

Coexistence of Oligocene toothed and baleen-assisted mysticetes in the northwestern Pacific

Cheng-Hsiu Tsai¹, Toshiyuki Kimura², Yoshikazu Hasegawa^{2,3}

¹ Department of Life Science, Institute of Ecology and Evolutionary Biology, Museum of Zoology, National Taiwan University, No. 1, Sec. 4, Roosevelt Rd., Taipei, 10617, Taiwan

² Gunma Museum of Natural History, 1674-1, Kamikuroiwa, Tomioka, Gunma 370-2345, Japan

³ Iida City Museum, 2-655-7, Otemachi, Iida, Nagano 395-0034, Japan

<https://zoobank.org/3E4B181B-8B6A-4567-9A58-A4A9ABFAD188>

Corresponding authors: Cheng-Hsiu Tsai (whaletsai@ntu.edu.tw, craniata@gmail.com); Toshiyuki Kimura (kimura@gmnh.pref.gunma.jp)

Academic editor: Johannes Müller ♦ Received 24 August 2023 ♦ Accepted 22 December 2023 ♦ Published 11 January 2024

Abstract

Oligocene mysticetes display an unparalleled diversity and morphological disparity in the evolutionary history of Mysticeti. However, their paleoecological aspects, such as the patterns of coexistence of different morphotypes, remain poorly explored. Here we describe an aetiocetid (toothed mysticete) from the Jinnobaru Formation (lower upper Oligocene, about 28 million years ago) of Umashima Island, Kitakyushu, Japan. Our description of a toothed mysticete from the Oligocene of Umashima exemplifies the coexistence of toothed and baleen-assisted mysticetes in the northwestern Pacific. Hopefully, new finds of Oligocene mysticetes will lead to a well-sampled dataset for analyzing this and other related paleoecological traits to understand the demise of “archaic” Oligocene mysticetes and the subsequent rise of the modern-looking baleen-bearing whales in Miocene times.

Key Words

Aetiocetidae, Chattian, Jinnobaru Formation, Mysticeti, toothed baleen whale, Umashima

Introduction

The coexistence of closely related species often shows niche partitioning under various mechanisms, such as resource, spatial, and temporal partitioning, habitat differentiation, or size disparity (Schoener 1974). Baleen whales (Cetacea: Mysticeti), the largest animals ever generally avoid intense competition through food partitioning. For example, blue whales consume euphausiids primarily, whereas fin whales predominantly forage on small fishes but also include euphausiids when abundant (Wursig et al. 2018). Yet, coexistence or competition of closely related mysticetes in the deep past has rarely been documented or discussed. The few remarkable examples include a large aetiocetid from the Oligocene of Hokkaido, which implies an early case of niche partitioning by size disparity in toothed mysticetes along the northwestern Pacific coast (Tsai and Ando 2016), and a

likely competitive exclusion between cetotheriid and eschrichtiid whales (Collareta et al. 2021). Here, we describe a newly collected aetiocetid specimen from the Oligocene of Umashima Island (Fukuoka, Japan; Fig. 1). This new specimen represents the first formally recognized toothed “baleen” whale from the Jinnobaru Formation. Given that the Jinnobaru Formation has also produced the well-preserved eomysticetid *Yamatocetus*, our discovery provides an opportunity to discuss the coexistence of different morphotypes of early mysticetes.

Institutional abbreviations

UCMP, University of California Museum of Paleontology, Berkeley, USA; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; **YM**, Yamaguchi Prefectural Museum, Yamaguchi, Japan.

Results

Systematic paleontology

Cetacea Brisson, 1762

Mysticeti Gray, 1864

Aetiocetidae Emlong, 1966

Aetiocetidae gen et sp. indet.

Fig. 2

Material. YM-G-100208, including the posterior part of the skull. A 3D file of YM-G-100208 is freely available at: <https://zenodo.org/record/8140997>.

Locality and age. YM-G-100208 was collected by Akito Makino on Umashima Island (about ten years ago, 33°57'58"N, 130°51'41"E; Fig. 1), Fukuoka Prefecture, Japan. YM-G-100208 was a floating nodule when discovered, resulting in an uncertain geological horizon. No microfossils, indicative of the geological age, have been recovered from the matrix with YM-G-100208. However, the matrix with YM-G-100208 is grayish and fine-grained sandstone, as typical of the Jinnobaru Formation of the Ashiya Group, which is the only exposed formation on Umashima (Nakae et al. 1998). In addition, YM-G-100208 is extensively eroded but still preserves some skull sutures, suggesting that the specimen was likely not transported far from the original locality. Thus, we regard the geological horizon producing YM-G-100208 to be part of the Jinnobaru Formation of the Ashiya Group. The Ashiya Group includes the Yamaga, Norimatsu, Jinnobaru, Honjo, and Waita formations in ascending order stratigraphically (Ozaki et al. 1993). The geological age of the Ashiya Group ranges from the latest Early to Late Oligocene based on fission-track dating, calcareous nannofossils, and planktonic foraminifera (Saito 1984; Okada 1992; Ozaki

et al. 1993), and the base of the Jinnobaru Formation was dated 28.91 ± 0.2 Ma by the sensitive high-resolution ion microprobe zircon U-Pb method (Sakai et al. 2014). The upper boundary of the Jinnobaru Formation remains uncertain, and we consider YM-G-100208 to be slightly younger than 28 Ma, about the early Late Oligocene, similar to *Yamatocetus canaliculatus*. The Jinnobaru Formation has produced abundant vertebrate fossils, including the eomysticetid *Yamatocetus canaliculatus* (Okazaki 1995; Okazaki 2012), the purported squalodontid "*Metasqualodon*" *symmetricus* (Okazaki 1982), and pterosaurs (Olson and Hasegawa 1996).

Description. YM-G-100208 preserves the post-frontal skull. The anteriormost serration likely indicates the frontal-parietal suture. Overall, the preserved part of the skull is eroded, and the natural sutures between bones are barely identifiable; the occipital complex is damaged. The right and left parietals meet at the dorsal midline, and the presence of the sagittal crest remains uncertain due to erosion. The anteriormost edge of the parietal is unclear, but the anteroposterior length of the parietal is much longer than its dorsoventral height. The posterior suture between the parietal and the supraoccipital is also eroded but shows a minor lateral extension of the supraoccipital, leaving a gentle overhang on the squamosal fossa posteriorly. The posterior-most margin of the parietal is also uncertain, but given the preserved morphology, it likely extends further back, only slightly anterior to the occipital condyle.

The supraoccipital is broadly triangular, and the anterior half is concave. Based on the surrounding morphology, the existence of a supraoccipital depression should be regarded as genuine. The suture between the supraoccipital and exoccipital likely remains partly unfused, but the post-mortem damage and compression hinder reliable judgment. The left occipital condyle is missing, but the overall preservation shows an oval shape

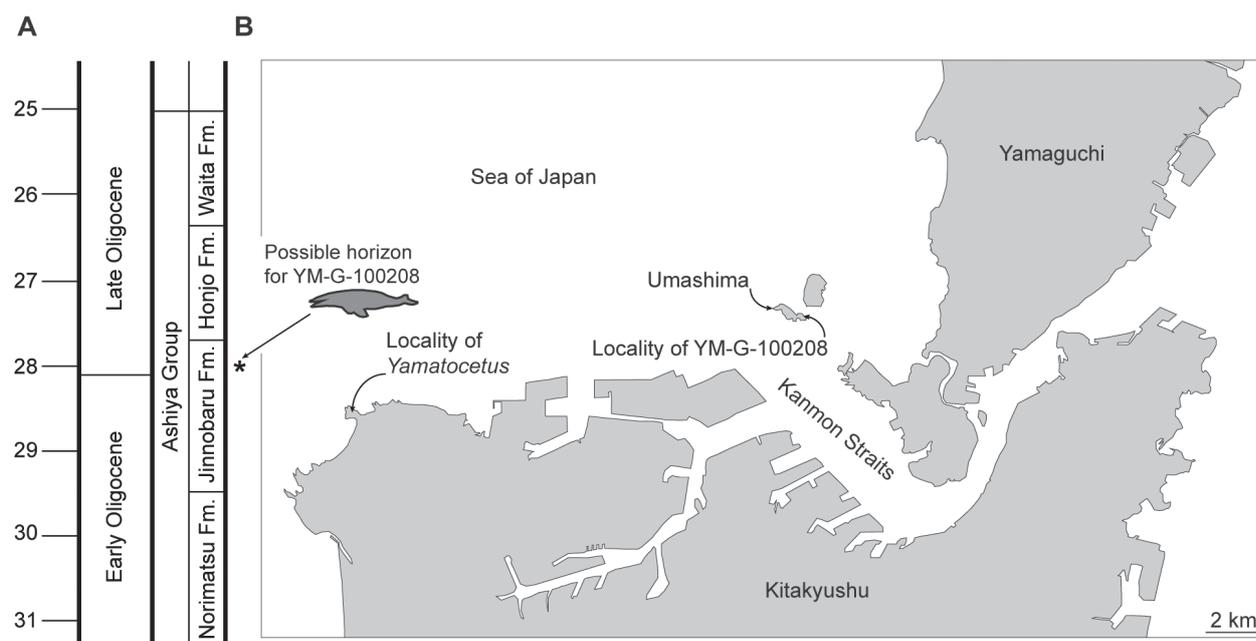


Figure 1. Geological horizon and locality of YM-G-100208. (A) Geological column to indicate the collecting horizon. (B) Geographic map to show the collecting locality.

of the magnum foramen (shorter dorsoventral height). Ventrally, the flat surface of the basioccipital is wide (about 63 mm), and the basioccipital crest is massive and bulbous. The basioccipital crest runs posterolaterally.

Anterior to the basioccipital, a partially well-developed keel of the vomer is observed, and the height reaches about 31 mm. The ventral margin of the keel is eroded, but it gently slopes to the surface of the basisphenoid/basioccipital posteriorly from the anterior margin of the pterygoid sinus. The vomer extends posteriorly at least to the level of the basioccipital crest. On the right side of the skull (the left side is eroded), the oval-shaped pterygoid sinus orients anteromedially, being much longer anteroposteriorly than wide. Posteriorly, the periotic is broken and eroded. The shape and degree of protrusion of the anterior process of the periotic remains uncertain due to erosion but shows a contact with the squamosal. The squamosal is also heavily eroded, but the base of the squamosal is robust based on the broken surface.

Body size and ontogenetic stage. We estimated that the bizygomatic width of YM-G-100208 is about 28 cm. Based on this estimation, we used Pyenson and Sponberg's equation (2011) for stem mysticetes:

$$\log(\text{TL}) = 0.92 * (\log(\text{BIZYG}[\text{in cm}]) - 1.72) + 2.68$$

to assess the body size of YM-G-100208, resulting in 268 cm – typical for aetiocetids. The skull sutures that can help assess the ontogenetic stage (Walsh and Berta 2011) are broadly eroded. But, given the fusion of some sutures, such as the suture between the basioccipital and basisphenoid, and robustness, we consider that YM-G-100208 represents a subadult at least.

Comment. YM-G-100208 shows its aetiocetid affinity by displaying the following combination of characters: body size less than 3 m long, outline of the supraoccipital broadly triangular, an anteriorly-thrust supraoccipital, straight lateral margins of the supraoccipital, a moderate exposure of parietals on the skull roof, and a well-developed basioccipital crest. YM-G-100208 differs from llanocetids in its small body size, lack of the sagittal trough, bulbous basioccipital crests, and the ventral keel of the vomer extending posteriorly to the level of the basioccipital crest. YM-G-100208 further differs from mammalodontids in having a broadly triangular supraoccipital, a less elongate intertemporal region, a well-developed and bulbous basioccipital crests, and the ventral keel of the vomer extending posteriorly to the level of the basioccipital crest. YM-G-100208 differs from eomysticetids in lacking the sagittal crest on the skull roof and the ventral keel of the vomer extending posteriorly to the level of the basioccipital crest. YM-G-100208 further differs from other crown mysticetes in having the parietals exposed on the skull roof. Due to the incompleteness of YM-G-100208, we provisionally identify it as belonging to Aetiocetidae gen. et. sp. indet. This taxonomic identification allows for the first recognition of coexisting toothed and baleen-assisted mysticetes in the northwestern Pacific.

Discussion

Our description of YM-G-100208 represents a formal recognition of the presence of aetiocetids in the Jinnobaru Formation, likely coexisting with the eomysticetid *Yamatocetus canaliculatus*. Interestingly, “*Metasqualodon*” *symmetricus* was originally named and recognized as an odontocete (Okazaki 1982), but later cladistic analyses suggested its placement in the mysticete lineage (Geisler et al. 2017; Boessenecker et al. 2023). The updated description and formal taxonomic revision of “*Metasqualodon*” *symmetricus*, which require a new generic identification, remain under progress (pers. comm. with Y. Okazaki). In addition, the lack of overlapping materials between YM-G-100208 and the holotype of “*Metasqualodon*” *symmetricus* hinders our interpretations of taxonomic similarities and the detailed composition of the mysticete communities of the Jinnobaru Formation. That said, the description of YM-G-100208 indicates a complex Oligocene ecosystem in the Jinnobaru Formation, with the co-occurrence of baleen-assisted eomysticetids and toothed mysticetes.

In the northwestern Pacific, two units, the Ashiya Group (including Jinnobaru Formation) in Kyushu and the Morawan Formation in Hokkaido, have yielded abundant Oligocene fossil cetaceans. However, the faunal composition of the two fossil whale-rich formations features an apparent discrepancy. Various species of toothed mysticetes were recovered from the Morawan Formation of Hokkaido, but no eomysticetids (Barnes et al. 1995; Tsai and Ando 2016), whereas both toothed mysticetes (this study) and eomysticetids (Okazaki 2012) have been documented (Fig. 2) from the Jinnobaru Formation of the Kyushu area. This faunal discrepancy, coupled with the fact that the Jinnobaru Formation (about 28 Ma) is older than the Morawan Formation (ranging from 26 to 24 Ma), may reflect an evolutionary scenario of the ecosystem structure along the northwestern Pacific. The competition between toothed mysticetes and baleen-assisted eomysticetids should have been less intense (a common resource-dependent niche partitioning). Then, toothed mysticetes may have dispersed north and differentiated to occupy various niches in the Oligocene waters of Hokkaido, resulting in the size disparity of toothed mysticetes (Tsai and Ando 2016).

Alternatively, the faunal discrepancy between the Jinnobaru and Morawan formations may indicate the need for more research effort in the Ashoro area, Hokkaido, which has produced various aetiocetid species but no baleen-assisted mysticetes (Barnes et al. 1995; Tsai and Ando 2016). On the other side of the North Pacific (Fig. 2), abundant Oligocene mysticetes, including both toothed and baleen-assisted species, inhabited both the northern and southern waters of the eastern North Pacific (ranging from Washington of the USA to Mexico) (Barnes et al. 1995; Marx et al. 2015; Peredo and Uhen 2016; Hernández-Cisneros 2022; Hernández-Cisneros and Nava-Sanchez 2022). Of note, a toothed mysticete, *Chonecetus sookensis*, has also been recovered from Canada (Russell 1968). Still, given the geographic locality and geological horizon, *Chonecetus sookensis*

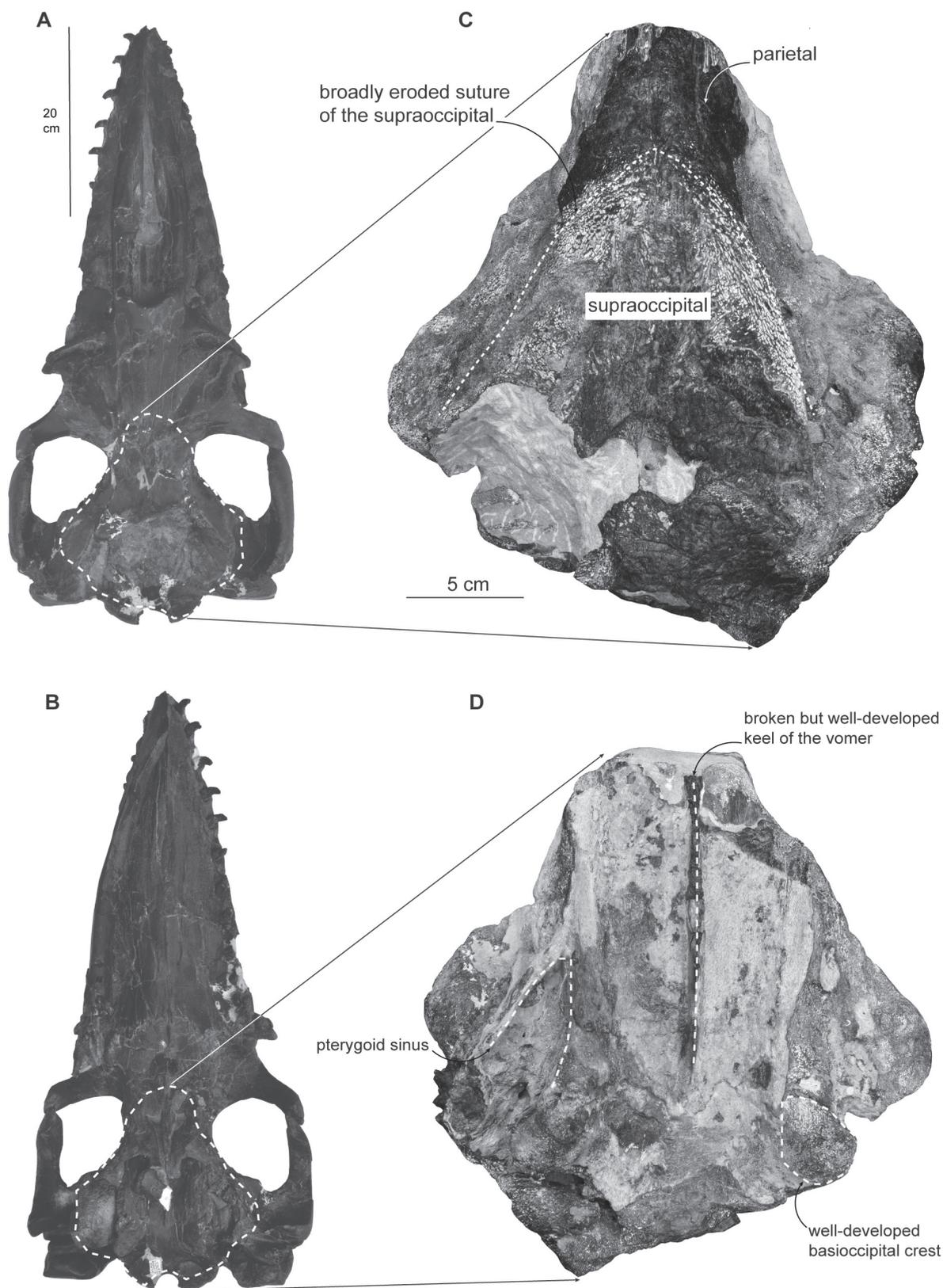


Figure 2. The skull of YM-G-100208 and a well-preserved skull of *Aetiocetus weltoni* (UCMP 122900) for comparison. (A) Dorsal view of *Aetiocetus weltoni* (UCMP 122900). (B) Ventral view of *Aetiocetus weltoni* (UCMP 122900). (C) Dorsal view of YM-G-100208. (D) Ventral view of YM-G-100208.

from the Oligocene of Canada can be considered as part of the faunal composition from the Oligocene sediments in Washington, USA. This distribution pattern suggests more abundant Oligocene mysticetes from the western

North Pacific. For example, the Oligocene mysticete composition between New Zealand and Australia also shows a prominent discrepancy; New Zealand includes various baleen-assisted and toothed species (Fordyce and

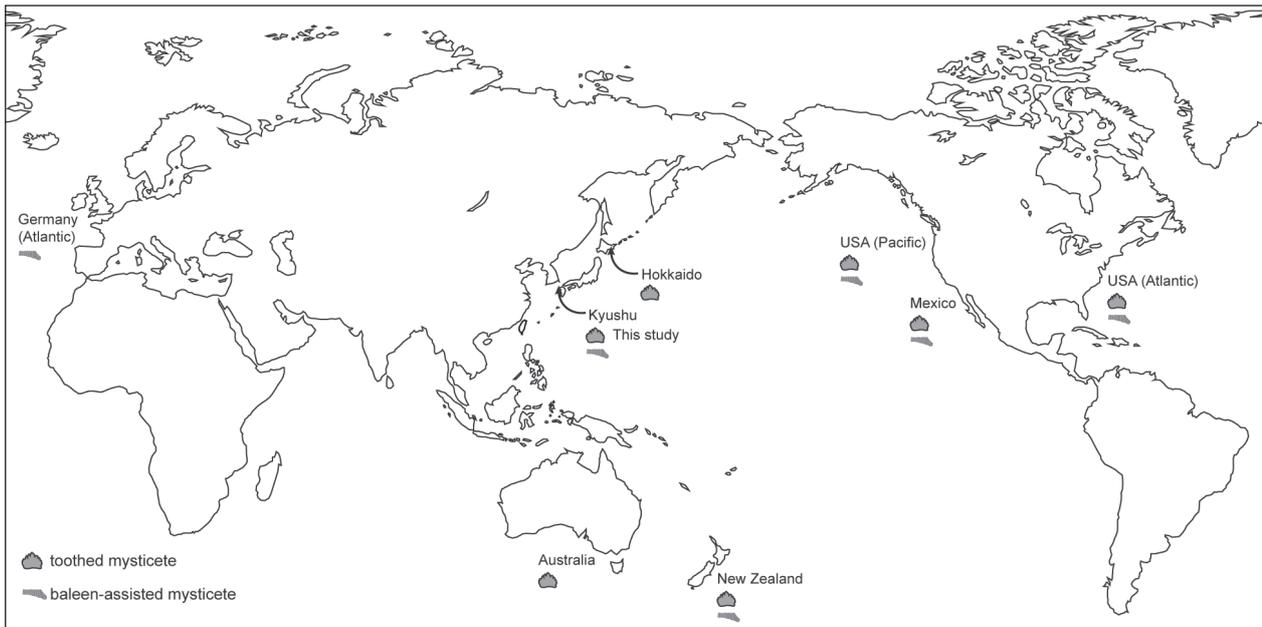


Figure 3. The global distribution of Oligocene toothed and baleen-assisted mysticetes.

Marx 2016; Boessenecker and Fordyce 2017; Tsai and Fordyce 2018), whereas toothed mysticetes represent the only Oligocene mysticetes in Australia (Fitzgerald 2006; Fitzgerald 2010). Interestingly, the supplementary information of a recent publication (Marx et al. 2019) listed 12 specimens (earbones: bullae) and identified as eomysticetids or chaemysticetes from the Oligocene of Australia. Future finds should substantiate this identification and provide a better understanding of the Oligocene mysticete communities of the Southern Ocean.

Oligocene mysticetes show an unparalleled diversity and morphological disparity in the evolutionary history of Mysticeti (Barnes et al. 1995; Fitzgerald 2010; Boessenecker and Fordyce 2015; Tsai and Fordyce 2015; Geisler et al. 2017; Peredo et al. 2018; Tsai 2023), and some of the most challenging questions in the mysticete evolution are whether toothed aetiocetids possessed proto-baleen and how the mysticete toothed-baleen transition occurred (Ekdale and Deméré 2022; Peredo et al. 2022). Such a transition in the structure of the feeding apparatus of baleen whales indeed played a critical role and attracts intense research efforts. Our description of a toothed mysticete from the Oligocene of Umashima (Kyushu, Japan) and a compilation of Oligocene mysticetes across the globe (Fig. 3) should draw more attention to finding more Oligocene mysticetes and lead to a well-sampled dataset for analyzing the coexistence pattern or other related paleoecological traits to understand the demise of “archaic” Oligocene mysticetes and give rise to the modern-looking baleen whales.

Acknowledgments

We thank A. Makino for collecting and donating YM-G-100208; A. Kameya and E. Akazaki of the Yamaguchi Prefectural Museum for access to YM-G-100208; P. Holroyd of the University of California Museum of Paleontology

for access to UCMP 122900; Alberto Collareta and Oliver Hampe for constructive and helpful comments. This research is partly supported by the Taiwan Ministry of Science and Technology (MOST 111-2621-B-002-006, 112-2621-B-002-005; now known as National Science and Technology Council, Taiwan), public donations (NTU FD107028), and Bestland Co., Ltd. based in Tsukuba to CHT.

References

- Barnes LG, Kimura M, Furusawa H, Sawamura H (1995) Classification and distribution of Oligocene Aetiocetidae (Mammalia; Cetacea; Mysticeti) from western north America and Japan. *Island Arc* 3: 392–431. <https://doi.org/10.1111/j.1440-1738.1994.tb00122.x>
- Boessenecker RW, Beatty BL, Geisler JH (2023) New specimens and species of the Oligocene toothed baleen whale *Coronodon* from South Carolina and the origin of Neoceti. *PeerJ* 11: e14795. <https://doi.org/10.7717/peerj.14795>
- Boessenecker RW, Fordyce RE (2015) A new genus and species of eomysticetid (Cetacea: Mysticeti) and a reinterpretation of ‘*Mauicetus*’ *lophocephalus* Marples, 1956: transitional baleen whales from the upper Oligocene of New Zealand. *Zoological Journal of the Linnean Society* 175: 607–660. <https://doi.org/10.1111/zoj.12297>
- Boessenecker RW, Fordyce RE (2017) A new eomysticetid from the Oligocene Kokoamu Greensand of New Zealand and a review of the Eomysticetidae (Mammalia, Cetacea). *Journal of Systematic Palaeontology* 15: 429–469. <https://doi.org/10.1080/14772019.2016.1191045>
- Brisson AD (1762) *Regnum animale in Classes IX. distributum, sive Synopsis methodica sistens generalem Animalium distributionem in Classibus IX, and duarum primarum Classicum, Quadrupedum scilicet and Cetaceorum, particularem divisionem in Ordines, Sectiones, Genera and Species.* Haak, Leiden, 296 pp. <https://doi.org/10.5962/bhl.title.40361>
- Collareta A, Marx FG, Casati S, Di Cencio A, Merella M, Bianucci G (2021) A cetotheriid whale from the upper Miocene of the Mediterranean. *Neues Jahrbuch für Geologie und Paläontologie* 301: 9–16. <https://doi.org/10.1127/njgpa/2021/0994>

- Ekdale EG, Deméré TA (2022) Neurovascular evidence for a co-occurrence of teeth and baleen in an Oligocene mysticete and the transition to filter-feeding in baleen whales. *Zoological Journal of the Linnean Society* 194: 395–415. <https://doi.org/10.1093/zoolin/zlab017>
- Emlong D (1966) A new archaic cetacean from the Oligocene of Northwest Oregon. *Bulletin of the Museum of Natural History, University of Oregon* 3: 1–51.
- Fitzgerald EMG (2006) A bizarre new toothed mysticete (Cetacea) from Australia and the early evolution of baleen whales. *Proceedings of the Royal Society B: Biological Sciences* 273: 2955–2963. <https://doi.org/10.1098/rspb.2006.3664>
- Fitzgerald EMG (2010) The morphology and systematics of *Mammalodon colliveri* (Cetacea: Mysticeti), a toothed mysticete from the Oligocene of Australia. *Zoological Journal of the Linnean Society* 158: 367–476. <https://doi.org/10.1111/j.1096-3642.2009.00572.x>
- Fordyce RE, Marx FG (2016) Mysticetes baring their teeth: a new fossil whale, *Mammalodon hakataramea*, from the Southwest Pacific. *Memoirs of Museum Victoria* 74: 107–116. <https://doi.org/10.24199/j.mmv.2016.74.11>
- Geisler JH, Boessenecker RW, Brown M, Beatty BL (2017) The origin of filter feeding in whales. *Current Biology* 27: 2036–2042. [e2032] <https://doi.org/10.1016/j.cub.2017.06.003>
- Gray JE (1864) On the Cetacea which have been observed in the seas surrounding the British Islands. *Proceedings of the Scientific Meetings of the Zoological Society of London* 1864: 195–248.
- Hernández-Cisneros AE (2022) A new aetiocetid (Cetacea, Mysticeti, Aetiocetidae) from the late Oligocene of Mexico. *Journal of Systematic Palaeontology* 20: 1–15. <https://doi.org/10.1080/14772019.2022.2100725>
- Hernández-Cisneros AE, Nava-Sanchez EH (2022) Oligocene dawn baleen whales in Mexico (Cetacea, Eomysticetidae) and palaeobiogeographic notes. *Paleontologia Mexicana* 11: 1–12.
- Marx FG, Fitzgerald EMG, Fordyce RE (2019) Like phoenix from the ashes: How modern baleen whales arose from a fossil “dark age”. *Acta Palaeontologica Polonica* 64: 231–238. <https://doi.org/10.4202/app.00575.2018>
- Marx FG, Tsai C-H, Fordyce RE (2015) A new Early Oligocene toothed ‘baleen’ whale (Mysticeti: Aetiocetidae) from western North America: one of the oldest and the smallest. *Royal Society Open Science* 2: 150476. <https://doi.org/10.1098/rsos.150476>
- Nakae S, Ozaki M, Ota M, Yabumoto Y, Matsuura H, Tomita S (1998) Geology of the Kokura District. With Geological Sheet Map at 1: 50,000. Geological Survey of Japan, 126 pp.
- Okada H (1992) Calcareous nannofossils and biostratigraphy of the Paleogene sequences of the northern Kyushu, Japan. *Journal of the Geological Society of Japan* 98: 505–528. <https://doi.org/10.5575/geosoc.98.509>
- Okazaki Y (1982) A Lower Miocene squalodontid from the Ashiya Group, Kyushu, Japan. *Bulletin of the Kitakyushu museum of natural history*: 107–112.
- Okazaki Y (1995) A new type of primitive baleen whale (Cetacea; Mysticeti) from Kyushu, Japan. *Island Arc* 3: 432–435. <https://doi.org/10.1111/j.1440-1738.1994.tb00123.x>
- Okazaki Y (2012) A new mysticete from the upper Oligocene Ashiya Group, Kyushu, Japan and its significance to mysticete evolution. *Bulletin of the Kitakyushu Museum of Natural History and Human History, Series A (Natural History)* 10: 129–152.
- Olson SL, Hasegawa Y (1996) A new genus and two new species of gigantic Plotopteridae from Japan (Aves: Pelecaniformes). *Journal of Vertebrate Paleontology* 16: 742–751. <https://doi.org/10.1080/02724634.1996.10011362>
- Ozaki M, Hamasaki S, Yoshii M (1993) Geology of the Orio district with geological sheet map at 1: 50,000. Geological Survey of Japan, 121 pp.
- Peredo CM, Pyenson ND, Marshall CD, Uhen MD (2018) Tooth loss precedes the origin of baleen in whales. *Current Biology* 28: 3992–4000. <https://doi.org/10.1016/j.cub.2018.10.047>
- Peredo CM, Pyenson ND, Uhen MD (2022) Lateral palatal foramina do not indicate baleen in fossil whales. *Scientific Reports* 12: 11448. <https://doi.org/10.1038/s41598-022-15684-8>
- Peredo CM, Uhen MD (2016) A new basal chaeomysticete (Mammalia: Cetacea) from the late Oligocene Pysht Formation of Washington, USA. *Papers in Palaeontology* 2: 533–554. <https://doi.org/10.1002/spp2.1051>
- Pyenson ND, Sponberg SN (2011) Reconstructing body size in extinct crown Cetacea (Neoceti) using allometry, phylogenetic methods and tests from the fossil record. *Journal of Mammalian Evolution* 18: 269–288. <https://doi.org/10.1007/s10914-011-9170-1>
- Russell LS (1968) A new cetacean from the Oligocene Sooke formation of Vancouver Island, British Columbia. *Canadian Journal of Earth Sciences* 5: 929–933. <https://doi.org/10.1139/e68-089>
- Saito T (1984) Oligocene calcareous plankton microbiostratigraphy of the Ashiya Group, North Kyushu. *Biostratigraphy and International correlation of the Paleogene System in Japan*: 85–87.
- Sakai T, Horie K, Takehara M (2014) An outcrop of unconformity at Natsugigahama. Vol. 16, Research Report of Cultural Property of Ashiya Town, 110 pp.
- Schoener TW (1974) Resource partitioning in ecological communities: Research on how similar species divide resources helps reveal the natural regulation of species diversity. *Science* 185: 27–39. <https://doi.org/10.1126/science.185.4145.27>
- Tsai C-H, Ando T (2016) Niche partitioning in Oligocene toothed mysticetes (Mysticeti: Aetiocetidae). *Journal of Mammalian Evolution* 23: 33–41. <https://doi.org/10.1007/s10914-015-9292-y>
- Tsai C-H, Fordyce RE (2015) The earliest gulp-feeding mysticete (Cetacea: Mysticeti) from the Oligocene of New Zealand. *Journal of Mammalian Evolution* 22: 535–560. <https://doi.org/10.1007/s10914-015-9290-0>
- Tsai C-H, Fordyce RE (2018) A new archaic baleen whale *Toipahau-tea waitaki* (early Late Oligocene, New Zealand) and the origins of crown Mysticeti. *Royal Society Open Science* 5: 172453. <https://doi.org/10.1098/rsos.172453>
- Tsai C-H (2023) In search of the origin of crown Mysticeti. *Journal of the Royal Society of New Zealand*. <https://doi.org/10.1080/03036758.2023.2249410>
- Walsh BM, Berta A (2011) Occipital ossification of balaenopteroid mysticetes. *The Anatomical Record* 294: 391–398. <https://doi.org/10.1002/ar.21340>
- Wursig B, Thewissen JGM, Kovacs KM (2018) *Encyclopedia of Marine Mammals*. Academic Press, 1190 pp.