A humpback whale, Megaptera novaeangliae (Borowski, 1781), from the Pleistocene Kioroshi Formation of Inba-mura, Chiba Prefecture, central Japan

Authors: Nagasawa, Kazuo, and Mitani, Yutaka

Source: Paleontological Research, 8(3) : 155-165

Published By: The Palaeontological Society of Japan

URL: https://doi.org/10.2517/prpsj.8.155

Paleontological Research, vol. 8, no. 3, pp. 155–165, September 30, 2004

A humpback whale, *Megaptera novaeangliae* (Borowski, 1781), from the Pleistocene Kioroshi Formation of Inba-mura, Chiba Prefecture, central Japan

KAZUO NAGASAWA[1] AND YUTAKA MITANI[2]

[1]*Kajo-gakuen Senior High School, 1-16-1 Jonan-machi, Yamagata City, Yamagata 990-8580, Japan (nagas@agate.plala.or.jp)*

[2]*Funabashi Hoden Senior High School, 4-1-1 Fujiwara, Funabashi City, Chiba 274-0047, Japan (mitani@m3.dion.ne.jp)*

Received February 18, 2003; Revised manuscript accepted June 18, 2004

Abstract. A humpback whale skull was discovered in the upper Middle Pleistocene sand bed of Inba-mura, Chiba Prefecture. The morphological features of the skull are summarized as follows: the supraorbital process of the frontal is elongated laterally and its posterior margin is straight; the orbit is relatively short considering the skull size; the squamosal is slender and protrudes anterolaterally at an obtuse angle; the squamosal sulcus is not developed at the base of the zygomatic process; the dorsal shape of the supraoccipital is equilaterally triangular; the basioccipital and the basisphenoid are fused, forming a wide plane on the ventral surface; the alisphenoid is not exposed in the temporal region. Based on these characteristics, the specimen was identified as *Megaptera novaeangliae* (Borowski, 1781). This is the first record of *M. novaeangliae* in the western North Pacific during Pleistocene time. No fossil has yet been described systematically as *M. novaeangliae* from Pleistocene strata. Therefore, there is a strong possibility that the new material is the oldest *M. novaeangliae* fossil in the world.

Key words: *Megaptera novaeangliae*, skull, alisphenoid, Kioroshi Formation, late Middle Pleistocene, central Japan, North Pacific

Introduction

Humpback whales are distributed in all oceans of the world. The only living species is *Megaptera novaeangliae* (Borowski, 1781) that has been flourishing recently, but its phylogeny and the process of its evolution have not been sufficiently elucidated. The reasons are that well preserved humpback whale fossils are scarce and *M. novaeangliae* itself has not been well described.

A new specimen of the humpback whale was discovered in Chiba Prefecture, central Japan. The fossil locality, a quarry of Otake, is situated in the northern Shimousa Upland of the Boso Peninsula (Figure 1). The fossil skull was found in the sand bed of the Kioroshi Formation (middle-upper Pleistocene) by students of Kogane Senior High School in May 1990. Only the skull, missing the rostrum, was excavated by students and Y. Mitani (Figure 2). Based on its morphological features, the fossil skull has been identified as *Megaptera novaeangliae* (Borowski, 1781). This specimen is the first record of the humpback whale in the Pleistocene western North Pacific, and it is clear that *M. novaeangliae* can be traced back to the late Middle Pleistocene.

Material and methods

The new material (CBM-PV662) was donated to the Natural History Museum and Institute, Chiba, and is housed in the Museum. CBM-PV662 was compared with skeletal specimens and literature figures of living and fossil baleen whales. Institutional abbreviations are as follows: CBM, Natural History Museum and Institute, Chiba; IPMM, Iwate Prefectural Museum; NSMT, National Science Museum, Tokyo; TWM, Taiji Whale Museum; YPM, Yamagata Prefectural Museum.

Extant species are as follows: *Balaena mysticetus*, one TWM specimen, Reeves and Leatherwood (1985, fig. 3); *Balaenoptera acutorostrata*, NSMT-M15941, NSMT-M21263, YPM2154 (Nagasawa, 1992, pls. 1–2), YPM3501, True (1904, pls. 22–26); *B. bonaerensis*, YPM6755 (Nagasawa *et al.*, 1998, pls. 1–6); *B. omurai*,

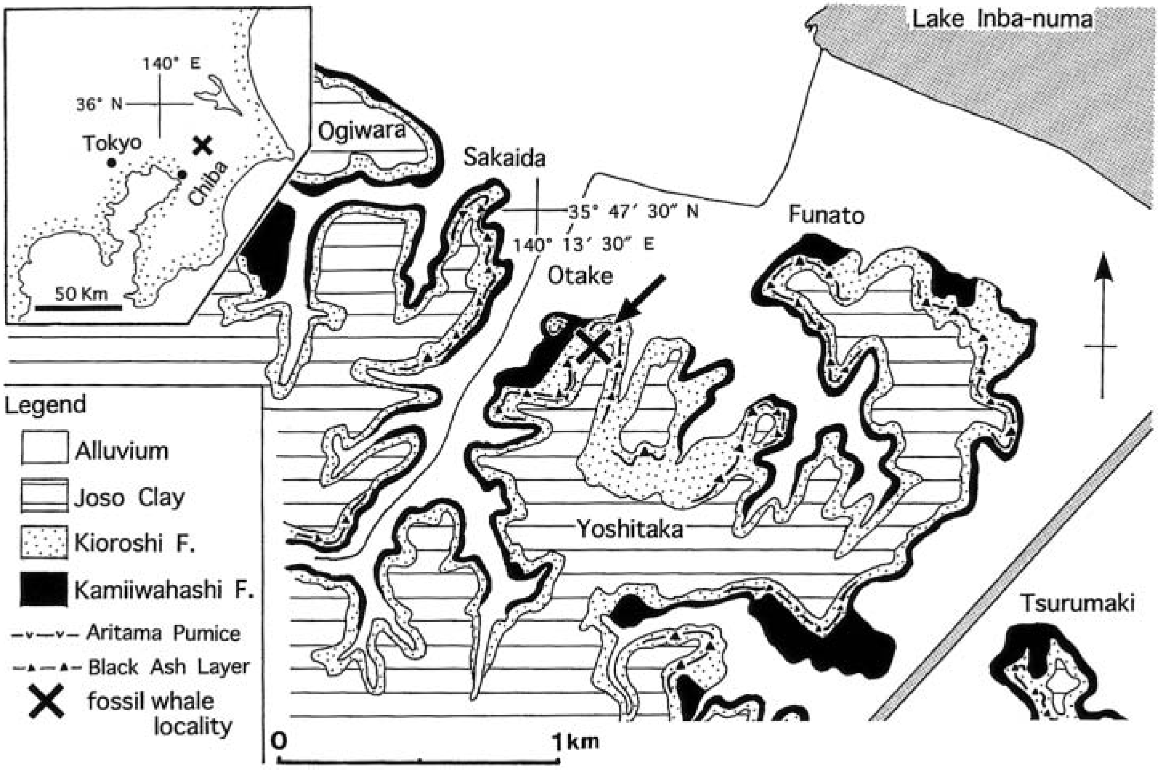

Figure 1. Geologic map around the fossil locality (arrow), Otake area, Inba-mura, Chiba Prefecture, central Japan.

Figure 2. Mode of occurrence of CBM-PV662, ***Megaptera novaeangliae*** (Borowski, 1781), at the excavation site, Otake, Inba-mura.

NSMT-M32505 (Wada *et al.*, 2003, fig. 1); *B. edeni*, Junge (1950, pls. 1–3); *B. brydei*, NSMT-M3538, Junge (1950, pls. 4–6); *B. borealis*, NSMT-M3536, one TWM specimen, Gambell (1985a, figs. 4–5); *B. physalus*, one NSMT specimen, True (1904, pls. 1–4), Gambell (1985b, figs. 5–7); *B. musculus*, Yochem and Leatherwood (1985, fig. 7); *Caperea marginata*, Baker (1985, figs. 3–4); *Eschrichtius robustus*, NSMT-M15940, one TWM specimen, True (1904, pl. 47), Wolman (1985, fig. 2); *Eubalaena glacialis*, NSMT-M5153, one TWM specimen, True (1904, pls. 42–43), Cummings (1985, figs. 8–10); *Megaptera novaeangliae*, NSMT-M8457, True (1904, pls. 29–33), Winn and Reichley (1985, figs. 4–6).

Neogene species are as follows: *Burtinopsis similis*, Van Beneden (1882, pls. 87–96); *B. minutus*, Van Beneden (1882, pls. 97–102); *Burtinopsis* sp., IPMM40063 (Oishi *et al.*, 1985, pl. 3); *Megaptera affinis*, Van Beneden (1882, pls. 40–48); *M. miocaena*, Kellogg (1922, pls. 1–4); *M. hubachi*, Dathe (1983, figs. 1–4, pls. 1–3).

Geological setting

Stratigraphy.—The upper Plio-Pleistocene marine strata, which ascend in order from the Kazusa to the Shimousa Groups, are widely distributed from the central to northern areas of the Boso Peninsula. The Shimousa Group is divided into the following formations; the Jizodo, the Yabu, the Kamiizumi, the

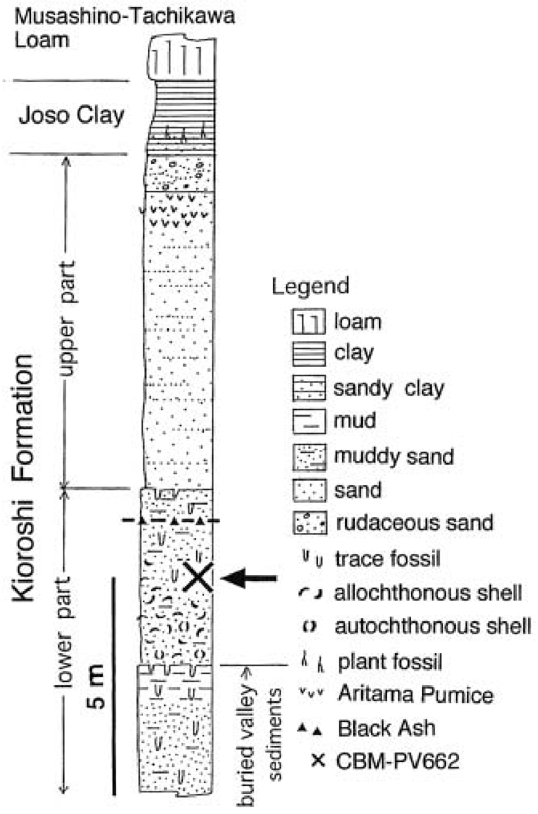

Figure 3. Columnar section of the fossil locality of Otake, Inba-mura.

Kiyokawa, the Yokota, the Kioroshi, the Anesaki Formations and the Joso Clay in ascending order (Tokuhashi and Endo, 1984). In the fossil locality area, the upper Shimousa Group (Kamiiwahashi Formation, Kioroshi Formation and Joso Clay), and the Musashino-Tachikawa Loam are distributed in ascending order (Figure 1). The Kamiiwahashi Formation is unconformable with the Kioroshi Formation (Shimousa Daichi Research Group, 1984), and is correlated to the Kiyokawa Formation (Nakazato, 1993). The Yokota and the Anesaki Formations are absent in this area. The Kioroshi Formation, which yielded the new fossil whale skull, is regarded as sediments of the latest interglacial stage (Kikuchi, 1974). Thus, this formation has buried valleys in its basal part. The Kioroshi Formation is divided into a lower part with a scoriaceous tephra (Black Ash) and an upper part with a pumiceous tephra (Aritama Pumice) (Shimousa Daichi Research Group, 1984). CBM-PV662 was found in the lower part of the Kioroshi Formation.

Occurrence.—The fossil locality, a quarry of Otake, is composed of the Kioroshi Formation (over 14 m thick), the Joso Clay (0.6 m thick) and the Musashino-Tachikawa Loam (over 1 m thick) in ascending order (Figure 3). The bottom of the lower part of the Kioroshi Formation at the site is also regarded as buried valley sediments, and is composed of a fine- to medium-grained sand bed (over 2 m thick) and a mud bed (ca. 0.8 m thick) in ascending order. These sediments are overlain by a massive muddy fine-grained sand bed (4 m thick) with abundant mollusks and the Black Ash (5–15 cm thick). The fossil skull was obtained from 1 to 1.4 m below the Black Ash. The skull missing the rostrum was laid parallel with the bedding and its dorsal was turned upward (Figure 2). The upper part of the Kioroshi Formation at the site is composed mainly of a parallel-laminated medium-grained sand bed (ca. 7.5 m thick) with the Aritama Pumice (0.8 m thick).

Age.—The lowermost part of the Joso Clay often interleaves with distinct tephras (KlP-6 and KlP-8). Their fission-track ages are dated as 128 ± 11 ka (KlP-6) and 132 ± 10 ka (KlP-8) (Machida and Suzuki, 1971). Another tephra (TAu-12) was found in the lower part of the Kioroshi Formation in the southern Shimousa Upland (Machida *et al.*, 1974; Sugihara *et al.*, 1978). Its fission-track age is dated as 143 ± 11 ka or 147 ± 9 ka (Machida, 1977). Accordingly, the age range of the Kioroshi Formation is estimated to be from 125 to 150 ka. The new specimen (CBM-PV662) was discovered in the lower part of this formation. Therefore, its age can be ascribed to the latest Middle Pleistocene time.

Systematic description

Class Mammalia Linnaeus, 1758
Order Cetacea Brisson, 1762
Suborder Mysticeti Flower, 1864
Family Balaenopteridae Gray, 1864
Subfamily Megapterinae Gray, 1864

Genus ***Megaptera*** Gray, 1846

Type species.—*Megaptera longimana* Gray, 1846 [= *Balaena novaeangliae* Borowski, 1781]

Emended diagnosis.—Supraorbital process of frontal elongated laterally with short orbit, both posterior margins of frontals straight transversely; squamosal slender, zygomatic protrudent anterolaterally, squamosal sulcus not developed; alisphenoid not exposed between parietal and pterygoid in temporal region.

Remarks.—Osteological description of Muller (1954) shows a large exposure of the alisphenoid in the temporal region in *M. novaeangliae.* But on the basis of reexamination of Muller's *Megaptera* specimen, Oishi (1999) argues that Muller (1954) has mistaken the alisphenoid for the pterygoid (Muller, 1954, fig. 2, g, table 2, description, p. 285). Therefore, it is plausible that the alisphenoid is not visible in *M. novaeangliae.*

Megaptera novaeangliae (Borowski, 1781)

Figures 4, 5

Types.—None in existence (Hershkovitz, 1966).

Diagnosis.—"Skull very broad; rostrum obtuse, sides slightly convex. Outer margin of intermaxillae (= premaxillae) sinuous. Nasals narrow, the anterior free margin acutely pointed. Orbital process (= supraorbital process) of frontal triangular, very broad transversely; orbital margin narrow, oblique, the posterior angle (= postorbital process) extending out much farther than the anterior (= antorbital process). Occiput (= supraoccipital) narrow anteriorly. Coronoid process of mandible low. (True, 1904, p. 299). " ; no squamosal sulcus at the base of zygomatic process (Oishi, 1999); no exposure of alisphenoid in temporal region (Ridewood, 1922; Oishi, 1999).

Referred material and depository.—CBM-PV662, incomplete skull; deposited in the Natural History Museum and Institute, Chiba; collected by students of Kogane Senior High School and Y. Mitani in May 1990; mentioned by Nagasawa and Mitani (1999).

Locality.—A quarry of Otake in Inba-mura, Chiba Prefecture, Japan.

Horizon and age.—1 to 1.4 m below the Black Ash in the lower part of the Kioroshi Formation, latest Middle Pleistocene.

Preservation.—CBM-PV662 (Figures 4, 5) is an incomplete skull lacking the bones of the rostrum, the

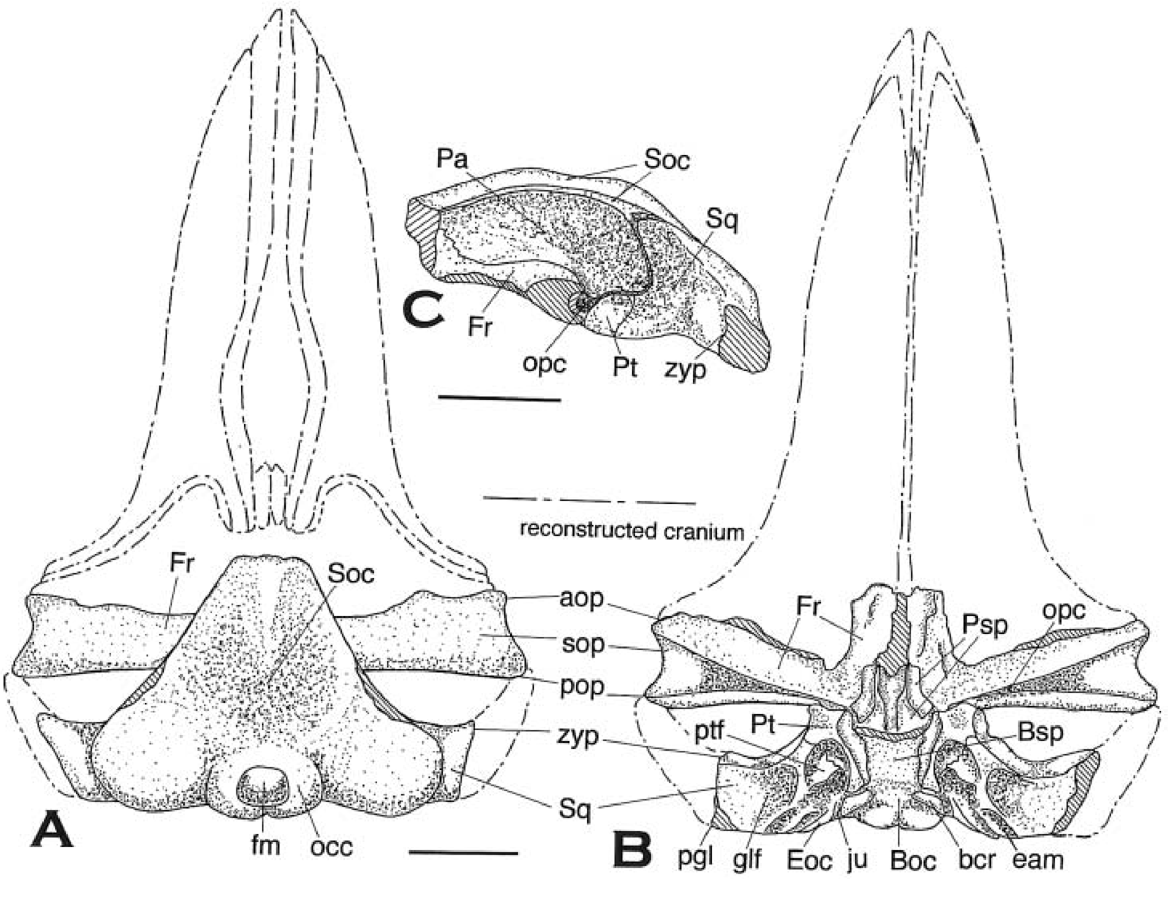

Figure 4. Drawings of the skull of CBM-PV662, ***Megaptera novaeangliae*** (Borowski, 1781). **A**, dorsal view; **B**, ventral view; **C**, left anterolateral view without supraorbital processes of frontals. Hatched areas indicate broken parts. Abbreviations: aop, antorbital process of frontal; bcr, basioccipital crest; Boc, basioccipital; Bsp, basisphenoid; eam, external auditory meatus; Eoc, exoccipital; fm, foramen magnum; Fr, frontal; glf, glenoid fossa; jn, jugular notch; occ, occipital condyle; opc, optic canal; pgl, postglenoid process; pop, postorbital process of frontal; Pa, parietal; Psp, presphenoid; Pt, pterygoid; ptf, pterygoid fossa; Soc, supraoccipital; sop, supraorbital process of frontal; Sq, squamosal; zyp, zygomatic process of squamosal. Scale bar equals 30 cm.

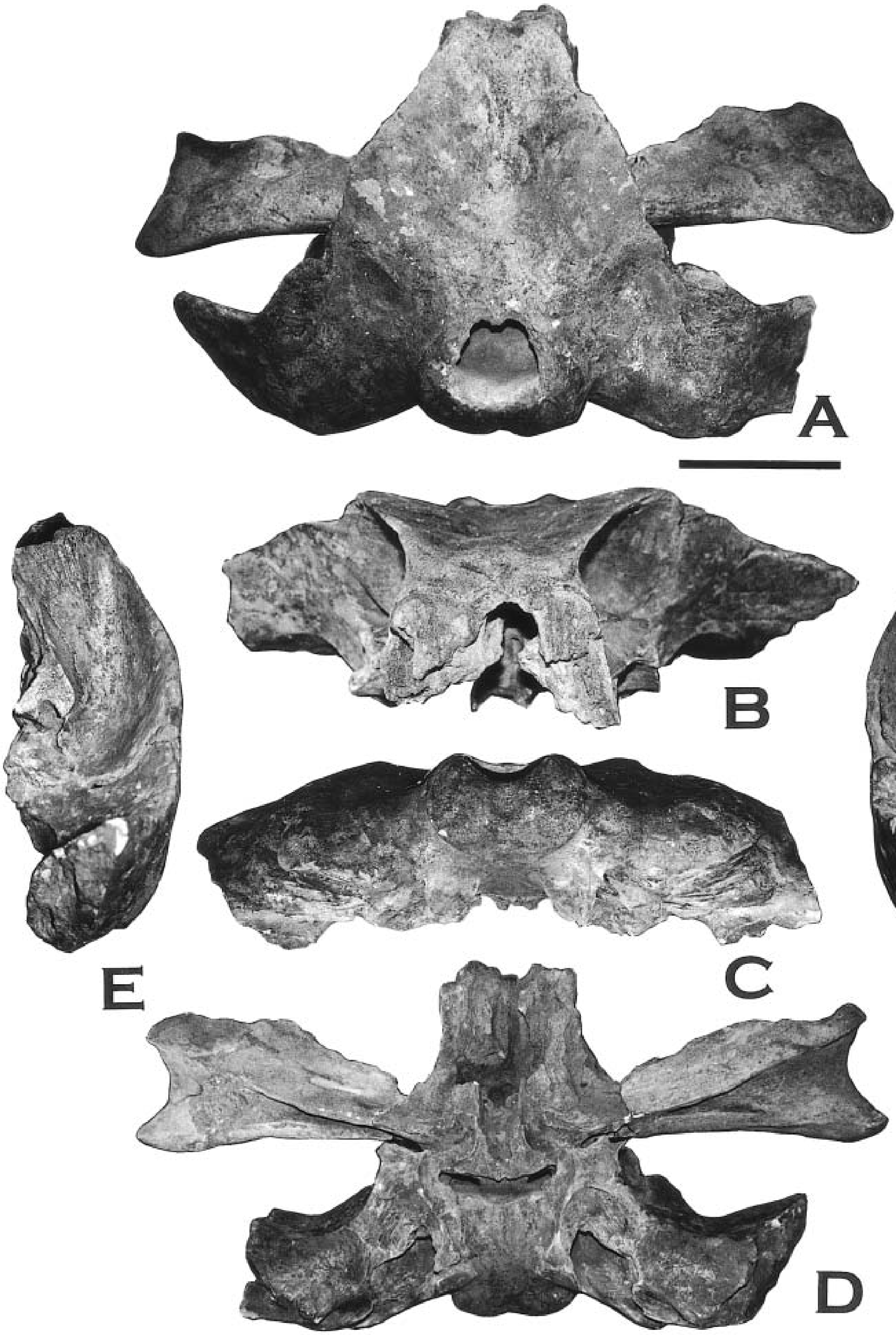

Figure 5. CBM-PV662, skull of ***Megaptera novaeangliae*** (Borowski, 1781), from the Kioroshi Formation of Otake, Inba-mura, Chiba Prefecture. **A**, dorsal view; **B**, anterior view without supraorbital processes of frontals; **C**, posterior view without supraorbital processes of frontals; **D**, ventral view; **E**, left lateral view without supraorbital processes of frontals; **F**, right lateral view without supraorbital processes of frontals. Scale bar equals 30 cm.

Table 1. Measurements (in cm) of CBM-PV662.

Greatest length of skull	76.4
Greatest breadth of skull across postorbital processes of frontals	142.5
Greatest breadth across zygomatic processes of squamosals as preserved	109.2
Height of skull as preserved	33.5
Length from anterior apex of supraoccipital to posterior margin of occipital condyle	69.6
Length from anterior apex of supraoccipital to dorsal rim of foramen magnum	57.7
Greatest breadth of supraoccipital	77.1
Greatest breadth across exoccipitals	77.8
Breadth across paroccipital processes of exoccipitals	70.2
Length of orbit, right	20.3
Width of foramen magnum	13.0
Height of foramen magnum	13.1
Breadth across occipital condyles	29.3
Height of occipital condyle, right	20.6
Greatest breadth of basioccipital across lateral margins of basioccipital crests	29.8
Length of basioccipital crest, right	7.7
Breadth of basioccipital crest, right	9.0
Least distance between basioccipital crests	11.3
Greatest distance between lateral margins of pterygoids at temporal fossae	48.6
Greatest distance between lateral margins of pterygoids at ventral surface	45.2
Greatest breadth of basisphenoid visible at ventral surface	21.5
Length of pterygoid, right	24.6
Breadth of pterygoid, right	15.3
Length of presphenoid	21.4
Breadth of presphenoid	22.0
Length of pterygoid fossa, right	16.1
Breadth of pterygoid fossa, right	12.1

lacrimals, the jugals, anterior parts of the frontals, both anterior parts of the zygomatic processes, the vomer, the palatines, ventral parts of the pterygoids, the tympanic bullae, and the periotics. The ventral surface is worn, but the outlines of the remaining elements are identifiable. The skull is slightly compressed dorsoventrally by the sedimentation. Owing to that, there is a transversal crack along the intersphenoidal suture in the ventral region. Measurements are shown in Table 1.

Frontal.—The supraorbital process of the frontal is elongated laterally. The orbital margin is slightly concave, and the postorbital process projects more laterally than the antorbital process. The length of the orbit is short considering the skull size. The optic groove on the ventral surface of the supraorbital process is isosceles triangle-shaped. The posterior margin of the frontal is not curved and both their posterior margins are lined up straight.

Parietal.—The parietal occupies the anterior region of the temporal fossa. The parietal is sutured with the squamosal at the posterior and with the supraoccipital at the dorsal margin. The dorsal margin of the temporal fossa is sharp-edged.

Squamosal.—The squamosal is slender and the zygomatic process protrudes anterolaterally at an obtuse angle. The turning at the base of the anterior margin of the zygomatic process shows an angle of ca. 130 degrees. At the base of the zygomatic process, the squamosal sulcus is not developed and this region is smooth (Figure 4, C). The glenoid fossa is narrow and shallow on the ventral surface of the squamosal. Both of the falciform processes of the squamosals are missing. Therefore, the foramina pseudoovale are not visible in the anteromedial corners of the glenoid fossae. The postglenoid process, which is partly broken, weakly projects posteriorly. The external auditory meatus is laid posterior to the glenoid fossa. The articular groove for the posterior process of the periotic runs along the immediate posterior to the external auditory meatus. The squamosal is sutured with the exoccipital in this articular groove.

Occipital.—In dorsal view, the supraoccipital is equilateral triangle-shaped. The foramen magnum is a large subtrapezoidal opening in shape. The occipital condyle is worn. As both the basioccipital crests are relatively separate from each other, the basioccipital shows a wide plane. The basioccipital is fused with the basisphenoid and the suture between them is obliterated. The visible basisphenoid on the ventral surface is also a wide plane. Therefore, the basal region composed of the basioccipital and the basisphenoid forms a large plane. The narrow groove of the jugular notch runs along the lateral of the basioccipital crest. The paroccipital process of the exoccipital is relatively small.

Sphenoid.—As the palatines and the vomer are missing, the presphenoid and the basisphenoid are visible. The ventral surface of the presphenoid is broken off. The intersphenoidal suture is rifted as a large crack. The basisphenoid and the basioccipital are intimately fused as mentioned above. In the temporal region, the alisphenoid is not exposed between the parietal and the pterygoid (Figure 4, C). The orbitosphenoid is not visible in the optic canal.

Pterygoid.—As both the inferior laminae with hamular processes of the pterygoids are broken off, the pterygoid fossae are visible as egg-shaped large cavities. The medial lamina of the pterygoid is lined up with the basioccipital crest.

Comparisons

Extant species.—Recent Mysticeti consists of four families: Neobalaenidae, Balaenidae, Eschrichtiidae and Balaenopteridae (Barnes *et al.*, 1985; Rice, 1998; Fordyce and Muizon, 2001).

The Neobalaenidae, having the only species *Caperea marginata*, shows the most distinct features in the Mysticeti, being different from CBM-PV662, as follows: the supraoccipital is isosceles triangle-shaped; the frontal and the squamosal are less developed laterally and both the frontals are analogous to the wings of a jet plane; the squamosal is noticeably broad with weakened zygomatic process. The Balaenidae also has different features from CBM-PV662. For example, the frontal and the squamosal are slender and more developed laterally; the zygomatic process of the squamosal projects anterolaterally at a larger obtuse angle. The Eschrichtiidae, having the only species *Eschrichtius robustus*, is slightly similar to *Balaenoptera*, but has also separate features from CBM-PV662. For example, both the frontal and the squamosal of the Eschrichtiidae are less developed laterally, and the posterior margin of the frontal is remarkably wavy.

The Balaenopteridae is composed of *Balaenoptera* and *Megaptera. Megaptera* has only the extant species *M. novaeangliae.* Recently extant *Balaenoptera* has been reclassified into eight species including one new species by analyses of external morphology, osteology and mitochodrial data (Wada *et al.*, 2003). These are as follows: *B. acutorostrata*, *B. bonaerensis*, *B. omurai*, *B. edeni*, *B. brydei*, *B. borealis*, *B. physalu*s, and *B. musculus*. There are evident differences between *Balaenoptera* and *Megaptera*, and besides CBM-PV662 is similar to *M. novaeangliae*. *Balaenoptera* species are distinguished from CBM-PV662 and *M. novaeangliae* by the following characteristics: the frontal is smaller and less developed laterally; both posterior margins of the frontals are not straight transversely; the orbit of the frontal is relatively longer; the squamosal is not slender; the zygomatic process of the squamosal protrudes more anteriorly; the squamosal sulcus is developed at the base of the zygomatic process (Miller, 1924; Oishi, 1999), but the squamosal sulcus does not occur in *M. novaeangliae* (Oishi, 1999); the alisphenoid is commonly exposed like a small patch between the parietal and the pterygoid around the subtemporal fossa, but the alisphenoid does not appear in *M. novaeangliae* (Ridewood, 1922; Oishi, 1999). Even in the foetal *M. novaeangliae*, the alisphenoid is not visible in the temporal region (Ridewood, 1922).

As a result, CBM-PV662 is the most conformable with *M. novaeangliae* among the extant mysticete species.

Neogene species.—There are four *Megaptera* species which have been described from the Neogene strata. These are as follows: *M. expansa* Cope, 1868 (cervical, thoracic and lumbar vertebrae); *M. affinis* Van Beneden, 1880 (a mandible, tympanic bullae and vertebrae); *M. miocaena* Kellogg, 1922 (a partial skull with tympanic bullae and periotics) and *M. hubachi* Dathe, 1983 (a moderately complete skull with associated elements). But it may be necessary to consider whether or not these species actually belong to the genus *Megaptera* with a thorough diagnostic examination of the genus *Megaptera*.

The type locality of *M. expansa* has not been described, but numerous vertebrae are presumed to be from the Upper Miocene of Maryland (Kellogg, 1968). Since *M. expansa* is based on a vertebral specimen, this species has been judged to be lacking in sufficient diagnostic characteristics (Kellogg, 1968). *M. affinis* is from the Pliocene of Belgium. Another species, *Megapteropsis robusta* Van Beneden, 1872, is regarded by Van Beneden as a synonym of *M. affinis* (Van Beneden, 1880, 1882). Deméré (1986) indicates that the mandible of *M. affinis* closely resembles that of extant *Eschrichtius robustus*. Consequently, there is a high possibility that *M. affinis* has mixed with some materials of variant taxa. Since *M. expansa* and *M. affinis* are defective as mentioned above, we have excluded these two species from our comparisons with CBM-PV662.

The other Neogene species related to CBM-PV662 are *M. miocanea* and *M. hubachi*. *M. miocaena* is from the Upper Miocene (Barnes, 1977) of California. This species is distinguished from CBM-PV662 and the living humpback whale by the following features: the frontal is narrower anteroposteriorly and less developed laterally; the orbit is longer; the supraoccipital is isosceles triangle-shaped; the basioccipital region is narrower. *M. hubachi* is from the Lower Pliocene of Coquimbo, Chile. This species is also distinguished from CBM-PV662 and the living humpback whale by the following features: the body size is remarkably smaller (body length, ca. 6 m); the frontal is also narrower anteroposteriorly and less developed laterally; the orbit is longer. Hence, CBM-PV662 is different from these species.

In addition to these, two related Neogene species belonging to the Balaenopteridae have been described as *Burtinopsis similis* Van Beneden, 1872 and *Burtinopsis minutus* Van Beneden, 1880 from the Pliocene of Belgium. Both materials are composed of mandibles, tympanic bullae and vertebrae. Kellogg (1922) regarded *Burtinopsis* and *Megapteropsis* as being synonyms for *Megaptera*. In accordance with this opinion, Dathe (1983) changed Van Beneden's names to *Megaptera similis*, *Megaptera minuta* [*sic*], and *Megaptera robusta* (= *M. affinis*). Afterward, different taxonomical views of the genus *Burtinopsis* were proposed. Deméré (1986) identifies *Burtinopsis* as *Balaenoptera* on the basis of the characteristics of the mandibles, and changed Van Beneden's names to *Balaenoptera similis* and *Balaenoptera minutis* [*sic*]. Oishi and Hasegawa (1995a) accepted the genus *Burtinopsis* on the basis of the characteristics of the tympanic bullae. Thus, opinions are divided among taxonomists on this subject. In this connection, Oishi and Hasegawa (1995a) assigned IPMM40063 as *Burtinopsis* species. IPMM40063, an almost complete skeleton from the Early Pliocene of Iwate (Oishi *et al.*, 1985), is much smaller and its skull is relatively similar to that of *Balaenoptera*. Therefore, we have excepted *Burtionpsis* from our comparisons with CBM-PV662.

There is an additional piece of evidence for the identity of the taxon of CBM-PV662. CBM-PV662 has no earbone, however, we verified that a tympanoperiotic bone from a living humpback whale (one CBM specimen) fits the articular groove and the pterygoid fossa of CBM-PV662 perfectly. The tympanic bulla of *M. novaeangliae* is different from that of the other living mysticete species (Oishi and Hasegawa, 1995a). The squamosal of *M. novaeangliae* is different from that of the other living mysticete species based on our observation and the above comparisons on mysticete squamosals. Therefore, the articulation of the periotic of *M. novaeangliae* with the squamosal is presumed to be also different from that of the other living mysticete species, and the fact that a periotic of *M. novaeangliae* fits CBM-PV662 can be explained quite naturally as both materials belonging to the same species.

In summary, almost all the features of CBM-PV662 are consistent with the extant humpback whale, and no Neogene species conform with CBM-PV662. As a result, CBM-PV662 can be identified as *Megaptera novaeangliae* (Borowski, 1781).

Body length.—The greatest breadth of the frontals of CBM-PV662 measures 142.5 cm (Table 1). Tomilin (1957) examines the relationship between the skull size and the body length of the humpback whales. His study indicates that the greatest breadth of the frontals is ca. 85–93% of the greatest breadth of the squamosals, and the greatest breadth of the squamosals is ca. 57–67% of the skull length, while the skull length is ca. 29–31% of the body length. Besides, the skull length rate of the body length in the humpback whales increases as ca. 22–30% with aging (Tomilin, 1957; True, 1904), because the skull of the humpback whales grows more rapidly in length than in breadth (Tomilin, 1957; Winn and Reichely, 1985).

The skull size and the condition of the cranial sutures of CBM-PV662 suggest that CBM-PV662 is an adult individual. On the basis of the above data (True, 1904; Tomilin, 1957; Winn and Reichely, 1985) and the assumption of CBM-PV662 as an adult, we evaluate that the greatest breadth of the frontals as ca. 90% of the greatest breadth of the squamosals, the greatest breadth of the squamosals as ca. 60% of the skull length, and the skull length as ca. 30% of the body length. Owing to these proportions, the body length of CBM-PV662 is estimated to be ca. 9 m.

Concluding remarks

CBM-PV662 is a rare specimen that can be traced back to Pleistocene time. In comparison, the living gray whale, *Eschrichtius robustus*, is dated back to the Middle Pleistocene (no more than 0.5 Ma; Barnes and McLeod, 1984). CBM-PV662 is the first Middle Pleistocene record of *M. novaeangliae* in the western North Pacific. Moreover, there is a significant possibility that CBM-PV662 is the oldest fossil of the species *M. novaeangliae* in the world, because there have been no publications regarding Pleistocene *M. novaeangliae* to date.

Living humpback whales are distinctive from the other balaenopterids in their external appearance. For exsample, *Megaptera* has a head studded with tubercles and a noticeably elongated pectoral fin. This suggests that *Megaptera* is derived from *Balaenoptera* in the early evolutionary process of the Balaenopteridae. *Megaptera miocaena*, the earliest species of the humpback whale, is from the Upper Miocene of California (Barnes, 1977). The Japanese oldest humpback whale fossil is also from the Upper Miocene (Kato, 1979; Oishi and Sato, 1991). Furthermore, the supposed ancestor of balaenopterids, including *Balaenoptera* and *Megaptera*, is the cetotheres (Cetotheriidae) (Barnes, *et al.*, 1985; Fordyce and Muizon, 2001). From this information, it can be inferred that *Megaptera* had diverged from the *Balaenoptera* lineage before the Late Miocene, probably in the Middle Miocene, and this taxon has had a wide range in the North Pacific since Late Miocene time. However, it is problematic to discuss the phylogeny of *Megaptera* and the evolutionary process which gave rise to it, because fossil humpback whales are rare.

The Japanese Islands are representative fossil localities of cetaceans in the western North Pacific. Therefore, this area is vital for the comparisons of the fossil cetacean assemblages between the eastern and western North Pacific. Lists of the Japanese fossil cetaceans have been reported (Kimura, 1992; Oishi and Hasegawa, 1995b). According to these references and Nagasawa (1999), there are six fossil records assigned as *Megaptera*, even though the species is unidentifiable. These materials are as follows: tympanic bullae, vertebrae and ribs from the Upper Miocene of Iwaki, Aomori (Oishi and Sato, 1991); a skull from the Upper Miocene of Yashima, Akita (Kato, 1979); mandibles from the Lower Pliocene of Mamurogawa, Yamagata (Nagasawa, 1999); a tympanic bulla from the Lower Pliocene of Sendai, Miyagi (Oishi and Sato, 1991); tympanic bullae from the Lower Pliocene of Choshi, Chiba (Oishi and Hasegawa, 1995a); vertebrae from the Holocene of Yokohama, Kanagawa (Hasegawa and Matsushima, 1968). Japanese fossils indicate that the humpback whales have been living in the western North Pacific since the Late Miocene, and the CBM-PV662 specimen is a supporting piece of evidence that the species *M. novaeangliae* has existed since the latest Middle Pleistocene.

Acknowledgements

We would like to thank the students of the Earth Science Club of Kogane Senior High School for their help with excavations and preparations of the fossil. We would like to thank Naoki Takahashi (Natural History Museum and Institute, Chiba) for making arrangements for the donation. We wish to thank Masayuki Oishi (Iwate Prefectural Museum), Toshiyuki Kimura (Gunma Museum of Natural History) and Hiroto Ichishima (Fukui Prefectural Dinosaur Museum) for their helpful comments and for providing relevant literature. We are especially indebted to Masayuki Oishi for his valuable advice and criticisms. We would like to express our gratitude to Tadasu K. Yamada (National Science Museum, Tokyo), Shoichi Shimoichi (Taiji Whale Museum) and Isao Jinbo (Yamagata Prefectural Museum) for permission to research the skeletal specimens housed in their Museum. We are grateful to Hajime Ishikawa (Institute of Cetacean Research) and the staff of his institute library for their help with our literature survey. We want to thank Suburu Oba and Ryuichi Abe for their assistance in measuring the specimen and taking pictures. We would like to thank Tohru Yamanoi (Yamagata University), Yoshiaki Ishida (Chitosegaoka Senior High School) and Hideo Yabe (Yoshida Construction) for their helpful comments. We wish to thank to Richard W. Jordan, Stephen B. Ryan (Yamagata University) and Gabrielle Piggin (Board of Education of Yamagata Prefecture) for correcting our English manuscript. Finally, we are grateful to referees of the Palaeontological Society of Japan for their valuable comments.

References

Baker, A. N., 1985: Pygmy right whale, *Caperea marginata* (Gray, 1846). *In*, Ridgway, S. H. and Harrison, R. J. *eds.*, *Handbook of Marine Mammals, vol. 3, The Sirenians and Baleen Whales*, p. 345–354. Academic Press, London.

Barnes, L. G., 1977: Outline of eastern North Pacific fossil cetacean assemblages. *Systematic Zoology*, vol. 25, p. 321–343.

Barnes, L. G. and McLeod, S., 1984: The fossil record and phyletic relationships of gray whales. *In*, Jones, M. L., Swartz, S. L. and Leatherwood, S. *eds., The Gray Whale: Eschrichtius robustus*, p. 3–32. Academic Press, Orlando, Florida.

Barnes, L. G., Domning, D. P. and Ray, C. E., 1985: Status of studies on fossil marine mammals. *Marine Mammal Science*, vol. 1, p. 15–53.

Borowski, G. H., 1781: *Gemeinnützige Naturgeschichte des Thierreiches*. vol. 2, p. 21 Berlin.

Brisson, M. J., 1762: *Regnum animale in classes IX distributum, sive synopsis methodica sistens generalem animalium distributionem in classes IX, & duarum primarum classium, quadripedum scilicet & cetaceorum, particularum divisionem in ordines, sectiones, genera, & species, Editio altera auctior*, 296 p. Theodorum Haak, Lugduni Batavorum (Leiden).

Cope, E. D., 1868: Second contribution to the history of the Vertebrata of the Miocene period of the United States. *Proceedings of the Academy of Natural Sciences of Philadelphia*, vol. 20, p. 184–194.

Cummings, W. C., 1985: Right whales, *Eubalaena glacialis* (Müller, 1776) and *Eubalaena australis* (Desmoulins, 1822). *In*, Ridgway, S. H. and Harrison, R. J. *eds., Handbook of Marine Mammals, vol. 3, The Sirenians and Baleen Whales*, p. 275–304. Academic Press, London.

Dathe, F., 1983: *Megaptera hubachi* n. sp., ein fossiler Bartenwal aus marinen Sandsteinschichten des tieferen Pliozäns Chiles. *Zeitschrift für Geologische Wissenschaften*, vol. 11, p. 813–848. (*in German with English abstract*)

Deméré, T. A., 1986: The fossil whale, *Balaenoptera davidsonii* (Cope, 1872), with a review of other Neogene species of *Balaenoptera* (Cetacea: Mysticeti). *Marine Mammal Science*, vol. 2, p. 277–298.

Flower, W. H., 1864: Notes on the skeletons of whales in the principal museums of Holland and Belgium, with descriptions of two species apparently new to science. *Proceedings of the Zoological Society of London 1864*, p. 384–420.

Fordyce, R. E., and Muizon, C. de, 2001: Evolutionary history of cetaceans: a review. *In*, Mazin, J. M. and Buffrénil. V. de *eds., Secondary Adaptation of Tetrapods to Life in Water: Proceedings of the International Meeting, Poitiers, 1996*, p. 169–233. Munich, F. Pfeil.

Gambell, R., 1985a: Sei whale, *Balaenoptera borealis* Lesson, 1828. *In*, Ridgway, S. H. and Harrison, R. J. *eds.*, *Handbook of Marine Mammals, vol. 3, The Sirenians and Baleen Whales*, p. 155–170. Academic Press, London.

Gambell, R., 1985b: Fin whale, *Balaenoptera physalus* (Linnaeus, 1758). *In*, Ridgway, S. H. and Harrison, R. J. *eds., Handbook of Marine Mammals, vol. 3, The Sirenians and Baleen Whales*, p. 171–192. Academic Press, London.

Gray, J. E., 1846: On the cetaceous animals. *In*, Richardson, J. and Gray, J. E. *eds., The Zoology of the Voyage of H. M. S. Erebus and Terror under the Command of Captain Sir James Clark Ross, R. N. F., R. S., during the Years 1839 to 1843*, vol. 1, p. 13–53. E. W. Janson, London.

Gray, J. E., 1864a: On the Cetacea which have been observed in the seas surrounding the British Islands. *Proceedings of the Zoological Society of London 1864*, p. 195–248.

Gray, J. E., 1864b: Notes on the whalebone whales; with a synopsis of the species. *The Annals and Magazine of Natural History, Ser. 3*, vol. 14, p. 345–353.

Hasegawa, Y. and Matsushima, Y., 1968: Fossil vertebrae of humpback whale from the alluvial deposits in Yokohama City. *Bulletin of the Kanagawa Prefectural Museum*, no. 1, p. 29–36, pl. 1.

Hershkovitz, P., 1966: Catalog of living whales. *United States National Museum Bulletin*, vol. 246, p. 1–259.

Junge, G. C. A., 1950: On a specimen of the rare fin whale, *Balaenoptera edeni* Anderson, stranded on Pulu Sugi near Singapore. *Zoologische Verhandelingen*, no. 9, p. 1–26, pls. 1–9.

Kato, M., 1979: Fossil cetaceans from Akita Prefecture. *Bulletin of Tohoku Branch, Geological Society of Japan*, no. 9, p. 17–18. (*in Japanese*)

Kellogg, R., 1922: Description of the skull of *Megaptera miocaena*, a fossil humpback whale from the Miocene diatomaceous earth of Lompoc, California. *Proceedings of the United States National Museum*, vol. 61, p. 1–18, pls. 1–4.

Kellogg, R., 1968: Miocene Calvert mysticetes described by Cope. *United State National Museum Bulletin*, vol. 247, p. 103–132.

Kikuchi, T., 1974: Characteristics of Quaternary tectonic movements in the Kanto District, Japan. *In*, Kakimi, T. and Suzuki, Y. *eds., Earthquake and Crustal Movements in the Kanto District*, p. 129–146. Ratisu, Tokyo. (*in Japanese*)

Kimura, M., 1992: Stratigraphy and inhabited environments of the Cetacea in Japan. *Memoirs of the Geological Society of Japan*, no. 37, p. 175–187. (*in Japanese with English abstract*)

Linnaeus, C., 1758: *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata*, 824 p. Impensis Direct. Laurentii Salvii, Holmiae (Stockholm).

Machida, H., 1977: *The Volcanic Ashes*, 324 p. Sojushobo, Tokyo. (*in Japanese*)

Machida, H., and Suzuki, M., 1971: Absolute ages of tephras and tephrochronological study in the late Quaternary. *Kagaku Science Journal*, vol. 41, p. 263–270. (*in Japanese*)

Machida, H., Arai, F., Murata, A. and Hakamada, K., 1974: Correlation and chronology of the Middle Pleistocene tephra layers in South Kanto. *Journal of Geography*, vol. 83, p. 22–58. (*in Japanese with English abstract*)

Miller, G. S. Jr., 1924: A pollack whale from Florida presented to the National Museum by the Miami Aquarium Association. *Proceedings of the United States National Museum*, vol. 66, p. 1–15.

Muller, J., 1954: Observations on the orbital region of the skull of the mystacoceti. *Zoologische Mededelingen*, no. 23, p. 279–290.

Nagasawa, K., 1992: A skull of minke whale from the bottom of the Japan Sea off Sakata City, Yamagata Prefecture, Northeast Japan. *Bulletin of the Yamagata Prefectural Museum*, no. 13, p. 11–18. (*in Japanese*)

Nagasawa, K., Yamada, T. K. and Ishikawa, H., 1998: Measurements of the skeleton of a minke whale (*Balaenoptera acutorostrata*) from the Antarctic Ocean. *Bulletin of the Yamagata Prefectural Museum*, no. 20, p. 1–19.

Nagasawa, K., 1999: Fossil whales from the Pliocene Noguchi Formation in Mamurogawa-machi, Yamagata Prefecture, Northeast Japan. *In*, Nagasawa, K. and Oba, S. *eds., Research Report on the Fossil Whale from Mamurogawa-machi in Yamagata Prefecture*, Yamagata Prefectural Museum, Yamagata, p. 11–52. (*in Japanese with English abstract*)

Nagasawa, K. and Mitani, Y., 1999: A fossil humpback whale from the Kioroshi Formation of the Shimousa Group in Inba-mura, Chiba Prefecture. *Abstract of the 1999 Annual Meeting of the Palaeontological Society of Japan*, p. 57. (*in Japanese*)

Nakazato, H., 1993: Stratigraphic relationship between the Kiyokawa and Kamiiwahashi Formations of the Middle-upper Pleistocene Shimosa Group, Chiba Prefecture, central Japan. *Journal of the Natural History Museum and Institute, Chiba*, vol. 2, p. 115–124.

Oishi, M., 1999: Comparison of the cranial elements around the subtemporal fossae of balaenopterid whales. *Nihonkai Cetology*, no. 9, p. 41–48. (*in Japanese with English abstract*)

Oishi, M., Hasegawa, Y. and Kawakami, T., 1985: Part IV. Fossil whale, the 2nd specimen from Maesawa-cho, Iwate Prefecture, Japan. *In*, Oishi, M., Ono, K., Kawakami, I., Sato, J., Nokariya, H. and Hasegawa, Y., Pliocene baleen whales and bony-toothed bird from Iwate Prefecture, Japan (Parts I–IV). *Bulletin of the Iwate Prefectural Museum*, no. 3, 150–154. (*in Japanese*)

Oishi, M. and Sato, T., 1991: On a fossil *Megaptera* from the foot of Iwaki Volcano, Aomori Prefecture and Mio-Pliocene balaenopterid whales in Northeast Japan. *Abstract of the 1991 Annual Meeting of the Palaeontological Society of Japan*, p. 66. (*in Japanese*)

Oishi, M. and Hasegawa, Y., 1995a: Diversity of Pliocene mysticetes from eastern Japan. *The Island Arc*, vol. 3, p. 436–452.

Oishi, M. and Hasegawa, Y., 1995b: A list of fossil cetaceans in Japan. *The Island Arc*, vol. 3, p. 493–505.

Reeves, R. R. and Leatherwood, S., 1985: Bowhead whale, *Balaena mysticetus* Linnaeus, 1758. *In*, Ridgway, S. H. and Harrison, R. J. *eds., Handbook of Marine Mammals, vol. 3, The Sirenians and Baleen Whales*, p. 305–344. Academic Press, London.

Rice, D. W., 1998: *Marine Mammals of the World, Systematics and Distribution*, 231p. Special Publication no. 4 of the Society for Marine Mammalogy, Lawrence, Kansas.

Ridewood, W. G., 1922: Observations on the skull in foetal specimens of whales of the genera *Megaptera* and *Balaenoptera*. *Philosophical Transactions of the Royal Society of London, Series B*, vol. 211, p. 209–272.

Shimousa Daichi Research Group, 1984: The relation between the shape of the base of the Kioroshi Formation and its facies, around Tega-mura, Chiba Prefecture, central Japan. *Earth Science* (*Chikyu Kagaku*), vol. 38, p. 226–234. (*in Japanese with English abstract*)

Sugihara, S., Arai, F. and Machida, H., 1978: Tephrochronology of the Middle to Late Pleistocene sediments in the northern part of the Boso Peninsula, central Japan. *Journal of the Geological Society of Japan*, vol. 84, p. 583–600. (*in Japanese with English abstract*)

Tokuhashi, S. and Endo, H., 1984: *Geology of the Anesaki District*. Quadrangle series, scale 1:50,000, 136 p. Geological Survey of Japan, Tsukuba. (*in Japanese with English abstract*)

Tomilin, A. G., 1957: Cetacea. *In*, Heptner, V. G. *ed., Mammals of the U.S.S.R. and Adjacent Countries*, vol. 9, 756 p. Izdatel'stvo Akademii Nauk SSSR, Moscow. (*English* *translation, 1967, 717 p., Israel Program for Scientific Translations, Jerusalem, translated from Russian by O. Ronen*).

True, F. W., 1904: The whalebone whales of the western North Atlantic compared with those occurring in European waters; with some observations on the species of the North Pacific. *Smithsonian Contributions to Knowledge*, vol. 33, p. 1–332, pls. 1–50.

Van Beneden, P. J., 1872: Les baleines fossiles d'Anvers. *Bulletin de l'Académie Royale des Sciences des Lettres et des Beaux-Arts de Belgique, Bruxelles, Sér. 2*, vol. 34, p. 6–20.

Van Beneden, P. J., 1880: Les mysticètes à courts fanons des sables des environs d'Anvers. *Bulletin de l'Académie Royale des Sciences des Lettres et des Beaux-Arts de Belgique, Bruxelles, Sér. 2*, vol. 50, p. 11–27.

Van Beneden, P. J., 1882: Description des ossements fossiles des environs d'Anvers, Troisième partie, Cétacés, genres: *Megaptera*, *Balaenoptera*, *Burtinopsis*, et *Erpetocetus*. *Annales du Musée Royal d'Histoire Naturelle de Belgique, Bruxelles, Sér. Paléontologique*, vol. 7, p. 1–90, pls. 40–109.

Wada, S., Oishi, M. and Yamada, T. K., 2003: A newly discovered species of living baleen whale. *Nature*, vol. 426, p. 278–281.

Winn, H. E. and Reichley, N. E., 1985: Humpback whale, *Megaptera novaeangliae* (Borowski, 1781). *In*, Ridgway, S. H. and Harrison, R. J. *eds., Handbook of Marine Mammals, vol. 3, The Sirenians and Baleen Whales*, p. 241–273. Academic Press, London.

Wolman, A. A., 1985: Gray whale, *Eschrichtius robustus* (Lilljeborg, 1861). *In*, Ridgway, S. H. and Harrison, R. J. *eds., Handbook of Marine Mammals, vol. 3, The Sirenians and Baleen Whales*, p. 67–90. Academic Press, London.

Yochem, P. K. and Leatherwood, S., 1985: Blue whale, *Balaenoptera musculus* (Linnaeus, 1758). *In*, Ridgway, S. H. and Harrison, R. J. *eds., Handbook of Marine Mammals, vol. 3, The Sirenians and Baleen Whales*, p. 193–240. Academic Press, London.