An Early Miocene enaliarctine pinniped (Carnivora: Otariidae) from the western North Pacific.

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下部中新統瑞浪層群より産出した エナリアークトス亜科の鰭脚類（食肉目：アシカ科）について

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(要　　旨)

瑞浪盆地に分布する前期中新世後期の瑞浪層群明世累層から産出した鰭脚類化石22点のうち、山野内層および久尻相から産出した頭蓋の一部、下顎骨など13点を同一種に属するものと認め、その形態からアシカ科の中で最も原始的なグループであるエナリアークトス亜科に属する鰭脚類として記載した。エナリアークトス亜科に属する鰭脚類は、これまで北東太平洋沿岸域（カリフォルニアおよびオレゴン）からのみ知られていたので、明世累層からのものはこの仲間のものとしては北西太平洋から最初の産出記録となる。明世累層より産出したこの仲間の下顎骨や頬歯には、これまでに北東太平洋から報告されたエナリアークトス類のそれらには見られない特徴が認められるため、これらがこれまでに知られていない種類に属するものである可能性が極めて高い。しかしながら、これまでのところ明世累層産の標本群の中に保存の良い頭蓋が含まれていないため、主に頭蓋形態に基づいて立てられているこの仲間の分類体系の中で他の属種との充分な比較検討ができない。よって、ここではこれらを Enaliarctine species A としてエナリアークトス亜科の中の属種不明種として分類するに留めている。

Enaliarctine species A は、陸生食肉類と同様な咬頭を残した原始的な頬歯を持つことや、体軸骨格や後肢骨等に陸生食肉類に見られる原始的特徴が認められることなど、エナリアークトス亜科を特徴づける数多くの原始形質を保持している一方で、仙椎が4つの仙骨から構成されていることや、距骨の後突起が極めてよく発達していることなど、いわゆるセイウチ類（イマゴタリア亜科やセイウチ亜科）に見られる派生形質をも合わせ持っており、この仲間がエナリアークトス亜科の鰭脚類の中でも特にイマゴタリア亜科やセイウチ亜科を導いた系統に属する種類であった可能性を暗示している。このことは同時に、前期中新世後期にはすでにセイウチ類の適応放散が始まっていたことをも暗示している。

(Abstract)

A primitive otariid pinniped is described from the late Early Miocene Akeyo Formation of the Mizumami Group in the Mizunami district, Gifu Prefecture, central Japan. It is a member of the archaic subfamily Enaliarctinae, here indentified as Enaliarctine species A, and is, therefore, the first record of the Enaliarctinae from the western North Pacific. Enaliarctine species A is char-

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acterized by a number of plesiomorphic dental and postcranial features typical of the subfamily Enaliarctinae while having several shared derived characters with some species within the subfamily Imagotariinae and Odobeninae. These features indicate that Enaliarctine species A might have been the first good candidate of the enaliarctine species from which the subfamily Imagotariinae and their extinct and extant relatives could have arisen, and also that the lineage ultimately leading to modern walruses might have already been differentiated from the lineages leading to other subfamilies by the late Early Miocene.

Introduction

This is a preliminary report of a presently unnamed enaliarctine pinniped, here identified as Enaliarctine species A, from the late Early Miocene Akeyo Formation of the Mizunami Group in the Mizunami district, Gifu Prefecture, central Japan.

Since Yoshiwara and Iwasaki (1902) described "a new fossil mammal", which was later named *Desmostylus japonicus* by the same authors in 1914, from the Akeyo Formation of the Mizunami Group, a number of vertebrate remains have been reported from the Mizunami Group in both the Kani and Mizunami basins (see Kamei and Okazaki, 1974 ; Okazaki, 1982). Since then, at least fifteen terrestrial and eleven marine mammals, as well as some species of birds and lower vertebrates, have been recognized in the Mizunami Group (Table 1). Although the marine mammal assemblage in the Mizunami Group includes some species of pinnipeds, they remain poorly known and alluded to only briefly in the literature (Kamei and Okazaki, 1974 : 284 ; Okazaki, 1977 : 12-13, 1978 : table 1, 142, 1982 : table 1 ; Kohno, 1990 : 84-85).

In the present article I provide a description of the cranial elements and dentary of the primitive pinniped, Enaliarctine species A, with a brief account of the postcranial bones that are provisionally referred to this species, from the Akeyo Formation. The importance of the fossil pinniped described here is that it is the first record of the subfamily Enaliarctinae from the western North Pacific and that it has some imagotariine-like or odobenine-like features in its dental and postcranial structures. In a subsequent paper (Kohno, in prep.), I will describe in detail the postcranial osteology and discuss the morphologic and phylogenetic importance of this animal in addition to considering its locomotor adaptations and paleoecology, based mainly on the structure of the pelvic girdle and hind limb elements.

Abbreviations

Abbreviations used in this paper are as follows:

CBMPV: Natural History Museum and Institute, Chiba, Japan; Vertebrate Paleontology Collection, Japan.

MFM: Mizunami Fossil Museum, Mizunami, Gifu Prefecture, Japan.

LACM: Natural Histoty Museum of Los Angeles County, Los Angeles, California.

USNM: United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Table 1. Faunal list (including lower vertebrates and birds) of the Mizunami Group.

	Terrestrial	Marine
Carnivora		
?Canidae gen. et sp. indet.	X	
?Musteloidea, gen. et sp. indet.	X	
Enaliarctine species A		X
Enaliarctinae gen. et sp. indet.		X
Otariidae gen. et sp. indet.		X
Proboscidea		
Gomphotherium annectens (Matsumoto, 1924)	X	
Desmostylia		
Desmostylus japonicus Tokunaga and Iwasaki, 1914		X
Paleoparadoxia tabatai (Tokunaga, 1939)		X
Perissodactyla		
Anchitherium hypohippoides Matsumoto, 1921	X	
Palaeotapirus yagii Matsumoto, 1921	X	
Chilotherium pugnator (Matsumoto, 1921)	X	
Chilotherium sp.	X	
Artiodactyla		
Palaeochoerus sp.	X	
Amphitragulus minoensis Matsumoto, 1918	X	
?Amphitragulus sp.	X	
Tragulidae gen. et sp. indet.	X	
Cetacea		
Eurhinodelphis minoensis Okazaki, 1976		X
Eurhinodelphis species A		X
Eurhinodelphis species B		X
Physeteriidae gen. et sp. indet.		X
Odontoceti, fam., gen. et sp. indet.		X
Mysticeti, fam., gen. et sp. indet.		X
Rodentia		
Youngofiber sinensis (Young, 1955)	X	
Sciuridae gen. et sp. indet.	X	
Myomorpha, fam., gen. et sp. indet.	X	
Rodentia, fam., gen. et sp. indet.	X	
Chelonia		
?Trionyx sp.	X	
Chelonia spp.	X	
Crocodilia		
Crocodylidae, fam., gen. et sp. indet.	X	
Aves		
Plotopterum sp.		X

Table 2. List of fossil pinnipeds from the Akeyo Formation of the Mizunami Group.

Reg.No.	Specimen	Ma	Member	Locality	Loc.No.	Discoverer	Year	Ref.
	Enaliarctine species A							
180120	Upper teeth, mandibles, atlas, etc.	17.5-17	Yamanouchi	Matsugase, Matsugase-cho, Mizunami	54	T. Niwa, N. Mitsuya	1990	4
180116	Mandibles	17.5-17	Yamanouchi	Matsugase, Matsugase-cho, Mizunami	54	H. Karasawa	1979	4
180113	Skull frag., upper cheek teeth, etc.	17.5-17	Yamanouchi	Matsugase, Matsugase-cho, Mizunami	54	T. Kaede, N. Kohno	1977	4
180115	Left mandible	17.5-17	Yamanouchi	Kohazama, Akeyo-cho, Mizunami	None	H. Karasawa	1978	4
180118	Lower premolar	17.5-17	Yamanouchi	Matsugase, Matsugase-cho, Mizunami	54	T. Kaede	1986	4
	Enaliarctine species A (provisionally referred)							
180109	Right femur, Lumbars, sacrum, etc.	17.5-17	Yamanouchi	ST-285, Togari, Akeyo-cho, Mizunami	49	M.F.M.	1972	3
180111	Lambar, femur, sacrum, pelvis, etc.	17.5-17	Yamanouchi	Matsugase, Matsugase-cho, Mizunami	54	M.F.M.	1976	3
180121	Lumbar, tibia, fibula, astragalus, etc.	17.5-17	Yamanouchi	Kohazama, Akeyo-cho, Mizunami	None	Y. Okumura	1991	4
180110	Femur, sacrum, pelvis, astragalus, etc.	17.5-17	Yamanouchi	Matsugase, Matsugase-cho, Mizunami	54	M.F.M.	1976	2
180102	Lumbars, Rib	17.5-17	Kujiri	Anabora, Kawai, Izumi-cho, Toki	40	M. Azuma	?	4
180105	Left mt 2, 4, cuboid	17.5-17	Kujiri	Anabora, Kawai, Izumi-cho, Toki	40	M. Tatematsu et al.	1965	1, 2
180106	Left mt 4, 5, cuboid	17.5-17	Kujiri	Nanamagari, Izumi-cho, Toki	19	S. Miura	1972	1, 2
180108	Left mt 2	17.5-17	Kujiri	Kujiri, Izumi-cho, Toki	None	T. Yoshida	1972	4
	Enaliarctinae gen. et sp. indet.							
180103	Right astragalus	17.5-17	Yamanouchi	Hitoichiba, Toki-cho, Mizunami	69	S. Ino	1952	None
180104	Left mc 4	17.5-17	Yamanouchi	Tentoku, Akeyo-cho, Mizunami	None	S. Ino	1952	None
180107	Left calcaneum	17.5-17	Kujiri	Kujiri, Izumi-cho, Toki	None	T. Yoshida	1972	None
180119	Right Astragalus	17.5-17	Togari	Terakawado-cho, Mizunami	79	T. Furuta	1989?	None
180123	Sacrum fragment	17.5-17	Togari	Ichihara, Toki-cho, Mizunami	78	T. Kaede	1991	None
	Otariidae gen. et sp. indet.							
180117	Humerus fragment	16	Shukubora	Oginoshima, Kamado-cho, Mizunami	7	T. Kaede	1983	None
180122	Radius	16	Shukubora	Oginoshima, Kamado-cho, Mizunami	7	T. Yamada	1991	None
180112	Left calcaneum fragment	16	Shukubora	Oginoshima, Kamado-cho, Mizunami	7	N. Kohno	1976	None
180114	Left calcaneum	16	Shukubora	Oginoshima, Kamado-cho, Mizunami	7	T. Fushimi	1977	None

References: 1, Kamei and Okazaki (1974); 2, Okazaki (1977); 3, Kohno (1990); 4, this study

Materials and Methods

The specimens have been collected over the past thirty years by numerous paleontologists, both professional and amateur, and have all been placed in the Mizumami Fossil Museum (Table 2). Most of the specimens have been found disassociated, thus the identification of these bones as the same species is based on those specimens that are morphologically identical with at least one element within each specimen.

The comparisons are made with the following specimens: Recent terrestrial and aquatic arctoid carnivorans (CBMPV collection); enaliarctine pinnipeds (LACM and USNM collections) including a nearly complete skeleton of *Enaliarctos mealsi* Mitchell and Tedford, 1973, represented by USNM 374272 ; and advanced pinnipeds both extinct and extant (CBMPV, LACM, and USNM collections). Additional osteological data were obtained from references cited.

The anatomical terminology used in this paper follows that of Howell (1929), Hershkovitz (1971), Barnes (1972, 1979), Repenning and Tedford (1977), Evans and Christensen (1979), and Berta (1991). Measurements of the specimens in tables are as defined by Barnes (1972, 1979), Repenning and Tedford (1977), and Berta (1991).

The classification of the otariid pinnipeds adopted here is that of Barnes (1989), in which the family Otariidae includes the subfamilies Enaliarctinae, Otariinae, Imagotariinae, Dusignathinae, Odobeninae, Desmatophocinae, and Allodesminae.

As discussed by Repenning and Tedford (1977), Barnes (1989, 1990, 1992), and Barnes *et al.* (1985), the subfamily Enaliarctinae is a paraphyletic basal group of primitive Otariidae from which several more derived lineages appear to have arisen (but see Wyss,

1987 ; Berta *et al.*, 1989 ; Berta and Ray, 1990 ; Berta, 1991).

The diagnosis of the subfamily Enaliarctinae is based on characters listed by Mitchell and Tedford (1973), Repenning and Tedford (1977), Barnes (1979, 1989, 1992), and Barta (1991), with appropriate modifications.

The MFM locality numbers used here are as defined by Itoigawa (1980).

Systematic Paleontology

Class Mammalia Linnaeus, 1758
Order Carnivora Bowdich, 1821
Infraorder Arctoidea Flower, 1869
Family Otariidae Gill, 1866
Subfamily Enaliarctinae Mitchell and Tedford, 1973

Type genus.—*Enaliarctos* Mitchell and Tedford, 1973.

Included genera.—*Enaliarctos* Mitchell and Tedford, 1973 ; *Pteronarctos* Barnes, 1989 ; *Pacificotaria* Barnes, 1992 ; and *Pinnarctidion* Barnes, 1979.

Emended Diagnosis of Subfamily.—A subfamily of the family Otariidae distinguished from other subfamilies by having the combination of following plesiomorphic characters: P^4 with an anterolingual or lingual protocone or a protocone shelf; P^4 with three or two roots; embrasure pit between P^4 and M^1; M_1 with well developed cusps on the trigonid and a hypoconid on the talonid; an inflated bulla; a deep nasolabialis fossa; a distinct lacrimal foramen; no large orbital vacuity; a relatively large paroccipotal mastoid crest; a prominent sulcus on cranium corresponding to pseudosylvian fissure of brain; relatively slender humerus with well developed supinator ridge; ulna lacking the posteriorly expanded olecranon process; radius lacking a strongly flattened and expanded distal end; femur with well developed pit on the head for the teres femoris ligament; conical patella; fibula with well defined processus lateralis fibulae; slightly laterally curved short ilium; six lumbar vertebrae; astragalus with slight posterior extension of calcaneal process; unreduced fifth intermediate phalanx of the manus; metapodial shafts rounded in cross section with keeled heads and strongly trochleated phalangeal articulations.

Known distribution.—Range in age from the late Late Oligocene to early Middle Miocene, California, Oregon, and Japan.

Enaliarctine species A

(Tables 4-6 ; Plates 35-43)

Canidae, gen. et sp. indet. Kamei and Okazaki, 1974 : 278.
Carnivora, gen. et sp. indet. Okazaki, 1977 : 12.
?*Neotherium* sp. Okazaki, 1982 : Table 1.
Neotherium sp. A. Kohno, 1990 : 84.

Comments.—Enaliarctine species A from the Akeyo Formation belongs possibly to at

least a new species within the subfamily Enaliarctinae as will be mentioned bellow. However, I have refrained from applying a name to this undetermined enaliarctine due to the lack of the cranial material among the available specimens that can be compared to other named species at the present time.

Formation and age.—The specimens came from the Ymanouchi Member and Kujiri facies (equivalent to the Togari and Yananouchi members) of the Akeyo Formation in the Mizunami Group (Table 3), which outcrops in the Mizunami district, Gifu Prefecture; late Early Miocene, Blow's Zone N7, correlative of Late Burdigalian of the European Chronology, Late Hemingfordian of the North American Land Mammal Age, Late Saucesian of the North American West Coast Foraminiferal Chronology, and approximately 17.5–17 Ma (Itoigawa, 1988 ; Kobayashi, 1989).

The geology and stratigraphy of this region was established by Itoigawa (1960, 1974), and more detailed accounts of the regional geology and chronology are given in Itoigawa (1980, 1988) and Kobayashi (1989).

Associated mammalian fauna.—The mammalian assemblage from the Mizunami Group in Kani and Mizunami basins have been the subject of many articles, in particular Matsumoto (1918, 1921, 1926), Takai (1939), Kamei and Okazaki (1974, 1976), Okumura *et al.* (1977), and Okazaki (1976, 1977, 1978, 1982). Okazaki (1982) summarized the previous studies on the mammalian assemblage from the Mizunami Group and recognized at least nineteen species of mammals, of which nine species were marine mammals. Recently, Tomida (1990) added a gigantic beaver, *Youngofiber sinensis* (Young, 1955), to the assemblage of the Mizunami Group. Until now, at least fifteen terrestrial and eleven marine mammals have been known in the Mizunami Group (Tables 1 and 3).

Refferred specimens and localities.—MFM 180120, young adult male, left and right I^2, right I^3, right P^2, left dentary with canine, P_1, and P_3, right dentary with incomplete canine, P_2, P_3, and M_1, keratohyoid, atlas, and rib bones; from the Yamanouchi Member at MFM locality 54, Matsugase, Matsugase-cho, Mizunami City; collected by Toshihito Niwa and Nobuyuki Mitsuya in 1990.

MFM 180116, young adult male, left dentary with canine and incomplete P_{2-4}, right dentary with incomplete canine, and a few vertebrae and rib bones (the last two bones have been lost); from the Yamanouchi Member at MFM locality 54, Matsugase, Matsugase-cho, Mizunami City; collected by Hiroaki karasawa in 1979.

MFM 180113, immature individual, frontals, parietals, occipitals, left P^3 (which has been lost) and P^4, atlas, 3 thoracic and 4 lumber vertebrae, rib bones, left innominate, right femur, left and right tibiae, and left and right fibulae; from the Yamanouchi Member at MFM locality 54, Matsugase, Matsugase-cho, Mizunami City; collected by Tatsuya Kaede and Naoki Kohno in 1977.

MFM 180115, immature male left dentary with canine and P_4; from the Yamanouchi Member at Kohazama, Akeyo-cho, Mizunami City; collected by Hiroaki Karasawa in 1978.

MFM 180118, left P_1 from the Yamanouchi Member at MFM locality 54, Matsugase, Matsugase-cho, Mizunami City; colleted by Tatsuya Kaede in 1986.

Table 3. Terrestrial and marine mammal assemblages in the Mizunami Group.

AGE (Ma)	15	16	17	18	19
BLOWS BIOZONE	N8		N7		
UNITS	III	II			I
GROUP	MIZUNAMI GROUP				
MIZUNAMI BASIN (marked with +)	Oidawara Mm.	Nataki Mm. / Shukubora facies	Hazama Mm.	Yamanouchi Mm. / Togari Mm. / Tsukiyoshi Mm. / Kujiri facies	Akeyo Fm. / Hongo Fm.	Oidawara Fm.	Toki Lignite-Bearing Fm.
KANI BASIN (marked with *)				?	Hiramaki Fm. (U / L)	?	Nakamura Fm. (U / L)
MAMMALIAN ASSEMBLAGE							
?Canidae gen. et sp. indet.							+
?Mustelidea, gen. et sp. indet.						+	
Gomphotherium annectens							+ *
Anchitherium hypohippoides					+ *		
Palaeotapirus yagii					+?		* *
Chilotherium pugnator				+?	+ * ?		* * *
Chilotherium sp.							* *
Palaeochoerus sp.				+			
Amphitragulus minoensis			+	+	+ *		*
?*Amphitragulus* sp.				+	+	+	
Tragulidae gen. et sp. indet.				+			
Youngofiber sinensis							*
Sciuridae gen. et sp. indet.			+			*	
Myomorpha fam., gen. et sp. indet.				+			
Rodentia fam., gen. et sp. indet.							*
Enaliarctine species A				+ +			
Enaliarctinae gen. et sp. indet.				+			
Otariidae gen. et sp. indet.		+	+				
Desmostylus japonicus				+			
Paleoparadoxia tabataí	+			+ +			
Eurhinodelphis minoensis				+			
Eurhinodelphis species A				+			
Eurhinodelphis species B	+						
Physeteridae gen. et sp. indet.				+			
Odontoceti, fam., gen. et sp. indet.	+	+		+ + +			
Mysticeti, fam., gen. et sp. indet.				+			

Provisionally refferred specimens and localities.—MFM 180109, referred male, rib bones, thirteenth and fourteenth thoracics, first, third, fourth, fifth, and sixth lumbars, right femur, and phalanx; from the Yamanouchi Member at MFM locality 49, ST-285, Togari, Akeyo-cho, Mizunami City; collected by staff of the Mizunami Fossil Museum in 1972.

MFM 180111, referred male, fifth or sixth lumbar, sacrum, 2 caudal vertebrae, fragment of right femur, and phalanx; from the Yananouchi Member at MFM locality 54, Matsugase, Matsugase-cho, Mizunami City; collected by staff of the Mizunami Fossil Museum in 1976.

MFM 180121, referred male, third or fourth lumbar vertebra, proximal half of left tibia and proximal end of right tibia, left fibula, ritht astragalus, right navicular, right metatarsal I, and right phalanges; from the Yamanouchi Member at Kohazama, Akeyo-cho, Mizunami City; collected by Yoshitsugu Okumura on 2 December 1991.

MFM 180110, referred female, left femur and proximal fragment of right femur, proximal half of left and right tibiae, right half of sacrum, left innominate, right astragalus and navicular (both of which have been lost), and right fifth metatarsal (misidentified as the distal end of the fibula in the previous report); partly described by Okazaki (1977 : 12-13, pl. 3), from the Yamanouchi Member at MFM locality 54, Matsugase, Matsugase-cho, Mizunami City; collected by staff of the Mizunami Fossil Museum in 1976.

MFM 180102, referred female, 2 lumbar vertebrae from the Kujiri facies at MFM locality 40, Anabora, Kawai, Izumi-cho, Toki City; collected by Mitoshi Azuma.

MFM 180105, referred female, left second and fourth metatarsal, and left cuboid; described by Kamei and Okazaki (1974 : 278, pl. 95), from the Kujiri facies at MFM locality 40, Anabora, Kawai, Izumi-cho, Toki City; collected by Masae Tatematsu, Haruo Ohsato, and Yoshihiko Okazaki in March 1965.

MFM 180106, referred female, left fourth and fifth metatarsal (misidentified as the distal end of the fibula in the previous reports), and left cuboid; described by Kamei and Okazaki (1974 : 279) and partly illustrated by Okazaki (1977 : pl. 3), from the Kujiri facies at MFM locality 19, Nanamagari, Jyorinji, Izumi-cho, Toki-City; collected by Satoshi Miura in August 1972.

MFM 180108, referred female left second matatarsal from the Kujiri facies at Kujiri, Izumi-cho, Toki City; collected by Takefumi Yoshida in 1972.

Description and Comparisons

Cranium and dentition:

Cranium (MFM 180113 ; Table 4, Pl. 35, Figs. 1-3).—The frontals, left and right parietals, and the occipitals of the immature individual are known of this species. These bones are separated into four sections along the line of sutures.

Occipitals—The basioccipital is relatively wide, parallel sided, and possess a medially excavated deep sinus on each lateral edge, as in ursids, species of enaliarctines, and some species of primitive imagotariines (Barnes, 1979 ; Hunt and Barnes, 1991 ; Kohno *et al.*, 1992). These sinuses have been lost in later pinnipeds (Barnes, 1989 ; Hunt and Barnes,

1991). The occipital condyles are widely spaced, diverging dorsally, and relatively close to the occipital shield. But the articular facet of the atlas of MFM 180120 indicates that the occipital condyles in an adult individual of Enaliarctine species A project prominently posteriorly from the occipital shield. This kind of difference is interpreted as ontogenetic variation such as is seen in Recent otariines (pers. observ.). There is a deep fossa on the dorsal margin of the foramen magnum near the medial side of the occipital condyle.

Parietal—The dorsal surfaces of the parietals are smooth and no sagittal crest is developed, however, the condition may also represent the immature state of this individual. A deep pseudosylvian sulcus is obliquely depressed on the lateral surface of the parietal.

Frontal—The anterior portion of the frontal is broken off. The intertemporal region is narrow and parallel sided. There is no paranasal sinus in the frontal as in typical otariids. The anterolateral corners of the braincase are expanded laterally, forming squared anterolateral margins.

Dentary (MFM 180115, 180116, 180120 ; Table 5, Pls. 36-39). —The dentaries of

Table 4. Measurements (in mm) of the skull and upper teeth of Enaliarctine species A. "e" indicates estimated measurements.

	MFM 180113	MFM 180120
Width across greatest intertemporal constriction	22.2	--
Width of braincase at anterior edge of glenoid fossa	64.8e	--
Greatest width across occipital condyles	43.7	--
Greatest width of foramen magnum	20.1	--
Greatest height of foramen magnum	21.2	--
I^1 anteroposterior diameter	--	5.1
I^1 transverse diameter	--	4.1
I^1 crown height (labial side)	--	4.8
I^2 anteroposterior diameter	--	4.9
I^2 transverse diameter	--	3.9
I^2 crown height (labial side)	--	4.9
I^3 anteroposterior diameter	--	6.6
I^3 transverse diameter	--	4.6
I^3 crown height (buccal side)	--	8.4
P^2 anteroposterior diameter	--	8.9
P^2 transverse diameter	--	5.4
P^2 crown height (buccal side)	--	6.2
P^3 anteroposterior diameter	--	--
P^3 transverse diameter	--	--
P^3 crown height (buccal side)	--	--
P^4 anteroposterior diameter	7.9	--
P^4 transverse diameter	6.7	--
P^4 crown height (buccal side)	5.4	--

Table 5. Measurements (in mm) of dentaries of Enaliarctine species A. "e" indicates estimated measurements. "a" indicates measurements of alveoli.

	MFM18020		MFM180116		MFM180115
	Left	Right	Left	Right	Left
Total length	160.0	160.8	155.2	154.8	--
Greatest length of symphysis	33.9	33.8	30.5	31.2e	--
Greatest breadth of symphysis	20.0	20.1	20.0	20.0	--
Symphysis angle relative to alveolar row	46	45	44	45	--
Length of alveolar row, C-M_2	69.8	68.6	69.0	69.3	--
Length of alveolar row, P_1-M_2	52.2	51.0	51.9	51.5	42.6e
Depth of horizontal ramus at P_3	28.8	28.4	28.0	27.0	17.8
Width of horizontal ramus at P_3	12.3	11.6	12.9	11.2	7.5
Depth of horizontal ramus at M_1	29.0	28.8	28.3	27.8	14.5
Width of horizontal ramus at M_1	12.2	11.6	11.7	11.2	5.4
Width of condyloid process	27.7	28.0	33.0	30.7	--
I_1 anteroposterior diameter	--	--	--	5.0a	--
I_1 transverse diameter	--	--	4.2e	3.2a	--
I_2 anteroposterior diameter	5.7a	--	--	6.0a	--
I_2 transverse diameter	4.1ae	--	--	4.1a	--
C anteroposterior diameter	12.1	--	12.1e	11.7e	--
C transverse diameter	9.0	8.5	8.9	8.5	--
P_1 anteroposterior diameter	6.7	6.6a	6.0a	7.0a	5.3a
P_1 transverse diameter	4.6	4.6a	4.6a	4.6a	3.2a
P_2 anteroposterior diameter	9.2a	8.5	--	9.2a	8.7a
P_2 transverse diameter	4.8a	4.8	5.4e	4.5a	4.3a
P_3 anteroposterior diameter	9.2	8.6	--	10.0a	9.8a
P_3 transverse diameter	5.0	4.9	--	4.8a	--
P_4 anteroposterior diameter	9.9a	8.2a	--	9.5a	10.0
P_4 transverse diameter	4.6a	4.0a	--	4.3a	--
M_1 anteroposterior diameter	11.3a	10.6	10.9a	10.6a	10.2a
M_1 transverse diameter	4.5a	5.5	4.4a	4.1a	3.2a
M_2 anteroposterior diameter	4.0a	4.1a	4.1a	4.3a	--
M_2 transverse diameter	3.7a	3.2a	2.8a	3.0a	--

MFM 180116 and 180120 are completely preserved. The horizontal ramus is relatively long and slender, and has parallel dorsal and ventral margins, like that of *Enaliarctos* spp. (Berta, 1991), but slightly deeper dorsoventrally. The symphysis is a rounded spindle shape, and the ventral margin of the symphysis flares downward into a prominent genial tuberosity beneath the P_1. There is a mental foramen on the anterior end of the horizontal ramus and there are two other foramina beneath the P_1 and P_3 on the midline of the horizontal ramus. As in other primitive otariids, the dentary of Enaliarctine species A has two incisors, one canine, four, premolars, and two molars. The alveoli indicate that the P_1 and M_2 are single-rooted and the P_2 to M_1 are distinctly double-rooted. In occlusal view, the cheek tooth rows are widely divergent posteriorly, and each row is straight with teeth moderately spaced. In *Enaliarctos emlongi* Berta, 1991, the cheek teeth are more widely spaced in the tooth row. On the contraty in *E. barnesi* Berta, 1991, the cheek tooth row is much shorter and more crowded (Berta, 1991). The coronoid process of the dentary is broad at the base and its dorsal apex is relatively high and rounded, unlike that of *Enaliarctos barnesi* in which it is not rounded but pointed posterodorsally. The masseteric

fossa on the lateral surface of the coronoid process is relatively deep and large in area. The mandibular foramen is relatively small, directed anteriorly, and lies midway between the anterior and posterior margins of the ascending ramus as in most otariids. According to Berta and Demêré (1986) the anterior margin of the mandibular foramen in *Enaliarctos mealsi* is directed anterodorsally. The digastric prominence is very weak and turned smoothly up to a long and shallow pterygoid process which is directed posteromedially. The condyloid process, which is transversely narrow, is elevated high above the level of the alveolar row, like that of *Enaliarctos* spp. (Berta, 1991).

Kamtschatarctos sinelnikovae Dubrovo, 1981, was originally described as a member of the Enaliarcninae on the basis of an incomplete skull and a right dentary with P_{2-4}, of Middle Miocene age from Kamchatka Peninsula, Russia (Dubrovo, 1981, 1984). Recently Barnes (1989) transferred this species from the Enaliarctinae to the Imagotariinae on the basis of its similarity to *Imagotaria downsi* Mitchell, 1968, rather than to the species within the Enaliarctinae, and I agree with Barnes' decision. The ventral margin of the dentary of *K. sinelnikovae* is nearly straight, the pterygoid process is relatively long and weak, and the condyloid process is lacated at the same level as the cheek tooth row, unlike the condition of Enaliarctine species A. In addition, the dentary of the former is much larger than that of the latter.

Barnes (1988) illustrated the anterior half of the dentary bearing the P_{2-4} of the primitive imagotariine (see Repenning and Tedford, 1977 ; Barnes, 1989) *Neotherium mirum* Kellogg, 1931, from the Middle Miocene Sharktooth Hill Bonebed, California, which has earlier been interpreted (Mitchell and Tedford, 1973 ; Mitchell, 1975) as a derived enaliarctine. From what can be seen in the illutration (Barnes, 1988 : fig. 4), the horizonal ramus of the dentary in *N. mirum* is similar in shape to that in Enaliarctine species A, however, it is much larger than that of the former. According to Barnes (pers. commun., 1991), the proportion and shape of ascending rami of unpublished dentaries in *N. mirum* are likewise very different from that in Enaliarctine species A.

Upper Dentition (Table 4, Pl. 35, Figs. 4-18). —Left and right I^2 (MFM 180120), right I^3 (MFM 180120), right P^2 (MFM 180120), left P^3 (MFM 180113 ; but the specimen has been lost), and left P^4 (MFM 180113), are known for this species.

The upper second incisor (Pl. 35, Figs. 4-9) is very small in size, and its root is extremely compressed transversely. The crown of the I^2 has transverse constriction, creating the effect of double cusps, of which the labial one is two times larger than the lingual one. This condition is distinguishable from that of *Enaliarctos* spp. (Berta, 1991) and *Pacificotaria hadromma* Barnes, 1992, in which the labial cusps of first and second incisors are as large as lingual ones.

The upper third incisor (Pl. 35, Figs. 10-12) is oval in cross section and has a prominent, asymmetrically curved posterior cingulum with no posterolateral cusp. There is a deep vertical wear facet on the lateral margins of the crown.

The upper second premolar (Pl. 35, Figs. 13-15) is posteromedially broad with a lingual cingulum that forms a small cingular shelf. The paracone is located centrally on the crown, and a small but distinct metacone and metastyle are located posterior to the

paracone. The P^2 has two distinctly separate roots, of which the anterior root is round in cross section, but the posterior one is slightly larger and expanded transversely.

The upper third premolar has been lost, however, from as much as can be seen in the only remaining illustration by the collector, it is similar in shape to the referred P^2 of MFM 180120 and has much more expanded posteroligual cingulum with two or three cuspules on it. The P^3 also had two distinctly separate roots.

The upper fourth premolar (Pl. 35, Figs. 16-18) is somewhat different in shape from the P^2 and P^3. The crown is shaped like an equilateral triangle in occlusal outline with a medially expanded, multiply cuspate cingulum with a protocone shelf, that is completely separated from the paracone and metacone by a sharp groove. The paracone is broad and low, and located at the midpoint on its crown. The metacone is anteroposteriorly enlarged, forming a blade-like ridge, and is separated from the paracone by a distinct notch. There is no parastyle. The crown is surrounded by a continuous cingulum. The buccal cingulum is slightly inflated, but the lingual one is much enlarged with multiple cuspules, a feature which represents an advenced condition among the Enaliarctinae. The P^4s in species of enaliarctines so far known are similer than that of MFM 180113, and they have no cuspules on their lingual cingula (see Barnes, 1979, 1989, 1990, 1992 ; Berta, 1991). The P^4 has two distinct roots, of which the anterior root is round in cross section and the posterior one is bilobed at the base.

Lower Dentition (Table 5, Pls. 36-39). —Left C (MFM 180115,180116,180120), P_1 (MFM 180118,180120), P_2(MFM 180120), P_3(MFM 180116,180120), P_4(MFM 180115 180116), and right C (MFM 180116,180120), P_2(MFM 180120), P_3(MFM 180120), M_1 (MFM 180120) are preserved.

The lower canine is large, and its crown is long and moderately worn. There is a slight cingulid on the lateral and medial sides of the base of the crown.

The lower first premolar is single rooted and has a centrally located simple protoconid with a small paraconid. The lingual cingulid is well developed at the lower margin of the crown, and is oblique to the long axis of the root.

The lower second premolar is similar to the P_1 but has two roots. The P_2 has an anteroposteriorly elongated, pointed protoconid and a small paraconid anterior to the protoconid. The lingual cingulid is well developed at the base of the crown.

The lower third and fourth premolars are nearly the same size and shape. They are similar in shape to the P_2 but much larger. Each tooth has a crown with three cusps, a relatively large paraconid, an anteroposteriorly elongated protoconid, of which there is a blade-like wear facet on the anterior margin, and a small but distinct metaconid. The metacconid is smaller than the paraconid and located close to the protoconid. The lingual cingulid is well developed on each tooth, as it is on the P_2.

The lower first molar also has two well separated roots. The crown of the M_1 consists of four cusps, a relatively large paraconid, an anteroposteriorly elongated protoconid, a distinct metaconid which is smaller and higher on the tooth than the paraconid, and a small hypoconid. The paraconid and metaconid are located slightly lingual to the anteroposterior axis of the crown. The hypoconid forms an anteroposteriorly shortened unicuspid talonid.

The trigonid of the M_1 shows signs of retaining a carnassial function (Pl. 37, Fig. 3).

Hyoid apparatus (MFM 180120 ; Pl. 35, Figs. 19-20). —The keratohyoid is only known element of the hyoid apparatus. The body of the bone is small, short, and slender. Its dorsal surface is excavated as a groove. The distal articular surface for the basihyoid and thyrohyoid is about twice as large as its proximal articular surface for the epihyoid.

Axial skeleton:

The complete vertebral column of Enaliarctine species A is not preserved in any specimen, but it probably was comprised of 7 cervicals, 14 thoracics, 6 lumbars, 4 sacrals, and an unknown number of caudals, as will be mentioned below.

Cervicals (MFM 180113,180120 ; Pl. 40, Figs. 1-8). —The atlas is only known cervical and agrees well in general morphology with otariid pinnipeds. The transverse foramen (= vertebraterial canal) is small and visible only from the posteriorly, as in most otariids except *Odobenus rosmarus* (Linnaeus, 1758), in which the transverse foramen is very large and visible from both dorsal and posterior views (see Wyss, 1988 : 17). The alar notch is distinct at the anterior base of the transverse process. It is well developed in most arctoid carnivorans and pinnipeds, but is very small in ursids (Berta and Ray, 1990).

Thoracics (MFM 180109,180113 ; Pl. 41, Figs. 1 and 3). —Although the thoracic vertebrae normally number fifteen in most pinnipeds, Enaliarctine species A is regarded as having fourteen thoracic vertebrae as in *Enaliarctos* and *Odobenus* (Berta and Ray, 1990). The thirteenth and fourteenth thoracics are preserved in MFM 180109. Each centrum is relatively small. The neural spine is low and elongated anteroposteriorly. The metapophysis is relatively large and forms a lateral support for the anterior zygapophysis. There is a large anapophysis that projects posteriorly beyond the centrum.

Lumbars (MFM 180102,180109,180110,180111,180113,180121 ; Pl. 41, Figs. 1-4). —Although only five lumbars are preserved in MFM 180109, the first lumbar does not articulate with the "second" lumbar because of the incompatibility in width between the postzygapophysis of the first lumbar and the prezygapophysis of the next one. It indecates that the original second lumbar was missing or was not preserved, and the preserved "second" lumbar is actually the third one. Therefore, I presume this animal possesses six lumbars. The lumbar vertebrae are all quite similar to each other and vary only in length of their neural spines and transverse processes. The neural spines are relatively short and vertical. They become long; the sixth lumbar vertebra has the longest neural spine. The posterior surfaces of the apices of the neural spines are bifid like those of *Odobenus rosmarus*. The transverse processes are flattened dorsoventrally and projected anteroventrally more than two or three times as long as wide.

Sacrum (MFM 180109,180110,180111 ; Pl. 41, Figs. 2,4,5-8). —The sacrum is composed of four well-fused vertebrae instead of three vertebrae as in ursids, musteloids, and typical otariids. Likewise, *Enaliarctos mealsi* has a sacrum being composed of three vertebrae as in most otariids (Berta and Ray, 1990). In *Odobenus rosmarus*, four vertebrae are always incorporated into the sacrum (Howell, 1929). In dorsal view, the lateral margins of the sacrum are tapered posteriorly, creating a reversed triangle in shape as in terrestrial

arctoids, unlike the rectanglar shape as in Recent otariids.

Caudals (MFM 180111 ; Pl. 41, Fig. 9). —Two caudal vertebrae are preserved in MFM 180111. On the larger one, possibly the first caudal vertebra, the bifurcated transverse process is well developed. The number of caudal vertebrae of this species is not determinable at present.

Rids (MFM 180102,180109,180110,180111,180113,180116,180120,180121). —The ribs are slender and are not as robust as in modern pinnipeds. Among all referred specimens, there is a shallow pit in the lateral surface of the proximal end of the shaft. This feature is lacking in terrestrial arctoids and other pinnipeds.

Appendicular skeleton:

No pectoral girdle nor forelimb bones are referred to this species. Only the pelvic girdle and some hind limb bones are known.

Pelvis (MFM 180109,180110,180111,180113 ; Table 6, Pl. 42, Figs. 1-3). —The pelvis is composed of a short ilium and elongated ischium and pubis as is characteristic of typical otariids. The ilium is curved laterally, approximately to the extent of that of *Enaliarctos* and *Odobenus*. Interestingly, the ischiatic spine is well developed dorsally in MFM 180110 (Pl. 42, Fig. 2), a feature that is not typical among the otariids, but is seen usually in the phocids. There is no obturator nerve foramen. The pelvis represented by MFM 180111 is approximately 23 percent larger than that of MFM 180110, and its posterior end is thick and rounded in shape. On the other hand, that of MFM 180110 is smaller in size, and its posterior end forms a thin and posteroventrally directed rectangular plate. Such differences in size and shape are interpreted to be the expression of sexual dimorphism as is characteristic of most otariid pinnipeds. Therefore, MFM 180111 is believed to be that of a male and MFM 180110 to be that of a female, respectively.

The femur (MFM 180109,180110,180111,180113 ; Table 6, Pl. 42, Figs. 4-9). —The femur is short, broad, and strongly flattened anteroposteriorly as is characteristic of all pinnipeds (Howell, 1929 ; Wyss, 1989 ; Berta and Ray, 1990). There is a well-defined pit on the cylindrical head for the teres femoris ligament (Pl. 42, Fig. 7). This pit is very reduced or absent in most pinnipeds except *Enaliarctos* spp. (Berta and Ray, 1990 ; Berta, 1991).

The tibia (MFM 180110,180113,180121 ; Table 6, Pl. 43 Figs. 1-6). —The tibia is long and slender. The proximal half of the shaft is slightly curved latrally. The tibia is separated proximally from (not fused) the fibula as in terrestrial carnivorans and primitive otariids such as *Thalassoleon mexicanus* Repenning and Tedford, 1977, allodesmines, and modern walruses (Repenning and Tedford, 1977 ; Berta *et al.*, 1989 ; Berta and Ray, 1990). The anterolateral and the post-tibial (=intercondyloid) fossae form a deep excavation in the proximal end of the shaft. These fossae are deeply developed in some fossil musteloids (Savage, 1957 ; Berta and Morgan, 1985), *Enaliarctos* spp. (Berta and Ray, 1990 ; Berta, 1991), and phocine phocids (King, 1983), whereas these are shallow in most terrestrial arctoids and most otariids (Berta and Ray, 1990). The medial malleoulus is well developed as a strong distal projection at the distal end.

The fibula (MFM 180113,180121 ; Table 6, Pl. 43, 1-2,5-6). —The fibula is also

Table 6. Measurements (in mm) of some postcranial bones of Enaliarctine species A, provisionally referred specimens. Parentheses indicate measurements of portions as preserved.

	MFM 180111	MFM 180121	MFM 180110	MFM 180113
Pelvis				
Greatest length	(283.9)	--	228.7	(148.4)
Ilium-acetabulum length	(91.5)	--	68.5	48.0
Acetabulum-ischium length	(166.4)	--	135.5	79.6
Femur				
Greatest length	--	--	101.4	(69.8)
Proximal width	--	--	51.8	(37.1)
Least width	--	--	25.5	18.5
Distal width	(60.0)	--	49.4	(36.5)
Tibia				
Greatest length	--	--	--	(123.3)
Proximal width	--	--	44.0	(34.0)
Distal width	--	51.2	--	(25.9)
Fibula				
Greatest length	--	30.4	--	(115.7)
Proximal width	--	54.5	--	--
Distal width	--	40.1	--	(20.0)
Astragalus				
Greatest length	--	66.2	47.2e	--
Greatest width	--	51.8	--	--

long and slender. On the distal end, the lateral malleolus displays a well-defined rounded keel, the processus lateralis fibulae, like that of *Enaliarctos* spp. (Berta and Ray, 1990 ; Berta, 1991). This feature is lacking in most otariids but is present in terrestrial arctoids and phocines.

Tarsus and Pes (MFM 180105,180106,180108,180109,180110,180111,180119,180121 ; Table 6, Pl. 43, Figs. 7-18).

Astragalus (MFM 180110,180121 ; Pl. 43, Figs. 7-12). —The astragalus is relatively slender. The posterior process is well developed and projected posteriorly as in species of imagotariines, odobenines, and in *Enaliarctos mealsi* (USNM 374272, pers. observ.). The astragalus of MFM 180110 (Okazaki, 1977 : pl. 3, fig. 6) is approximately 29 percent smaller than that of MFM 180121, further indication of sexual dimorphism in the sample.

Cuboid (MFM 180105,180106 ; Kamei and Okazaki, 1974 : pl. 95, figs. 1 a-c ; Okazaki, 1977 : pl. 3, figs. 3 a-b) —The cuboid is rectangular in shape and has large, broad proximal and distal articular facets.

Navicular (MFM 180123 ; Pl. 43, Figs. 13-14). —The navicular is dorsoventrally deep. The proximal surface is concave, ovoid in shape, and articulates with the head of the astragalus.

Metatarsal (MFM 180101,180103,180105,180111,180123). —The metatarsal I (Pl. 9, Figs. 15-18), II (Kamei and Okazaki, 1974 : pl. 95, fig. 3 ; Okazaki, 1977 : pl. 3, fig. 4), IV (Kamei and Okazaki, 1974 : pl. 95, fig. 2), and V (Okazaki, 1977 : pl. 3, figs. 2 and 5) are known for this species. Each metatarsal is long and round in cross section, and

bears a keeled trochlea at the distal end. The shaft of metatarsal I is curved dorsally, a feature that is not typical among the otariids, but is seen in some phocids.

Phalanges (MFM 180111, 180112, 180123). —The phalanges are broad and flat with expanded ends, as is characteristic of all pinnipeds.

Discussion

Enaliarctine species A is apparently a member of the most primitive otariid subfamily, Enaliarctinae, a group which have been previously known only from the eastern North Pacefic Ocean in rocks ranging from Late Oligocene to early Middle Miocene age. The taxon is, therefore, the first record of the subfamily from the western North Pacific. It is based on some cranial fragments, denataries, and provisionally referred postcranial elements from the Yamanouchi Member and Kujiri fasies (equivalent to the Togari and Yamanouchi members) of the Akeyo Formation, approximately between 17.5 and 17 million years old. The primitive characters that Enaliarctine species A shares with previously known enaliarctines are: P^4 with a lingual protocone shelf; M_1 with a well developed paraconid, protoconid, and metaconid on the trigonid and a hypoconid on the talonid; dorsoventrally slender dentary with a dorsally positioned condyloid process; femur with a well developed pit on the head for the teres femoris ligament; fibula with a well-defined processus lateralis fibulae; and six lumbar vertebrae.

In comparison with previously known enaliarctines, Enaliarctine species A has much larger and dorsoventrally deeper dentary with higher positioned condyloid process, a different type of bifid crown on the I^1 and I^2, and the P^4 with a relatively large sized cuspules on the more prominent lingual cingulum. These features of Enaliarctine species A can be interpreted as being derived states for the Enaliarctinae. Therefore, the mandibular and tooth morphologies of Enaliarctine species A are more derived than, and are differentiated from those of any other known member of the subfamily Enaliarctinae. However, I refrain from applying a name to this undetermined enaliarctine due to the scarcity of the cranial material among the available specimens. In fact, the dentaries of the most species of the Enaliarctinae are not yet sufficiently known in the published materials at the present time to differentiate this spesies. Any discussion of the classification and relationships of Enaliarctine species A among the species of the Enaliarctinae will be more meaningful when more sufficient cranial material of the former is known.

Although the mandibular and dental features of Enaliarctine species A mentioned above are primitive and generalized among the otariid pinnipeds, its postcranial osteology is relatively specialized. Indeed, the fossil pinnipeds from the Akeyo Formation had previously been assigned to the primitive imagotariine genus *Neotherium* Kellogg, 1931 (Okazaki, 1982 ; Kohno, 1990) within the subfamily Imagotariinae on the basis of its postcranial similarities to the latter species, especially the similarities of the proportion and shape of the astragalus (Kohno, 1990). The astragalus from the Akeyo Formation has a relatively well developed calcaneal process, the character which has been interpreted as diagnostic for the Imagotariinae and Odobeninae (Wyss, 1987 ; Berta and Ray, 1991 ;

Berta, 1991). In addition to this character, Enaliarctine species A has some more imagotariine-like or odobenine-like features in its postcranial elements such as a sacrum that consists of four vertebrae, and lumbar vertevrae with very long and anteroventrally projecting transverse processes. In this respect, Enaliarctine species A might have represented a late adaptive radiation of an enaliarctine lineage leading to the origin of the Imagotariinae and their relatives including modern walreses, and the lineage might have already been differentiated from other enaliarctine lineages leading to other subfamilies by late Early Miocene time or much earlier. However, more detailed investigation of the cranial and postcranial osteology is needed before any judgement on the phylogenetic position of this animal can be made, and such work will be carried out in detail in a subsequent paper (Kohno, in prep.).

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PLATES 35-43

Plate 35

Figs. 1-20. Enaliarctine species A from the late Early Miocene Yamanouchi Member of the Akeyo Formation, MFM locality 54.

1-3. Skull fragments, MFM 180113, × 0.7.

1. Dorsal view.
2. Posterior view.
3. Ventral view.

4-6. Left upper second incisor, MFM 180120, × 1.4.

7-9. Right upper second incisor, MFM 180120, × 1.4.

10-12. Right upper third incisor, MFM 180120, × 1.4.

4, 7, 10. Lateral view.
5, 8, 11. Medial view.
6, 9, 12. Lingual view.

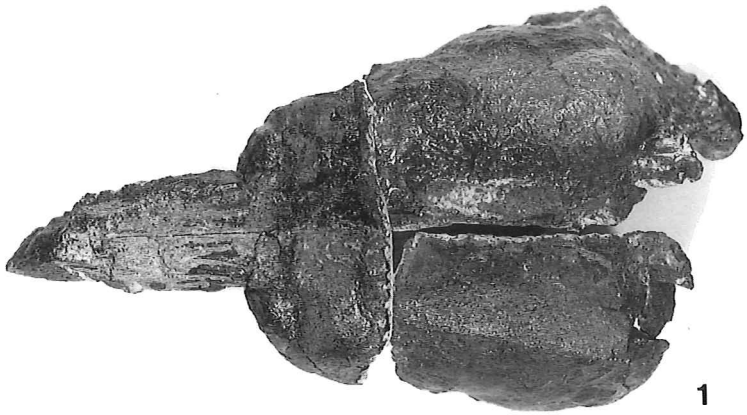
13-15. Right upper second premolar, MFM 180120, × 1.4.

16-18. Left upper fourth premolar, MFM 180113, × 1.4.

13, 16. Buccal view.
14, 17. Lingual view.
15, 18. Occlusal view.

19, 20. Keratohyoid, MFM 180120, × 1.4.

19. Lateral view.
20. Medial view.


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Plate 36

Figs. 1-4. Enaliarctine species A, referred male, MFM 180120 from MFM locality 54, × 0.7.

1, 2. Left dentary

1. Lateral view.
2. Medial view.

3, 4. Right dentary

3. Medial view.
4. Lateral view.

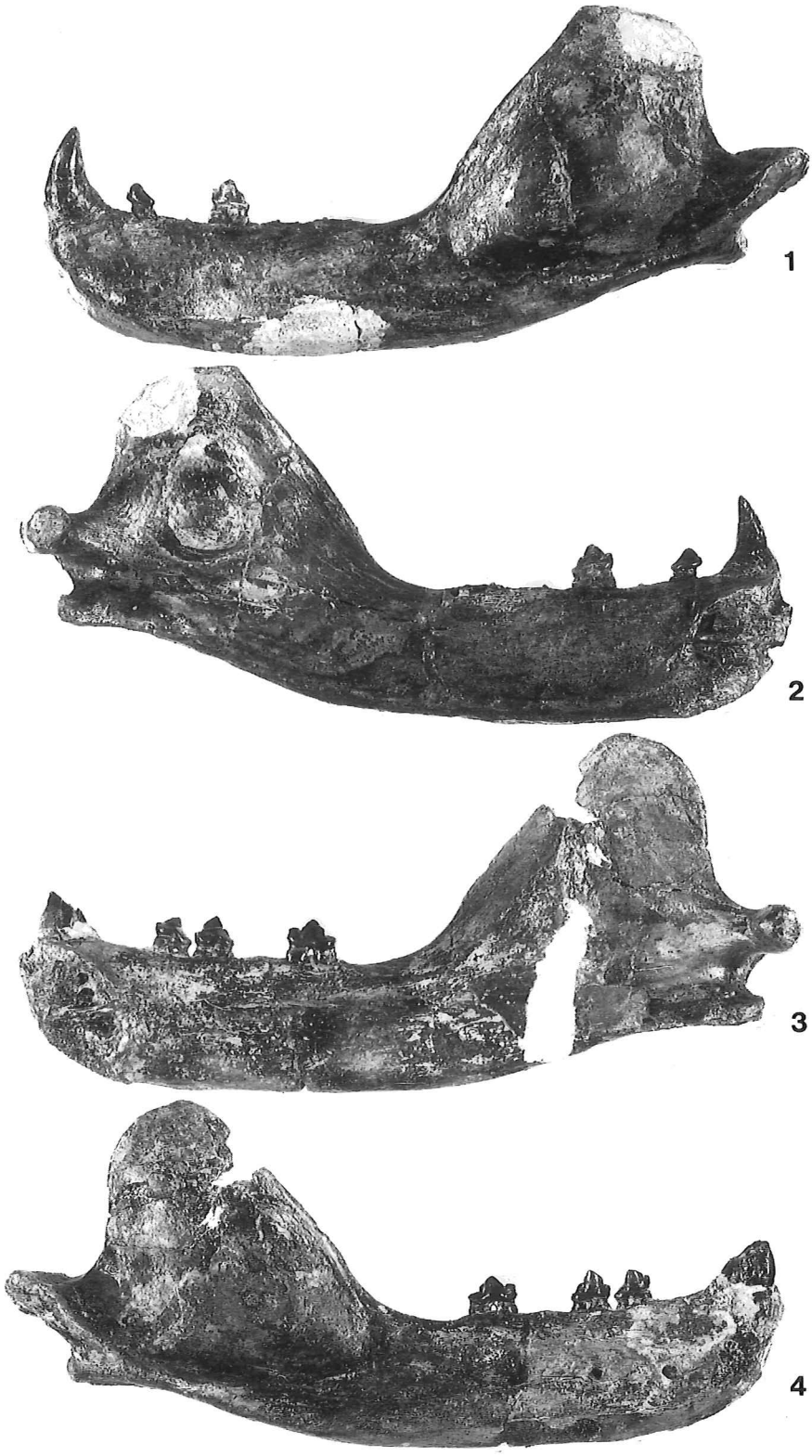

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Plate 37

Figs. 1-3. Enaliarctine species A, referred male, MFM 180120 from MFM locality 54.

1. Occlusal view of left and right dentary, × 0.7.
2. Stereophotograph of tooth row of left dentary, × 1.4.
3. Stereophotograph of tooth row of right dentary, × 1.4.



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Plate 38

Figs. 1-4. Enaliarctine species A, referred male, MFM 180116 from MFM locality 54, × 0.7.

1, 2. Left dentary

1. Lateral view.
2. Medial view.

3, 4. Right dentary

3. Medial view.
4. Lateral view.


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Plate 39

Figs. 1. Enaliarctine species A, referred male, MFM 180116 from MFM locality 54.

1. Left and Right dentary, occlusal view, × 0.7.

2-5. Left dentary, MFM 180115 from Kohazama, Akeyo-cho, Mizunami City.

2. Lateral view, × 0.7.

3. Medial view, × 0.7.

4. Occlusal view, × 0.7.

5. Stereophotograph of occlusal view, × 1.4.

6, 7. Left lower first premolar, MFM 180118 from MFM locality 54.

6. Buccal view, × 1.4.

7. Lingual view, × 1.4.



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Plate 40

Figs. 1-8. Enaliarctine species A from MFM locality 54, × 0.7.

1-4. Atlas, MFM 180120.

5-8. Atlas, MFM 180113.

1, 5. Dorsal view.

2, 6. Ventral view.

3, 7. Anterior view.

4. Left lateral view.

8. Right lateral view.



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Plate 41

Figs. 1-9. Provisionally referred Enaliarctine species A, × 0.35.

1-4. Vertebral column, thirteenth and fourteenth thoracics, and first lumbar (figs. 1, 3), and third, fourth, fifth, sixth lumbars, and anterior fragment of sacrum (figs. 2, 4), referred male, MFM 180109 from MFM locality 49.

1, 2. Dorsal view.

3, 4. Left lateral view.

5, 6. Sacrum, referred male, MFM 180111 from MFM locality 54.

5. Dorsal view.

6. Left lateral view.

7, 8. Sacrum, referred female, MFM 180110 from MFM locality 54.

7. Dorsal view.

8. Right lateral view.

9. Caudal vertebra, MFM 180111 from MFM locality 54, dorsal view.

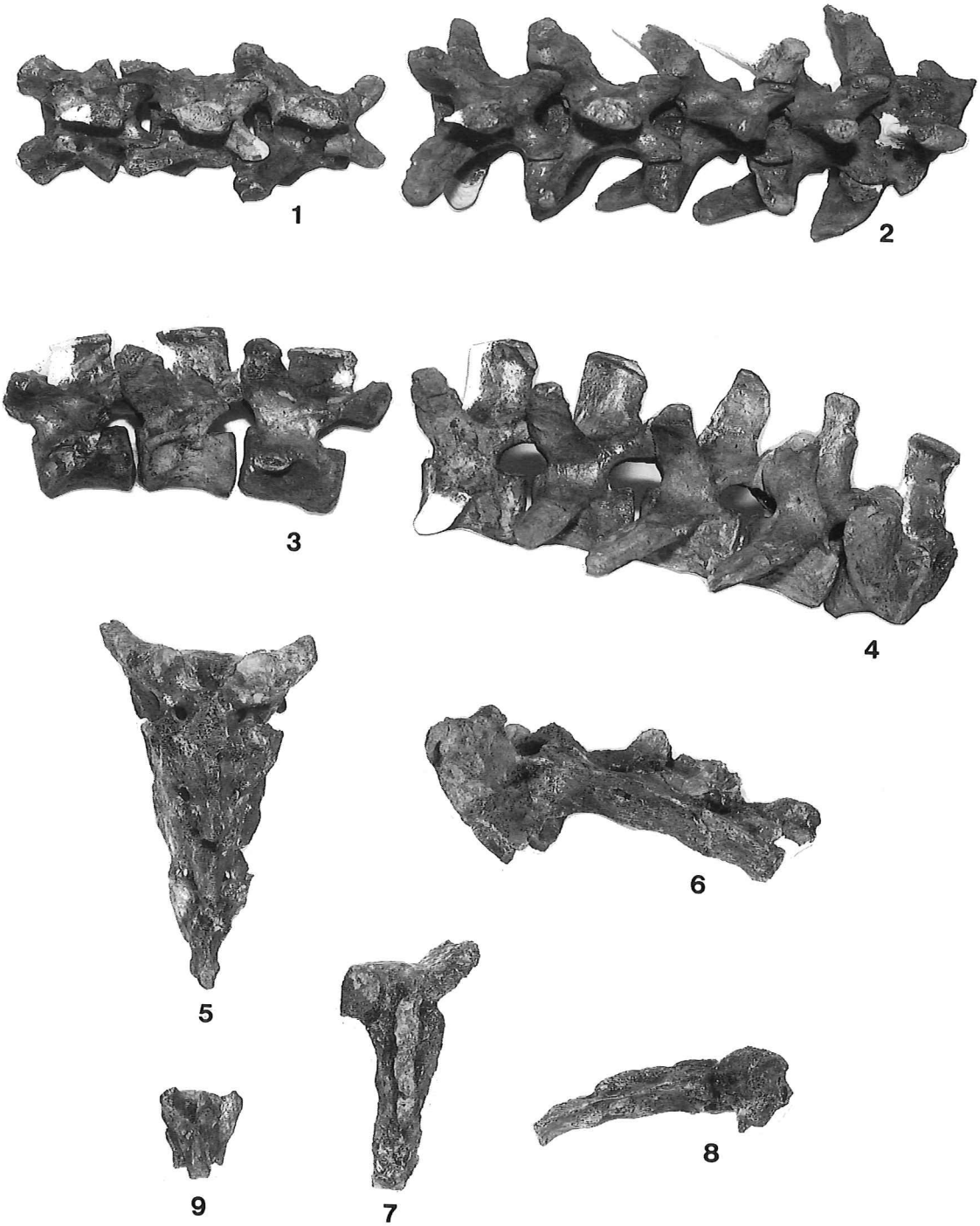

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Plate 42

Figs. 1-9. Provisionally referred Enaliarctine species A from MFM locality 54, × 0.35.

1-3. Left innominates, left lateral views.

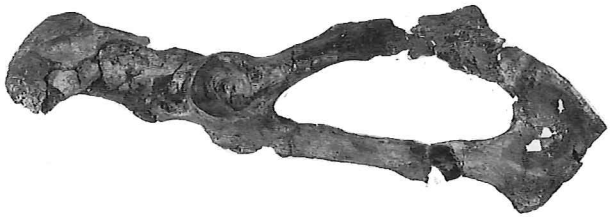
1. Referred male, MFM 180111.
2. Referred female, MFM 180110.
3. Immature individual, MFM 180113.

4-9. Femora.

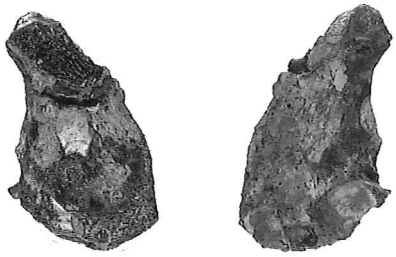
4, 5. Right femur, referred male, MFM 180111.
6, 7. Left femur, referred female, MFM 180110.
8, 9. Right femur, immature individual, MFM 180113.
4, 6, 8. Anterior views.
5, 7, 9. Posterior views.



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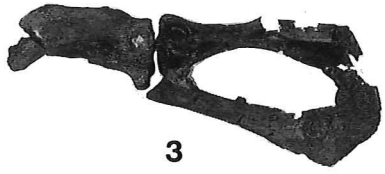


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Plate 43

Figs. 1-17. Provisionally referred Enaliarctine species A, × 0.35.

1-6. Left tibiae and fibulae.

1, 2. Referred male, MFM 180121 from Kohazama, Akiyo-cho, Mizunami City.

3, 4. Referred female, MFM 180110 from MFM locality 54.

5, 6. Immature individual, MFM 180113 from MFM locality 54.

7. Right astragalus, referred male, MFM 180121 from Kohazama, Akeyo-cho, Mizunami City.

7. Dorsal view.

8. Ventral view.

9. Distal view.

10. Proximal view.

11. Lateral view.

12. Medial view.

13, 14. Right navicular, referred male, MFM 180121 from Kohazama, Akeyo-cho, Mizunami City.

13. Proximal view.

14. Distal view.

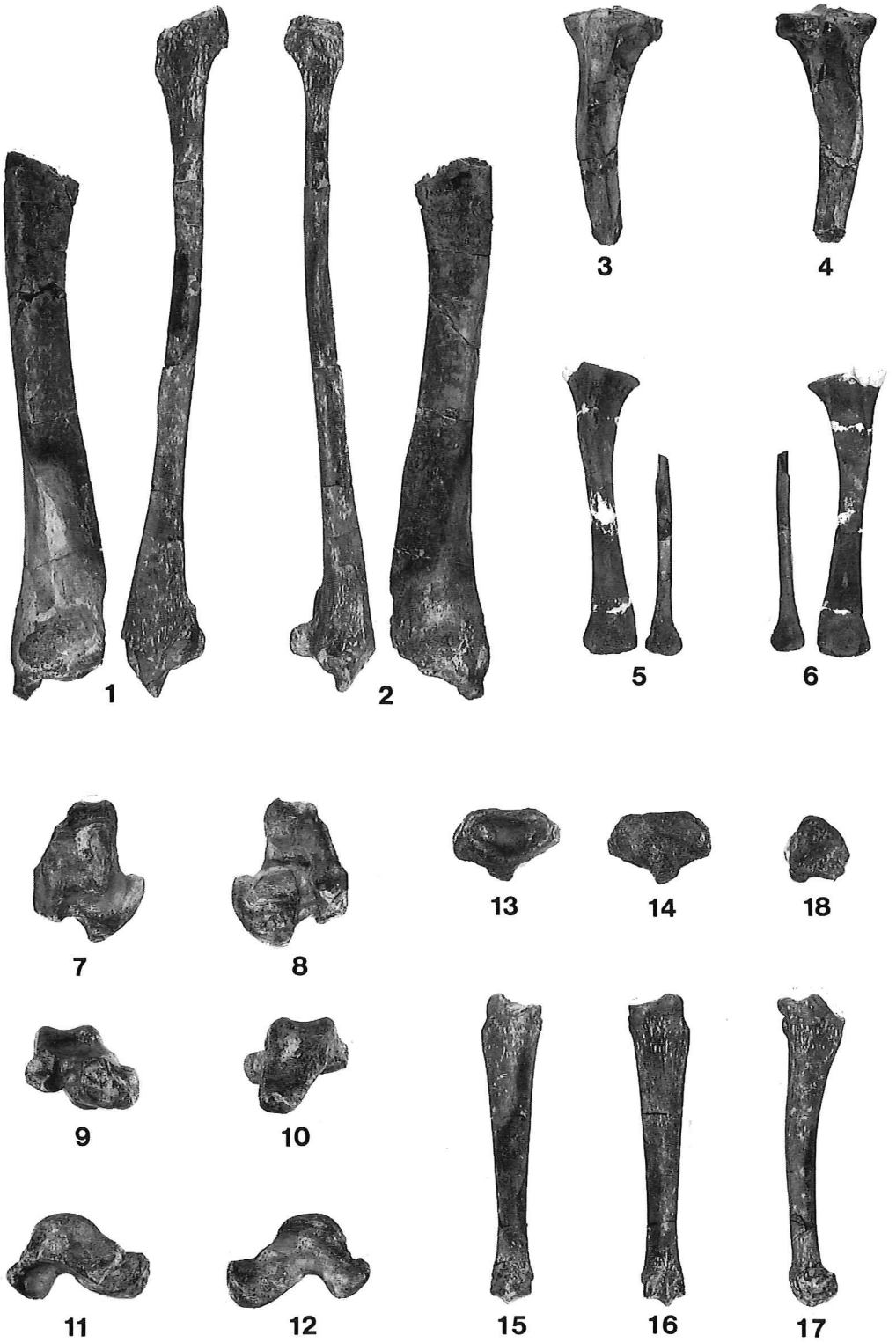
15-18. Left first metatarsal, referred male, MFM 180121 from Kohazama, Akiyo-cho, Mizunami City.

15. Dorsal view.

16. Ventral view.

17. Lateral view.

18. Proximal view.


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