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and its significance to mysticete evolution**

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# A new mysticete from the upper Oligocene Ashiya Group, Kyushu, Japan and its significance to mysticete evolution

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**ABSTRACT** — The Ashiya Group (Late Oligocene) is distributed in the northern part of the Kyushu Island, West Japan, yields many cetacean fossils. Among them, an archaic mysticete is reported here. The fossil occurred at the Wakamatsu Coast of Kitakyushu City (Tominohana (cape), 33°56'09"N, 130°41'08"E), from siltstone of the Jinnobaru Formation, Ashiya Group. The material is composed of an almost complete skull with both dentaries, cervical vertebrae, anterior thoracic vertebrae, several ribs, and fore limb elements. Deformation of bones is limited. The specimen is described as *Yamatocetus canaliculatus*, new genus and new species in the Eomysticetidae SANDERS and BARNES, 2002. *Yamatocetus canaliculatus* has following characters: the rostrum is wide and long, indicating the presence of functional baleen: there are several alveoli along the grooves of lateral margin of upper jaws and dorsal margin of dentaries. The external naris opens anteriorly as seen in *Eomysticetus whitmorei* SANDERS and BARNES 2002, but different from *E. whitmorei* at the uplift of nasals and other features. *Yamatocetus canaliculatus* has advanced features in the anterior limb for swimming, the lengths of bones are different from extant species of mysticetes. The ribs are mostly two-headed, indicating a less flexible nature of the rib cage. It indicates that the whale was not adapted enough for deep diving, compared to extant baleen whales which have a limited number of two-headed ribs. The occurrence of *Yamatocetus canaliculatus* is important for discussion of early stage of the mysticetes, especially at the stage of loss of teeth. There are several species of such evolutionary stage in west coast of North Atlantic Ocean and New Zealand. They have migrated rapidly in the Late Oligocene.

**KEY WORDS:** Oligocene, Mysticete, Ashiya Group, Northern Kyushu, Japan

## INTRODUCTION

In October 1981, Mr. Toshiyuki KAMEI found an exposure of a column of fossil vertebrae at Tominohana in Wakamatsu, Kitakyushu (Fig. 1) through his fossil collecting in the Ashiya Group. The fossil was collected and cleaned by the author, Kitakyushu Museum and Institute of Natural History (KMNH). The specimen was catalogued as KMNH VP 000,017, stored in the Kitakyushu Museum of Natural History and Human History, which succeeded the former Museum in 2002. Preparation revealed a complete skull with both dentaries, left pectoral limb bones, cervical vertebrae, incomplete thoracic vertebrae and several ribs. The skull occurred in ventral side up, in articulation with cervical vertebral column. Mandibles were associated with the skull internal side up.

The Ashiya Group has yielded many tetrapod fossils as seen in the Table 1. All of them are marine vertebrates with an exception of an amynodontid perrisodactyl leg bone from the Umashima Island. The fauna is very important because of its

Late Oligocene age; there is only contemporaneous fauna from Hokkaido district in the western North Pacific.

## SYSTEMATIC PALEONTOLOGY

**Cetacea** BRISSON, 1762

**Mysticeti** FLOWER, 1864

**Family Eomysticetidae** SANDERS and BARNES, 2002

**Included genera.** *Eomysticetus* SANDERS and BARNES, 2002;

*Yamatocetus* new genus

**Genus** *Yamatocetus* new genus

**Included species.** *Yamatocetus canaliculatus* new species

**Diagnosis.** Same as the species

**Etymology.** Yamato (Japanese), old name of Japan, and cetus or cete (Latin, from Greek ketos), whale

***Yamatocetus canaliculatus* new species**

(Figs. 2–29; Tables 2–6)

**Diagnosis.** *Yamatocetus canaliculatus* differs from other named eomysticetids in; without elevation at midline of nasals; with gingival grooves on both upper and lower jaws; with large supraorbital process with parallel anterior and posterior margins in dorsal view; with rather blunt tip of rostrum.

**Holotype.** Holotype specimen; KMNH VP 000,017, stored in the Kitakyushu Museum of Natural History and Human History. A skull with both dentaries, cervical vertebrae, anterior thoracic vertebrae, several ribs, and fore limb elements (Fig. 2).

**Type locality.** The holotype specimen was collected at coast of Tominohana (cape) in Wakamatsu Ward, Kitakyushu City, 33°56'09"N, 130°41'08"E (Fig. 1).

**Geology and age.** The fossil was from the Jinnobaru Formation (OZAKI *et al.*, 1993) of the Ashiya Group. The geologic age of the Ashiya Group has been determined by micropaleontology and fission-track estimations as the latest Early Oligocene to Late Oligocene (SAITO and OKADA, 1984; OKADA, 1992; OZAKI *et al.*, 1993), which is closely concordant to the knowledge of cetacean evolution. There are no direct estimations of the Jinnobaru Formation by these methods but underlying Norimatsu Formation is estimated as early Late Oligocene based on planktonic foraminifer and calcareous nannofossil chronologies (P21). On the other hand, there is no evidence of existence of Miocene fauna of both macro- and micro-fossils from the Ashiya Group. These estimations suggest that the age of the Jinnobaru Formation is estimated to be early Late Oligocene.

**Etymology.** *Canaliculatus*, with groove.

Table 1. Tetrapod fossils from the Ashiya Group

Reptilia	
Chelonia, gen. and sp. undet.	unreported
<i>Tryonyx</i> sp.	unreported
<i>Indotestudo takasago</i>	MATSUMOTO, 1923
Crocodylia, gen. and sp. undet.	ARISHIMA and OKAZAKI, 1995
Aves	
<i>Copepteryx hexeris</i>	OLSON and HASEGAWA, 1996
<i>Copepteryx titan</i>	OLSON and HASEGAWA, 1996
Plotopteridae, spp.	HASEGAWA <i>et al.</i> , 1979
Odontopterigiformes, gen. and sp. undet.	OKAZAKI, 1989
Mammalia	
Sirania	
Dugongidae, gen. and sp. undet.	OKAZAKI, 1984
Mysticeti	
<i>"Metasqualodon" symmetricus</i>	OKAZAKI, 1982; OKAZAKI, 1985
aff. <i>Chonecetus</i>	
Aetiocetidae? gen. and sp. undet.	OKAZAKI, 1987
<i>Yamatocetus canaliculatus</i> , n. sp.	this paper
<i>Mysticeti</i> , gen. and spp. undet.	
Odontoceti	
Odontoceti, gen. and sp. undet.	
Agorophiidae, gen. and sp. undet.	
Squalodontidae, gen. and spp. undet.	OKAZAKI, 1988
Perissodactyla	
<i>Amynodon?</i> sp.	OKAZAKI, 1994

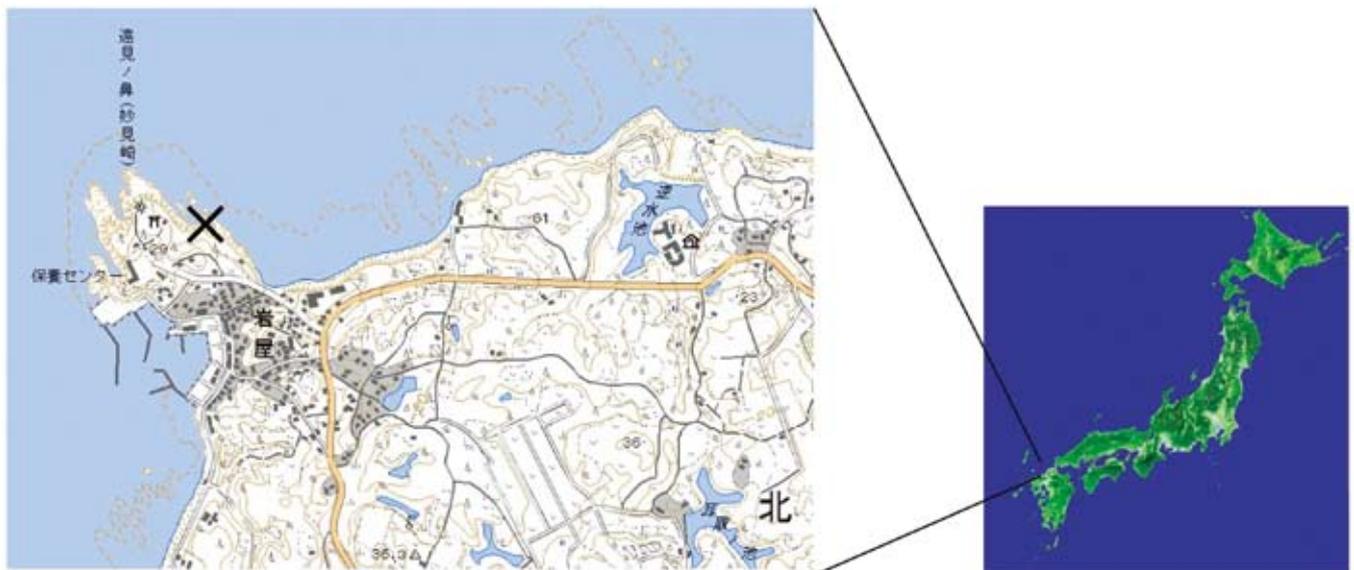


Fig. 1. Locality of the KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Tominohana, Wakamatsuku, Kitakyushu, Japan. Data from "Iwaya" topographical map (1:25,000) of Geospatial Information Authority of Japan.

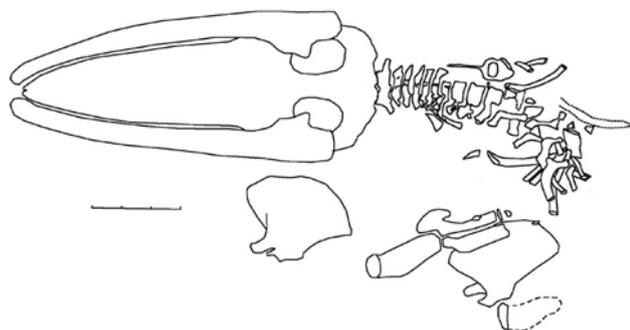


Fig. 2. Occurrence of the KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Scale: 30 cm.

## DESCRIPTION

**General Description.** A skull with both dentaries, cervical vertebrae, anterior thoracic vertebrae, several ribs, and fore limb elements are preserved (Fig. 2). Deformation of each bone is limited such as inclination of neural spines in cervical and thoracic vertebrae.

**Skull.** The skull (Figs. 3, 4, 5) is slender and flat, with a wide and flat rostrum. Supraorbital process of frontal is long sagittally. Zygomatic process is also large. Rostrum has a bluntly acute tip with a parabolic profile in dorsal view; posterior margins are subparallel. The margin of rostrum has several semicircular notches. These notches are not post-mortem, because they have round edges. On the rostrum, the exposure of maxilla is large as other mysticetes. Medial outlines of maxillae are almost parallel except anterior part. Premaxilla is very long, reaching to the position of eyes. Anterior parts of both premaxillae are attached together or even left premaxilla piled upon right in midline (This situation is probably post-mortem). Anterior to narial opening, premaxilla is convex transversely but almost flat in anterior expanded part. Narial opening is situated about mid-length of the rostrum. The dorsal outline of nasal is not elevated above the margin of the premaxilla anterior to the nasal opening. Posterior extremities of premaxillae and nasals are traced by the suture on the frontal. Mesorostral groove is open in dorsal view. Nasals of both side are mostly symmetrical. Posterior small part of right side is damaged. Nasal is also very long with almost parallel sides. Anterior extremity of nasal has a short projection into narial opening. Ascending process of left maxilla somewhat triangular. Right side of projection is not preserved. In ventral flat face of rostrum, there are eight grooves in total. A narrow and straight groove is located in anterior left maxilla, about 58 mm in length, with its anterior end on the margin of gingival border of 120 mm posterior to the tip. The corresponding groove of right side is about 154 mm in length, with its anterior end on the margin of gingival border of 150 mm posterior to the tip. There is an opening with anterior groove at left maxilla 424

mm posterior to the tip. The corresponding right opening is at 350 mm posterior from the tip. There are three short oblique grooves with posterior openings in middle right maxilla. The corresponding left side has only one groove and opening.

Along the anterior margin of maxilla and premaxilla, there is a shallow vestigial alveolar groove. In the posterior part, the groove, apart from the outline, is directed straight caudally, reaching about the position of eyes. The groove has deep alveoli in several places (Fig. 4). The groove is interrupted at two places; position of the posterior end of nasal opening in left side, and about the middle of the nasal opening in right side. In these places, maxillary margins eroded with smooth surface, suggesting that they existed in lifetime. The suture of maxilla and palatine on the ventral surface is meandering. The midline of both palatines is elevated sharply forming a medial crest.

There is a weak oblique ridge from the antorbital notch directing to the nasal opening. Lacrymal is preserved only left side, exposes at the anterolateral corner of the supraorbital process, forming a subcylindrical depression.

The anterior margin of frontal is not so clearly preserved in outline. Supraorbital process is almost flat both anteroposteriorly and laterally. Orbitotemporal crest is sharp or even overhanging in internal part but blunt in lateral. The posterior face of the supraorbital process does not carry a fossa for temporal muscle. The suture between frontal and parietal situated relatively posterior position; parietal reaches posterior to the posteromedial part of supraorbital process. Parietal is short, with distinct sagittal crest at midline. In dorsal and ventral view, the intertemporal region is elongate with parallel sides. Supraoccipital shield is triangular in dorsal view, concave with weak midcrest. Nuchal crest is very high. In lateral part, nuchal crest is overhanging against parietal. Squamosal is robust and relatively long, and diverges gently anteriorly. In ventral view, it appears slightly bowed outwards; in lateral view, it is markedly arched dorsally with a prominent facet for the jugal on the ventral apex.

In ventral view of posterior to rostrum, the exposure of vomer beneath the braincase is rhomboidal and convex laterally. Internal nasal opening is situated at posterior to the vomer, a little anterior to the position of the tympanic bullae. Internal nasal opening is separated longitudinally at its middle. Exposure of alisphenoid is below the suture between frontal and parietal. Jugal is spoon-shaped, its wider side is directed to zygomatic process. Narrow anterior part contacts with maxilla. The condyles appear to be on short condylar pedicles. Articular surface of the occipital condyles is much convex, both dorso-ventrally and laterally, than recent mysticetes.

**Tympanic bulla.** Left tympanic bulla (Fig. 6) is preserved imperfectly. Ventral surface of outer posterior prominence and median furrow is destroyed. Length from the anterior margin to the outer posterior prominence is 68.3 mm, and the maximum width is 42.8 mm. In ventral view, the tympanic bulla is rounded



Fig. 3. Skull of the KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Dorsal (above) and ventral (below) views. Scale: 10 cm.

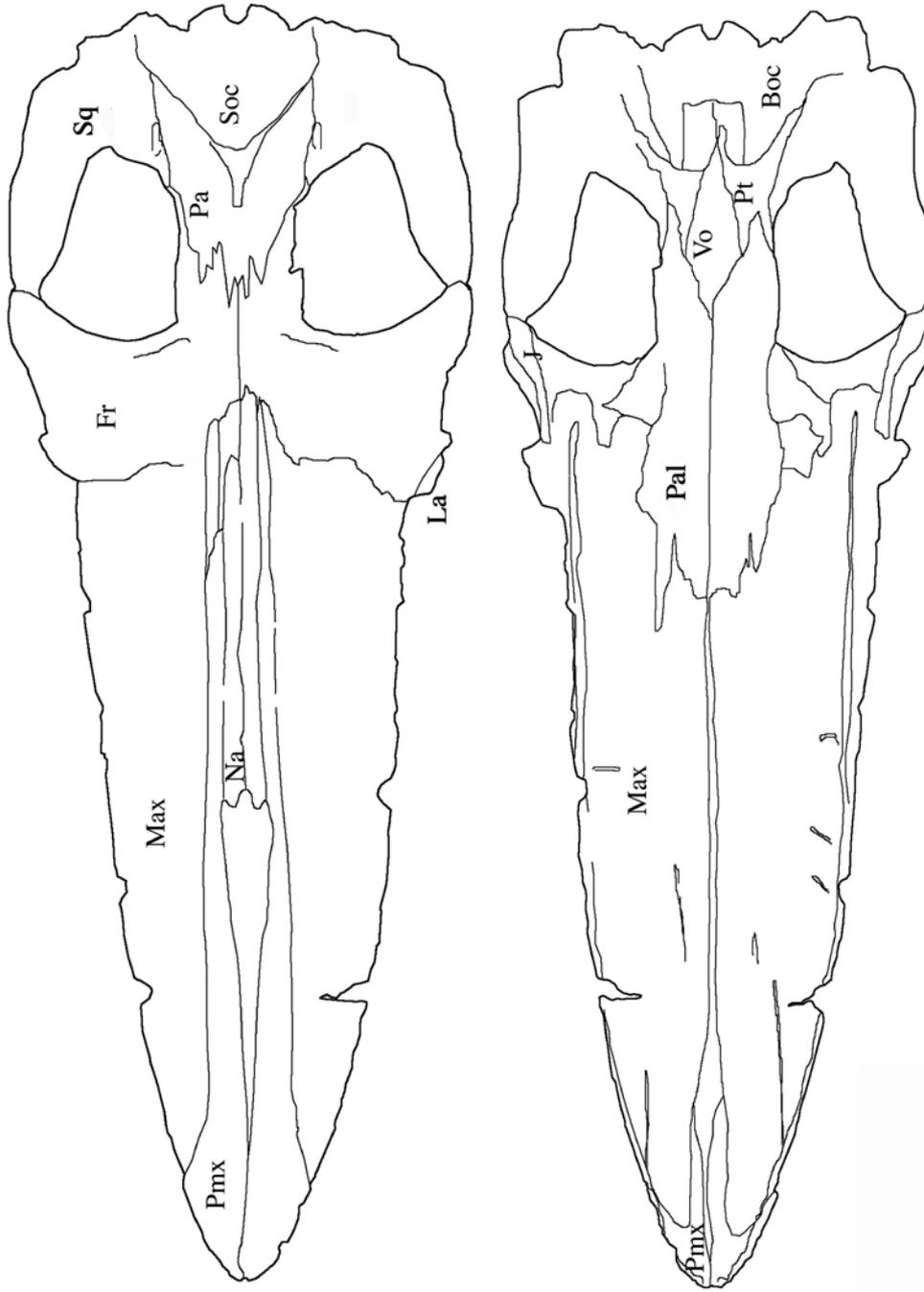


Fig. 4. Sketch of skull, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Dorsal (above) and ventral (below) views. Abbreviations—Boc; basioccipital, Fr; frontal, J; jugal, La; lacrymal, Max; maxilla, Na; nasal, Pa; parietal, Pal; palatine, Pmx; premaxilla, Pt; pterygoid, Soc; supraoccipital, Sq; squamosal, Vo; vomer.



Fig. 5. Skull of KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Ventral view of anterior rostrum (upper left). Scale 5 cm. Arrows indicate positions of alveoli. Caudal view (upper right). Scale: 10 cm. Lateral view (below). Scale: 10 cm.



Fig. 6. Left tympanic bulla, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Ventral, medial, dorsal and lateral views from left to right. Scale 5 cm.

subquadrate, rather elongate with subparallel lateral and medial faces. A horizontal ridge is present between the posterolateral and posteromedial prominences. Ventral keel developed. Anterior part is not pointed and the end is truncated, and is a bit flattened. Lateral furrow is significant as a mysticete. Sigmoid process is small. There is a flat face on the median side. The malleus is present, but is broken and in matrix.

**Dentaries.** Both side of dentaries are almost perfectly preserved (Figs. 7, 8). Condylod process is preserved only right dentary. Lateral curvature of dentaries in dorsal view is distinct, especially in anterior part. Anterior part of horizontal ramus is rather lifted than middle or posterior. Height of horizontal ramus is almost uniform. Coronoid process is very large and concave dorso-ventrally in lateral surface. Condylod process is also large,

Table 2. Measurement of skull (in mm)

Skull		
a.	Length from anterior end of premaxilla to occipital condyle	1,162
b.	Length from anterior end of premaxilla to apex of supraoccipital	1,072
c.	Length from anterior end of premaxilla to anterior end of temporal fossa	919
d.	Length from anterior end of premaxilla to posterior end of nasal (left)	864
e.	Length from anterior end of premaxilla to posterior end of premaxilla (left)	845
f.	Length from anterior end of premaxilla to anterior end of frontal	768
g.	Length from anterior end of premaxilla to posterior end of nasal opening	488
h.	Length from anterior end of premaxilla to anterior end of maxilla in dorsal surface	97
i.	Greatest length of left temporal fossa	193
j.	Greatest length of right temporal fossa	198
k.	Greatest width of both premaxillae	125
l.	Width of both premaxilla at middle of nasal opening	87
m.	Greatest width of nasal opening	48
n.	Width of both nasals	70
o.	Width of rostrum at nasal opening	280
p.	Width of rostrum at base at the antorbital notches	320
q.	Greatest width of frontal	440
r.	Width between temporal fossae	105
s.	Maximum bizygomatic width	460
t.	Width of supraoccipital shield	210
u.	Width of occipital condyles	95
v.	Length from anterior end of premaxilla to anterior end of palatine	674
w.	Length from anterior end of premaxilla to anterior end of vomer exposure	953
x.	Length from anterior end of premaxilla to posterior end of vomer exposure	1,101
y.	Width of both alveolar grooves at posterior end	280
Dentary		
a.	Length from anterior end to posterior end of left dentary	1,182
b.	Length from anterior end to posterior end of right dentary	1,176
c.	Height of coronoid process from ventral end of dentary: left	215
d.	Height of coronoid process from ventral end of dentary: right	220
e.	Horizontal distance from posterior end of condyle to apex of coronoid process :left	160
f.	Horizontal distance from posterior end of condyle to apex of coronoid process :right	175
g.	Length from posterior end of condyle to anterior end of orifice for mandibular canal :left	180
h.	Length from posterior end of condyle to anterior end of orifice for mandibular canal :right	196
i.	Greatest vertical diameter 320 mm behind anterior end of left ramus	95
j.	Greatest transverse diameter 320 mm behind anterior end of left ramus	39
k.	Greatest vertical diameter 630 mm behind anterior end of left ramus	92
l.	Greatest transverse diameter 630 mm behind anterior end of left ramus	49
m.	Greatest vertical diameter 335 mm behind anterior end of right ramus	95
n.	Greatest transverse diameter 335 mm behind anterior end of right ramus	39
o.	Greatest vertical diameter 855 mm behind anterior end of right ramus	98
p.	Greatest transverse diameter 855 mm behind anterior end of right ramus	40
q.	Greatest vertical diameter behind coronoid process of left ramus	124
r.	Greatest vertical diameter behind coronoid process of right ramus	130



Fig. 7. Dentaries, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. From top to bottom, lateral view and medial view of left dentary, medial and lateral views of right dentary. Scale: 10 cm.

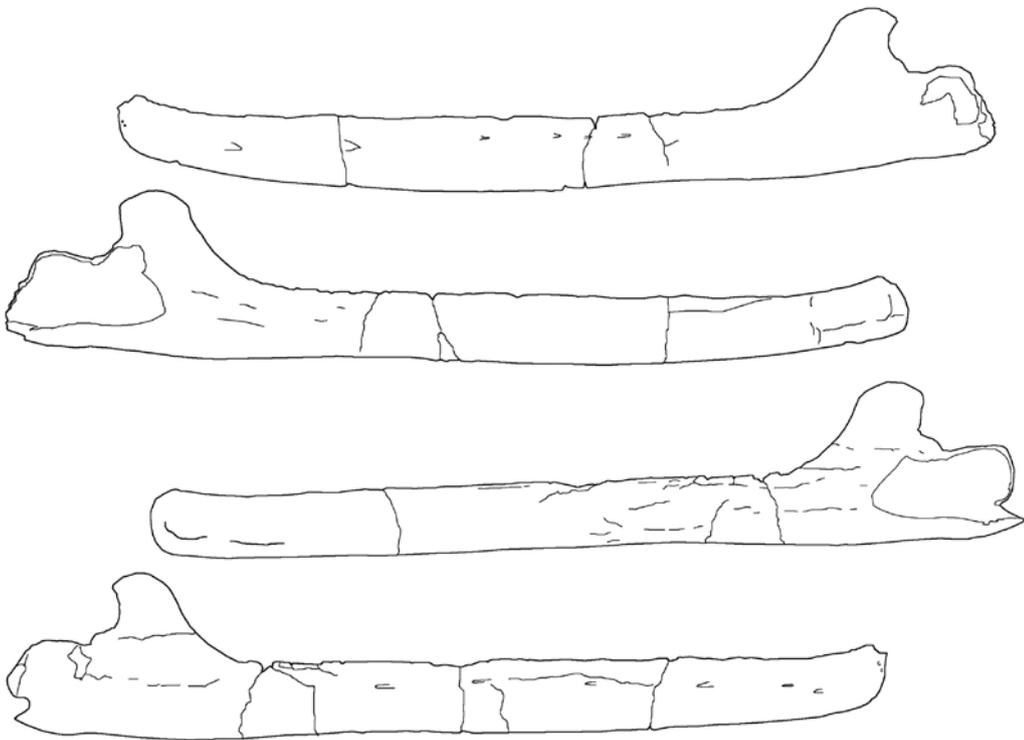


Fig. 8. Sketch of dentaries, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. From top to bottom, lateral view and medial view of left dentary, medial and lateral views of right dentary.



Fig. 9. Hyoid bones, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Scale 5 cm. Left row; top to bottom, ventral, dorsal, left antero-lateral and right antero-lateral views of basihyoid and fused thyrohyoids. Right row; two views of a hyoid element referred to stylohyoid or epihyoid.

Table 3. Measurements of the cervical vertebrae and thoracic vertebrae (in mm)

Cervical vertebrae								
	Atlas	Axis	C3	C4	C5	C6	C7	
a. Anteroposterior length of centrum	61.3	48.1	23.6	23.2	26.2	31.1	31.6	
b. Minimum anteroposteior length of pedicle of neural arch	31.4	21.3	9.5	14.1	16.0	21.0	27.6	
c. Transverse diameter of neural canal	36.0	49.9	51.0	54.7	58.1	63.0	65.3	
d. Vertical diameter of neural canal at middle	50.7	23.4	30.0	25.5	27.2	29.5	27.9	
e. Distance between ends of transverse processes	195.7	150.2	154.0	160.8	165.4	168.9	197.2	
f. Height of neural spine from the neural canal	28.2+	37±	11.8	17.8	19.2	25.0	44.6	
g. Length of Neural arch at base of neural spine	32.8	69.3	12.8	14.1	15.6	15.0	21.5	
h. Maximum distance between anterior zygapophyses	—	—	67.5	75.5	85.5	91.5	101.8	
Thoracic vertebrae								
	T1	T2	T3	T4	T5	T6	T7	T9?
a. Anteroposterior length of centrum	44.0	47.6	48.4	—	—	—	—	—
b. Minimum anteroposteior length of pedicle of neural arch	17.0	17.0	21.6	27.4	27.0	—	—	—
c. Transverse diameter of neural canal	63.9	59.4	58.1	53.5	50.5	50±*	—	53.8
d. Vertical diameter of neural canal at middle	29.0	28.9	28.3	—	—	—	—	34.5
e. Distance between ends of transverse processes	153.8	151.1	150.2	141.2	127±	125±	—	—
f. Height of neural spine from the neural canal	75.9	97.4	100.5	101.9	108.2	115.4	—	133.0
g. Length of Neural arch at base of neural spine	31.4	33.4	38.0	39±	43.2	53±	—	—
h. Maximum length across neural spine	29.9	40.5	43.2	42.5	46.0	48.1	50.0	50.9
i. Maximum distance between anterior zygapophyses	114.1	109.3	92.5	88.0	69±*	69±*	—	—

\*measured half and twiced

with concave face, which forms the inner surface of mandibular foramen. Mandibular foramen is very large. Angular process is also large, projected straight, thin-walled and subcylindrical. Dorsal margin of the mandibular foramen reaches to the base of coronoid process. There is a series of mental foramina in lateral face of dentaries. Groove for symphyseal ligament is prominent. Along the dorsal margin of dentary, a vestigial alveolar groove is situated, from anterior tip to just anterior to the coronoid process. In several places, the vestigial alveolar groove, there has deep holes which could be alveoli (or could be openings of the terminal branches of the mandibular canal), but no teeth are observed in or around the skull.

**Hyoid bones.** Basihyoid and proximal part of both thyrohyoid (Fig. 9) are preserved. These bones are fused together incompletely at articular facets. In the middle part, the basihyoid is broken; the pieces were separated in sediments. Basihyoid is short in width, flat at dorsal surface. Thyrohyoid is also flat at dorsal surface, with wide distal part. Another bone is referred to the stylohyoid or possibly epihyoid. Orientation and side of the bone is indeterminable. The bone is rod-like with its internal surface flat. One end is flattened and curved and the other end is triangular in section.

**Cervical vertebrae.** A complete series of seven cervical vertebrae (Figs. 10–15) is preserved. The cervical vertebrae are situated in articulation with both skull and thoracic vertebrae. The atlas (first cervical vertebra) has deep concave articular faces to skull. Transverse process of atlas is large, oriented obliquely dorsally, and is imperforate; the neural canal is deep and parallel-sided. Facet for the odontoid process is small. Posterior articular facets are flat. The neural spine of the axis is large and triangular in lateral view; the neural spine is elongated anteroposteriorly and overlaps the atlas anteriorly. The third to seventh cervicals are unfused and flattened anteroposteriorly. The articular faces of the third to seventh cervicals are almost flat. The lengths of the centrum of third to seventh cervicals increase posteriorly. The third to seventh cervicals have vertebral arterial canals, although the canal in the seventh cervical is very small. The neural spine of the third to seventh cervicals increase height posteriorly.

**Thoracic vertebrae.** The first to seventh thoracic vertebrae (Figs. 12, 16–19) are preserved in articulated position. Among them, posterior ones are more eroded ventrally by weathering. The first thoracic vertebra is completely preserved; in lateral view, position of the lateral process is almost similar to the dorsal margin of centrum. The second thoracic vertebra missing ventral



Fig. 10. First to third cervical vertebrae, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Scale 5 cm. Cranial (upper row) and caudal (lower row) views.



Fig. 11. Fourth to sixth cervical vertebrae, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Scale 5 cm. Cranial (upper row) and caudal (lower row) views.



Fig. 12. Seventh cervical vertebra and first to second thoracic vertebrae, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Scale 5 cm. Cranial (upper row) and caudal (lower row) views.



Fig. 13. First to seventh cervical vertebrae, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Scale 5 cm. Dorsal (upper row) and left lateral (lower row) views.

part of centrum; in lateral view, position of the lateral process is higher than the first thoracic vertebra. The third thoracic vertebra missing ventral-right half of centrum. The fourth thoracic vertebra missing whole centrum, the fifth and sixth missing centrum and right transverse process, and the seventh is preserved only neural spine and fragmental left transverse process. Adding to those, one thoracic vertebra (Fig. 20) is preserved beside the vertebral column. The neural spine and other character indicate that the detached vertebra may be close to the seventh, and treated here as the ninth thoracic. The anterior surface of centrum and prezygapophyses of the ninth thoracic vertebra is missing. There is articular facet for rib on centrum at posterior edge.

**Ribs.** The first to fourth left ribs, third to seventh right ribs (Figs. 21, 22) are preserved only their proximal part. Mostly, ends of these ribs are already broken at sedimentation. Adding to them, nine fragmental ribs are preserved. The first to fourth left ribs are occurred in articulation to thoracic vertebrae. The left first rib has a pointed head. Distance between head to tubercle is short. Tubercle is large with an elongated vertebral articular facet. The distance between tubercle to rib angle is long. The left second

Table 4. Measurement of hyoid (in mm)

Basihyoid	Right Left	
	a. Maximum width as preserved	204.9
b. Width of both cornu minor	80.4	
c. Maximum width of basihyoid	55.1	
d. Minimum length of basihyoid	24.5	
e. Thickness of basihyoid at middle	13.5	
f. Preserved length of thyrohyoid	108.0	113.4
g. Width of thyrohyoid at middle	19.7	19.5
h. Thickness of thyrohyoid at middle	14.8	14.8
Stylohyoid or Epihyoid		
a. Length	139.8	
b. Width at middle	16.6	
c. Thickness at middle	8.4	

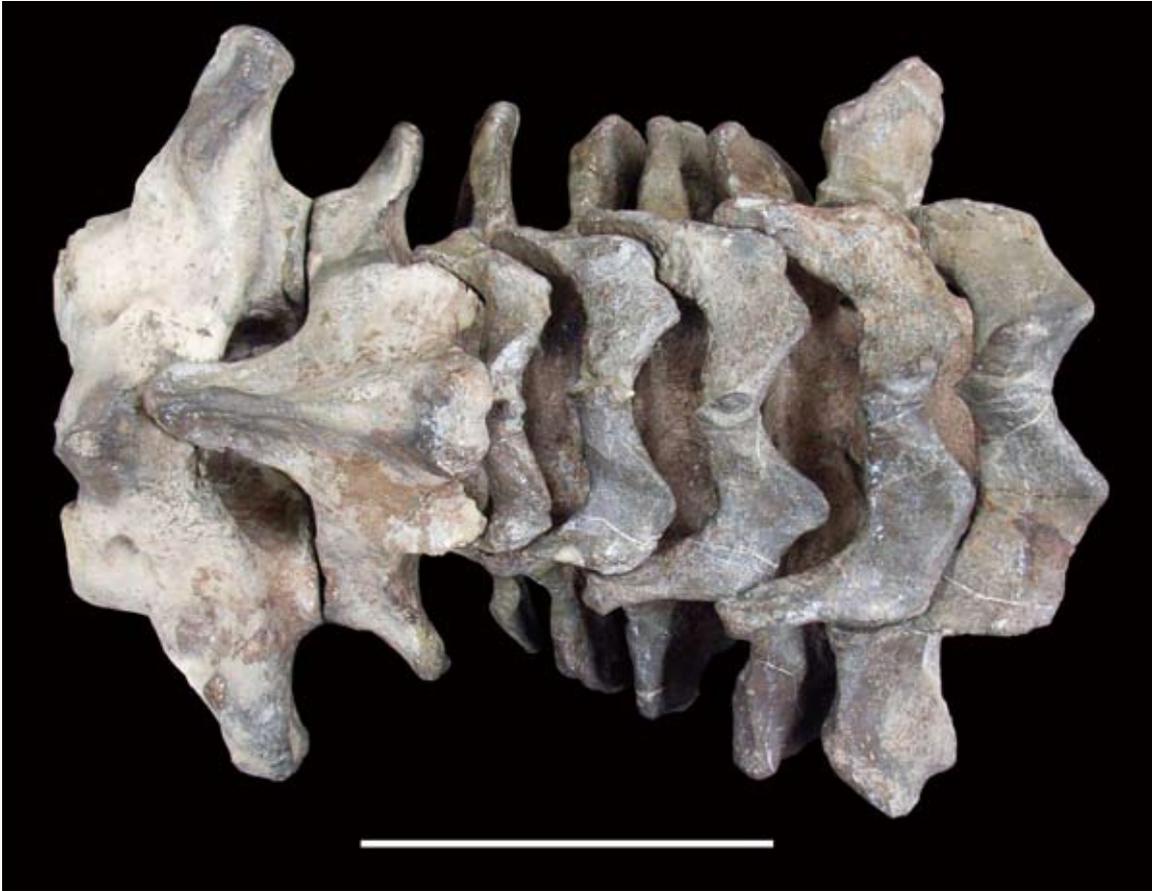


Fig. 14. First to seventh cervical vertebrae, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Scale 5 cm. Dorsal view, in the articulated position.



Fig. 15. First to seventh cervical vertebrae, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Scale 5 cm. Left lateral view, in the articulated position.



Fig. 16. First to third thoracic vertebrae, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Scale 5 cm. Dorsal (upper row) and left lateral (lower row) views.

rib has a blunt head. Distance between head to tubercle is longer than that of first rib. Tubercle is smaller with a rounded vertebral articular facet. The distance between tubercle to rib angle is short. The left third rib has a truncated head. Distance between head to tubercle is long. Tubercle is smaller with an elongated vertebral articular facet. The distance between tubercle to rib angle is long. The right third rib has a truncated head. Distance between head to tubercle is long. Tubercle is smaller with a short vertebral articular facet. The distance between tubercle to rib angle is long. The left fourth rib is fragmental. The right fourth rib has a truncated head and narrow neck. Distance between head

to tubercle is long. Tubercle is smaller with a short vertebral articular facet. The distance between tubercle to rib angle is long. The right fifth rib has a round head. Distance between head to tubercle is long. Tubercle is smaller with a small vertebral articular facet. The right sixth rib has a round and large head. Distance between head to tubercle is short. Tubercle is smaller with a small vertebral articular facet. There is a rib fragment which has a truncated single head.

**Forelimb.** Left forelimb is preserved in articulation (Fig. 23) without digit nor metacarpi. One carpal bone is preserved, but



Fig. 17. Fourth to sixth thoracic vertebrae, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Scale 5 cm. Dorsal (upper row) and left lateral (lower row) views.

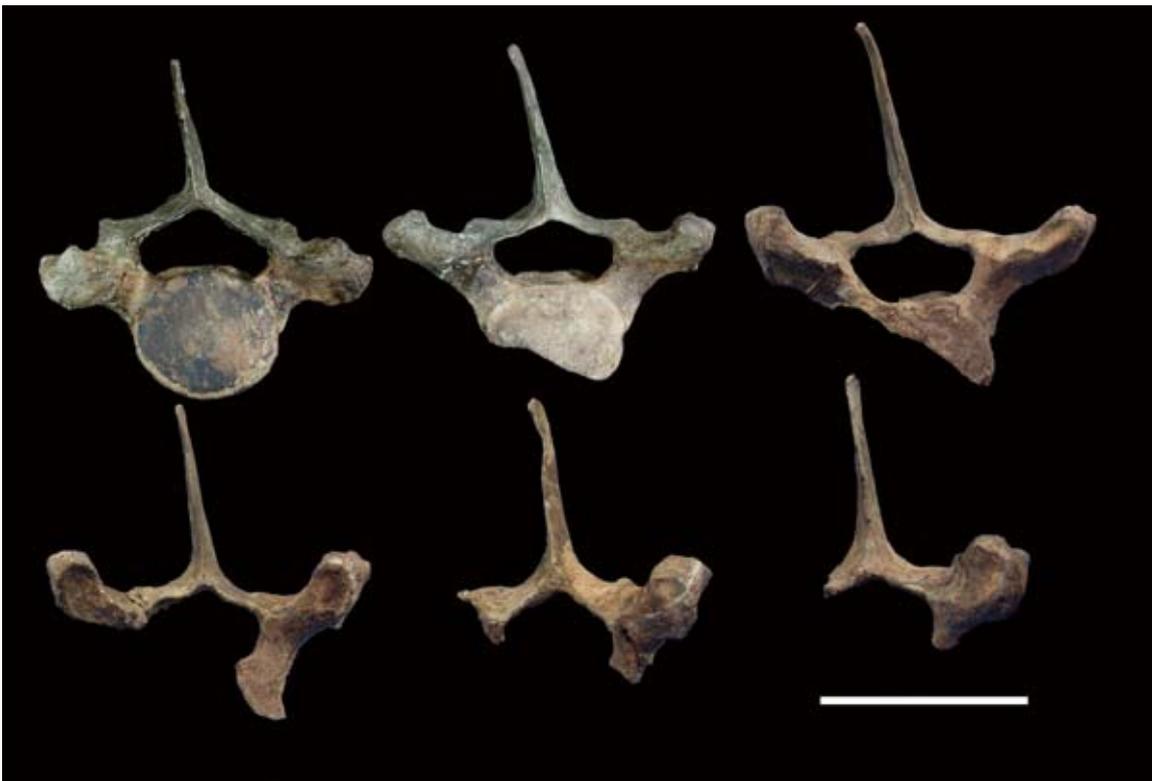


Fig. 18. First to sixth thoracic vertebrae, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Scale 5 cm. Cranial view.



Fig. 19. First to seventh thoracic vertebrae, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Scale 5 cm. Left lateral (upper) and dorsal (lower) views.



Fig. 20. Presumed ninth thoracic vertebra, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Scale 5 cm. Cranial, caudal, left lateral, and dorsal views, from left to right.



Fig. 21. Vertebral part of ribs, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Scale 5 cm. Internal views; left first to fourth (upper) and right third to sixth and posterior ribs (lower).



Fig. 22. Vertebral part of ribs, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Scale 5 cm. Lateral views; left first to fourth (lower) and right third to sixth and posterior ribs (upper).

the position is undecided. Several right forelimb elements are preserved but mostly fragmental. The left humerus, radius and ulna are articulated.

**Scapula:** Complete left scapula (Fig. 24) and fragmental right scapula are preserved. Description is based on the left. Scapula is wide. Glenoid cavity is suboval and shallow. Anterior margin is S-shaped. Acromion is rather large with parallel sides, and it is directed anteriorly. Coracoid process is short but robust, with a blunt tip. Posterior margin is straight in its medial part. Internal face of scapula is concave, and separated by a blunt ridge running from the glenoid to the middle of medial margin.

**Humerus:** Left humerus (Fig. 25) is completely preserved. Natural mold of right humerus is partly preserved in original matrix. Humerus is long. Head of humerus is round and large. Body of humerus is flattened laterally. Deltoid crest is developed. Articulation facet for ulna is almost flat. Articulation facet for radius is also flat but in different plane of the ulnar facet, indicating the elbow joint is not rotating joint.

**Radius:** Both left and right radii (Figs. 26, 27) are preserved. Radius is short, flattened laterally. Anterior margin of radius is thinner than the posterior margin.

**Ulna:** Left ulna (Fig. 26) is completely preserved. Oleclanon is very largely developed. Coronoid process is not distinct. Posterior margin of radius is thinner than the anterior margin.

## DISCUSSION

**Comparisons to closely related taxa.** This species has many similarities to *Eomysticetus whitmorei* SANDERS and BARNES, reported from South Carolina, USA in fundamental structure of the skull or position of the external nares. SANDERS and BARNES (2002) presented a new subfamily Eomysticetidae including a single new genus *Eomysticetus*. But the diagnosis of their new subfamily Eomysticetidae is presented as “the same as for the genus.” *Yamatocetus* and *Eomysticetus* share characters

Table 5. Measurement of ribs (in mm)

	Left				Right				
	1	2	3	4	3	4	5	6	7
a. Distance between head to outer broken end	147.1	139.6	124.5	—	122.7	196.2	98.2	91.8	—
b. Distance between tuberosity to outer broken end	163.5	141.0	111.9	—	101.4	200.1	62.6	68.7	51.0
c. Maximum length from head to tuberosity	62.6	75.7	80.3	—	84.9	79.5	65.0	45.0	—
d. Width of rib at broken end	27.8	23.5	28.0	—	31.0	18.8	20.5	17.2	17.9
e. Thickness of rib at broken end	13.8	11.8	12.3	—	11.5	15.3	17.0	19.0	12.8



Fig. 23. Left forelimb, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Scale 10 cm. Articulated position.



Fig. 24. Left scapula, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Scale 10 cm. Lateral, Internal and anterior views in upper row, and the face to the humerus articulation below.

such as; differing from all other baleen-bearing Mysticeti by having an elongate and narrow intertemporal region; extremely long zygomatic processes of squamosals; humerus as long as radius and ulna; differing from Balaenopteridae, Balaenidae, Neobalaenidae and Eschrichtiidae by having naris near mid-length of rostrum, exceptionally elongate nasal bones; parietals exposed along intertemporal region between frontals and apex of supraoccipital; large coronoid process of dentary.

The most significant difference of *Yamatocetus* and *Eomysticetus* is seen in the outline seen from side of rostrum, almost flat in the present species (Fig. 5), but longitudinally elevated nasals in *E. whitmorei*. In dorsal view, anterior margin of the rostrum is bluntly pointed in the present species, but sharply pointed in *E. whitmorei*. Deltoid crest is significantly higher and over-hanged in the present species. The vestigial alveolar groove is observed in both upper and lower jaws in the present species but exists only lower jaws in *E. whitmorei*. The frontal of the present species is stout and with parallel anterior and posterior margins in the present species, but weak and with constricted margins in *E. whitmorei*. Furthermore, the outline of the dentaries observed from side is almost horizontal throughout the ramus in the present species but bends downward in *E. whitmorei*.

**Skull structure, nasal opening and telescoping.** The morphology and position of the nasal opening offers good information for the first stage of evolution of mysticetes. Nasals are very long and straight, reaching posteriorly almost to the



Fig. 25. Left humerus, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Scale 10 cm. Posterior, lateral and internal views from top to bottom.



Fig. 26. Left ulna and radius, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Scale 10 cm. Lateral and internal views from top to bottom.



Fig. 27. Right radius, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Scale 10 cm. Lateral and internal views from top to bottom.

Table 6. Measurement of limb bones (in mm)

Left scapula		
	greatest length from anterior-vertebral end to posterior end	388
	length of anterior margin	290
	length of posterior margin	194
	distance from humerus articulation to vertebral end	278
	length of coracoid process	120
	greatest diameter of humerus articulation	78
	smallest diameter of humerus articulation	59
Left humerus		
	greatest length	276
	anteroposterior diameter of head	85
	anteroposterior diameter of shaft at deltoid crest	98
	anteroposterior diameter of shaft at distal end	67
	greatest transverse diameter at proximal end	93
Left ulna		
	greatest length	280
	greatest distance between proximal end to distal angle of olecranon process	121
	length between humerus articulation to distal end	94
	greatest distance between radius facet to posterior end of olecranon process	95
	anteroposterior diameter at distal end	55
	transverse diameter at distal end	27
Left radius		
	greatest length	225
	anteroposterior diameter at proximal end	52
	anteroposterior diameter at widest portion	61
	anteroposterior diameter at distal end	59
	transverse diameter at distal end	32
Right radius		
	greatest length	218
	anteroposterior diameter at proximal end	60
	anteroposterior diameter at widest portion	64
	anteroposterior diameter at distal end	57
	transverse diameter at distal end	32

position of eyes. It indicates the backward telescoping of the posterior end of nasals occurred before migration of the nasal opening.

**Phylogeny and auditory bulla.** The somewhat quadrate ventral outline of the auditory bulla (Fig. 6) is one of the most significant features of *Yamatocetus canaliculatus*. Several characteristics of the auditory bulla, such as medial and lateral outlines in ventral view are straight, anterior projection is not sharp and truncated, are seen in many “toothed mysticetes”, such as *Mammalodon colliveri* PITCHARD from Australia, *Kekenodon onamata* HECTOR and other archaic mysticetes from New Zealand. Furthermore, *Llanocetus denticrenatus* (MITCHELL) from Antarctic Peninsula shares similar characteristics above in auditory bulla (Fig. 28), although the age is older than *Yamatocetus canaliculatus*. These characters are also seen in, in part, several archaeocetes. On the other hand, advanced Oligocene mysticetes such as *Mauicetus lophocephalus* MARPLES from New Zealand (MARPLES, 1956) has different shape, such as sides which are not parallel, and pointed anterior end of the bulla.

**Gingival groove and food.** It is obvious that *Yamatocetus canaliculatus* had baleen plates and enough space for the

activity of filter feeding, because the rostrum is very wide and long. Furthermore, the nutrient grooves with distinct openings of canals on the ventral face of rostrum are good indicator of the existence of baleen plates, even though the number of the openings is fewer compared to the extant baleen whales. Such small number is also seen in the Oligocene “toothed whales” such as aetiocetids (DEMÉRÉ, *et al.*, 2008). As in the case of the aetiocetids, *Yamatocetus canaliculatus* also had teeth, at least some stage of its ontogeny, because of the vestigial alveolar grooves along the margins of both upper and lower jaws. Especially the presence of three pairs of deep holes, comparable to alveoli, in the groove of premaxilla suggests the presence of teeth. So, the present species occupies a transitional stage during the evolutionary loss of teeth.

The oldest “toothed mysticete”, *Llanocetus denticrenatus* MITCHELL, from the Early Oligocene of Antarctic Seymour Island (MITCHELL, 1989), has also a very wide rostrum and separately situated large cheek teeth with two roots. Their function would be somewhat limited because of their long distance between teeth. The present species had smaller and more distant teeth than *Llanocetus denticrenatus* MITCHELL and the root is single. Therefore the function of the teeth in *Yamatocetus canaliculatus* is much more limited than the latter. On the other hand, the

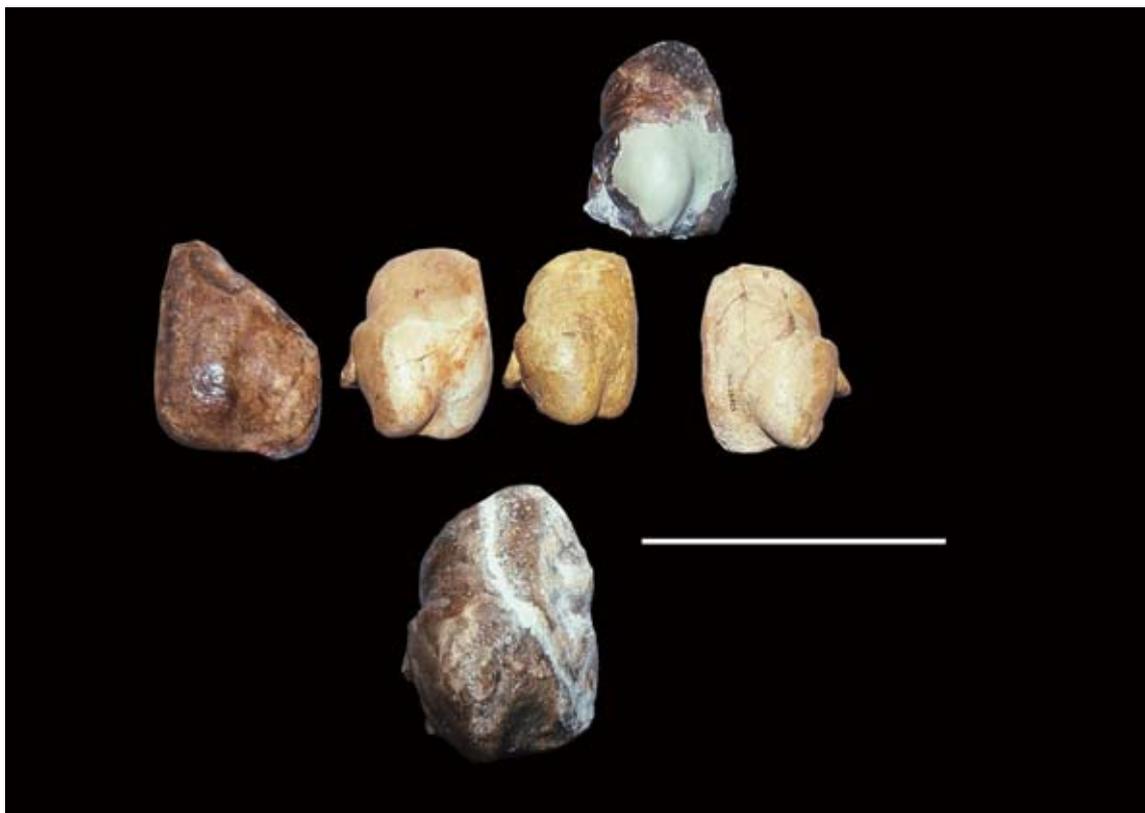


Fig. 28. Several auditory bullae of archaic mysticetes. Scale 10 cm. Top row: KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Middle row (left to right): NMNZ Ma 306, *Kekenodon onamata* HECTOR, 1881; OU 22036, mysticete; MUGD 1874, *Mammalodon colliveri* PRITCHARD, 1939; OU No number, “toothed mystecete”. Bottom row: additional specimen of *Llanocetus denticrenatus* MITCHELL, 1989.

margins of rostrum are concordant with the curve of dorsal margin of dentaries, suggesting the margin of upper and lower jaws fit together. The movement and function of *Yamatocetus canaliculatus* is simple, compared with extant rorquals, and almost without alpha rotation (LAMBERTSEN *et al.*, 1995).

**Rib structure and diving.** Among the ribs, proximal parts of left anterior ribs are articulated to first to fifth thoracic vertebrae (Fig. 29). They have both head and tubercle articular facets (double-headed). Ribs of right side are not in anatomical position. The shapes of them indicate that there are third and fourth of right side. There are at least two double-headed ribs of right side more-posterior than the fourth. So, there are at least six double-headed ribs in each side. It is not clear whether vertebrae posterior to the second thoracic actually had a rib articulation on the centrum. But one dislocated thoracic vertebra has a centrum articulation facet. This vertebra is posterior than seventh, maybe eighth or ninth, judging from the shape and structure. Therefore, the *Yamatocetus canaliculatus* had more than 8 double-headed ribs in each side. This character is also seen in *Eomysticetus whitmorei*, which has at least 9 double-headed ribs (SANDERS and BARNES, 2002).

There are fewer double-headed ribs in the recent mysticetes. In *Balaenoptera brydei*, for example, only one the first (anterior-

most) rib is double-headed; the “additional head” articulates to the seventh thoracic vertebra, while all others articulate only to lateral process of vertebrae. Reduction of the double-headed rib articulation is an adaptation to deep diving, giving much flexibility to the rib cage. Therefore, there is not advanced adaptation to deep diving in the present species.

**Anterior limb.** The holotype of *Yamatocetus canaliculatus* includes almost perfect scapula, humerus, radius and ulna at the left side. In the scapula, the costal side is concave, as an ancestral feature among mysticetes. Also, the scapula has a ridge from olecranon to the middle of vertebral margin. This character is not seen in extant baleen whales, and not seen in *Basilosaurus cetoides* OWEN, reported by KELLOGG (KELLOGG, 1936).

Fundamental structures of humerus, radius and ulna are almost similar to those of extant mysticetes, indicating that their functional changes to flipper had been already obtained. The elbow articulation has angled flat faces to radius and ulna respectively, showing limited movement at elbow. This structure is seen in mysticetes, but not seen in archaeocetes such as *Basilosaurus cetoides* OWEN and *Zygorhiza kochii* (REICHENBACH) (KELLOGG, 1936). But, looking at the ratio of the length of forelimb, humerus is much longer compared to recent mysticetes. This condition is also seen in *Eomysticetus whitmorei*



Fig. 29. Photograph taken during the preparation of vertebral column and ribs, KMNH VP 000,017, holotype, *Yamatocetus canaliculatus*, n. gen. and n. sp. Oblique left lateral view; second cervical vertebra (partly) to fourth thoracic vertebra with articulated first to third left ribs.

(SANDERS and BARNES, 2002). It suggests less swimming ability in eomysticetids than later mysticetes.

## CONCLUSION

In the present report, the author described a new genus and species of an archaic mysticete, *Yamatocetus canaliculatus*, from the Upper Oligocene Ashiya Group, Kyushu Island, Japan. Closest species is *Eomysticetus whitmorei* SANDERS and BARNES from the Late Oligocene of South Carolina, USA, which shares many skull characters such as anterior-situated outer nare and wide rostrum. The age of both species is important time for radiation of archaic mysticetes including “toothed mysticetes” (FORDYCE, 1992). *Yamatocetus canaliculatus* is very important for the research of evolution of archaic mysticetes, because of its excellent preservation, such as the backward transition of nasal opening, feature of gingival grooves, and feature of mandibular articulation. Looking at the evolutionary history of mysticetes, *Yamatocetus canaliculatus* has progressive morphology, such as the rostrum shape or construction of forelimb, or transitional morphology, such as the position of nasal opening or tooth remnant, and also ancestral morphology, such as the function of jaws, two-headed ribs, and scapula curvature. The filter feeding had mostly obtained, but ancestral in jaw movement. Swimming apparatuses are also obtained but imperfect, such as the ratio of forearm, and the adaptation to deep diving is not obtained.

It is very interesting that there is no comparable species in the fauna of the same age from Hokkaido (BARNES *et al.*, 1995) and West Coast of the United States (EMLONG, 1966; BARNES *et al.*, 1995). However, there are close forms in New Zealand (FORDYCE, 1992) and the eastern United States (FORDYCE and BARNES, 1994). The radiation and dispersal of mysticetes were very rapid and complicated in the Northern Hemisphere than Southern Hemisphere (FORDYCE, 1977).

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