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A feeding organ the basihyal and thyrohyal tells which size of prey do true baleen whales (Cetacea, Chaeomysticeti) eat

Yoshihiro Tanaka

ABSTRACT

Modern baleen whales are filter feeders. The Chaeomysticeti is a group of true baleen whales including extinct and all extant baleen whales. The early feeding strategy of the Chaeomysticeti has been discussed but not enough. Considering evolution of feeding strategy of baleen whales, fossils of the Chaeomysticeti are important key to describe how filter feeding in whales began and diversified.

To answer such questions, this study examined the relationships of the basihyal-thyrohyal shape and feeding strategy among extinct and extant baleen whales, and hypothesized evolution of the prey types.

As the result of analysis, small prey feeders such as balaenids, *Caperea marginata,* and *Eschrichtius robustus* share the basihyal-thyrohyal with small articular processes, and a wide and shallow notch between the articular processes. On the other hand, large prey feeders eating fish primarily show very long articular processes and anteriorly oriented lateral portions of the basihyal-thyrohyal, which is a unique condition owned by *Balaenoptera edeni* among baleen whales. A member of the most basal chaeomysticete: *Yamatocetus canaliculatus* was plotted close to the cluster of the small prey feeders.

This result suggests that the early Chaeomysticeti fed on small prey using the baleen plates for filtering. In the Miocene, the Cetotheriidae and Balaenopteridae started having both large and small prey. Then, a few members of Balaenopteridae such as *Balaenoptera musculus* and *B. edeni* were specialized in prey types. In short, prey type of the Chaeomysticeti started from small-sized prey such as small invertebrates then diversified through evolution.

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INTRODUCTION

Modern baleen whales (the Mysticeti) are filter feeders, who feed on much smaller prey to develop and maintain huge bodies. The Chaeomysticeti is a group of toothless and true baleen whales including extinct and all extant baleen whales. Considering evolution of feeding strategy of baleen whales, fossils of the Chaeomysticeti are important key to describe how filter feeding whales began and diversified.

Chaeomysticetes with the baleen plates appeared in the Late Oligocene about 30 to 27 m.y.a. (Boessenecker and Fordyce, 2017). Prior to them, there were toothed mysticetes from the latest Eocene (about 36 m.y.a.) (Lambert et al., 2017). For example, an early toothed mysticete *Mystacodon* having large teeth with worn crowns is thought as a raptorial feeder (De Muizon et al., 2019).

Feeding strategies such as prey capture tactics and prey types of extant baleen whales are varied. Prey capture tactics of extant baleen whales are known as skim, lunge, and benthic suction feedings (Werth, 2000). Skim feeding is employed by the Balaenidae (right and bowhead whales) and *Caperea marginata* (pygmy right whale) and is "generating continuous negative pressure" within the mouth cavity with a steady forward propulsion (Brodie and Vikingsson, 2009). Lunge feeding is employed by most of balaenopterids (rorquals and humpback whales) and is "intermittent engulfment and subsequent filtration" (Croll et al., 2018). Benthic suction feeding is employed by *Eschrichtius robustus* (gray whale) and involves the filtering of invertebrates from the sea bottom (Ray and Schevill, 1974). Some baleen whales such as *Balaenoptera borealis* (sei whale) and *E. robustus* employ combinations of such feeding tactics (Nemoto, 1970; Jefferson et al., 2008; Werth, 2000), which can be called multiple prey capture tactics (Tanaka, 2022).

Baleen whales feed on different sizes of prey (Figure 1). Such prey can be divided into small size prey (about 0.1 to 5 cm) and large size prey (about 10 cm or larger). The Balaenidae and *Caperea marginata* feed on small size prey of copepods and other invertebrates with skim feeding (Nemoto, 1970; Jefferson et al., 2008). Most members of the Balaenopteridae feed on a wide range of prey such as copepods to large fish with lunge feeding (Nemoto, 1970; Jefferson et al., 2008). Only a few balaenopterids are different from the others. *Balaenoptera edeni* (Bryde's whales) primarily feeds schooling fish such as pilchard, anchovy, sardine, mackerel, and herring (Jefferson et al., 2008). *Balaenoptera musculus* (blue whales) feeds krill with lunge feeding (Jefferson et al., 2008). *Balaenoptera borealis* uses multiple prey capture tactics, which includes not only lunge but also skim feedings. *B. borealis* eats copepods and small prey with skim feeding, and krill, sardines and anchovies with lunge feeding (Jefferson et al., 2008; Brodie and Vikingsson, 2009). *Eschrichtius robustus* also uses multiple prey capture tactics including benthic suction, skim and lunge feedings, and feed on

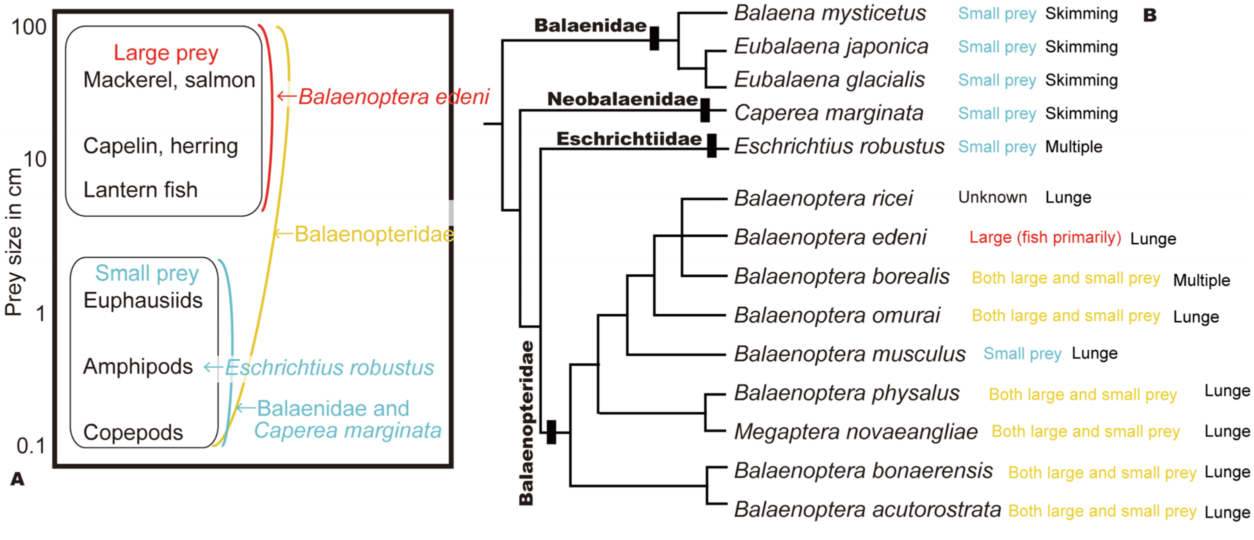

FIGURE 1. A. Prey size of baleen whales modified from Gaskin (1982) with prey information in Jefferson et al. (2008). B. Modern baleen whale phylogeny and information of prey types + prey capture tactics. Phylogeny was combined the tree of the Balaenopteridae in Rosel et al. (2021) and the tree in Steeman et al. (2009) for the relationships of others.

mysids, amphipods, tube worm, and so on (Scammon, 1874; Nemoto, 1970; Werth, 2000; Jefferson et al., 2008). Such variety of feeding strategies might be related to niche partitioning, diversification, and evolution (Woodward et al., 2006; Werth et al., 2018).

For understanding true baleen whale evolution, early members of the Chaeomysticeti are keys. Early feeding strategy of the Chaeomysticeti has been discussed recently, but not enough. An early work briefly mentioned that fossil mysticetes were structurally similar to balaenopterids and *Eschrichtius robustus,* in a review about the baleen whale feeding mechanism (Pivorunas, 1979). A later work more clearly mentioned that none of archaic baleen whales have arched or robust rostra like the Balaenidae and *E. robustus,* thus lunge feeding was earned by archaic baleen whales (Fordyce and de Muizon, 2001). After the studies, some studies discussed about early Chaeomysticeti feeding strategy as benthic feeding based on osteosclerotic bones (Beatty and Dooley, 2009), skim feeding based on lack of gulp feeders' features (Boessenecker and Fordyce, 2015), lunge feeding based on mandible morphology (Tsai and Fordyce 2018). One of the latest study analyzed rostrum morphology variation among the Chaeomysticeti and stated that the feeding strategy of early chaeomysticetes was not skim and benthic feedings, but the answer is still unsolved (Tanaka, 2022).

There are difficulties for restoring feeding strategies of extinct animals. Even among living whales, we cannot observe what is happening in their mouth. Thus, creating hypotheses and running experimental works are two ways to improve our understanding on the black box (Werth and Potvin, 2016; Goldbogen et al., 2017). There is another way in paleobiology. Comparing the shape among living species and tracing the shape change of fossil species helps in understanding their evolution.

An analysis of relationships between the rostrum shape and prey capture tactics of the Chaeomysticeti recognized convergent evolution (Tanaka, 2022). The Balaenidae and *Caperea marginata* shifted from unknown feedings (some sort of primitive ones) to skim feeding independently through evolution. Tanaka (2022) could not find certain variation in rostral morphology among lunge feeders of the Balaenopteridae, which has various prey types as above. Because lunge feeding can be observed only among modern balaenopterids, and it was not possible to recognize convergent evolution. However, analysis of different anatomical elements might reveal different factors of feeding strategy adaptation to understand baleen whale evolution.

A single fused element of the basihyal-thyrohyal (Figure 2) forms a part of the hyoid. The hyoid has an important role for feeding. It provides numerous attachments to muscles to the larynx, sternum, and tongue (Werth, 2007), which work for moving the tongue and swallowing (Gray et al., 1887). An early study of *Balaenoptera borealis* introduced five muscles from the basihyal and thyrohyal (Schulte, 1916), and the knowledge of the bones and muscles' relationships and their function on baleen whales has been developed as shown in Table 1 and Figure 2 show (Reidenberg and Laitman, 1994; Kienle et al., 2015; Werth and Ito, 2017).

The basihyal and thyrohyal have been compared among extant baleen whales (Omura, 1964; Werth, 2007), and analyzed extant whales, dolphins, and porpoises (Johnston and Berta, 2011). But the element has not been analyzed with extinct members of the Chaeomysticeti yet. A member of early Chaeomysticeti, *Yamatocetus canaliculatus* is a key taxon showing an early condition of the basihyal and thyrohyal among the true baleen whale group. This study examines the basihyal and thyrohyal using geometric morphometric analysis, recognizes shared features of the element, then finds morphological traits with feeding strategies to describe evolutionary history of feeding strategy among the Chaeomysticeti.

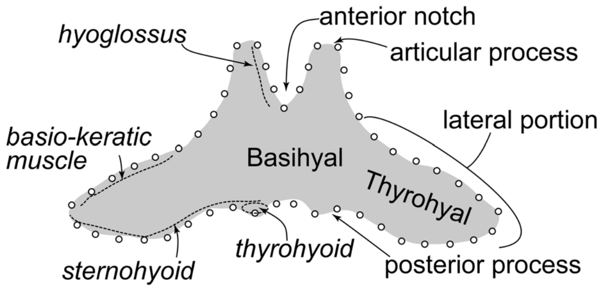

FIGURE 2. Example semi-landmark in the ventral view of the basihyal and thyrohyal with anatomical terms. The one of *Balaenoptera musculus* number 66 in Table 1 is used. The origins for the muscles were modified from Schulte (1916) with minor modification following Reidenberg and Laitman (1994) on the omohyoid muscle insertion.

TABLE 1. Muscles attached to the basihyal and thyrohyal.

Muscles	Muscle attachments on the basihyal + thyrohyal	Other side of the muscle attachments	Function	Reference of function
Hyoglossus muscle	Anterior suraface of the anterior process and lateral portion of the body.	It ends left and right sides of the tongue	The hyoglossus pulls the tongue ventrally	Werth and Ito, 2017: rorquals
Geniohyoid muscle	The anterior surface of the body	The mandibular symphysis	The geniohyoid muscle protracts the tongue	Werth and Ito, 2017: rorquals
Basio-keratic muscle	The anterolateral border of the lateral portion	The stylohyal	The basio-keratic muscle flexes the thyrohyal posteriorly and decreases the angle forme by the thyrohyal and ceratohyal	Kienle et al., 2015: gray whales
Sternohyoid muscle	The medial part of the posterior border	The sternum	The sternohyoid and thyrohyoid similaryly retract and depress the tongue root	Werth and Ito, 2017: rorquals
Thyrohyoid muscle	The posterior process	The tyroid cartilage	The sternohyoid and thyrohyoid similaryly retract and depress the tongue root	Werth and Ito, 2017: rorquals

MATERIALS AND METHODS

The anatomical terms follow Reidenberg and Laitman (1994) and Werth (2007) for the basihyal and thyrohyal and Schulte (1916) for myology. In Schulte (1916), the label 8 in figure 7 did not have a name of muscle, and the label 7 genioglossus did not match for the explanation in the text, which said that the muscle runs from the mandible to the tongue. Here, label 7 genioglossus is not followed, and the label number 8 is stated as the hyoglossus following later anatomical studies (Werth, 2007; Kienle et al., 2015).

In total 85 Basihyal-thyrohyal data were collected from photos and illustrations having the right views in previous studies (Figure 3 and Table 2, see also Appendix 1). They include 14 extant species of 81 specimens, representing all extant baleen whale species except *Eubalaena australis*. Bryde's whales are treated as *Balaenoptera edeni* (Table 2), following the latest list of species and subspecies of Society for Marine Mammalogy (Committee on Taxonomy, 2022).

Fossil toothless baleen whales (members of the Chaeomysticeti) were selected through the preservation of their basihyal-thyrohyal. Some specimens were reconstructed using a preserved right or left side of the specimens. An early Chaeomysticeti *Yamatocetus canaliculatus* has the basihyal and thyrohyal with broken lateral ends, which is identified as a minor damage based on preserved rounded outline.

The materials were classified by feeding strategies (Heithaus and Dill, 2018). Feeding strategies includes foraging tactics (skim, lunge, or multiple prey capture tactics) (Nemoto, 1970; Croll et al., 2018; Tanaka, 2022), and prey type (feed on small, large, or both small and large prey) (Jefferson et al., 2008; Cerchio and Yamada, 2018). The feeding strategies of *Balaenoptera ricei,* which is a recently established extant species and extinct true baleen whales were assigned as unknown (not observed) (Rosel et al., 2021).

Institutional Abbreviations

AMNH, American Museum of Natural History, New York, USA. KMNH, Kitakyushu Museum of Natural History, Fukuoka, Japan. MNHN, Muséum national d'Histoire naturelle, Paris, France. MPST, Museo Paleontologico di Salsomaggiore Terme, Italy. NFL, Numata Fossil Museum, Hokkaido, Japan. NMNS, National Museum of Nature and Science, Tsukuba, Japan. NMV, Museum Victoria, Australia. OMNH, Osaka Museum of Natural History, Osaka, Japan. USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Data Collection

Landmark acquisition was managed using the TPS program package such as tpsUtil v1.78 and tpsDig v2.31 (Rohlf, 2015). Semi-landmarks (Figure 2) were measured on each specimen. Lines on the outline of the basihyal-thyrohyal were taken as semi-landmarks from/to the most posterior position of the anterior margin of the basihyal-thyrohyal at the center, on pictures in dorsoventral view. They were divided into 50 semi-landmarks at equal distances. Non-shape information (size and rotation) was removed from the landmark configurations using the New Procrustes Fit implemented in MorphoJ 1.07a (Klingenberg, 2011).

FIGURE 3. Outlines of analyzed true baleen whale specimens. Numbers are given in Table 1 and Appendix 1. Abbreviations mean prey capture tactics (Sk: Skim, Mu: Multiple, Lu: Lunge) and prey types (Sm: Small, Bo: both large and small prey, La: Large, Un: Unknown).

Morphometric Analysis

Geometric morphometric analysis was used to access the shape variation of basihyal-thyrohyal morphology and test the hypothesis that specific basihyal-thyrohyal morphologies facilitate specific feeding strategies. Analyzes were run with MorphoJ 1.07a (Klingenberg, 2011) and PAST 4.13 (Hammer et al., 2001).

To reduce the dimensionality of the data and display the major axes of variation for extant and extinct true baleen whales, principal component analysis (PCA) was used in MorphoJ (Figures 4 and 5) and was tested on PC1 and 2 by Multivariate Analysis of Variance (MANOVA) in PAST.

Hypotheses were fixed as below. If specific basihyal-thyrohyal morphologies facilitate specific feeding strategies, then clusters of phylogenetically separated linages with the same feeding strategies will be closely associated. For example, on prey capture tactics, some phylogenetically separated groups having small prey such as balaenids, *Caperea marginata, Eschrichtius robustus,* and *Balaenoptera musculus* will be grouped together in the morphospace. Only one primary fish feeder *Balaenoptera edeni* will be separated from other balaenopterids. For example, on prey type, *Balaenoptera borealis* has not only lunge but also skim feedings (multiple prey capture tactics) and will appear far from other lunge feeder balaenopterids in the morphospace, but will be close to *Eschrichtius robustus*, which also has a multiple prey capture tactics. In addition, examined specimens will appear as clusters of prey types.

To examine which groups united by feeding strategy (prey capture tactics and prey types) differ from each other, pairwise Hotelling's tests was used in PAST (Table 3).

Cladograms

To consider the evolution of feeding strategies among the Chaeomysticeti, strategies of both extant and extinct baleen whales are adapted to cladograms. The cladograms represent two phylogenetic hypotheses on the phylogenetic position of included three named extinct taxa analyzed in this study. There are numerous phylogenetic hypotheses, which can be recognized as two types of *Pelocetus calvertensis* positions. Type A locates *P. calvertensis* basal to the Balaenopteridae (Lambert et al., 2017; Buono et al., 2017; De Muizon et al., 2019; Marx et al., 2019; de Lavigerie et al., 2020;

TABLE 2. Specimens used for analysis in this study with variation in prey capture tactics and prey types among extant mysticetes. See cited references in Appendix 2.

Family	ID	Scientific name	Abbreviation	Prey capture tactics	Prey types	Specimen number or ID	Reference
Balaenidae	0	*Balaena mysticetus*	MYS	Skim	Small prey	-	Nishiwaki and Kasuya, 1970
	1	*Eubalaena glacialis*	EUG	Skim	Small prey	Plate XV, 1	Omura, 1964
	2	*Eubalaena glacialis*	EUG	Skim	Small prey	Plate XV, 3	Omura, 1964
	3	*Eubalaena glacialis*	EUG	Skim	Small prey	Plate XV, 4	Omura, 1964
	4	*Eubalaena glacialis*	EUG	Skim	Small prey	Plate XV, 5	Omura, 1964
	5	*Eubalaena japonica*	EUJ	Skim	Small prey	61A	Omura et al., 1969
	6	*Eubalaena japonica*	EUJ	Skim	Small prey	61B	Omura et al., 1969
	7	*Eubalaena japonica*	EUJ	Skim	Small prey	-	Omura, 1958
Neobalaenidae	8	*Caperea marginata*	CAP	Skim	Small prey	NMV C40064	Evans EvoMorph Lab. 2020
Eschrichtiidae	9	*Eschrichtius robustus*	ESC	Multiple	Small prey	M-804A	Nakamura and Kato, 2014
	10	*Eschrichtius robustus*	ESC	Multiple	Small prey	M-804B	Nakamura and Kato, 2014
	11	*Eschrichtius robustus*	ESC	Multiple	Small prey	AMNH 34260	Andrews, 1914
	12	*Eschrichtius robustus*	ESC	Multiple	Small prey	-	Kienle et al 2015
Balaenopteridae	13	*Megaptera novaeangliae*	MEG	Lunge	Both large and small prey	USNM 21492	Cope, 1871
	14	*Megaptera novaeangliae*	MEG	Lunge	Both large and small prey	Plate XIV, 1	Omura, 1964
	15	*Megaptera novaeangliae*	MEG	Lunge	Both large and small prey	Plate XIV, 2	Omura, 1964
	16	*Megaptera novaeangliae*	MEG	Lunge	Both large and small prey	Plate XIV, 3	Omura, 1964
	17	*Megaptera novaeangliae*	MEG	Lunge	Both large and small prey	Plate XIV, 4	Omura, 1964
	18	*Megaptera novaeangliae*	MEG	Lunge	Both large and small prey	Plate XIV, 5	Omura, 1964
	19	*Megaptera novaeangliae*	MEG	Lunge	Both large and small prey	Plate XIV, 6	Omura, 1964
	20	*Megaptera novaeangliae*	MEG	Lunge	Both large and small prey	Plate XIV, 10	Omura, 1964
	21	*Megaptera novaeangliae*	MEG	Lunge	Both large and small prey	NMNS M 24369	-
	22	*Megaptera novaeangliae*	MEG	Lunge	Both large and small prey	OMNH-M 3042	-
	23	*Balaenoptera acutorostrata*	ACU	Lunge	Both large and small prey	Plate XIII, 1	Omura, 1964

TABLE 2 (continued).

Family	ID	Scientific name	Abbreviation	Prey capture tactics	Prey types	Specimen number or ID	Reference
	24	*Balaenoptera acutorostrata*	ACU	Lunge	Both large and small prey	Plate XIII, 2	Omura, 1964
	25	*Balaenoptera acutorostrata*	ACU	Lunge	Both large and small prey	Plate XIII, 3	Omura, 1964
	26	*Balaenoptera acutorostrata*	ACU	Lunge	Both large and small prey	Plate XIII, 4	Omura, 1964
	27	*Balaenoptera acutorostrata*	ACU	Lunge	Both large and small prey	Plate XIII, 6	Omura, 1964
	28	*Balaenoptera acutorostrata*	ACU	Lunge	Both large and small prey	Plate XIII, 7	Omura, 1964
	29	*Balaenoptera acutorostrata*	ACU	Lunge	Both large and small prey	Plate XIII, 8	Omura, 1964
	30	*Balaenoptera acutorostrata*	ACU	Lunge	Both large and small prey	Plate XIII, 9	Omura, 1964
	31	*Balaenoptera acutorostrata*	ACU	Lunge	Both large and small prey	Plate XIII, 10	Omura, 1964
	32	*Balaenoptera acutorostrata*	ACU	Lunge	Both large and small prey	Plate XIII, 11	Omura, 1964
	33	*Balaenoptera acutorostrata*	ACU	Lunge	Both large and small prey	-	Arnold et al., 1987
	34	*Balaenoptera acutorostrata*	ACU	Lunge	Both large and small prey	NMNS M 24347	-
	35	*Balaenoptera acutorostrata*	ACU	Lunge	Both large and small prey	NMNS M 24355	-
	36	*Balaenoptera acutorostrata*	ACU	Lunge	Both large and small prey	NMNS M 24357	-
	37	*Balaenoptera bonaerensis*	BON	Lunge	Small prey	Plate I, 4	Satake and Omura, 1974
	38	*Balaenoptera bonaerensis*	BON	Lunge	Small prey	Plate I, 5	Satake and Omura, 1974
	39	*Balaenoptera bonaerensis*	BON	Lunge	Small prey	Plate I, 6	Satake and Omura, 1974
	40	*Balaenoptera bonaerensis*	BON	Lunge	Small prey	Plate I, 7	Satake and Omura, 1974
	41	*Balaenoptera bonaerensis*	BON	Lunge	Small prey	Plate I, 8	Satake and Omura, 1974
	42	*Balaenoptera bonaerensis*	BON	Lunge	Small prey	Plate I, 9	Satake and Omura, 1974
	43	*Balaenoptera bonaerensis*	BON	Lunge	Small prey	Plate I, 11	Satake and Omura, 1974
	44	*Balaenoptera bonaerensis*	BON	Lunge	Small prey	Plate II, 15	Satake and Omura, 1974
	45	*Balaenoptera bonaerensis*	BON	Lunge	Small prey	Plate II, 17	Satake and Omura, 1974

TABLE 2 (continued).

Family	ID	Scientific name	Abbreviation	Prey capture tactics	Prey types	Specimen number or ID	Reference
	46	*Balaenoptera bonaerensis*	BON	Lunge	Small prey	Plate II, 24	Satake and Omura, 1974
	47	*Balaenoptera bonaerensis*	BON	Lunge	Small prey	Plate II, 25	Satake and Omura, 1974
	48	*Balaenoptera borealis*	BOL	Multiple	Both large and small prey	Plate VI, 3	Omura, 1964
	49	*Balaenoptera borealis*	BOL	Multiple	Both large and small prey	Plate VI, 8	Omura, 1964
	50	*Balaenoptera borealis*	BOL	Multiple	Both large and small prey	Plate VIII, 1	Omura, 1964
	51	*Balaenoptera borealis*	BOL	Multiple	Both large and small prey	Plate VIII, 10	Omura, 1964
	52	*Balaenoptera borealis*	BOL	Multiple	Both large and small prey	-	Nishiwaki and Kasuya, 1971
	53	*Balaenoptera edeni*	EDE	Lunge	Large prey (fish prymarily)	Plate X, 6	Omura, 1964
	54	*Balaenoptera edeni*	EDE	Lunge	Large prey (fish prymarily)	Plate X, 10	Omura, 1964
	55	*Balaenoptera edeni*	EDE	Lunge	Large prey (fish prymarily)	Plate X, 11	Omura, 1964
	56	*Balaenoptera edeni*	EDE	Lunge	Large prey (fish prymarily)	Plate XI, 1	Omura, 1964
	57	*Balaenoptera edeni*	EDE	Lunge	Large prey (fish prymarily)	Plate XI, 5	Omura, 1964
	58	*Balaenoptera edeni*	EDE	Lunge	Large prey (fish prymarily)	Plate XI, 7	Omura, 1964
	59	*Balaenoptera edeni*	EDE	Lunge	Large prey (fish prymarily)	Plate XI, 9	Omura, 1964
	60	*Balaenoptera edeni*	EDE	Lunge	Large prey (fish prymarily)	Plate XI, 10	Omura, 1964
	61	*Balaenoptera edeni*	EDE	Lunge	Large prey (fish prymarily)	77N62, Plate 1	Omura et al., 1981
	62	*Balaenoptera ricei*	RIC	Unknown	Unknown	USNM 594665	Rosel et al., 2021
	63	*Balaenoptera musculus brevicauda*	MUS	Lunge	Small prey	Plate I, 1	Omura, 1964
	64	*Balaenoptera musculus brevicauda*	MUS	Lunge	Small prey	Plate I, 2	Omura, 1964

TABLE 2 (continued).

Family	ID	Scientific name	Abbreviation	Prey capture tactics	Prey types	Specimen number or ID	Reference
	65	*Balaenoptera musculus brevicauda*	MUS	Lunge	Small prey	Plate I, 3	Omura, 1964
	66	*Balaenoptera musculus brevicauda*	MUS	Lunge	Small prey	Plate I, 5	Omura, 1964
	67	*Balaenoptera musculus brevicauda*	MUS	Lunge	Small prey	Plate I, 6	Omura, 1964
	68	*Balaenoptera musculus brevicauda*	MUS	Lunge	Small prey	Plate I, 8	Omura, 1964
	69	*Balaenoptera musculus brevicauda*	MUS	Lunge	Small prey	-	Omura et al., 1970
	70	*Balaenoptera physalus*	PHY	Lunge	Both large and small prey	Plate II, 3	Omura, 1964
	71	*Balaenoptera physalus*	PHY	Lunge	Both large and small prey	Plate II, 4	Omura, 1964
	72	*Balaenoptera physalus*	PHY	Lunge	Both large and small prey	Plate II, 5	Omura, 1964
	73	*Balaenoptera physalus*	PHY	Lunge	Both large and small prey	Plate II, 7	Omura, 1964
	74	*Balaenoptera physalus*	PHY	Lunge	Both large and small prey	Plate II, 9	Omura, 1964
	75	*Balaenoptera physalus*	PHY	Lunge	Both large and small prey	Plate IV, 8	Omura, 1964
	76	*Balaenoptera physalus*	PHY	Lunge	Both large and small prey	Plate IV, 10	Omura, 1964
	77	*Balaenoptera physalus*	PHY	Lunge	Both large and small prey	Plate IV, 12	Omura, 1964
	78	*Balaenoptera physalus*	PHY	Lunge	Both large and small prey	Plate IV, 13	Omura, 1964
	79	*Balaenoptera physalus*	PHY	Lunge	Both large and small prey	OMNH-M 1000	-
	80	*Balaenoptera physalus*	PHY	Lunge	Both large and small prey	OMNH in the 3rd exhibition room	-
	81	*Balaenoptera omurai*	OMU	Lunge	Both large and small prey	NMNS	Shinohara, 2011
Extinct taxa							
Balaenopteridae	82	*"Megaptera" hubachi*	HUB	Unknown	Unknown	MPST 240505	Bisconti, 2010
Cetotheriidae	83	*Piscobalaena nana*	PIS	Unknown	Unknown	MNHN SAS 1617	Bouetel and de Muizon, 2006

TABLE 2 (continued).

Family	ID	Scientific name	Abbreviation	Prey capture tactics	Prey types	Specimen number or ID	Reference
Eomysticetidae	84	*Yamatocetus canaliculatus*	YAM	Unknown	Unknown	KMNH VP 000,017	Okazaki, 2012
-	85	Mysticeti indet.	NFL	Unknown	Unknown	NFL 2634	Shinohara, 2011

Kimura and Hasegawa, 2021). Type B locates *P. calvertensis* basal to the Balaenopteridae+Cetotheriidae clade (Gol'din, 2018). These cladograms were chosen from numerous phylogenetic hypotheses with confluency of molecular phylogenetic analysis (Nikaido et al., 2006; Sasaki et al., 2006; McGowen et al., 2009; Steeman et al., 2009; Rosel et al., 2021).

Qualitative Comparison

To see differences and unique features among the Balaenopteridae, detailed morphological features in the basihyal-thyrohyal such as notches and projections were compared (Table 4).

To know conditions among early mysticetes, *Fucaia buelli* phylogenetically placed basal to the Chaeomysticeti (Marx et al., 2015) is included in qualitative comparison as an outgroup. This specimen has isolated basihyal and thyrohyal. Thus, it does not show original orientation of the lateral portion. Limitedly preserved holotype bone of *Pelocetus calvertensis* is also included in qualitative comparison.

RESULTS

Principal Component Analysis

The first two PCs combined explain 83.3% of the variation (PC1=54.1%, PC2=29.2%, PC3=5.9%, PC4=3.1%, PC5= 2.6%, PC6 = 0.8%), and the results of MANOVA in the shape of feeding strategies were significant (P<0.001) (Appendix 2).

Principal component 1 represents the orientation of the lateral portion and the curvature of the posterior border of the basihyal-thyrohyal. To the right end (the positive side) of PC 1, the posterior border of the basihyal-thyrohyal is strongly anteriorly excavated and the lateral portion of the basihyal-thyrohyal oriented posterolaterally. By contrast, to the left (the negative side), the posterior border of the basihyal-thyrohyal is posteriorly expanded and the lateral portion of the basihyal-thyrohyal oriented anterolaterally (Figure 4).

A primary fish feeder *Balaenoptera edeni* has negative PC1 scores associated with an anterolaterally oriented lateral portion of the basihyal-thyrohyal. Some of small prey feeders such as the Balaenidae*, Caperea marginata, and Eschrichtius robustus* have positive PC1 scores associated with posterolaterally oriented lateral portions of the basihyal-thyrohyal. However, another small prey feeder *Balaenoptera musculus* has near zero PC1 scores like other balaenopterids feed on both small and large prey plotted between the two groups of large prey feeders and small prey feeders (Figure 4).

Principal component 2 is characterized by relative position of the articular process against the lateral portion. Positive PC2 scores were related to an anteriorly elongated articular process against the whole part of the basihyal-thyrohyal with an angle at the lateral portion, that can be seen *Balaenoptera musculus*, which has very high PC2 scores. *Balaenoptera edeni* and *B. borealis* show relatively low PC2 scores. However, this does not mean that *Balaenoptera edeni* and *B. borealis* has short articular process (see Qualitative morphological comparison).

As a result, the Balaenidae, *Caperea marginata*, and *Eschrichtius robustus* share the basihyal-thyrohyal morphology by eating small-size prey. However, *Balaenoptera musculus* is plotted far from the three linages (the Balaenidae, *Caperea marginata*, and *Eschrichtius robustus*).

Prey capture tactics do not affect strongly in PCA (Figure 5). Lunge feeders are not bound closely and separated into three groups by prey types (Figure 5). Thus, prey types effect morphology of the basihyal-thyrohyal strongly.

This is also supported by the result of pairwise Hotelling's tests. P-values for pairwise Hotelling's tests are all significant ($p<0.05$) in groups categorized by prey types, but are limitedly in groups categorized by feeding tactics (Table 3). Multiple prey capture tactics are discriminated from lunge feed-

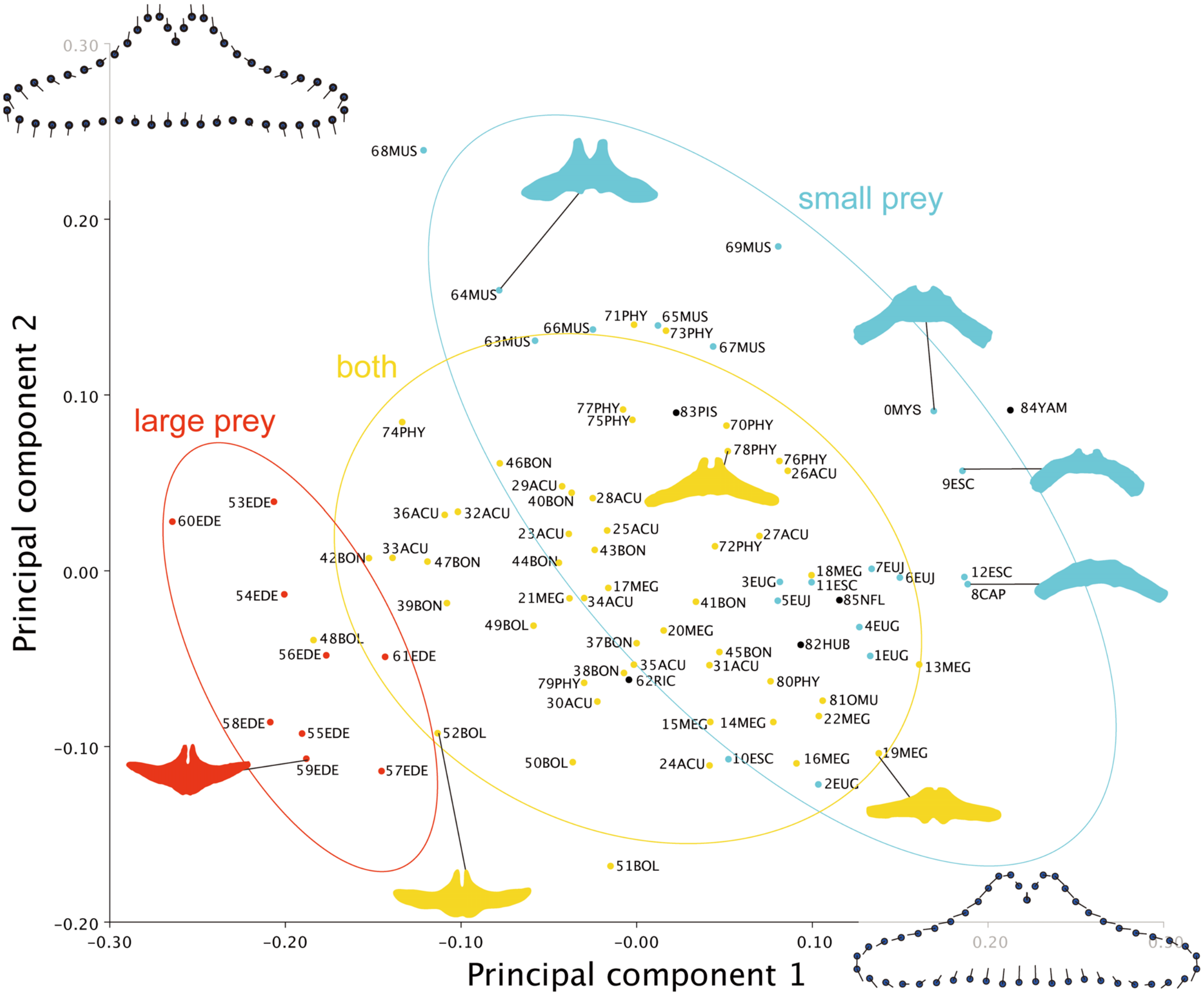

FIGURE 4. The results of principal component analysis. Ovals represent 90% confidence intervals for prey types of the extant taxa. Diagrams of the shape changes in the positive directions are given along each axis. Numbers and letters are IDs and abbreviations of scientific names (see Table 2).

ing significantly, but from skim feeding not significantly.

Most fossil taxa are closely associated with the clusters of the lunge feeders having both small and large prey (most of balaenopterids), and small prey feeders with skimming (the Balaenidae and *Caperea marginata*) or multiple prey capture tactics (*Eschrichtius robustus*), but far from the clusters of the lunge feeders having fish primary (*Balaenoptera edeni*) and small invertebrates (*Balaenoptera musculus*) in the morphospace (Figure 5).

The early Chaeomysticeti *Yamatocetus canaliculatus* shows that high positive PC1 score among the analyzed specimens, which makes *Yamatocetus canaliculatus* closest to the clusters of the small prey feeders (the Balaenidae, *Caperea marginata*, and *Eschrichtius robustus*).

Qualitative Morphological Comparison

Balaenoptera edeni shows a unique combination of features such as very long articular processes, deep notch between the articular processes, large and wide processes at the posterior margin, and anterolaterally oriented lateral portions (Table 4). On the other hand, most of baleen whales have a short articular process, wide notch between the articular process, and laterally oriented lateral portions.

Among the Chaeomysticeti including the Balaenopteridae, only *Balaenoptera musculus* shows anteroposteriorly expanded lateral portions.

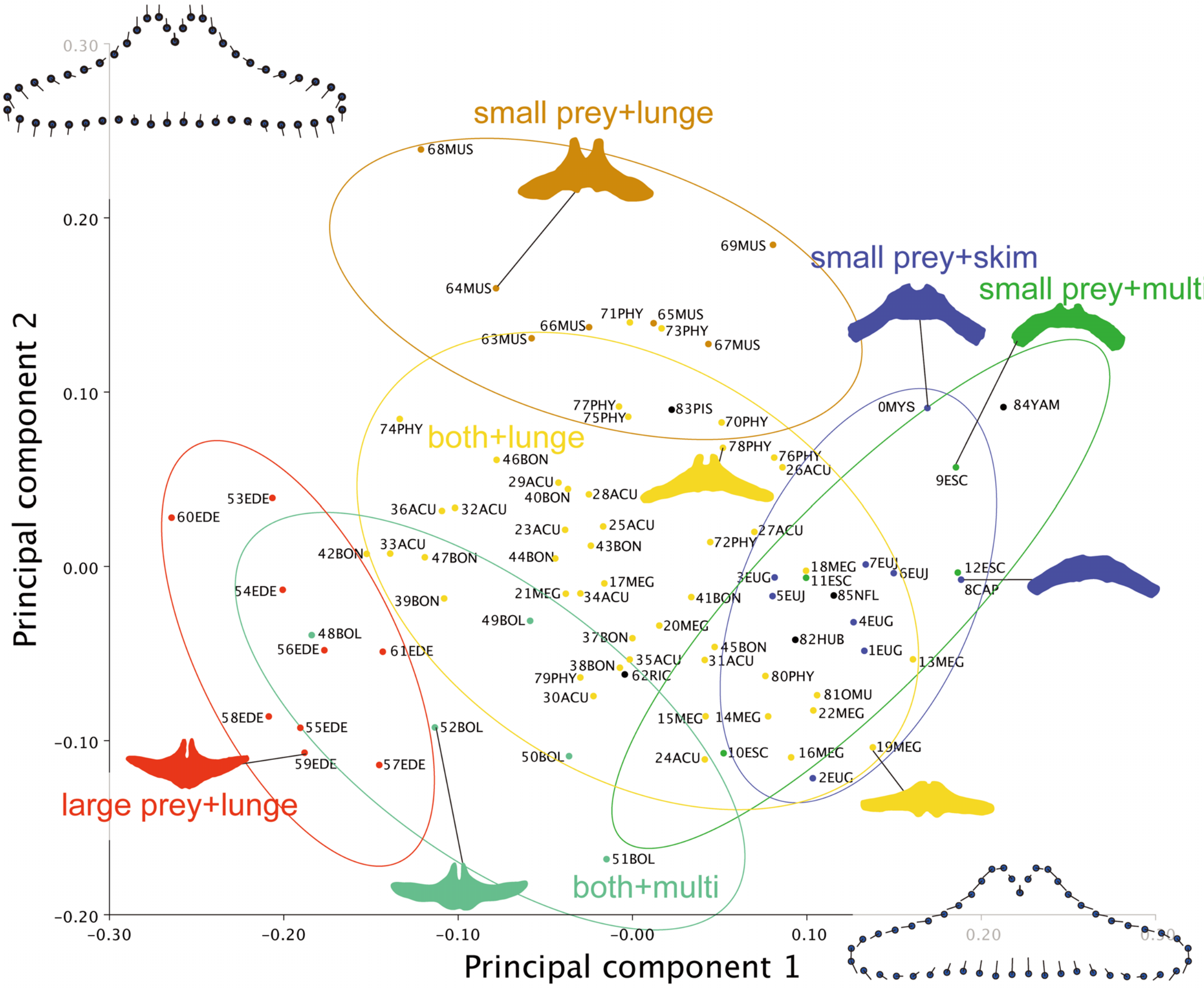

FIGURE 5. Same results as in Figure 4 with 90% confidence intervals for combinations of prey capture tactics and prey types. Numbers and letters are IDs and abbreviations of scientific names (see Table 2).

TABLE 3. P-values for pairwise Hotelling's tests. Significant values (<.005) are in bold.

	Invertebrates	**Both**	**Fish**
Invertebrates		**8.26E-07**	**5.23E-10**
Both	**8.26E-07**		**2.36E-09**
Fish	**5.23E-10**	**2.36E-09**	
	Skim	**Multiple**	**Lunge**
Skim		0.056496	**7.05E-05**
Multiple	0.056496		**0.035062**
Lunge	**7.05E-05**	**0.035062**	

This expansion forms an angle at the middle of the lateral portion of the basihyal-thyrohyal.

The all extant non-balaenopterids (the Balaenidae, *Caperea marginata*, and *Eschrichtius robustus*) show small articular and posterior processes, shallow notch, and posteriorly oriented lateral portions.

Most of examined extinct species show the same conditions of the features to those of other extant groups (the Balaenidae, *Caperea marginata*, and *Eschrichtius robustus*). An aetiocetid *Fucaia buelli* and an early member of the Chaeomysticeti *Yamatocetus canaliculatus* show primitive conditions of the basihyal-thyrohyal. They have very short and not anteriorly well-projected articular processes. *Yamatocetus canaliculatus* shows most posteriorly oriented lateral portion. A Middle to Late

TABLE 4. Qualitative morphological comparison. The articular process is categorized by the ratio of the width and length of the process (Very short [Over 3.0], Short [2.9 to 1.2], Long [1], Very long [less than 1]). The notch between the articular process is categorized by the ratio of the width and length of the notch (Narrow [less than 0.3], Wide [over 0.5]).

Scientific name	**articular process**	**notch between the articular processes**	**processes at the posterior margin**	**orientation of lateral portion**	**lateral portion anteroposerior expansion**
Extant taxa					
Balaena mysticetus	short	wide	absent	posterolaterally	absent
Eubalaena glacialis	short	wide	small	posterolaterally	absent
Eubalaena japonica	short	wide	small	posterolaterally	absent
Caperea marginata	short	wide	small	posterolaterally	absent
Eschrichtius robustus	short	wide	small or absent	posterolaterally	absent
Megaptera novaeangliae	short	wide	small or absent	laterally / posterolaterally	absent
Balaenoptera omurai	short	wide	large and pointed	laterally	absent
Balaenoptera bonaerensis	short	wide	small or absent	laterally	absent
Balaenoptera acutorostrata	short	wide	small or large	laterally / posterolaterally	absent
Balaenoptera physalus	long to short	wide to narrow	large and pointed	posterolaterally	absent
Balaenoptera musculus	short	wide	large and pointed	posterolaterally	present
Balaenoptera ricei	short	narrow	large and pointed	laterally	absent
Balaenoptera borealis	long to short	wide to narrow	large and wide	anterolaterally	absent
Balaenoptera edeni	very long	narrow	large and wide	anterolaterally	absent
Extinct taxa					
"Megaptera" hubachi	short	wide	absent	laterally	absent
Pelocetus calvertensis	short	wide	absent	laterally	absent
Piscobalaena nana	short	wide	absent	posterolaterally	absent
NFL 2634	short	wide	absent	posterolaterally	absent
Yamatocetus canaliculatus	very short	wide	absent	more posteriorly	absent
Fucaia buelli	very short	wide	-	-	absent

Miocene cetotheriid *Piscobalaena nana* and a Late Miocene chaeomisticeti *Pelocetus calvertensis* have short articular processes, which are similar to these of extant balaenopterids. An Early Pliocene balaenopterid “*Megaptera” hubachi* has laterally oriented lateral portion.

Prey size and the size of the basihyal-thyrohyal are varied. The size of the basihyal-thyrohyal of small prey feeders are from a small size of the Balaenidae (about 70 to 90 cm wide) to large size of *Balaenoptera musculus* (about 120 to 130 cm wide). The size of the basihyal-thyrohyal of both large and small prey feeders are from small size of *Balaenoptera acutorostrata* (about 30 to 40 cm wide) to large size of *Balaenoptera borealis* (about 60 to 80 cm wide).

DISCUSSION

Morphological Traits by Prey Types

Some morphological features are related to prey types more strongly instead of prey capture tactics based on PCA and pairwise Hotelling’s tests (Figure 5 and Table 3). The clusters of small prey feeders with different prey capture tactics such as balaenids, *Caperea marginata*, and *Eschrichtius robustus* are plotted very closely (Figure 4). Such small prey feeders share the basihyal-thyrohyal with a small articular process, and a wide and shallow notch between the articular processes.

A lunge + small prey feeder *Balaenoptera musculus* is differentiated from other small prey feeders (balaenids, *Caperea marginata*, and *Eschrichtius robustus*) by having the basihyal-thyrohyal with a large articular process, and a narrow and deep notch between the articular processes. In addition, *B. musculus* uniquely shows an anteroposteriorly expanded lateral portion of the basihyal-thyrohyal. This fact implies that *B. musculus* are specialized and adapted to consume small prey in different ways.

Most of balaenopterids' feeding of both small and large prey are located at the center in the morphospace (Figures 4 and 5). Such balaenopterids have moderate-sized articular process and narrow notch between the processes.

On the other hand, the primarily fish feeders (*Balaenoptera edeni*) are distant from the center of the confidence ellipse of balaenopterids. The primarily fish feeder *Balaenoptera edeni* having a very long articular process and anterolaterally oriented lateral portion. These features are very rare among the Chaeomysticeti.

Some *Balaenoptera borealis* is similar to *B. edeni* in having slender articular process. However, the articular process of *B. borealis* is shorter than that of *B. edeni*. In *B. borealis*, orientation of lateral portion is varied, but some of them have anterolaterally oriented ones. *B. borealis* is known as a generalist feeding wider range of prey compared to other extant baleen whales (Horwood, 2018). *B. borealis* might have more fish compared to other balaenopterids excluding *B. edeni*.

Morphology of the Basihyal-Thyrohyal and Function of the Tongue

Since the hyoid bone provides muscles for moving the tongue and swallowing, differences of the bone shape may reflect difference of the tongues themselves such as hardness, function of the tongue, and swalloing manner.

How whales use their tongues? The members of the Balaenidae and *Caperea marginata* are skim feeders, and they use their sturdy tongues for cleaning baleen with trapped prey and swallowing (Werth and Crompton, 2023). *Eschrichtius robustus* retract their muscular tongue to expand the oral cavity and generate negative pressure to take prey from the mud sea floor (Werth, 2001). The members of the Balaenopteridae are thought to use their flabby tongues for transporting accumulated prey posteriorly in their mouth (Werth and Ito, 2017).

The hardness of the tongue possibly relates to the basihyal-thyrohyal morphology. The tongues of *Eschrichtius robustus* and the Balaenidae are muscular, but the ones of the Balaenopteridae are soft. Whales with muscular tongues share the basihyal-thyrohyal morphology with a small articular process, and a wide and shallow notch between the articular processes. The tongue of *Balaenoptera edeni* was described with other balaenopterids such as *B. borealis, B. acutorostrata,* and *Megaptera novaeangliae* as a poorly muscled tongue (Nemoto, 1970; Lambertsen, 1983).

It might be possible that among the Balaenopteridae detailed comparison of the tongue in not only hardness, but also dimensions and shape. *B. edeni* can be differentiated from other members. The relationships between basihyal-thyrohyal morphology and tongue are still unclear. At least, *B. edeni* has some sort of different tongue usage from other balaenopterids.

Having a long articular process and anteriorly oriented lateral portion are unique features for *B. edeni*, which can be thought as a features of fish eaters.

Having a long articular process possibly allows to provide the insertions of the hyoglossus muscle longer than these of other balaenopterids. The hyoglossus is a paired muscle on the left and right sides of the tongue (Kienle et al., 2015). The hyoglossus is originated from the articular process of the basihyal-thyrohyal (Carte and Macalister, 1868; Schulte, 1916). Having long articular process associated to having an anteroposteriorly long origin for the hyoglossus.

The lateral portion provides muscle attachments such as the sternohyoid muscle running to the sternum and the geniohyoid muscle running to the mandibular symphysis (Werth and Ito, 2017). The sternohyoid muscle retracts and depresses the tongue root (Werth and Ito, 2017). As mentioned above, the members of the Balaenopteridae use their flabby tongues for transporting accumulated prey posteriorly in their mouth.

Anteriorly oriented lateral portion makes the anteroposterior distance between the lateral portion and anterior border of the anterior process shorter in *B. edeni* than these of other balaenopterids. These differencese of *B. edeni* from other balaenopterids might be related to swallowing large size prey such as fish.

Fossil Species

Morphology of the basihyal-thyrohyal of fossil species suggests that prey type of the Chaeomysticeti started from small-sized prey such as small invertebrates then diversified through evolution.

The early Chaeomysticeti: a member of the Eomysticetidae *Yamatocetus canaliculatus* is closest to the clusters of small prey feeders (balaenids, *Caperea marginata*, and *Eschrichtius robustus*), but far from balaenopterids in the morphospace (Figure 5). An aetiocetid *Fucaia buelli* is included in qualitative comparison as outgroup, which shares

TABLE 5. Estimated feeding strategies for extinct taxa and *Balaenoptera ricei*.

Family	ID	Scientific name	Estimated prey types	Specimen number
Balaenopteridae	62	*Balaenoptera ricei*	Both large and small prey	USNM 594665
Balaenopteridae	82	*"Megaptera" hubachi*	Both large and small prey, or small prey	MPST 240505
Cetotheriidae	83	*Piscobalaena nana*	Both large and small prey	MNHN SAS 1617
Eomysticetidae	84	*Yamatocetus canaliculatus*	Small size prey	KMNH VP 000,017
-	85	Mysticeti indet.	Both large and small prey, or small prey	NFL 2634

some conditions with the early Chaeomysticeti: *Y. canaliculatus* has very small and not anteriorly well-projected anterior process and wide notch (Table 4). These conditions are supposed as primitive condition at least among the Chaeomysticeti based on comparison with outgroup.

In this study, morphology of the basihyal and thyrohyal represents prey types. *Y. canaliculatus* can be hypothesized as a small prey feeder. Previously, *Y. canaliculatus* was identified as “not a skim and multiple prey capture feeder” as seen on modern baleen whales based on rostrum morphology and was closer to the cluster of lunge feeders (Tanaka, 2022). Of note, *Y. canaliculatus* has very small and not anteriorly well-projected articular processes and more posteriorly oriented lateral portions, which are not the same to all compared baleen whales (Table 4). The Eomysticetidae: an early member of the Chaeomysticeti likely had unknown feeding strategies different from all extant baleen whales.

"Megaptera" hubachi and NFL 2634 are plotted in the three overlapped clusters of small prey, and both small and large prey feeders (Figure 5). Their prey types are still unknown, but at least, they were not large prey feeders like *Balaenoptera edeni* (Table 5).

A cetotheriid *Piscobalaena nana* possibly had both small and large prey. An amazingly preserved fossil stomach of a cetotheriid from the Pisco Formation, Peru contained *Sardinops* scales and bones (Collareta et al., 2015). Unusual among the Malacostraca, Krill have no unequivocal fossil records (Jarman, 2001), because difficulty of preservation. Thus, the fossil cetotheriid including *P. nana* might have not only fish but also krill.

Here, prey type diversification among the Chaeomysticeti is hypothesized (Figure 6). Early members of the Chaeomysticeti started to have small size invertebrates, then some linages such as the Cetotheriidae and Balaenopteridae adapted to have fish in the Miocene. Among the Balaenopteridae, at least one linage of *B. musculus* being back to a small invertebrate feeder but in different way to other linages (balaenids, *Caperea marginata*, and *Eschrichtius robustus*). Another linage in the Balaenopteridae *B. edeni* adapted to feeding fish primarily.

CONCLUSION

This study examined the relationships of the basihyal-thyrohyal shape and feeding strategy among extinct and extant baleen whales, and hypothesized evolution of the prey types. As the result of analysis, small prey feeders such as balaenids, *Caperea marginata*, and *Eschrichtius robustus* share the basihyal-thyrohyal with small articular processes, and a wide and shallow notch between the articular processes. On the other hand, large prey feeders eating fish primarily show very long articular processes and anteriorly oriented lateral portions of the basihyal-thyrohyal, which is a unique condition owned by *Balaenoptera edeni* among baleen whales. A member of the most basal family Eomysticetidae: *Yamatocetus canaliculatus* was plotted close to the cluster of the small prey feeders. This result suggests that the early Chaeomysticeti fed small prey using the baleen plates for filtering. In the Miocene, the Cetotheriidae and Balaenopteridae started having both large and small prey. Then, a few members of Balaenopteridae such as *Balaenoptera musculus* and *B. edeni* were specialized in prey types. In short, morphology of the basihyal-thyrohyal of fossil species suggests that prey type of the Chaeomysticeti started from small-sized prey such as small invertebrates then diversified through evolution. This study revealed that the early member of the Chaeomysticeti represents a combination of prey type and prey capture tactics, which is not the same with combinations of any extant baleen whales. We still do not know how primitive feeding strategies worked among the Chaeomysticeti. More morphological comparison possibly allows us to provide better idea to consider combination of prey capture tactics, prey types and so on.

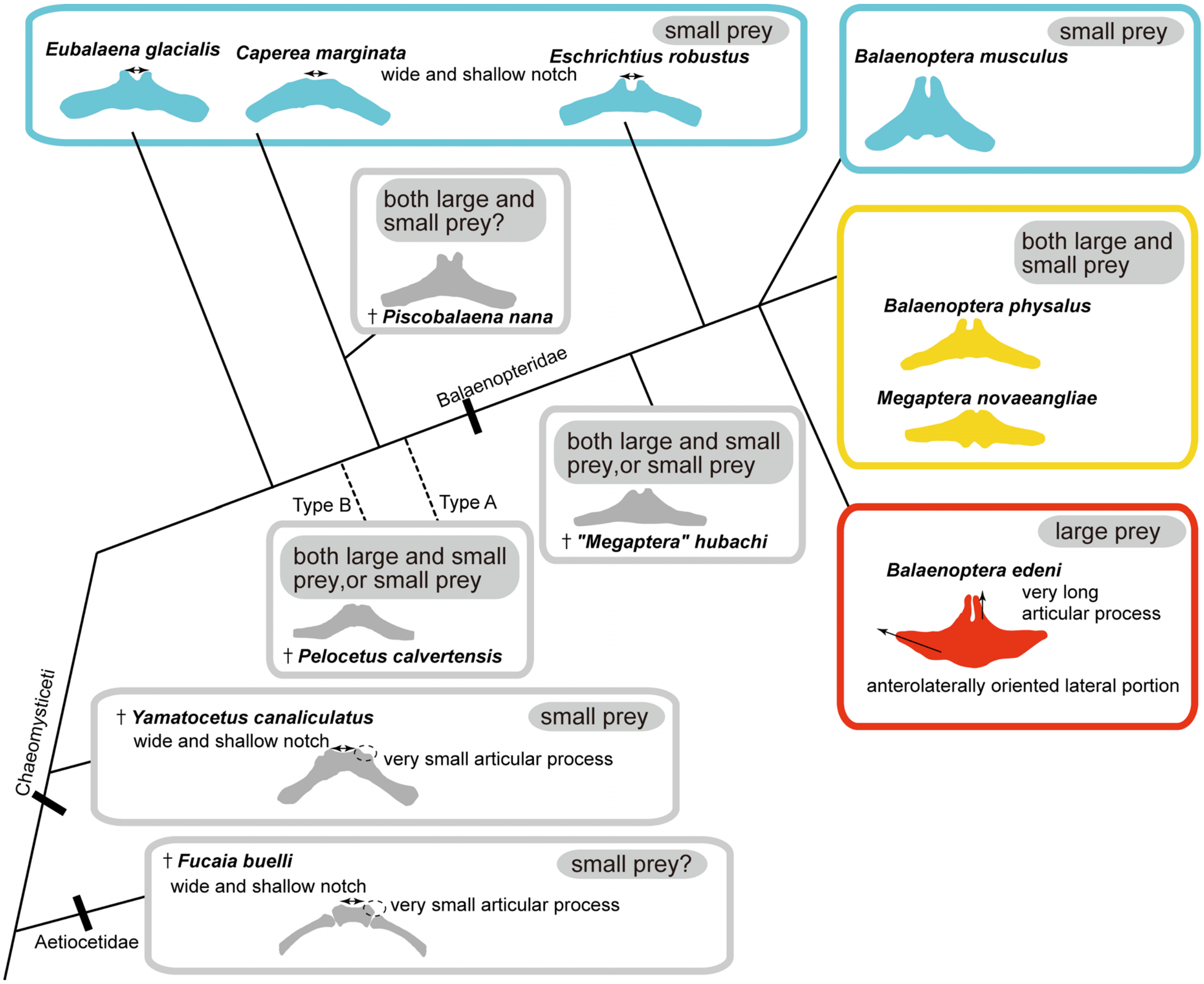

FIGURE 6. Morphological traits of the basihyal and thyrohyal among the Chaeomysticeti separated by prey types. Boxes gray in colour are extinct baleen whales, which ID number 4, 8, 11, 33, 40, 53, 61, 70 in Table 2 are used here. *Piscobalaena nana* shows two different types of phylogenetic hypotheses (see in cladogram section).

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APPENDIX 1.

Original references of analyzed specimens. See Figure 3 and Table 1.

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APPENDIX 2.

MANOVA in the PCA.

MANOVA PC1 and 2 in prey types			
Wilks´ lambda:	0.3934	Pillai trace:	0.6205
df1:	6	df1:	6
df2:	162	df2:	164
F:	16.05	F:	12.29
p (same):	1.91E-14	p (same):	2.10E-11
MANOVA PC1 and 2 in feeding tactics			
Wilks´ lambda:	0.7072	Pillai trace:	0.3066
df1:	6	df1:	6
df2:	162	df2:	164
F:	5.107	F:	4.948
p (same):	7.88E-05	p (same):	0.000111