteriorly, but becomes markedly thickened, up to 8 mm., at the level of the opening of the anterior lacerate foramen. At this same level the ventromedial margin of the strut, including at this point both palatine bone and alisphenoid bone, is produced into a thin flaring ridge which runs back to project into the ventral floor of the braincase medial to the glenoid fossa. As it passes the posterior opening of the alisphenoid canal and the foramen ovale it forms the sharp medial lip of these foramina. The ridge beneath the opening of the anterior lacerate foramen is projected ventrally approximately 5 mm. to form a small pterygoid process that does not project below the ventrolateral margin of the entire palate. Although preservation is something of a problem at this point, our interpretation holds that there is no well-developed pterygoid hamulus.

The internal choana is 15 mm. high and 24 mm. wide. The dorsal roof of the choana, that is, the regions of the palatine, presphenoid, and basisphenoid bones, is laterally concave and forms a long, straight trough whose surface is continuous back to the scars for the insertion of the longus capitis and rectus capitis anterior muscles on the ventral surface of the braincase. Two very small, fine sutures or breaks define

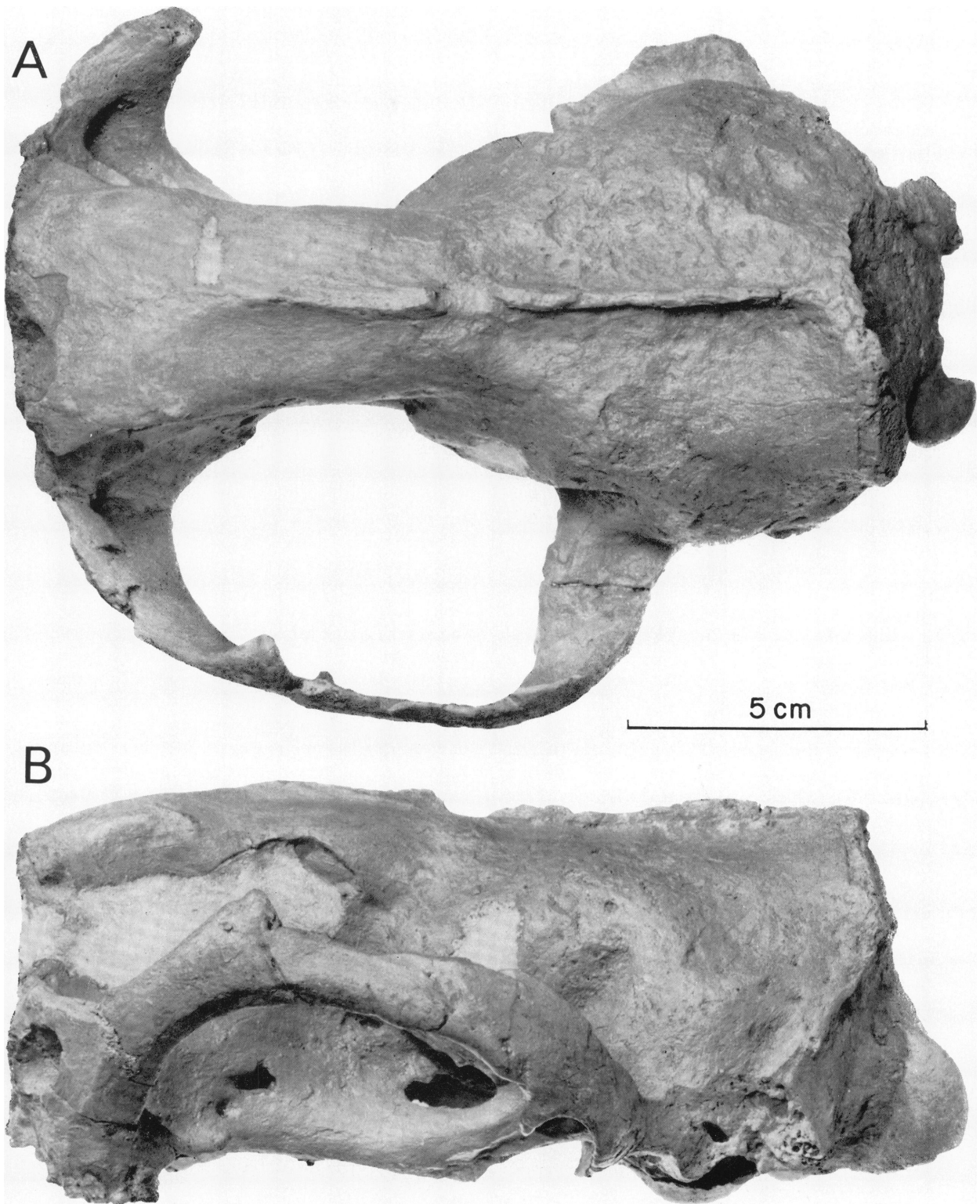


FIG. 6. Holotype skull of *Enaliarctos mealsi*, LACM 4321, from LACM Loc. 1627, Pyramid Hill Sand Member, Jewett Sand, early Miocene, at Pyramid Hill, Kern County, California. A. Dorsal view. B. Left lateral view.

the pterygoid bones from the basisphenoid. A small hole on the left side might represent the posterior foramen of the pterygoid canal.

The zygomatic arch (figs. 6, 7) bows out markedly at the posterior end, then slopes inward to its junction with the snout. It is generally thin, sharp, and high vertically, and is most massive and more rounded just lateral to and ventral to the infraorbital canal. The maxillary process of the zygomatic arch takes origin from the skull immediately above P⁴ and M¹. The ventral root of the process below the infraorbital canal is about 18 mm. or more in antero-posterior length, and is about twice as thick dorsoventrally as the dorsal root above the infraorbital canal. The dorsal root projects laterally from the skull, and the ventral root projects dorsolaterally 35 degrees. Both are directed posteriorly about 25 degrees. Distally the process has a slight dorsoventral constriction, then expands in the vertical plane into two processes. We cannot find the suture between the maxillary and jugal bones. A blunt, wide-based, inferior postorbital process curves dorsomedially, and a long, slender zygomatic process articulates with the squamosal bone over a distance of at least 45 mm. This is obvious, even though some of the zygomatic process of the squamosal bone has been broken off, because of definite articulation facets between the two bones. The zygomatic arch, as seen in lateral view, curves to its highest point far anterior to its midlength. It is not reflected anteriorly in a recurve, such as in many otariids where the zygomatic arch forms an S-shaped curve.

The anterior tip of the zygomatic process of the squamosal bone lies 8 mm. behind the tip of the inferior postorbital process. It continues as a thin vertical plate of bone becoming deeper posteriorly until it attains a depth of 16 mm. in front of the glenoid fossa. At this point the plate becomes somewhat thicker and twists ventromedially to join with the braincase. The entire horizontal portion of the process making up the roof of the glenoid fossa is relatively thin and contoured. The anterior border runs medially and slightly posteriorly, then curves gracefully dorsomedially as a slight crest on the antero-ventrolateral margin of the braincase, running just below a large sulcus in the side of the braincase. The posterior border of the horizontal portion of the zygomatic process of the squamosal bone is a continuation of the dorsal border of the

zygomatic arch, and runs posteroventrally, forming the posterior border of a shallow fossa and then abutting into the braincase near the dorsal margin of the external auditory meatus. The glenoid fossa is wide and straight and would receive a condyloid process some 10 mm. in diameter and 30 mm. wide. Its anterior margin runs laterally and slightly ventrally and ends as a process hanging down from the zygomatic arch, whereas the posterior border begins abruptly 6 mm. lateral to the foramen ovale, forming the postglenoid process and then runs laterally and dorsally to merge with the zygomatic arch.

The braincase of the holotype of *Enaliarctos mealsi* is rather square. In lateral view the top of the braincase is slightly concave in outline, dropping below the surface of the roof of the interorbital area by about 2 mm. at the level of the anterior lacerate foramen. It rises again gently to a large, posteriorly pronounced lambdoidal crest by almost 11 mm. The roof of the braincase slopes roundly to join with the lateral walls. The braincase is widest above the external auditory meati, approximately 78 mm. This wide, bulbous portion of the braincase is continuous ventrally and slightly anteriorly with the root of the zygomatic process of the squamosal bone. Anterior to this bulbous portion is a very large sulcus, actually a triangular fossa about 4 to 5 mm. deep, with the apex of the triangle pointing 45 degrees posterodorsally. A much smaller sulcus parallels the larger one 11 mm. anteriorly. Anterodorsal to this sulcus the braincase is again bulbous, ending so abruptly that it would not be incorrect to term this point the anterolateral corner of the braincase. This corner overhangs the anterior lacerate foramen to a considerable extent, approximately 17 mm. On the dorsal surface of the braincase, at the level of the orbital fissure, there is a pair of slight depressions. Small foramina perforate the floor of the depressions, which we term the parasagittal fossae. The anterior margins of the fossae have a higher edge than the posterior margins, the break in slope effectively marks the junction between the interorbital area and the braincase proper.

The occipital shield is a structure of great surface relief (fig. 7). A thin, median supra-occipital crest runs dorsally to meet the heavy lambdoidal crest, effectively separating a pair of very deep fossae for the insertion of neck

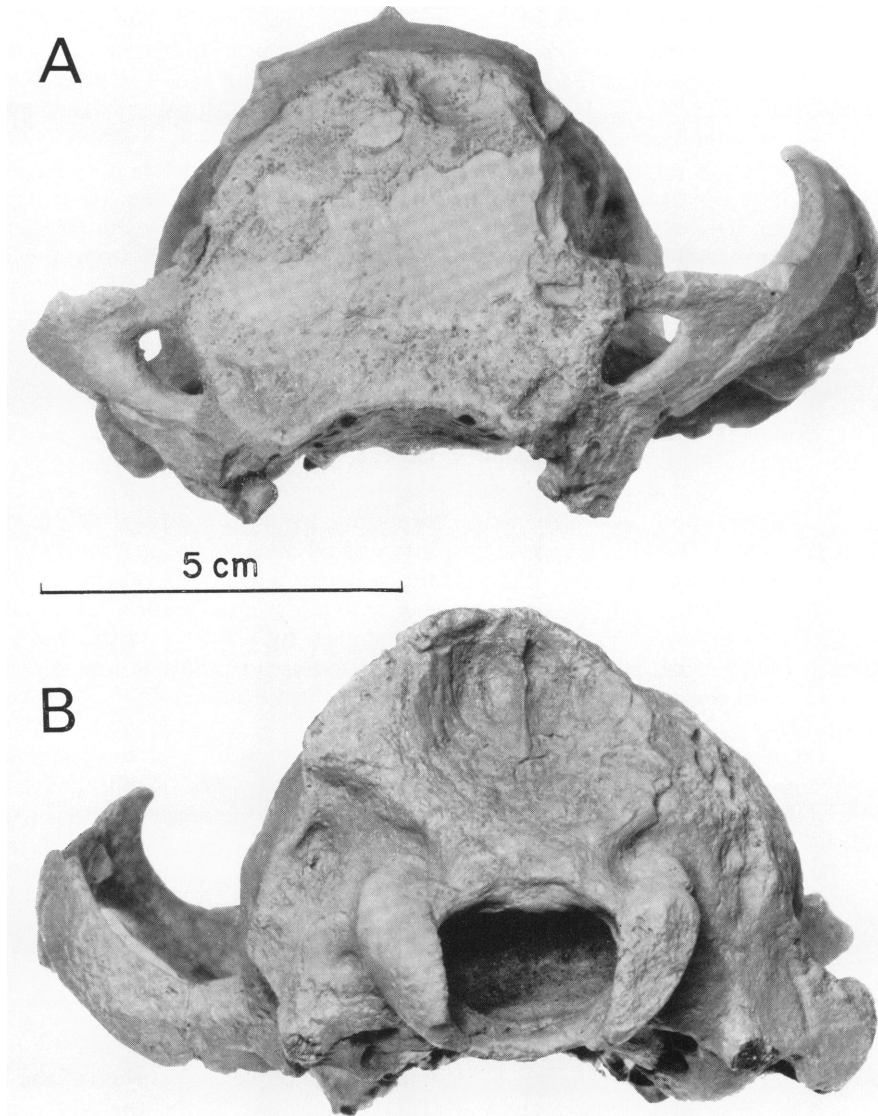


FIG. 7. Holotype skull, LACM 4321, of *Enaliarctos mealsi*, Pyramid Hill Sand Member, Jewett Sand, early Miocene, at Pyramid Hill, Kern County, California, LACM Loc. 1627. A. Anterior view. B. Posterior view.

muscles. Lateral and ventral to these pits the shield is almost vertical and forms a definite, heavy crest. In posterior view this crest originates from the dorsolateral corners of the foramen magnum and curves outward to a point far beyond the width of the condyles, outlining a symmetrical, fan-shaped area.

The lambdoidal crest around the dorsal

margin of the fan-shaped portion of the occipital shield is almost completely broken away, but it is certain that it was large and heavy out to a point 7 mm. lateral to the occipital condyle, then very much reduced from this point down to the posterodorsal corner of the mastoid process. The exoccipital portion of the occipital shield has an irregular surface pitted with numerous

small fossae, some deep and some shallow. The occipital condyles are well defined from the shield by raised borders. The widest articulatory surface on the left condyle is near the bottom of the condyle and runs in an anteroposterior plane. The condyles are 25 mm. apart above the foramen magnum and end approximately 15 mm. apart below that structure. The ventral border of the foramen magnum is a thin plate of bone, less than 4 mm. thick, which is concave in outline. The dorsal border of the foramen is almost straight and at each end curves down to the ventral border. Within the foramen magnum, leading anteriorly and slightly laterally into the body of each condyle, is a condyloid foramen 4 mm. in diameter with a thin medial wall. Smaller foramina lead dorsally from the lip of the condyloid foramen into the root of the foramen magnum. No other foramina are visible in this specimen through the foramen magnum. Shallow grooves for transmission of the occipital venous sinus traverse the roof of the foramen magnum medial to the condyloid foramina.

Notable in the external features of the auditory region is the great width of the basicranial area, particularly across the basioccipital (fig. 5). On the lateral margin of the basioccipital adjacent to the large posterior lacerate foramina are two prominent fossae, anterolateral to which are low processes for insertion of the rectus and longus capitis muscles. Anterior to these arcuate processes the basicranial area is dorsally arched and the lateral wings of the basioccipital are deflected ventrally against the median walls of the bullae.

Terminology used herein for basicranial and specifically middle ear anatomy follows Mitchell (1968).

The auditory bullae are slightly inflated, smooth, and flask-shaped, deepest near their median borders. Their longitudinal axes are slightly oblique to the midline of the skull. The external surface of the bulla does not show such structures as an apical bullar spur or fossa, or a posterior bullar projection (Mitchell, 1968). There is a definite but shallow fossa on the ventral surface, situated halfway between the ventralmost point of the bulla and the tip of the mastoid process, anteromedial to foramen stylomastoideum. Anterolaterally the bulla is ankylosed to the base of the postglenoid process. One or two small foramina, possibly homologous with the postglenoid foramen, pierce the junc-

tion of the bulla and postglenoid process. At the median end of the postglenoid process a slitlike foramen at the bulla-squamosal suture probably represents the opening of the canal for the chorda tympani (fissura petrotympanica). The median lacerate foramen and the canalis musculotubarius (which includes the eustachian tube and tendon of the tensor veli palatini muscle in carnivores) lie in a common opening in the anteromedial corner of the bulla. Internally a septum (lateral wall of the carotid canal) separates the eustachian or auditory tube and the median lacerate foramen. A stout styliform process projects over the anterior opening of the canalis musculotubarius. Posteriorly the bulla is sutured to the base of the paroccipital process, contacting both the mastoid and exoccipital bones. Laterally it is fused to the base of the mastoid process. It sends out a weak process behind the stylomastoid foramen which partially separates this foramen from the vagina processus styloidei. Medially the bulla is loosely sutured to the ventrally deflected lateral wings of the basioccipital.

The external auditory meatus is directed slightly anteriorly and is formed by the bulla anteriorly and ventrally, the mastoid posteriorly, and the squamosal dorsally. The meatus is relatively small and elliptical in cross section with the long axis of the ellipse directed in a dorsoanterior-ventroposterior plane. A supra-meatal fossa in the meatal portion of the squamosal is lacking. The ventral wall of the external auditory meatus is quite thick, particularly anteriorly. There is a very small bulge in the ventroexternal edge of the floor of the meatus, in the region where an inframeatal spine is found in many otariids (Mitchell, 1968).

The facial nerve exits from the middle ear via the foramen stylomastoideum and passes antero-ventrally in a groove in the mastoid. The stylomastoid foramen is a large opening on the basicranial surface surrounded by the mastoid laterally and the bulla medially; posteriorly it is separated from the pit for the tympanohyal (vagina processus styloidei) by a thin process of the bulla.

At the posterior end of the auditory bulla lies the large posterior lacerate foramen which is elliptical with its major axis oriented antero-posteriorly. The posterior carotid foramen is large and closely associated with the posterior lacerate foramen. On the left side a small

foramen penetrates the bulla wall on the bony bridge between the posterior carotid foramen and posterior lacerate foramen. On the right side only two minute foramina pierce this bridge. The carotid canal deeply grooves the median wall of the bulla immediately in front of the posterior lacerate foramen. Posteriorly the carotid canal is open medially, but anteriorly it is enclosed within the wall of the bulla. The anterior opening of the carotid canal is just concealed in ventral view by the anteromedian lip of the bulla, but LACM (CIT) 5302 shows that the portion of the canal containing the internal carotid artery enters the braincase in the region of the median lacerate foramen, flexing sharply dorsoposteriorly, the bend being supported dorsally by a groove in the edge of the basi-sphenoid.

The mastoid process is larger than the paroccipital process. Both processes are abraded on the right side of the holotype. They are connected by a strong but narrow ridge of bone bearing a shallow depression ventrally. The mastoid process is stout, uninflated, quadrangular in form, and bears a groove for the facial nerve ventromedially. The paroccipital process is short, pyramidal in form, and directed postero-ventrolaterally. It is composed about equally of the mastoid bone and the paroccipital projection of the exoccipital bone. Lying about halfway between the occipital condyles and the posterior lacerate foramina on the basioccipital surface are small, posteromedially directed hypoglossal foramina.

In order to describe the internal features of the auditory region, the ventral wall of the bulla was removed on the left side of the skull (figs. 8, 9). The walls of the bulla are thick (1.5 mm.) anteriorly, less so (1.2 mm.) posteriorly, and composed of rather dense bone. Internally the bulla walls are smooth. The tympanic cavity is relatively narrow and deep. It does not extend into any of the surrounding bony elements insofar as our preparation shows. The foramen magnum bulla, the open space dorsally rimmed by the dorsalmost edges of the ectotympanic and entotympanic bones, is large. It is roofed over by pars petrosa, pars squamosa, and other elements. A low septum is developed anteriorly within the bulla, passing from the anterolateral wall of the carotid canal to the anterolateral corner of the bulla. A pointed process projects posteriorly and slightly dorsally into the middle ear cavity from

the edge of this anterior horizontal septum. The wall of the carotid canal forms a ledge in the median wall of the bulla. It is almost straight anteroposteriorly but curves slightly dorsally in its course from the posterior carotid foramen to near the median lacerate foramen. Near its posterior end, there is a small, almost horizontal flange projecting from the wall of the carotid canal. The flange underlies the posteromedial corner of the promontorium. The crista tympani is of small diameter and lies at an acute angle to the basicranial plane; its ventral border is produced as a free edge into the auditory cavity. An anterior and a ventral strut radiate from the crista tympani.

The promontorium (fig. 8) is situated at the rear of the auditory cavity; its exposed ventral surface is smooth and pear-shaped. The fenestra cochlea (or fenestra rotunda) faces posteriorly, opening very close to the posterior wall of the hypotympanic sinus, whereas the slightly smaller fenestra vestibuli (or fenestra ovale, for the footplate of the stapes) faces anteroventrolaterally. Between these openings the promontorium smoothly curves dorso-externally to the edge of the facial canal. Lateral to the fenestra vestibuli is the narrow groove (sulcus or canalis facialis) that runs posterolaterally to the foramen stylo-mastoideum primitivum and becomes a tube exiting at the foramen stylo-mastoideum definitum (above simply called "stylo-mastoid foramen," formed by the bulla and mastoid). Anterior to the fenestra vestibuli and lateral to the promontorium is the rather shallow, elliptical fossa for the tensor tympani. The lateral margin of this fossa is slightly reflected over the fossa itself. Its grooved anterior margin continues as a shallow sulcus converging with the groove for the eustachian tube. A shallow, elongate fossa in the anterior portion of the facies tympanica of pars petrosa, immediately medial to the fossa tensor tympani, leads into a foramen (possibly the promontory foramen of Van Valen, 1966) at the petrosal-sphenoid suture. This fossa and foramen may mark the exit of the promontory branch of the entocarotid artery where it leaves the braincase to join the Circle of Willis. No groove was present on the promontorium for this vessel, but the small foramen in the posteromedian wall of the bulla described above could mark its entrance to the middle ear cavity.

The shallow groove for the eustachian tube

passes lateral to the fossa for the tensor tympani, its lateral margin being defined ventrolaterally by septum canalis musculotubarii. At the anterior edge of the epitympanic recess there is a bluntly pointed process on the septum canalis musculotubarius. The epitympanic recess lies dorsal, lateral, and mostly posterior to the fossa for the tensor tympani. These two pits communicate via a broad, shallow groove. The epitympanic recess is filled with hard matrix from which a portion of the incus protrudes. The full extent of the recess thus cannot be determined, but it approximates in size that found in terrestrial canoids of similar cranial dimensions.

The posterolateral wall of the bulla is bent inward under the pit for the stapedial muscle, coming very close to the projecting tip of the promontorium between the fenestrae vestibuli and cochleae (fig. 9). The reflected margin of the bulla passes immediately posterior to the dorsal lip of the fenestra cochleae and thence anteriorly under the body of the promontorium. The auditory cavity (specifically the dorsal portion of the hypotympanic sinus) is prolonged only a very short distance behind and medial to the promontorium. There is no indication of an eminentia vagina processus hyoidei or styloidei on the posterior wall of the bulla.

Partly exposed within the matrix remaining in the epitympanic recess is the incus. Over half of the incus, including the long crus with a recurved apex and most of the articular surface for the malleus, is visible. The body of the incus appears to be about two-thirds the size of the epitympanic recess. The mastoid process on the left side of the holotype is broken deeply enough to expose what we interpret as the large cerebellar or parafloccular fossa (fossa cerebellaris) lying medial to the trace of the lambdoidal crest.

Some features of the dentition (table 3) can be discerned on the holotype. It bears portions of the right and left upper carnassials, a complete left first molar (fig. 10), and the alveoli of the right first molar and right and left second molars. The carnassials are nearly identical to the isolated complete fourth premolar recovered from LACM Loc. 1626. They are described along with this better preserved tooth (discussion below and fig. 15).

The upper first molar (fig. 10) is much reduced relative to P⁴ over the normal fissiped condition. It is very low crowned and bears three roots of which the lingual root is the

largest; the labial roots are smaller and crowded together. This tooth is quadrate in occlusal outline and about as long as wide. The parastyle is large and projects anterolabially. A weakly developed, but continuous, labial cingulum is present. The paracone is much larger than the metacone; both cusps are compressed transversely giving them a bladelike form. In addition the paracone is deflected labially following the parastyle so that the labial border of the tooth shows a strong curvature when viewed from the occlusal surface. The hypocone and protocone are small cusps barely distinguishable at the state of wear of the holotype. There is little development of a lingual cingulum so that the talon seems to taper posteriorly. Wear has broken through the enamel between the protocone and hypocone and along the anterior face of the M¹. These areas received the single cusp of the talonid and the posterior surface of the protoconid of the lower carnassial, respectively. Remnants of low anterior and posterior cingula remain where not removed by wear.

A single-rooted M² is present in this species. It was apparently highly reduced judging from the size of its root (a fragment of such a tooth is described below).

REFERRED SPECIMENS

The following cranial fragments and isolated teeth are referred to *Enaliarctos mealsi*: LACM (CIT) 5303, a cranium lacking the rostrum anterior to the P¹ and the posterior portions of both zygomatic arches. Most of the bone forming the braincase and palate has been eroded away. Both right and left P¹⁻³ and M¹⁻² are represented by alveoli, the fourth premolars by their roots. This specimen was collected in 1950 by Chester Stock at the locality of the holotype [LACM (CIT) Loc. 481], and was a float specimen partially contained within a concretion. The exact stratigraphic position is unknown but the matrix filling the cranial and narial cavities and the orbital area prior to preparation consisted of a dark gray, fine-grained, well-sorted, calcareous cemented quartz sand which is a more common lithology in the upper part of the "grit zone."

LACM (CIT) 5302, a braincase with little surface bone remaining. This specimen has been prepared on its left side to expose the natural endocranial cast. It was collected in 1950 by Chester Stock at the holotype locality [LACM

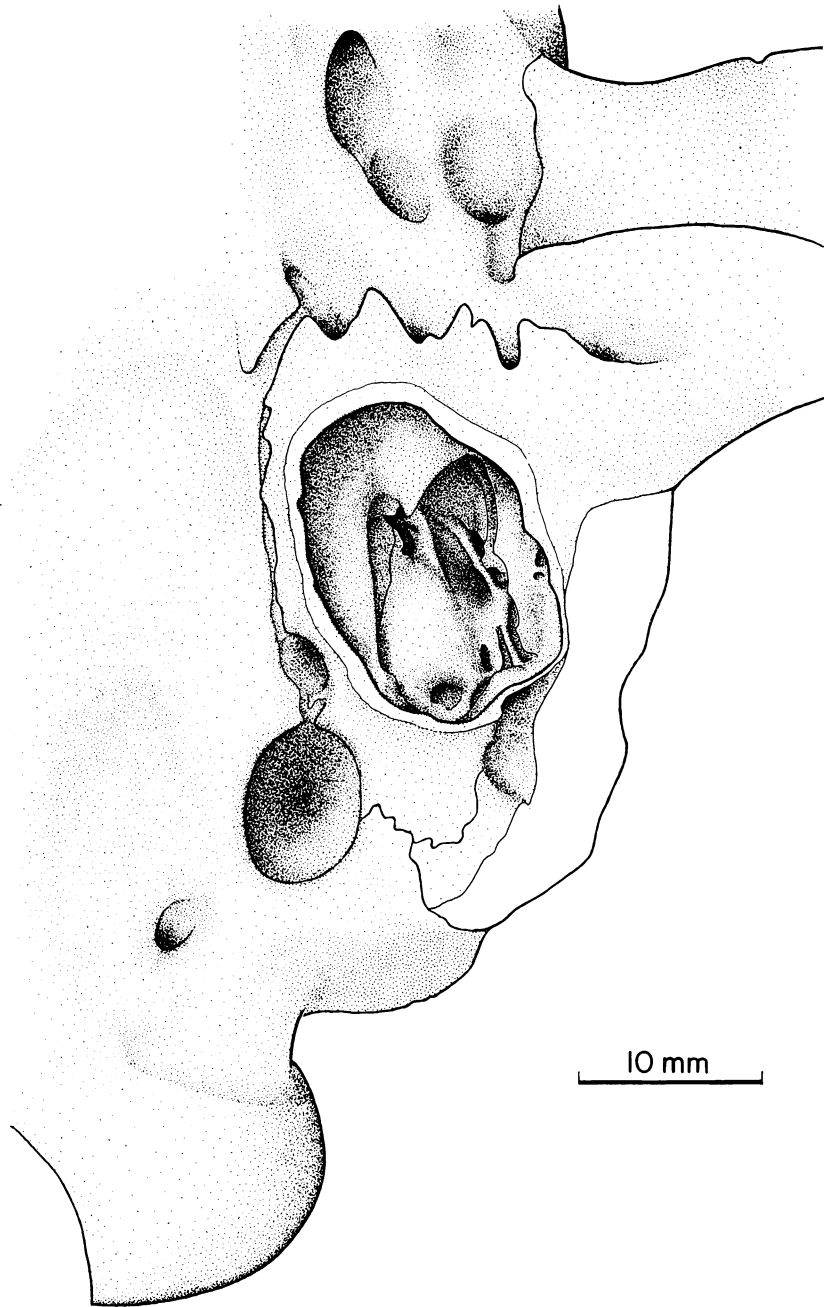


FIG. 8. Ventral view of left side of basicranium of holotype skull of *Enaliarctos mealsi*, LACM 4321. Ventral wall of auditory bulla has been removed to show anatomy of middle ear; blank area denotes broken region. Anterior end is at top. Scale is approximate.

(CIT) 481] and was a float specimen. The exact stratigraphic position of this specimen is unknown. The braincase is filled with a yellow

weathering gray, fine-grained, well-sorted, calcareous cemented quartz sand. This lithology is more common within the Pyramid Hill Sand in

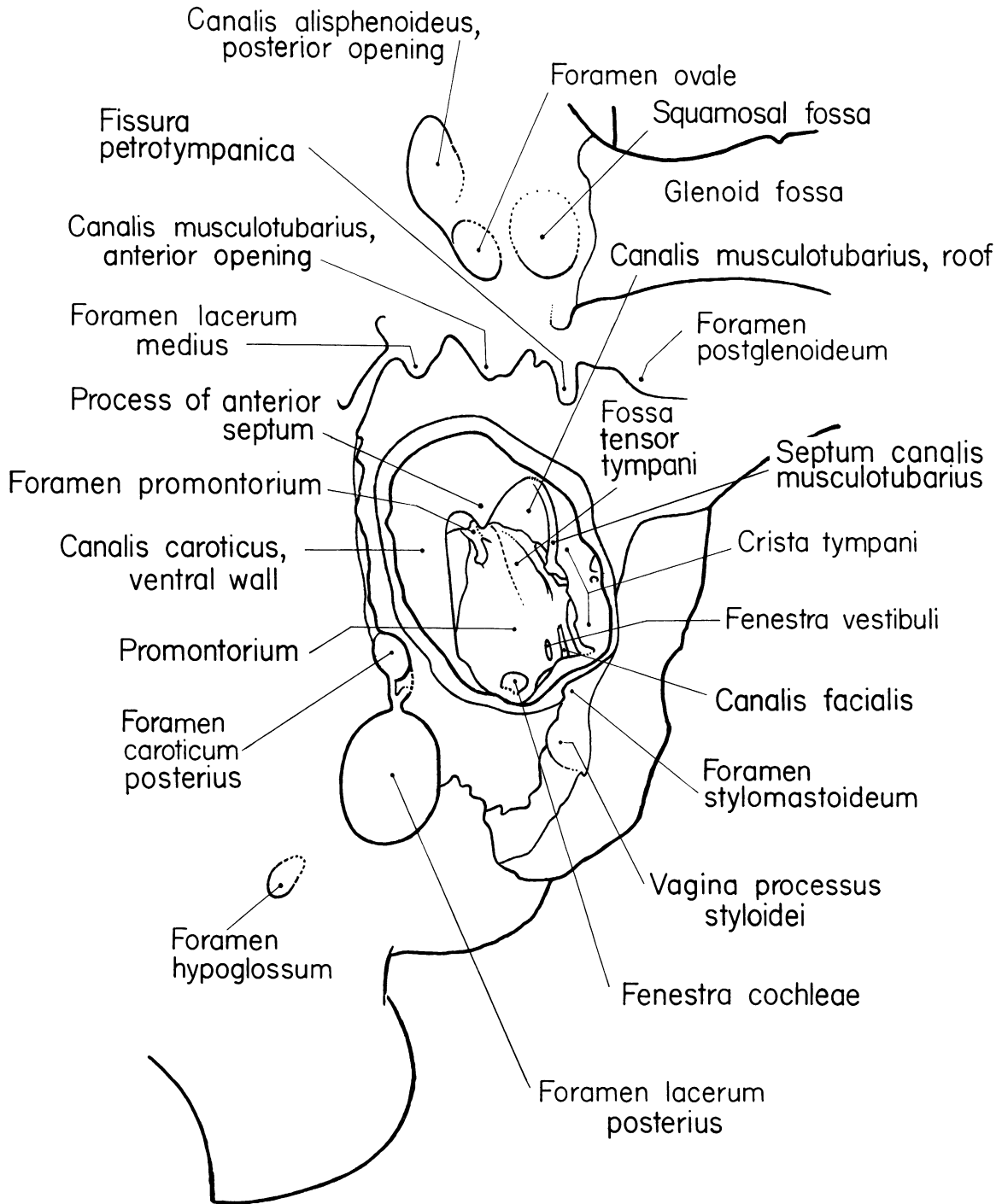


FIG. 9. Ventral view of left side of basicranium of holotype skull of *Enaliarctos mealsi*, LACM 4321. Anterior end is at top. Same scale as in figure 8. Terminology follows Mitchell (1968).

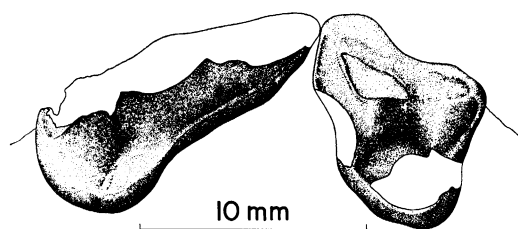


FIG. 10. Occlusal view of upper left carnassial and first molar of holotype skull, LACM 4321. Blank areas denote broken regions.

the upper part of the "grit zone," but finer sand lenses are not infrequent within the basal coarse grits.

The following referred teeth were all collected by Harold S. Meals at LACM Loc. 1626 (SW $\frac{1}{4}$ NW $\frac{1}{4}$ SE $\frac{1}{4}$ sect. 15, T. 28 S, R. 29 E) from the "grit zone" at the base of the Pyramid Hill Sand Member of the Jewett Sand, early Miocene, late Arikareean, late Vaquerosian: LACM 4364, left P⁴, lacking both anterior roots and tip of posterior root; LACM 4576, protocone of left P⁴ with part of its root; LACM 4574, left M₁ complete; and LACM 4575, left Dp₄, lacking the talonid. From the same locality Richard Bishop collected isolated lower cheek teeth which probably pertain to *Enaliarctos*: LACM 17036, an unworn left M₁ lacking roots; and LACM 20517, a worn fragment of right M² lacking the paracone but with complete root.

The snout and orbital area of LACM (CIT) 5303 (figs. 11, 12) is poorly preserved, the tip of the snout from the canines anteriorly is missing, as is the remainder of the skull from the olfactory lobes posteriorly except for an endocranial cast. On many parts the surface bone has been broken away, exposing the matrix filling the underlying cavities and canals, but in other areas, especially on the dorsum of the snout, preservation allows sutures to be picked out with a better degree of certainty than in the case of the holotype of *E. mealsi*.

The snout and orbital area is in many respects quite similar to the same region in the holotype except that it is much more delicately built and slightly smaller. For example, the zygomatic process of the maxillary bone is only about two-thirds the thickness of that on the holotype, yet there is not an equivalent disparity in the depth of the arch. Features within the orbit and inter-orbital region are as in the holotype, as far as can be ascertained.

The snout of LACM (CIT) 5303 curves down to the level of the tooth row at a consistent angle, and it may be inferred that the animal probably had a short snout. The snout as preserved is relatively wide, tapering from a minimum 55 mm. width in front of the infraorbital canals to 44 mm. at a noticeable constriction at the level of premolar one.

About 10 mm. anterolateral to the supra-orbital ridge is a triangular, shallow fossa on the

TABLE 3
MEASUREMENTS (IN MILLIMETERS) OF THE TEETH OF *Enaliarctos mealsi*

	L	LP	Dimensions			
			W	AW	PW	HP
Upper cheek teeth						
P ⁴ , LACM 4364	13.7	6.2	—	9.4	5.7	8.4
P ⁴ , LACM 4576	—	5.4	—	—	—	—
RP ⁴ , LACM 4321, holotype	—	7.2	—	—	—	—
LP ⁴ , LACM 4321, holotype	—	7.2	—	—	—	—
M ¹ , LACM 4321, holotype	8.1	—	9.0	—	—	—
M ² , LACM 20517	4.0	—	ca.5	—	—	ca.1.5
Lower cheek teeth						
Dp ₄ , LACM 4575	—	—	—	3.9	—	5.8
M ₁ , LACM 4574	12.8	—	—	5.9	5.7	7.7
M ₁ , LACM 17036	12.3	—	—	5.5	5.4	6.4

Abbreviations: L, maximum length; LP, length of protocone of upper carnassial; W, width of transverse diameter of upper molars; AW, width across anterior root of premolars, trigonid of M₁; PW, width across posterior root of premolars, talonid of M₁; HP, labial height of principal cusp, metacone in upper molars.

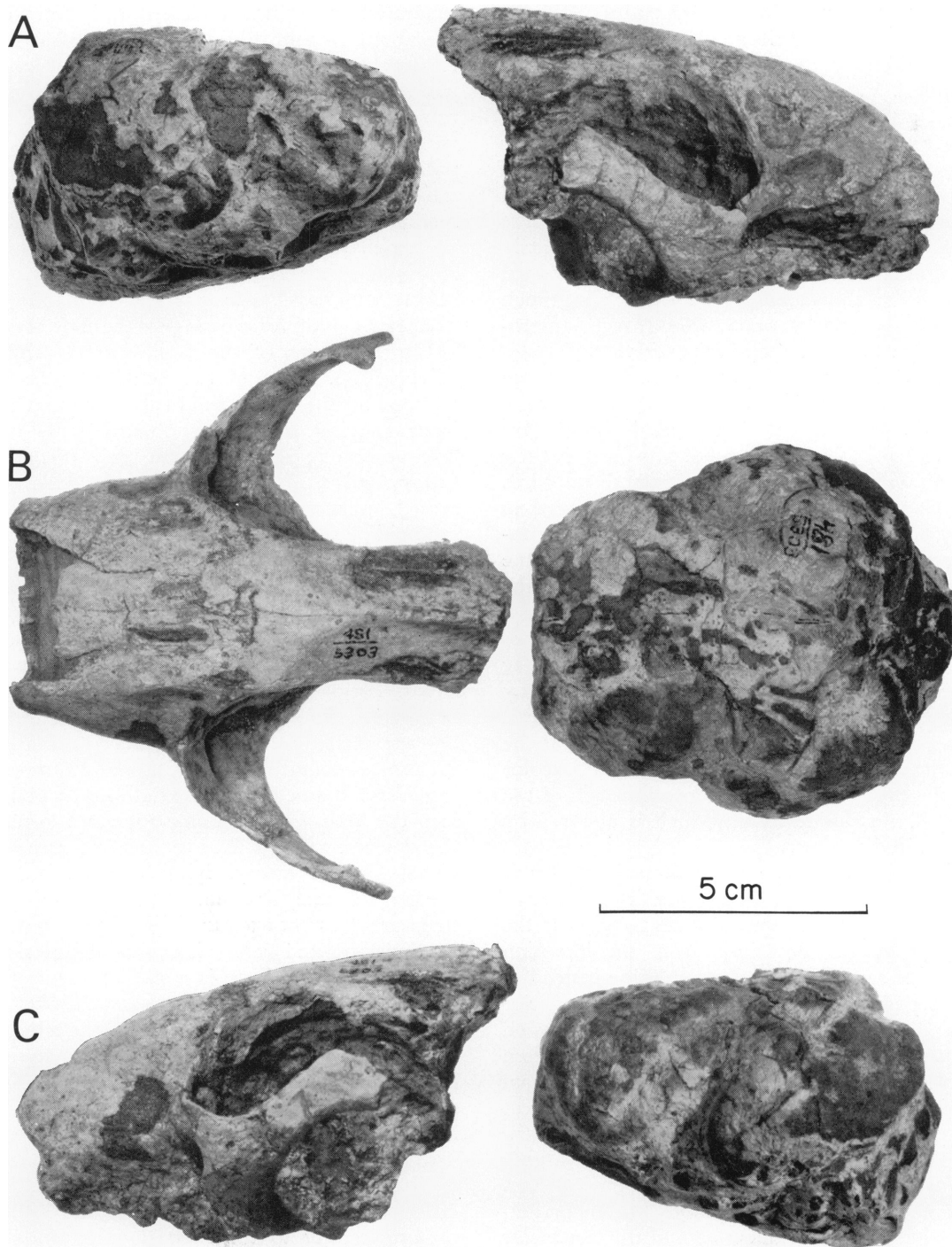


FIG. 11. Referred skull of *Enaliarctos mealsi* LACM (CIT) 5303, from LACM (CIT) Loc. 481, Pyramid Hill Sand Member, Jewett Sand, early Miocene, at Pyramid Hill, Kern County, California. A. Right lateral view of endocranial cast and associated anterior portion of skull. B. Dorsal view of endocranial cast and associated anterior portion of skull. C. Left lateral view of anterior portion of skull and associated endocranial cast.

side of the snout, with the apex of the triangle pointed dorsoposteriorly. Ventrally the fossa becomes indistinct above the level of the lacrimal foramen. Ventral and anterior to this fossa the snout attains its greatest width, about 16 mm. above the level of the palate. Seen in anterior view, the greatest snout width is at the level of the middle of the external choana. The nasal bones, which penetrate the frontal bones at the level of the lacrimal foramen, end approximately 28 mm. anterior to this foramen. In a dorsal view, then, the short nasals indicate that much of the external choana would face antero-dorsally and not directly anteriorly.

The maxillary bones meet the frontal bones along an oblique suture behind the level of the frontal-nasal suture. The nasal bones are parallel sided for the proximal two-thirds of their length, but flare out laterally in the distal third. At this point, they are arched much more than they are proximally. The sagittal suture is continued caudally from between the nasals to the beginning of the sagittal crest, between the frontals.

The broken anterior end of the snout discloses that the palate at the level of the first premolar is up to 7 mm. thick. A pair of large alveoli, 4 by 6 mm., for the reception of a pair of incisors, can be seen in the cross section of the palate near the midline. Dorsal and a little lateral to the alveolus for the first premolar is the cross section of the root of the canine tooth, which is about 5 by 7 mm. in diameter.

The palate of the referred snout is similar to that of the holotype. The posteriormost pair of posterior palatine foramina is obvious; the furrows leading anteriorly from the foramina converge slightly toward the midline instead of being parallel as in the holotype. The anterior two pairs are not readily identifiable. The alveoli of the cheek tooth series P^1 to M^1 converge from posterior to anterior on the midline at an internal angle of about 25 degrees on each side, whereas the left alveolus for M^2 , much larger than in the holotype, is oriented along a line converging toward the midline from anterior to posterior. There is less of a palatine process of the horizontal plate of the maxillary behind the last molar than in the holotype.

The broken rear surface of the specimen as preserved (fig. 12) shows the anterior end of the endocranial cavity and a cross section of the choana. Paired fossae for the olfactory bulbs,

separated by a thin vertical septum 1 mm. wide, are about 18 mm. high and 7 mm. wide. The choana, 11 mm. behind the M^2 , is 13 mm. high and 23 mm. wide. At this spot there seem to be remnants of an incipient vertical plate of the vomer and a small vertical spine from the palatine bones, but the complete vertical septum must have been even farther anterior. The medial wall of the orbit, i.e. the lateral wall of the choana, is at this point less than 1 mm. thick. Above the choana and below the fossae for the olfactory bulbs is a pair of canals about 4 mm. in diameter, evidently for passage of the optic nerves.

Little remains of the braincase of LACM (CIT) 5303. Most of the lamellar bone has chipped off the endocranial cast, leaving a thin layer covering, and largely obscuring, the cast. The ventral two-thirds of the bases of the olfactory bulbs, at the level of the section preserved, were separated by a narrow vertical ethmoid plate. The bulbs at this level are a total of 13.0 mm. across and 20.0 mm. deep.

The auditory bullae have been broken away, but on each side there are remnants of the promontorium and the fossae for the tensor tympani muscles (fig. 12). The least distance between the left and right fenestra cochleae is 50.0 mm.; between the fenestra vestibulae 55.0 mm. On the left side, the fenestra vestibuli is seen to be about 2.4 mm. in longitudinal, and about 1.6 mm. in transverse, diameter. On the right side is plainly seen the fossa within the basisphenoid forming the dorsoanterior wall of the canal for the internal carotid artery, lying anterior to the median lacerate foramen. On the left side this structure does not appear to be present, but the median lacerate foramen is expanded anteriorly into this region. There is a slitlike opening on both sides between the petrosal and alisphenoid separated medially by fragments of the reflected walls of the bullae. This opening appears homologous with that observed within the middle ear cavity of the holotype and likewise is believed to transmit the promontory artery. The promontory is abraded in such a way that the basal whorl of the cochlea is exposed. This cross section has a long axis oriented slightly posterolaterally to the sagittal axis. On both sides abrasion of the mastoid has revealed the large parafloccular or cerebellar fossae which open into the braincase.

For the most part the sutures are obscure on this specimen, but the sutures surrounding the

well-fused petrosal and mastoid bones are clearly shown. The petro-occipital suture, in which the posterior lacerate foramen opens, runs antero-internally about 10.5 mm. between the basioccipital and petrosal to join with a petrosquamosal suture running about 20.5 mm. from the median lacerate foramen out to the ventrolateral edge of the braincase. This suture runs along the ventroexternal side of the canal for the inferior petrosal venous sinus. The canal is deeply excavated in the lateral margin of the basioccipital so that the basioccipital forms a large part of its floor. The median margin of the petrosal is also grooved for this canal. A squamous suture can be traced between the mastoid and the exoccipital and squamosal bones.

Many of the remaining basicranial foramina can be observed and measured on this specimen. The least distance between the hypoglossal (condyloid) foramina is 24.6 mm., between the posterior lacerate foramina 29.0 mm., between the median lacerate foramina 31.0 mm., between the foramina ovale 34.6 mm., between the large orbital fissures about 10.4 mm., between the optic canals at the level of the pterygoideus process of the braincase about 7.2 mm. At this point the optic canals are round, about 3.0 mm. in diameter. As shown in the holotype, they open via the optic foramina anterior to the level of the pterygoideus process (the antero-externoventral corner of the braincase) beneath the pterygoideus-frontal ridge (or the superior orbital crest). On the right side the anterior end of the alisphenoid canal, the foramen rotundum (opening into the orbital fissure) is about 3.4 mm. in diameter. The posterior end of the alisphenoid canal opens anterior but adjacent to the foramen ovale.

As deduced from the holotype, the canalis pterygoideus nerve from the sphenopalatine ganglion exits from the pterygoid canal in the external edge of the orbital fissure. The cast shows on the right side that this canal curves ventrally around the wall of the orbital fissure before it exits.

Chipped and worn away as it is, the relatively thin layer of basisphenoid bone remaining is breached by a hole in the region of the hypophysal fossa that almost certainly represents that fossa. Thus the back edge of the hypophysis lies at the level of the front edge of the foramen ovale.

The condyloid canal, for the condyloid vein,

on the left side is up to 3.5 mm. in diameter; the hypoglossal foramen is 2.2 mm. in diameter. The occipital shield is mainly abraded away; thus the transverse sinus is visible as a major feature on the braincase as preserved, posteroventral to and paralleling the lambdoid crest. On the left side the transverse sinus is at least 4.0 mm. wide and the dorsal sagittal sinus is about 2.6 mm. wide. Right and left dorsal sagittal sinuses are about 6.8 mm. apart halfway along the braincase. About midlength, a major canal branches laterally off the left dorsal sagittal sinus and disappears into the lateral sulcus. This can be identified as a left dorsal cerebral vein. A small posterior twig from this trunk might be the left parietal diploic vein. Farther forward in the region of the frontal gyrus can be found a cast of a canal for another dorsal cerebral vein, and between these two yet a third branch from the dorsal sagittal sinus. The position of foramen impar is difficult to assess. Dorsal to this region, on the left side of the braincase roof, are two canals converging anteriorly. The dorsalmost of these two canals, both of about 2.5 mm. bore, is possibly part of the straight sinus, although it might be too superficial to justify identification as this particular venous sinus. Another canal, probably a venous sinus, lies on the right side even more superficially and is directed, from the region of confluens sinuum or higher, antero-externally for 17.7 mm., then anteriorly. At this point it is 2.1 mm. in diameter, but cannot be traced farther due to defects of preservation.

A number of canals of smaller caliber, on the order of 0.7 to 0.3 mm., can be seen particularly on the lateral portions of the damaged braincase. These are largely middle meningeal vessels, and anteriorly possibly some external ethmoidal vessels are visible. These are preserved in more detail on the endocast LACM (CIT) 5302, and will be described therewith.

The natural endocranial cast, LACM (CIT) 5303, shows little detail of brain structure, although it was prepared further than the illustrations indicate. Accordingly we prepared LACM (CIT) 5302 for other of these details, and description of this specimen is found below. However, the following general comments can be based on endocast LACM (CIT) 5303 (figs. 11, 12).

The endocranial cavity is about 71.7 mm. in greatest width, and the plane of greatest width lies about 24 mm. anterior to the hypoglossal foramina, near the anterior tips of the petrosal

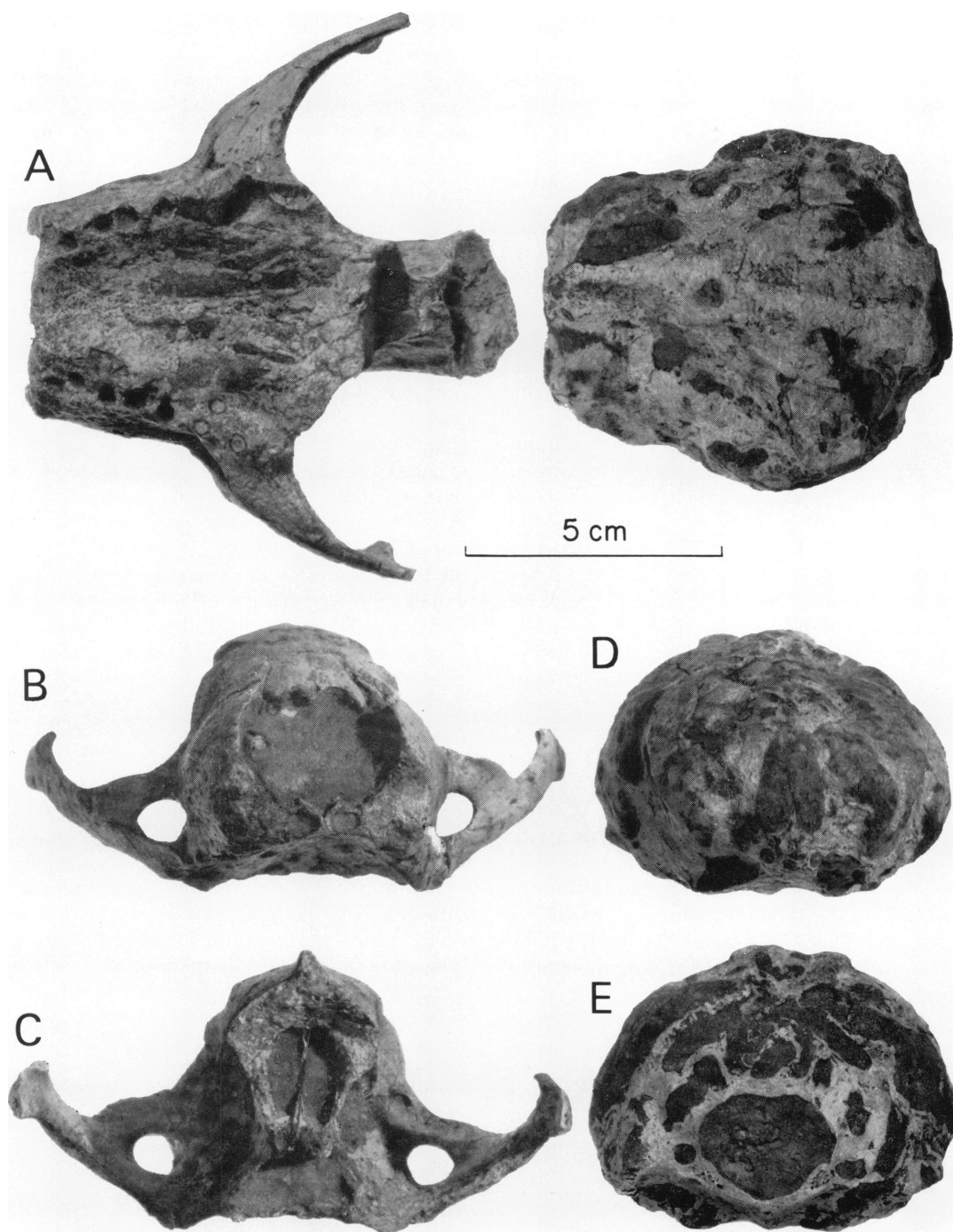


FIG. 12. Referred skull of *Enaliarctos mealsi*, LACM (CIT) 5303, from LACM (CIT) Loc. 481, Pyramid Hill Sand Member, Jewett Sand, early Miocene, at Pyramid Hill, Kern County, California. A. Ventral view of anterior portion of skull and associated endocranial cast. B, C. Anterior portion of skull. B. Anterior view. C. Posterior view. D, E. Endocranial cast associated with skull. D. Anterior view. E. Posterior view.

bones. Measured from the ventral margin of the foramen magnum to the blunt anterior end of the cast as preserved (i.e. to the inferior frontal gyrus), the cranial cavity, exclusive of the ethmoidal fossae for olfactory bulbs, was approximately 80.5 mm. long. A width/length index would be $71.7/80.5=0.89$. Comparable measurements for LACM (CIT) 5302 are: $72.6/81.2=0.89$. Subtracting in each instance 2.0 mm. for braincase wall thickness, the estimated measurements for the holotype are: $73.6/86.8=0.85$. The endocast is 55.1 mm. wide anterior to the fossa pseudosylvia and 55.1 mm. wide across the fossa, thus giving a quadrate appearance to the presylvian portion of the neopallium. The greatest depth of the endocast is approximately 51.7 mm., and it is 43.4 mm. deep in the transverse plane through the level of the hypophysis. Endocranial volume was determined, by displacement, to be approximately 164 cubic cm. or slightly less.

As noted above, the olfactory bulbs are reduced, and markedly narrowed, and the olfactory tracts may have been rather short. Few other aspects of the rhinencephalon can be deduced from this cast.

The major convolutions of the neopallium show to better advantage on the endocast LACM (CIT) 5302, but cast LACM (CIT) 5303 shows that there is only one major gyrus behind the widespread gyrus suprasylvius posterior, best termed gyrus postlateralis. The striking feature of the endocast is the deep fossa sylvia (or more correctly fossa pseudosylvia), enlarged to a broad and deep crease down the side of the brain and effectively separating the cerebrum into front and back halves. Even in this incompletely prepared endocast it is obvious that sunken within this fossa is the gyrus arcuatus primus. This is normally the first step in the opercularization of the gyrus arcuatus primus, in which this cortical region is covered by the bordering cortical field, the gyrus arcuatus secundus (Kappers, Huber, and Crosby, 1936, p. 1542).

We have prepared part of the left cerebral hemisphere of LACM (CIT) 5302 (figs. 13, 14), and the following description is based on that side, with some information from the unprepared right side and from the endocast LACM (CIT) 5303 as well. The description covers size and proportions, remaining braincase, nerves, arteries and veins, cerebrum, and cerebellum.

In size and proportions the endocast matches

that of individual LACM (CIT) 5303 closely. As presented above, the width/length index is identical. The endocast is 59.7 mm. wide across the coronal gyri, but constricted to an estimated 57.8 mm. across the sulcus pseudosylvia. Its greatest depth is 54.5 mm., more accurately measurable here than on LACM (CIT) 5303, and at the level of the hypophysis is about 46.0 mm. deep. The olfactory bulbs are broken off and further enhance the square proportions of the entire cast (fig. 13). The presylvian portion is quadratic in shape, the postsylvian portion almost so. In side view the cast tapers from great depth in back to a less deep but still blunted forward region.

The remaining braincase on the right side and beneath the left is battered and broken. The skull roof in the region of the foramen impar was about 1.6 to 3.0 mm. thick. There is a slight lambdoid ridge on a fragment of bone in this area that might indicate that the sagittal crest was not yet developed in this individual. The small fossae in the occipital shield undercutting the dorsal end of each condyle are much deeper than in the holotype. On the left side the posterior lacerate foramen is well preserved, as is the petro-occipital suture, and the anterior part of the dorsal roof of the carotid canal is represented by a fossa in the basisphenoid. The floor of the braincase in the rectus capitis fossa is 0.5 mm. thick. The foramen magnum is about 24.5 mm. wide and 18.6 mm. high.

The olfactory bulbs are broken away. Only a few nerves can be interpreted on the cast, the size and position of these inferred only from foramina. The optic nerve lay in an optic canal about 4.3 by 2.4 mm. in caliber; the optic chiasma is at the level of sulcus coronalis. The alisphenoid canal exits anteriorly into the orbital fissure, but presumably transmits no nerve. Within the orbital fissure in the living animal would be found the oculomotor, trochlear, trigeminal, and abducens nerves, but these have left no trace in the cast. The foramen rotundum, evidently opening into the alisphenoid canal as in canids (Miller, Christensen, and Evans, 1964), transmits the maxillary branch of the trigeminal. The foramen ovale clearly shows in this specimen. The mandibular nerve and the motor root of the trigeminal pass through a canal about 2.6 by 4.0 mm. in diameter and exit at the foramen ovale. As mentioned, the dorsoanterior roof of the carotid canal is represented by a

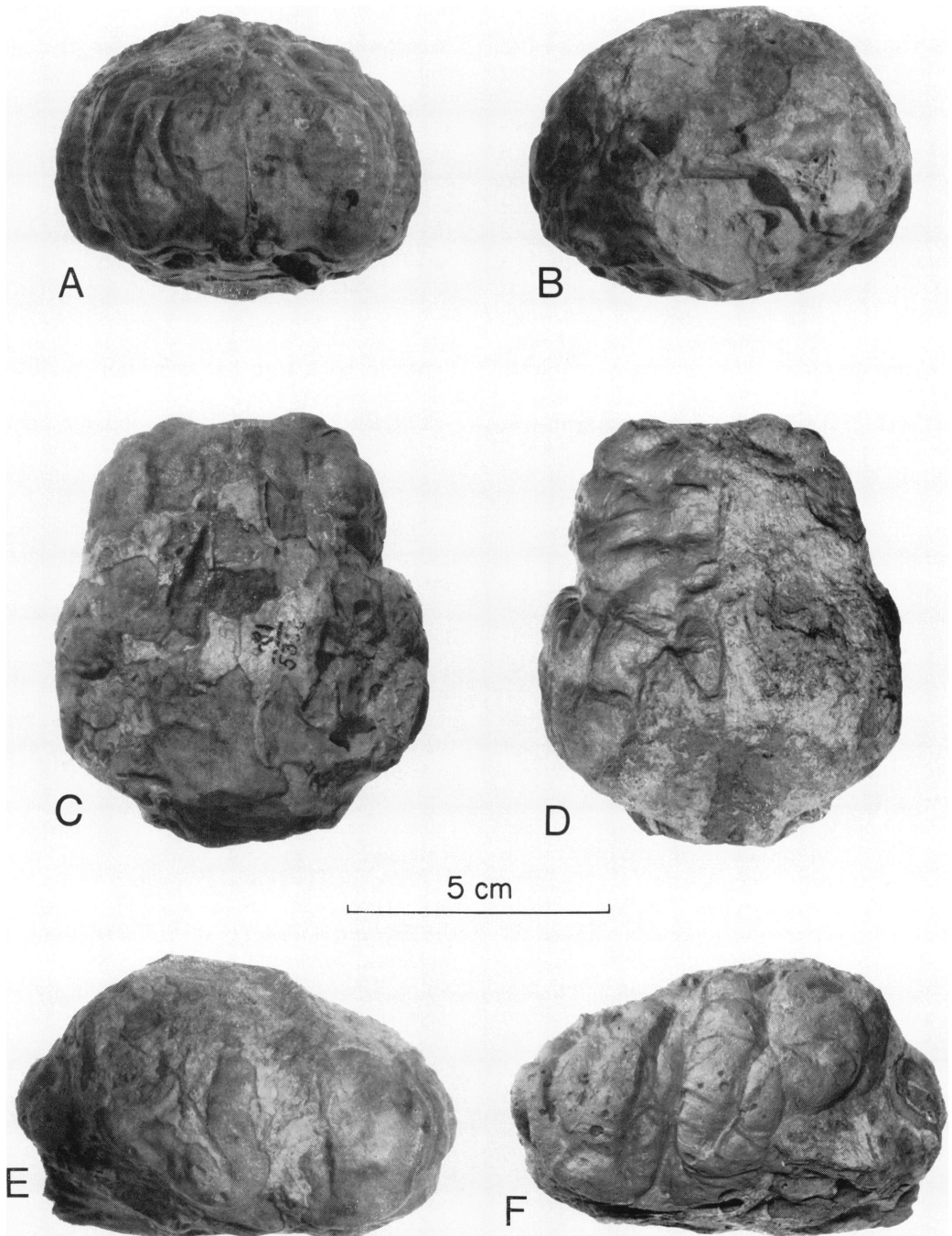


FIG. 13. Referred natural endocranial cast of *Enaliarctos melesi*, LACM (CIT) 5302, from LACM (CIT) Loc. 481, Pyramid Hill Sand Member, Jewett Sand, early Miocene, at Pyramid Hill, Kern County, California. Bone has been chipped off this cast on the left side, exposing details of the surface of the endocranial wall. A. Anterior view. B. Posterior view. C. Ventral view, anterior toward top of page. D. Dorsal view, anterior toward top of page. E. Right lateral view. F. Left lateral view.

fossa in the basisphenoid, anterior to the foramen lacerum medium, preserved on the left side. The median lacerate foramen would have carried, in addition to blood vessels, a division of the internal carotid nerve. In the large posterior lacerate foramen would be found the glossopharyngeal, vagus, and spinal accessory nerves. The large condyloid foramen would transmit the hypoglossal nerve and the foramen magnum the spinal cord. The above pattern accords in all specifics with the arrangement in Carnivora, but the relative sizes of the foramina differ slightly. The posterior lacerate foramen, for example, is enlarged as in some Pinnipedia.

The imprint of some arteries and veins of the endocast may be observed more directly in some cases. Aside from the arteries that are transmitted through the canals and foramina (see Story, 1951, for a list of contents of the foramina in *Procyon*), there are casts of vessels on the neopallium. Dissection of part of the occipital canal on the left side reveals a large (6 mm.) elliptical anterior opening deep within the posterior wall of the posterior lacerate foramen. The canal leads from this point to the condyloid foramen entirely within the exoccipital bone. At the condyloid foramen a large canal continues dorsally, still within the exoccipital bone, paralleling but posterior to the transverse sinus which lies within the cranial cavity. Presumably the described venous sinus penetrates the supraoccipital and joins the transverse sinus near the confluens sinuum. Such a vessel does not appear to be present on the right side of LACM (CIT) 5302, nor is there any clear evidence of such a structure on the abraded braincase LACM (CIT) 5303. The small foramina leading dorsally from the condyloid foramina in the holotype may represent these venous sinuses. Clearly seen are dorsal cerebral veins arising in the sulcus lateralis and emptying into the dorsal sagittal sinus. Many twigs of the middle cerebral artery or middle meningeal vein run from within the pseudosylvian fissure, either forward over gyrus ectosylvius anterior or caudad over gyrus ectosylvius posterior. One major arterial trunk on the surface of gyrus suprasylvius posterior parallels sulcus suprasylvius posterior over most of its length.

Both arterial supply and venous drainage seem to be as rich as in any carnivore as indicated by the large caliber of the venous trunks dorsally.

The cerebral hemispheres are large, relatively flat on top, and project back to cover most of the cerebellum in a dorsal view. Three major neopallial convolutions are evident. Of these the gyrus arcuatus primus (gyrus ectosylvius anterior and posterior) and secundus (gyrus suprasylvius posterior and medius, and gyrus coronalis) can be followed for nearly their entire length. The terminology we use follows Kappers, Huber, and Crosby (1936) and Davis (1964), and is presented in figure 14.

The major vertical crease in the side of the endocast is broad and deep, but not due alone to sulcus pseudosylvius. The latter comprises the posterior margin of the crease, the gyrus ectosylvius anterior, the internal wall of the crease, and the sulcus suprasylvius anterior, the forward margin of the crease. This prominent gutter forms a major feature of the shape of the endocast and of the braincase as a whole. Gyrus ectosylvius anterior is sunken in from the surface of the endocast as a whole and is partly covered by gyrus coronalis. It extends posterodorsally 32 degrees from a vertical plane. Gyrus ectosylvius posterior is inclined at a like angle, but its external surface is 7.6 mm. more superficial than the surface of the gyrus ectosylvius anterior. Preservation is worse in some of the ventral regions, but it is clear that gyrus temporalis inferior, at the bottom of and continuous with gyrus ectosylvius posterior, was in turn confluent with gyrus suprasylvius posterior. The sulcus suprasylvius posterior ends ventrally without any subsidiary sulci. The gyrus suprasylvius posterior shows a notable enlargement dorsally, comparable with the expansion of the gyrus coronalis. Behind gyrus suprasylvius posterior the braincase has not been removed so information cannot be obtained on the shape and possible subdivision of gyrus lateralis, but the latter appears to be extensively overlapped by the former. Dorsal to the expansion of the gyrus suprasylvius posterior there is a prominent sulcus, and from this region forward the gyrus may be termed gyrus suprasylvius medialis. Evidently most of the medial margin of gyrus suprasylvius posterior and medius along sulci postlateralis, lateralis, and coronalis is highly convoluted. This is particularly the case in the region of gyrus suprasylvius medialis.

Gyrus coronalis overlaps gyrus ectosylvius anterior over the entire length of sulcus suprasylvius anterior and defines the anterior wall of

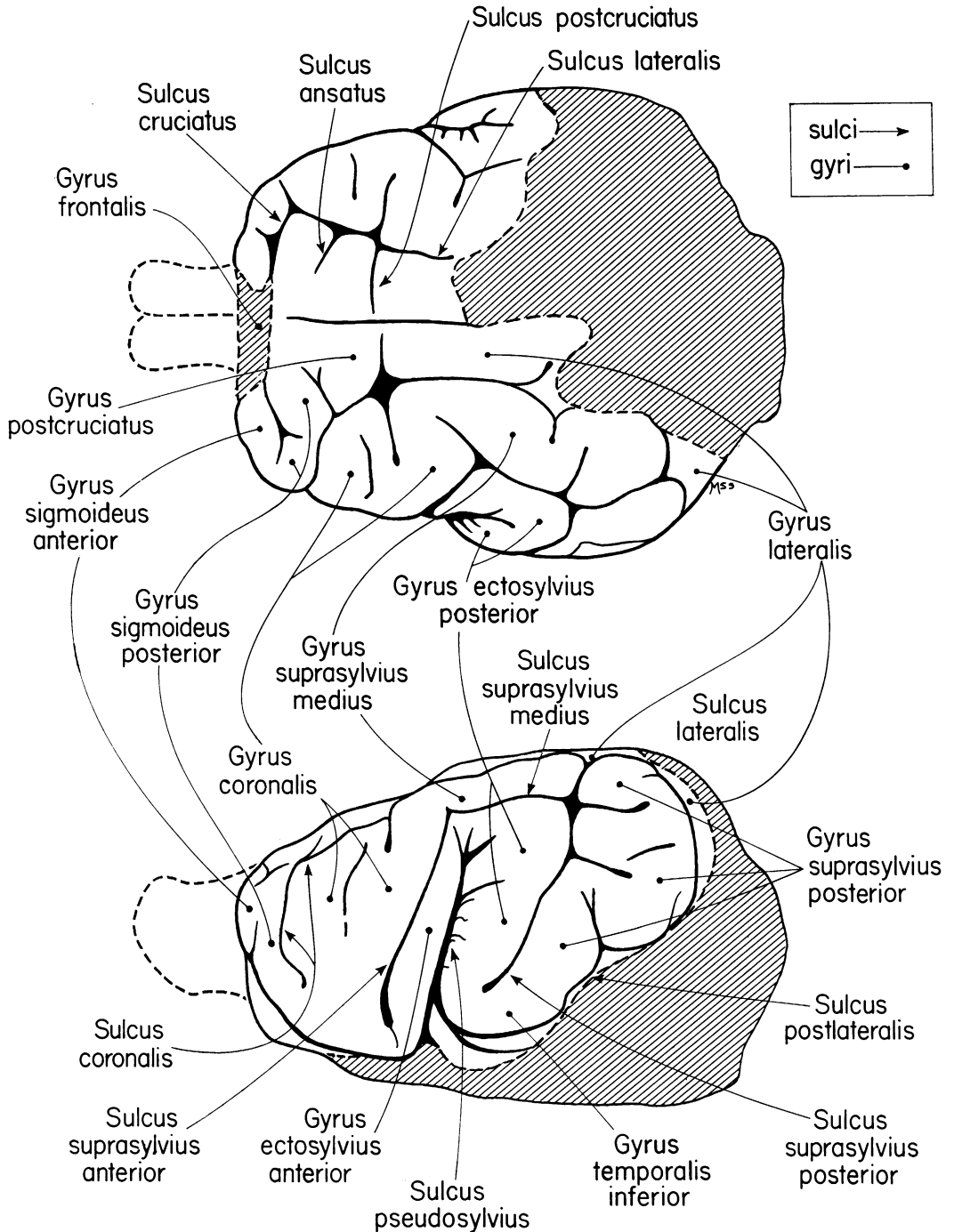


FIG. 14. Outline drawings of dorsal and left lateral side of endocranial cast referred to *Enaliarctos mealsi*, LACM (CIT) 5302, to show interpretation of gyri and sulci adopted in this paper. From LACM (CIT) Loc. 481, Pyramid Hill Sand Member, Jewett Sand, early Miocene, at Pyramid Hill, Kern County, California. Shaded areas denote matrix and eroded surfaces.

the large braincase crease, or sylvian fossa. Thus its back edge is relatively smooth and straight. The anteroposterior expansion of the gyrus coronalis is one of the more striking features of the endocast. At its maximum width it is creased by a shallow, elongate fossa.

On the dorsal surface, the gyrus lateralis extends anteriorly to the prominent sulcus postcruciatu, which is occupied on the right side of LACM (CIT) 5302 by a branch of the dorsal sagittal venous sinus. Anterior to this the gyrus postcruciatu is outlined by the sulcus ansatus anteriorly and the sulcus postcruciatu posteriorly. The anteromedially directed sulcus ansatus arises from the sulcus coronalis and carries a large branch of the sagittal venous sinus on the left side of both endocasts.

This endocast shows that the anterior end of the brain has been compressed backward, shortening and widening it. Thus the ventralmost limb of gyrus coronalis extends down below the level of gyrus temporalis inferior and to the level of the bottom of the endocast anteriorly. The anterior end of the sulcus coronalis is almost vertical when viewed from the side, and the gyrus sigmoidea posterior inclines slightly dorso-anteriorly. The identification of some of these structures, and the delineation of their outlines, is hampered by poor preservation in the anterior region of the endocast. What we identify as sulcus cruciatu may be divided into two limbs: an anterior short limb terminating on the anterior face of the endocast; and a posterior limb paralleling the sulcus coronalis and dividing the gyrus sigmoideus into anterior and posterior portions. In a dorsal view the eroded area anterior and medial to the sulcus cruciatu may represent the small gyri frontalis superior and medialis.

The cerebellum is largely covered by the cerebrum and not exposed through the posterior region of the braincase so little can be mentioned of it. The region of the pons is broad transversely and pronounced downward; behind the pons the pyramids lie in a single, deep, V-shaped groove which runs back to the foramen magnum. No vestige of the ventral median fissure between the pyramids can be found on the endocast. At its widest point the cerebellum did not extend out beyond the cerebral lobes laterally although it comes close by extension into the deep para-floccular fossae. The cerebellum appears to have been overlapped far posteriorly and laterally by

the cerebrum, with the region of gyrus supra-sylvius posterior and gyrus postlateralis covering the cerebellum more than halfway down the side of the endocast.

Several isolated complete teeth and fragments of teeth referred to this species were recovered from LACM Loc. 1626. These specimens include a complete upper carnassial, two lower carnassials, a lower deciduous carnassial, and an M². The lower carnassials are referred on the basis of their morphology and occlusal relationships with the upper teeth.

The upper incisors are unknown and only the bases of the roots of the canines can be seen in the referred specimen [LACM (CIT) 5303]. These do not seem to be more different in size, relative to the cheek teeth, than in other arctoid carnivores. The P¹ and P² are present as judged from the alveoli in LACM (CIT) 5303. P¹ is single rooted and P², double rooted. The size of these roots indicates that the P² is nearly as large as P³.

The upper carnassial (figs. 10, 15) is almost twice as long as M¹. Its general structure is that of a rather typical fissiped carnassial with three roots bearing a crown composed of a trenchant paracone and metacone and shelflike talon or protocone. This tooth is completely encircled by

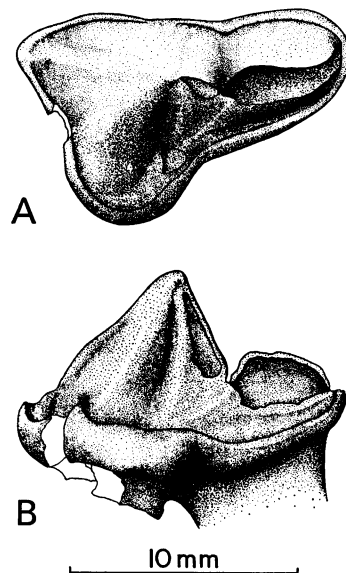


FIG. 15. Left upper carnassial tooth referred to *Enaliarctos mealsi*, LACM 4364. A. Occlusal view. B. Lingual view. Blank areas denote broken regions.

a well-defined cingulum. The paracone is separated from the blade-like metacone by a sharp groove. The metacone is deflected labially, giving the labial edge of P⁴ a concave outline when viewed from the occlusal surface. Wear has broken through the enamel on the postero-lingual surface of the paracone in LACM 4364 (fig. 15). The whole lingual surface of the metacone is worn in this specimen. There is no parastyle, only a slight spur is developed on the cingulum at this position. The protocone is a broad shelf on the lingual surface of the paracone. It is surrounded by a strong cingulum which is not produced into cuspules in the specimens at hand. In the holotype this shelf bears a transverse groove. Wear has broken the enamel on the posterior end of the protocone shelf. This wear facet is connected with the facet on the posterior surface of the paracone indicating that the protocone receives the point of the paraconid of the lower carnassial, a relationship which is confirmed on examining the wear facets on the lower tooth and experimenting with its occlusion with P⁴.

A referred right second upper molar (LACM 20517) lacks the anterolabial corner of the tooth and paracone. The preserved part of the crown is low and flat and surrounded by a cingulum. The metacone is worn nearly to its base but was apparently a low cusp like the centrally placed, low, rounded protocone which is the only cusp in the talon. There is a single root, but longitudinal grooving clearly indicates that this is a composite structure in which the labial cusps each bear smaller contributions than the lingual root supporting the talon. The root structure, although modified, is thus analogous to that seen in M¹.

Two isolated left lower carnassials of identical morphology but slightly different size have been recovered from LACM Loc. 1626. One moderately worn lower carnassial (LACM 4574), occludes so well with the holotype that it may represent another individual of *E. mealsi*. The rather low crown is borne on two strong roots which are nearly identical in size and shape. Cingula surround the anterior and lateral, but not the posterior, surface of the crown. The trigonid comprises over half the crown, with the protoconid the largest cusp. The paraconid is directly in front of the protoconid, the hypoconid directly behind, and the metaconid is tiny so that this tooth consists effectively of three cusps:

paraconid, protoconid, and hypoconid, arranged in a linear row. There is no trace of an entoconid in the unicusped talonid. The hypoconid is placed only slightly labial of the midline. It is separated by a broad notch from the base of the protoconid. The unworn carnassial (LACM 17036, fig. 16) is slightly smaller than LACM 4574 and has weaker roots, but otherwise is morphologically identical.

In LACM 4574 wear has breached the enamel on the crest and labial side of the paraconid, anterolabial side of the protoconid, and tip of the hypoconid. Heavy wear on the crest of the paraconid corresponds to the occlusion of this cusp with the protocone shelf on P⁴. Wear on the labial side of the protoconid results from shearing action against the lingual side of the metacone of P⁴. The hypoconid fits into the basined talon of M¹.

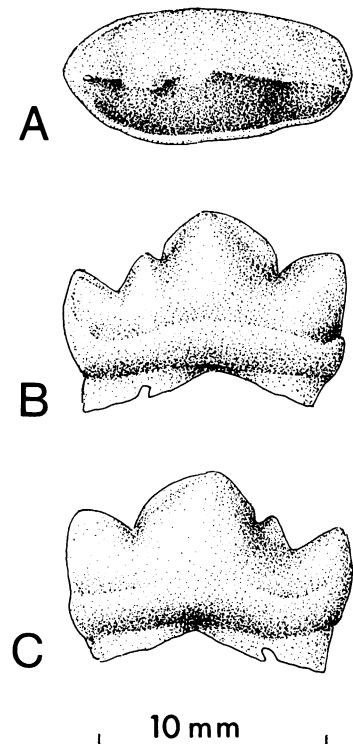


FIG. 16. Lower cheek tooth, left M₁, LACM 17036, referred to *Enaliarctos mealsi* from LACM Loc. 1626, Pyramid Hill Sand Member, Jewett Sand, early Miocene, near Pyramid Hill, Kern County, California. Scale is approximate. A. Occlusal view. B. Lingual view. C. Labial view.

The trigonid of a deciduous fourth premolar (LACM 4575) is assigned to the species on the basis of its close similarity to M_1 described above. As far as the preserved parts go this tooth is virtually a miniature of M_1 . The only conspicuous difference is the relative size of the metaconid, which is a better developed cusp in the deciduous tooth.

The dentition of the referred snout of *Enaliarctos mealsi* [LACM (CIT) 5305, fig. 12] is not preserved, but some of the dental pattern can be determined from the remains of the alveoli. The tooth row, from the anterior margin of the alveolus of P^1 to the posterior margin of M^2 alveolus, was approximately 54 mm. in length on the left side of the palate. M^2 is missing on the right. The palate is 23 mm. wide between the most medial alveoli for P^2 and approximately 42 mm. wide between the alveoli for M^1 . The tooth row was quite straight: a line may be drawn through the center of the alveolus for P^1 and the medial root of M^1 that angles back about 10.5 degrees from the midline on the left and about 9.0 degrees from the midline on the right side. P^1 was situated directly behind and slightly medial to the canine. Directly behind and medial to P^1 , the anterior root of P^2 was the most medially situated of any of the cheekteeth alveoli. P^3 and P^4 alveoli are linearly aligned along the alveolar margin of the palate. The three alveoli for the broadly based left P^4 fall within a triangle that is 13 mm. on its external side, 9 mm. on its anteromedial side, and 13 mm. on its posteromedial side. The same measurements for the right P^4 alveoli are 11 mm., 8 mm., and 12 mm. respectively. The medial root of the tri-rooted M^1 is the largest and also the most posterior of the three roots, whereas the medial root of P^4 is internal and medial to the other two roots. M^2 is single rooted.

Based on the above descriptions of the holotype and referred specimens, we present a restoration of the skull of *Enaliarctos mealsi* (fig. 17).

ONTOGENETIC AGE AND SEX

There are a number of methods by which marine mammals may be aged from cranial material: suture closure, wear of teeth, size and ossification of the skull, growth zones in teeth, and so on. But all of these methods presuppose a large series of specimens, which are not known in this case. None of the teeth were sacrificed for

sectioning. Because the skull of the holotype is completely ossified, with only major sutures open, the skull is judged to be that of a fully mature adult. The molars preserved are not notably worn. Assuming that normal feeding in the life of this species would result in moderate to great attrition, we conclude that the holotype represents a fully mature but not aged adult.

The snout and endocranial cast of the referred specimen is about 9 percent smaller than the skull of the holotype. Although poorly preserved, it too seems to have been well ossified. The sutures of the nasal bones show in the snout of the referred specimen but not in the holotype, as does a slight metopic suture between the frontal bones. If not due to excessive abrasion of the snout, one interpretation would be that the snout represents a younger animal than does the holotype. If the sutures show because of abrasion, the smaller specimen might be interpreted as a female, the larger as a male. As the transverse oblique diameter of the orbit is almost the same in the larger skull of the holotype (40 mm. diameter: BD of 54 mm.) and the relatively smaller skull of the referred snout (39 mm. diameter: BD of 50 mm.), we conclude that the snout simply represents a younger individual of unknown sex.

Because the isolated braincase [LACM (CIT) 5302] shows some indication of a low lambdoid crest, we recognize the possibilities it represents: a large but young animal of unknown sex, a female with suppressed lambdoid and sagittal crests, versus the holotype which might then be from a male since it has a sagittal crest, or a species other than *E. mealsi*. We incline toward the first speculation.

COMPARISON WITH FISSIPEDS

SKULL: The skull of *Enaliarctos mealsi* is in some ways similar to that of the sea otter *Enhydra lutris* and river otter *Lutra canadensis*. Similarities that may be pointed out are: a short rostrum, low skull, wide and relatively flat basicranium, broad and flat palate, and other features. But there are as many notable differences. For example, the braincase of *Enaliarctos* is relatively square with a pronounced anterior margin and a deep ventrolateral pseudosylvian sulcus externally, whereas in the otters the braincase is broadly inflated with no decided anterior margin and the sylvian sulcus is shallow. The eye of the otter is relatively smaller: the ratio of

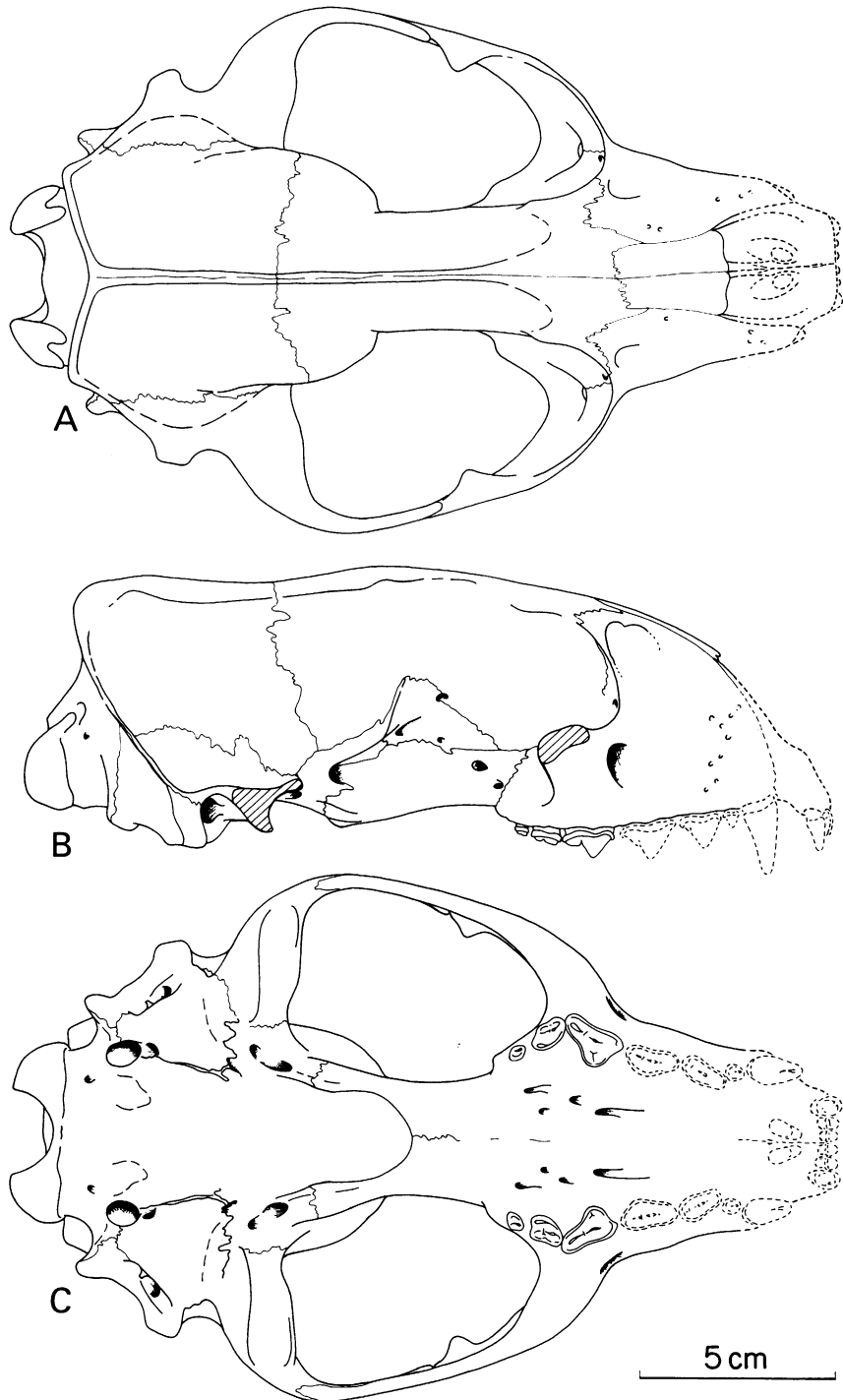


FIG. 17. Restoration of skull of *Enaliarctos mealsi* based upon specimens studied in this report. Shaded region anterior to the nasal bones is unknown, and is drawn after comparable region in skull of *Procyon lotor*. Scale is approximate. Specimen size is based on LACM 4321. A. Dorsal view. B. Right lateral view. C. Ventral view.

the oblique transverse diameter of the orbit to the BD (basal dimension, see Measurements for explanation) in *E. mealsi* holotype is 0.74; in the *E. mealsi* snout it is 0.78; in *Enhydra lutris* (LACM M1572 and M1737) it is 0.52 and 0.54 respectively; and in *Lutra canadensis* (LACM 190 and M980) it is 0.67 and 0.64 respectively. Relative to snout width, the orbit of *Enaliarctos* is clearly larger than that of the sea otter, in which the orbit is even smaller than in the river otter. In otters the eye is placed far forward where the anterior margin of the orbit lies over P³ but in *Enaliarctos* it lies more posteriorly, over P⁴. The river otter bears a well-marked supra-orbital process, but this is less pronounced in the sea otter. It is almost absent in *Enaliarctos*. The muzzle of the otters is blunt, but it is much less so in *Enaliarctos*. There are any number of other differences, quite aside from the obvious heritage differences, sufficient to demonstrate that the skull of *Enaliarctos* does not approximate the plan of sea or river otter skulls very well.

Another obvious comparison is with *Potamotherium*, the Oligocene lutrine demonstrated by Savage (1957) to be a highly specialized freshwater "otter." Available for comparisons are: two partial skulls of *Potamotherium*, AMNH 22520, and the illustrations and descriptions of Savage (1957). These skulls are superficially similar to that of *E. mealsi*: the *Potamotherium* skull is elongate and low, deep in front, with a long interorbital region, without major supra-orbital processes, with an elongate braincase having a crease in the region of the pseudosylvian fissure, with sharp overhanging lips around the glenoid fossa, a long palate and a tubular internal choana, an internal nares at a level far behind the front end of the braincase, a lacrimal bone and lacrimal canal, an imperforate interorbital wall, a sagittal crest, expanded narial chamber, a flattened dorsal surface on the skull, a small to absent postglenoid foramen, a large posterior lacerate foramen, small olfactory bulbs, and other features. As an aside we note that Savage discussed the absence of the postglenoid foramen in *P. valletoni*. We have found that in a *Potamotherium* skull (AMNH 22520a) that is long relative to overall skull width and height, the postglenoid foramen seems to be present but small. This should not affect Savage's argument about drainage of the brain significantly, however. The shape and proportions of the *E. mealsi* and *Potamotherium*

skulls are exceptionally similar, and along with similarities in basicranial features and brain, we believe these similarities to be of phyletic importance (see discussion below).

The holotype and only known specimen of the "procyonid" *Kolponomos clallamensis* (Stirton, 1960) is sufficiently complete to allow comparisons to both the holotype and referred snout of *Enaliarctos*, and the following comments pertain to both specimens.

The anterior ridges leading from the supra-orbital ridges to the beginning of the sagittal ridge of *Enaliarctos* are much less well developed than in *Kolponomos*, and the nasals do not extend posteriorly as far. In the snout, the ratio of the distance from the level of the anterior border of the lacrimal foramen to the posterior end of the nasal bones divided by the BD is 0.12 and the same ratio in *Kolponomos* is 0.40. There is no supraorbital ridge leading back from the dorsal preorbital ridge in *Kolponomos* as there is in *Enaliarctos*, accordingly the posterodorsal limits of the orbit are not so well defined. The tips of the nasal bones are raised at their distal end, not deflected as in *Enaliarctos*, and the entire snout is much longer, narrower, and higher than in *Enaliarctos*. For example, the breadth across the fossae for the quadratus labii superioris muscles (the levator-quadratus fossae of Stirton, 1960) divided by the BD is 0.64 in both specimens of *Enaliarctos* and 0.78 in *Kolponomos*.

In anterior view, the anterior choana in *Enaliarctos* is very much wider and the nasal chamber is more inflated than in *Kolponomos*. The zygomatic arches flare laterally much more and evidently enclosed a substantially larger orbit in *Enaliarctos mealsi*.

The palate of *Kolponomos* is relatively less broad anteriorly and is much more arched than it is in the *Enaliarctos* snout. The bony palate in *Kolponomos* ends at the level of M² or slightly anterior, whereas in *Enaliarctos* it is continued caudad well behind the tooth row and the orbit, ending about halfway between M² and the anterior lacerate foramen.

In summary, the skull of *Enaliarctos mealsi* differs markedly from that of *Kolponomos clallamensis*. *Kolponomos* is constructed like many primitive fissipeds, with a long, deep skull and relatively small eyes. Conversely, *Enaliarctos* has a long, low skull with a short muzzle and relatively larger eyes that are directed more dorsally. Clearly the two are related only by

virtue of being derived from a common canoid stock.

AUDITORY REGION: Hough's work (1944, 1948) on the morphology of the auditory region of fossil canoid Carnivora has convincingly demonstrated that the characteristic procyonid, mustelid, and canid patterns can be traced back into mid-Tertiary time. More recently de Beaumont (1965) has shown that the ursids have an equally long history.

In the Oligocene, ursid, procyonid, and mustelid types of auditory structures are present. These primitive forms, like their modern descendants, are similar in many ways, and these similarities are the basis for union into a common superfamily, the Arctoidea (Flower, 1869; Hough, 1953). The Oligocene species differ in the following basicranial features:

1. Ursidae (exemplified by *Cephalogale* Jourdan early to late Oligocene, Europe; early Miocene, Asia). Longitudinal axis of bulla slightly oblique to midline; bulla co-ossified only with base of mastoid process, loosely sutured at base of paroccipital and postglenoid processes; mastoid process of petrosal prominent, downward directed; paroccipital process widely separated from bulla, but closely associated with mastoid process and joined to latter by a crest; external auditory meatus a short tube, its opening of moderate size; auditory cavity not expanded posterior to promontorium and contains no septa; facial canal exits from skull via foramen stylomastoideum definitum, which lies dorsal to and in a common pit with tympanohyal; shallow suprimeatal fossa may be present; fossa for tensor tympani deeply excavated into side of promontorium; promontorium greatly overlapped by bulla (i.e., portion carrying carotid canal) medially, exposed part low and pear-shaped, small in area relative to roof of tympanic cavity; posterior carotid foramen in common fossa with posterior lacerate foramen; carotid canal within median wall of bulla, petrosal not grooved for canal; alisphenoid canal present.

2. Procyonidae (exemplified by *Plesictis* Pomel, mid to late Oligocene and early Miocene, Europe; *Plesiogale* Pomel, late Oligocene, Europe; *Zodiolestes* Riggs, early Miocene, North America). Longitudinal axis of bulla nearly parallels midline; bulla co-ossified with base of mastoid processes, loosely sutured to base of paroccipital and postglenoid processes; mastoid process laterally directed, shelflike, prominent in

larger forms such as *Zodiolestes*, less so in *Plesiogale*, small in *Plesictis*; paroccipital process widely separated from mastoid, without connecting crest; short tubular external auditory meatus of moderate caliber; middle ear cavity slightly expanded posterior to promontorium and contains no septa; facial canal and tympanohyal enclosed in common "stylomastoid foramen"; suprimeatal fossa present, deeply excavated into mastoid process of squamosal; fossa for tensor tympani (muscularis major) an oval depression deeply excavated in lateral side of promontorium; promontorium not greatly overlapped by bulla, exposed surface low and globose; posterior carotid foramen widely separate from posterior lacerate foramen; carotid canal a tube in median wall of bulla, traverses ventral surface of petrosal; petrosal not grooved ventrally for carotid canal; alisphenoid canal lacking.

3. Mustelidae (exemplified by *Paleogale* von Meyer, early Oligocene to early Miocene, Europe and North America; middle Oligocene, Asia; *Paragale* Petter, late Oligocene, Europe). Longitudinal axis of bulla oblique to midline; bulla co-ossified with mastoid at base of mastoid process and between paroccipital process and stylomastoid foramen, sutured or co-ossified with base of postglenoid process; mastoid process prominent in larger genera (*Paragale*), laterally directed; paroccipital process widely separated from mastoid process by sloping shelf or shallow, broad groove, no crest connects these processes; tubular external auditory meatus of small caliber in *Paragale*, lacking in *Paleogale* where meatus is of large diameter; auditory cavity expanded posterior to promontorium; low transverse septa on median wall of bulla in *Paleogale*; facial canal surrounded by mastoid laterally and bulla medially; tympanohyal in separate pit ventral to foramen stylomastoideum definitum; suprimeatal fossa lacking; in *Paleogale* fossa for tensor tympani oval and deep but not deeply excavated into side of promontorium; exposed part of promontorium elongate, inflated about fenestra cochlea in *Paleogale*; posterior carotid foramen small, separate but close to posterior lacerate foramen; carotid canal within medial wall of bulla throughout its course in *Paragale*, only within bulla wall anteriorly in *Paleogale*, parallels median border of petrosal in *Paleogale*; alisphenoid canal lacking.

The primitive canid auditory region differs from the ursid, procyonid, and mustelid in

several ways as described below. The extent of divergence from the Arctoidea has been thought to justify their separation as a distinct superfamily, the Cynoidea (Flower, 1869). Other authors united the canids, ursids, procyonids, and mustelids in a common superfamily, Canoidea (Simpson, 1945), or group them with the felids as a superfamily, Cynofeloidea (Hough, 1953), based on the similarity of the early felid auditory region to that of the canids. We have chosen the arrangement followed by Simpson (1945), although we employ the informal term "arctoid" as a collective for the families Ursidae, Procyonidae, and Mustelidae, and use the informal term "cynoid" as a synonym of Canidae.

4. Canidae [exemplified by *Hesperocyon* Scott (= *Pseudocynodictis* Schlosser) early to late Oligocene and early Miocene, North America; *Mesocyon* Scott, middle to late Oligocene and early Miocene, North America]. Longitudinal axis of bulla slightly oblique to midline; posterior edge of external auditory meatus may be fused to mastoid, but bulla otherwise not co-ossified with surrounding elements, sutured to base of postglenoid and paroccipital processes; mastoid process a low rugose knob; paroccipital process widely separated from mastoid, joined to latter by low crest; external auditory meatus of large caliber, not produced into tube; low septum present at entotympanic-ectotympanic junction; middle ear cavity expanded posterior to promontorium; facial canal surrounded by mastoid laterally and bulla medially, shares common opening ("stylomastoid foramen") with tympanohyal; a shallow supra-meatal fossa may be present in *Hesperocyon*; fossa for tensor tympani (*muscularis major*) a prominent, broadly oval to circular depression not deeply excavated in lateral wall of promontorium; exposed portion of promontorium elongate, pear-shaped, somewhat inflated and large relative to area of roof of auditory cavity; posterior carotid foramen small, separate from but close to posterior lacerate foramen; carotid canal a deep groove in medial wall of bulla, occasionally completely enclosed within bulla wall anteriorly, traverses ventral surface of petrosal in a groove; alisphenoid canal present.

Of the four types of auditory regions, the canid type seems to be the most stable in the sense of having undergone less modification during the course of evolution in the later

Cenozoic. The only major changes seem to have been development of a short and ventrally incomplete tubular meatus, enlargement of the septum, and union of the posterior carotid foramen and posterior lacerate foramen. The ursids too have been relatively stable in the major features of the auditory region. In the ursid lineage leading to the living genera increasing size and a shift in feeding habits from carnivorous to omnivorous has been accompanied by modifications in the bones surrounding the auditory region in accord with the realignment of the jaw musculature. Consequently the bulla has become flat relative to the surrounding processes, a phyletic development which is repeated ontogenetically in living bears as shown by Firbas and Wicke (1968). In addition, in ursids the middle ear cavity has been expanded through invasion of the floor of the external auditory meatus by the hypotympanic sinus. In both the procyonids and mustelids evolution has tended to modify the bullae in the direction of greater complexity of structure. *Bassariscus* Coues represents the least modified condition of the auditory region among living procyonids; its structure differs little from Oligocene forms. The tendency in this family has been to develop a tubular auditory meatus, expand the auditory cavity posterior to the petrosal, and shift the posterior opening of the carotid canal anteriorly along the median margin of the bulla. In the mustelids the same trends are seen. In the latter group, however, expansion of the auditory cavity proceeded farther than in the Procyonidae in that some of the surrounding bony elements were invaded. This trend seems to be already underway in the early Oligocene. The bulla develops septa which may proliferate to the extent of forming a complex network of diploe lining the walls of the auditory cavity. The expansion of the bulla laterally overlaps the mastoid process, enclosing the facial canal in a long tube. Characteristically in later mustelids the foramen stylomastoideum definitum is almost completely surrounded by the expanded bulla.

Of the four families *Enaliarctos* seems most closely allied to the primitive arctoids in the structure of the auditory region and surrounding bones. There appears to be a close morphological resemblance to the ursid *Cephalogale*, and the alleged lutrine mustelid *Potamotherium* Geoffroy. *Potamotherium* in particular appears to resemble

Enaliarctos sufficiently to deserve close comparison, especially in view of the aquatic adaptation of both genera. The known procyonids seem less closely allied particularly in the morphology of the mastoid and paroccipital processes, position of the posterior carotid foramen, lack of alisphenoid canal, form of the promontorium and presence of a large suprameatal fossa.

Potamotherium has consistently been placed in the Mustelidae and it is usually grouped with the later Cenozoic otters in the Lutrinae. Studies of the magnificently preserved skeletal material of *P. vallentoni* Geoffroy from the Allier district in France (Helbing, 1921; Savage, 1957) demonstrate clearly that this late Oligocene ("Aquitanian") species is already too specialized for aquatic life to be considered an ancestor for the later lutrines. In the auditory region, aquatic adaptation is probably responsible to some degree for such structural differences from the primitive canoid condition as: great reduction of postglenoid foramen, probably correlated with increase in size of the posterior lacerate foramen; great reduction of the fossa for the tensor tympani muscle; and enlargement of the auditory ossicles and the surrounding epitympanic recess. To a greater or lesser degree these features also distinguish *Enaliarctos* from other canoids.

The auditory region of *Enaliarctos* was compared with two crania of *Potamotherium vallentoni* from St. Gerand-le-Puy (AMNH 22520) and the proportions of the basicranial region and external morphology of their parts were found to be quite similar. The only noteworthy differences, making allowances for the disparity in size, is that in *Enaliarctos* the mastoid process is directed downward and close to the paroccipital process to which it is connected by a strong but narrow ridge of bone, whereas in *Potamotherium* the mastoid is laterally directed and widely separated by a broad sloping shelf from the paroccipital process. In both species the posterior carotid foramen and posterior lacerate foramen lie in a common fossa which is round or slightly oval in form in *Potamotherium*, but strongly elliptical in *Enaliarctos* due to the great posterior prolongation of the posterior lacerate foramen. In addition the articulation of the hyoid apparatus in *Enaliarctos* occurs in a pit posterior to the stylomastoid foramen, whereas in *Potamotherium* this articulation lies ventral and slightly anterior to the stylomastoid foramen. There is no alisphenoid canal in *Potamotherium*.

Comparison of the internal structures of the auditory region of the two genera also reveals considerable general similarity. In both the auditory cavity is small relative to that in many later Cenozoic arctoid carnivores. The posterior wall of the bulla is virtually coincident with the posterior border of the promontorium. There are, however, some important differences in details of structure of the middle ear cavity. In *Enaliarctos* the auditory cavity is markedly narrower and deeper than in *Potamotherium*. *Potamotherium* differs from *Enaliarctos* in lacking the low septum across the anterior end of the bulla. In *Potamotherium* the crista tympani is of large diameter, but it is not produced into the auditory cavity to the extent in *Enaliarctos*. Consequently there is no extension of the hypotympanic sinus into the wall of the meatus. *Potamotherium* thus retains what appears to be the primitive condition of the tympanic annulus in fissipeds with ossified bullae. Such extension of the hypotympanic sinus is a trend seen in all arctoid families, although *Enaliarctos* and the ursids show exceptionally well-developed sinuses in the wall of the meatus and the crista tympani are of relatively small diameter. The surface of the promontorium in *Potamotherium* is more irregular, less inflated than in *Enaliarctos*. However, in shape, degree and manner of inflation, and area relative to the roof of the tympanic cavity, the promontorium in both genera agrees with the ursids specifically among the canoids. The fossa for the muscularis major is shallower in *Potamotherium* than in *Enaliarctos*. In both genera this fossa is shallow relative to the condition in terrestrial canoids, a condition which may reflect adaptation to an aquatic mode of life.

The differences between *Potamotherium* and *Enaliarctos* discussed in the previous paragraphs are similar in kind and degree to those which are held to be diagnostic within the earliest known arctoids. Among the particularly noteworthy features are the form and relationships of the mastoid and paroccipital processes, discounting the effect of the larger size of *Enaliarctos*. The pendant mastoid process, closely associated and strongly connected with the paroccipital process, appears to be a diagnostic ursid feature of *Enaliarctos*, contrasting with the mustelid or procyonid, laterally directed, isolated mastoid in *Potamotherium*. The close association of tympanohyal with the opening of the facial canal in *Potamotherium* is a primitive canoid feature and

its posterior position and separation from the stylomastoid foramen in *Enaliarctos* is specifically like that in late Tertiary ursids and otariids. *Enaliarctos*, like all ursids, possessed an alisphenoid canal, whereas *Potamotherium*, the mustelids, and procyonids lacked this structure even in their earliest known representatives. In the ursids the hypotympanic cavity is narrow and deep, and includes a prominent extension into the auditory meatus anterior and ventral to the small diameter crista tympani. *Enaliarctos* possesses a similar auditory cavity in contrast to the wider, shallower cavity of *Potamotherium* and Oligocene mustelids and procyonids which have larger diameter crista tympani. In *Enaliarctos* the exposed part of the promontorium is smooth and appears inflated and pear-shaped (the "stem end" pointing toward the stylomastoid foramen) rather than anteroposteriorly elongate and flat as in *Potamotherium*, although both types more closely compare with early ursids than with representatives of other families. Despite these morphological differences there is an overall similarity in structure, including those features which can be or are suspected to be related to aquatic adaptation. These similarities relate to their close proximity in time to a common arctoid ancestor, resulting from a common adaptation to an aquatic mode of life. We conclude that *Potamotherium* and *Enaliarctos* share many features with primitive arctoid Carnivora and hence should be regarded as a part of the Oligocene radiation of this group. Both genera agree best in auditory structure (and other features brought out in these pages) with the ursid phase of this radiation as exemplified by the Oligocene genus *Cephalogale*. A common origin close to *Cephalogale* is implied by these similarities, which are explored in more detail for *Enaliarctos* in the following paragraphs. The relationships of *Potamotherium* will be further investigated in a paper being prepared by Tedford.

In the skull, and especially the dentition, *Enaliarctos* shows trends that are almost the antithesis of those involved in the evolution of the ursids, yet the auditory regions in these forms are very similar. It is difficult to ascribe these similarities in the ear region to parallelism in animals that otherwise are adaptively so distinct; therefore, it is believed that this similarity must be regarded as evidence for some degree of phyletic relationship.

Cephalogale is the best-known Oligocene ursid and the comparisons presented above of *Enaliarctos* with this family were based on the former genus. Some further comparison seems in order to establish the relationship between these genera. De Beaumont (1965) has recently figured and described the auditory region of both *C. minor* Filhol (approx. Sannoisian, Phosphorites de Quercy) and *C. gracile* (Pomel) (Aquitanian, St. Gerand-le-Puy). We have on hand the Vienna cranium (Vienna A4445; we are indebted to Dr. F. Bachmayer for permission to prepare the middle ear region of this specimen) figured and described by de Beaumont (1965); a cast (AMNH 39298) of the cranium of *C. gracile* (Lyon St. G. 795) figured by Viret (1929, pl. 9, fig. 4a); and the acid-prepared cranial fragment figured and described by de Beaumont (1965, Basel St. G. 2158). Comparisons are made chiefly with these specimens. We are also indebted to Dr. Donald E. Savage for notes on the auditory region of Lyon St. G. 795.

Compared with the width of the basicranium, the bulla seems relatively smaller in *Enaliarctos*. The form of the bulla, however, is similar in both genera, especially with *Cephalogale minor*; in *C. gracile* it is somewhat deeper medially, resembling *Procyon*. There is a tubular meatus directed laterally and slightly anteriorly, forming a little more than the ventral half of the auditory meatus. In *Cephalogale* the meatus is not fused anteriorly with the postglenoid process as in *Enaliarctos*, and a large postglenoid foramen occurs just lateral to the pit in the squamosal for the anterior horn of the tympanic ring. The postglenoid foramen is, of course, tiny or absent in *Enaliarctos*. The bulla lacks fusion with any of the surrounding elements except the mastoid in *Cephalogale*, whereas in *Enaliarctos* the bulla is strongly joined to the postglenoid, mastoid, and paroccipital processes. The mastoid and paroccipital processes are closely associated and connected by a strong ridge which is especially prominent in *Enaliarctos*. A lesser although clearly homologous development is seen in *C. gracile* and in *C. minor*. The pit for the tympanohyal lies posterior to the stylomastoid foramen in *Enaliarctos* but lies ventral to the stylomastoid foramen in a common fossa in *Cephalogale*. In both genera a common fossa at the postero-medial edge of the bulla encloses the posterior carotid foramen and the posterior lacerate

foramen, although in *Enaliarctos* the latter foramen is greatly extended posteriorly.

As far as can be determined the structure of the roof of the auditory cavity is similar in *Cephalogale* and *Enaliarctos*. In both, the tympanic cavity is deep, particularly with respect to the median basicranial bones whose lateral flanges overlap the medial margin of the auditory bullae. The tympanic cavity is narrow and is extended laterally into the meatus forming a hypotympanic sinus in both genera. The low promontorium is pear-shaped in both, slightly more inflated in *Enaliarctos*, and broadly overlapped medially by the wall of the auditory bulla containing the carotid canal. The important differences in structure seem to be related to the aquatic adaptation of *Enaliarctos*. These include the small diameter of the crista tympani, the larger size of the epitympanic recess relative to the size of the middle ear cavity, the shallow fossa for the tensor tympani muscle, and the somewhat larger size of the fenestra cochlea relative to the fenestra ovalis.

These comparisons, although admittedly incomplete, clearly indicate the fundamental similarity of *Cephalogale* and *Enaliarctos*. As far as the auditory region is concerned, the terrestrial *Cephalogale* possesses structures that make a logical morphological base from which the more modified auditory structures of the aquatic *Enaliarctos* could be derived.

BRAIN: The endocast of *E. mealsi* appears to show as much neocortical convolution as in *Lutra* (cf. Gervais, 1870, pl. 9, fig. 8; Jelgersma, 1934, 145-149; Kappers, Huber, and Crosby, 1936, fig. 663; Savage, 1957, fig. 13d; and Radinsky, 1968, fig. 4); more than in *Potamotherium valletoni* (Savage, 1957, fig. 13; and Radinsky, 1968, figs. 5, 6); and probably about the same as in *Enhydra lutris* (Gervais, 1870, pl. 6, fig. 9). The neocortex of *L. lutra* is more complex than that of *P. valletoni* (Savage, 1957, p. 182; and Radinsky, 1968, figs. 4-6). The conclusion is inescapable that, in terms of absolute neocortical complexity, *E. mealsi* was highly specialized for an early Miocene carnivore, but comparisons are meaningful only if correlated with absolute size, and we cannot make comparisons at this time.

The squared appearance of the *E. mealsi* endocast is due partly to an elaboration and expansion of the presylvian section of the cortex, and partly to anteroposterior compression. Par-

ticularly large are the postsigmoidal (motor I) and coronal (somatic afferent) areas. Davis (1964) noted the same elaboration, and others, in procyonids and bears, and cited evidence that it is associated with a corresponding elaboration of the motor and sensory functions. The opercularization of gyrus ectosylvius anterior by gyrus coronalis is a direct morphological result of this trend. Also the anteroventrolateral corner of the endocast is enlarged, in part by gyrus sigmoideus posterior, and we speculate that this enlargement was related to facial and masticatory functions.

Davis (1964) pointed out that in procyonids the postcruciate area, part of somatic afferent area I, is expanded and as a result the continuity of the coronal-lateral sulcus is interrupted. In *E. mealsi* the postcruciate area is large but the sulcus coronalis and sulcus lateralis are broadly continuous as in the Ursidae. Thus *E. mealsi* approaches *Procyon* and differs from the Ursidae and other carnivores in the size of the part of somatic afferent area I devoted to the forepaw.

Comparing the endocast of *E. mealsi* with the illustrations of *P. valletoni* and *L. lutra* given by Savage (1957, fig. 13) and Radinsky (1968, figs. 4-6) and with the endocast of *P. valletoni* studied by Radinsky (AMNH 22520), the resemblance between *E. mealsi* and *P. valletoni* is striking. Both show similarities in the shape of gyrus ectosylvius anterior and posterior, particularly in the region where they join, and in expansion of gyrus coronalis and suprasylvius posterior. In *E. mealsi* the pseudosylvian sulcus is oriented more nearly vertical, is slightly more inclined backward in *P. valletoni*, and is farther inclined in *L. lutra*. The gyrus ectosylvius anterior is already somewhat opercularized in *E. mealsi*, and little or not at all in the geologically older *P. valletoni*. As in *E. mealsi*, the sulcus cruciatus in *Potamotherium* is situated on the anterior edge of the endocast (Radinsky, 1968), but in *E. mealsi* this sulcus is better developed than in *Potamotherium*. Such differences may also be related to the elaboration of the sigmoid area and its more complex function in *Enaliarctos*.

In the elaboration of the coronal, sigmoidal, and postcruciate regions of the cortex, *E. mealsi* approaches the Ursidae and Mustelidae, and differs from the Canidae and Felidae. The idea of concomitant elaboration of manual functions in Ursidae and Procyonidae might be extended to *E. mealsi* as well.

The question of the "ursine lozenge" remains. The "ursine lozenge" according to Davis (1964, p. 297) is present in ursids (including *Ailuropoda* Milne Edwards), and many mustelids, rudimentary in procyonids, and absent in other carnivores. When present it is a diamond-shaped region on the dorsal surface of the front half of the brain, where the gyrus frontalis superior is externally visible, bounded by sulcus praecruciatius and cruciatius. Our interpretation of the anterior region of the *E. mealsi* endocast [LACM (CIT) 5302] indicates the presence of a cruciate area, but as this is situated on the anterior portion of the endocast it does not assume the form found in terrestrial arctoids (in which the cruciate area has a more dorsal exposure). Its presence on the brain surface clearly allies *Enaliarctos* with the Arctoidea, a group in which this structure appears at an early phylogenetic stage (Radinsky, 1971).

DENTITION: The brain and auditory region of *Enaliarctos* clearly indicate affinity with the arctoid carnivores; consequently, the most meaningful comparison of the dentition will be with primitive members of the Mustelidae, Procyonidae, and Ursidae.

Enaliarctos differs from all the arctoids compared in the relative size of the known teeth. The degree of reduction of the upper molars compared with the premolars (as judged by their alveoli) is greater than in any of the known early Miocene and Oligocene arctoids, yet M^2 is retained.

The quadrate form of M^1 eliminates many of the contemporary and older arctoids from further comparison. Both primitive procyonids (*Plesiictis*, *Plesiogale*, and *Zodiolestes*) and primitive mustelids (*Paleogale*, *Paragale*, *Oligobunis* Cope, and *Promartes* Riggs) have transversely elongate first molars, and a tendency to greatly reduce the size of the metacone relative to the paracone and to develop a prominent labial shelf. In *Enaliarctos* this tooth, although reduced in size, retains a quadrate, cynoid outline. The only group of primitive arctoids that has a quadrate molar is the hemicyonine ursids. In the procyonids and mustelids compared, the protocone on the upper carnassial is directed more anterolingually, not so directly lingual as in *Enaliarctos*, and it often bears a distinct cusp. Despite its narrow, transversely elongate M^1 , *Potamotherium* makes a close approach in the structure of its carnassial to that of *Enaliarctos*,

but the protocone shelf is much larger and its root is opposite the paracone root, not behind it as in *Enaliarctos* (i.e., the protocone is more anterolingual in position). Here again, the hemicyonines, and particularly *Cephalogale*, make the closest approach to the condition in *Enaliarctos*.

Cephalogale is most similar in the known features of the dentition to *Enaliarctos*. Lower jaw fragments of *C. minor* (AMNH 10072 and 10073) and the cheek teeth in the Vienna skull (Vienna A4445) of *C. minor* were available for direct comparison, as well as a cast of *C. gracile* (AMNH 39298, Lyon St. G. 795). These specimens show that P^4 in *Cephalogale* is similar in size to that of *Enaliarctos*. In labial view the relative sizes of the paracone and metacone appear similar; there is no parastyle in either genus. The most conspicuous difference in P^4 involves the enlargement of the protocone shelf in *Enaliarctos*, which is, however, not greatly hypertrophied over the condition in *C. minor*.

M^1 is three rooted in both *Enaliarctos* and *Cephalogale*, but the labial roots are small and tightly appressed in *Enaliarctos*. This tooth is quadrate in occlusal outline in both genera, but in *Enaliarctos* the hypocone is placed at the posterolingual corner of the tooth and the lingual cingulum is reduced. This cusp is also in the posterolingual position in *C. minor* but there is a much stronger lingual cingulum. The labial cingulum is also better developed in *Cephalogale*, but not the parastyle which is a stronger structure in *Enaliarctos*. The enlarged parastyle and oblique paracone crest resemble the condition in *Potamotherium* and give the labial border a curved appearance when viewed from the occlusal surface rather than the straight border shown in *Cephalogale*. However, these features are not so well developed in *Enaliarctos*; the quadrate rather than transversely elongate outline of M^1 differs markedly from that of *Potamotherium*. M^2 of *Enaliarctos*, although much reduced, could be derived from a three-rooted tribosphenic condition similar to M^2 of *Cephalogale*.

In the lower carnassial there are differences between these genera which reflect modifications of the upper molars. The talonid is effectively unicuspid (hypoconid) in *Cephalogale* with a strong crest running along the lingual border of the talonid. This crest and the hypoconid enclose the talonid basin, which receives the protocone of M^1 . There is no lingual cingulum. In

Enaliarctos the talonid lacks the lingual crest, the hypoconid is separated from the trigonid by a broad groove and is more centrally placed, there is a low lingual cingulum around the talonid, and the metaconid is much reduced over the condition in *Cephalogale*. The talonid in *Enaliarctos* resembles that in *Potamotherium* in the prominence of the hypoconid and lack of an entoconid crest, but the large metaconid and approximation of trigonid cusps again bar close relationship to *Enaliarctos*.

In summary the dentition of *Enaliarctos* is closest to *Cephalogale* and to a lesser extent to *Potamotherium* among known arctoid carnivores. As in the case of the auditory region the generalized arctoid *Cephalogale* makes a reasonable structural ancestor for *Enaliarctos*. In the dentition of *Enaliarctos* we see an intermediate stage in the transformation of the generalized fissiped dentition from a multipurpose structure to a specialized device for capturing fish and nektonic invertebrates. Further modification for the aquatic carnivorous mode of life would result in eventual loss of M^2 and "premolarization" of M^1 . The loss of the functional relationship of M^1 and the talonid of M_1 would result in reduction of the latter to a two-cusped condition (paraconid and protoconid). The homodonty displayed by later Cenozoic pinnipeds is the logical end product of this functional shift from the requirements of a terrestrial carnivore to that of a pelagic carnivore.

COMPARISON WITH PINNIPEDS

SKULL: Comparison of the *Enaliarctos mealsi* skull and referred snout with members of the Otariidae reveals a great number of similarities. In the skulls of *Enaliarctos* and the living otariids *Callorhinus* Gray, *Arctocephalus* Geoffroy and Cuvier, *Zalophus* Gill, *Neophoca* Gray, *Phocarctos* Peters, *Eumetopias* Gill, and *Otaria* Peron there are to be found: a long and low skull with a straight dorsal profile, a slight to moderate sagittal ridge, a braincase with an abrupt and ventroposteriorly sloping anterolateral wall, a forward sloping supraoccipital shield, a relatively narrow and parallel-sided interorbital bridge between the snout and braincase, very large orbits oriented dorsoanteriorly, and other major resemblances. Of course the basicranium is slightly different as emphasized below, and the palate differs in that the *Enaliarctos* tooth rows are not parallel and contain molariform pos-

terior teeth. The pterygoid struts, between the palate and the braincase, are inflated much as in some otariid species.

Arctocephalus is a widespread polytypic genus of otariid with a typical skull comparable in size to that of *Enaliarctos*. We pick it for detailed comparison with *Enaliarctos* both as a matter of convenience and because it is of equivalent size. We hope in this way to circumvent discussion of some features, such as excessively massive lambdoid and sagittal crests and extensive exostoses, which are clearly features associated with old age and great size in pinnipeds. A detailed comparison of the skull and snout of *Enaliarctos mealsi* with three skulls of *Arctocephalus* [USNM 23331, BM (NH) 1950.11.14.4, and LACM M1656] reveals the similarities enumerated above and more. The arctocephaline palate broadens posteriorly as does that in *Enaliarctos*, and on the posterolateral margin, behind the last (sixth) postcanine tooth, is a small spur of maxillary bone that is the homologue of the flange behind M^2 of *E. mealsi*. Posterior to this maxillary spur the palate in both genera narrows to cover the internal nares for some distance posteriorly. The pterygoid struts are inflated and are very similar in shape. The thin and delicate zygomatic arches are similar, being broadest directly anterior to the glenoid fossa and having a straight body sloping anteromedially to the level of M^2 . The glenoid fossa differs slightly in shape. In the Arctocephalini it has a straight anterior border, whereas in *Enaliarctos* there is a prominent preglenoid process which wraps around the mandibular condyle, as in *Lutra*. The smooth and relatively uninflated bulla of *E. mealsi* is similar to the triangular bulla of a male *Arctocephalus galapagoensis* (LACM M1656). There is more space between the glenoid fossa and the bulge of the bulla in *Enaliarctos*, notwithstanding the fact that the glenoid fossa is relatively much farther back on the braincase. In *Arctocephalus* the glenoid fossa and the bulla are far anterior on the skull, and the meatus is directed about 10 to 13 degrees anteriorly from the transverse plane. In *E. mealsi* this angle is 15 degrees or more. Proportions of some basicranial foramina are different: for example, the posterior lacerate foramen is long and ovate in *Arctocephalus*, shorter and rounder in *Enaliarctos*.

Relative to skull size, the palate and interorbital region of *E. mealsi* is much broader, the

braincase narrower, and the occipital condyles project farther posteriorly from the skull. The mastoid ridge is much larger and projects ventrolaterally in the Arctocephalini. The pterygoid strut drops anteroventrally, then anterodorsally, in *E. mealsi*, unlike the relatively straight strut in *Arctocephalus* that is continuous with the palatal margin. The *Enaliarctos* skull is deeper at the level of the anterior orbital margin, but drops off to an attenuated snout in lateral profile more abruptly than in *Arctocephalus*. The tip of the snout is unknown in *Enaliarctos*.

The Otariinae, but not the Phocidae, show a patent interorbital septum developed anterior to an interorbital perforation associated with the optic foramen. The optic canals lead from within the braincase to open in the orbital wall, which in the Otariinae is a single thin lamina in the region of the presphenoid bone. This thin vertical lamina, the interorbital septum, is formed by the orbitosphenoid bones that lie mostly anterior to the optic foramen. Its back edge forms the single, common anterior edge of the optic foramina, which thus form an interorbital perforation through the interorbital region. In some individuals the presphenoid runs between the orbitosphenoids back into the common canal for the optic nerves as a midline septum, but in Otariidae never so far back as to preclude the entire transverse perforation through which one can peer. Although the interorbital septum is not developed in Phocidae, the "see through" condition of the optic perforation can be present [*Leptonychotes weddelli* (Lesson) BM (NH) 1908. 2.20.16].

In *Enaliarctos mealsi* the interorbital region, although narrow, is not reduced to a single lamina. The optic canals are subparallel and paired, and the optic foramina are far apart, without a common anterior margin. The fossil thus resembles fissipeds, phocids, and odobenines rather than most of the Otariinae. The presence and extent of the thin interorbital septum and the perforation, are correlated with matters of cranial geometry related mainly to the mutual relationships of the nasal cavity, the brain cavity, and the nasopharyngeal duct. Haines (1950) concluded that the orbital septum was emphasized in microsmatic mammals with large eyes, long and narrow skulls, and thin (not excessively cancellous) cranial bones. *Enaliarctos mealsi* is obviously trending in these directions,

but had not yet attained the extreme situation found in the Otariinae.

The step between *E. mealsi* and some species of *Arctocephalus* would be represented by: simplification of P⁴, M¹, and M², broadening of the anterior corners of the braincase and loss of the lateral braincase sulcus along with a general expansion of the brain, development of larger supraorbital processes, suppression of the lacrimal bone, and some, but not many, modifications in the middle ear region as mentioned below. The resemblances are striking. Most of the changes could be expected with increasing adaptation to amphibious life, especially pre-molarization and lacrimal bone changes.

The above comparison with *Arctocephalus* serves to show a few of the similarities and differences between *E. mealsi* and living otariids, especially the Arctocephalini. The question as to whether the Arctocephalini or the Otariini are the more generalized remains moot and does not significantly affect the outcome of the comparison as they differ so little that we have taken *Arctocephalus* as representative of living otariids. Of all the extinct otariid species yet described, *Desmatophoca oregonensis* Condon is the most generalized and primitive (Condon, 1906; Mitchell, 1966a).

Desmatophoca oregonensis was a highly adapted otariid having a homodont dentition (insofar as known) and other attributes of living otariids, yet retaining such primitive features as separate mastoid and paroccipital processes. *Enaliarctos mealsi* in some respects differs markedly from *D. oregonensis*, yet the two species show interesting similarities. *Enaliarctos mealsi*, the smaller of the two, is known from early Miocene rocks in California; *D. oregonensis*, from middle Miocene rocks in Oregon. Both have long interorbital regions; when viewed dorsally, the interorbital bar is parallel-sided in both; and there are no well-developed supraorbital processes. The infra-orbital foramen is medium-sized to small, the zygomatic arch relatively thin and widely bowed, the sagittal crest low and thin, the orbits large, the braincase squared off in front, and the premolars simplified grasping teeth. These and other features are shared by both forms. The snout of *E. mealsi* is unknown, but may have been relatively deeper than in *Desmatophoca* Condon.

In *E. mealsi* there is a pair of slight depressions on the dorsal roof of the braincase, midway

between the orbit and the lambdoid crest. In the same position, these depressions are duplicated and emphasized on the skull of *D. oregonensis* (Mitchell, 1966a, pl. 29). Their function is unknown to us, and Howell (1929) did not observe in *Zalophus* any of the muscles or tendons originating in the region of the parasagittal fossae (as we so name them here) that we find in *Desmatophoca* and *Enaliarctos*. We have not made an exhaustive search, but have found analogous parasagittal fossae in *Odobenus* Brisson and some phocids.

The ventral margin of the glenoid fossa is subtended more ventroanteriorly in *E. mealsi* than in most living otariids, but approximates the condition in *D. oregonensis*. The large posterior palatine foramina of *E. mealsi*, found to some extent in *D. oregonensis*, also are much diminished in size in living otariids.

Although *D. oregonensis* is advanced beyond *E. mealsi* and on a different line emphasizing some different features, the above comparison confirms the suggested resemblances of *E. mealsi* to otariids. The *D. oregonensis* skull is relatively much longer and more slimly built, yet there are similarities in the dorsal and lateral aspect of the skulls. *Desmatophoca oregonensis* is a primitive otariid, but not sufficiently generalized to serve as an ancestor for all the Otariidae (Mitchell, 1968, p. 1888). We suspect that *D. oregonensis* may be a separate stock (Desmatophocinae) within the family Otariidae having little to do with the ancestry of the Otariinae. If this is so, then the possibility exists that *E. mealsi* could have given rise to the Otariinae (Mitchell, 1968, fig. 16). Such features in *Desmatophoca* as discontinuous paroccipital and mastoid processes, among others, precludes *E. mealsi* from desmatophocine and allodesmine ancestry. Thus, *E. mealsi* is not ancestral to *D. oregonensis* and the question hinges on the relation of *D. oregonensis* to the Otariinae.

In the following features the skull of *E. mealsi* differs from that of phocids: the jugal-squamosal contact is of a simple overlapping type and not a more complex interlocking type as in all Phocidae, as well as in Allodesminae and to a lesser degree in Odobeninae; the bullae are less inflated; an alisphenoid canal is present; the skull is more heavily ossified and has no major vacuities; the pterygoid struts are inflated; pre-glenoid processes are present but are absent or

reduced in many Phocidae; the interorbital region is longer and wider than in some phocids; the skull is almost as deep at the level of the infraorbital foramina as at the level of the auditory bullae; there is a major external crease corresponding with the pseudosylvian fissure in the braincase wall; the sagittal crest is stronger than in some phocids, and the lambdoid crests are reflected far back on the braincase as in some phocids; the mastoid is not inflated, and a conspicuous mastoid process is joined by a ridge with the paroccipital process; there are no major interorbital vacuities as in many Phocidae; the braincase is relatively longer; and other differences. The general resemblances in the skull we regard as due mainly to convergence in aquatic adaptation, a subject we discuss further below.

AUDITORY REGION: Because of the many adaptive structures suggesting an aquatic mode of life for *Enaliarctos* comparison of its auditory region with that of the pinnipeds is of great interest. The holotype of *Enaliarctos mealsi* was compared with some of the living phocids, otariids, and the Miocene otariid *Allodesmus kelloggi* (holotypic partial skull, LACM 4320, and left otic region of another individual, LACM 4565). The internal features of the middle ear were examined in specimens of *Phoca vitulina* Linnaeus, *Monachus tropicalis* (Gray), *Erignathus barbatus* (Erxleben), *Lobodon carcinophagus* (Hombron and Jacquinot), *Hydrurga leptonyx* (Blainville), *Leptonychotes weddelli* (Lesson), *Cystophora cristata* (Erxleben), *Mirounga angustirostris* (Gill), *Arctocephalus townsendi* Merriam, *Zalophus californianus* (Lesson), *Eumetopias jubata* (Schreber), and *Odobenus rosmarus* (Linnaeus).

EXTERNAL FEATURES: The bulla is more inflated in *Enaliarctos* and its surface less rugose than in living otariids or *Allodesmus*. In adult individuals of living otariids the ectotympanic forms three-quarters or more of the auditory bulla in such a way that the entotympanic composes little more than the carotid canal. *Enaliarctos* seems to show this pattern as suggested by a groove and chain of nutrient foramina extending posteriorly from the anteromedial corner of the bulla to the vagina processus hyoidei (pit for the tympanohyal). The inflation of its bulla is thus attributable to the ectotympanic rather than to the entotympanic as is typical of phocids.

Allodesmus shows a condition like that of newborn otariids in which the entotympanic forms nearly one-third (up to one-half in *Odobenus*) of the bulla. In Recent otariids there are one or two tubercles or ridges on the ventral surface of the bulla near the median border of the ectotympanic.

The auditory meati in living species appear no longer, and in many cases are relatively shorter, than in *Enaliarctos*. In *Allodesmus* the bulla is very flat, flatter than in any living otariid studied, and without prominent processes although the ventral surface is rugose. The external auditory meatus is very short. The bulla is firmly ankylosed to the posterior surface of the postglenoid process and strongly fused to the anteromedian margin of the mastoid process in all genera compared. In addition adult otariines and *Allodesmus* show fusion of the bulla with the mastoid between the tympanohyal pit and stylomastoid foramen and with the petrosal anterior to the base of the paroccipital process. *Odobenus* adults show variable fusion of the bulla and mastoid between the tympanohyal and stylomastoid foramen but not behind the tympanohyal pit. *Enaliarctos* is closer to the otariines, but lacks strong union of the bulla and mastoid between the tympanohyal pit and stylomastoid foramen. In *Potamotherium* the tympanohyal is apparently fused with the bulla ventral to the stylomastoid foramen as in primitive arctoids.

All otariids lack the postglenoid foramen but a tiny remnant is present in *Enaliarctos*. The styloform process is tiny in *Allodesmus*, larger in *Enaliarctos* and living otariids. The median lacerate foramen at the alisphenoid-basisphenoid junction is covered by the anteromedian wall of the bulla in the specimens of *Allodesmus* examined, but two small foramina in the bulla wall allow access to this foramen. This condition is found in varying modes of development in all the otariids studied from the completely open condition in *Enaliarctos* to the covered foramen described for *Allodesmus*.

In the otariids the posterior carotid foramen and posterior lacerate foramen lie in a common fossa as in *Enaliarctos*, the posterior lacerate foramen is elongated anteroposteriorly. *Enaliarctos* has a straight carotid canal as in living otariids, but unlike them, the internal carotid artery issues from the anterior carotid foramen and turns sharply dorsally, and posteriorly the

loop formed lies in a short groove in the ventral surface of the basisphenoid as in ursids, canids (including the Oligocene canid *Hesperocyon*), and some procyonids (Segall, 1943; Story, 1951). Living otariids have a straight carotid canal and the artery enters the median lacerate foramen with a short dorsal flexure. *Potamotherium* is more like *Allodesmus* and most phocids in that the anterior part of the carotid canal turns dorsally within the median wall of the bulla, and the internal carotid artery enters the braincase directly through the median lacerate foramen without the strong flexure as in *Enaliarctos*.

The mastoid process is a strong, roughly quadrangular, pendant projection in *Enaliarctos* and in all otariids studied. It may be greatly enlarged in old otariid males. In the otariids, including *Allodesmus*, a wedgelike bony element (ossiculum mastoideum, Cave and King, 1964) is generally visible interposed between the mastoid-squamosal suture on the tip of the mastoid process. This element cannot be detected in the holotype of *Enaliarctos* but does occur in the terrestrial arctoid families Ursidae and Mustelidae (Segall, 1943).

The paroccipital process in both *Enaliarctos* and the otariids is well developed and composed of contributions from both the mastoid and exoccipital. The mastoid is produced into a continuous crest from the mastoid process to the paroccipital process, forming a large shelf when viewed ventrally, which in living otariids makes up much of the posterolateral surface of the basicranium. In *Allodesmus* the paroccipital processes are likewise formed by the exoccipital and mastoid bones, they project more laterally, and are longer and narrower than in *Enaliarctos* and in later otariids.

The bulla is greatly inflated, particularly the entotympanic, in living phocids examined and its surface is relatively smooth. The entotympanic forms more than one-half of the bulla. The external auditory meatus is longer than in most otariids, similar to that in *Enaliarctos*. Anteriorly the bulla is sutured to the base of the postglenoid process. A small postglenoid foramen may be present in the phocids, as in *Enaliarctos* and *Potamotherium*, on this suture anterior to the lip of the external auditory meatus.

In the living phocids studied the anterior edge of the bulla covers the cranial opening of the median lacerate foramen and extends forward to the posterior edge of the foramen ovale. In

Hydrurga Gistel a strong styloid process medial to the eustachian opening extends anteriorly beyond the foramen ovale. The styliiform process is variably formed in the phocids ventral or medial to the opening for the eustachian tube. Medially the bulla either lacks any sutural contact with the basioccipital, or it may be loosely sutured as in *Enaliarctos*, *Potamotherium*, and the otariids. Only in *Hydrurga* is the lateral edge of the basioccipital and basisphenoid turned downward along the medial side of the bulla in the manner seen in the otariids and *Enaliarctos*.

In contrast with the condition in *Enaliarctos*, *Potamotherium* and the otariids, the posterior carotid foramen and posterior lacerate foramen are well separated by a flange of the ectotympanic so that the carotid opening lies distinctly ventral to and in advance of the lacerate foramen. The internal carotid artery lies in a canal within the medial wall of the bulla and follows a dorsally or dorsolaterally curving path to the anterior carotid foramen, from which it enters the braincase via the median lacerate foramen by dorsomedial flexion. There is no groove in the basisphenoid for the bend of the artery as in *Enaliarctos*.

In living phocids the ectotympanic portion of the bulla is loosely sutured to the petrosal well in advance of the base of the paroccipital process. As in other bulla-bearing carnivores there is a strong fusion of the ectotympanic to the mastoid process. The mastoid process in most of the phocids studied is a low laterally projecting knob, but in *Hydrurga* and *Monachus* Fleming this structure is produced laterally to a greater extent approximating the condition in *Potamotherium*. An ossiculum mastoideum is unknown in the phocids. A unique phocid feature, especially well developed in the Phocinae, is the inflation of the region between the paroccipital and mastoid processes, evidently related to the enlarged condition of the cerebellar or subarcuate fossa within the petrosal and pachyostosis of the petrosal about this fossa. The cerebellar fossa is large in *Potamotherium* and *Enaliarctos* although it is not accompanied by a corresponding inflation through pachyostosis of the region between the mastoid and paroccipital processes. Many other canoid genera also show a large fossa, and this condition may be primitive in carnivores. A relatively shallow pit represents the cerebellar fossa in the otariids,

including *Allodesmus*. The otariines and arctocephalines do not develop pachyostosis of the petrosal, but rather show a unique lateral expansion of the cerebellum (see Murie, 1874, p. 529 for description in *Otaria*) into the petrosal above and behind the shallow subarcuate fossa. *Odobenus* does not show such an extreme expansion as in other otariids, but it still exceeds the condition in the phocids. As far as can be determined *Enaliarctos* is similar to the walrus in the expansion of the dorsalmost part of the petrosal. *Cephalogale*, *Potamotherium*, and the phocids are similar to other carnivores.

In the phocids the facial nerve passes from the foramen stylomastoideum definitum in a well-defined groove in the mastoid which extends anterolaterally along the side of the external auditory meatus. An equally well-defined groove extends posteromedially from the stylomastoid foramen, or a secondary foramen behind the opening of the facial canal when the latter is closed behind by a process of the bulla. Such a posterior groove is lacking in the otariids and *Enaliarctos*. Some individuals of *Potamotherium* have a posterior foramen and groove as in the phocids. The tympanohyal of the phocids is included in the bulla just anterior and ventral to the stylomastoid foramen, not lodged in a pit posterior to this foramen as in *Enaliarctos* and the otariids. *Potamotherium* shows a condition like that of the phocids.

INTERNAL FEATURES. In all the phocid genera studied the bulla walls are thick anteriorly (especially so in *Hydrurga*) and formed of dense bone tissue, particularly the ectotympanic and median wall of the ectotympanic below the carotid canal. Otariine bullae do not show a comparable pachyostosis of the ectotympanic: the thickest part of the floor of the bulla lies along the ectotympanic-ectotympanic suture, and here the thickened bulla is formed by cancellous bone. *Odobenus* shows pachyostosis of the ectotympanic similar to the phocids. *Enaliarctos* and *Potamotherium* also show thickening of the ectotympanic over the condition in the ectotympanic, but this thickened bulla floor is formed by cancellous bone. With the exceptions mentioned below the floor of the pinniped bulla is smooth, but medially is rugose along the carotid canal, and a few low transverse septa radiate from the crista tympani. Low septa following the ectotympanic-ectotympanic fusion were observed in a young adult *Monachus*

tropicalis [AMNH (M) 35354] and a young juvenile *Odobenus* [AMNH (M) 35159]. These examples have septa comparable with those possessed by the Oligocene canid *Hesperocyon*. No arctoids known to us show such septa. None of the pinnipeds examined show any extension of the tympanic cavity into the surrounding elements. Nevertheless the phocid tympanic cavity is relatively more capacious than that of the otariids, principally due to the greater inflation of the ventral portion of the bulla. *Enaliarctos* agrees with the otariids in the small size of the tympanic cavity. In *Enaliarctos* the crista tympani is relatively small in diameter and is produced into the tympanic cavity as a consequence of the extension of the hypotympanic sinus along its ventral side. Comparable development is seen in *Arctocephalus* and *Zalophus*. *Potamotherium*, *Odobenus*, and the phocids show relatively large diameter crista tympani, which are not so strongly produced into the tympanic cavity. Posterodorsolaterally the inbent margin of the bulla in *Enaliarctos* comes close to, but does not underlap, the apex of the promontorium as in the otariids. In most of the phocids studied, the apex of the promontorium and most or all the fenestra cochlea are underlapped by the bulla. Only *Monachus* showed a condition similar to the otariids. It is difficult to ascertain the condition in *Potamotherium* with the material in hand, but the situation seems to be much as in *Enaliarctos*.

The promontorium is smooth and pear-shaped in the otariines studied and in *Enaliarctos*. *Odobenus* shows a promontorium of similar form, as does *Potamotherium*, but both lack the degree of inflation seen in the foregoing. In the phocids examined the promontorium is ventrally produced and inflated above the fenestra cochlea and often underlapped medially by the bulla to a greater extent than seen in any of the other genera studied.

In the pinnipeds studied the fossa for the tensor tympani (fossa muscularis major) is either lacking entirely (Otariinae) or possibly represented by a very shallow groove or irregular pit lateral to the promontorium and parallel to the eustachian canal (Phocidae). Dissection failed to reveal the tensor tympani in *Eumetopias jubata* (Odend'hal, 1965). A well-defined but shallow groove occurs in this position in *Enaliarctos*, suggesting that the tensor tympani may have been present. The condition in *Potamother-*

ium closely resembles that in the phocids. By contrast the epitympanic recess that houses the auditory ossicles is very large in the phocids and *Odobenus*, corresponding to the hypertrophy of these bones. In all otariids (except *Odobenus*) this recess is small and the auditory ossicles are consequently moderate in size. In *Allodesmus*, however, the auditory ossicles are greatly enlarged ["five times more massive than in any otarioid," (Mitchell, 1966a)] and the epitympanic recess is also capacious. Savage (1957) also reported that the auditory ossicles in *Potamotherium* are rather larger than those of *Lutra*, and the epitympanic recess in this form is also relatively larger than in *Lutra*. In *Enaliarctos* the epitympanic recess is slightly larger than it is in *Arctocephalus* skulls of similar basal length. Its incus appears to be similar in size to that of *Arctocephalus*.

In summary, the above comparison of the auditory region of *Enaliarctos* with that of the otariid and phocid pinnipeds suggests that it more closely approaches the otariids than the phocids. Particularly striking otariid features are: the small size of the bulla relative to the basal length of the skull; the great size of the ectotympanic relative to the entotympanic; the anteroposteriorly elongated posterior lacerate foramen forming a common fossa with the large posterior carotid foramen; the straight carotid canal; the articulation of the tymphanohyal posterior to the stylomastoid foramen; the strong roughly quadrangular and pendant mastoid process connected via a ridge with the paroccipital process; small size of the tympanic cavity; crista tympani of small size strongly produced into tympanic cavity; and the smooth, pear-shaped promontorium. In addition, in neither the known otariids nor in *Enaliarctos*, does the petrosal show the pachyostosis of the petrosal between the mastoid and paroccipital process as in most phocids. The incus in *Enaliarctos* does not seem to be enlarged as in the phocids and *Odobenus*; as far as can be determined it is approximately the size of that in otariids of similar skull size. In all these features *Enaliarctos* and the otariids contrast with the phocids.

BRAIN: The opercularization of the gyrus arcuatus primus (gyrus sylvius) by the gyrus arcuatus secundus (gyrus ectosylvius) begins in many mammalian groups by insinking or covering of the region lying in front of the

pseudosylvian sulcus (Kappers, Huber, and Crosby, 1936). In the pinnipeds the pseudosylvian sulcus sinks into the island along with the anterior limb of the gyrus arcuatus primus (Turner, 1888a; and other authors cited by Kappers, Huber, and Crosby, 1936). This, also, is the case in *E. mealsi*.

Opercularization takes differing forms in living pinnipeds. In the otariids (Turner, 1888a; Fish, 1899, 1903) the entire anterior margin of the gyrus ectosylvius is overlapped by the gyrus coronalis, whereas in phocids (Fish, 1899) only the ventral portion of the gyrus ectosylvius is overlapped along the sulcus suprasylvius. *Enaliarctos* follows the pattern shown by sea lions and walruses.

In side view the cerebellum in phocids is prominent, occupying up to one-half the depth of the entire brain at that point (e.g., in *Lep-tonychotes weddelli*, Hepburn, 1913, plate, fig. 2; *Phoca vitulina*, Fish, 1899, pl. 6; USFWS cast 64-508; and Jelgersma, 1934, figs. 103-104). But in otariids the posterolateral edge of the cerebral hemispheres overlaps the cerebellum much more and may cover it far ventrolaterally. *Enaliarctos* approximates the latter condition, and in general proportions shows an endocast more like that of otariids than phocids. The phocid brain is much more bulbous and is highly convoluted [*Erignathus barbatus*, *Pusa hispida* (Schreber), and *Phoca vitulina*, Kükenthal, 1889, pl. 13; *Mirounga leonina*, Turner, 1888b, pl. 8 and also p. 197 in Turner, 1912].

The endocast of *E. mealsi* shows less neocortical convolution than any otariid compared. The following, in the order given, represent an approximation of a structural series showing an increasing degree of complexity of folding of the cerebral cortex: *E. mealsi* [LACM (CIT) 5302], *Callorhinus ursinus* (Fish, 1899, pl. 5; and USFWS cast 61-510), *Odobenus rosmarus* (Fish, 1903), *Otaria byronia* (Murie, 1874, pl. 78), *Zalophus californianus* (Fish, 1899, pl. 7; and USFWS cast 62-294). This is our conclusion based on gross appearance of the above specimens and illustrations, but Fish (1899) concluded from preserved materials that the brain of *Callorhinus ursinus* showed a greater number of minor fissures and more intricate branching of larger ones than did the brains he examined of *Zalophus*, *Phoca*, and *Ursus*.

Despite this complexity there is a general uniformity in overall shape and relative size of

neocortical convolutions within the Otariidae, different from the less cohesive pattern found within the more diverse Phocidae. As numerous authors have emphasized, in this context the ursid brain and the otariid brain are more similar than different, and both differ from phocid brains in many of the same ways. The pattern of cortical elaboration in *Enaliarctos* places it, at first sight, within the ursid-otariid pattern, and in such a way that it forms a base from which otariid patterns may be derived.

In the description of the endocast of *E. mealsi* we noted the expansion of the gyri coronalis and suprasylvius posterior. In the pinnipeds the suprasylvius posterior is also expanded but the coronalis is not proportionally enlarged. A possible reason for this difference lies in the transformation of the front limbs (somatic sensory area I, gyrus coronalis, Welker and Seidenstein, 1959) from tactile manipulatory organs to organs of locomotion in the pinnipeds. *Enaliarctos* may have retained a grasping, yet webbed front foot, as in *Potamotherium*, rather than developing the flippers of its otariid descendants.

No satisfactory casts have yet been made of the endocranial cavity of the otariid *Allodesmus kelloggi*, but the holotype of another middle Miocene otariid, *Desmatophoca oregonensis*, shows some of an endocast through a damaged braincase wall (Mitchell, 1966a, pl. 29). Comparison of the specimens shows notable similarities of the endocasts of *E. mealsi* and *D. oregonensis*, including: squared corner of braincase anteroventrolaterally; presylvian half of endocast much smaller than postsylvian half, presylvian half with parallel to subparallel sides when viewed from above; deep pseudosylvian sulcus; and gyrus suprasylvius posterior extending far backward and downward over cerebellum. Evidently the neocortical convolutions were more complicated in *D. oregonensis* than in *E. mealsi*.

DENTITION: Pinnipeds are a very old, possibly heterogenous, and certainly diverse group of animals. As might be expected, there are a number of pinnipedian tooth types, patterns related more to adaptive tendencies than to ancestry. The tusks and peg teeth of the odobenines *Odobenus* and *Prorosmarus* Berry and Gregory are approximated by long canines and thick cheek teeth in the genus *Dusignathus* Kellogg (Mitchell, 1966a, 1968).

Within the Phocidae there is a wide range of cheek tooth types, ranging from the nearly smooth, slightly wrinkled crowns of the peglike teeth of *Mirounga* Gray through the simple step-like teeth with a small posterior cusp of *Cystophora* Nilsson, *Ommatophoca* Gray, *Leptonychotes* Gill, and *Halichoerus* Nilsson. The species of *Pusa* Scopoli and *Phoca* Linnaeus (figs. in Douth, 1942, for example) generally have a major blade-like cusp preceded by a small sharp cusp and followed by one (upper) or two (lower) sharp posterior cusps, all linearly arranged. In *Hydrurga* Gistel, the cheek teeth have greatly produced and attenuated cusps for piercing and grasping. The cusps in *Lobodon* Gray are so complex that they form a sieve when the upper and lower dentition is occluded (King, 1961). The few cheek teeth referred to *Enaliarctos mealsi* are not comparable with either the peglike or complicated teeth seen in phocids and odobenines.

Teeth of the Otariini and Arctocephalini generally have a major cusp that is conical in shape but flattened side to side, with a short accessory cusp projecting anteromedially from the heavy medial cingulum. The sharp edge running down the back of the main cusp meets a smaller but usually distinct posterolateral accessory cusp sitting on the cingulum, usually appressed to the main cusp. The following notation gives the features of the upper left postcanine series of a female *Arctocephalus australis* [BM (NH) 1950.11.14.4] skull: Anterior accessory and main cusps occur on PC¹–PC⁵, posterior accessory and main cusps occur on PC¹ and PC⁴–PC⁶. The left lower series is identical except that there is no postcanine 6. But such cusps are variable: the first and the fifth lower postcanines of a male *Arctocephalus galapagoensis* (LACM M1656) show all three structures but most of the intermediate three teeth show only the anterior accessory and main cusps.

Anterior cingular cusps are pronounced in one male skull of *Phocarctos hookeri* (Gray), as is a simple internal cingulum, but posterior cingular cusps are absent or relatively small. Medial and anterior, but not posterior, cingular cusps are marked on the upper cheek teeth of one male skull of *Neophoca cinerea* (Péron) [BM (NH) 1925.10.8.32]. Chiasson (1957, fig. 6) has illustrated a tooth of *Otaria* with pronounced anterior and posterior accessory cusps, a condition probably not typical. The cusps are relatively larger than

any of those figured by Hamilton (1934, pls. 10, 13; 1939, pl. 29), which show instead teeth with crowns that are composed of a high, conical main cusp and often an anterior accessory cusp, but seldom a posterior cusp, which is smaller if present at all.

There appears to be a pattern to otariine teeth: a main cusp with a small anterior cingular cusp and a variable posterior one. The first postcanine tooth is single rooted, the intermediate teeth partially double rooted, and the fourth and fifth postcanines are often patently double rooted.

The upper carnassial tooth (fig. 15) referred to *E. mealsi* is three rooted, unlike most pinniped teeth. The two upper molars, preserved in the holotype, are completely unlike any other pinniped tooth. In the lower carnassial of *Enaliarctos* the crown is dominated by the paraconid, protoconid, and hypoconid, which form a linear series resting on a double-rooted base. This approximates the form of the posterior postcanine teeth of some otariids.

Comparison of the *E. mealsi* teeth with those of *Desmatophoca oregonensis* (Condon, 1906) results in the same conclusions. The *Desmatophoca* teeth are all double rooted except the first postcanine. The second molar has been lost, and the crowns are inflated to a degree; they have internal cingula with small anterior and posterior cusps and a high main cusp. The fourth postcanine has a transversely widened posterior root that supports an internal shelf. This might be derivable from a carnassial like that referred to *E. mealsi*, but *D. oregonensis* is clearly not a descendant of *E. mealsi* on other evidence.

The teeth of other extinct otariids like *Allodesmus* and *Dusignathus* are peglike, with inflated crowns and suppressed auxiliary cusps. One interesting tooth, supposedly from the Shark-tooth Hill local fauna (Kellogg, 1922, figs. 3–5), bears a main cusp, small anterior and posterior cingular cusps, and a tuberculated internal cingulum. As it has only one root, it probably is a first postcanine tooth. Mitchell (1966a, p. 19) suggested that it was from *Neotherium mirum* Kellogg. The possibility is thus raised that there is an ancestor-descendant relationship between *E. mealsi* and *Neotherium mirum*, for the "molar" of Kellogg is such that it might fit nicely into the (still hypothetical) premolar dentition of *E. mealsi*.

In summary, the postcanine dentition of *Enaliarctos* might serve as a loose structural stage in the evolution of otariid cheek teeth, but this does not in itself demonstrate a true phyletic relationship. Reduction of molars to two-rooted,

haplodont cheek teeth, obliteration of the external cingulum, and de-emphasis of large bladelike posterior cusps would have been necessary if *Enaliarctos* were strictly ancestral to any of the otariid pinnipeds.

MORPHOLOGIC EVIDENCE FOR AQUATIC ADAPTATION

THERE ARE FEW positive features to be found in an isolated skull that might unequivocally demonstrate that an animal is aquatic rather than fossorial or cursorial. But a number of features, taken together, suggest that *Enaliarctos* was an aquatic mammal. Remains of *E. mealsi* were found in marine, near-shore deposits and although this is not in itself convincing proof of aquatic life it will add weight to our argument based on morphological indications of such an existence. In addition unabraded remains of three individuals and isolated teeth indicating several more were found in the same marine rocks, lending weight to our conclusions that *E. mealsi* lived at or near the site of deposition.

Because the sense of smell has evidently been lost by some kinds of cetaceans (Kellogg, 1928, and others), attention has been directed toward the loss of olfactory capacity as a correlate of adaptation to aquatic life. But, as Edinger (1955) has emphasized, much of the evidence in cetaceans has been misinterpreted, and this trend is by no means clearcut even through a series of structural grades culled from various orders of mammals. However, with this qualification in mind, we can accept Howell's (1930) generalizations about the reduction in size of the olfactory bulbs in some groups. This is not a strict indication of loss of efficiency or usefulness. Certainly pinnipeds, for example, depend somewhat on olfaction in socially oriented behavior when on land. We do point out that in *E. mealsi* the endocast shows that the brain was short and wide, and that the olfactory bulbs were narrow and relatively small. A conservative interpretation of this reduction in size, along with other indications of aquatic life, is that olfaction was reduced or functioned differently in *E. mealsi* in comparison with most terrestrial carnivores.

In marine mammals, the lacrimal foramen is often reduced or lost entirely. In the pinnipeds (lacrimal bone absent in some phocids, Dornesco and Marcoci, 1958; usually absent, or imperforate when present, in adult otariids, Howell, 1929, p. 12), in the Sirenia (Reinhart, 1959, p. 9, but the lacrimal foramen is found in early sirenians, p. 106) and in the Desmostylia (lacrimal present, lacrimal foramen absent, VanderHoof, 1937, p. 178) this is also the case.

In some odontocetes this trend toward reduction was thought by some to result in the absence of the lacrimal bone itself, but evidence indicates that it may instead fuse with the malar bone (Schulte, 1917, pp. 390–391, 398). VanderHoof (1937) and Reinhart (1959) agree that absence of the lacrimal foramen in desmostylians is an aquatic feature found in amphibious mammals. In *E. mealsi* the lacrimal bone is present and is relatively large, covering much of the anterior rim of the orbit, and bordering a large lacrimal foramen. This is the condition also in *Potamotherium valletoni* (Savage, 1957) and in *Enhydra lutris* (we examined AMNH CA 41353). Savage (1957, p. 166) has stated that the presence in *Potamotherium* of a lacrimal rather larger than in *Lutra* is a primitive character persisting in spite of advanced aquatic adaptation. Whatever interpretation attaches to its retention, the presence of a lacrimal bone and foramen in *Enaliarctos* is another feature in which it parallels *Potamotherium* and *Enhydra* in structural plan at this stage of aquatic adaptation.

The interorbital constriction in *E. mealsi*, the large size of the orbits, and their placement high on the skull is an aquatic adaptation also found in *Potamotherium* (Savage, 1957, p. 168), in pinnipeds, hippopotamuses, desmostylians, and a number of other aquatic species (Howell, 1930, and others). Savage in particular has pointed out that it may increase the field of binocular vision, but other factors enter here and we emphasize only that in *Enaliarctos* the eyes were high on the head and might therefore break the water surface without exposing much of the animal.

We are particularly struck by the rich venous drainage of the brain of *E. mealsi*, indicated by the large caliber of the dorsal cerebral veins and dorsal sagittal sinuses found on the endocasts. Pinnipeds also have such enhanced circulation to and from the brain, similarities possibly related to diving adaptations.

A postglenoid foramen is rare in feloids but usually present in canoids. It is absent (Savage, 1957) or small (present paper) in *Potamotherium*, and small in *E. mealsi* and in pinnipeds. As the brain is drained by three main groups of veins, one of which, the external jugular vein, exits

through the postglenoid foramen, the other two routes must be emphasized in these species. Significantly, one of these, the posterior lacerate foramen through which issues the internal jugular vein, is enlarged in all. Thus, the same pattern is found in *Enaliarctos* as in other aquatic carnivores and serves to strengthen the idea that it was aquatic.

Howell (1930, p. 88) has emphasized that broadening of the muzzle is an aquatic adaptation found in such mammals as the tenrec, *Potamogale*, and the Carnivora. As we have pointed out, the muzzle in *E. mealsi* is relatively short and broad, much as in *Enhydra* and pinnipeds. The significance of the broad muzzle in *E. mealsi* is difficult to interpret. The maxillo-turbinal bones in *Potamotherium* were much larger than the ethmo-turbinal bones, and functioned to filter and perhaps warm inspired air (Savage, 1957, p. 173). Perhaps in *E. mealsi* the same condition held, as the olfactory senses may have been diminished as attested by the small size of the olfactory bulbs. The turbinals in pinnipeds used particularly in warming inspired air are emphasized (see, for example, Gregory, 1910), and a similar adaptation would have been an obvious advantage to *Enaliarctos* in marine waters.

We do not know if asymmetry is more prevalent in aquatic than in terrestrial quadrupedal mammals, but asymmetry in at least some pinnipeds has been reported. Of course the classic case of asymmetry is that found in many odontocete cetaceans (see, for example, Abel, 1902, and Howell, 1930), but we are quick to point out that a number of other aquatic groups have quite symmetrical skulls. We can find little asymmetry in the specimens of *E. mealsi* available, but should mention that enough of a disparity in size and position of the following structures exist to lead us to conclude that the specimens before us were asymmetrical: nasolabial fossae, foramina lateral to foramen ovale, foramina ventral to lacrimal foramen, alveoli for M^2 , spurs of bone and other structures on the bullae and basicranium, the zygomatic arches, and other minor features. It might be worth noting that the holotype skull of *Kolponomos clallamensis* Stirton is slightly asymmetrical and that in pinnipeds (observations by Mitchell; Howell, 1925, 1930, p. 13), in desmostylians (VanderHoof, 1937, fig. 10), and in other amphibious mammals, asymmetry is not uncommon.

The palate of *E. mealsi* is arched transversely, extended far posteriorly, and pierced by many foramina. These conditions are common in many terrestrial carnivores as well, but we note that they are found in almost all otariid pinnipeds and are carried to extremes in *Otaria byronia*, in which the internal choanal tube is also projected far posteriorly. Again we speculate that such similarities are indicative of common adaptations to feeding and breathing in an aquatic medium.

The teeth of aquatic mammals have undergone a spectacular series of changes. In some (e.g., in *Enhydra*) the teeth have become broad crushing batteries adapted to crack invertebrate armor. In others, such as *Hydrodamalis* Retzius, teeth have been lost and a horny plate functions in herbivorous feeding. In baleen whales the teeth have given way to a filter feeding apparatus. But in most carnivorous species the cheek teeth, particularly, have become simplified into sharp points for grasping of slippery, fast moving fish and invertebrates (Howell, 1930, p. 82 *et. seq.*). In *E. mealsi* the suppression in size of the upper molars and the premolarization of the lower carnassial are also viewed as trends

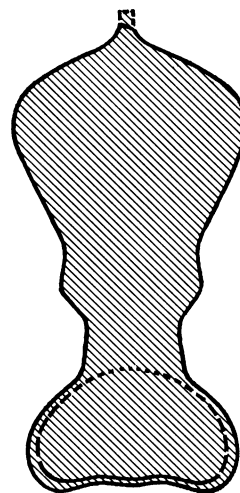


FIG. 18. Schematic cross section of holotype of *Enaliarctos mealsi*, LACM 4321, taken along a vertical transverse plane anterior to braincase and posterior to palate, to show skull configuration.

toward the establishment of a haplodont dental battery of the type best illustrated by later Cenozoic pinnipeds.

We speculate that, as the spacing and shape of the premolars are much like those in pinnipeds, the adaptive trend in these features paralleled the nekton capturing mechanisms of pinnipeds. Perhaps *Enaliarctos* fed on fish or cephalopods. The incisors are unknown, but the canines evidently projected downward more than forward from the axis of the palate as judged from the curvature of the canine alveoli.

Between the wide, short rostrum and the box-like braincase there extends an interorbital region built much like an I-beam. A cross section of the skull anywhere between the front of the braincase and M² would show thin interorbital plates bounded dorsally by transverse supra-

orbital ridges and ventrally by an expanded palatine-alisphenoid-pterygoid region (fig. 18). We suggest that this reinforcement is an adaptation for structural rigidity, and for accommodation of large eyes, a choanal tube of adequate diameter, and overall streamlining.

The presence of a sagittal crest, the shape of the braincase, the fact that the glenoid fossae tightly control all but rotary movements of the mandibular condyles, and the simplification of some of the premolars and molars all indicate to us that *E. mealsi* was beginning to evolve a feeding mechanism capable of rapid closure of the jaws.

We conclude that *E. mealsi* was adapted to life in the water, and the above points support our thesis that the species lived at or near the site of deposition in a neritic environment.

PHYLETIC RELATIONSHIPS

THE PIONEERING STUDIES of Hough (1948) on the auditory region of the fossil arctoid and cynoid Carnivora have shown that the morphology of the auditory region of these carnivores has been rather stable relative to other parts of the skeleton since the appearance of these groups in early Oligocene time. Some modification of the auditory region has, of course, occurred in later Cenozoic time, but certain apparently fundamental morphological patterns are discernible from earliest times which serve to distinguish the families Canidae, Ursidae, Procyonidae, and Mustelidae. In the Oligocene these families were somewhat closer allied in basicranial structure than they appear to be in the late Cenozoic, reflecting a diverging evolutionary pattern away from a common pre-Oligocene ancestor. Thus the characters that Flower (1869) used to group the fissiped families into superfamilies in his classic study of the living Carnivora break down somewhat when traced back to their earliest representatives. This appears to be the principal reason Simpson (1945) chose to group Flower's Arctoidea (Procyonidae, Mustelidae, and Ursidae) and Cynoidea (Canidae) into a single superfamily Canoidea. Nevertheless, it is convenient in discussion to recognize Flower's superfamilies. The arctoid families for instance seem to be more closely related to one another than to the cynoids. Their later Cenozoic evolu-

tion has been very complex, involving many parallel, as well as diverging adaptive trends. The cynoids, on the other hand, have remained more conservative in their evolution, although they too show interesting parallels with some of the arctoids.

The auditory region of *Enaliarctos* shows definite structural relationship to the arctoids among terrestrial carnivores. It resembles that of the canids only in features common to the auditory region of both the cynoids and arctoids. Among the middle Tertiary arctoids, the closest affinity is with the aquatic otter-like *Potamotherium*.

Potamotherium is geochronologically older than *Enaliarctos* and correspondingly more primitive in some cranial features. *Potamotherium vallentoni* diverges enough in some ways (e.g., in the lack of alisphenoid canal) to make it an unsuitable ancestor for *E. mealsi*, yet the degree of morphological resemblance in all the cranial structures available for comparison, demonstrates that these animals are closely related.

We have tried to show that primitive members of the ursid subfamily Hemicyoninae represent an arctoid group generalized enough to serve as the ancestral stock from which *Enaliarctos* arose. They also seem to be a product of the late Eocene radiation of the Carnivora. The earliest member of this group (*Cephalogale*) bears many

resemblances in skull and dentition to other arctoids, as well as some resemblances (mainly in the dentition) to the cynoids, all of which manifest the close relationship of these groups and their common early Tertiary origin. In assigning the hemicyonine genera *Cephalogale* Jourdan, *Hemicyon* Lartet, and *Dinocyon* Jourdan and others to the Canidae (as Amphicyodontinae) Simpson (1945, p. 224) followed the generally accepted view that the mid-Tertiary genera were "completely canid in character," while admitting that the later Tertiary genera (*Hemicyon* and *Dinocyon*) were more ursid-like. The amphicyodontines were supposed to contain the representatives of the canid-ursid intergradation. De Beaumont (1965) has demonstrated, and we concur, that in fact at least one of the earliest amphicyodontines (*Cephalogale*) is clearly arctoid, not cynoid, in basi-cranial structure, and hence more logically allied with the families Mustelidae, Procyonidae, and Ursidae.

As the fossil record demonstrates that the arctoid families can be traced as distinct groups from the late Cenozoic into the Oligocene, it seems to us far more logical and consistent with phyletic principles in classification to include *Cephalogale* and its close allies *Hemicyon* (including *Plithocyon* Ginsburg and *Phoberocyon* Ginsburg) and *Dinocyon* as a subfamily within the family Ursidae despite Simpson's admonition that "it leads to . . . difficulty and confusion in practical taxonomy" (1945, p. 224). The intergradation of these genera with those of the Ursidae has long been noted.

Schlosser (1899, 1902) and others (Viret, 1951; Dehm, 1950) have advocated the origin of *Ursavus* Schlosser and, thus, the Ursidae (*sensu* Simpson, 1945) from the European "canid" *Cephalogale* Jourdan, 1862 (see Erdbrink, 1953, for a review). These authors supported this view by demonstrating that the dental features of *Ursavus* were foreshadowed by *Cephalogale*, particularly among the smaller species, such as *C. minor* of the Phosphorites. Frick (1926) created the subfamily Hemicyoninae for *Hemicyon*, *Dinocyon*, *Ursavus*, and *Agriotherium* Wagner (= *Hyaenarctos* Falconer and Cautley, including *Indarctos* Pilgrim as a subgenus) and presented considerable evidence for their inclusion in the Ursidae, although he specifically refrained from doing so. Pilgrim (1931, pp. 4-5, 20-21) placed the "Cynodontinae" (*Cynodon* Aymard = *Amphi-*

cynodon Filhol and *Cephalogale*) and Frick's Hemicyoninae in the Ursidae and gave a revised diagnosis of that family including these primitive forms. More recently de Beaumont (1965) and Ginsburg (1961, 1966) have supported this view on the basis of new studies of some of the critical European genera. De Beaumont does not consider the amphicyodontine genera *Amphicyonodon* and *Pachycynodon* Schlosser, but Pilgrim (1931) and Ginsburg (1966) admitted one or both of these to the Ursidae. We have chosen a conservative course in this matter by considering as Hemicyoninae only those genera [*Cephalogale*, *Hemicyon* (*sensu lato*, see above) and *Dinocyon*] that have been shown to be ursids. When detailed studies on the other amphicyodontine genera have been presented, it may be shown that most if not all those forms grouped in that subfamily are best considered primitive Ursidae or an independent arctoid group of family rank. In any event the family Ursidae becomes comparable with other canoid families in terms of history and diversity of adaptation and its late Tertiary origin from the Canidae specifically denied.

The detailed comparisons presented in the previous pages, we believe, have provided a basis for the following conclusions as to the phyletic relationships of *Enaliarctos melesi*: (1) *Enaliarctos* is clearly an arctoid carnivore closest in known morphology to the Aquitanian otter-like *Potamotherium*; (2) both genera appear to have diverged from a common terrestrial arctoid stock best approximated by the Oligocene ursid genus *Cephalogale*; (3) the decided similarity of the cranium of *Enaliarctos* to that found in the Otariidae, and its many important distinctions from that of the Phocidae, strongly suggests that it represents a structural step in the evolution of the otariid pinnipeds from terrestrial hemicyonine ursid ancestors.

We think the evidence warrants erection of a separate subfamily, the Enaliarctinae, for this genus in recognition of its intermediate phyletic status. We favor assignment of this new group to the Otariidae on the basis of its many specific resemblances and degree of aquatic adaptation, recognizing that a degree of arbitrariness is involved in this action, which may create some difficulty in dealing with closely related forms (e.g., *Potamotherium*).

As mentioned below there is some evidence, from the early Miocene Woody local fauna from

the Kern River district, that more specialized pinnipeds may have been in existence during the time of deposition of the lower part of the Pyramid Hill Sand. Thus *Enaliarctos* itself may be too late in time to warrant consideration as an otariid and specifically otariine ancestor, but the evidence inclines us toward the hypothesis

that such an ancestor may be found among members of its subfamily or the immediately antecedent Hemicyoninae. Whatever the exact phyletic connection may be, this paleontological evidence supports the widely held notion of relationship between the Ursidae and Otariidae (see McLaren, 1960, for summary).

OTHER SUPPOSED AQUATIC CARNIVORES IN THE NORTH PACIFIC

THERE ARE A NUMBER of species of canoid carnivores from marine and lacustrine rocks around the North Pacific basin that have remained in questionable status since they were described. Represented by very few fossils that are usually disparate elements of the skeleton, and therefore not directly comparable, these species will remain poorly understood until additional fossils are discovered and all the bones are re-examined and re-illustrated. Many of these species have been variously considered as pinnipeds and fissipeds, but most have been thought to have lived an otter-like mode of life.

We herein use the term "otter-like form" to refer to a morphotype or adaptive type, and not to mustelid carnivores such as *Lutra* and *Enhydra* alone. The record of the marine otter *Enhydra lutris* in the North Pacific has been documented and summarized elsewhere (Mitchell, 1966c). Other otter-like forms include *Semantor macrurus* Orlov, *Kolponomos clallamensis*, and possibly *Neotherium mirum*.

Orlov (1931a, 1931b, 1933) described *Semantor macrurus* from deposits in western Siberia now regarded as late Miocene to early Pliocene in age (references in Kirpichnikov, 1955), and thought of it as a new type of pinniped. Only the posterior portion of the skeleton was preserved and Orlov's conclusions were disputed by many. Thenius (1949) concluded that *Semantor* was not a pinniped but a lutrine convergent on pinnipeds, but Kirpichnikov (1955) reiterated Orlov's view that it represented a kind of pinniped. Chapskii (1961) firmly excluded the Semantoridae from the Phocoidea.

Recently another aquatic fissiped, first described on the basis of postcranial bones found in limestones of Apsherian age (late Pliocene) in

the vicinity of Baku by Bogachev (1940) as *Necromites nestoris*, has been compared with *Semantor macrurus* by Akhundov (1963). Bogachev had placed *N. nestoris* in the Semantoridae, but Akhundov concluded that it was more highly adapted to aquatic life than *S. macrurus*, resembled seals, and could not remain in the Semantoridae. Unfortunately he did not specifically state that *N. nestoris* should or should not be placed among the Phocidae or elsewhere. Thus the systematic position of the family Semantoridae is still unresolved, as is the status

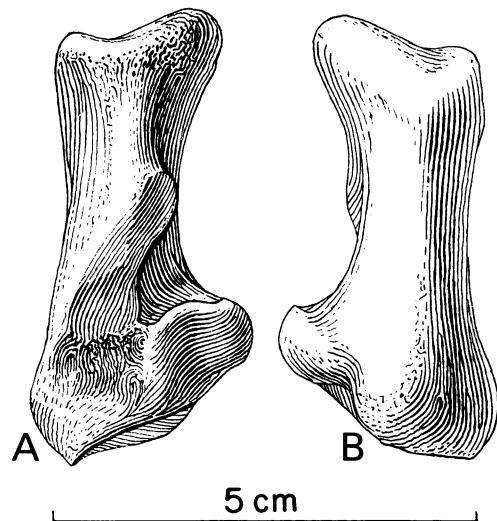


FIG. 19. Right calcaneum, lectotype of *Neotherium mirum* Kellogg, 1931, USNM 11542, from the late Miocene Round Mountain Silt at Sharktooth Hill, Kern County, California. A. Dorsal view. B. Ventral view. Drawings by Sydney Prentice. (From Kellogg, 1931, figs. 65, 66.)

of *N. nestoris*. Neither of these animals is represented by a skull, hence no comparisons are possible with *Enaliarctos*.

We find the diagnostic characters of *Kolponomos clallamensis* (Stirton, 1960) so different from those of *E. mealsi* that further comparisons are unnecessary (see above).

Otter-like forms are known from marine sediments in western North America. *Neotherium mirum* was described by Kellogg (1931) from the late Miocene Sharktooth Hill fauna (Mitchell, 1965), and was regarded as an otariid (or possibly allodesmid) pinniped by Kellogg. In the original description of this taxon Kellogg (1931, p. 296) did not designate a holotype, but instead based the species and the genus on four specimens that he termed "type material," a right calcaneum (USNM 11542), a right astragalus (USNM 11543), a right cuboid (USNM 11552), and a left navicular (USNM 11548). As there is no mention of these specimens having been found articulated or in association, and because some other bones referred by Kellogg to *Neotherium mirum* may be found to represent

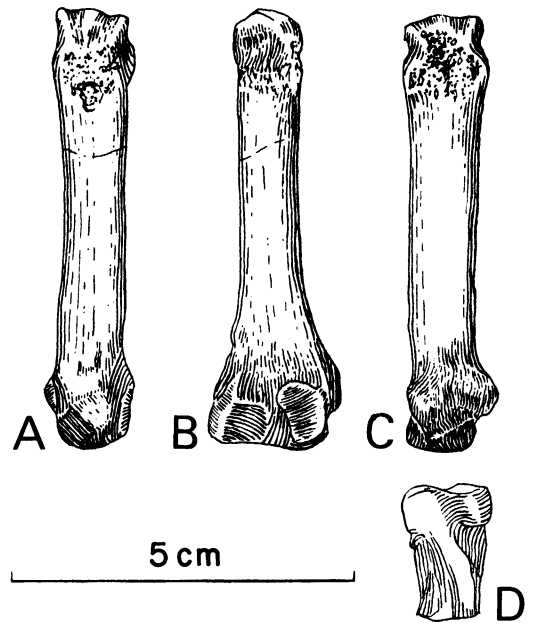


FIG. 21. Left metatarsal ?III, LACM 4360, possibly *Neotherium*, from late Miocene Round Mountain Silt at Sharktooth Hill, LACM Loc. 1557, Kern County, California. A. Ventral view. B. External view. C. Dorsal view. D. Proximal view. Drawings by Pam Immel.

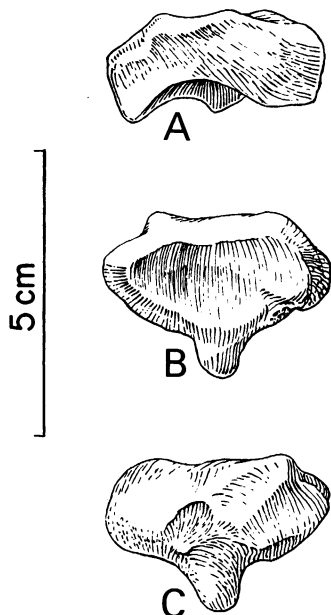


FIG. 20. Navicular, LACM 4733, possibly *Neotherium*, from late Miocene Round Mountain Silt at Sharktooth Hill, LACM Loc. 1557, Kern County, California. A. Dorsal view. B. Proximal view. C. Distal view. Drawings by Bonnie Gordon.

Allodesmus or even another pinniped, and because another pinniped or aquatic fissiped may yet be found in the Sharktooth Hill fauna, we believe that the type material should be restricted. As Kellogg listed the calcaneum first, and owing to the fact that the calcaneum can be compared with known calcanea of other fossil pinnipeds, we here fix the right calcaneum (USNM 11542, our fig. 19) as the lectotype of *Neotherium mirum* and regard the three other syntypes as paratypes. The type locality was given by Kellogg as Sharktooth Hill, Kern County, California, and the material was collected by Charles Morrice in 1924. Morrice's collections of that year almost certainly came from the bone bed at Sharktooth Hill, which is in the Round Mountain Silt of the "Temblor Group," Barstovian age (see fig. 1). Some doubt was expressed by Downs (1956, p. 129) as to the validity of this taxon, but it is almost certainly a distinct taxon of otariid pinniped or aquatic fissiped even if its relationship to other species is not understood (Mitchell, 1966a, 1968).

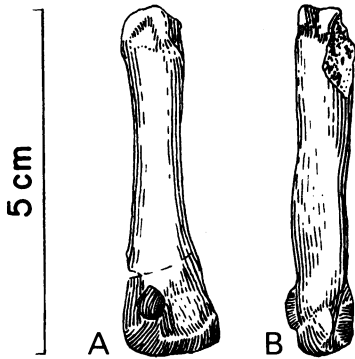


FIG. 22. Left metatarsal III, LACM 4570, possibly *Neotherium*, from Miocene rocks at Wilson Cove, San Clemente Island, California, LACM Loc. 1683 (Mitchell and Lipps, 1964, 1965). A. Internal view. B. Ventral view. Drawings by Pam Immel.

Neotherium mirum, according to Kellogg, is probably smaller than a female *Zalophus californianus*, as attested by the small size of the type material. But Kellogg referred bones from a

relatively larger pinniped to *Neotherium mirum*, such as femur CAS 4300, that may be found to belong to another species, possibly *Allodesmus kelloggi*. The possibility exists that *N. mirum* is an aquatic fissiped distantly or not at all related to pinnipeds. New, critical fossils are needed to establish its relationships.

In figures 20 and 21 we illustrate some additional bones from the Sharktooth Hill local fauna, the type locality of *N. mirum*, that are not now assignable to known pinnipeds other than *N. mirum*. The metatarsal pictured (fig. 21) is closely matched by another from Miocene rocks on San Clemente Island (fig. 22), suggesting that this species, whatever its identity, was widespread in Miocene marine environments.

Wilson (1935) described a humerus from the Pyramid Hill Sand near Woody, Kern County, California, and referred it to the Phocidae. We have examined this humerus (YPM 13433) and found that it has some features in common with a humerus (LACM 4319) from the Sharktooth Hill fauna that Mitchell previously referred to *Neotherium* (Mitchell, 1961, p. 15; our fig. 23).

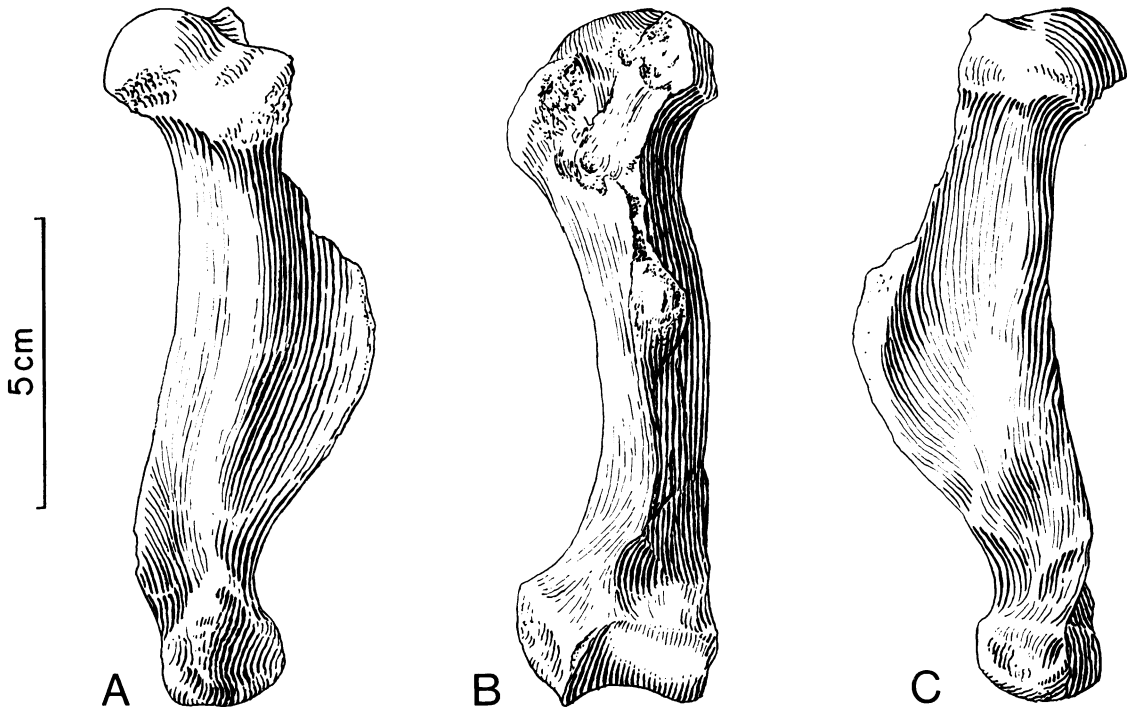


FIG. 23. Left humerus, LACM 4319, referred to *Neotherium* by Mitchell, 1961, from late Miocene Round Mountain Silt at Sharktooth Hill, LACM Loc. 1557, Kern County, California. A. Internal view. B. Anterior view. C. External view. Drawings by Mary Butler.

In view of the occurrence in the same stratigraphic unit with *E. mealsi* it is at least a possibility that the species represented by the humerus described by Wilson (1935) is related to *E. mealsi* on the family level or lower. These in turn may be related to the geologically younger *Neotherium mirum*. (See discussion below of Woody local fauna.)

Perhaps this array of otter-like marine mammals indicates that there were no true marine otters of lutrine ancestry in the eastern North Pacific in the early and middle Miocene, since other species might have excluded them. The earliest record of true marine otter is earliest Pleistocene (Mitchell, 1966c).

ASSOCIATED FAUNA

BONES AND TEETH of *Enaliarctos mealsi* have been recovered from the "grit zone" of the Pyramid Hill Sand at Pyramid Hill. Addicott (ms; see also table 1, present paper) listed approximately 62 species of gastropods, pelecypods, scaphopods madreporarians, and cirripeds from the "grit zone" of the Pyramid Hill Sand Member of the Jewett Sand, and noted that this fauna is correlative with the uppermost Vaqueros faunal zone of Loel and Corey. Loel and Corey (1932, pp. 136-137) listed 32 species of gastropods and pelecypods from this zone, as well as the echinoid *Scutella norrisi* Pack. Addicott (1965, p. C104) also pointed out that the "grit zone" contains a "previously unreported element of northern mollusks characteristic of late Oligocene to middle Miocene formations of Oregon and Washington . . ." We have seen abundant wood fragments in the "grit zone," many of which are pierced by borings of marine invertebrates, and pine cones are occasionally collected from this horizon. "That myriads of marine vertebrates existed is evidenced by the enormous quantities of bone material so characteristic of Vaqueros marine sediments . . ." (Loel and Corey, 1932, p. 164).

This sequence of beds, then, contains invertebrate megafossils in abundance, as well as fragments of wood, bones, and teeth. In a broad sense the environment could be termed marine, shallow water, and near shore. The following enumeration of the vertebrates in the Pyramid Hill local fauna and the Woody local fauna may yield additional evidence bearing on the habitat of *Enaliarctos mealsi*.

PYRAMID HILL LOCAL FAUNA

A diverse fauna of marine and terrestrial vertebrates occurs in the "grit zone" or lower

10 ft. of the Pyramid Hill Sand Member of the Jewett Sand at Pyramid Hill. Some of the vertebrates have already been mentioned in the literature. Jordan and Hannibal (1923, p. 52) mentioned the occurrence of *Isurus hastalis* (Agassiz) on the "south and west slope of Pyramid Hill." Kellogg (1932) described a new species of eurhinodelphid porpoise, *A. joaquinensis*, and referred it to the Patagonian lower Miocene genus *Argyrosetus*. The skull of this animal was found 1000 ft. west of Pyramid Hill and "about 75 feet below the top of the Vedder zone" (Kellogg, *Ibid*, p. 1). This is probably the Pyramid Hill Sand, as the Vedder Formation does not crop out in that area, and the mollusks identified (Barbat, *In* Kellogg, 1932, p. 1) at the site are typical of the "grit zone" of the Pyramid Hill Sand.

The following comments are based on new specimens and information (see table 4), and while they should not be construed as an attempt to describe the Pyramid Hill vertebrate fauna, they will give some idea of the size and diversity of the assemblage and, hopefully, stimulate further work on this early marine mammal fauna.

SHARKS AND RAYS: Shelton P. Applegate (*in litt.*, April 18, 1962) kindly provided the following: "Approximately thirty species of sharks and rays are represented in the Los Angeles County Museum collection from locality 1626, the Pyramid Hill Sand Quarry (Kern County, California). These are presently under study by Richard Bishop and myself, and are as follows: *Heterodontus* sp., *Hexanchus* sp. A, *Hexanchus* sp. B, *Squatina* cf. *lerichei*, *Squalus* cf. *serriculus*, *Echinorhinus blakei*, *Pristophorus* sp., new genus probably orectolobid, *Odontaspis ferox*, *Isurus benedini*, *Isurus* sp. A, *Isurus* sp. B, *Carcharodon angustidens*,

Cetorhinus sp., *Alopias* cf. *exigua*, *Alopias latidens*, *Alopias* cf. *vulpinus*, *Cephaloscyllium* sp., cat shark (new genus and species), *Mustelus* sp., *Galeorhinus* cf. *latus*, *Negaprion* cf. *elongata*, *Galeocerdo medius*, *Carcharhinus* sp., *Sphyrna* sp. A, *Sphyrna* sp. B, *Zapteryx* cf. *californicus*, ?*Rhinobatis* or *Squatina*, *Raja* sp., and *Myliobatis californicus*.

"Sharks and rays may move at will out of their normal habitats. However, if we consider the habitats of related species of Recent sharks and rays we can at least infer the approximate depth and proximity to shoreline of the Pyramid Hill environment. *Alopias*, *Isurus*, and *Cetorhinus* are pelagic and are not commonly found near shore except in deep water. *Hexanchus* may be predominantly a deep water type when adult; as yet little is known about its life history or habits, although it has been collected in shallow as well as in deep water. *Galeocerdo* may be pelagic or, like *Negaprion* and *Squalus*, a nektonic shallow-water inshore type. *Cephaloscyllium*, *Heterodontus*, *Squatina*, *Zapteryx* and *Myliobatis* are inshore bottom feeders. *Raja* is both a shallow water and a deep water genus. The Pyramid Hill sharks and rays suggest near-shore and shallow water, as well as deep water, habitat. The genera *Echinorhinus* and *Pristophorus*, and *Odontaspis ferox* are indicative of depths of 40 fathoms or more. Thus both shallow and deep water forms occur together.

"The geographical range of the living species of the Pyramid Hill genera in waters off California is as follows: *Notorhynchus* and *Squalus* occur commonly in shallow water in northern California and in deep water in southern California. *Alopias*, *Myliobatis*, *Raja*, *Zapteryx* and *Rhinobatis* range both north and south of southern California. Typical southern California sharks are *Isurus*, *Squatina* and *Heterodontus*, all being rare in northern California. *Negaprion* is known only from tropical waters.

"The whole fauna is indicative of warmer waters than now exist in this region; this might be explained by the shifting of currents or by a generally warmer climate."

TELEOSTS: We have observed fish bones of varying sizes in the "grit zone" and, although few have been collected and none studied, we think that there is a very large bony fish fauna present in the beds. John Fitch, of the California Department of Fish and Game, has collected teleost otoliths from Pyramid Hill and is presently studying them. He has been kind

TABLE 4
LIST OF LOCALITIES

Locality	Description
LACM (CIT) 258	"NE $\frac{1}{4}$ of Sect. 19, T. 27 S., R. 29 E., M.D.B. and M. Branch of Adobe Canyon about 2 mi. north of Poso Creek, Kern County, approx. 50' below top of Pyramid Hill Sand-Vaqueros" (from CIT locality catalogue). "Collector Alex Clark 10-24-34" (from original label).
LACM (CIT) 481	"Pyramid Hill (Elevation 2161') Sect. 14, T. 28 S., R. 29 E. Caliente Quad., USGS, Kern County, California. Exposures of lower Miocene Marine beds with porpoise remains (nat. brain casts) seal skulls and brain casts. Ledges of fossiliferous concretionary sandstone. Coll. Jan. 1950 by Dr. C. Stock" (from CIT locality catalogue).
LACM 1603	"Pyramid Hill, Kern County, California. W $\frac{1}{2}$ SE $\frac{1}{4}$ Sect. 14, R. 29 E., T. 28 S., Rio Bravo Ranch Quad. USGS 1954. In bottom bed. = EDM F-257" (from LACM locality catalogue).
LACM 1626	Southwestern slope of Pyramid Hill, Kern County, California, at approx. 1400 ft. elevation in SE $\frac{1}{4}$ NW $\frac{1}{4}$ SE $\frac{1}{4}$ Sect. 15, T. 28 S., R. 29 E., Rio Bravo Ranch Quad., USGS 1954 ed., 1:24,000. Loose sands of "grit zone," base of Pyramid Hill Sand Member of the Jewett Sand (EDM F-256 ^a).
LACM 1627, 1628	Southern slope of Pyramid Hill, Kern County, California, at approx. 1800 ft. elevation in NE $\frac{1}{4}$ SW $\frac{1}{4}$ NE $\frac{1}{4}$ SW $\frac{1}{4}$ Sect. 14, T. 28 S., R. 29 E., Rio Bravo Ranch Quad., USGS 1954 ed., 1:24,000. LACM 1627 in "grit zone" at base of Pyramid Hill Sand Member of the Jewett Sand; LACM 1628 (EDM F-268) approx. 40 ft. above LACM 1627 (EDM 267) in Pyramid Hill Sand Member.

^aEdward D. Mitchell field number.

enough to prepare the following statement on the Pyramid Hill fishes (*in litt.*, July 22, 1965; and see, for example, Fitch, 1969):

"I have only looked through about 20 pounds of screenings from Pyramid Hill [Sand Quarry =LACM locality 1626] for fish otoliths, but this is enough material for me to say they are neither abundant nor very easy to obtain entire in this deposit. I have not made any serious attempt to identify these or any other otoliths of Miocene vintage or older, but the 50 or 60 otoliths and otolith fragments I have from Pyramid Hill can be separated into 15 species belonging to at least nine families: Coryphaenoididae (cods), 2 species; Macruridae (cods), 1 species; Gadidae (cods), 1 species; Bothidae (flatfish), 1 species; Pleuronectidae (flatfish), 2 species; Sciaenidae (croakers), 3 species; ?Embiotocidae (perches), 1 species; ?Scorpaenidae (rockfishes), 1 species; and 3 species of unidentified family. By today's standards, some of these (cods) are deep-water forms, whereas the rest inhabit shallow to moderate depths. All prefer living above sandy, sandy-mud, or muddy substrates, and most are in direct contact with the bottom as adults."

CHELONIANS: A turtle bone fragment (LACM 17032) was collected from LACM Loc. 1626 in 1961, and other fragments including bony shell plates have been seen and collected since. They evidently represent a large marine turtle, and some of the plates are reminiscent of those figured by Palmer (1909, pl. 31). Such plates also occur in the Sharktooth Hill local fauna, higher in the section, and it is not improbable that a leatherback turtle like *Psephophorus* occurred in both faunas. Gilmore (1937) described the first turtle known from the Sharktooth Hill local fauna, but referred it questionably to *Chelonia* because of lack of knowledge at that time. Since then *Psephophorus* cf. *calvertensis* has been identified in the Sharktooth Hill assemblage (Mitchell, 1966a, pp. 28-29), and it is at least possible that further study will show these two records to be conspecific. *Psephophorus* is known also from the middle Miocene of Oregon (Packard, 1940).

BIRDS: A single bird was collected from LACM Loc. 1626 in 1963 by Richard Bishop. The partial coracoid, LACM 8927, evidently represents an extinct marine bird, *Plotopterum joaquinensis*, type of a new avian family, the Plotopteridae (Howard, 1969).

SQUALODONT CETACEANS: Two skull fragments (LACM 17033 and 17034) and three associated teeth of a single individual of shark-

tooth whale were collected from the "grit zone" at LACM Loc. 1627. The best specimen is a skull fragment of the right side containing parts of the crowns of the last two molars and the roots of a third (LACM 17033). The maxillary-vomer suture is clearly visible on this fragment along with the badly eroded, posteriorly extended premaxillary bone. The disposition of these bones and the presence of a mesorostral gutter indicates that this individual is a squalodont rather than an archaeocete, although some archaeocetes have similar teeth (Kellogg, 1936, fig. 81). The cheek teeth are double rooted with a bridge of dentine joining the roots proximally. The crowns are compressed and covered with rugose enamel, strongly developed anterior and posterior accessory cusps are present, but there is little development of carinae on the cutting edges of these teeth. These features indicate comparison with the long-beaked group of *Squalodon* species (Kellogg, 1923).

Other squalodonts have been reported from the northeastern Pacific, the most pertinent of these being *Squalodon errabundus* Kellogg (1931, p. 373), first described and as yet known only from the late Miocene Sharktooth Hill local fauna (Mitchell, 1965, 1966a). Cornwall (1922, p. 121) and Clark and Arnold (1923) refer to bones associated with remains of *Cornwallius sookensis* (Cornwall) in the Sooke Formation of Vancouver Island that might possibly be from a squalodont cetacean. Hanna (1936a, 1936b) mentioned the jaw (CAS cast 27625) of a possible squalodont from Miocene rocks in Carneros Creek, Kern County, California, without accessory cusps on the leading edge, much as in the *Neosqualodon* group. Hoots (1930, pp. 255-256) mentioned another California record that he said came from below the middle of the San Lorenzo Formation in the lower part of Wagner and Schilling's "Pleito Formation," San Joaquin Valley, California. The two lumbar vertebrae were identified as "Squalodontidae," and were mentioned as the first fossil whales from pre-Miocene rocks in the northeastern Pacific. Thus fragmentary squalodont material has been discovered in the eastern North Pacific but little of a definitive nature has been published. Squalodonts will probably be found commonly in marine mammal local faunas of the appropriate age in the North Pacific in the future, just as they have been well documented in the earlier Miocene of the southern Pacific and elsewhere.

Mitchell (1966b) has presented a restoration of one of the northeastern Pacific squalodonts, and likened its habits to those of the living but unrelated killer whale, *Orcinus orca* (Linnaeus). The Pyramid Hill squalodont seems to represent a type of rapacious predator to be expected in a well-balanced faunal assemblage of large marine vertebrates.

DELPHINOID CETACEANS: Numerous uncurated and unprepared specimens of delphinoid cetaceans from the vicinity of Pyramid Hill are in the collections of the Los Angeles County Museum. The Stock collection from LACM (CIT) Loc. 481 includes portions of natural endocranial casts, skulls, vertebral elements, snouts and jaws, and other bones representative of at least two or perhaps three species. Some of

these rostral fragments show the premaxillae closely appressed dorsal to the mesorostral gutter, one of the diagnostic features of members of the family Eurhinodelphidae (Kellogg, 1925; Abel, 1905). A slab of sandstone (LACM 8791) contains a porpoise skull, evidently that of a delphinid, with ribs, atlas, and other bones in association, but preparation is needed before the specimen can be positively identified. Numerous other porpoises are present in the collections. As mentioned, Kellogg (1932) described the new species of long-beaked porpoise, *Argyrocetus joaquinensis*, from the vicinity of Pyramid Hill and probably from the basal Pyramid Hill Sand.

MYSTICETE CETACEANS: In the Stock collection from LACM (CIT) Loc. 481 is a fragment

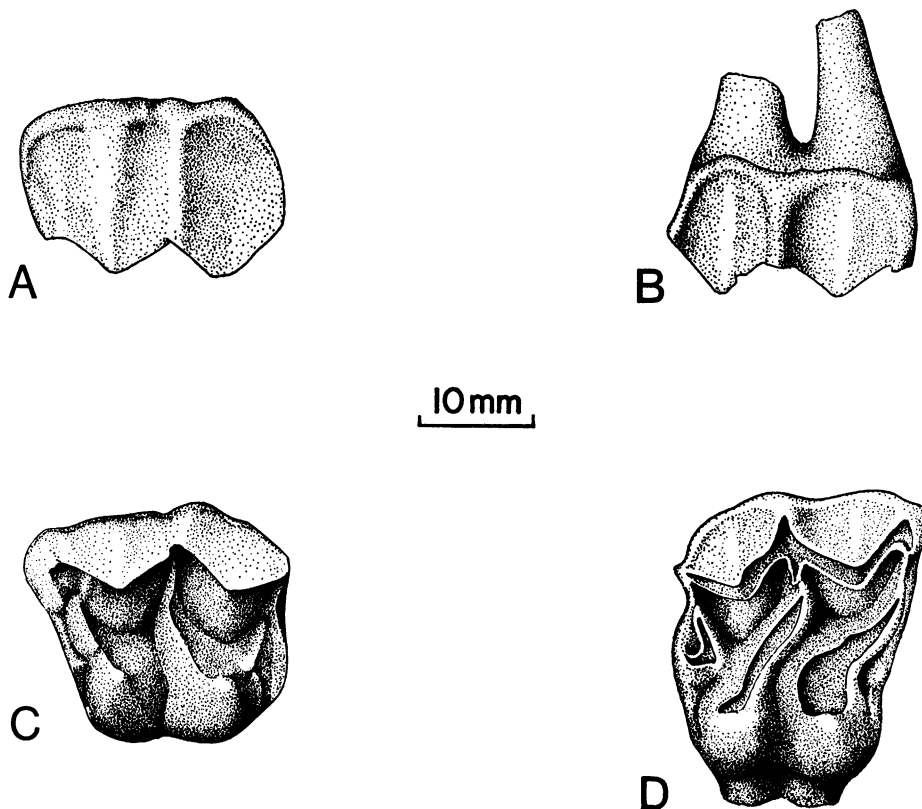


FIG. 24. Cheek teeth of horse *Anchitherium* sp. from Pyramid Hill local fauna, collected from LACM Loc. 1626, from Pyramid Hill Sand Member, Jewett Sand, early Miocene, near Pyramid Hill, Kern County, California. A, B. Left second upper premolar, LACM 4359. A. Labial view. B. Occlusal view. C, D. Right second upper molar, LACM 4332. C. Labial view. D. Occlusal view.

of a mysticete skull showing portions of the palatine, frontal, parietal, and nasal bones. We have collected a concretion containing a transverse section of another, much smaller mysticete skull. Mysticetes definitely occur in the assemblage, but better specimens and more preparation is needed to obtain specific identifications.

CARNIVORES: Isolated postcranial bones occur at LACM Locs. 1603, 1626, and 1627, and at other collecting stations in the same horizons that have yielded the teeth and skulls of *Enaliarctos mealsi*. cursory inspection of some of these bones suggest that they belong to some pinniped or pinniped-like species, but we are unwilling to describe and refer any of these bones to *Enaliarctos* pending the acquisition of new specimens showing definite anatomical associations of the cranial and postcranial elements.

EQUIDS: A left second upper premolar (LACM 4359) and a right second upper molar (LACM 4332) of a large species of the horse *Anchitherium* Meyer were obtained by Harold S. Meals from LACM Loc. 1626. These teeth (fig. 24) are not specifically determinable, but they agree best in height of crown and size with later Arikareean forms such as *A. agatensis* (Osborn) from the Harrison Formation in Nebraska. The Pyramid Hill teeth have weaker ribs and more strongly united metalophs and ectolophs than in referred specimens of *A. agatensis* (Romer, 1926). In these features they approach early (Hemingfordian) species of the genus *Hypohippus* Leidy. Measurements are: LACM 4359: maximum length of ectoloph 24.0 mm.; width across mesostyle at base of enamel 20.9 mm.; height of crown along mesostyle 13.2 mm. LACM 4332: maximum length of ectoloph 21.7 mm.; width across mesostyle at base of enamel 25.3 mm.; height of crown along mesostyle 9.6 mm.

TAYASSUIDS: A single upper fourth premolar of a peccary (LACM 4567, evidently from LACM Loc. 1626) was sent to the late R. A. Stirton of the University of California, Berkeley.

Stirton informed us (*in litt.*, September 21, 1964) that this tooth is "apparently referable to the genus *Desmathyus*. It is more advanced than the specimen from the upper John Day and less progressive than *Desmathyus pinensis* Matthew" from the Harrison and Rosebud formations of South Dakota (see Macdonald, 1963).

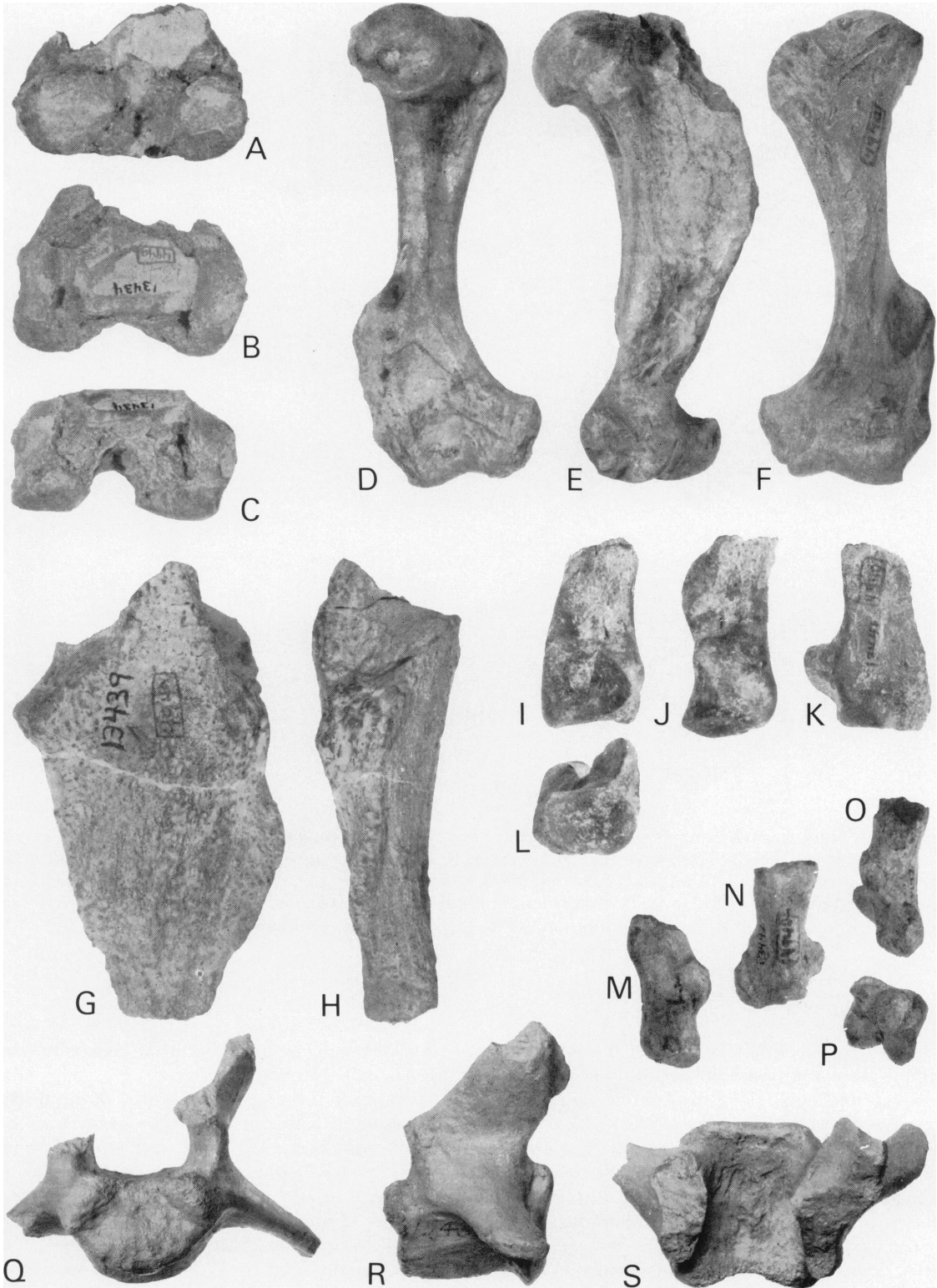
WOODY LOCAL FAUNA

In 1935 Leslie E. Wilson described marine mammals from exposures of the Pyramid Hill Sand west of Willow Spring Creek, north and south of the road to Woody, 14 miles north of Pyramid Hill (SW $\frac{1}{4}$ of sect. 12, NW $\frac{1}{4}$ of sect. 13, T. 26 S, R. 28 E). As discussed elsewhere in this paper we believe that Wilson's material comes from horizons well up in the Pyramid Hill Sand, stratigraphically above the level of occurrence of the Pyramid Hill local fauna. For this reason we are reluctant to consider these assemblages contemporaneous and have accordingly given them different faunal names.

Wilson (1935) described the following marine mammals from the Woody local fauna: a baleen whale, Cetotheriidae genus and species indeterminate; a new platanistoid species, *Doliodelphis littlei*; a new eurhinodelphid species, *Eurhinodelphis extensus*; four new delphinid species, *Allodelphis pratti*, *Macrodelphinus kelloggi*, *Acrodelphis bakersfieldensi*, and *Miodelphis californicus*; two sea lions (Otariidae, genus and species indeterminate); *Allodesmus* (cf. *A. kernensis*), and a seal (Phocidae, genus and species indeterminate).

Wilson (1935) referred to the Otariidae two calcanea (YPM 13441 and 13442; fig. 25) which are in some ways similar to the calcaneum of *Neotherium mirum* (Kellogg, 1931, p. 299), an otariid pinniped or aquatic carnivore known only from the later Miocene Sharktooth Hill local fauna (Mitchell, 1965). Kellogg stated that *N. mirum* was no larger and probably smaller than a female *Zalophus californianus*. A humerus

FIG. 25. Appendicular and axial skeletal elements of Wilson's (1935) "phocid" and "Otariid indet." from Woody local fauna, Pyramid Hill Sand Member, Jewett Sand, early Miocene, vicinity of Woody, Kern County, California. A-C. Distal end of femur, YPM 13434. ca. $\times .79$. A. Posterior or ventral view. B. Anterior or dorsal view. C. Distal view. D-F. Left humerus, YPM 13433. ca. $\times .59$. D. Posterior view. E. Internal view. F. Anterior view. G-H. Manubrium, YPM 13439. ca. $\times .6$. G. Ventral view. H. Lateral view. I-L. Right calcaneum, YPM 13441. ca. $\times .57$. I. Dorsal view. J. Internal view. K. Ventral view. L. Distal view. M-P. Left calcaneum, YPM 13442. ca. $\times .57$. M. Internal view. N. Ventral view. O. External view. P. Distal view. Q-S. Lumbar vertebra, YPM 13434a. ca. $\times .57$. Q. Anterior view. R. Left lateral view. S. Dorsal view.



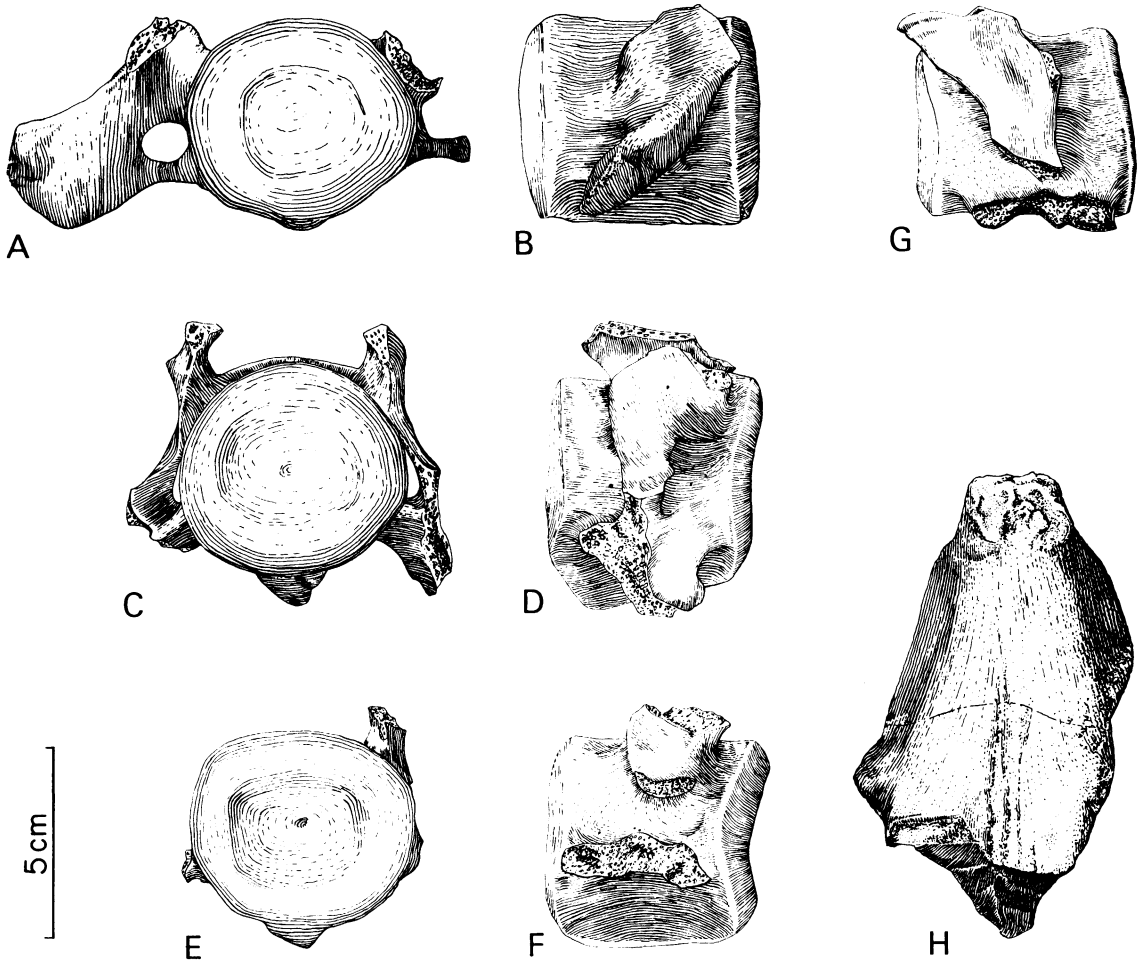


FIG. 26. Axial skeletal elements of Wilson's (1935) "otariid" from Woody local fauna, in early Miocene rocks in the vicinity of Woody, Kern County, California. A, B. Cervical vertebra, YPM 13436b. A. Anterior view. B. Right lateral view. C, D. Cervical vertebra, YPM 13435b. C. Posterior view. D. Right lateral view. E, F. Cervical vertebra, YPM 13435a. E. Posterior view. F. Right lateral view. G. Left lateral view of cervical vertebra, YPM 13436a. H. ? Dorsal view of manubrium, YPM 13439. Drawings by Pamela Immel.

termed "cf. *Neotherium*" by Mitchell (1961, p. 15) differs from the fragment of a humerus originally referred by Kellogg to *N. mirum*, and differs in turn from the humerus (YPM 13433) that Wilson (1935, p. 126 *et seq.*) referred to the "Phocidae." Wilson had cause to state that "the humerus resembles that of the recent *Callorhinus alascanus* . . . more closely than other otariids . . . with which it was compared." And this humerus, described by Wilson and illustrated herein (fig. 25) in turn compares favorably in some

respects with a humerus that Kirpichnikov (1955) called *Semantor macrurus*.

It is obvious that a large number of pinnipeds and aquatic fissipeds must have existed in the middle and early Miocene, and most of them are still poorly known or undescribed. Hence our reluctance to add to the confusion by referring bones to *Enaliarctos mealsi* that may actually belong to another fissiped or pinniped. The animals mentioned by Wilson (1935) were collected from stratigraphic horizons within the

Pyramid Hill Sand that are higher than the "grit zone," but it is certain that they still should be included in a discussion of the early Miocene marine fauna in the region of southern California.

Wilson (1935) listed "Phocidae; Otariidae, genus and species indeterminate; Allodesmidae, *Allodesmus* (cf. *A. kernensis*)" in his collections. Mitchell doubted Wilson's identification of "*Allodesmus* (cf. *A. kernensis*)" in the YPM collections (1966a, p. 20, pl. 24) and instead termed the bones in question an undetermined marine mammal. The phocid record is also in doubt. Nevertheless it is not improbable that three or more pinnipeds would be found in the same area in the past, for it is not uncommon in the North Pacific Ocean at present to find two or more

pinnipeds hauling out on the same rookeries, and two otariids and an odobenid-like pinniped are known from the Purisima Formation in the area of Santa Cruz (Mitchell, 1962, p. 22). The Sharktooth Hill local fauna, just a few thousand feet stratigraphically above the Pyramid Hill and Woody local faunas, contains two pinnipeds and possibly more, as Kellogg (1931, p. 227) intimated (see also Mitchell, 1966a).

To assist others in checking Wilson's determinations, we have prepared illustrations of the "otariid" and the "phocid" bones originally described in his 1935 study. We present these without further comment in figures 25, 26 (and see Mitchell, 1966a, pl. 24, as well as our discussion above on other aquatic carnivores in the North Pacific Ocean).

PALEOECOLOGY.

THE ABOVE SURVEY of the Pyramid Hill and Woody vertebrate local faunas sheds some light upon the ecology and associations of *Enaliarctos mealsi*. The invertebrate and vertebrate species found in the Pyramid Hill local fauna may or may not have been closely associated in life, but information derived from them is broadly consistent. The shark and ray assemblage is of near-shore, warm and shallow water aspect, with modern relatives living at the same or more southerly latitudes at present. The evidence from bony fish suggests that a mixture of deep, moderate, and shallow water species lived above sandy to muddy substrates. The possible presence of a leatherback turtle lends a tropical or warm water aspect to the assemblage. Most of the marine mammals remain unstudied, but can be regarded as a well-balanced assemblage, broadly antecedent to the Sharktooth Hill local fauna. It may be construed as a warm water assemblage of near shore aspect.

Addicott (1965, p. C104) has stated that the mollusks from the "grit zone" (our table 1), in which the early Miocene Pyramid Hill local fauna occurs, include some species of distinctly northern aspect. The species *Epitonium clallamense* Durham, *Mioleionea weaveri* Tegland, *Priscofusus* aff. *P. geniculus* (Conrad), *Priscofusus medialis* (Conrad), *Bruclarkia yaquinana* (Anderson and Martin), and *Mytilus middendorffi* Grewingk are found in late Oligocene to middle Miocene rocks along the shores of Oregon and Washington. In a later and more detailed analysis of the paleotemperature relationships of the molluscan faunas of the San Joaquin Basin, Addicott (1970b) concluded that the mollusca from the Jewett Sand lived in a warm-water environment, but one not so warm as that of the mid-Miocene (Temblor Stage), when marine paleotemperatures in the basin reached a peak.

SUMMARY AND CONCLUSIONS

ON THE BASIS of two partial skulls and two natural endocranial casts representing three individuals and several isolated upper and lower cheek teeth, we have described and compared the new genus and species *Enaliarctos mealsi* and concluded that it represents a hitherto unknown otariid subfamily, the Enaliarctinae, differing in structure from its probable ancestor among the terrestrial ursid subfamily Hemicyoninae in features related to aquatic adaptation.

The holotype and referred specimens were found in the basal part of the early Miocene Pyramid Hill Sand Member of the Jewett Sand at Pyramid Hill, Kern County, California. We presented the details of the physical stratigraphy and biostratigraphy of the sites, and have concluded from the contained vertebrates and invertebrates that the Pyramid Hill Sand can be assigned to the later Arikareean Land Mammal Age, the Vaqueros Molluscan Stage, and that these rocks lie close to or include the boundary between the Zemorrian and Saucesian foraminiferal stages. The following observations and conclusions were derived from the study of the specimens of *Enaliarctos*, their associated invertebrate and vertebrate fauna, and stratigraphy:

1. *Enaliarctos mealsi* was a medium-sized carnivore (see figure 27), comparable in cranial dimensions with such smaller living otariids as *Callorhinus*. The resemblance of the skull to that of most otariid pinnipeds is enhanced by the short, deep snout; large orbits; great interorbital constriction (emphasized by the great reduction in the olfactory region of the brain); anteriorly expanded braincase; strong mastoid-paroccipital crest; anteriorly sloping occipital plate; and tendencies to haplodonty in the dentition. Resemblance to terrestrial arctoid fissipeds and particularly the ursids is shown by the presence and form of the upper and lower carnassials, presence of two reduced but still molariform upper molars of quadrate form, and the degree of inflation and the form of the bullae. The cranial dental formula was apparently $I^2/C^1/P^{1-4}/M^{1-2}$.

The endocranial casts of *E. mealsi* show that the anterior limb of the gyrus ectosylvius is partly opercularized by the gyrus coronalis. The

neocortex shows fewer convolutions than in any otariid. The "ursine lozenge" is present but because of the great anteroposterior compression of the brain, it occupies a more anterior position than in many arctoids. The arteries and veins preserved in the endocasts include venous trunks of relatively large caliber, and we conclude that both arterial supply and venous drainage is quite rich in the brain of *E. mealsi*.

2. We conclude that *E. mealsi* was aquatically adapted because it has an enlarged narial chamber, reduced olfactory bulbs, a wide muzzle, a long hard palate that is transversely arched, tendencies toward premolarization of the molars, a narrow interorbital region with eyes placed high on the head, good arterial supply to and enlarged venous drainage of the brain, including an enlarged posterior lacerate foramen. There are a number of other features in which it resembles *Enhydra*, *Potamotherium*, members of the Otariidae, and other aquatic or amphibious mammals.

3. We have adopted the view of many European workers (Pilgrim, de Beaumont, and Ginsburg, among others) that the family Ursidae should be enlarged to include certain primitive forms of canid habitus and arctoid basicranial structure. The genus *Cephalogale* (Sannoisian-Burdigalian, Europe and Asia) represents such a generalized type of arctoid, structurally ancestral to such later genera as *Hemicyon* and *Dinocyon* (as well as *Enaliarctos* and later ursids). The subfamily Hemicyoninae Frick, 1926, seems to be the most appropriate available name for the group of terrestrial primitive ursids including *Cephalogale*, *Hemicyon*, and *Dinocyon* (see de Beaumont, 1965).

In *Enaliarctos* adaptation to aquatic life has produced many modifications of the terrestrial ursid structure and consequently a distinct departure from the morphology of any previously recognized ursids. A new subfamily, the Enaliarctinae, appears to be justified.

Consideration of all available evidence leads to the conclusion that *E. mealsi* represents a transitional arctoid that departed in structure from the terrestrial Hemicyoninae and evolved in the direction of aquatic Otariidae due to the requirements for adaptation to aquatic life. The



FIG. 27. Artist's conception of head of *Enaliarctos mealsi* as it would have appeared in life. Notable features are the long, low head with large, dorsally directed eyes and short muzzle. Shape of ear and nose is conjectural. *Enaliarctos mealsi* was an early Miocene carnivore of medium size, phylogenetically related to early ursids and pinnipeds. It is a transitional arctoid that departed in structure from terrestrial Hemicyoninae and evolved toward aquatic Otariinae in the northeast Pacific. Restoration by Bonnie Dalzell under the direction of Mitchell (from Mitchell, 1966b, fig. 1).

following features we think serve to demonstrate its ancestry among the primitive Ursidae: the form and composition of the auditory bulla and its relationship to surrounding bones; the strongly produced crista tympani; the narrow and deep tympanic cavity, not extended into any of the surrounding bones; the size and shape of the promontorium; the transmission of the entocarotid artery within the median wall of the bulla and its sharp flexure before entering the foramen lacerum medius; the position of the pit for the tympanohyal posterior to the foramen stylomastoideum definitum; the prominent mastoid and paroccipital processes, joined by a strong crest of bone; the upper carnassial with large posteriorly placed protocone shelf; the quadrate form of the upper first molar; and the development of the sulcus cruciatus and presence of the "ursid lozenge" on the anterodorsal surface of the cerebrum.

4. *Enaliarctos* approximates in many ways the structure of later and possibly generalized otariid pinnipeds such as the Arctocephalini. There are few important features of the cranium that suggest affinity with the Phocidae; much of the evidence is in the otariid direction. We have placed the new subfamily Enaliarctinae in the Otariidae, emphasizing the evidence for aquatic adaptation and the many specific morphological resemblances to the otariid pinnipeds. The following structural sequence can be drawn, trending from land to water: Hemicyoninae—Enaliarctinae—Otariinae. The chronologic relationships between these ursid and otariid subfamilies corroborate this view. Thus with a graded morphological sequence of fossils, in correct chronological arrangement, there is good reason to believe that *Enaliarctos mealsi*, or a closely related member of the same subfamily, was involved in the ancestry of some of the Otariidae.

5. The view of McLaren (1960) and others (Mitchell, 1961, 1967) that the available evidence suggests that phocids and otariids had their origin in separate terrestrial ancestors, is relevant to the discovery and interpretation of *E. mealsi*. If *E. mealsi* is at all involved in the evolutionary origins of otariid pinnipeds, as we believe, and *Potamotherium* is related to *Enaliarctos*, as we believe, then it seems that the diphyly question now revolves around the relationship of phocids to still earlier Arctoidea. In all features of phyletic import, we believe

that *Enaliarctos* is generally unlike known phocids and only resembles mustelids and procyonids in features that are common to all early arctoid carnivores or that have evolved in parallel fashion during adaptation to aquatic life. We conclude that we have demonstrated a sequence from hemicyonines to otariids that leaves little room for phocid origin. Reasonable morphological and other evidence exists demonstrating the wide differences between Otariidae and Phocidae (McLaren, 1960). As the earliest otariids are found in early Miocene rocks around the North Pacific and the earliest phocids occur in early Miocene deposits of the Tethys (Aslanova, 1965), the Pinnipedia consist of two major groups that have long, separate histories.

6. We believe that the sum total of the paleontological and zoological evidence indicates that the known fossil and living pinnipeds were fundamentally derived from arctoid ancestry. At the present time it is not possible to be certain of the exact stocks from which specific families were derived beyond the evidence presented here for the ursid origin of some of the otariids. We recognize the possibility that desmatophocines and their close allies might represent yet a third major pinniped group independently derived from the middle Tertiary arctoid adaptive radiation. Evidence for this view will be further explored by Mitchell.

7. In view of our concept of the Pinnipedia as polyphyletically derived, we believe that the pinniped families should be arranged with their terrestrial relatives within the Canoidea, emphasizing the fact that they, along with terrestrial families, are the result of a broad, middle Tertiary adaptive radiation of the Carnivora. Thus we feel that the diphyly issue is spurious, and that emphasis should be placed on the divergences, convergences, and parallelisms within all Carnivora. The following classification seems to best reflect our views:

Order Carnivora

Superfamily Canoidea Simpson, 1931

Family Canidae Gray, 1821

Family Procyonidae Bonaparte, 1850

Family Ursidae Gray, 1825

Family Otariidae Gray, 1825, *sensu lato* (including Odobenidae Allen, 1880; this is the Otarioidae of recent workers like Scheffer, 1958, and Mitchell, 1966a)

Family Mustelidae Swainson, 1835

Family Semantoridae Orlov, 1931
 Family Phocidae Gray, 1825

We therefore suggest that the terms Pinnipedia and Fissipedia be held in abeyance pending the accumulation of additional evidence on the arctoid adaptive radiation. We emphasize that, within the Otariidae, the true walruses represent only one of a number of different adaptive types (Mitchell, 1961; 1966a, p. 36; 1968). If Enaliarctinae is ancestral to Otariinae, then other otariid subfamilies may be related to Enaliarctinae by as yet unknown Oligocene precursors. The following subfamilies of Otariidae include all the genera in the same arrangement as listed by Mitchell, 1968:

Family Otariidae Gray, 1825
 Subfamily Enaliarctinae, new subfamily
 Subfamily Desmatophocinae Hay, 1930
 Subfamily Odobeninae Allen, 1880
 Subfamily Dusingathinae Mitchell, 1968
 Subfamily Allodesminae Kellogg, 1931
 Subfamily Imagotariinae Mitchell, 1968
 Subfamily Otariinae Gray, 1825

As mentioned above, we believe that *Neotherium mirum* Kellogg, 1931, might be related less to otariines than to enaliarctines, and thus we would include it in the Enaliarctinae rather than in some other subfamily of the Otariidae (Kellogg, 1931) or in Otariidae, *incertae sedis* (Mitchell, 1966a).

8. The area of origin and the center of dispersal of *Enaliarctos mealsi* are not known, but we infer that the North Pacific basin is the most likely site. The Eurasiatic distribution of the earlier ancestral ursids, and the known geographic distribution of their otariid descendants in the North Pacific, agrees with the concept of Davies (1958) and McLaren (1960). We point out that a number of independent arctoid carnivores and other aquatic or amphibious mammalian groups have presumably originated or radiated (or both) from the vicinity of the North Pacific and Arctic. These now include: *Enaliarctos mealsi* of arctoid stock, *Neotherium mirum* of possible enaliarctine affinities, *Kolponomos clallamensis* of assumed "procyonid" affinities, *Thalarctos maritimus* of ursid ancestry, *Enhydra lutris* of mustelid ancestry, other otariid pinnipeds of arctoid ancestry, desmostylians of paenungulate affinities, and probably some groups within the Cetacea.

9. *Enaliarctos mealsi* may be found to be a

relative of *Neotherium mirum* Kellogg, 1931, known from the late Miocene Sharktooth Hill local fauna, in rocks near the type locality of the former. We fix the right calcaneum (USNM 11542) as the lectotype of *N. mirum*, and regard the remaining three syntypes as paratypes.

10. We emphasize that we have no postcranial material which can be unequivocally referred to *Enaliarctos mealsi*. Isolated humeri previously and herein described from marine Miocene rocks in southern California and elsewhere in the eastern North Pacific are similar in many ways to a humerus referred to a semantorid from the Caspian Basin. A number of other isolated bones from marine rocks in this region indicates that there were many species of aquatic carnivores of otter or pinniped habitus that have not yet been described.

11. The Pyramid Hill local fauna is named and characterized from the "grit zone" or basal unit of the Pyramid Hill Sand Member of the Jewett Sand at Pyramid Hill, California. The invertebrate fauna includes more than 16 species of gastropods, 25 species of pelecypods, one species of scaphopod, one or more species of barnacle, and, among the vertebrates, 15 species of elasmobranchs, 15 species of teleosts, one species of chelonian, one avian species, one squalodont cetacean, two species or more of delphinoid cetaceans, one or more mysticete cetacean, the aquatic *Enaliarctos mealsi*, one or more unidentified carnivores, one equid (*Anchitherium* cf. *A. agatensis*), one tayassuid (*Desmathyus* sp.), and other species. This and other evidence leads us to conclude that the fauna is a well-balanced assemblage, which for the most part indicates the presence at the site of deposition of a warm water, near-shore environment.

12. We have summarized the occurrences of squalodont cetaceans in the northeastern Pacific and find four published records from the late Oligocene to the middle Miocene from Vancouver Island to California. None of these has been extensively restudied and published in the detail that each merits, including our new material from the Pyramid Hill local fauna, but we conclude that squalodonts are not uncommon in marine mammal faunas of the appropriate age in the northeastern Pacific.

13. The Woody local fauna is named from and characterized by fossils from exposures of the Pyramid Hill Sand Member of the Jewett Sand west of Willow Spring Creek, 14 miles

north of Pyramid Hill. We have no new material from this local fauna, but we list the marine mammals described by Wilson (1935) and question his identifications of the reputed pinnipeds. We doubt the validity of his phocid record and hesitate to accept his specific and generic identifications of the supposed otariids. In addition to

these marine mammals of questionable identity, the fauna includes, according to Wilson, a platanistoid, a eurhinodelphoid, and four delphinids. We believe that this material comes from a horizon stratigraphically higher than the level of the Pyramid Hill local fauna within the Pyramid Hill Sand.

LITERATURE CITED

- ABEL, O.
1902. Die Ursache der Asymmetrie des Zahnwalschädels. Sitzungberichten der kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Cl., vol. 111, art. 1, pp. 510-526, 1 pl.
1905. Les Odontocètes du Boldérien (Miocène Supérieur) d'Anvers. Mém. Mus. Roy. Hist. Nat. Belgique, vol. 3, pp. 1-55.
- ADDICOTT, W. O.
[MS.] Miocene stratigraphy northeast of Bakersfield, California. Ph.D. Thesis, Dept. Paleont., Univ. California, Berkeley, 1956, 207 pp.
1965. Miocene macrofossils of the southeastern San Joaquin Valley, California. U. S. Geol. Surv. Prof. Paper no. 525-C, pp. C101-C109.
1970a. Miocene gastropods and biostratigraphy of the Kern River Area, California. *Ibid.*, no. 642, pp. iv+174.
1970b. Tertiary paleoclimatic trends in the San Joaquin Basin, California. *Ibid.*, no. 644-D, pp. D1-D19, figs. 1-7.
- AKHUNDOV, F. M.
1963. Morfologicheskie ofichiya *Necromites nestoris* ot semeist va Semantoridae (Mammalia, Pinnipedia). [Morphological distinctions of *Necromites nestoris* from the family Semantoridae (Mammalia, Pinnipedia).] *Izv. Akad. Nauk Azerbaizhanskoi S.S.R.*, ser. geol. nauk nefti, no. 3, pp. 9-14.
- ANDERSON, F. M.
1905. A stratigraphic study of the Mount Diablo Range of California. *Proc. California Acad. Sci.*, ser. 3, vol. 2, pp. 155-248.
1911. The Neocene deposits of Kern River, California, and the Temblor Basin. *Ibid.*, ser. 4, vol. 3, pp. 73-148.
- ANDERSON, F. M., AND B. MARTIN
1914. Neocene record in the Temblor Basin, California, and Neocene deposits of the San Juan district, San Luis Obispo County. *Proc. California Acad. Sci.*, ser. 4, vol. 4, pp. 15-112.
- ASLANOVA, S. M.
1965. Tiülen iz nizhnemiotenovyx otlozhenii Azerbaidzhana. [Seal in the lower Miocene deposits in Azerbaidjan.] *Dok. Akad. Azerbaizhanskoi S.S.R.*, vol. 21, no. 6, pp. 46-48 [In Russian].
- BOGACHEV, V. V.
1940. Nakhoda novogo morskogo mlekopitaiushchego v apsheronskom yaruse bliz Baku. [A finding of a new sea mammal in the Apsheron stage near Baku.] *Priroda*, 1940, pp. 94 (in Russian). [Also *Izv. Az. F.A.N. S.S.S.R.*, 1940, no. 1, cited by Akhundov, 1963.]
- CAVE, A. J. E., AND J. E. KING
1964. The ossiculum mastoideum of the otariid skull. *Ann. Mag. Nat. Hist.*, ser. 13, vol. 7, pp. 235-240.
- CHAPSKII, K. K.
1961. Sovremennoe sostoyanie i problemy sistematiки lastonogikh. [Present status and problems in the systematics of seals.] Moscow, Tr. soveshch. po ekol. promyslu morskikh mlekop. Tr. soveshchanii ikhtiol. komissii A.N. S.S.S.R., vyp. 12, Moscow.
- CHIASSON, R. B.
1957. The dentition of the Alaskan fur seal. *Jour. Mammal.*, vol. 38, no. 3, pp. 310-319.
- CLARK, B. L., AND R. ARNOLD
1923. Fauna of the Sooke Formation, Vancouver Island. *Univ. California Publ. Dept. Geol. Sci.*, vol. 14, pp. 123-179.
- CONDON, T.
1906. A new fossil pinniped (*Desmatophoca oregonensis*) from the Miocene of the Oregon coast. *Univ. Oregon Bull.*, suppl. vol. 3, no. 3, pp. 1-14.
- CORNWALL, I. E.
1922. Some notes on the Sooke Formation, Vancouver Island, B.C. *Canadian Field-Nat.*, vol. 36, pp. 121-123.
- DAVIES, J. L.
1958. The Pinnipedia: an essay in zoogeography. *Geogr. Rev.*, vol. 48, pp. 474-493.

- DAVIS, D. D.
1964. The giant panda. A morphological study of evolutionary mechanisms. Chicago Nat. Hist. Mus., Fieldiana: Zool. Mem., vol. 3, pp. 1-339.
- DE BEAUMONT, B.
1965. Contribution à l'étude du genre *Cephalogale* Jourdan (Carnivora). Schweiz Palaeont. Abhandl., vol. 82, pp. 1-34.
- DEHM, R.
1950. Die Raubtiere aus dem Mittel-Miocän (Burdigalium) von Wintershof-West bei Eichstatt in Bayern. Abhandl. Bayerische Akad. Wiss., Math.-Nat. Abt., vol. 58, pp. 1-141.
- DIBBLEE, T. W., JR., W. G. BRUER, O. HACKEL, AND A. M. WARNE
1965. Geologic map of the southeastern San Joaquin Valley. In Geology of southeastern San Joaquin Valley. AAPG, SEG, SEPM (Pacific Section) Guidebook, 40 pp.
- DORNESCO, G. T., AND G.-V. MARCOCI
1958. Étude comparative du crâne des pinnipèdes. Ann. Sci. Nat., Zool. Biol. Animale, sér 11, vol. 20, pp. 157-182.
- DOUTT, J. K.
1942. A review of the genus *Phoca*. Ann. Carnegie Mus., vol. 29, pp. 61-125.
- DOWNES, T.
1956. A new pinniped from the Miocene of southern California: with remarks on the Otariidae. Jour. Paleont., vol. 30, pp. 115-131, pl. 26.
- DURHAM, J. W., R. H. JAHNS, AND D. E. SAVAGE
1954. Marine-nonmarine relationships in the Cenozoic section of California. Bull. California Div. Mines 170, chap. 3, pp. 59-71.
- EAMES, F. E., F. T. BANNER, W. H. BLOW, AND W. J. CLARKE
1962. Fundamentals of mid-Tertiary stratigraphical correlation. Cambridge Univ. Press, 163 pp., 17 pls.
- EDINGER, T.
1955. Hearing and smell in cetacean history. Monatsschr. Psychiat. Neurol, Basle, vol. 129, no. 1-3, pp. 37-58.
- ERDBRINK, D. P.
1953. A review of fossil and recent bears of the Old World. With remarks on their phylogeny. Based upon their dentition. Deventer, Drukkery Jan de Lange, xii+597 pp.
- EVERNDEN, J. F., D. E. SAVAGE, G. H. CURTIS, AND G. T. JAMES
1964. Potassium-argon dates and the Cenozoic mammalian chronology of North America. Amer. Jour. Sci., vol. 262, pp. 145-198.
- FIRBAS, W., AND W. WICKE
1968. Über das postnatale Wachstunder Bärenbulla. Anat. Anz., vol. 122, pp. 120-128.
- FISH, P. A.
1899. The brain of the fur seal, *Callorhinus ursinus*; with a comparative description of those of *Zalophus californianus*, *Phoca vitulina*, *Ursus americanus* and *Monachus tropicalis*. In Jordan, D. S., The fur seals and fur seal islands of the North Pacific Ocean. Washington, pt. 3, pp. 21-41.
1903. The cerebral fissures of the Atlantic walrus. Proc. U.S. Nat. Mus., vol. 26, no. 1325, pp. 675-688, pls. 28, 29.
- FITCH, J. E.
1969. Fossil lanternfish otoliths of California, with notes on fossil Myctophidae of North America. Los Angeles County Mus. Contrib. Sci., no. 173, pp. 1-20.
- FLOWER, W. H.
1869. On the value of the characters of the base of the cranium in the classification of the order Carnivora, and on the systematic position of *Bassaris* and other disputed forms. Proc. Zool. Soc. London, 1868, pp. 4-37.
- FRICK, C.
1926. The Hemicyoninae and an American Tertiary bear. Bull. Amer. Mus. Nat. Hist., vol. 56, pp. 1-119.
- GERVAIS, M. P.
1870. Mémoire sur les formes cérébrales propres aux carnivores vivant et fossiles suivi de remarques sur la classification de ces animaux. Nouv. Arch. Mus. Hist. Nat., Paris, Mém. vol. 6, pp. 103-162, pls. 3-9.
- GILMORE, C. W.
1937. A new marine turtle from the Miocene of California. Proc. California Acad. Sci., ser. 4, vol. 23, pp. 171-174.
- GINSBURG, L.
1961. La faune des Carnivores Miocènes de Sansan. Mem. Mus. Natl. Hist. Nat., ser. C, vol. 9 (new ser.), pp. 1-190.
1966. Les amphicyons des Phosphorites du Quercy. Ann. Paleont., vol. 52, pp. 23-44.
- GREGORY, W. K.
1910. The orders of mammals. Bull. Amer. Mus. Nat. Hist., vol. 27, pp. 1-524.
- HACKEL, O., AND K. F. KRAMMES
1958. Stratigraphy. In San Joaquin Geol. Soc. Guidebook, 1958 Spring Field Trip, Round Mountain Area, p. 10-11, 14-15.
- HAINES, R. W.
1950. The interorbital septum in mammals. Jour. Linnean Soc. London, vol. 41, pp. 585-607.
- HAMILTON, J. E.
1934. The southern sea lion, *Otaria byronia* (de

- Blainville). *Discovery Repts.*, vol. 8, pp. 269-318, pls. 1-13.
1939. A second report on the southern sea lion, *Otaria byronia* (de Blainville). *Discovery Repts.*, vol. 19, pp. 121-164, pls. 26-33.
- HANNA, G. D.
- 1936a. Interesting whale jaw from Kern County, California. *Proc. Geol. Soc. Amer.*, 1935, p. 419 (abstr.).
- 1936b. Interesting whale jaw from Kern County, California. *Pan-Amer. Geol.*, vol. 64, pp. 79-80 (abstr.).
- HELBING, H.
1921. Zur Skelettrekonstruktion eines oberoligo-cänen Fischotters. *Verhandl. Schweizerischen Ges. Naturwiss.*, vol. 101, no. 2, pp. 209-210.
- HEPBURN, D.
1913. Scottish National Antarctic Expedition: Observations on the anatomy of the Weddell Seal (*Leptonychotes weddelli*). Part IV: The brain. *Trans. Roy. Soc. Edinburgh*, vol. 48, pt. 4, no. 30, pp. 827-847, 1 pl.
- HOOTS, H. W.
1930. Geology and oil resources along the southern border of San Joaquin Valley, California. *U.S. Geol. Surv. Bull.* 812-D, pp. i-vi, 243-332.
- HOUGH, J. R.
1944. The auditory region in some Miocene carnivores. *Jour. Paleont.*, vol. 18, pp. 470-479.
1948. The auditory region in some members of the Procyonidae, Canidae and Ursidae. Its significance in the phylogeny of the Carnivora. *Bull. Amer. Mus. Nat. Hist.*, vol. 92, pp. 67-118.
1953. Auditory region in North American fossil Felidae: its significance in phylogeny. *U.S. Geol. Surv. Prof. Paper* 243-G, pp. 95-115.
- HOWARD, H.
1969. A new avian fossil from Kern County, California. *Condor*, vol. 71, no. 1, pp. 68-69.
- HOWELL, A. B.
1925. Asymmetry in the skulls of mammals. *Proc. U.S. Natl. Mus.*, vol. 67, no. 27, pp. 1-18, pls. 1-8.
1929. Contribution to the comparative anatomy of the eared and earless seals (genera *Zalophus* and *Phoca*). *Ibid.*, vol. 73, art. 15, pp. 1-142, 1 pl.
1930. Aquatic mammals. Springfield, C. C. Thomas, 338 pp.
- JAHNS, R. H. (ED.)
1954. Geology of Southern California. *Bull. California Div. Mines* 170, chap. 2.
- JELGERSMA, G.
1934. Das Gehirn der Wassersäugetiere. Eine Anatomische Untersuchung. Leipzig, J. A. Barth, viii+238 pp.
- JORDAN, D. S., AND H. HANNIBAL
1923. Fossil sharks and rays of the Pacific Slope of North America. *Bull. Southern California Acad. Sci.*, vol. 22, pp. 27-68.
- KAPPERS, C. U. A., G. C. HUBER, AND E. C. CROSBY
1936. The comparative anatomy of the nervous system of vertebrates, including man. New York, Macmillan Co., 2 vols., i-xx+1-864, i-xiv+865-1845 pp.
- KEEN, A. M.
1943. New mollusks from the Round Mountain Silt (Temblor) Miocene of California. *Trans. San Diego Soc. Nat. Hist.*, vol. 10, pp. 25-60.
- KELLOGG, R.
1922. Pinnipeds from Miocene and Pleistocene deposits of California . . . and a résumé of current theories regarding origin of Pinnipedia. *Univ. California Publ. Geol. Sci.*, vol. 13, pp. 23-132.
1923. Description of two squalodonts recently discovered in the Calvert Cliffs, Maryland; and notes on the shark-toothed cetaceans. *Proc. U.S. Natl. Mus.*, vol. 62, pp. 1-69.
1925. On the occurrence of remains of fossil porpoises of the genus *Eurhinodelphis* in North America. *Ibid.*, vol. 66, pp. 1-40.
1928. The history of whales - their adaptation to life in the water. *Quart. Rev. Biol.*, vol. 3, pp. 29-76, 11 figs.
1931. Pelagic mammals from the Temblor Formation of the Kern River region, California. *Proc. California Acad. Sci.*, ser. 4, vol. 19, pp. 217-397.
1932. A Miocene long-beaked porpoise from California. *Smithsonian Misc. Coll.*, vol. 87, no. 2, pp. 1-11.
1936. A review of the Archaeoceti. *Carnegie Inst. Washington Publ.* 482, pp. 1-366.
- KING, J. E.
1961. The feeding mechanism and jaws of the crabeater seal (*Lobodon carcinophagus*). *Mammalia*, vol. 25, no. 4, pp. 462-466.
- KIRPICHNIKOV, A. A.
1955. Novye dannye o semantore [New data on *Semantor*.] *Voprosy Geol. Azii (A.N., S.S.S.R.)*, vol. 2, pp. 810-814 [In Russian].
- KLEINPELL, R. M.
1938. Miocene stratigraphy of California. *Tulsa, Amer. Assoc. Petrol. Geol.*, 450 pp.
- KLEINPELL, R. M., AND D. W. WEAVER
1963. Oligocene biostratigraphy of the Santa Barbara Embayment, California. *Univ. California Publ. Geol. Sci.*, vol. 43, pp. i-vi, 1-250.

- KÜKENTHAL, W.
1889. Vergleichend-anatomische und entwicklungsgeschichtliche Untersuchungen an Walthieren. Denkschr. Med.-Naturwisse. Gesell. Jena, vol. 3, pt. 1, x+220 pp., pls. 1-13.
- LIPPS, J. H.
1967. Planktonic foraminifera, intercontinental correlation and age of California mid-Cenozoic microfaunal stages. *Jour. Paleont.*, vol. 4, pp. 994-999.
- LOEL, W., AND W. H. COREY
1932. The Vaqueros Formation, lower Miocene of California. I. Paleontology. Univ. California Publ. Bull. Dept. Geol. Sci., vol. 22, pp. 31-410.
- MACDONALD, J. R.
1963. The Miocene fauna from the Wounded Knee area, western South Dakota. *Bull. Amer. Mus. Nat. Hist.*, vol. 125, pp. 141-238.
- MCLAREN, I. A.
1960. Are the Pinnipedia biphyletic? *Syst. Zool.*, vol. 9, pp. 18-28.
- MILLER, L. H.
1961. Birds from the Miocene of Sharktooth Hill, California. *Condor*, vol. 63, pp. 399-402.
1962. A new albatross from the Miocene of California. *Ibid.*, vol. 64, pp. 471-472.
- MILLER, M. E., G. C. CHRISTENSEN, AND H. E. EVANS
1964. Anatomy of the dog. Philadelphia, Saunders Co., xii+941 pp.
- MITCHELL, E.
1961. A new walrus from the Imperial Pliocene of southern California: with notes on odobenid and otariid humeri. *Los Angeles County Mus. Contrib. Sci.*, vol. 44, pp. 1-28.
1962. A walrus and a sea lion from the Pliocene Purisima Formation at Santa Cruz, California: with remarks on the type locality and geologic age of the sea lion *Dusignathus santacruzensis* Kellogg. *Ibid.*, vol. 56, pp. 1-24.
1965. History of research at Sharktooth Hill, Kern County, California. *Bakersfield, Kern Co. Hist. Soc., Special Publ.*, pp. i-vi, 1-45.
1966a. The Miocene Pinniped *Allodesmus*. *Univ. California Publ. Geol. Sci.*, vol. 61, pp. i-viii, 1-105.
1966b. Faunal succession of extinct North Pacific marine mammals. *Norsk Hvalfangsttidende*, vol. 55, no. 3, pp. 47-60.
1966c. Northeastern Pacific Pleistocene sea otters. *Jour. Fish. Res. Board Canada*, vol. 23, no. 12, pp. 1897-1911.
1967. Controversy over diphyly in pinnipeds. *Syst. Zool.*, vol. 16, no. 4, pp. 350-351.
1968. The Mio-Pliocene pinniped *Imagotaria*. *Jour. Fish. Res. Board Canada*, vol. 25, pp. 1843-1900, 12 unnum. pls.
- MITCHELL, E., AND J. H. LIPPS
1964. Miocene marine vertebrates from San Clemente Island, California. *Geol. Soc. Amer., Special Paper 76*, pp. 214-215.
1965. Fossil collecting on San Clemente Island. *Pacific Discovery*, vol. 18, no. 3, pp. 2-8.
- MURIE, J.
1874. Researches upon the anatomy of the Pinnipedia. Part III. Descriptive anatomy of the sea-lion (*Otaria jubata*). *Trans. Zool. Soc. London*, vol. 8, pt. 9, pp. 501-582.
- ODEND'HAL, S.
1965. Selected topics on the regional anatomy of *Eumetopias jubata* (Steller Sea Lion). *Proc. 2nd Ann. Conf. Biol. Sonar Diving Mammals*, Stanford Res. Inst., pp. 29-36.
- ORLOV, YU. A.
1931a. Na khodka iskopaemogo lastonogo b. Sibiri. *Priroda*, 1931, no. 1, pp. 91-94.
1931b. Über die Reste eines primitiven Pinnipediens aus den neogenen Ablagerungen Westsiberiens. *Compt. Rend. Acad. Sci. U.R.S.S.*, ser. A, no. 3, pp. 67-70.
1933. *Semantor macrurus* (ordo Pinnipedia, fam. Semantoridae fam. nova) aus den Neogen-Ablagerungen Westsiberiens. *Trav. Inst. Paléozool. Acad. Sci. U.R.S.S.*, vol. 2, 1932 [1933], pp. 165-262, 10 pls.
- PACKARD, E. L.
1940. A new turtle from the marine Miocene of Oregon. *Oregon State Monogr., Studies Geol.*, no. 2, pp. 1-31.
- PALMER, W.
1909. Description of a new species of leatherback turtle from the Miocene of Maryland. *Proc. U.S. Natl. Mus.*, vol. 36, pp. 369-373.
- PILGRIM, G. E.
1931. Catalogue of the Pontian Carnivora of Europe. London, Trustees, Brit. Mus. (Nat. Hist.), vi+174 pp.
- RADINSKY, L. B.
1968. Evolution of somatic sensory specialization in otter brains. *Jour. Comp. Neurol.*, vol. 134, no. 4, pp. 495-506.
1971. An example of parallelism in carnivore brain evolution. *Evolution*, vol. 25, no. 3, pp. 518-522.
- REINHART, R. H.
1959. A review of the Sirenia and Desmostylia. *Univ. Calif. Publ. Geol. Sci.*, vol. 36, no. 1, pp. 1-146.
- REPENNING, C. A., AND J. G. VEDDER
1961. Continental vertebrates and their stratigraphic correlation with marine mollusks, eastern Caliente Range, California. *U.S. Geol. Surv. Prof. Paper no. 424*, pp. 235-239.

- ROMER, A. S.
1926. A lower Miocene horse *Anchitherium agatense* (Osborn). Amer. Jour. Sci., vol. 212, pp. 323-335.
- RUDEL, C. H.
1965. Rock units of the general eastside area, Cottonwood Creek to Tejon Hills. In Geol. of southeastern San Joaquin Valley, AAPG, SEG, SEPM, (Pacific Section), Guidebook, 1965, 40 pp.
- SAVAGE, R. J. G.
1957. The anatomy of *Potamotherium* an Oligocene lutrine. Proc. Zool. Soc. London, vol. 129, no. 2, pp. 151-244.
- SCHEFFER, V. B.
1958. Seals, sea lions and walruses. Stanford, Stanford Univ. Press, pp. 1-179.
- SCHLOSSER, M.
1899. Ueber die Bären und bärenähnlichen Formen des europäischen Tertiärs. Paleontographica, vol. 46, pp. 95-147.
1902. Beiträge zur Kenntniss der Säugetierreste aus den Süddeutschen Bohnerzen. Geol. Paläont. Abhandl., new ser., vol. 5, pp. 117-258.
- SCHULTE, H. VON W.
1917. The skull of *Kogia breviceps*. Bull. Amer. Mus. Nat. Hist., vol. 37, art. 17, pp. 361-404.
- SEGALL, W.
1943. The auditory region of the arctoid carnivores. Field Mus. Nat. Hist., zool. ser., vol. 29, pp. 33-59.
- SIMPSON, G. G.
1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., vol. 85, pp. 1-350.
- SIVERTSEN, E.
1954. A survey of the eared seals (Family Otariidae) with remarks on the Antarctic seals collected by Mik "Norvegia" in 1928-29. Det Norske Vidensk. Akad. Oslo, no. 36, pp. 1-76.
- SMITH, A. R.
1965. Bakersfield sheet. Geol. Map California (O. P. Jenkins, ed.), 1:250,000.
- STIRTON, R. A.
1960. A marine carnivore from the Clallam Miocene Formation, Washington, its correlation with nonmarine faunas. Univ. California Publ. Geol. Sci., vol. 36, pp. 345-368.
- STORY, H. E.
1951. The carotid arteries in the Procyonidae. Chicago Nat. Hist. Mus., Fieldiana: Zool., vol. 32, no. 8, pp. 477-557.
- THENIUS, E.
1949. Über die systematische und phylogenetische Stellung der Genera *Promeles* und *Semantor*. Sitzber. Österreiches Akad. Wiss., pt. 1, vol. 158, art. 4, pp. 323-335.
- TURNER, W.
1888a. Comparison of the convolutions of the seals and walrus with those of the Carnivora, and of apes and man. Jour. Anat., vol. 22, pp. 554-581.
1888b. Report on the seals. Zoology of the Voyage of H.M.S. Challenger, vol. 26, no. 68, pp. 89-134.
1912. The marine mammals in the Anatomical Museum of the University of Edinburgh. London, Macmillan and Co., Ltd., xvi+207 pp.
- VANDERHOOF, V. L.
1937. A study of the Miocene sirenian *Desmostylus*. Univ. California Publ. Dept. Geol. Sci., vol. 24, no. 8, pp. 169-262.
- VAN VALEN, L.
1966. Deltatheridia, a new order of mammals. Bull. Amer. Mus. Nat. Hist., vol. 132, pp. 1-126.
1968. Monophyly or diphyly in the origin of whales. Evolution, vol. 22, pp. 37-41.
- VIRET, J.
1929. Les faunes de mammifères de l'Oligocène supérieur de la Limagne bourbonnaise. Ann. Univ. Lyon, new ser., no. 47, pp. 1-328.
1951. Catalogue critique de la faune des mammifères miocènes de La Grive Saint-Alban (Isère). Première partie: Chiroptères, carnivores, edentés, pholidotes. Nouv. Arch. Mus. Hist. Nat., Lyon, vol. 3, pp. 3-104.
- WEAVER, C. E., ET AL.
1944. Correlation of the marine Cenozoic formations of western North America. Bull. Geol. Soc. Amer., vol. 55, pp. 509-598.
- WELKER, W. I., AND S. SEIDENSTEIN
1959. Somatic sensory representation in the cerebral cortex of the raccoon (*Procyon lotor*). Jour. Comp. Neurol., vol. 111, p. 469-501.
- WETMORE, A.
1930. Fossil bird remains from the Temblor Formation near Bakersfield, California. Proc. California Acad. Sci., ser. 4, vol. 19, pp. 85-93.
- WILSON, L. E.
1935. Miocene marine mammals from the Bakersfield region, California. Peabody Mus. Nat. Hist. Bull., vol. 4, pp. 1-143.
- WOOD, H. E. ET AL.
1941. Nomenclature and correlation of the North American continental Tertiary. Bull. Geol. Soc. Amer., vol. 52, pp. 1-48.

