

A New Walrus (Carnivora, Odobenidae) from the Middle Pleistocene of the Boso Peninsula, Japan, and its Implication on Odobenid Paleobiogeography

By

Yukimitsu TOMIDA

Department of Geology, National Science Museum, Tokyo

Abstract Odobenid fossil remain from the early middle Pleistocene Mandano Formation, Kisarazu City, is designated as the holotype of a new species of the genus *Odobenus*. The new species, *O. mandanoensis*, is characterized mainly by (1) mandibular symphysis very robust and thick, (2) dentary bone laterally thickened above the mental foramen posterior to C₁, (3) wide diastema between C₁ and P₂, and (4) obliquely implanted teeth. *O. mandanoensis* provides evidence that *Odobenus* emigration from the Atlantic Ocean to the Pacific was older than previously presumed and happened at least twice.

Introduction

The Pleistocene sequence of the Boso Peninsula has been well known for the occurrences of a number of mammalian fossils, both terrestrial and marine (KAMEI *et al.*, 1988; WATANABE, 1980; HORIKAWA *et al.*, 1985; and references therein). The Mandano Formation (abbreviated as Fm. afterward) and its westward equivalent Nagahama Fm. of the upper Kazusa Group (MITSUNASHI and YAMAUCHI, 1988; Fig. 1) are one of the productive deposits among them (MATSUMOTO, 1924, 1926, 1939; Mandano Fossil Research Group, 1987; and other unpublished material).

The odobenid remain described below is also from the Mandano Fm., adding another element to the fauna. The fossil specimen was found in a sand and gravel mine near Mandano village, Kisarazu City (Fig. 2) by Mr. Shigehisa TOKUMARU in 1982.

Modern walrus *Odobenus rosmarus* in the North Pacific Basin has been presumed to have emigrated from the Atlantic Ocean through the Arctic Ocean sometime in the late Pleistocene after the long history of evolution in the Atlantic (REPENNING and TEDFORD, 1977; REPENNING *et al.*, 1979). The fossil walrus from Mandano described below provides evidence for an earlier emigration of *Odobenus* to the Pacific and for a more complicated evolutionary history of the genus.

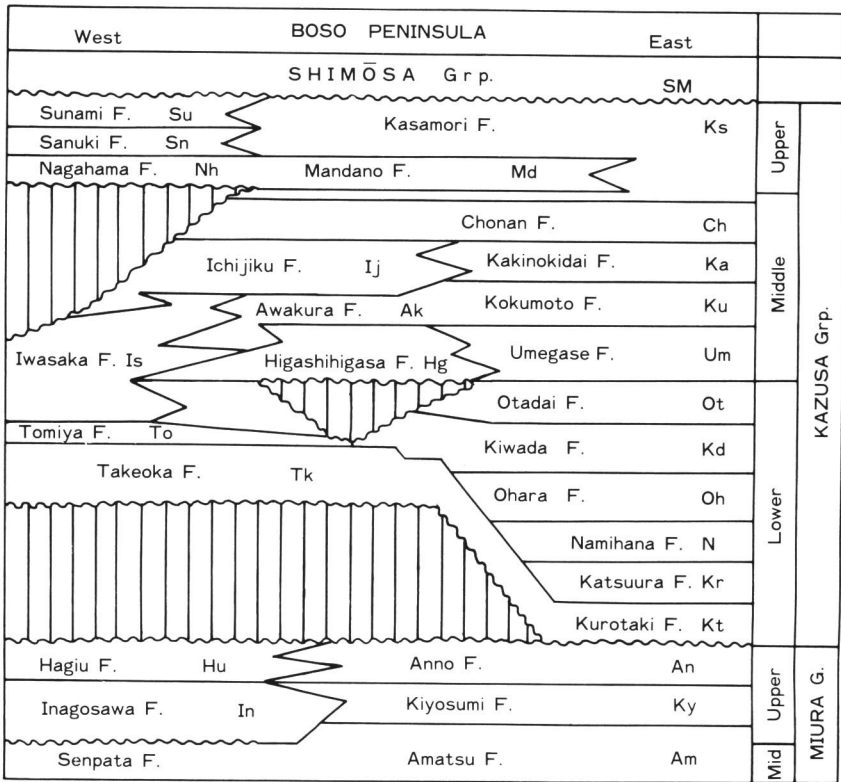


Fig. 1. Stratigraphy of the Kazusa and Miura (upper) Groups at the Boso Peninsula. Abbreviations of the formation names are the same as those in figure 2 (re-drawn after MITSUNASHI and YAMAUCHI, 1988).

Systematic Description

Order Carnivora BOWDICH, 1821

Suborder Pinnipedia ILLIGER, 1811

Family Odobenidae ALLEN, 1880

Genus *Odobenus* BRISSON, 1762

Odobenus mandanoensis sp. nov.

(Figs. 3 and 4)

Holotype: National Science Museum, Vertebrate Paleontology (NSM-PV) 18911, mandibular symphyseal portion of left and right mandibles of an adult, male individual with roots of left C_1 , P_2 , and right C_1^* .

* For tooth homology, I follow FAX (1982) who designated four functional mandibular teeth as $C_1P_2P_3P_4$.

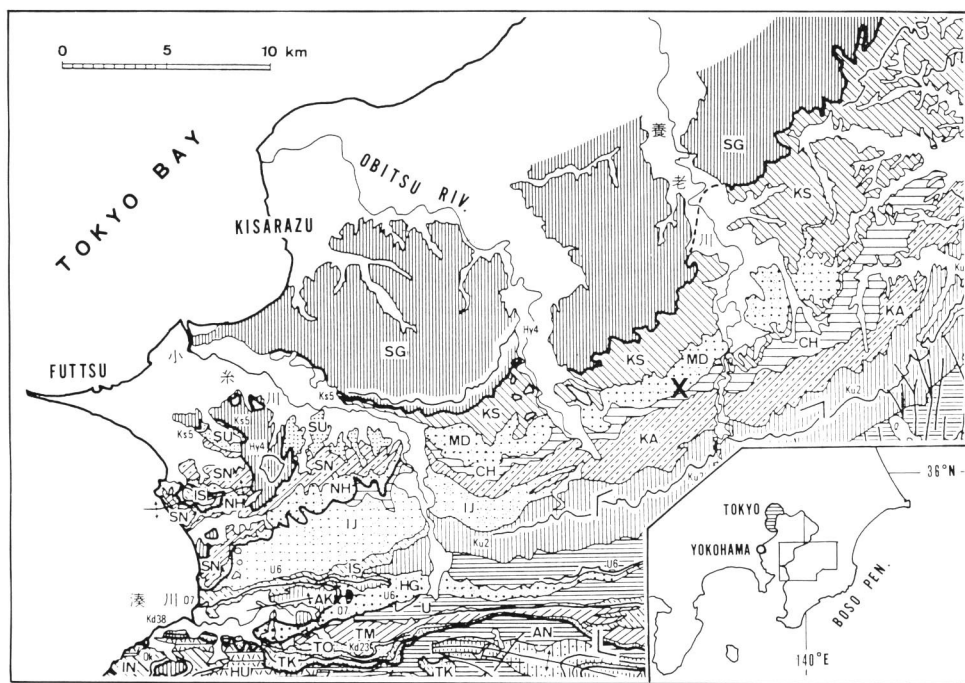


Fig. 2. Geologic map of the central part of the Boso Peninsula with the type locality (X mark) of *Odobenus mandanoensis*. Abbreviations of the formation names are the same as those in figure 1 (geologic map after MITSUNASHI and YAMAUCHI, 1988).

Type locality: A sand and gravel mine located 1.5 km directly west of the Itabu Station of Kominato Railroad, and 0.8 km east of Mandano village, Kisarazu City, Chiba Prefecture.

Horizon and age: Mandano Formation, Kazusa Group; early middle Pleistocene, approximately 0.5 Ma.

Etymology: After the type locality as well as the fossil bearing formation.

Diagnosis: A walrus of about the same size to, or somewhat larger than, the recent Pacific subspecies *Odobenus rosmarus divergens*; mandibular symphysis robust and vertically thick; dentary bone thickens laterally above the level of the mental foramen posterior to C_1 ; diastema between C_1 and P_2 wide; teeth being implanted obliquely, leaning anteriorly.

Description: The holotype is the only specimen known. The specimen had probably been originally complete or nearly so, but the posterior portion was broken off at the position near P_2 when collected (Fig. 3). It is 137 mm in length and 123 mm in width. The specimen is coated by thin limonite layer, and the detail of fine sculpture of the surface is not observable.

The mandibular symphysis is extremely massive and robust; its ventral surface

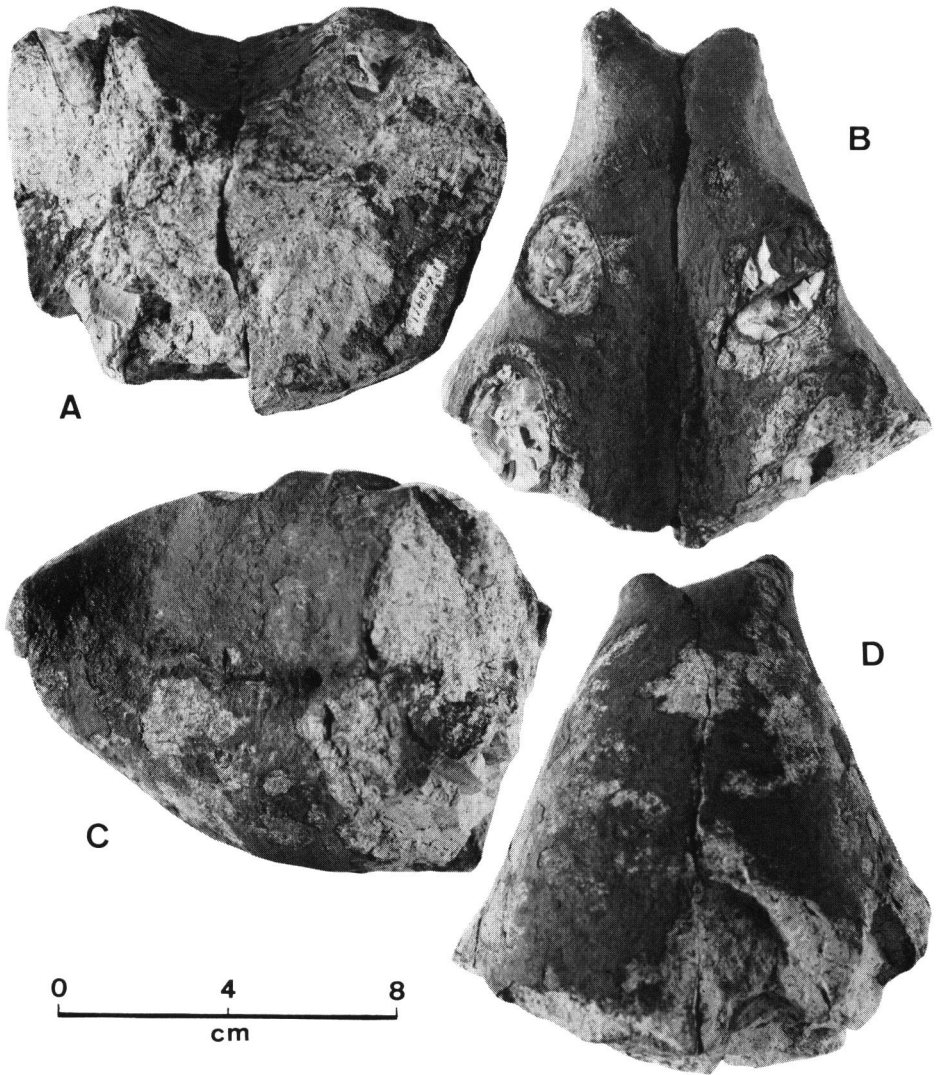


Fig. 3. *Odobenus mandanoensis* n. sp., holotype, NSM-PV 18911. A: posterior view (note the root of left P_2). B: dorsal view. C: ventral view. D: left lateral view.

forms a gentle curve in lateral view. Notable constriction is present anterior to C_1 ; anterior ends of both left and right dentaries project antero-laterally, forming a vertical depression at the anterior face of mandibular symphysis. Vertical thickness of the mandibular symphysis is very thick, making the slope of the upper surface of the symphysis gentle (Fig. 3-A, Table 1).

Dorsal half of the dentary bone thickens extremely laterally posterior to C_1

Table 1. Measurements (in mm on items 1 through 7 and in degree on item 8) of the holotype of *Odobenus mandanoensis* and modern Pacific subspecies *O. rosmarus divergens*.

	<i>O. mandanoensis</i> NSM-PV 18911	<i>O. rosmarus</i> <i>divergens</i> *
(1) Maximum antero-posterior length of mandibular symphysis	125+	112
(2) Maximum width of mandible at the position of constriction	56	57
(3) Maximum width of mandible at the position of C ₁	84	80
(4) Maximum width of mandible at the position of P ₂	ca. 117	106
(5) Maximum height of dentary at the position between C ₁ and P ₂	97	97
(6) Length between lateral borders of left and right C ₁ 's	70	71
(7) Diastema between C ₁ and P ₂ alveoli	13	4
(8) Angle formed by lines connecting C ₁ and P ₂	ca. 40	42

* The specimen belongs to the Department of Geology, Tohoku University but not catalogued; the skull of the same individual was used as a comparative material in MATSUMOTO (1926).

(compare Figs. 4-B and -C), which makes the thickness of the dentary lateral to P₂ root extreme (Fig. 3-A and Fig. 4-C); and the maximum width of the mandible posterior to C₁ occurs higher than the level of the mental foramen. The mental foramen is located between C₁ and P₂ at a position slightly lower than the midpoint of the height of the dentary.

Most of the roots of left C₁, P₂, and right C₁, and tip of the right P₂ root are preserved, of which roots of P₂'s are observable because of the breakage. All four teeth are implanted obliquely, leaning anteriorly and slightly laterally. Diastema between C₁ and P₂ alveoli is wide and measures approximately 13 mm. C₁ is oval in cross section. P₂ is also oval in cross section, but anteroposteriorly more elongated than C₁. The straight lines connecting left C₁ and P₂ and right C₁ and P₂ cross somewhat anterior to the anterior end of the mandible, with the angle of approximately 40 degrees (Table 1; Fig. 4-G).

Comparisons: (1) massiveness of the mandibular symphysis, (2) constriction of the dentary anterior to C₁, (3) vertical depression on the anterior face of the mandible, and (4) angle formed by the lines connecting left C₁ and P₂ and right C₁ and P₂ distinguish the present species from the genera *Prorosmarus* and *Alachtherium* and place it in the genus *Odobenus* (BERRY and GREGORY, 1906).

A single extant species (*O. rosmarus*) and a single extinct species (*O. huxleyi*) have been recognized within the genus *Odobenus* (REPENNING and TEDFORD, 1977). *O. huxleyi* is known from C₁'s (LANKESTER, 1865, 1883; RAY, 1960) and skulls (RUTTEN, 1907; Van DEINSE, 1964); no mandibular remains are currently known. Thus, *O. mandanoensis* can not be compared directly with *O. huxleyi*, and future finds may serve the two to be synonymous.

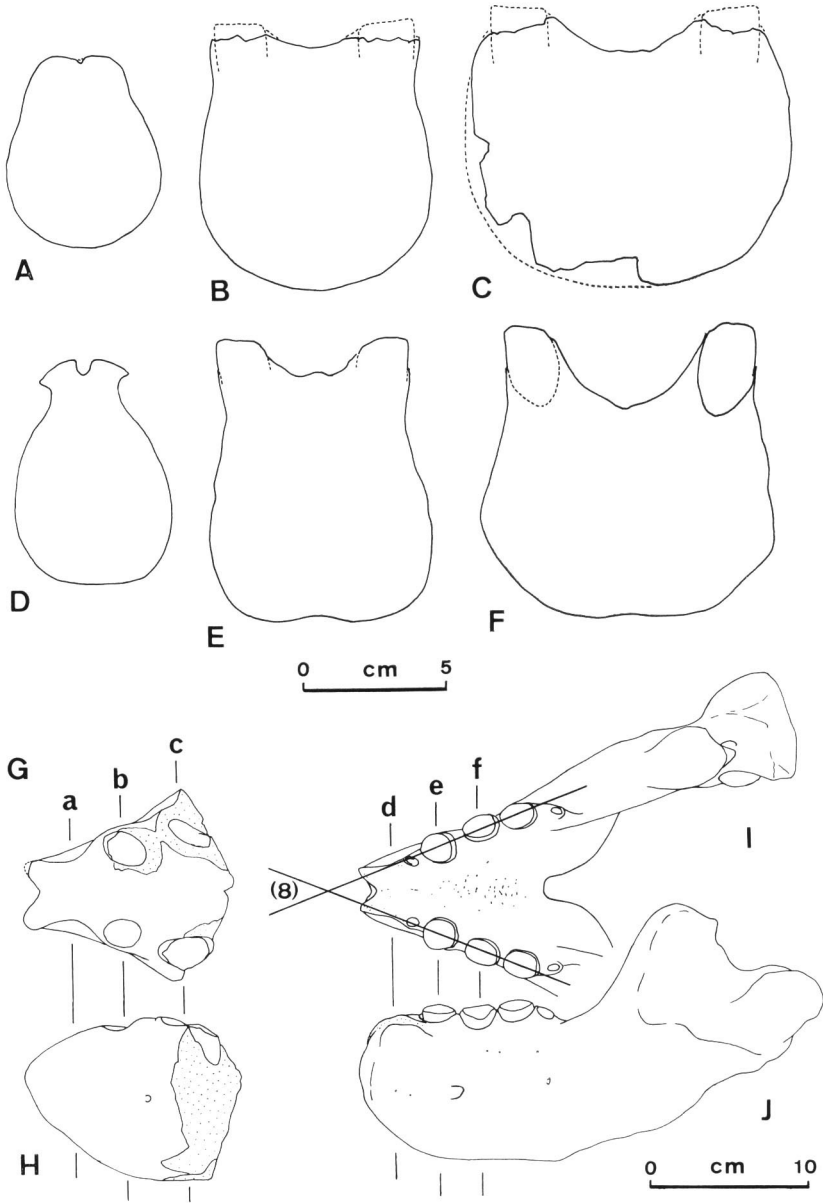


Fig. 4. Cross sections of the mandibles of *O. mandanoensis* and *O. rosmarus divergens*. A–C, G, H: *O. mandanoensis*, holotype, NSM-PV 18911. D–F, I, J: *O. rosmarus divergens*, Tohoku University specimen. Lines a–c of figures G and H and d–f of figures I and J indicate the positions where the cross sections A–F, respectively, were drawn. Angle (8) of figure I indicates the angle measured and listed on item (8) of table 1.

REPENNING and TEDFORD (1977, p. 55) listed *O. koninckii* as a dubious extinct species. *O. koninckii* is known from a tusk fragment, a dentary fragment, and a number of post cranial elements (VAN BENEDEN, 1877). Systematic evaluation of the species is not attempted here, but comparison of the dentary fragment with *O. mandanoensis* is possible. According to the illustrations and descriptions of VAN BENEDEN (1877), the mandible of *O. koninckii* differs from that of *O. mandanoensis* in that (1) one large canine and four functional, aligned, post-canine teeth are present, (2) area of the mandibular symphysis is small, and (3) dorsal surface of the symphyseal portion is steeply sloped posteriorly. Thus, *O. koninckii*, if valid, is distinct (may be even generically) from *O. mandanoensis*.

Direct comparisons with the modern walrus were made with two adult male specimens: one is the Atlantic subspecies, *O. r. rosmarus*, NSMT-M 27860 from Greenland, and the other is Pacific subspecies *O. r. divergens*, a Tohoku University specimen from unknown locality in northern Pacific (Table 1, footnote). The mandible of Atlantic subspecies is slenderer and less robust, and the mandibular symphysis is anteroposteriorly shorter and vertically much thinner than the Pacific subspecies (ALLEN, 1880). In these characters and in size, *O. mandanoensis* is more similar to the Pacific subspecies than the Atlantic subspecies.

However, in other characters *O. mandanoensis* further differs from both subspecies. Most remarkable is the lateral thickening (swelling) of the dentary bone above the mental foramen starting at posterior to C_1 toward backward. This is most obvious in cross section of the mandible. General outline of the cross section anterior to C_1 is similar between the Mandano specimen and *O. r. divergens* (A vs. D and B vs. E in Fig. 4), whereas the one at P_2 differs (C vs. F in Fig. 4). That is also obvious from the fact that the dentary bone lateral to P_2 root is extremely thick in the Mandano specimen, whereas it is very thin in *O. r. divergens* (Fig. 3-A vs. Fig. 4-F; COBB, 1933, pls. 2 and 6) and in *O. r. rosmarus*. In modern walrus, the masseteric crest begins approximately directly below the mental foramen and continues postero-dorsally toward the coronoid process; the masseteric crest forms the widest point of the dentary as in Fig. 4-F. Whether or not the lateral thickening (swelling) of the dentary bone above the mental foramen in *O. mandanoensis* is the anterior extremity of the masseteric crest is not certain; posterior continuation of the masseteric crest can not be traced because of breakage.

Mandible is more robust, and the symphysis is vertically thicker than *O. r. divergens*; hence the dorsal surface of symphyseal portion between the left and right tooth rows slopes more gently than the case of *O. r. divergens*. All four teeth are implanted obliquely, leaning anteriorly in *O. mandanoensis*, whereas they are nearly vertical, or only slightly leaning anteriorly in case of C_1 (COBB, 1933, pls. 4 and 5), in *O. rosmarus*.

Diastema between C_1 and P_2 in *O. mandanoensis* is much wider than that of *O. rosmarus*: it measures 13 mm (approx. 60% of diameter of C_1 alveolus) in Mandano specimen, whereas it is 4 mm (approx. 18% of diameter of C_1 alveolus) in the Tohoku

University specimen of *O. r. divergens*; it is about 12–20% (measured on the illustrations) in two other specimens of *O. r. divergens* in COBB (1933, pls. 2 and 6), and also approx. 15% (3.5 mm/22.5 mm) in NSMT-M 27860 of *O. r. rosmarus*.

KIMURA *et al.* (1983) mentioned and figured the occurrence of a mandible of *Odobenus* sp. from the early middle Pleistocene (approx. 0.7 Ma) of Hokkaido. As far as I can determine from the illustration (KIMURA *et al.* 1983, pl. 3, fig. 4), the dentary bone lateral to P₂ root is thin, and masseteric crest starts approximately between C₁ and P₂ low on the dentary and continues backward. In these characters, *Odobenus* sp. of KIMURA *et al.* resembles the modern walrus *O. rosmarus* and is not comparable with *O. mandanoensis* described above.

Discussion

General phylogeny, dispersal, and paleobiogeography of the family Odobenidae by REPENNING (1976), REPENNING and TEDFORD (1977), and REPENNING *et al.* (1979) have been widely accepted (eg. THENIUS, 1980; KING, 1983; FAY in MACDONALD, 1984; CARROLL, 1988), although the family-group level systematics remains controversial (BARNES *et al.*, 1985). According to the literatures above, an early odobenine odobenid entered to the Atlantic Ocean through the Central American Seaway sometime in the late Miocene, and adapted to the cooler environments and evolved into the genus *Odobenus* by approximately Plio-Pleistocene. Meanwhile all other Pacific odobenids disappeared, and present Pacific *Odobenus* entered to the North Pacific via the Arctic Ocean sometime during the late Pleistocene. The oldest *Odobenus* fossil specimen from the Pacific known to REPENNING and others was from Alaska, the geologic age of which is Sangamon (REPENNING and TEDFORD, 1977, p. 82) which is approx. 0.12–0.07 Ma in recent estimation (HAQ and VAN EYSINGA, 1987). Although REPENNING *et al.* (1979, fig. 2) estimated 0.6 Ma for the age of the emigration of *Odobenus* to the Pacific, there was no older evidence known to them other than the Alaskan material mentioned above. Thus, new findings of older material from the Pacific side bear on the age of *Odobenus* emigration.

Several Pleistocene *Odobenus* fossils are known from northwestern Pacific: (1) a skull from Sakhalin (MATSUMOTO, 1926), (2) a skull from off the Cape Erimo (SASA and OKAZAKI, 1967), (3) a skull from Tokyo (HASEGAWA, 1972, 1977), (4) a snout from Chiba Pref. (HORIKAWA *et al.*, 1985), and (5) a mandible from Kitahiroshima, Hokkaido (KIMURA *et al.*, 1983). Of these, only the first two specimens are described, but their geologic ages are unknown. The last three have not been described, but were referred to either as *Odobenus* sp. or simply walrus. The skull from Tokyo (no. 3 above) is from the upper Tokyo Fm. (HASEGAWA, 1972) and is about 0.15 Ma in age (KIKUCHI, 1986); the snout from Chiba (no. 4 above) is from the Yabu Fm. (HORIKAWA *et al.*, 1985) and is about 0.25–0.3 Ma in age (KIKUCHI, 1986).

The mandible from Kitahiroshima (no. 5 above) is from the Shimonopporo Fm. whose age has been estimated as approximately 0.7 Ma (KIMURA *et al.*, 1983). The

holotype of *O. mandanoensis* is from the Mandano Fm., approximately 0.5 Ma in age (KIKUCHI, 1986). Thus, although KIMURA *et al.* (1983) did not provide any description of the specimen nor mention its implication to the odobenid paleobiogeography, the mandible from Kitahiroshima is the oldest *Odobenus* (the illustration is clear enough to establish the generic assignment) known from the North Pacific. This revises somewhat the scenario by REPENNING *et al.* (1979); the age of emigration of *Odobenus* to the Pacific is slightly older than previously estimated.

Although the age is slightly younger, *O. mandanoensis* complicates the scenario. That is, no matter where *O. mandanoensis* evolved (and even if it is synonymized with *O. huxleyi*), the emigration of *Odobenus* from the Atlantic to the Pacific (or vice versa) happened at least twice (*O. mandanoensis* itself or its ancestor and modern *O. rosmarus*). In addition, if *O. mandanoensis* originated in the Pacific, its ancestor should have emigrated there significantly earlier.

Although they were not noted by REPENNING (1976), REPENNING and TEDFORD (1977), and REPENNING *et al.* (1979), two Pliocene odobenid specimens had been known from Japan by that time. Both are tusk fragments and had been identified as *Odobenus* sp.: one is from the Yotsukura Fm. in Fukushima Pref. (NAORA, 1944), and the other is from the Shiranuka Fm. at Atsunai, Hokkaido (SASA and OKAZAKI, 1967). The geologic ages of those formations are approx. 3 and 5–3 Ma respectively, by recent micro-fossil biostratigraphy and chronology (TSUCHI *et al.*, 1981). In addition, another tusk was recently found from the Yotsukura Fm. in Fukushima Pref. (HASEGAWA and KOHDA, 1988). All of them resemble, at least superficially, *O. huxleyi* (LANKESTER, 1883; RAY, 1960) and also undescribed and unidentified tusks from the Pliocene Yorktown Fm. of Virginia, U.S.A. Once they are described and identified (a review in prep.), the scenario by REPENNING *et al.* (1979) on dispersal and paleobiogeography of odobenines will probably be required considerable revision, a task beyond the scope of the present paper.

Acknowledgments

I am grateful to Mr. Shigehisa TOKUMARU who collected and kindly donated the specimen described above to the National Science Museum. My thanks also go to Prof. Dr. Kei MORI of the Tohoku University and Dr. Nobuyuki MIYAZAKI of the National Science Museum for their permission to examine the modern walrus specimens under their care, and Mr. Naoki KOHNO of the Natural History Museum and Institute of Chiba for providing some literature information. I am also indebted Mr. Andre R. WYSS of the American Museum of Natural History for his reading and suggestions on the manuscript. Financial support was provided in part by a Grant-in-Aid for Scientific Research (nos. 61304010 and 61540578) from the Ministry of Education, Science and Culture of the Government of Japan.

References

- ALLEN, J. S., 1880. History of North American pinnipeds. A monograph of the walruses, sea-lions, sea-bears, and seals of North America. *Dept. Inter. U.S. Geol. Geogr. Survey Terr. Misc. Pub.*, **12**: xvi+773.
- BARNES, L. G., D. P. DOMNING, & C. E. RAY, 1985. Status of studies on fossil marine mammals. *Marine Mam. Sci.*, **1** (1): 15-53.
- BERRY, E. W. & W. K. GREGORY, 1906. *Prorosmarus alleni*, a new genus and species of walrus from the upper Miocene of Yorktown, Virginia. *Amer. Jour. Sci.*, ser. 4, **21** (40): 444-450.
- CARROLL, R. L., 1988. Vertebrate paleontology and evolution. New York, W. H. Freeman and Co., xiv+698.
- COBB, W. M., 1933. The dentition of the walrus, *Odobenus obesus*. *Proc. Zool. Soc. London*, **103**: 645-668, pls. 1-6.
- FAY, F. H., 1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. *U.S. Dept. Inter. Fish Wildlife Serv., North Amer. Fauna*, **74**: vi+279.
- 1984. Walrus. In MACDONALD, D. (ed.) *The encyclopaedia of mammals: 1*. London, George Allen & Unwin, p. 264-269.
- HAQ, B. U. & F. W. B. VAN EYSINGA, 1987. Geological time table. Amsterdam, Elsevier Sci. Pub.
- HASEGAWA, Y., 1972. [A walrus fossil found in Tokyo.] *Nat. Sci. Mus. News*, (43): 1 (In Japanese.)
- 1977. [History and distribution of the vertebrates.] In WATANABE, N. et al. (eds.) *Quaternary studies in Japan*. Tokyo, Univ. Tokyo Press, p. 227-243 (In Japanese.)
- & Y. KOHDA, 1988. [A Pliocene walrus fossil from Tomioka-cho, Futaba-gun, Fukushima Prefecture.] *Abst. 1988 Ann. Meet. Palaeont. Soc. Japan*, p. 85 (In Japanese.)
- HORIKAWA, H. & seven others, 1985. On the fossil Pinnipedia from Japan. *Assoc. Geol. Collabor. Japan Monogr.*, **30**: 91-96 (In Japanese.)
- KAMEI, T., Y. KAWAMURA, & H. TARUNO, 1988. Mammalian stratigraphy of the late Neogene and Quaternary in the Japanese Islands. *Mem. Geol. Soc. Japan*, **30**: 181-204 (In Japanese with English abstract.)
- KIKUCHI, T., 1986. [Quaternary-Outline-] In OMORI, M., Y. HAYAMA, & M. HORIGUCHI (eds.) *Regional geology of Japan Part 3 Kanto*. Tokyo, Kyoritsu Shuppan, p. 137-142 (In Japanese.)
- KIMURA, M., T. TONOSAKI, M. AKAMATSU, Y. KITAGAWA, M. YOSHIDA, & T. KAMEI, 1983. Occurrences of early-middle Pleistocene mammalian fossils from the Nopporo Hills in the Ishikari Lowland, Hokkaido. *Chikyu Kagaku (Earth Science)*, **37** (3): 162-177 (In Japanese with English abstract.)
- KING, J. E., 1983. *Seals of the world*. 2nd ed. London, Brit. Mus. (Nat. Hist.), 240 pp.
- LANKESTER, E. R., 1865. On the sources of the mammalian fossils of the Red Crag, and on the discovery of a new mammal in that deposit, allied to the walrus. *Geol. Soc. London Quart. Jour.*, **21** (3): 221-232.
- 1883. On the tusks of the fossil walrus, found in the Red Crag of Suffolk. *Linnean Soc. London Trans.*, ser. 2, Zool., **2** (6): 213-221, 1 pl.
- Mandano Fossil Research Group, 1987. On a fossil of Otariidae (Mammalia) from the Middle Pleistocene Mandano Formation of Ichihara City, Chiba Prefecture, Japan. *Chikyu Kagaku (Earth Science)*, **41** (6): 327-330.
- MATSUMOTO, H., 1924. [Preliminary notes on fossil elephants in Japan.] *Jour. Geol. Soc. Tokyo*, **31**: 255-272 (In Japanese.)
- 1926. On two species of fossil Pinnipedia from Kazusa and Saghalin. *Sci. Rep. Tohoku Imp. Univ.*, ser 2, **10** (1): 13-16, pls. 6-7.
- 1939. On two species of fossil mammals from Kazusa. *Zool. Mag. Tokyo*, **51**: 257-266, (In Japanese with English summary.)
- MITSUNASHI, T. & S. YAMAUCHI, 1988. Tectonic evolution of the sedimentary basin of the Kazusa

- Group, Kanto District, Japan. *Mem. Geol. Soc. Japan*, **30**: 67–75 (In Japanese with English abstract.)
- NAORA, N., 1944. [Mammalian history in Japan.] Tokyo, Yotokusha, 265 pp (In Japanese.)
- RAY, C. E., 1960. *Trichecodon huxleyi* (Mammalia: Odobenidae) in the Pleistocene of southeastern United States. *Bull. Mus. Comp. Zool. Harvard Univ.*, **122** (3): 129–142, 2 pls.
- REPENNING, C. A., 1976. Adaptive evolution of sea lions and walruses. *System. Zool.*, **25** (4): 375–490.
- , C. E. RAY, & D. GRIGORESCU, 1979. Pinniped biogeography. In GRAY, J. & A. J. BOUCOT (eds.) *Historical biogeography, plate tectonics, and the changing environment*. Eugene, Oregon State Univ. Press, p. 357–369.
- & R. H. TEDFORD, 1977. Otarioid seals of the Neogene. *U.S. Geol. Surv. Prof. Pap.*, **992**: vi+93, 24 pls.
- RUTTEN, L., 1907. On fossil trichechids from Zealand and Belgium. *Proc. Akad. Wet. Amsterdam*, **10**: 2–14.
- SASA, Y. & Y. OKAZAKI, 1967. [Walrus fossils from the Pacific coast of Hokkaido.] In ASANO, K. et al. (eds.) *Commemorative volume on 77th Anniversary of Prof. Ichiro Hayasaka*. Kanazawa, Kanazawa Univ., p. 181–184, pl. 8 (In Japanese.)
- THENIUS, E., 1980. *Grundzuge der Faunen- und Verbreitungs- geschichte der Säugetiere*. Stuttgart, Gustav Fischer Verl., 375 pp.
- TSUCHI, R. & IGCP-114 National Working Group of Japan, 1981. Bio- and chronostratigraphic correlation of Neogene sequences in the Japanese Islands. In TSUCHI, R. (ed.) *Neogene of Japan- Its biostratigraphy and chronology-*. IGC-114 National Working Group of Japan, Shizuoka, p. 91–104.
- VAN BENEDEN, P. J., 1877. Description des ossements fossiles des environs d'Anvers. Première partie. Les phoques ou les amphiteriens. *Ann. Mus. Hist. nat. Belgique*, **1**: 1–88, pls. 1–18.
- VAN DEINSE, A. B., 1964. De fossiele en recente walrussen van Nederland. *Zool. Meded. Leiden*, **39**: 187–205, pl. 13.
- WATANABE, K., 1980. [III. Boso Peninsula.] In IGO, H. et al. (eds.) *Regional geology of Japan, Kanto District*. Tokyo, Asakura Shoten, p. 257–280 (In Japanese.)

