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

By

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Abstract Odobenid fossil remian from the early middle Pleistocene Mandano Formation, Kisorazu 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one of the productive deposits among them (MATSUMOTO, 1924, 1926, 1939; Mandano Fossil Research Group, 1987; and other unpublished material).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 (REPPENNING and TEDFORD, 1977; REPPENNING 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.
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 symphysial portion of left and right mandibles of an adult, male individual with roots of left C₁, P₃, and right C₁*.

* For tooth homology, I follow Fay (1982) who designated four functional mandibular teeth as C₁,P₂,P₃,P₄.
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 C₁; diastema between C₁ and P₂ 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 P₂ 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* p. sp., holotype, NSM-PV 18911. A: posterior view (note the root of left P₂). B: dorsal view. C: ventral view. D: left lateral view.

forms a gentle curve in lateral view. Notable constriction is present anterior to C₁; 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 C₁,
Table 1. Measurements (in mm on items 1 though 7 and in degree on item 8) of the holotype of *Odobenus mandanoensis* and modern Pacific subspecies *O. rosmarus divergens*.

<table>
<thead>
<tr>
<th>Description</th>
<th><em>O. mandanoensis</em></th>
<th><em>O. rosmarus divergens</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) Maximum antero-posterior length of mandibular symphysis</td>
<td>125+</td>
<td>112</td>
</tr>
<tr>
<td>(2) Maximum width of mandible at the position of constriction</td>
<td>56</td>
<td>57</td>
</tr>
<tr>
<td>(3) Maximum width of mandible at the position of C₁</td>
<td>84</td>
<td>80</td>
</tr>
<tr>
<td>(4) Maximum width of mandible at the position of P₂</td>
<td>ca. 117</td>
<td>106</td>
</tr>
<tr>
<td>(5) Maximum height of dentary at the position between C₁ and P₂</td>
<td>97</td>
<td>97</td>
</tr>
<tr>
<td>(6) Length between lateral borders of left and right C₁’s</td>
<td>70</td>
<td>71</td>
</tr>
<tr>
<td>(7) Diastema between C₁ and P₂ alveoli</td>
<td>13</td>
<td>4</td>
</tr>
<tr>
<td>(8) Angle formed by lines connecting C₁ and P₂</td>
<td>ca. 40</td>
<td>42</td>
</tr>
</tbody>
</table>

* 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 antero-posteriorly 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* (Repennin 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.
REPPENING and TEDFORD (1977, p. 55) listed *O. konincki* as a dubious extinct species. *O. konincki* 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. konincki* 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 symphysial portion is steeply sloped posteriorly. Thus, *O. konincki*, 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, toward backward. This is most obvious in cross section of the mandible. General outline of the cross section anterior to C 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, differs (C vs. F in Fig. 4). That is also obvious from the fact that the dentary bone lateral to P 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 symphysial 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* (COBB, 1933, pls. 4 and 5), in *O. rosmarus*.

Diastema between *C* and *P* in *O. mandanoensis* is much wider than that of *O. rosmarus*: it measures 13 mm (approx. 60% of diameter of C alveolus) in Mandano specimen, whereas it is 4 mm (approx. 18% of diameter of C 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 P₃ root is thin, and masseteric crest starts approximately between C₃ and P₃ 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 (e.g. 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 Kitahirosima 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.

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