Review of the fossil balaenids from Japan with a re-description of *Eubalaena shinshuensis* (Mammalia, Cetacea, Mysticeti)

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*SUMMARY: About fifty specimens of fossil balaenids, representing at least 33 individuals, have been found in Japan. While the oldest of these specimens is Upper Miocene in age, the family seems to have reached its highest diversity in this area of the North Pacific during the Pliocene, with representatives of at least three genera (*Balaena, Balaenula, *and* Eubalaena*) dating from this time having been identified so far. This abrupt increase in the number of balaenid* taxa *during the Pliocene of Japan may ultimately have been the result of Neogene marine environmental changes, which led to an increase in krill and copepod productivity in the North Pacific.*
***Key words**: Balaenidae, western North Pacific, Japan*, Eubalaena shinshuensis, Balaena, Balaenula.

RIASSUNTO: Circa cinquanta esemplari di balenidi fossili, che rappresentano al massimo 33 individui, sono stati rinvenuti in Giappone. Mentre il più antico di questi campioni è databile al Miocene superiore, la famiglia sembra aver raggiunto la più alta diversità, in quest'area del Nord Pacifico, durante il Pliocene, con rappresentanti di almeno tre generi (*Balena, Balenula* e *Eubalena*) attribuiti a questo periodo. Questo brusco aumento del numero di *taxa* di balenidi durante il Pliocene in Giappone potrebbe essere stato il risultato dei cambiamenti dell'ambiente marino del Neogene con conseguente incremento di krill e di copepodi nel Pacifico settentrionale.
Parole chiave: Balaenidae, Pacifico Nordoccidentale, Giappone, *Eubalaena shinshuensis*, *Balaena, Balaenula.*

Introduction

At least 39 species of extant cetaceans can be found in the western North Pacific (Kasuya, 1996), including representatives of the two living genera of the family Balaenidae, *Eubalaena* (right whales) and *Balaena* (bowhead whale). Though now generally considered to comprise at least three extant species (Mead, Brownell 2005), the systematics of the genus *Eubalaena* is still controversial (e.g., Cummings, 1985; Jefferson *et al*., 1993; Rice, 1998; Rosenbaum *et al*., 2000; Gaines *et al*., 2005). Living right whales have a global distribution, ranging from temperate to subpolar latitudes in all of the world's oceans (Kenney, 2002). In the North Pacific, there have been reported sightings ranging from about 25˚ to 60˚N (Cummings, 1985). Prior to heavy exploitation by commercial whaling, there were large numbers of right whales in the western North Pacific around Japan (Braham, Rice, 1984). The living bowhead, *Balaena mysticetus*, is found in high latitude areas in the northern hemisphere. While the population in the Sea of Okhotsk is generally confined to the area north of 57˚N (Moore, Reeves, 1993), a young bowhead was captured by a fisherman in Osaka Bay (33˚28'N), Japan in 1969 (Nishiwaki, Kasuya, 1970). Although this individual may have been astray, this is the southernmost confirmed record of this species (Reeves, Leatherwood, 1985; Moore, Reeves, 1993), and thus members of both of the living balaenid genera have been sighted around Japan.

In addition to the large number of extant species, a variety of fossils found in Japan point to a diverse cetacean fauna in the Neogene of the western North Pacific (Oishi, Hasegawa, 1995b;

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Kimura, Ozawa, 2002). Although the fossils recovered to date include the remains of a number of extinct right whales, details of the evolution of balaenids in the western North Pacific have never been documented. Indeed, most of the balaenid fossils from Japan have never been diagnosed to species level, the only two exceptions being *Eubalaena shinshuensis* from the Gonda Formation, Nagano Prefecture, originally described by Kimura *et al.* (2007), and *E. glaciais* from the Holocene of Akita Prefecture, reported by Nishiwaki and Hasegawa (1969). The purpose of the present paper is to review the fossil balaenids found in Japan and re-describe the recently named fossil right whale *Eubalaena shinshuensis*.

Institutional Abbreviations: FM, Fukushima Museum, Aizuwakamatsu, Fukushima Prefecture, Japan; GMNH, Gunma Museum of Natural History, Tomioka, Gunma Prefecture, Japan; HUES, Hokkaido University of Education Sapporo, Sapporo, Hokkaido, Japan; IC, Iwaki City Coal and Fossil Museum, Iwaki, Fukushima Prefecture, Japan; KPM, Kanagawa Prefectural Museum of Natural History, Odawara, Kanagawa Prefecture, Japan; NFL, Numata Fossil Laboratory, Numata, Hokkaido, Japan; NSMT, National Science Museum, Tokyo, Japan; SFM, Shinshushinmachi Fossil Museum, Shinshushinmachi, Nagano Prefecture, Japan; USNM, United States National Museum of Natural History, Smithsonian Institution, USA; YK, Y. Kurihara collection; YPM, Yamagata Prefectural Museum, Yamagata, Yamagata Prefecture, Japan

Re-description of the Holotype of *Eubalaena shinshuensis*

Order Cetacea Brisson, 1762

Suborder Mysticeti, Flower, 1864

Family Balaenidae Gray, 1825

Genus *Eubalaena* Gray, 1864

Eubalaena shinshuensis Kimura, Narita, Fujita, and Hasegawa, 2007

(Figs. 1, 2, 3C-D; Plate 1)

Holotype: SFMCV-0024, cranium and lumbar vertebra.

Locality: SFMCV-0024 was found in 1938 by S. Nishizawa in Matatara, Yamahokari, Shinshushinmachi, Kamiminouchi County, Nagano Prefecture, Japan (Yagi, 1939).

Formation and Age: Gonda Formation, Late Miocene-Early Pliocene; SFMCV-0024 was collected from the lowermost part of the Gonda Formation. The Gonda Formation is overlain by the Johshita Formation, which in turn intercalates with the Kumeji pyroclastics. K-Ar dating places the geological age of the Kumeji pyroclastics at 4.2±0.3 Ma (Kato, 1989). Furuta and Amano (1993) reported the geological age of the Takafu Formation, which is a contemporaneous heterotopic facies of the Gonda Formation, as 4.3±0.2Ma. Hoyanagi *et al*. (1998) suggested the age of the lowermost part of the Gonda Formation to be between 5.5 and 6.3 Ma in age based on the sequence boundary. Similarly, Nagamori *et al*. (2003) and Motoyama and Nagamori (2006)

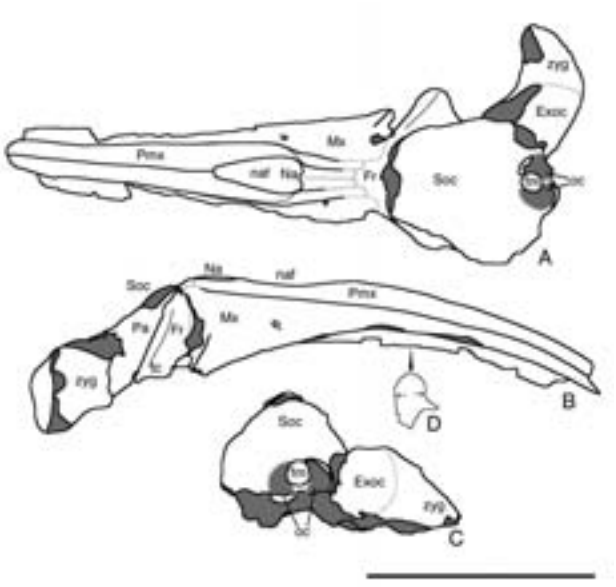

Fig. 1 - *Eubalaena shinshuensis* (SFMCV-0024). Cranium in dorsal (A), lateral (B), and posterior (C) views, and cross-sectional view of rostrum (D). Dashed lines indicate unpreserved and/or estimated structures, and grey areas indicate damaged portions. Arrows (in D) show the suture between the premaxilla and maxilla. Scale bar equals 1 m. Abbreviations: Exoc, exoccipital; fm, foramen magnum; Fr, frontal; Mx, maxilla; Na, nasal; naf, nasal fossa; oc, occipital condyle; Pa, parietal; Pmx, premaxilla; Soc, supraoccipital; Sq, squamosal; tc, temporal crest; zyg, zygomatic process of squamosal. (Kimura *et al*., 2007).

Fig. 1 - Eubalaena shinshuensis *(SFMCV-0024). Cranio in visione dorsale (A), laterale (B), posteriore (C), e sezione trasversale del rostro. Le linee punteggiate indicano strutture non conservate e/o ricostruite, le aree in grigio indicano porzioni danneggiate. Le frecce (D) mostrano le suture tra le ossa premascellari e mascellari. Barra: 1 m. Abbreviazioni: Exoc, esoccipitale; fm, foramen magnum; Fr, frontale; Mx, mascella; Na, nasale; naf, fossa nasale; oc, condilo occipitale; Pa, parietale; Pmx, premascellare; Soc, sopraoccipitale; Sq, squamoso; tc, cresta temporale; zyg, processo zigomatico dello squamoso (Kimura* et al., *2007).*

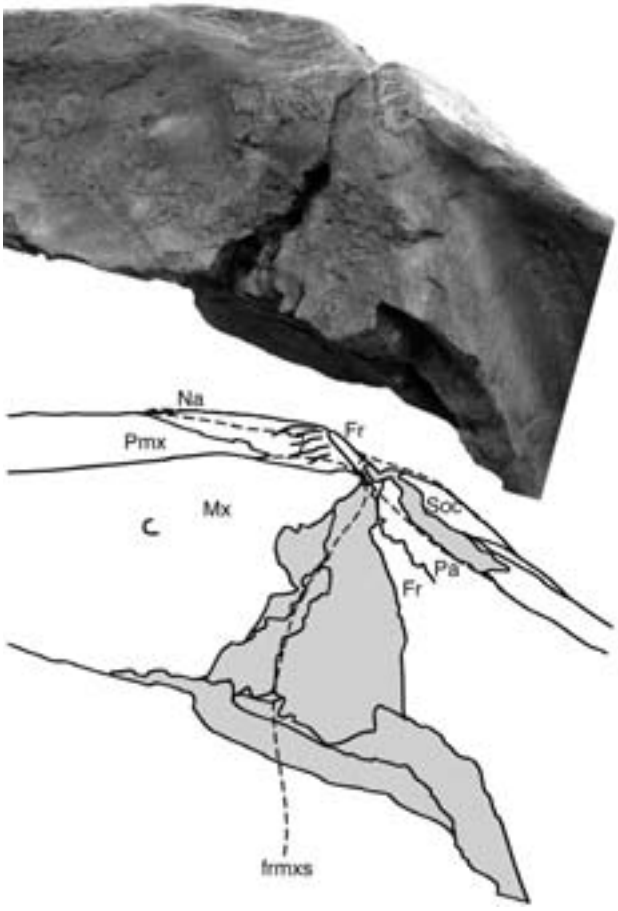

Fig. 2 - *Eubalaena shinshuensis* (GMNH-PV-1700; cast of holotype (SFMCV-0024)). Photograph and line drawing of left lateral view showing part of the cranium. Dashed lines indicate unpreserved and/or estimated structures. Grey areas indicate damaged portions. Abbreviations: Fr, frontal; frmxs, frontomaxillary suture; Mx, maxilla; Na, nasal; Pa, parietal; Pmx, premaxilla; Soc, supraoccipital. After Kimura *et al*. (2007).

Fig. 2 - Eubalaena shinshuensis *(GMNH-PV-1700; calco dell'holotipo (SFMCV-0024)). Fotografia e schema della vista laterale sinistra mostrante parte del cranio. Le linee tratteggiate indicano strutture non conservate e/o ricostruite, le aree in grigio indicano porzioni danneggiate. Abbreviazioni: Fr, frontale; frmxs, sutura frontomacellare; Mx, mascella; Na, nasale; Pa, parietale; Pmx, premascellare; Soc, sopraoccipitale. (Kimura* et al., *2007).*

also proposed the lowermost part of the Gonda Formation to date back to the late Miocene.

Diagnosis: A species of *Eubalaena* differing from other species of this genus by having a more robust premaxilla, a more posteriorly protruded squamosal (its posteriormost surface being extended to a point posterior to the level of the occipital condyles), a more slender nasal, and a relatively less arched cranium.

Remarks: Several authors briefly mentioned this specimen (Matsumoto, 1939; Tokunaga, 1939; Yagi, 1939; 1943), which originally included many parts of the skeleton. Unfortunately, however, most of it was subsequently lost and only the cranium and one lumbar vertebra are preserved now (Kimura *et al*., 2007). Measurements of 16 consecutive vertebrae (now lost) are shown in Matsumoto (1939), Tokunaga (1939) and Yagi (1939; 1943).

Description: The cranium lacks the anterior tip of the rostrum, both supraorbital processes of the frontal, and the left squamosal (Fig. 1, Plate 1). Most of the bone surfaces are slightly damaged by weathering, making it difficult to trace some of the suture lines. The ventral side of the cranium is badly damaged. Since the holotype specimen is heavy and broken into several pieces, it is difficult to measure it accurately. The measurements appearing in the following description were taken using the cast of the holotype (GMNH-PV-1700), unless otherwise stated.

The cranium is large, measuring 3217+mm in anteroposterior length as preserved (measured in a straight line). In lateral view, there is a distinctly angled apex between the rostral and cranial bones, a kind of curvature also seen in *Balaenula* and *Eubalaena* and unlike the continuously convex outline of the skull of *Balaena* (Miller, 1923; Bisconti, 2003; 2005). The rostrum is transversely compressed and highly arched dorsoventrally, the curvature being more pronounced anteriorly.

The premaxilla is quite robust. In front of the narial fossa, each premaxilla deepens and meets its opposite along the midline of the rostrum. Its dorsal surface is highly convex transversely. At the centre of the rostrum, the lateral surface of the premaxilla slightly overhangs the maxilla (Fig. 1D). Posteriorly, each premaxilla is lodged between the nasal and maxilla and contacts the frontal, though damage caused by weathering has obscured the exact outline of the posterior borders of both premaxillae. The premaxilla attains its maximum width (112 mm: right premaxilla) in front of the narial fossa; at this point, the height of the right premaxilla is 113mm.

Except for their anterior thirds, the original outer edges of the maxillae are entirely missing. The preserved parts of the outer edges suggest that most of the maxilla was compressed transversely. The dorsal surface of the anterior part of the maxilla gradually slopes downward from the level of the maxilla-premaxilla suture to its

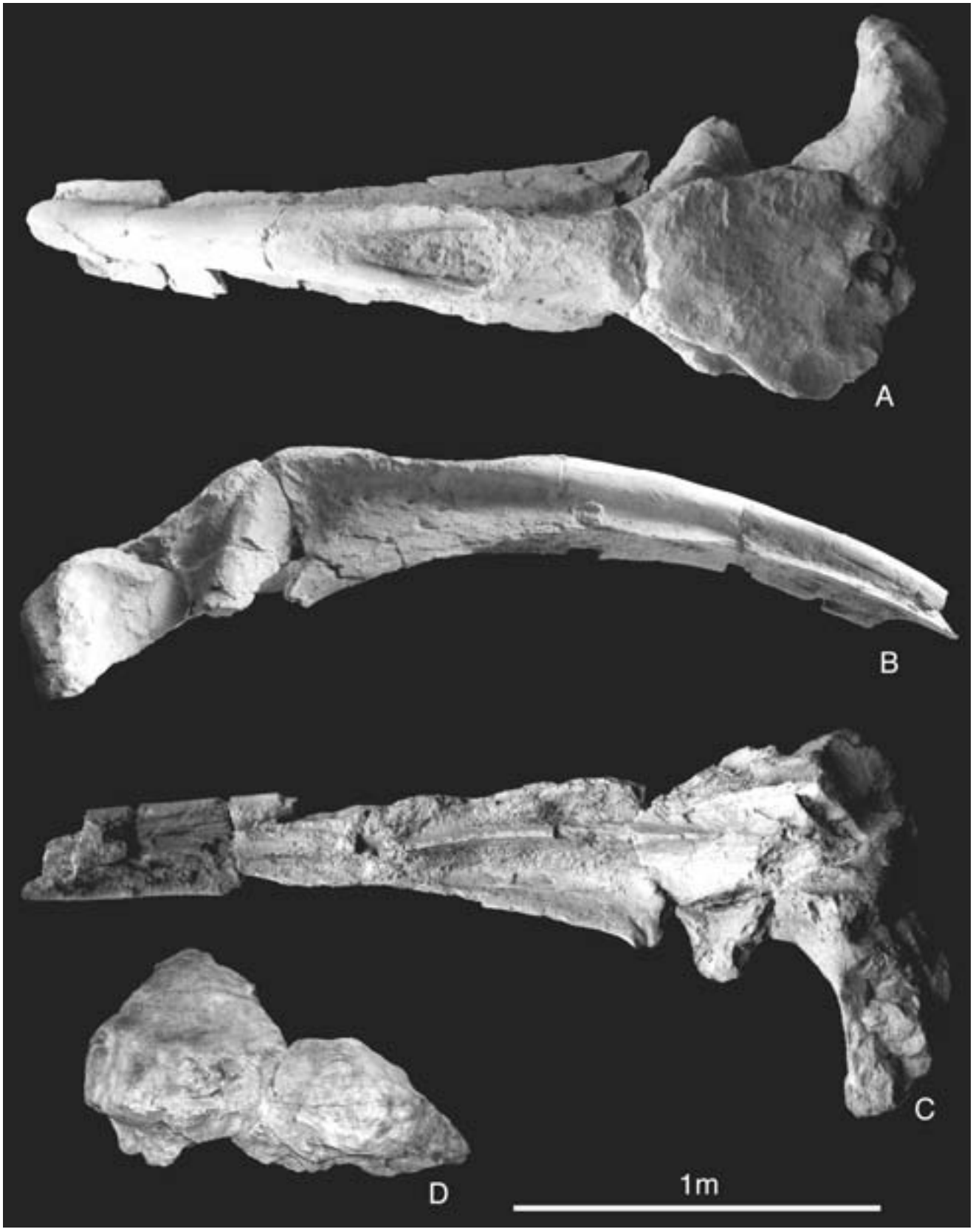

Plate 1 - *Eubalaena shinshuensis* (NSMT-PV20176; cast of holotype (SFMCV-0024)). Cranium in dorsal (A), lateral (B), ventral (C), and posterior (D) views. Scale bar equals 1 m. After Kimura *et al.* (2007).
Tavola 1 - Eubalaena shinshuensis *(NSMT-PV20176; calco dell'olotipo (SFMCV-0024)). Cranio in vista dorsale (A), laterale (B), ventrale (C) e posteriore (D). Barra: 1m. (Kimura* et al.*, 2007).*

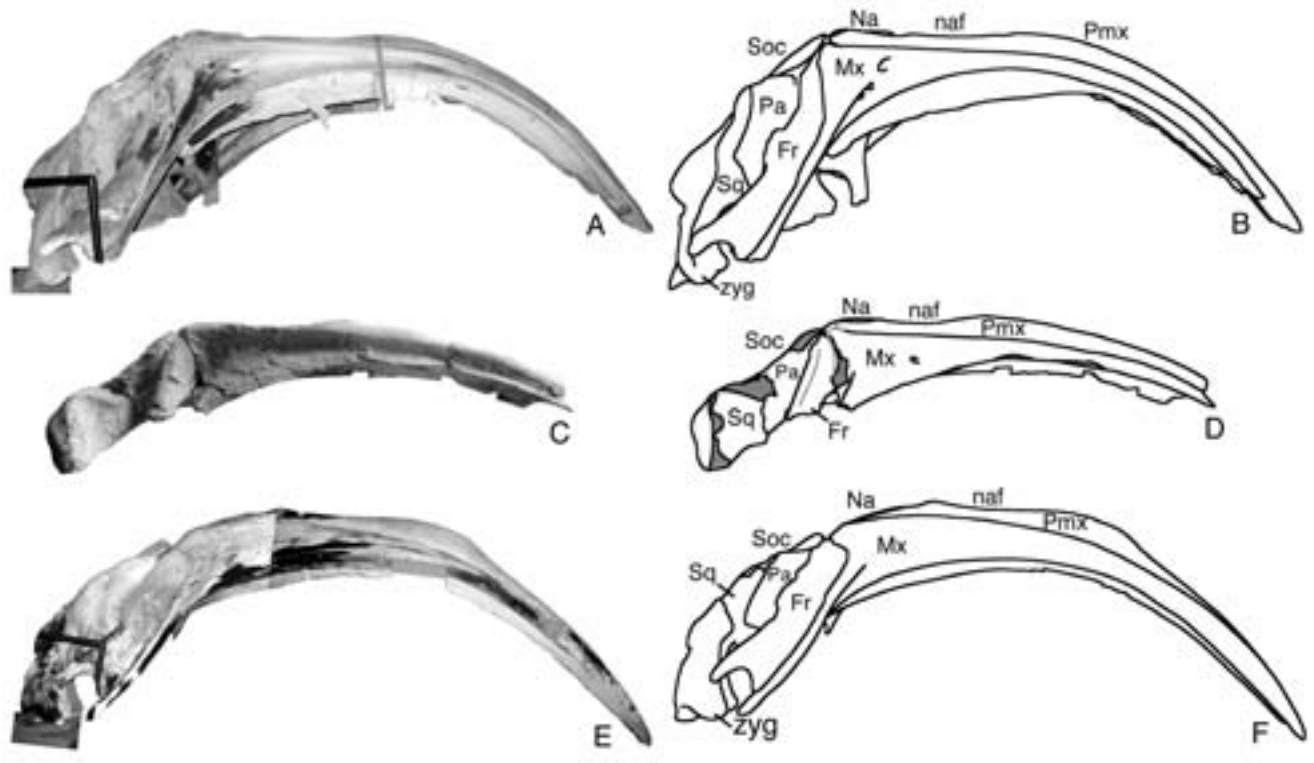

Fig. 3 - Comparison of the cranium in lateral view. A-B, *Eubalaena glacialis* (USNM23077); C-D, *Eubalaena shinshuensis* (NSMT-PV20176; cast of holotype (SFMCV-0024)); E-F, *Balaena mysticetus* (USNM257513). Dashed lines indicate unpreserved and/or estimated structures. Grey areas indicate damaged portions. Not to scale. Abbreviations: Fr, frontal; Mx, maxilla; Na, nasal; naf, nasal fossa; Pa, parietal; Pmx, premaxilla; Soc, supraoccipital; Sq, squamosal; zyg, zygomatic process of squamosal. After Kimura *et al*. (2007).

Fig. 3 - Confronto tra i crani in vista laterale. A-B, Eubalaena glacialis *(USNM23077); C-D,* Eubalaena shinshuensis *(NSMT-PV20176; calco dell'holotipo (SFMCV-0024)); E-F,* Balaena mysticetus *(USNM257513). Le linee tratteggiate indicano strutture non conservate e/o ricostruite, le aree in grigio indicano porzioni danneggiate. Non in scala. Abbreviazioni: Fr, frontale; Mx, mascellare; Na, nasale; naf, fossa nasale; Pa, parietale; Pmx, premascellare; Soc, sopraoccipitale; Sq, squamoso; zyg, processo zigomatico dello squamoso. (Kimura* et al.*, 2007).*

outer edge. At least one maxillary foramen is present on the dorsal surface of this bone. The maxilla extends back to at least the level of the apex of the occipital shield (Fig. 2), though it should be noted that, because of the weathering, the exact position of the suture with the frontal is unclear. The posteromedial angle of each maxilla is widely superimposed on the frontal. The posterior border of the maxilla (frontomaxillary suture: Fig. 2, 3C, D) is gently curved as seen in *Eubalaena* (Fig. 3A, B). By contrast, it abruptly turns posterolaterally in *Balaena* (Fig. 3 E, F).

The nasals, located anterior to the level of the estimated preorbital angles of the frontals, are long and rectangular in outline, and each of them bears a shallow notch on the anterior face. Although, because of the weathering, the exact positions of their posterior borders are unclear, the nasals are at least 214 mm long and measure 54 mm (left) and 60 mm (right) in anterior width, respectively. The ratio of nasal length versus width is about 3.5 in *E. shinshuensis*. In *Balaena*, this ratio is about 3 (McLeod *et al*., 1993), whereas it is only about 2 in living right whales (McLeod *et al*., 1993), indicating that *E. shinshuensis* retains elongated nasal bones as a primitive feature. The vomer is posteriorly elongated and reaches to at least the level of the posterior edge of the temporal fossa.

The frontals are narrowly exposed between the posterior ends of the medial rostral elements (maxillae, premaxillae, and nasals) and the supraoccipital. The supraorbital processes are largely missing and only their bases are preserved. From what remains, it seems that the supraorbital process of the frontal sloped uniformly and steeply downward from the vertex to its outer end, with a low ascending temporal crest being present on

No.	Specimen	Formation and Age	Locality	References
1	*Eubalaena shinshuensi* (SFMCV-0024)	Gonda F.: L. Miocene-E. Pliocene	Shinshushinmachi, Nagano	Matsumoto (1939), Tokunaga (1939), Yagi (1939, 1943), Kimura *et al* . (2007)
2	*Eubalaena glacialis*	Holocene	Nikaho, Akita	Nishiwaki and Hasegawa (1969)
3	*Balaena* sp. (YPM7873)	Noguchi F.: E. Pliocene	Mamurogawa, Yamagata	Nagasawa (1999)
4	*Balaena* sp. (YK01 etc)*	Na-arai F.: l.E. Pliocene	Choshi, Chiba	Oishi and Hasegawa (1995)
5	*Balaenula* sp. (HUES10003)	Chichibubetu F.: e.E. Pliocene	Fukagawa, Hokkaido	ERGFW (1982)
6	*Balaenula* sp. (HUES10005)	Rumoi F.: e.E. Pliocene	Rumoi, Hokkaido	Kimura and Matsubara (1990)
7	*Balaenula* sp. (NSMT-PV177998 etc)**	Na-arai F.: l.E. Pliocene	Choshi, Chiba	Oishi and Hasegawa (1995)
8	Balaenidae	Senmi M., Aoki F.: L. Miocene	Ogawa, Nagano	Nagasawa and Tanabe (1994)
9	Balaenidae	Gonda F.: L. Miocene-E. Pliocene	Shinshushinmachi, Nagano	Matsumoto (1939)
10	?Balaenidae (HUES(NFL3))	Horokaoshirarika F.: e.E. Pliocene	Numata, Hokkaido	Kimura et al. (1987)
11	Balaenidae (IC7)	Yotsukura F.: E. Pliocene	Iwaki, Fukushima	IECC (1989), Ichishima (2005)
12	Balaenidae (IC9)	Yotsukura F.: E. Pliocene	Iwaki, Fukushima	IECC (1989)
13	Balaenidae (IC15)	Yotsukura F.: E. Pliocene	Iwaki, Fukushima	IECC (1989)
14	Balaenidae	Tomioka F.: l.E.-e.L. Pliocene	Futaba, Fukushima	Hasegawa *et al* . (1993), Ichishima (2005)
15	Balaenidae (KPM-NN5228)	Nakatsu G.: L. Pliocene	Aikawa, Kanagawa	Koizumi (1988), Hasegawa *et al* . (1991)

* 17 specimens (at least 9 individuals)

** 20 specimens (at least 11 individuals)

Tab. 1 - List of fossil balaenids from Japan.
Tab. 1 - Lista dei balenidi fossili del Giappone

its dorsal surface. The parietal overrides the base of the supraorbital process of the frontal at least to some extent.

The right squamosal is relatively well preserved, but lacks the apex of the zygomatic process. The latter seems robust and was almost certainly directed outwards. The temporal surface of the squamosal is more or less flat. In dorsal view, the squamosal protrudes posteriorly to a point well posterior to the level of the occipital condyles.

In dorsal view, the outline of the supraoccipital shield is triangular with a wide anterior tip. The exoccipital is deflected posteriorly and

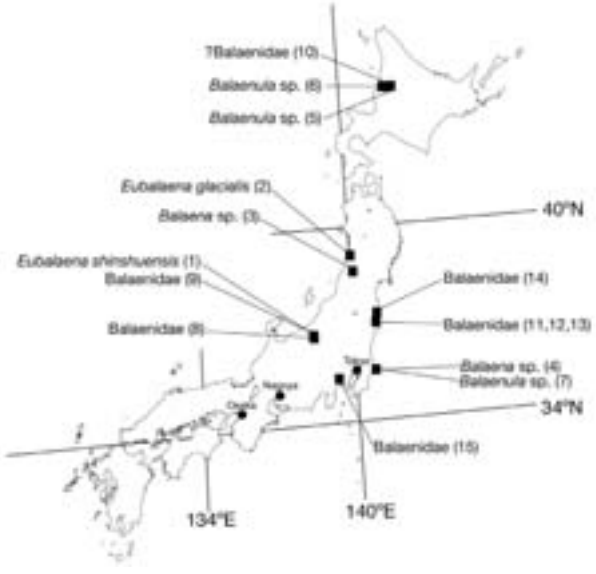

Fig. 4 - Locality map of fossil balaenids from Japan. Numbers in parentheses correspond to those in Tab.1.
Fig. 4 - Mappa dei siti di ritrovamento di fossili di balenidi del Giappone. I numeri in parentesi corrispondono alla tabella 1.

extends well posterior to the level of the occipital condyles. In posterior view, the ventral edge of the exoccipital is located below the level of the ventral margin of the foramen magnum. The dorsoventral and mediolateral diameters of the right occipital condyle are 165+ mm and 72+ mm, respectively. The foramen magnum is circular in outline, with a dorsoventral diameter of 85mm and a transverse diameter of 76 mm.

Fossil Balaenids From Japan

At least 33 individuals of fossil balaenids have been found in Japan (Tab. 1 and Fig. 4). Here, I provide a summary of the general information (fossil material, formation, age, and locality), as well as some brief comments on every fossil. Artificially buried remains of right whales have also been recovered from archaeological sites in Japan (Kasuya, 2002), but these are not included here.

Eubalaena shinshuensis (no. 1 in Tab. 1; Fig.1-3; Plate 1)

Material: SFMCV-0024; cranium and lumbar vertebra.

Formation and Age: Gonda Formation, Late Miocene-Early Pliocene

Locality: Shinshushinmachi, Nagano Prefecture

As stated above.

Eubalaena glacialis (no. 2 in Tab. 1; Fig. 5)

Material: incomplete cranium

Age: Holocene

Locality: Nikaho, Akita Prefecture

This specimen is a subfossil individual (Nishiwaki, Hasegawa, 1969). The zygomatic process

Fig. 5 - *Eubalaena glacialis* from Kisagata shell bed, Nikaho, Akita Prefecture, Japan. Cranium in posterior (A) and ventral (B) views. Scale bar equals 1 m (Nishiwaki, Hasegawa, 1969).
Fig. 5 - Eubalaena glacialis *proveniente da Kisagata shell bed, Nikaho, Akita Prefecture, Giappone. Vista posteriore (A) e ventrale (B) del cranio. Barra: 1 m (Nishiwaki, Hasegawa, 1969).*

of the squamosal is short and directed outwards. In posterior view, the postglenoid process of the squamosal deepens medially. Based on the size and shape of the squamosal and the occipital condyle, Nishiwaki and Hasegawa (1969) diagnosed this specimen as *Eubalaena glacialis*. The specimen was found just under the Kisagata Shell Bed (Nishiwaki, Hasegawa, 1969). All the species found from the Kisagata Shell Bed are living and inhabit along the coast near the low tide level (Nishiwaki , Hasegawa, 1969). On 10th July 1804, a large earthquake was occurred in this area (Kisakata (not Kisagata) earthquake: Hatori, 1986). This earthquake caused upheaval of ground and most part of this area were changed to paddy field (Imamura, Ogasawara, 1942). This suggests that the specimen was buried before

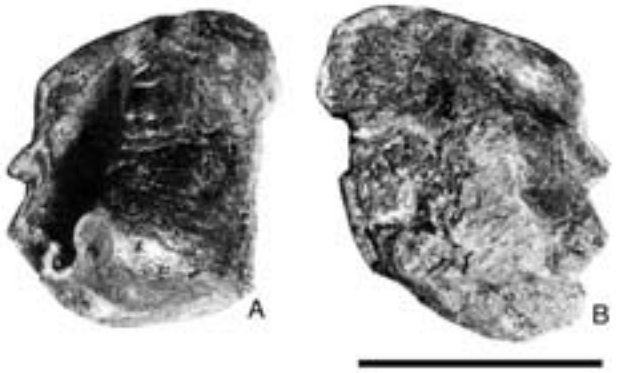

Fig. 6 - *Balaena* sp. from the Noguchi Formation, Mamurogawa, Yamagata Prefecture, Japan. Left tympanic bulla in ventral (A) and dorsal (B) views. Scale bar equals 10 cm (Nagasawa, 1999).
Fig. 6 - Balaena *sp. proveniente dalla Formazione Noguchi, Mamurogawa, Yamagata Prefecture, Giappone. Bulla timpanica sinistra in visione ventrale (A) e dorsale (B). Barra: 10 cm (Nagasawa, 1999).*

1804 (Nishiwaki, Hasegawa, 1969). However, the exact age of the Kisagata shell bed is unclear (Nishiwaki, Hasegawa, 1969).

***Balaena* sp.** (no. 3 in Tab. 1; Fig. 6)
Material: YPM7873; right tympanic bulla
Formation and Age: Noguchi Formation, Early Pliocene
Locality: Mamurogawa, Yamagata Prefecture
Nagasawa (1999) reported a balaenid fossil from the Lower Pliocene Noguchi Formation, Mamurogawa, Yamagata Prefecture. This specimen was numbered as "TY-MA" in Nagasawa (1999) and shows some typical balaenid characteristics, such as a shallow tympanic cavity and no involucral elevation.

The outline of the bulla is nearly rectangular in dorsal view. In ventral view, the lateral profile of the involucrum is nearly flat. Nagasawa (1999) suggested the age of the horizon in which the specimen was found to be between 4.5 and 5 Ma in age, based on studies of planktic foraminifera, diatoms, radiolarians, calcareous nannofossils, fission-track dating, and molluscan fossils (Aita *et al*., 1999; Nagasawa *et al*., 1999; Ogasawara *et al*., 1999).

***Balaena* sp.** (no. 4 in Tab. 1)
***Balaenula* sp.** (no. 7 in Tab. 1)
Material: YK01, NSMT-PV177998 etc. (37 specimens); tympanic bullae
Formation and Age: Na-arai Formation, late

Early Pliocene

Locality: Choshi, Chiba Prefecture

Many cetacean fossils have been found in the basal conglomerate of the Na-arai Formation, Choshi, Chiba Prefecture (Oishi, Hasegawa 1995a). Oishi and Hasegawa (1995a) examined more than 300 mysticete tympanic bullae (representing at least 195 individuals) and identified 37 bullae as balaenids. Within the balaenid specimens, they recognized two morphological groups based on overall size, and described the larger one (17 specimens, at least nine individuals) as *Balaena* sp. and the smaller one (20 specimens, at least 11 individuals) as *Balaenula* sp. Kohno (2002) reviewed previous studies on the Na-arai Formation and estimated the basal conglomerate to be late Early Pliocene in age.

***Balaenula* sp.** (no. 5 in Tab. 1; Fig. 7)

Material: HUES10003 (Oishi, Hasegawa, 1995b); incomplete cranium, tympanic bullae, periotics, mandible, vertebrae, ribs and sternum

Formation and Age: Chichibubetsu Formation, Fukagawa Group, early Early Pliocene

Locality: Fukagawa, Hokkaido

This specimen was described by ERGFW (1982). The supraorbital process of the frontal is anteroposteriorly narrow, oriented transversely to the long axis of the cranium and slopes steeply, but uniformly from the vertex to its orbital rim. A well-developed ascending temporal crest is present on the dorsal surface of the supraorbital process. The parietal overrides the base of the supraorbital process, which is a synapomorphic character of the clade comprising *Balaenula* and *Eubalaena* (Bisconti, 2005). The zygomatic process of the squamosal is short and slender, and directed ventrolaterally and slightly anteriorly. The outline of the supraoccipital seems to be triangular in dorsal view and its anterior apex was probably rounded. The anterior part of the mandible shows a high degree of torsion.

Fig. 7 - *Balaenula* sp. (HUES10003) from the Chichibubetsu Formation, Fukagawa, Hokkaido, Japan. Cranium in dorsal view. Scale bar equals 20 cm (ERGFW, 1982).
Fig. 7 - Balaenula *sp. (HUES10003) proveniente dalla Formazione di Chichibubetsu, Fukagawa, Hokkaido, Giappone. Cranio in visione dorsale. Barra: 20 cm (ERGFW, 1982).*

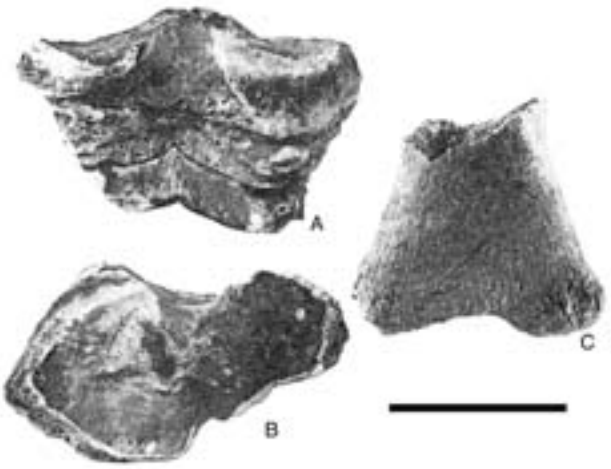

Fig. 8 - *Balaenula* sp. (HUES10005) from the Rumoi Formation, Rumoi, Hokkaido, Japan. Second (axis) to seventh cervical vertebrae in dorsal view (A), axis in anterior view (B), and distal part of the supraorbital process of the right frontal in dorsal view (C). Scale bar equals 10 cm. (Kimura, Matsubara, 1990).
Fig. 8 - Balaenula *sp. (HUES10005) dalla Formazione di Rumoi, Rumoi, Hokkaido, Giappone. Vertebre cervicali dalla seconda epistrofeo alla settima in visione dorsale (A),norma anteriore dell'epistrofeo (B), e parte distale del processo sopraorbitario del frontale destro in vista dorsale (C). Barra: 10 cm (Kimura, Matsubara, 1990).*

***Balaenula* sp.** (no. 6 in Tab. 1; Fig. 8)

Material: HUES10005 (Oishi, Hasegawa, 1995b); fragment of the supraorbital process of the frontal, vertebrae and ribs

Formation and Age: Rumoi Formation, early Early Pliocene

Locality: Rumoi, Hokkaido

This specimen was described by Kimura and Matsubara (1990). All cervical vertebrae apart from the atlas are well-preserved and fused to each other. Only a small portion of the distal part of the right supraorbital process of the frontal is preserved. The latter is narrow anteroposteriorly and does not bear any ascending temporal crest on its dorsal surface. The completely fused cer-

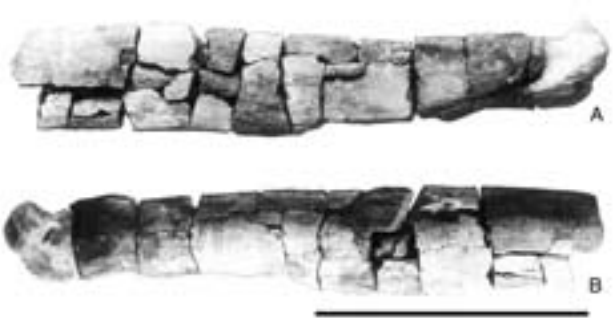

Fig. 9 – Balaenidae gen. et sp. indet. from the Aoki Formation, Ogawa, Nagano Prefecture, Japan. Right dentary in medial (A) and lateral (B) views. Scale bar equals 1 m. (Nagasawa, Tanabe, 1994).
Fig. 9 - Balaenidae gen. et sp. indet. proveniente dalla Formazione di Aoki, Ogawa, Nagano Prefecture, Giappone. Ramo mandibolare destro in visione mediale (A) e laterale (B). Barra: 1 m. (Nagasawa, Tanabe, 1994).

vical vertebrae and the anteroposteriorly narrow supraorbital process of the frontal suggest that the specimen belongs to the family Balaenidae. Based mainly on the morphology of the cervical vertebrae, Kimura and Matsubara (1990) concluded that this specimen belongs to the genus *Balaenula*.

Balaenidae gen. et sp. indet. (no. 8 in Tab. 1; Fig. 9)

Material: right dentary

Formation and Age: Senmi Member, Aoki Formation, Late Miocene

Locality: Ogawa, Nagano Prefecture

Nagasawa and Tanabe (1994) originally described this specimen as Balaenidae or Eschrichtiidae gen. et sp. indet. The specimen consists of a right dentary lacking its anterior tip. The mandibular condyle extends dorsally and posteriorly, and its posterior surface is located posterior to the angle of the mandible. A mylohyoidal sulcus is present on the medial surface of the dentary. The mental foramina open into an anteriorly directed groove on the lateral surface. Together, these characters suggest that this specimen belongs to the family Balaenidae. The radiometric age of the lowermost part of the Senmi Member is 6.7±0.4 Ma, as determined by fission track dating (Nagamori *et al*., 2003).

Balaenidae gen. et sp. indet. (no. 9 in Tab. 1)

Material: rostral part of cranium, humerus, ribs and vertebra

Formation and Age: Gonda Formation, Late Miocene-Early Pliocene

Locality: Shinshushinmachi, Nagano Prefecture

This specimen was described by Matsumoto (1939), who referred it to Balaenidae. Matsumoto (1939) also mentioned a sternum, but the bone he described was elongate (180 cm) and dissimilar to that of typical balaenids (e.g., True, 1904). Unfortunately, the specimen, which was formerly housed in local school, was lost when the school was closed down (Kimura *et al*., 2007), making a reassessment of the sternum impossible. The cranium was quite large, with a preserved length measuring 480cm (Matsumoto, 1939), and marked by a transversely compressed and highly arched rostrum (Matsumoto, 1939). The head of the humerus was large, globular, and extended dorsally. Together, these morphological traits clearly suggest that this specimen was a balaenid. It was found in the vicinity of the type locality of *E. shinshuensis*, and indeed in almost the same horizon as the latter. Kimura *et al*. (2007) implied an affinity of this specimen with *E. shinshuensis*.

?Balaenidae gen. et sp. indet. (no. 10 in Tab. 1; Fig. 10)

Material: HUES(NFL3) (Oishi and Hasegawa, 1995b); left mandible

Formation and Age: Horokaoshirarika Formation, Fukagawa Group, early Early Pliocene

Locality: Numata, Hokkaido

This specimen was described by Kimura *et al*. (1987) as the remains of a balaenid. The specimen consists of a left dentary lacking both the proximal and distal ends. It is nearly straight in

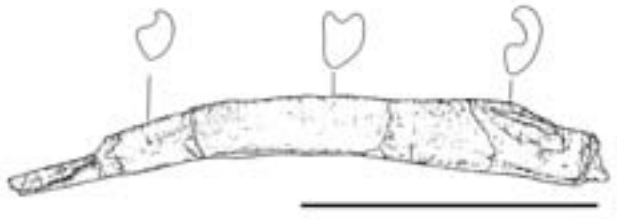

Fig. 10 - ?Balaenidae gen. et sp. indet. (HUES(NFL3)) from the Horokaoshirarika Formation, Numata, Hokkaido, Japan. Left dentary in lateral view with cross sections. Scale bar equals 50 cm. (Kimura *et al*., 1987).
Fig. 10 - ?Balaenidae gen. et sp. indet. (HUES(NFL3)) proveniente dalla Formadione di Horokaoshirarika, Numata, Hokkaido, Giappone. Ramo mandibolare sinistro in visione laterale e sezioni trasversale. Barra: 50 cm. (Kimura et al., *1987).*

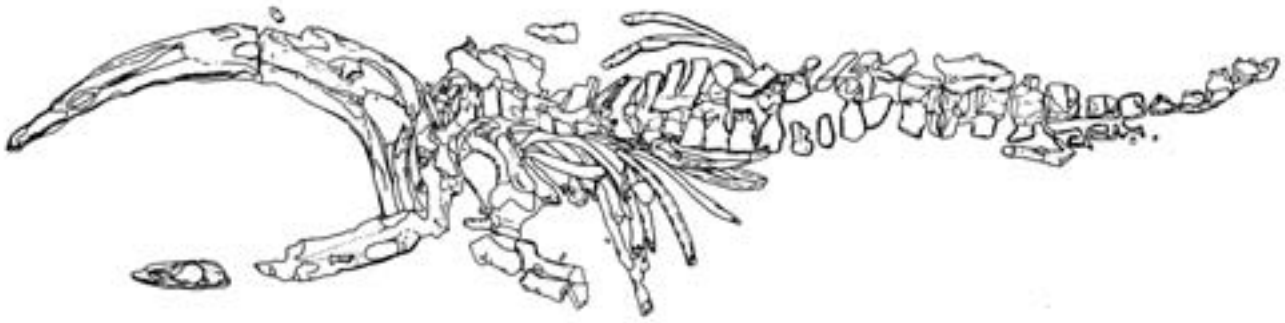

Fig. 11 - Balaenidae gen. et sp. indet. (IC7) from the Yotsukura Formation, Iwaki, Fukushima Prefecture, Japan. After IECC (1989).
Fig. 11 - Balaenidae *gen. et sp. indet. (IC7) dalla Yotsukura Formation, Iwaki, Fukushima Prefecture, Giappone. IECC (1989).*

dorsal view. As preserved, the horizontal ramus does not seem to be rotated around its axis. In lateral view, the ventral profile of the horizontal ramus is concave. The cross-sectional shape of the ventral margin is rounded, as opposed to the well-defined angular edge found in balaenopterids. However, the presence of a mylohyoidal groove is questionable (pl. 6 in Kimura *et al*., 1987), casting some doubt on the balaenid affinities of this specimen. Here, I tentatively refer it to ?Balaenidae. The horizon in which the specimen was found is overlain by a layer of tuff with a radiometric age of 5.0±0.2 Ma, as determined by fission track dating (Kimura *et al*., 1987).

Balaenidae gen. et sp. indet. (no. 11 in Tab. 1; Fig. 11)

Material: nearly complete skeleton (IC7)

Formation and Age: Yotsukura Formation, Early Pliocene

Locality: Iwaki, Fukushima Prefecture

This specimen was originally reported by IECC (1989) as Eschrichtiidae gen. et sp. indet. Based on the figure published in IECC (1989), the specimen shows the following characteristics: a large cranium compared to its total body length, a highly arched rostrum, and a relatively short radius and ulna. Together, these morphological traits clearly suggest that the specimen belongs to the family Balaenidae. Ichishima (2005) also regarded this as a balaenid based on the shape of the cranium and the tympanic bulla. The Yotsukura Formation is placed in nannofossil zone CN10c-11 (c.a. 4 Ma), based on calcareous nannofossil biostratigraphy (IECC, 1989).

Balaenidae gen. et sp. indet. (no. 12 in Tab. 1)

Material: IC9, incomplete cranium, tympanic bullae, vertebrae, scapula, radius, ulna and ribs

Formation and Age: Yotsukura Formation, Early Pliocene

Locality: Iwaki, Fukushima Prefecture

This specimen was reported by IECC (1989) as Balaenidae gen. et sp. indet. Without providing a morphological description, IECC (1989) referred this specimen to Balaenidae based on the morphology of the scapula, the radius, and the tympanic bulla. It was recovered from almost the same horizon as IC7 reported by IECC (1989).

Balaenidae gen. et sp. indet. (no. 13 in Tab. 1)

Material: IC15, incomplete cranium, mandible, tympanic bullae, vertebrae, scapula and ribs

Formation and Age: Yotsukura Formation, Early Pliocene

Locality: Iwaki, Fukushima Prefecture

This specimen was reported by IECC (1989) as Balaenidae gen. et sp. indet. Without providing a morphological description, IECC (1989) briefly noted that this specimen was referred to Balaenidae based on the morphology of the cranium and the tympanic bulla. It was recovered from almost the same horizon as IC7 reported by IECC (1989).

Balaenidae gen. et sp. indet. (no. 14 in Tab. 1; Fig. 12, 13)

Material: FM-NK000001, incomplete cranium, periotics, vertebrae, ribs, scapulae, humerus, radii and ulna

Formation and Age: Tomioka Formation, late Early-early Late Pliocene

Locality: Futaba, Fukushima

This specimen was originally described by Hasegawa *et al*. (1993) as Mysticeti gen. et sp. indet. It exhibits a number of balaenid characteristics, such as a hypertrophied anterior process of the

Fig. 12 - Balaenidae gen. et sp. indet. (FM-NK000001) from the Tomioka Formation, Futaba, Fukushima Prefecture, Japan. Periotic in ventral view. Scale bar equals 10 cm. (Hasegawa *et al*., 1993).
Fig. 12 - Balaenidae gen. et sp. indet. (FM-NK000001) proveniente dalla Formazione Tomioka, Futaba, Fukushima Prefecture, Giappone. Vista ventrale dell'osso periotico. Barra: 10 cm (Hasegawa et al.*, 1993).*

periotic, a distinct groove for the tensor tympani muscle developed on the periotic, a globular and well-developed head of the humerus, a relatively short radius and ulna, and a narrow scapula with a reduced coracoid process. An olecranon process is retained on the ulna, probably representing the primitive condition for Balaenidae. Ichishima (2005) also regarded this specimen as a balaenid based on the periotic, scapula and humerus. Hasegawa *et al*. (1993) estimated the age of the fossil horizon as between 2.5 and 4 Ma in age based on radiolarian and diatom biostratigraphy.

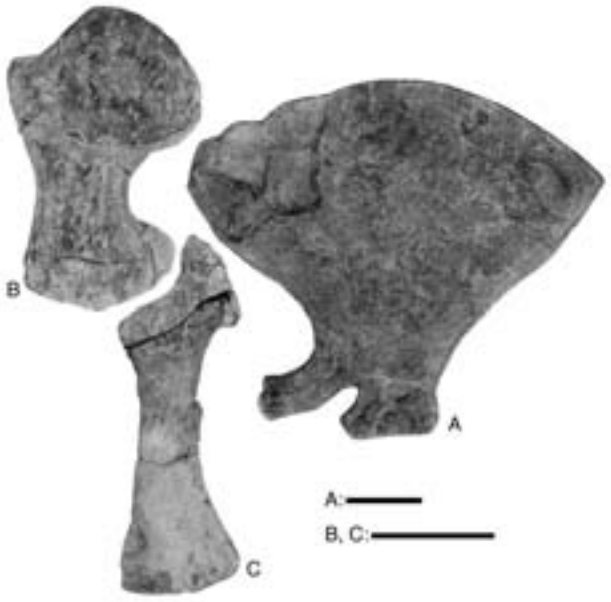

Fig. 13 - Balaenidae gen. et sp. indet. (FM-NK000001) from the Tomioka Formation, Futaba, Fukushima Prefecture, Japan. Right scapula (A), humerus (B), and ulna (C) in lateral views. Scale bars equal 20 cm (Hasegawa *et al*., 1993).
Fig. 13 - Balaenidae gen. et sp. indet. (FM-NK000001) proveniente dalla Formazione Tomioka, Futaba, Fukushima Prefecture, Giappone. Scapola destra (A), omero (B) e ulna (C) in visione laterale. Barra: 20 cm (Hasegawa et al.*, 1993).*

Balaenidae gen. et sp. indet. (no. 15 in Tab. 1; Fig. 14)

Material: KPM-NN5228; fragment of left dentary

Formation and Age: Nakatsu Group, Late Pliocene

Locality: Aikawa, Kanagawa Prefecture

This specimen consists of the anterior part of a left dentary and was described by Koizumi (1988) and Hasegawa *et al*. (1991, specimen 850503-1) as Balaenidae gen. et sp. indet. The cross-sectional shape of the ventral margin of the dentary is rounded. The lateral surface of the horizontal ramus is convex, while the medial surface is more or less flattened. The horizontal ramus shows a high degree of anterior torsion, suggesting that the specimen belongs to the family Balaenidae. Saito (1988) used planktic foraminifera to place the Nakatsu Group in Zone N21 of Blow (1969) and, based on this and unpublished palaeomagnetostratigraphic data, estimated the age of the Nakatsu Group to be between 1.9 and 2.9 Ma in age.

In addition to the specimens listed in Tab. 1, two further balaenid specimens have been

Fig. 14 - Balaenidae gen. et sp. indet. (KPM-NN5228) from the Nakatsu Group, Aikawa, Kanagawa Prefecture, Japan. Left dentary in lateral (A) and dorsal (B) views. Scale bar equals 10 cm. (Hasegawa *et al*., 1991).
Fig. 14 - Balaenidae gen. et sp. indet. (KPM-NN5228) proveniente dal Nakatsu Group, Aikawa, Kanagawa Prefecture, Giappone. Vista laterale (A) e dorsale (B) del ramo mandibolare sinistro. Barra: 10 cm. (Hasegawa et al*., 1991).*

reported. Omi (1986) described a rib fragment from the Pliocene Sakiyama silt, Ishikawa Prefecture, as belonging to a balaenid. However, the specimen is too incomplete to allow an accurate identification. Here, I refer it to Mysticeti fam., gen. et sp. indet. Hasegawa and Kato (1974) reported an incomplete skeleton of a fossil baleen whale from the Funakawa Formation, Akita Prefecture as *Morenocetus*? sp. The typical shape of the balaenid scapula is relatively narrow and is distinguished by its greater proportional height compared to that of rorquals. However, the scapula of the specimen from the Funakawa Formation is relatively wide, unlike that of other known balaenids. Subsequent studies suggested an affinity of this specimen with Balaenopteridae (Kato, 1979; Oishi, Hasegawa, 1995b) and Eschrichtiidae (Kato, 1996). However, the latter was strongly contradicted by Oishi *et al*. (2001) and Ichishima (2005).

Discussion

About fifty specimens of fossil balaenids, representing at least 33 individuals, have been reported from Japan (Fig. 4, Tab. 1), the oldest being Upper Miocene in age (no.8 in Tab. 1, Fig. 9). The number of balaenid fossils abruptly increases in deposits dating from the Pliocene (Fig. 15), during which the family apparently attained its greatest diversity, with at least three genera (*Balaena*, *Balaenula*, and *Eubalaena*) being present in the western North Pacific around Japan. Since the oldest balaenid was found in rocks dating from the Upper Oligocene of New Zealand (Fordyce, 2002), it is unlikely that this abrupt increase in diversity during the Pliocene can be explained by the evolutionary appearance of the group at that time. This poses the question what else could have accounted for this sudden change in the number of fossil balaenids. Here I propose a scenario explaining the evolutionary history of the members of this family in the western North Pacific in terms of the relationship between their specialized feeding strategy and their primary food sources.

Most of the extant families of baleen whales are widely distributed. At present, three families of baleen whales (Balaenopteridae, Eschrichtiidae, and Balaenidae) are present in the western North Pacific, with their ranges overlapping each other (Jefferson *et al*., 1993). In general, in order to coexist, species must differ in their ecological requirements or niches (Ballance, 2002). Niche partitioning based on primary food sources has been observed in living mysticetes (Ballance, 2002). Because the nature of these sources is often closely linked to the main way food is being obtained by the animal (Nemoto, 1959), it can be assumed that niche partitioning in living baleen whales is established by the unique feeding strategies of each family. The latter are generally divided into three types: engulfment feeding, found in balaenopterids, mud scooping (benthic suction feeding), found in eschrichtiids, and skim feeding, found in balaenids (Nemoto, 1959; Brodie, 1977; Pivorunas, 1979; Berta and Sumich, 1999). All of these feeding strategies generally manifest themselves in a variety of morphological traits relating to such structures as the baleen plates, the mandible, and the cranium (Kawamura, 1980; Heyning, Mead, 1996; Berta, Sumich, 1999; Kimura, 2002). Indeed, some of the morphological traits closely related to a particular method of feeding are sometimes regarded as diagnostic characters of the family (e.g. numerous throat grooves in Balaenopteridae, or a highly arched rostrum with long and fine baleen plates in Balaenidae).

The balaenopterids are fast swimmers being characterized by short baleen plates and numerous throat grooves found on the ventral side of the body. They feed by engulfing vast quantities of water containing their prey, and then expel-

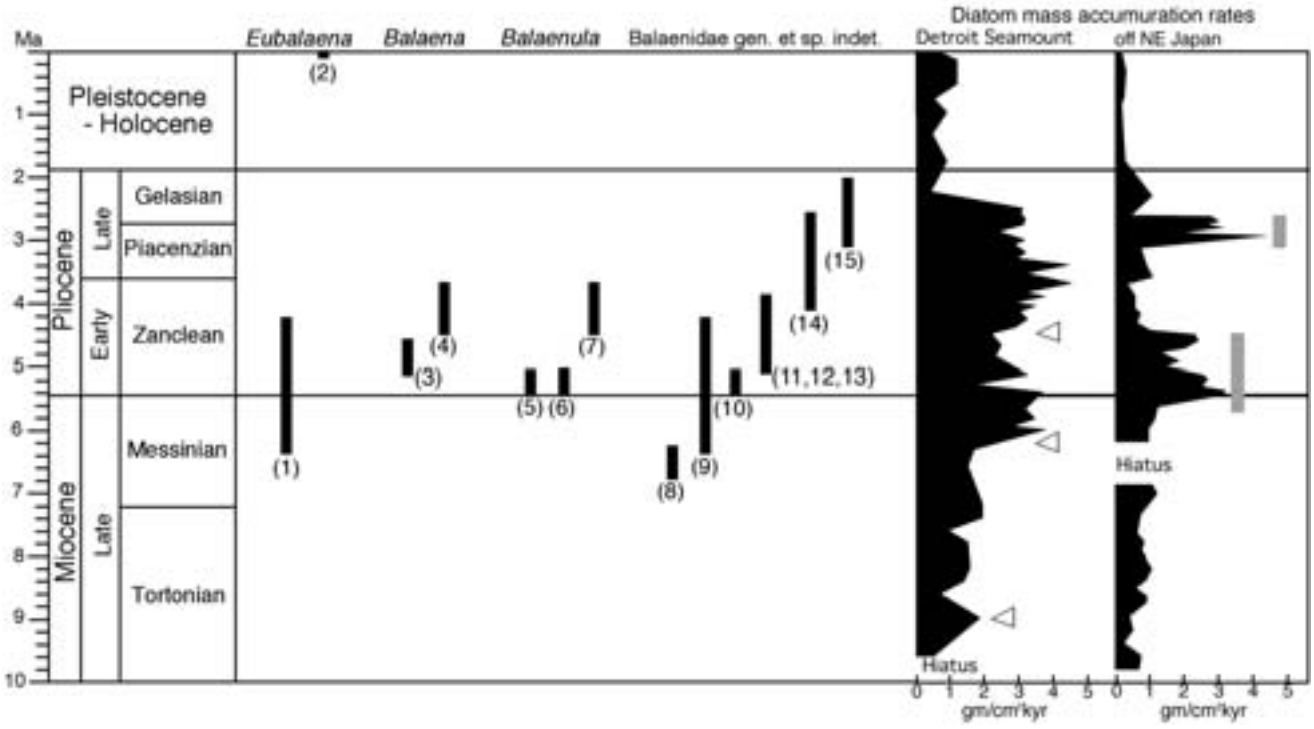

Fig. 15 - Stratigraphic distribution of fossil balaenids from Japan with diatom mass accumulation rates for the western North Pacific. Diatom mass accumulation rates are after Barron (1998). Arrows and diagonally striped lines indicate events of increased diatom mass accumulation rates as suggested by Barron (1998). Numbers in parentheses correspond to those in Tab.1.
Fig. 15 - Distribuzione stratigrafica dei fossili di balenidi del Giappone in relazione al tasso di accumulo delle masse di diatomiti nel Pacifico Nordoccidentale. Il tasso di accumulo di diatomiti è tratto da Barron (1998). Le frecce e le barre con linee diagonali indicano gli episodi di aumento dell'accumulo di massa diatomitica in accordo con Barron (1998). I numeri in parentesi corrispondono a quelli della tabella 1.

ling the water through their baleen plates. Their main food source is small zooplankton, but they also feed on squid and many kinds of fish (Nemoto, 1959; Pauly *et al*., 1998 and references cited therein; Bannister, 2002). By contrast, the primary food sources of eschrichtiids are benthic invertebrates (Nemoto, 1959; Pauly *et al*., 1998 and references cited therein; Bannister, 2002), which they obtain by sucking bottom sediments in shallow waters over continental shelves (Pivorunas, 1979; Jones, Swartz, 2002). This type of suction feeding is achieved by creating a negative pressure in the mouth cavity through retraction of the large, muscular tongue (Jones, Swartz, 2002). Finally, the balaenids are slow swimmers with a highly arched rostrum, greatly elongated and finely textured baleen plates, and an anterior gap between the left and right baleen rows (Miller, 1923; Pivorunas, 1979; Lowry, 1993; McLeod *et al*., 1993; Berta, Sumich, 1999; Bisconti, 2003). When feeding, they swim forward through a concentration of zooplankton with their mouths opened. This causes prey-laden water to flow into the mouth through the anterior gap between the baleen rows. Once inside the mouth, small zooplankton contained in the water becomes trapped in the finely frayed inner edges of the baleen plates (Pivornous, 1979). Balaenids feed almost exclusively on krill and copepods (Nemoto, 1959; Pauly *et al*., 1998 and references cited therein; Bannister, 2002), making their prey smaller and less evasive than that of other baleen whales. Unlike balaenopterids, they are therefore able to feed on relatively scattered zooplankton (Nemoto, 1959; Sanderson, Wassersug, 1993).

The evolution of mysticetes is closely linked with the availability of their primary food sources. Indeed, Fordyce (1980; 1989) suggested that their very emergence might have been triggered by the onset of high plankton productivity in response to the establishment of the Circum Antarctic Current, following the increasing physical isolation of Antarctica. The production of zooplankton is closely related to the quantity and quality of available food (Checkley, 1980; Jónasdóttir *et al*., 1995; Ross *et al*., 2000). Both dinoflagellates and

diatoms have been found to be important components of the diet of copepods (Kleppel *et al*., 1991). Diatoms in particular are also considered to be the primary food source of krill (Haberman *et al*., 2003), a hypothesis supported by a close relationship between diatom productivity and krill abundance (Ross *et al*., 2000).

Neogene changes in the productivity of diatoms and dinoflagellates have been studied by several authors (e.g., Bujak, 1984; Barron, 1998). It is logical to assume that such changes may have affected the abundance of krill and copepods, and thus the primary food sources of the balaenids. Bujak (1984) studied core samples of Deep Sea Drilling Project (DSDP) sites in the Bering Sea and the northern North Pacific and noted that dinoflagellate cysts are generally less common in sections older than the Late Miocene. He also identified a distinct change in the assemblages of dinoflagellate cysts in the Late Miocene and linked it to the onset of high diatom productivity in these areas. Barron (1998) worked on core samples of Ocean Drilling Program (ODP) sites (Leg 145) along an east-west transect in the subarctic North Pacific and pointed out major changes in diatom mass accumulation rates during the last 10 myr. In particular, he found at least three major events of increased diatom mass accumulation rates (at 9.0, 6.2, and 4.5 Ma, respectively) in the western North Pacific (Detroit Seamount, 50°N; Site 883) (Fig. 15). In addition, he also recognized two intervals of markedly increased diatom mass accumulation rates (5.7-4.5 Ma and 3.1-2.6 Ma) based on the core sample of a DSDP site off northeast Japan (40°N; Site 438) (Fig. 15).

High diatom and dinoflagellate productivity during the Late Miocene would have led to an increase in the abundance of krill and copepods, the primary food sources of the balaenids. It is thus logical to assume that this sudden increase in krill and copepod productivity may have been linked with the appearance of balaenids in the western North Pacific during this time. This hypothesis is supported by the fact that this surge in krill and copepod abundance was followed by an abrupt increase in the number of balaenids, as shown by the numerous fossils found in Japan (Fig. 15). Palaeodiversity should be carefully examined, because some authors questioned whether it reflects genuine biological signal not overwhelmed by biases (e.g., outcrops) (e.g., Smith, Mc Gowan, 2007). There are no enough data to discuss it in the western North Pacific. But, Marx (2009) clearly indicated that such biases do not mislead the estimation of the palaeodiversity in Europe. This may support the adequacy of above discussion on the palaeodiversity of western North Pacific.

Overall, cetacean diversity was very high during the Tortonian, before abruptly decreasing in the Messinian (Uhen, Pyenson, 2007; Marx, 2009). Surprisingly, though, the latter was also the time when balaenids first appeared in the western North Pacific, thus seemingly defying the general trend. Since balaenids almost exclusively feed on krill and copepods (Nemoto, 1959; Pauly *et al*., and references cited therein; Bannister, 2002), it is possible that they might have been more affected by changes in the abundance of these animals than other cetaceans. Thus, the abrupt increase in the number of balaenid fossils in the Pliocene of Japan may ultimately have been the result of Neogene marine environmental changes which led to an increase in krill and copepod productivity in the North Pacific.

It should be noted that this abrupt diversification of fossil balaenids during the Pliocene was not restricted to the western North Pacific (e.g., Barnes, 1977). The balaenids have a long independent history: the oldest fossil balaenid was found in rocks dating from the Upper Oligocene of New Zealand (Fordyce, 2002), while the oldest named species, *Morenocetus parvus*, is known from the earliest Miocene of Argentina (Cabrera, 1926). However, a large gap seems to exist in the fossil record, separating those earliest balaenids from the more modern taxa appearing from the Late Miocene onwards. To elucidate balaenid evolution, detailed studies of those early balaenid remains, as well as further studies on the effects of Neogene marine environmental changes in other parts of the world ocean are needed.

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Riassunto

In questo lavoro viene presentata per la prima volta una revisione dei balenidi fossili giapponesi e una nuova descrizione, in lingua inglese, della nuova specie *Eubalaena shinshuensis*. La nuova specie viene dalla Formazione Gonda che è collocabile stratigraficamente tra 5.3 e 4.2±0.3 milioni di anni fa tra la fine del Miocene e il Pliocene Inferiore. La nuova specie *E. shinshuensis* è rappresentata da un cranio incompleto e da una vertebra lombare; gran parte dello scheletro di questo animale è andata distrutta nel corso del tempo anche se misure e descrizioni delle parti oggi mancanti sono riportate nella precedente letteratura scientifica. *Eubalaena shinshuensis* è attribuita al genere *Eubalaena* (che oggi comprende le balene franche) per la presenza di un angolo pressoché retto tra processo laterale del mascellare e processo sovraorbitario del frontale, per l'estensione laterale del parietale alla base del processo laterale del frontale (carattere condiviso con *Balaenula*), per l'estensione trasversale del sovraoccipitale, e per la curvatura irregolare del rostro. La specie può essere inequivocabilmente distinta dalle altre specie di balenidi a causa di una proiezione molto marcata degli squamosi e degli esoccipitali i cui bordi posteriori vanno a posizionarsi più posteriormente delle superfici articolari dei condili occipitali. *Eubalaena shinshuensis* mantiene lunghe ossa nasali come carattere di primitività. Questa specie è particolarmente importante perché riempie, in parte, il gap nella documentazione fossile della famiglia *Balaenidae* nel senso che si colloca in un punto stratigraficamente intermedio tra il più antico balenide descritto e denominato (*Morenocetus parvus*) che proviene dal Miocene inferiore (circa 23 milioni di anni fa) dell'Argentina e le specie più recenti che sono tutte plio-pleistoceniche.

Tra gli altri reperti di balenidi revisionati in questo lavoro si trova un ulteriore reperto attribuito ad *Eubalaena* e proveniente da strati olocenici, un reperto attribuibile a *Balaena* (il genere a cui appartiene la balena della Groenlandia), 2 reperti di *Balaenula* (una forma di balenide di piccole dimensioni diffuso nel Miocene superiore e nel Pliocene in vari bacini oceanici del mondo) del Pliocene Inferiore, 37 reperti consistenti in ossa uditive e attribuibili o a *Balaena* o a *Balaenula* sempre dal Pliocene inferiore e 8 reperti di *Balaenidae* gen. et sp. indet. Di questi ultimi 2 sono collocati nel Miocene superiore, 4 nel Pliocene inferiore e 2 nel Pliocene superiore.

Per interpretare l'abbondanza di balenidi fossili nel Pliocene del Giappone viene presentata un'ipotesi basata sullo studio delle variazioni dell'abbondanza delle fonti di cibo di questi animali nel corso del Neogene. E' infatti noto che i balenidi si nutrono per lo più di copepodi calanoidi e krill. Questi invertebrati, a loro volta, si nutrono di dinoflagellati e diatomee. Lo studio dell'accumulo delle cisti di dinoflagellati e diatomee nel corso del Neogene ha rivelato che questi organismi sono rari nei depositi giapponesi almeno fino al Miocene superiore. Distinti picchi di accumulo di diatomee, ad esempio, si osservano tra i 9 e i 4.5 milioni di anni fa e poi un picco ulteriore è stato registrato a 2.6 milioni di anni fa. I balenidi appaiono nella documentazione paleontologica del Giappone intorno ai 6 milioni di anni fa, in un momento in cui la presenza di abbondanti diatomee e dinoflagellati suggerisce anche abbondanza di krill e copepodi calanoidi. L'aumentata disponibilità di fonti di cibo può essere la causa dell'incremento dell'abbondanza di balenidi nella documentazione fossile del Giappone e può interpretare la diversità tassonomica del gruppo in quest'area dell'oceano Pacifico settentrionale e occidentale.