

Pliocene Tusked Odobenids (Mammalia: Carnivora)
in the Western North Pacific, and
Their Paleobiogeography

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Abstract Four fossil tusks belonging to the tribe Odobenini DEMÉRÉ, 1994b, in the subfamily Odobeninae of the family Odobenidae, are described from Pliocene rocks in Japan. The previous hypothesis, that the tusked walrus originated in the North Atlantic in the latest Miocene and that the Recent walrus genus *Odobenus* evolved in the North Atlantic and entered into the North Pacific via the Arctic Ocean in the Middle Pleistocene, are revised on the basis of the succession of occurrences of the tusked odobenids in the North Pacific from Late Miocene until Recent time. It suggests that the tusked odobenids might have evolved in the North Pacific Ocean during the late Late Miocene and never disappeared from the North Pacific. Likewise, the genus *Odobenus* might have originated in the North Pacific and immediately spread out into the North Atlantic through the Arctic Ocean during the Late Pliocene on the basis of their earlier records in the North Pacific.

Introduction

The modern walrus is a highly evolved and aberrant, Holarctic, fin-footed carnivore with curiously elongated, ever-growing, large vertical tusks in its upper jaw. It is classified as the only surviving constituent of the Family Odobenidae ALLEN, 1880, and divided into two subspecies, the Pacific walrus, *Odobenus rosmarus divergens* (ILLIGER, 1815) and the Atlantic walrus, *O. r. rosmarus* (LINNAEUS, 1758). The North Pacific walrus population has been interpreted as an immigrant from the North Atlantic via the Arctic Ocean during Middle Pleistocene times (e.g., REPENNING *et al.*, 1979).

Although REPENNING *et al.* (1979) delineated the origin and paleobiogeography of the Odobenidae in the North Pacific and North Atlantic on the basis of the fossil records of walrus known by the time of their publication, their discus-

sion had been restricted for the most part to the fossil records only from the eastern North Pacific and North Atlantic realm. Consequently, the fossil records in the western North Pacific had remained poorly understood and almost excluded from the discussions in the subsequent papers (see also BARNES *et al.*, 1985). This was due partly to the extreme incompleteness of the available specimens, and partly because of the inaccessibility of the material and literature regarding the fossil odobenids from the western North Pacific (see also TOMIDA, 1989).

Following the reviews of REPENNING and TEDFORD (1977) and REPENNING *et al.* (1979), a number of new fossil tusked odobenids have been discovered from the North Pacific realm (e.g., HASEGAWA & KOHDA, 1987; TOMIDA, 1989;

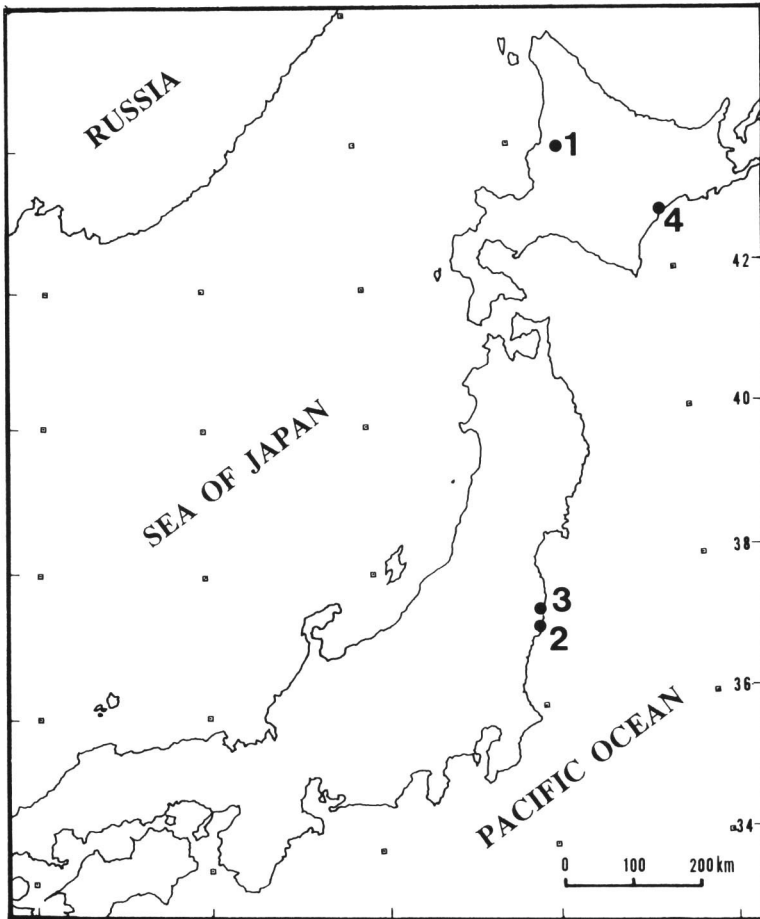


Fig. 1. Index map showing the localities of tusked odobenids described herein. 1, Numata-cho, Uryu-gun, Hokkaido; 2, Yotsukura-cho, Iwaki City, Fukushima; 3, Tomioka-cho, Futaba-gun, Fukushima; 4, Urahor-cho, Tokachi-gun, Hokkaido.

KIMURA & FURUSAWA, 1991; MIYAZAKI *et al.*, 1992; ISHIGURI & KIMURA, 1993; DEMERE, 1994a). An attempt to determine the precise taxonomic affinities and geologic ages of these material might immediately produce some interesting systematic and biogeographic results.

In this paper, we describe four fossil tusks belonging to the tribe Odobenini DEMERE, 1994b in the subfamily Odobeninae of the family Odobenidae from Pliocene deposits in Japan (Fig. 1) and re-consider the origin and paleobiogeography of the tusked odobenids in the North Pacific and North Atlantic.

Abbreviations

FM-N	Division of Natural History, Fukushima Museum, Aizuwakamatsu, Fukushima, Japan.
HMH	Historical Museum of Hokkaido, Sapporo, Hokkaido, Japan.
KCM	Kushiro City Museum, Kushiro, Hokkaido, Japan.
LACM	Vertebrate Paleontology Section, Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A.
NFL	Numata Fossil Laboratory, Numata-cho, Hokkaido, Japan.
NMJH	National Museum of Japanese History, Sakura, Chiba, Japan.
NSM-PV	Division of Vertebrate Paleontology, National Science Museum, Tokyo, Japan.
SDSNH	Department of Paleontology, San Diego Natural History Museum, San Diego, California, U.S.A.
TPM	Tottori Prefectural Museum, Tottori, Japan.
USNM	Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D. C., U.S.A.
WUHH	Waseda University Honjo Senior High School, Honjo, Saitama, Japan.
YWSM	Wakkanai Science Museum for the Youth, Wakkanai, Hokkaido, Japan.

Systematic Paleontology

Class Mammalia LINNAEUS, 1758

Order Carnivora BOWDICH, 1821

Suborder Caniformia KRETZOI, 1945

Infraorder Arctoidea FLOWER, 1869

Unranked Pinnipedia (ILLIGER, 1811) BERTA *et al.*, 1989

Family Odobenidae ALLEN, 1880

Subfamily Odobeninae (ALLEN, 1880) ORLOV, 1931

Tribe Odobenini DEMÉRÉ, 1994b

Odobenini DEMÉRÉ, 1994b, p. 117

Emended diagnosis: Distinguished from other odobenines by having the following derived characters: external narial opening elevated above the incisive margin, palate arched transversely and longitudinally, palatine telescoped beneath alisphenoid, zygomatic portion of squamosal blunt and thick, orbital vacuity posteriorly placed, optic foramen funnel-shaped, temporal fossa shortened, mastoid processes as widest part of cranium, upper canine elongated to be ever-growing tusk with globular osteodentine filling vacated pulp cavity, lower canine reduced to be molariform, postcanine tooth crowns lacking enamel in adult stage, deltoid tubercle of humerus located on lateral edge of deltopectoral crest. For other postcranial diagnosis see DEMÉRÉ (1994b: 117).

Type genus: *Odobenus* BRISSON, 1762.

Included genera: *Odobenus* BRISSON, 1762 (incl. *Trichecodon* LANKESTER, 1865; *Hemicaulodon* COPE, 1869); *Ontocetus* LEIDY, 1859 (*nomen dubium*, see Discussion); *Alachtherium* DU BUS, 1867; *Prorosmarus* BERRY and GREGORY, 1906; *Pliopedia* KELLOGG, 1921 (see DEMÉRÉ, 1994b: 118); *Valenictus* MITCHELL, 1961.

Distribution: Ranges in age from the latest Miocene to Recent in the North Pacific and from the Early Pliocene to Recent in the North Atlantic.

Odobenini gen. et sp. indet.

Fig. 2

Odobenus sp., KIMURA and FURUSAWA, 1990, NQ-5.

Material: NFL 12, left upper canine, two upper premolars, and hyoid fragment of one individual, collected on 3 November 1987 by Tadashi SETO and Toshihiro MATSUBARA.

Locality: Bank of Horonitachibetsu River, Ebishima, Numata-cho (Town), Uryu-gun (County), Hokkaido, Japan.

Formation and age: The specimen was collected from the middle part of the Horokaoshirarika Formation. According to FURUSAWA *et al.* (1993), fission track ages of the two tuffaceous layers (namely "Ops" and "Nt-3" in ascending order) occurring in the middle part of the Horokaoshirarika Formation are 4.5 ± 0.7 Ma and 5.0 ± 0.2 Ma, respectively.

A sample of siltstone extracted from the pulp cavity of the tusk was processed for microfossils by Yoshihiro TANIMURA (NSM) and produced a diatom flora that corresponds to the *Thalassiosira oestrupii* Zone of KOIZUMI (1985) or the upper part of the *Neodenticula kamtschatica* Zone of AKIBA (1985).



Fig. 2. *Odobenini* gen. et sp. indet., NFL 12, from the Horokaoshirarika Formation. A–D, left upper canine (NFL 12-a); E–F, upper premolar (NFL 12-b); G–H, upper premolar (NFL 12-c). A, E, G, medial view; B, F, H, lateral view; C, anterior view; D, cross section of proximal end (anterior is to the left). Scale bar equals 5 cm.

Thus, the geologic age of the middle part of the Horokaoshirarika Formation is estimated to be Early Pliocene, approximately 3.8–5.2 Ma.

Description: The upper canine (NFL 12-a) is large and posteriorly curved in the parasagittal plane, and its axis is slightly twisted anteromedially (counterclockwise torsion) from the proximal to the distal end. The curvature of the tusk in the parasagittal plane is extreme, and the radius of the arc along the posterior margin of the tusk is about 386 mm and along its anterior margin, about 360 mm. Although the proximal portion of the tusk is broken away, the distal end of the tusk is very worn and shows extreme abrasion and breakage that occurred during life. On the lateral surface of the tusk, there are two broad longitudinal grooves, of which anterior one is deeper and wider. There is an additional narrow groove on the posterolateral surface of the tusk. The medial surface of the tusk has one strong longitudinal groove located anterior to the midline.

Internally the tusk is composed of a central column of globular osteodentine, a surrounding ring of dense compact orthodentine, and a thin outer layer of cementum, characteristic of the odobeninine odobenids (RAY, 1960; DEMÉRÉ, 1994a). There is no enamel remaining on the crown. The cementum layer is well preserved for most of the tusk and is thin anterodistally because of wear. The

maximum thickness of the cementum layer is 2.3 mm on the posterior surface of the tusk. The surface of the proximal end of the tusk is smooth because of the thick cementum and is marked by closely spaced transverse striations as alternating weak ridges (averaging approximately 20 mm intervals), indicating annual growth layers. The center of the column represents the vestige of the pulp cavity, indicating that the preserved portion of this tusk include the clinical root near the base of the intra-alveolar portion.

The cheek teeth (NFL 12-b and 12-c) are relatively large and robust, and have no enamel crown. Each tooth is relatively long and gently curved medially in the paratransverse plane indicating that both may be maxillary teeth (COBB, 1933). There are two distinct wear facets on the anterior and posterior sides of the apex of the crown. The anterior wear facet is procumbent and the posterior one is recumbent by occlusion against the lower cheek teeth. NFL 12-b measures 26.2 mm in greatest mesiodistal diameter, 23.0 mm in greatest buccolingual diameter, and 40.3 mm in tooth length as preserved. NFL 12-c measures 20.4 mm in greatest mesiodistal diameter, 22.1 mm in greatest buccolingual diameter, and 40.3 mm in tooth length.

Odobenini gen. et sp. indet.

Fig. 3

Odobenidae gen. et sp. indet., TOKUNAGA, 1934, p. 41.

Odobenus sp., NAORA, 1944, p. 144.

Material: Left (NMJH N-004) and right (WUHH IX-95) upper canines belonging to the same individual; collected by Shigeyasu TOKUNAGA. No date given but prior to 1934. Casts are preserved as NSM-PV 20039.

Locality: According to TOKUNAGA (1934), the tusks were collected from a tuffaceous sandstone deposit at Yotsukura-cho, Iwaki City, Fukushima Prefecture, Japan.

Formation and age: The formation which outcrops in the vicinity of Yotsukura Town is the Yotsukura Formation (MITSUI *et al.*, 1973). Based on diatom and radiolarian biostratigraphy, the age of the Yotsukura Formation is estimated to be Early Pliocene, approximately 3.7–4.7 Ma (TAKAYANAGI *et al.*, 1988). A sample of siltstone adhering to the right tusk was processed for microfossils by Y. Tanimura (NSM) and produced a diatom flora which corresponds to the *Thalassiosira oestrupii* Zone of KOIZUMI (1985) or the upper part of the *Neodenticula kamtschatica* Zone of AKIBA (1985), which is identical with the estimated age of the Yotsukura Formation.

Description: Two upper canine fragments belonging to the same individual were briefly mentioned by TOKUNAGA (1934), and the left one was later il-

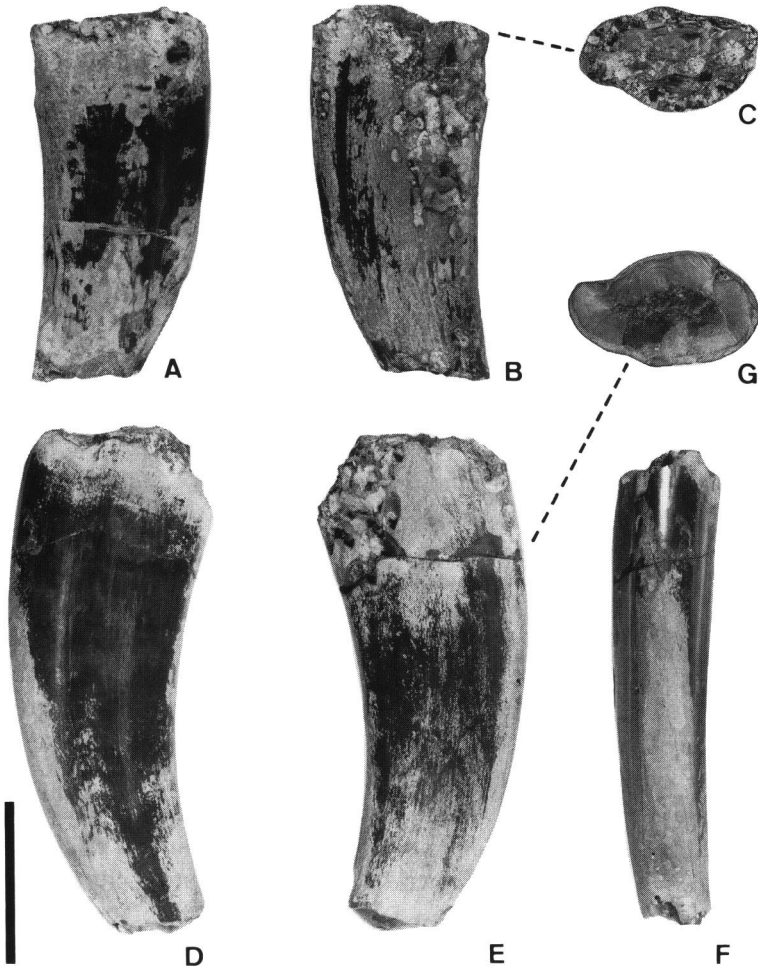


Fig. 3. *Odobenini* gen. et sp. indet., from the Yotsukura Formation. A-C, right canine (WUHH IX-95); D-G, left canine (NMJH N-004). A, D, lateral view; B, E, medial view; F, anterior view; C, G, cross section of proximal part. Anterior is to the left in each section. Scale bar equals 5 cm.

illustrated by NAORA (1944: 96). Each specimen consists of the anterior tip of an enlarged tusk. The proximal end of each one was penetrated by some marine organisms during or prior to fossilization. The curvature of each tusk in the parasagittal plane is relatively extreme, and this curvature is enhanced by the wear on the anterodistal surface of the tusk. Radii of the arc along the posterior and anterior margins of the left tusk are 165 and 125 mm, respectively. There are two shallow longitudinal grooves on the relatively flattened lateral surface of each tusk. The anterior one is prominent, but the posterior one is shallow

and indistinct at the mid-portion of the tusk. On the convex medial side there is one longitudinal groove anterior to the midline. It diminishes in depth distally and disappears at the distal end of the tusk, due to strong anterolateral wear (Fig. 2-D).

The surfaces of the tusks are surrounded by a thin layer of cementum and are marked by closely spaced transverse striations as alternating weak ridges (averaging approximately 20 mm intervals), indicating annual growth layers. This surface is smooth, glossy, and are well preserved on the left tusk, but it is exfoliated on most of the right tusk, perhaps due in part to postmortem corrosion. In the well preserved left tusk, the cementum layer is worn away anterolaterally, and the central column of the globular osteodentine is exposed externally at the anterodistal tip of the tusk.

Odobenini gen. et sp. indet.

Fig. 4

cf. *Hemicaulodon effodiens* Cope, 1869, HASEGAWA and KOHDA, 1988, p. 85.

Material: FM-N 9600001, right upper canine, collected in 1955 by Hideo HASHIMOTO.

Locality: Makabe, Shimokohriyama, Tomioka-cho, Futaba-gun, Fukushima Prefecture, Japan.

Formation and age: Although HASEGAWA and KOHDA (1988) did not reveal the formation that produced the specimen, the formation which outcrops in the area of the locality is the Tomioka Formation (YANAGISAWA *et al.*, 1989). According to HASEGAWA and KOHDA (1988), the diatom flora from matrix adhering to the tusk corresponds to the *Denticulopsis seminae* var. *fossilis-D. kamtschatica* Concurrent Range Zone of AKIBA (1985), which is indicative of late Early to early Late Pliocene age, and approximately between 2.7 and 3.8 Ma (BARRON & GLADENKOV, in press).

Description: The specimen, preliminarily reported by HASEGAWA and KOHDA (1987), is a very large, posteriorly curved tusk with a very slight clockwise torsion of the axis from the proximal to the distal end. It measures 460 mm along its posterior margin. The curvature of the tusk in the parasagittal plane is rather strong and the radius of the arc along the posterior margin of the tusk is about 509 mm and its anterior margin is about 469 mm. There are two broad longitudinal grooves on the lateral surface and one longitudinal groove on the relatively flattened medial surface, extending nearly to the distal end of the tusk, although the intervening ridge on the lateral surface of the proximal half of the tusk is badly broken. There is an additional shallow groove on the anterior surface only at the intralveolar region of the tusk.

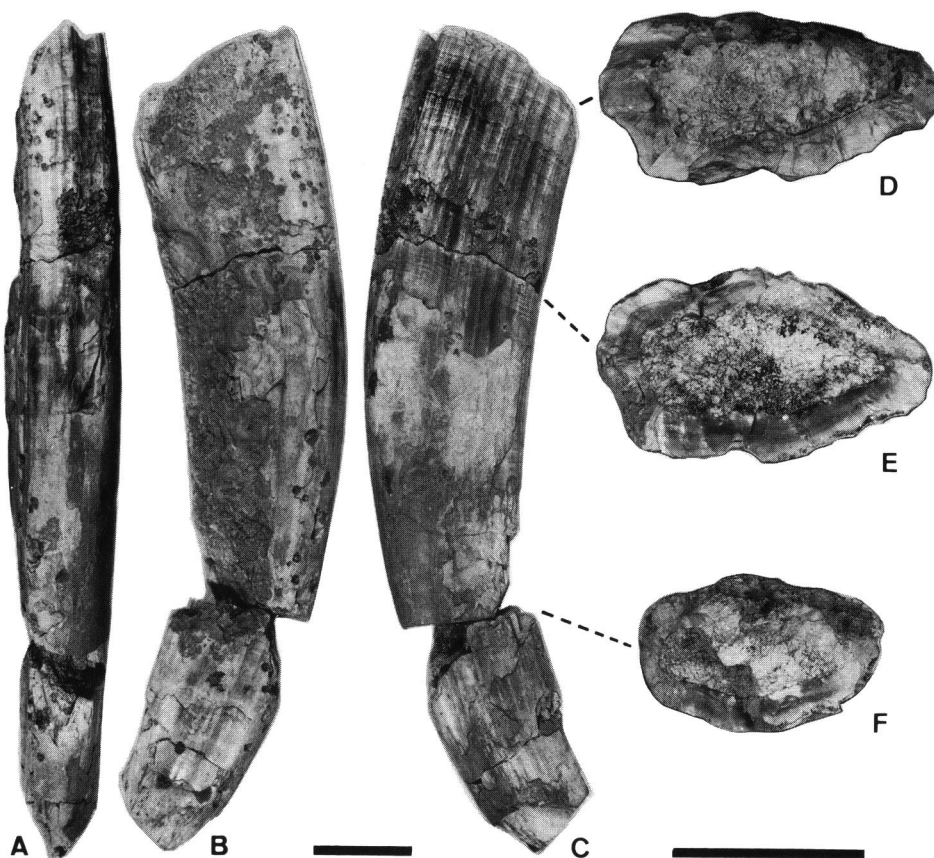


Fig. 4. *Odobenini* gen. et sp. indet., from the Tomioka Formation, right upper canine (FM-N 9600001). A, anterior view; B, lateral view; C, medial view; D, cross section of proximal part; E, cross section of middle part; F, cross section of distal part. Anterior is to the left in each section. Scale bars equal 5 cm.

The cementum layer is well preserved for the most part on the medial surface but almost exfoliated on the posterolateral surface of the tusk. The maximum thickness of the cementum layer is 2.4 mm measured in the anterior groove on the lateral side of the tusk. It thins toward the anterodistal edge, because of wear, and the thickness of the cementum layer is less than 0.2 mm on the tip of the crown as preserved. On the proximal 122 mm of the tusk, probably the intralveolar portion, the surface of the cementum layer is marked by a number of closely spaced transverse striations as alternating strong and weak ridges, indicating annual and/or seasonal growth layers. Although the rim of the pulp cavity is broken away, the proximal end of the tusk is occupied by globular osteodentine and shows no pulp cavity.

Odobenus species indet.

Fig. 5

Odobenus sp., SASA and OKAZAKI, 1967, p. 181.

Material: KCM unnumbered, right upper canine; collected by Katsuo YOKOTA, date unknown but pre-1967. A cast is preserved as NSM-PV 20041.

Locality: Sea cliff near Chokubetsu, Urahor-cho, Tokachi-gun, Hokkaido, Japan.

Formation and age: The Urahor specimen was collected from the middle part of the Shiranuka Formation (SASA & OKAZAKI, 1967). A sample from the matrix enclosing the tusk was processed for microfossils by Y. TANIMURA (NSM) and produced a diatom flora that corresponds to the *Neodenticula koizumii* Zone of AKIBA (1985). Thus, the age of the fossil is estimated to be Late Pliocene, approximately 2.0–2.7 Ma (BARRON & GLADENKOV, in press).

Description: The specimen, preliminarily reported by SASA and OKAZAKI (1967), is an extremely elongated, nearly straight tusk. There exists a slight clockwise torsion of the axis of the tusk from the proximal to the distal end. The tusk is so nearly straight that the radius of the arc along both the posterior and anterior margins of the tusk in the parasagittal plane is more than 999 mm. The distal half of the tusk is badly broken, and the medial side of the natural surface is nearly totally exfoliated. Although both the proximal and distal ends are broken away, it extends 570 mm in length as preserved, and is estimated to have originally extended more than 700 mm from the alveolar margin. At the proximal end, it measures 104.6 mm anteroposteriorly by 63.4 mm transversely in cross section. On the lateral surface of the tusk, there are two shallow, broad, longitudinal grooves, of which the anterior one is more prominent. An additional narrower groove is present on the posterolateral surface of the tusk. These grooves decrease in depth distally and disappear at a point approximately 150 mm from the preserved distal end. On the medial surface of the tusk, there is one shallow, broad, longitudinal groove at the midline on the surface.

The outer cementum layer is well-preserved, and thins distally because of wear. The maximum thickness of cementum in the medial groove on the tusk is 2.8 mm and that on the intervening ridges on the tusk is 2.1 mm. At the proximal portion of the tusk (probably still clinical crown portion), the surface of the orthodontine, which is exposed by exfoliation of the cementum layer, is marked by a number of closely spaced transverse striations indicating annual and/or seasonal growth layers. The central core of the fractured proximal end of the tusk is filled completely by globular osteodontine and has no pulp cavity.

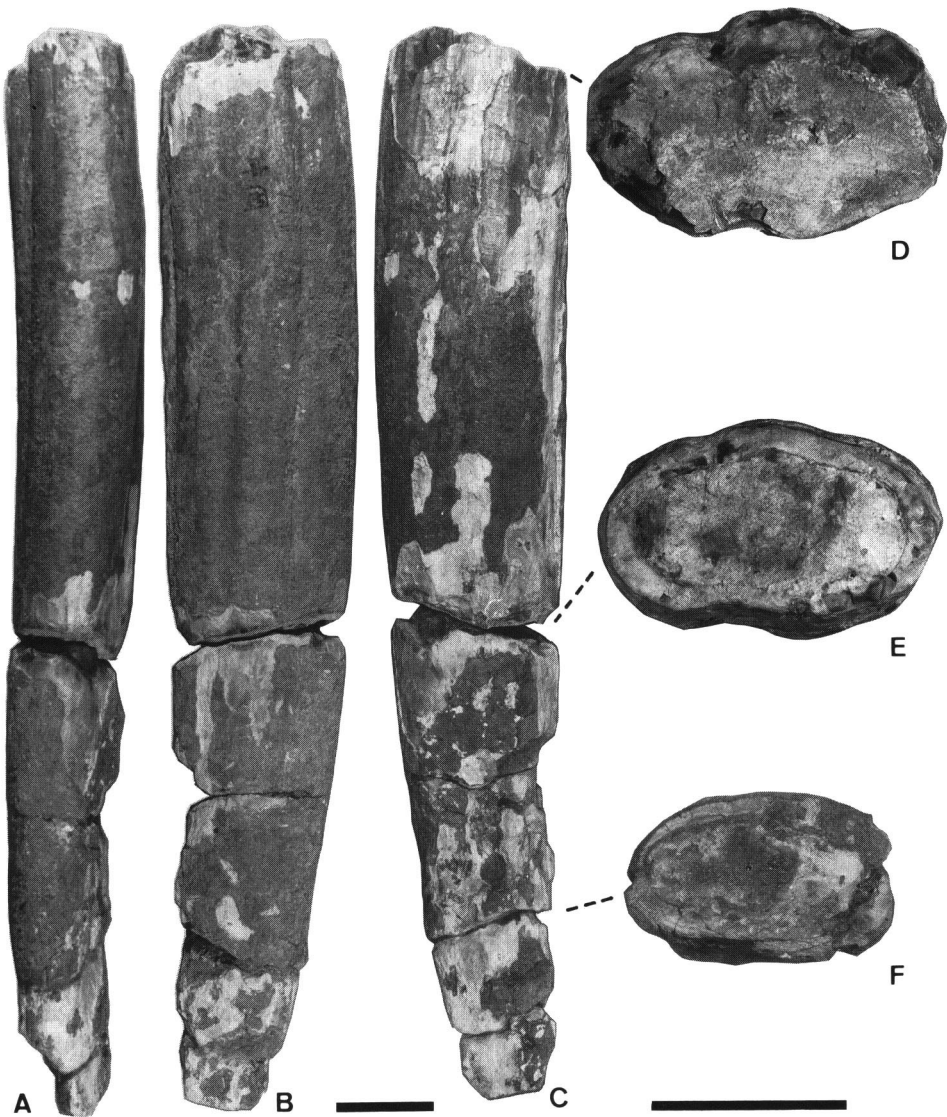


Fig. 5. *Odobenus* species indet., from the Shiranuka Formation, right upper canine (KCM un-numbered). A, anterior view; B, lateral view; C, medial view; D, cross section of proximal end; E, cross section of middle part; F, cross section of distal part. Anterior is to the left in each section. Scale bars equal 5 cm.

Discussion

The general structure and proportion, especially the well-developed central column of globular osteodentine in the tusks described herein agree with the

upper canines of the tusked walruses of the tribe Odobenini of DEMÉRÉ (1994b), and consequently preclude an identification of these tusks as other taxa having elongated tusks without globular osteodentine, such as some dusignathine odobenids (e.g., *Gomphotaria* BARNES and RASCHKE, 1991), cetaceans (e.g., *Odobenocetops* DE MUIZON, 1993), or proboscideans. In addition, the direct comparison of these Pliocene tusks with that of the Recent walrus, *Odobenus rosmarus* (LINNAEUS, 1758), clearly shows the significant differences between the two, and therefore, detract also from the assignment of the tusks to that of *O. rosmarus*. Such differences seen in the Japanese Pliocene tusks (except for KCM specimen) include greater robustness (greatest anteroposterior diameter more than 95 mm), greater curvature (radii of curvature less than 510 mm), greater lateral compression (ratios of transverse to anteroposterior diameters 0.58–0.61), stronger and deeper longitudinal surface fluting, and thinner cementum (less than 2.8 mm).

The Late Pliocene eastern North Pacific “edentulous” walrus, *Valenictus chulavistensis* DEMÉRÉ, 1994a, also has strongly curved upper canines, but it seems to be discernible from the Japanese Pliocene tusks in its smaller size (greatest anteroposterior diameter up to 81 mm) and weaker longitudinal grooves on both lateral and medial surfaces of the tusk. It is also distinguishable from at least NFL 12 in lacking the cheek teeth.

The characters seen in the Japanese Pliocene tusks mentioned above are previously recognized for the tusks of the Pliocene North Atlantic walruses, *Prorosmarus alleni* (REPENNING & TEDFORD, 1977; C. E. RAY, oral communication in 1992), *Alachtherium cretsii* (HASSE, 1908; EEDBRINK & VAN BREE, 1990), and Plio-Pleistocene Atlantic walrus, *Odobenus huxleyi* (LANKESTER, 1880; RAY, 1960; ERDBRINK & VAN BREE, 1986). However, variations of tusks of those named species are not sufficiently known (REPENNING & TEDFORD, 1977), and no one character listed above can be regarded as absolutely diagnostic for those species as has already been pointed out by several authors (e.g., RAY, 1960; REPENNING & TEDFORD, 1977; MIYAZAKI *et al.*, 1992). In most respects, therefore, although the Pliocene walrus tusks in Japan may be assigned to an extinct form, which might be previously known from the Pliocene and Pleistocene of the North Atlantic realm, they should be regarded only as Odobenini, genus and species indeterminate.

In the case of the huge tusk from the Late Pliocene Shiranuka Formation (KCM specimen), it has almost the same character combination as in Early Pliocene tusks mentioned above (see also Table 1), which include very robust form (greatest anteroposterior diameter more than 100 mm), strong lateral compression (ratio of transverse to anteroposterior diameters 0.61), prominent longitudinal surface fluting, and thin cementum (2.8 mm). However, its straightened proportion (radius of arc more than 999 mm) seems to exceed the variation of tusk curvature of the Pliocene North Atlantic extinct genera (i.e., *Prorosmarus*

Table 1. Measurements (in mm) of the Pliocene odobenine tusks described herein. (L) and (R) indicate left and right canines of the same individual.

Specimen	NFL 12	NMJH N-004 (L)	WUHH IX-95 (R)	FM-N 9600001	KCM unnumbered
Total length, arc of anterior surface	220 [†]	180 [†]	125 [†]	460 [†]	580 [†]
Total length arc of posterior surface	—	150 [†]	115 [†]	380 [†]	555 [†]
Length, tangent of arc of lateral midline	200 [†]	164 [†]	114 [†]	376 [†]	550 [†]
Radius of curvature, anterior surface	360*	160*	125*	469*	999<
Radius of curvature, posterior surface	386*	180*	165*	509*	999<
Greatest anteroposterior diameter	73.9	64.0	58.8	98.3	104.6
Greatest transverse diameter	45.2	36.9	34.4	58.9	63.4
Ratio of transverse to ant-posterior diameters	0.61	0.58	0.58	0.60	0.61
Greatest anteroposterior diameter, osteodentine	46.5	34.1	72.3	72.3	75.3
Greatest transverse diameter, osteodentine	20.1	11.6	30.5	30.5	39.7
Maximum thickness, orthodentine	10.1	14.6	12.1	12.1	14.8
Maximum thickness, cementum	2.3	2.8	2.5	2.4	2.8

“†” indicates measurements that are as preserved. “*” indicates estimated measurements.

and *Alachtherium*) and might be seen only in the genus *Odobenus* (FAY, 1982). Comparisons among the known species in *Odobenus* is, unfortunately, difficult at present because of the incompleteness of specimens: *O. huxleyi* is known only from a few tusks; Middle Pleistocene North Pacific extinct walrus, *O. mandanoensis* TOMIDA, 1989 is known only from the mandibular fragment. Therefore, it is uncertain that the KCM specimen falls within the range of variation in size and robustness of *O. huxleyi* or *O. mandanoensis*. Accordingly, this tusk is best regarded as *Odobenus* species indeterminate.

During the Pliocene and Pleistocene there might have existed more than two species of tusked odobenids in the North Pacific, and certain species might be conspecific or congeneric with the North Atlantic extinct walruses. However, nomenclatural and taxonomic problems surround the Plio-Pleistocene North Atlantic tusked walruses. For instance, *Ontocetus emmonsii* LEIDY, 1859 from “Miocene of North Carolina” which was initially believed to be a sperm whale tooth, is known from a large tusk-like tooth with globular osteodentine, that was later re-identified as a tusk of an extinct walrus by RAY (1975). Although the description of the holotype tusk, now USNM 329064, was given in fact as a minutes in the Proceedings of the Academy of Natural Sciences of Philadelphia by an anonymous reporter, Leidy’s remarks have not included any diagnostic character for his new taxon. According to C. E. RAY (in REPENNING & TEDFORD, 1977: 13), large isolated walrus tusks have been found in the Yorktown Formation which produced the holotype dentary of *Prorosmarus alleni*, and some of those tusks strongly resemble USNM 329064 (personal observation).

This and presumed stratigraphic association as inferred from its locality and age suggest that *O. emmonsii* may be conspecific with *P. alleni*. *Ontocetus emmonsii* is here retained in the Odobenini, but generically and specifically it is a *nomen dubium*. In addition to this, other Plio-Pleistocene walruses in the North Atlantic are also less well known from comparable material with each other as mentioned above. In those respects, the comprehensive description and considerable revision of the taxa in the North Atlantic will be needed before the identification of the North Pacific walrus tusks, a task however is beyond the scope of the present paper.

Biogeographic and Chronologic Distribution

The Pliocene tusked odobenids in Japan described above and other critical fossils recently recovered from the North Pacific realm (e.g., TOMIDA, 1989; MIYAZAKI *et al.*, 1992; DEMÉRÉ, 1994a; HORIKAWA *et al.*, 1994) shed new light on the interpretation of the paleobiogeography of the odobenine odobenids in the North Pacific and North Atlantic, and consequently require some modifications of their hypothesized origin and paleobiogeographic succession as outlined by REPENNING and TEDFORD (1977) and REPENNING *et al.* (1979).

REPENNING and TEDFORD (1977) presumed that the ancestral representative of the lineage leading to the tusked odobenines was primarily subtropical in habit and was represented by *Aivukus cedrosensis*, a non-tusked odobenid from the late Late Miocene (ca. 6–8 Ma) of coastal Mexico. Other lineages within the Odobenidae (i.e., “Imagotariinae” and Dusignathinae) were warm to mild temperate in habit in the mid-latitudes of the North Pacific Ocean, and their southern limits were believed to be northern-most coastal Mexico, approximately 33° North latitude.

The species next to the ancestral subtropic representative of the odobenine odobenids known to REPENNING and TEDFORD (1977) was from the North Atlantic realm, represented by the obviously tusked odobenine, *Prorosmarus alleni*, in the Yorktown Formation (ca. 3.3–4.8 Ma) in Virginia and North Carolina. No other record of tusked walruses was known to them at that time in the North Pacific basin except for the Late Pleistocene record of the genus *Odobenus* from Alaska. This evidence led REPENNING and TEDFORD (1977) and REPENNING *et al.* (1979) to emphasize the following scenario for the evolution and dispersal of the odobenine odobenids: (1) The subtropical or tropical *Aivukus*-like non-tusked walrus in coastal Mexico between 6 and 8 Ma dispersed southward and must have passed through the Central American Seaway into Caribbean waters sometime during the latest Miocene. (2) Subsequently, the “proto-walrus” moved northward with the paleo-Gulf Stream along the coast of North America and evolved to *Prorosmarus* known in Virginia and North

Carolina at about 3.3–4.8 Ma. (3) This primitive walrus was replaced sometime during the Pliocene by its possible direct descendant *Alachtherium* at about 2–4 Ma in the eastern North Atlantic. (4) *Odobenus* also had arisen in the North Atlantic from the *Prorosmarus*-like walrus by Late Pliocene time, probably independently with *Alachtherium*. (5) The Recent walrus *O. rosmarus* in the North Pacific Ocean (i.e., *O. r. divergens*) was, therefore, the “immigrant” that returned from the Atlantic Ocean through the Arctic Ocean sometime in the Middle Pleistocene (ca. 0.6 Ma) after the species adapted for Arctic waters in the Atlantic region.

Although this scenario by REPENNING and TEDFORD (1977) and REPENNING *et al.* (1979) was based on the limited fossil record from the eastern North Pacific and North Atlantic realms, since REPENNING and TEDFORD (1977) and REPENNING *et al.* (1979) had reviewed almost all the fossil records available for them by that time, this hypothesis was widely accepted by many workers (e.g., THENIUS, 1980; KING, 1983; CARROLL, 1988).

A few key points as will be discussed below call this scenario into question. REPENNING and TEDFORD (1977) and REPENNING *et al.* (1979) considered that *Aivukus cedrosensis*, latest Miocene non-tusked odobenine walrus, was the morphologically closest representative to the later tusked walruses. They also considered that after *Aivukus* the odobenine odobenids had disappeared in the North Pacific Ocean during the period between the Pliocene and Pleistocene. These hypotheses were the most important key points to delineate the details (1), (2), (4), and (5) of the scenario summarized above. However, some Pliocene tusked walruses had been reported from Japan by that time (i.e., NAORA, 1944; SASA & OKAZAKI, 1967) when REPENNING *et al.* (1979) reviewed the fossil odobenid records, as has already been pointed out by TOMIDA (1989). In addition to those records, some distinct odobenine odobenids have recently been recovered from the Pliocene deposits of California and Japan (BARNES & PERRY, 1989; MIYAZAKI *et al.*, 1992; DEMÉRÉ, 1994a; HORIKAWA *et al.*, 1994). For this evidence, TOMIDA (1989) and MIYAZAKI *et al.* (1992) suggested that recognition of the genus *Odobenus* in the Late Pliocene and Pleistocene of the western North Pacific demonstrates that *Odobenus* might have come back from the North Atlantic at least by the Late Pliocene or might originate in the North Pacific. DEMÉRÉ (1994a) also mentioned that recognition of the tusked odobenine genus *Valenictus* in Californian Tertiary deposits illustrates that tusked odobenines remained a part of the North Pacific pinniped fauna at least into the Late Pliocene. In this respect, the widely accepted theory of the dispersal and paleobiogeography of the tusked odobenids outlined by REPENNING *et al.* (1979) now should be revised.

As described above, the oldest record of the undoubted tusked walrus in the western North Pacific is an upper canine and cheek teeth (NFL 12) from the

Table 2. The western North Pacific Odobenini with chronostratigraphic controls.

1, KIMURA and FURUSAWA (1990); 2, TOKUNAGA (1934); 3, NAORA (1994);
 4, HASEGAWA and KOHDA (1988); 5, SASA and OKAZAKI (1967);
 6, MIYAZAKI *et al.* (1992); 7, ISHIGURI and KIMURA (1993); 8, TOMIDA (1989);
 9, HASEGAWA (1988); 10, HOSHI and AKAGI (1994); 11, this paper.

Taxa/specimen	Locality	Formation	Age (Ma)	References
Odobenini gen. et sp. indet.				
NFL 12	Numata-cho, Hokkaido	Horokaoshirarika Fm.	3.8–5.2	1, 11
NMJH N-004	Yotsukura-cho, Fukushima	Yotsukura Fm.	3.7–4.7	2, 3, 11
WUHH IX-95				
FM-N 9600001	Tomioka-cho, Fukushima	Tomioka Fm.	2.7–3.5	4, 11
<i>Odobenus</i> spp.				
KCM unnum.	Urahoru-cho, Hokkaido	Shiranuka Fm.	2.0–2.7	5, 11
YWSM 1	Off shore, Sakhalin	Sea bottom	2.0–2.7	6
HMH 125898	Shimonopporo, Hokkaido	Shimonopporo Fm.	ca. 0.7	7
NSM-PV 18911	Mandano, Chiba	Mandano Fm.	ca. 0.5	8
NSM-PV 15157	Bunkyo-ku, Tokyo	Tokyo Fm.	0.1–0.2	9
TPM 1 and 2	Off shore, Shimane	Sea bottom	ca. 0.03	10

Early Pliocene Horokaoshirarika Formation (ca. 3.8–5.2 Ma) in Hokkaido or tusk fragments (NMJH N-004 and WUHH IX-95) from the Early Pliocene Yotsukura Formation (ca. 3.7–4.7 Ma) in Fukushima, and the other fossil records of the Odobenini listed in Table 2 illustrate the continuous existence of the tusked walruses at least in the mid-northern latitudes of the North Pacific realm. In addition to these records, HORIKAWA *et al.* (1994) has reported the “primitive odobenine walrus,” which might be a sister taxon to the tusked walruses, from the Early Pliocene Tamugigawa Formation in Niigata Prefecture, Japan.

Moving to the eastern North Pacific records, the earliest tusked walruses have dated back to the latest Miocene (5–6 Ma) of California (REPENNING & TEDFORD, 1977; DEMÉRÉ, 1994b), and their descendants have been known from the Late Pliocene of southern California (DEMÉRÉ, 1994a). In addition to these records, BARNES and PERRY (1989) have announced another primitive tusked walrus from the Purisima Formation (ca. 3.5–5 Ma) in California.

Therefore, the odobenine odobenids apparently never disappeared in the circum North Pacific during the Pliocene and Pleistocene. Furthermore, the earliest record of the tusked walruses in the North Pacific, *Pliopedia* and *Valenicetus* of approximately 5–6 Ma, is earlier than that of the North Atlantic tusked walrus, *Prorosmarus* of approximately 4.5 Ma (see also Fig. 6).

It would appear that soon after its origin the non-tusked odobenines were replaced quickly by the modernized walruses, having procumbent, tusk-like upper canines with a central column of globular osteodentine. They became dominant in the North Pacific, replacing the predominant “imogatariine” and dusignathine odobenids. The tusked odobenine lineage appears to have dispersed into the

SPEC.	AGE	PLIOCENE		PLEISTOCENE	
		MIOCENE	Early	Late	Early
Pacific					
Odobenini					
NFL		FT, D			
NMJH		D, R			
FM-N			D		
<i>Pliopedia</i>		M			
<i>Valenictus</i>		M		F, M	
<i>Odobenus</i>				D	
KCM				D	
					D, N
Atlantic					
<i>Prorosmarus</i>			F, D		
<i>Alachtherium</i>				M	
<i>Odobenus</i>					M

Fig. 6. Geochronologic distribution of the Odobenini in the North Pacific and North Atlantic. Solid lines represent the records traced by published material. Dashed lines represent no fossil or no published record. Abbreviations: F, foraminifera; FT, fission track; D, diatom; N, nanno plankton; M, mega-fossils. Sources of fossil record of *Odobenus* include BORISSIAK (1930), ERDBRINK and VAN BREE (1986, 1990), HASEGAWA (1988), HOSHIMI and AKAGI (1994), ISHIGURI and KIMURA (1993), LANKESTER (1865, 1880), MATSUMOTO (1926), MIYAZAKI *et al.* (1992), REPENNING and TEDFORD (1977), RUTTEN (1907), TOMIDA (1989), VAN BENEDEN (1877), VAN DEINE (1964), and VAN DER FEEN (1968).

North Atlantic through the Central American Seaway or the Arctic Ocean during the latest Miocene. According to HOPKINS (1972), glacial conditions at the Arctic region probably did not exist before the Mid-Pliocene, and it was not very cool around the Holarctic region. Therefore, it does not seem necessary to consider the Arctic Ocean as a formidable barrier for the tusked odobenine dispersal from the North Pacific to the North Atlantic. However, the existence of the Arctic route of the odobenine dispersal from the North Pacific to the North Atlantic is presently unproved.

The Recent walrus genus *Odobenus* might have evolved from the unknown *Prorosmarus*-like ancestor in the northern North Pacific sometime during the Late Pliocene on the basis of their earlier records in the North Pacific (Fig. 6). The genus *Odobenus*, therefore, immediately spread out into the Holarctic region and re-entered into the North Atlantic by the latest Pliocene. The previous thought, that the genus *Odobenus* evolved in the North Atlantic and entered into the North Pacific through the Arctic Ocean in the Middle Pleistocene, should therefore be revised. However, until the cranial material corresponding to the large tusks with great curvature might be discovered from the Pliocene of both North Pacific and

North Atlantic, the relationship of the genus *Odobenus* to other Pliocene extinct genera is still open to question.

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