

Large-sized cetacean fossils from the Tonohama Group in the Iwado area, Muroto City, Kochi Prefecture, Japan

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Abstract Two cetacean specimens (humerus and lumbar vertebrae) derived from the latest Miocene to early Pliocene shallow marine deposit (ca. 5.6–3.8 Ma) in the Iwado area, Muroto City, Kochi Prefecture, Shikoku, Japan, are reported. Owing to the partially preserved state of the specimens, it is difficult to identify them even at the suborder level. However, on the basis of their morphological features and a comparison of extant cetaceans, the humerus specimen was derived from a large-sized (11 to 15 m) cetacean and the lumbers also as large as, or larger medium-sized (4 to 10 m) cetacean, indicating both specimens of whale-sized cetacean provenance. This is the first report of large-sized cetacean fossil from Shikoku. At present, some species of large-sized cetaceans inhabit offshore waters around Kochi (e.g., Eden's whale (*Balaenoptera edeni*) in Tosa Bay). Therefore, this study indicates that large-sized cetaceans have lived in the area since at least the early Pliocene (Zanclean: ca. 3.8 Ma). Although the divergence of cetaceans in Japanese waters during the middle Miocene to Pliocene is considered to be associated with the development of the Kuroshio Current, which flows along the southern coast of Japan with its northern limit being located off the coast of the Boso Peninsula in Chiba Prefecture, this is only supported by fossil fauna from limited areas: the Kakegawa fauna of Okinawa Pref., southernmost Japan. This study indicates that the distribution of cetaceans around the southern coast of Japan was more extensive along the Kuroshio Current during the late Miocene to Pliocene.

Key words: cetaceans, Kuroshio Current, Muroto, Tonohama Group

Introduction

The Kuroshio Current, a representative warm current system, has a strong influence on marine life, including cetaceans (porpoises, dolphins, and whales) (e.g., Kanaji *et al.*, 2014; Nagai *et al.*, 2019). The current appeared during the early to middle Miocene (Ogasawara, 2011), and it is considered that the present system was established no later than the end of the Pliocene (Gallagher *et al.*, 2015). The Kakegawa fauna (Otsuka, 1939) is scattered along the Pacific coast of Japan and comprises warm-current molluscan fossils associated with the Kuroshio Current (e.g., Ozawa *et al.*, 1995; Yamaoka, 2017). Although studies of these molluscan fossils have been well conducted, cetacean fossils associated with the current have been poorly studied.

In the present paper, we report two cetacean specimens from the shallow marine deposit in the Iwado area, Muroto City, Kochi Pref., Shikoku, Japan (Fig. 1). This locality was once correlated with the Ananai Formation of the Tonohama Group based on occurrences of the Pliocene molluscan fossils (Mitusio *et al.* 1990; Mimoto, 1992). Yamaoka (2017) recently suggested that the age of the deposit is older (the upper Miocene to the lower Pliocene: ca. 5.6–3.8 Ma) than previously suggested on the basis of the indications of calcareous nannofossils. He also precisely studied molluscan fossils and recovered the Kakegawa fauna which contains *Amussiopecten praesignis* (Yokoyama, 1922), *Mimachlamys satoi* (Yokoyama 1928), and *Megacardita panda* (Yokoyama, 1926). Here, the cetacean specimens are systematically described, and the relationship between the development of the Kuroshio Current and divergence of cetaceans is

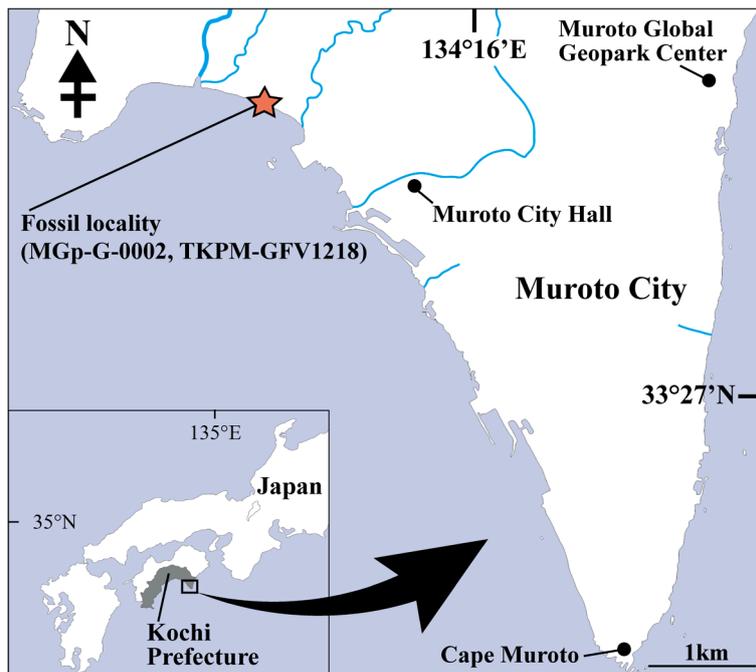


Fig. 1. Star represents the locality at which the present specimens were discovered, on the coast of the Iwado area, Muroto City, eastern Kochi Prefecture.

discussed.

Material and methods

MGp-G-0002 and TKPM-GFV1218 were personally observed for taxonomical identification. MGp-G-0002 was mechanically prepared in the preparation room of Department of Geology and Paleontology, National Museum of Nature and Science, Japan (NMNS). Morphological terminology follows that of Flower (1885), and Carwardine (2020) for body-size categories in cetaceans (small: up to 3 m, medium: 4 to 10 m, large: 11 to 15 m, extra large: more than 15 m). Photographs were taken using a DSLR camera (OM-D E-M10 Mark II; OLYMPUS Corp., Tokyo, Japan). Measurements were taken using a digital caliper (CD-20APX; Mitutoyo Corp., Kanagawa, Japan) and measures.

Institutional abbreviations are as follows: MGp, Muroto Geopark, Kochi, Japan; NMNS, National Museum of Nature and Science, Ibaraki, Japan; TKPM, Tokushima Prefectural Museum, Tokushima, Japan.

Systematic Paleontology

Class Mammalia Linnaeus, 1758

Order Cetacea Brisson, 1762

Fam., gen. et sp. indet.

(Fig. 2; Table 1)

Material: Right humerus (MGp-G-0002).

Locality and horizon: The cetacean-fossil-bearing horizon is uncertain because the specimen was collected as a float at the Narashi Beach in the Iwado area, Muroto City, Kochi Pref., Shikoku, Japan (Fig. 1). However, on the basis of a matrix with molluscan fossils, it was derived from a shallow marine deposit in the Iwado area. The deposit mainly consists of blue-grey coarse sand to fine sand, and its thickness is about 30 m or more. The age of deposit is considered to be the upper Miocene to the lower Pliocene (ca. 5.6–3.8 Ma) based on the indications of calcareous nannofossils (Yamaoka, 2017). The molluscan fossil assemblage is characterized by subtropical species and upper sublittoral species (Yamaoka, 2017).

Description: This specimen consists of blade- and dome-shaped bone elements. The blade-shaped bone is badly broken. It has two facets that form a rectangle with rounded corners and a transversally long elliptical shape (Figure 2C). The former is

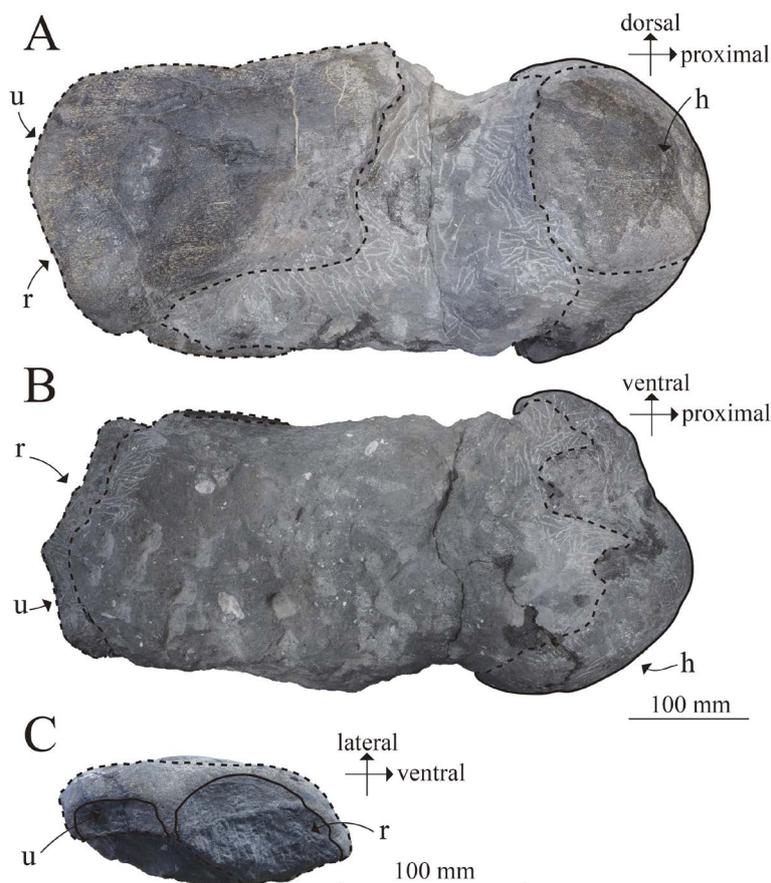


Fig. 2. Cetacean humerus (MGp-G-0002). Photographs in lateral (A), medial (B), and proximal (C) views. Scale bars are equal to 100 mm. h, head of humerus; r, facet for radius; u, facet for ulna.

Table 1. Measurements (in cm) of the humerus (MGp-G-0002). +, incomplete.

| | |
|---|--------|
| dorsoventral length of head in lateral view | + 125 |
| proximodistal length of head in lateral view | + 14.0 |
| maximum dorsoventral length of distal end | + 15.5 |
| maximum dorsoventral length of facet for ulna | + 5.0 |
| maximum dorsoventral length of facet for radius | + 5.1 |

smaller than the latter. These facets are unconnected. The dome-shaped bone has a large hemisphere. On the opposite side of the hemisphere, this bone is badly broken, but forms a nearly flat.

Identification and comparison: The two divided facets on the blade-shape bone, one smaller and one larger, correspond to the articular facets of the cetacean ulna and radius, respectively. In addition, the flat body that resembles a blade is a morphological feature of cetaceans (Flower, 1885; Cooper *et al.*, 2007; Marx *et al.*, 2016). Therefore, this specimen is the distal part of a cetacean humerus. Meanwhile, the hemisphere of the dome-shaped bone corresponds to the head of a cetacean humerus (Marx *et al.*, 2016). On the basis of the occurrence and morphological features of the fossil, these bones possi-

bly originate from a single individual. On the basis of the above, we identified MGp-G-0002 as a cetacean humerus. The epiphyses of the humerus is fused, indicating the specimen is an adult individual. The poor preservation of the specimen makes it difficult to identify it at the suborder level. However, based on the comparison with extant cetaceans, it is suggested to belong to the large-sized cetaceans (Table 3).

Fam., gen. et sp. indet.

(Fig. 3; Table 2)

Material: Four lumbar vertebrae (TKPM-GFV1218).

Locality and horizon: This specimen was collected as a float at the same place as MGp-G-0002 (Fig. 1). However, on the basis of a matrix with molluscan fossils, it was also derived from the same deposit as MGp-G-0002.

Description: The present specimen consists of four large vertebrae. In all vertebrae, the centrum is well preserved, but the transverse process, spinous

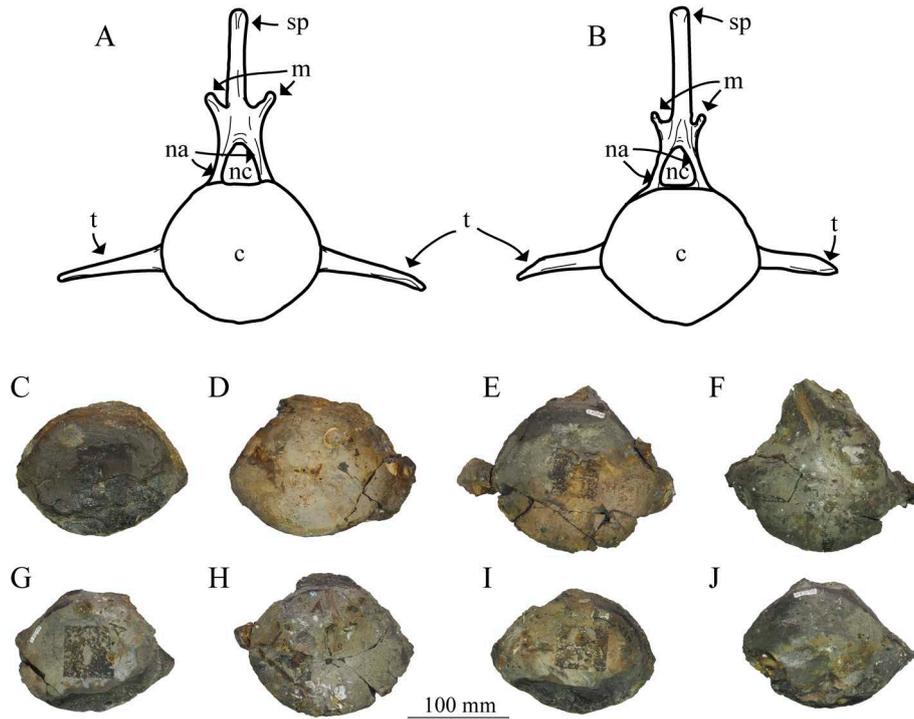


Fig. 3. Cetacean lumbar vertebrae (TKPM-GFV1218). Line drawings of lumbar vertebra (extant cetaceans) in anterior (A) and posterior (B) views for morphological terms. Photographs of TKPM-GFV1218-1 (C, D); -2 (E, F); -3 (G, H); -4 (I, J) in anterior (C, E, G, I) and posterior (D, F, H, J) views. Scale bar is equal to 100 mm. c, centrum; m, metapophysis; na, neural arch; nc, neural canal; sp, spinous process; t, transverse process.

Table 2. Measurements (in cm) of the lumbar (TKPM-GFV1218). +, incomplete.

| | 1218-1 | 1218-2 | 1218-3 | 1218-4 |
|--|--------|--------|--------|--------|
| transverse width of anterior centrum | 14.5 | 16.0 | 14.0 | 12.3 |
| dorsoventral height of anterior centrum | 12.0 | 15.0 | + 12.5 | 11.7 |
| transverse width of posterior centrum | 15.5 | + 15.0 | + 14.8 | 13.5 |
| dorsoventral height of posterior centrum | 13.8 | + 15.0 | 13.2 | 12.5 |
| anteroposterior length of centrum | 15.8 | + 16.0 | 15.0 | 14.5 |

process, and neural arch are badly broken. The centrum is an oval in anterior or posterior views. The transverse process is flat and anteroposteriorly wide, and it projects ventrolaterally from the lateral side of the centrum. Each vertebra has a neural arch that projects vertically. The hemal process is absent.

Identification and comparison: Regarding the fossil occurrence, all vertebrae are in alignment within a single rock. On the basis of their provenance, they belong to a single individual. We identified TKPM-GFV1218 as cetacean lumbar vertebrae based on the following morphological features: the oval centrum, the flat and anteroposteriorly wide transverse process that projects slightly ventrolaterally from the lateral side of the centrum, the vertically projecting neural arch, the absence of the hemal process (Flower, 1885; Marx *et al.*, 2016). Based on comparisons with the extant species, the

specimen was derived from at least estimated to be as large as, or larger than medium-sized cetaceans (Table 4). In terms of the ration of the centrum transverse width to dorsoventral height (F in Table 4), the value of the specimen is included in the ranges of *Eubalaena japonica* (Lacépède, 1818) (North Pacific right whale), *Physeter macrocephalus* Linnaeus, 1758 (Sperm whale), and *Berardius minimus* Yamada, Kitamura and Matsuishi, 2019 (Sato's beaked whale). However, the indicator is suggested to be difficult to use for classification because of the large overlap of values in extant cetaceans. In the ration of the centrum transverse width to anteroposterior length (G in Table 4), the present specimen is very different from *Eu. japonica*, *Eschrichtius robustus* (Lilljeborg, 1861) (Grey whale), *Megaptera novaeangliae* (Borowski, 1781) (Humpback whale), *Balaenoptera omurai* Wada,

Table 3. Measurements (in cm) of the humerus of MGp-G-0002 and extant whale-sized cetaceans. +, incomplete; BL, body length.

| Specimen number | Suborder | Family | Scientific name | BL | A: dorsoventral length of head in lateral view | | B: proximodistal length of head in lateral view | | C: maximum dorsoventral length of distal end | | D: maximum dorsoventral length of facet for ulna | | E: maximum dorsoventral length of facet for radius | |
|-----------------|------------|----------------------------------|------------------------------|-------|--|--------|---|--------|--|--------|--|-------|--|-------|
| | | | | | L | R | L | R | L | R | L | R | L | R |
| MGp-G-0002 | ? | Cetacea fam., gen. et sp. indet. | <i>Eubalaena japonica</i> | ? | — | + 12.5 | — | + 14.0 | — | + 15.5 | — | + 5.0 | — | + 8.5 |
| NMNS-M55028 | Mysticeti | Balaenidae | <i>Eubalaena japonica</i> | 881 | 15.2 | 14.0 | 14.0 | 13.2 | 21.5 | 22.0 | 10.5 | 9.8 | 12.0 | 12.5 |
| NMNS-M52579 | Mysticeti | Eschrichtiidae | <i>Eschrichtius robustus</i> | 890 | 13.2 | — | 10.2 | — | 20.5 | 21.0 | 12.0 | 12.2 | 8.2 | 9.0 |
| NMNS-M29617 | Mysticeti | Balaenopteridae | <i>Balaenoptera musculus</i> | 2350 | 32.4 | 35.2 | 24.5 | 27.7 | 35.4 | 36.2 | 20.8 | 22.1 | 15.8 | 14.1 |
| NMNS-M42442 | Mysticeti | Balaenopteridae | <i>Ba. borealis</i> | 1236 | 14.5 | 15.3 | 11.5 | 12.2 | 18.2 | 17.8 | 8.7 | 8.5 | 9.5 | 9.7 |
| NMNS-M33622 | Mysticeti | Balaenopteridae | <i>Ba. edeni</i> | 745 | — | — | — | — | — | 12.8 | — | 5.8 | — | 6.8 |
| NMNS-M42012 | Odontoceti | Ziphiidae | <i>Berardius minimus</i> | 662 | 10.5 | 9.8 | 9.5 | 9.8 | 10.0 | 10.3 | 3.8 | 4.2 | 5.1 | 5.4 |
| NMNS-M52660 | Odontoceti | Ziphiidae | <i>Ziphius cavirostris</i> | 616.4 | 7.8 | 7.5 | 6.5 | 6.8 | 7.7 | 7.8 | 3.5 | 3.7 | 3.9 | 4.0 |

Table 4. Measurements (in cm) of the lumbers of TKPM-GFV1218 and extant whale-sized cetaceans. +, incomplete; BL, body length; Min and Max, the minimum and maximum values of the lumber vertebrae in a single individual.

| Specimen number | Suborder | Family | Scientific name | BL | A: transverse width of anterior centrum (Min–Max) | | B: dorsoventral height of anterior centrum (Min–Max) | | C: transverse width of posterior centrum (Min–Max) | | D: dorsoventral height of posterior centrum (Min–Max) | | E: anteroposterior length of centrum (Min–Max) | | F: A/B (Min–Max) × 100(%) | | G: A/E (Min–Max) × 100(%) | | H: B/E (Min–Max) × 100(%) | |
|-----------------|------------|----------------------------------|-------------------------------|-------|---|-----------|--|-----------|--|-----------|---|-------------|--|-------------|---------------------------|-----------|---------------------------|-----------|---------------------------|-----------|
| | | | | | (Min–Max) | (Min–Max) | (Min–Max) | (Min–Max) | (Min–Max) | (Min–Max) | (Min–Max) | (Min–Max) | (Min–Max) | (Min–Max) | (Min–Max) | (Min–Max) | (Min–Max) | (Min–Max) | (Min–Max) | (Min–Max) |
| TKPM-GFV1218 | ? | Cetacea fam., gen. et sp. indet. | | ? | 12.3–16.0 | 11.7–15.0 | 13.5–15.5 | 12.5–15.0 | 13.5–15.5 | 12.5–15.0 | 14.5–16.0 | 105.1–106.7 | 84.8–100.0 | 80.7–93.8 | | | | | | |
| NMNS-M55028 | Mysticeti | Balaenidae | <i>Eubalaena japonica</i> | 881 | 20.8–23.8 | 18.7–22.8 | 21.7–24.7 | 19.2–23.2 | 21.7–24.7 | 19.2–23.2 | 8.2–10.8 | 111.2–104.4 | 253.7–220.4 | 228.0–211.1 | | | | | | |
| NMNS-M52579 | Mysticeti | Eschrichtiidae | <i>Eschrichtius robustus</i> | 890 | 18.3–22.0 | 14.8–18.7 | 19.0–19.7 | 14.7–21.5 | 19.0–19.7 | 14.7–21.5 | 10.5–13.0 | 123.6–117.6 | 174.3–169.2 | 141.0–143.8 | | | | | | |
| NMNS-M33734 | Mysticeti | Balaenopteridae | <i>Megaptera novaeangliae</i> | 960 | 21.7–24.3 | 18.2–21.8 | 23.2–25.5 | 18.2–22.6 | 23.2–25.5 | 18.2–22.6 | 10.8–13.5 | 119.2–114.5 | 200.9–180.0 | 168.5–161.5 | | | | | | |
| NMNS-M29617 | Mysticeti | Balaenopteridae | <i>Balaenoptera musculus</i> | 2350 | 36.8–39.6 | 28.9–30.6 | 37.9–40.1 | 29.6–31.5 | 37.9–40.1 | 29.6–31.5 | 28.5–31.5 | 127.3–129.4 | 129.1–125.7 | 101.4–97.1 | | | | | | |
| NMNS-M42442 | Mysticeti | Balaenopteridae | <i>Ba. borealis</i> | 1236 | 22.3–26.0 | 22.3–26.5 | 23.5–27.5 | 22.6–27.8 | 23.5–27.5 | 22.6–27.8 | 18.4–25.5 | 100.0–98.1 | 121.2–102 | 121.2–103.9 | | | | | | |
| NMNS-M32992 | Mysticeti | Balaenopteridae | <i>Ba. omurai</i> | 710 | 12.8–15.7 | 9.2–13.1 | 13.2–16.1 | 9.4–13.4 | 13.2–16.1 | 9.4–13.4 | 8.9–12.5 | 139.1–119.8 | 143.8–125.6 | 103.4–104.8 | | | | | | |
| NMNS-M5152 | Mysticeti | Balaenopteridae | <i>Ba. acutorostrata</i> | 760 | 13.3–16.0 | 11.3–14.5 | 13.7–17.6 | 11.4–15.2 | 13.7–17.6 | 11.4–15.2 | 14.8–18.9 | 117.7–110.3 | 89.9–84.7 | 76.4–76.7 | | | | | | |
| NMNS-M19792 | Mysticeti | Balaenopteridae | <i>Ba. bonaerensis</i> | 980 | 19.6–22.3 | 16.8–19.8 | 19.8–22.8 | 16.9–20.8 | 19.8–22.8 | 16.8–22.2 | 16.8–22.2 | 116.7–112.6 | 116.7–100.5 | 100.0–89.2 | | | | | | |
| NMNS-M33072 | Mysticeti | Balaenopteridae | <i>Ba. brydei</i> | 786 | 14.8–17.8 | 11.4–14.9 | 15.8–18.3 | 11.4–15.2 | 15.8–18.3 | 11.4–15.2 | 9.8–12.7 | 129.8–119.5 | 151.0–140.2 | 116.3–117.3 | | | | | | |
| NMNS-M3538 | Mysticeti | Balaenopteridae | <i>Ba. edeni</i> | 1219 | 22.0–25.4 | 15.8–21.8 | 22.7–25.0 | 16.7–19.5 | 22.7–25.0 | 16.7–19.5 | 19.5–23.8 | 139.2–116.5 | 112.8–106.7 | 81.0–91.6 | | | | | | |
| NMNS-M3539 | Odontoceti | Pyseteridae | <i>Physeter macrocephalus</i> | 1219 | 25.0–25.8 | 23.5–25.3 | 25.2–27.8 | 24.0–25.6 | 25.2–27.8 | 24.0–25.6 | 16.2–19.0 | 106.4–102.0 | 154.3–135.8 | 145.1–133.2 | | | | | | |
| NMNS-M3535 | Odontoceti | Ziphiidae | <i>Berardius bairdii</i> | 1066 | 19.8–23.7 | 16.8–21.9 | 20.7–25.8 | 17.5–22.6 | 20.7–25.8 | 17.5–22.6 | 22.4–29.3 | 117.9–108.2 | 88.4–80.9 | 75.0–74.7 | | | | | | |
| NMNS-M42012 | Odontoceti | Ziphiidae | <i>Be. minimus</i> | 662 | 10.4–13.2 | 9.8–13.1 | 11.5–14.0 | 10.7–14.2 | 11.5–14.0 | 10.7–14.2 | 14.8–20.5 | 106.1–100.7 | 70.3–64.4 | 66.2–63.9 | | | | | | |
| NMNS-M52660 | Odontoceti | Ziphiidae | <i>Ziphius cavirostris</i> | 616.4 | 11.5–14.2 | 10.2–12.4 | 12.3–15.3 | 10.4–12.3 | 12.3–15.3 | 10.4–12.3 | 15.4–19.5 | 112.7–114.5 | 74.7–72.8 | 66.2–63.6 | | | | | | |
| NMNS-M62797 | Odontoceti | Ziphiidae | <i>Mesoplodon ginkgodens</i> | 480 | 8.4–10.3 | 6.7–9.4 | 8.8–10.9 | 7.3–10.4 | 8.8–10.9 | 7.3–10.4 | 10.7–14.6 | 125.4–109.6 | 78.5–70.5 | 62.6–64.4 | | | | | | |

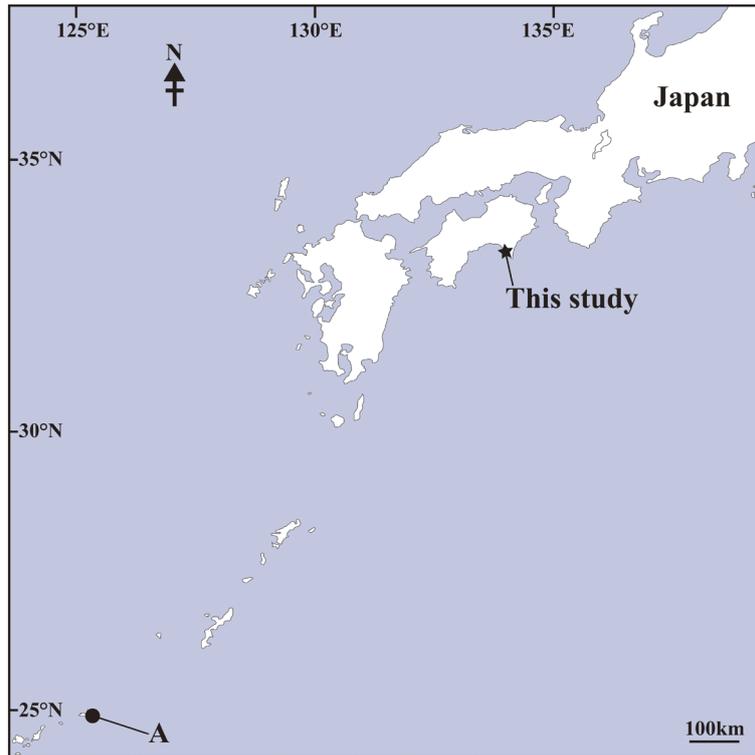


Fig. 4. Localities of cetacean fossils associated with the Kuroshio Current during the late Miocene to Pliocene. A, a balaenopterid fossil from the upper Miocene Okamishima Formation, Shimajiri Group in Miyako Island, Okinawa Pref. (Kimura *et al.* 2015). Star indicated this study.

Oishi and Yamada, 2003 (Omura's whale), *Balaenoptera brydei* Olsen, 1913 (Sei whale), *P. macrocephalus*, *Be. minimus*, *Ziphius cavirostris* Cuvier, 1823 (Cuvier's beaked whale), and *Mesoplodon ginkgodens* Nishiwaki and Kamiya, 1958 (Ginkgo-toothed beaked whale). On the other hand, regarding the ration of the centrum dorsoventral height to anteroposterior length (H in Table 4), the specimen has a very similar value to that of *Balaenoptera edeni* Anderson, 1878 (Bryde's whale). These measurements suggest the specimen does not belong to the large toothed whale group. It is also indicated that the specimen is different from lumbar vertebrae of *Eu. japonica*, *Es. robustus*, and *Meg. novaeangliae* in baleen whales, implying a member of the genus *Balaenoptera*. However, because the specimen is partially preserved and the measurements does not reflect intra-species variations, we kept our identification of the specimen as Cetacea fam., gen. et sp. indet.

Discussion

It is difficult to identify these specimens at the suborder level, however, on the basis of their mor-

phological features, the humerus specimen was derived from a large-sized cetacean, and the lumber specimens as large as, or larger than medium-sized cetacean. Japan has rich records of cetacean fossils, but such records are limited in western Japan (Oishi, 1985; Kimura, 1992; Oishi and Hasegawa, 1995; Oishi, 1997; Ichishima, 2005; Kimura, 2009; Nagasawa, 2016). The only cetacean fossil from Shikoku is that of a finless porpoise (*Neophocaena phocaenoides* Cuvier, 1829), belonging the small-sized cetacean (dolphins and porpoises), dredged from the Seto Inland Sea (Hasegawa, 1988; Kimura and Hasegawa, 2005). Therefore, this study is the first report of the large-sized cetacean (whales) fossil from Shikoku. At present, some species of large-sized cetaceans inhabit the offshore waters around Kochi, such as Eden's whale (*Balaenoptera edeni*) in Tosa Bay (Ohdachi *et al.*, 2015). On the basis of the present study, large-sized cetaceans have lived in the area since at least the early Pliocene (Zanclan: ca. 3.8 Ma).

Molluscan fossils of the Tonohama Group are characterized by the Kuroshio Current-related Kakegawa fauna (Otsuka, 1939; Tsuchi, 1961; Yamaoka, 2017). The fauna is distributed along the

Pacific coast of Japan from the Shimajiri Group (Miocene to lower Pleistocene) in Nansei Islands, Okinawa Pref. to the Kume Group (Pliocene) in Ibaraki Pref. (e.g., Ozawa *et al.*, 1995; Yamaoka, 2017). Because the Kuroshio Current, which flows along the southern coast of Japan with its northern limit being located off the coast of the Boso Peninsula in Chiba Prefecture, is one of the major currents dividing marine biogeographic zones (e.g., Roden, 1991; Nagai *et al.*, 2019), it affects a great number of marine life (e.g., Hidaka *et al.*, 2003; Watanabe *et al.*, 2009) including, of course, cetaceans (e.g., Konishi *et al.*, 2009; Kanaji *et al.*, 2014). It is known that the molluscan fauna changed as the current developed (e.g., Ozawa, 1983; Yamaoka *et al.*, 2015). However, the relationship between the evolution of cetaceans and the development of the Kuroshio Current during the late Miocene to Pliocene is not well understood. There has been just one report of cetaceans along the current so far: balaenopterid fossil from the upper Miocene Okamishima Formation, Shimajiri Group in Miyako Island, Okinawa Pref., southernmost Japan (A in Fig. 4) (Kimura *et al.*, 2015). The present study indicates that cetaceans inhabiting around the southern coast of Japan were more widespread along the Kuroshio Current during the Miocene to Pliocene (Fig. 4).

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