JOURNAL OF THE ROYAL SOCIETY OF NEW ZEALAND
2024, VOL. 54, NO. 5, 696–710
https://doi.org/10.1080/03036758.2023.2277739

RESEARCH ARTICLE

OPEN ACCESS

A review of New Zealand Eomysticetidae (Mammalia, Cetacea) and implications for the evolution of baleen whales: new specimens, functional anatomy, and phylogeny

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ABSTRACT

Eomysticetidae are a clade of early diverging functionally toothless, longirostrine and likely baleen-bearing stem mysticete whales. Eomysticetid fossils are rare but known worldwide from Oligocene strata. The richest assemblage of eomysticetids has been uncovered in New Zealand from the Kokoamu Greensand and Otekaike Limestone (North Otago and South Canterbury regions, South Island). This includes some of the largest known eomysticetids, *Tokarahia kauaeroa* and *Tokarahia lophocephalus*, some older and more archaic forms such as *Matapanui waihao*, the fragmentary *Tohoraata raekohao* and *Tohoraata waitakiensis*, and the well-known *Waharoa ruwhenua* represented by several well-preserved skulls and mandibles of adults and juveniles. Studies of these New Zealand fossils strongly indicates monophyly of Eomysticetidae and suggest possible skim feeding behaviour, possession of non-functional teeth and baleen, extreme rostral lengthening during growth and peramorphic evolution, rostral kinesis, use of Zealandia as a calving ground, and probable extinction at or near the Oligo-Miocene boundary.

ARTICLE HISTORY
Received 21 June 2023
Accepted 21 October 2023

HANDLING EDITOR
Jeffrey Robinson

KEYWORDS
Cetacea; Mysticeti; Eomysticetidae; marine mammals; Oligocene

Introduction

Modern cetaceans include toothed whales (Odontoceti) and the baleen whales (Mysticeti), which are toothless as adults and instead possess racks of keratinous baleen used to filter feed for krill, amphipods, copepods, and fish. The cetacean crown clade, Neoceti, diverged from ancestral basilosaurid archaeocete whales into these groups during the late Eocene, and a host of fossils documenting the archaeocete-neocete transition has been unearthed from late Eocene and Oligocene rocks. The early evolution of mysticetes is illuminated by a variety of fossil toothed forms lacking baleen (Mammalodontidae, Llanocetidae, Coronodonidae; Mitchell 1989; Fitzgerald 2006, 2010; Geisler et al. 2017; Lambert et al. 2017; Fordyce and Marx 2018; Boessenecker et al. 2023), fossil

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toothed mysticetes potentially also possessing baleen (Aetiocetidae; Deméré et al. 2008; Ekdale and Deméré 2022; Gatesy et al. 2022; but see Marx et al. 2016; Peredo et al. 2017, 2018, 2021), and early baleen-bearing mysticetes lacking functional teeth (Eomysticetidae; Sanders and Barnes 2002b; Okazaki 2012; Boessenecker and Fordyce 2015a, 2015c, 2017a) – all late Eocene or Oligocene in age.

The Eomysticetidae are the largest known Oligocene cetaceans and possess large skulls nearing 2 m in length with broad, flat, purportedly toothless palates, large attachments for the temporalis muscle, and delicately constructed bow-like mandibles initially interpreted as lacking teeth (Sanders and Barnes 2002b; Boessenecker and Fordyce 2015a, 2015c; Figure 1A-F). Eomysticetids are chiefly known from rocks of late early Oligocene and late Oligocene age (~30-23 Ma) from South and North Carolina, Japan, and New Zealand (Sanders and Barnes 2002b; Boessenecker and Fordyce 2015a, 2015b, 2015c, 2017a), with possible survival into the earliest Miocene (Boessenecker and Fordyce 2017b; Boessenecker 2022; but see Marx et al. in press, in regards to OU 22744). Considerable debate over the evolution of baleen has emerged in recent years (Marx et al. 2016; Geisler et al. 2017; Peredo et al. 2017, 2018, 2021; Ekdale and Deméré 2022; Gatesy et al. 2022) and some eomysticetid-like cetaceans (e.g. *Maiabalaena*) have been proposed to constitute major transitional fossils in the teeth-baleen transition, even indicating an intermediate stage where mysticetes lacked both teeth and baleen (Peredo et al. 2018; but see Ekdale and Deméré 2022; Gatesy et al. 2022; Boessenecker et al. 2023). This review focuses on Eomysticetidae from New Zealand, which has historically produced the most anatomically informative and diverse assemblage of eomysticetids worldwide, and further reviews the broader role of eomysticetids in understanding mysticete evolution and reevaluates hypotheses of baleen evolution based on eomysticetid-like whales and the phylogenetic relationships of these taxa.

Geologic background

New Zealand's Eomysticetidae have been predominantly recovered from the southern margin of the Canterbury Basin, in the Waitaki region (Field and Browne 1989; Boessenecker and Fordyce 2017a). During the late Oligocene, the region consisted of predominantly mid to outer continental shelf setting on a broad shelf exhibiting paleotopography, with a general trend of shallower marine facies westwards towards a paleo-high (Fordyce et al. 1985; Ayress 1993; Fordyce and Richards 2016; Barrier et al. 2019). This oceanic setting with little terrigenous sedimentary input and upwelling from deeper water resulted in time-condensed beds of authigenic minerals (glauconitic and phosphatic deposits) on the seafloor. This is known as the Kokoamu Greensand of a lower-mid Chattian age (upper Whaingaroan to Duntroonian local NZ Stage) (Gage 1957). The greensand has an unconformity at its base that appears to represent a large sea level drop with subaerial expousure in the mid-Cenozoic (32-30 Ma; Barrier et al. 2019). In the mid-upper Duntroonian (mid Chattian) there was a shift to carbonate-dominated deposition and there was a gradational shift in seabed composition until bioclastic, fine grained limestones of the Otekaike Formation predominated basin-wide up until after the disappearance of Eomysticetidae towards or in the Waitakian Stage near the end of the Oligocene. Early in the Miocene, marine sediments developed a stronger terrigenous-signal due to the increasing intensity of mountain-building and erosion on the western inner

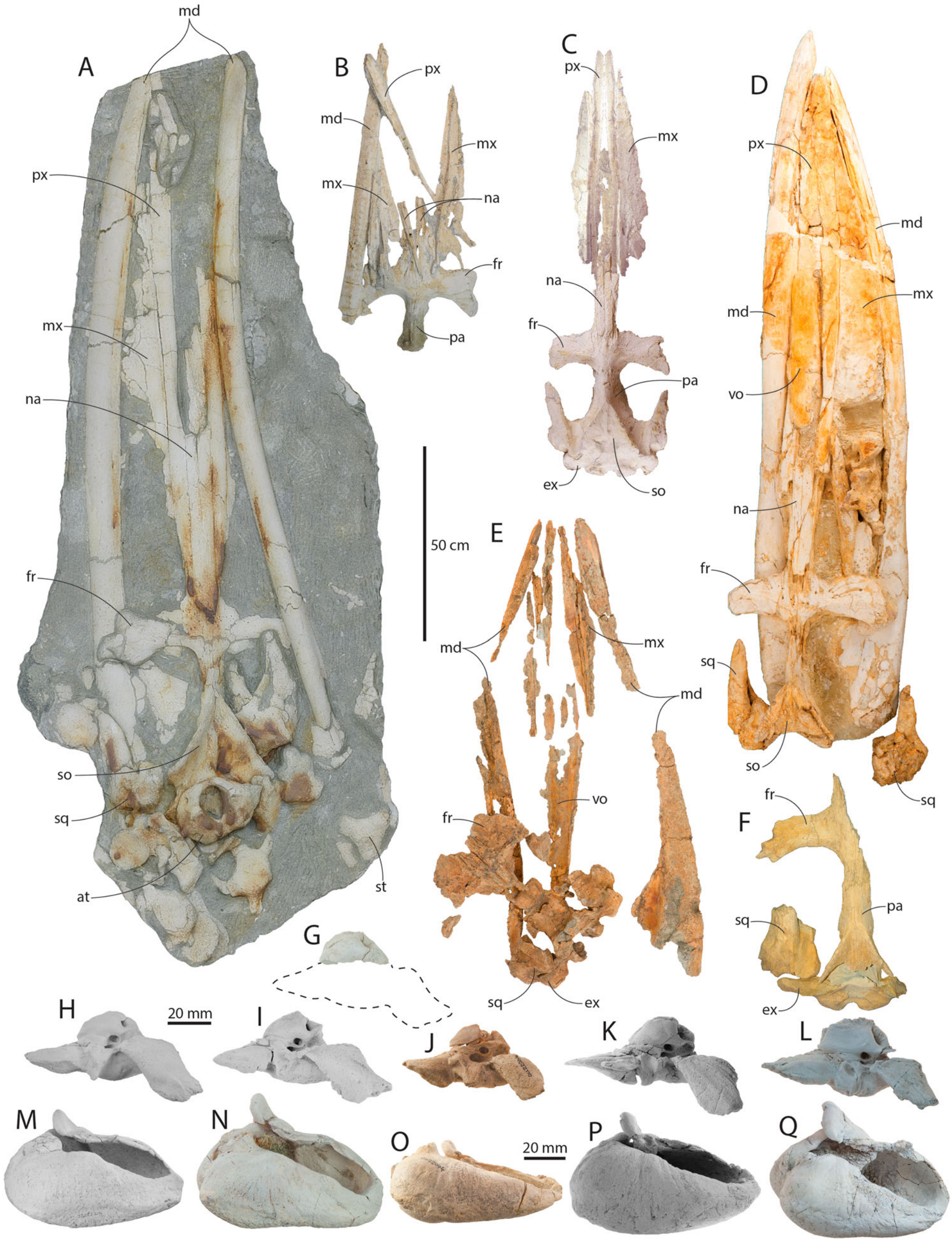

Figure 1. Previously reported material of Eomysticetidae from New Zealand. **A,** *Tokarahia kauaeroa* holotype skull (OU 22235); **B,** *Waharoa ruwhenua* juvenile (OU 22075); **C,** *Waharoa ruwhenua* juvenile and paratype (OU 22163); **D,** *Waharoa ruwhenua* adult and holotype skull (OU 22044); **E,** *Matapanui waihao* holotype skull (OU 12918); **F,** *Tohoraata raekohao* holotype skull (OU 22178); **G,** holotype periotic of *Tokarahia lophocephalus* (OM GL 412); **H,** holotype periotic of *Tokarahia kauaeroa*; **I,** referred periotic of *Tokarahia lophocephalus* (OU 22081); **J,** holotype periotic of *Waharoa ruwhenua* (OU 22044); **K,** holotype periotic of *Tohoraata raekohao* (OU 22178); **L,** holotype periotic of *Matapanui waihao* (OU 12918); **M,** holotype bulla of *Tokarahia kauaeroa* (OU 22235); **N,** holotype bulla of *Tokarahia lophocephalus* (OM GL 412); **O,** holotype bulla of *Waharoa ruwhenua* (OU 22044); **P,** holotype bulla of *Tohoraata raekohao* (OU 22178); **Q,** holotype bulla of *Matapanui waihao* (OU 12918). Abbreviations: at, atlas; ex, exoccipital; fr, frontal; md, mandible; mx, maxilla; na, nasal; pa, parietal; px, premaxilla; so, supraoccipital; sq, squamosal; st, sternum; vo, vomer.

margin of the basin (Gage 1957; Field and Browne 1989). Both the Kokoamu and Otekaike formations typically reflectcalm bottom conditions and do not exhibit an abundance of warm-water indicator species (Beu and Maxwell 1990; Ayress 1993; Fordyce and Maxwell 2003). In comparison, northern, western and southern basins were rich in warm water indicators. This indicates a dominance of currents of colder water coming from the south, as found on the eastern coast of the South Island today. Inner to mid shelf deposits at Haughs Quarry yield warm water indicators not found elsewhere in the basin for the late Oligocene. The low accumulation rate of Late Oligocene sediments in the Waitaki area (eg: seen in the inner marginal basin deposits of Haughs Quarry, Hakataramea) is an important factor contributing toward a high density of relatively closely-associated cetacean skeletons that can be found today throughout the outcrops in the region (Fordyce and Maxwell 2003).

History of study of eomysticetidae

The very first discovered cetacean now considered to belong to Eomysticetidae was collected in the 1940s by New Zealand entomologist Brian J. Marples (U. Otago), who discovered a number of partial cetacean skeletons in the soft weathering Kokoamu Greensand. Marples excavated and prepared these specimens and named them *Mauicetus lophocephalus*, *Mauicetus waitakiensis*, and *Mauicetus brevicollis* (Marples 1956). The type species of *Mauicetus*, *M. parki* (Benham 1937), represents a much more derived cetacean (Boessenecker and Fordyce 2015b, 2015c). Owing to fragmentary preservation and the loss of the informative holotype skull of *M. lophocephalus* in the 1960s or 1970s (Boessenecker and Fordyce 2015c), little sense was made of these specimens until the discovery of *Eomysticetus whitmorei* from the Oligocene Chandler Bridge Formation of South Carolina (Sanders and Barnes 2002b). This taxon is represented by a partial skull with a fragmentary rostrum, nearly complete braincase, well-preserved tympanoperiotics, mandibles, and postcrania. A similar specimen from the Oligocene Jinnobaru Formation of Japan was briefly reported by Okazaki (1995) and later formally described as *Yamatocetus canaliculatus* by Okazaki (2012) based on a complete skull in a concretion with associated mandibles, thoracic postcrania and forelimbs.

A large suite of eomysticetid material was collected by R.E. Fordyce and associates from the South Island of New Zealand in the 1980s and 1990s including several skulls and skeletons from the Kokoamu Greensand and Otekaike Limestone (Figures 1 and Figure 2). This collection at OU, along with surviving material from the Marples collection at Otago Museum, formed the basis for the Ph.D. thesis research of the lead author. These studies resulted in the recognition of eomysticetid monophyly as well as the recognition that '*Mauicetus waitakiensis*' and '*Mauicetus*' *lophocephalus* were not congeneric (Boessenecker and Fordyce 2015b, 2015c); these were reassigned to the newly named genera *Tohoraata* and *Tokarahia*, along with *Tohoraata raekohao* and *Tokarahia kauaeroa* (Boessenecker and Fordyce 2015b, 2015c). Additional eomysticetids named from New Zealand include *Matapanui waihao* and *Waharoa ruwhenua* (Boessenecker and Fordyce 2015a, 2017a), taxa recovered during Fordyce's four decades of extensive fieldwork and surprisingly undetected by early fieldwork by Marples. One of R. Ewan Fordyce's final large fossil excavations was a field expedition to collect an eomysticetid

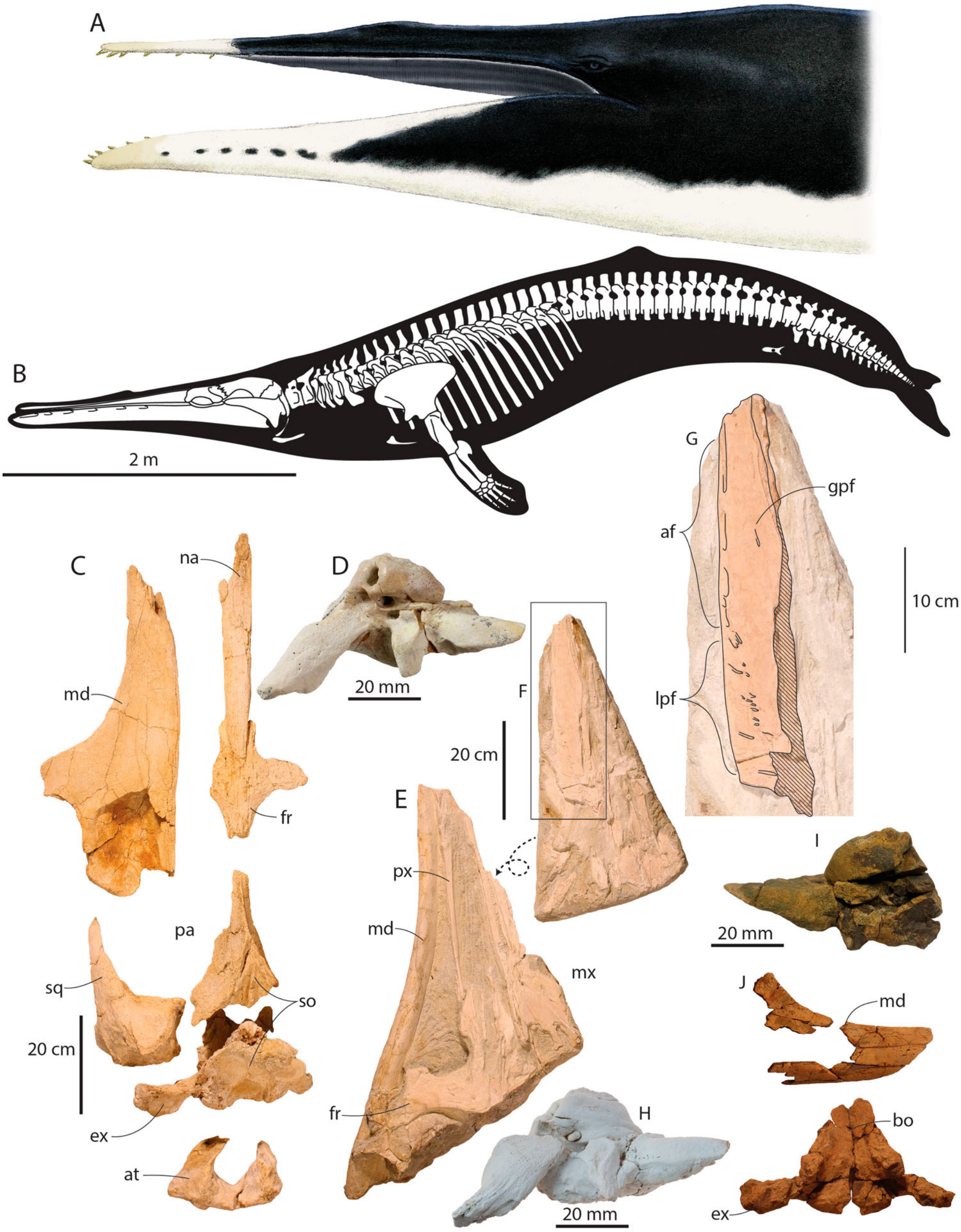

Figure 2. Life and skeletal restorations of Eomysticetidae and newly reported material of New Zealand Eomysticetidae. **A,** life restoration of *Waharoa ruwhenua* with vestigial dentition (from Boessenecker and Fordyce 2015a); **B,** skeletal restoration of *Tokarahia kauaeroa* (from Boessenecker and Fordyce 2015b); **C-D,** referred skull and periotic of *Tokarahia* sp., OU 22783; **E-H,** referred skull (OU 22120) and possibly associated periotic (OU 22743) of *Matapanui waihao*; **I-J,** referred skull and periotic of *Matapanui* sp. (OU 22028). Abbreviations: af, alveolar foramina; bo, basioccipital; gpf, greater palatine foramina; lpf, lateral palatal foramina.

partial skeleton in September, 2016 (*Tokarahia* sp., OU 22783), with the process being documented on film (*Modern Dinosaurs* 2017; season 1 episode 6 - Violent Seas).

More recently, two eomysticetid-like Oligocene chaeomysticetes were reported from Oligocene deposits of Oregon and Washington, USA. These include *Sitsqwayk cornishorum* based on a partial skeleton with a proportionally robust skull from the Pysht Formation of Washington (Peredo and Uhen 2016) and *Maiabalaena nesbittae* from the Alsea Formation of Oregon (Peredo et al. 2018). Though not immediately recognised as eomysticetids by these initial studies, phylogenetic analysis strongly confirms placement within Eomysticetidae (Boessenecker et al. 2023). Isolated bullae from the Jan Juc Marl confirm the first records of Eomysticetidae from Australia (Marx et al. 2019); we provisionally identify these bullae as cf. *Tokarahia* (Marx et al. 2019: fig. S1D, S2A), cf. *Waharoa* (Marx et al. 2019: fig. S2B) and cf. *Matapanui* (Marx et al. 2019: fig. S2C). Most recently, a partial skull with unusually enlarged nasal process of the premaxilla was described as an eomysticetid from the El Cien Formation of Baja California, Mexico (Hernández-Cisneros and Nava-Sánchez 2022).

Eomysticetid morphology

Eomysticetid baleen whales possess a mixture of unusually derived and unusually archaic features. Derived features are mostly present in the rostrum: the rostrum is elongated, dorsoventrally flattened, and the palate possesses a series of relatively small lateral palatal foramina and sulci – osteological correlates of baleen (Deméré et al. 2008; Figure 1A-F, Figure 2E-G). The rostrum appears to have at least some kinesis as the maxilla-premaxilla and maxillofrontal sutures are open and do not possess mortised articular surfaces (Boessenecker and Fordyce 2015a). The overall shape of the rostrum resembles many other Chaeomysticeti, generally suggestive of filter feeding habits. A palatal keel is not developed (Okazaki 2012; Boessenecker and Fordyce 2015a). The nasal bones are unusually long, even longer than in basilosaurid archaeocetes; similarly, the bony nares are positioned quite far anteriorly on the rostrum (Sanders and Barnes 2002b; Okazaki 2012; Boessenecker and Fordyce 2015a, 2015c). The supraorbital process of the frontal is typically delicate, horizontally oriented, and anteroposteriorly short; the orbitotemporal crest is shifted anteriorly onto the posterodorsal surface of the frontal. The intertemporal region is quite long and narrow, with most eomysticetids possessing a tall sagittal crest (Figure 1A, D). The occipital shield of nearly all Eomysticetidae is narrow and triangular (Figure 1A, C-D). The zygomatic processes lack a supramastoid crest, are elongate and somewhat cylindrical in shape, medially rotated, and possess a large squamosal prominence at their base; a secondary squamosal fossa is also developed. The periotics and bullae (Figure 1G-Q) are quite archaic and generally resemble their counterparts in toothed mysticetes and basilosaurid archaeocetes. The periotics are distinguished from most other early Mysticeti by possessing a discontinuous superior process with anterior and posterior apices; the bulla is narrower and possesses a longer median furrow on the ventral surface.

The mandibles of Eomysticetidae (Figure 1A, E-D) are long with parallel dorsal and ventral margins of the horizontal ramus, an unfused symphysis and symphyseal groove, a lobate dorsal-dorsolaterally oriented coronoid process, a large mandibular foramen and fossa with thin ‘pan bone’ (Figure 2C) resembling other stem mysticetes, archaeocetes, and odontocetes. The mandible is slightly laterally bowed. A series of gingival foramina are present along the dorsal crest, and there are some large foramina in a row anteriorly initially interpreted by Boessenecker and Fordyce (2015a) as tooth alveoli. Eomysticetid forelimbs (Figure 2B) have elongate humeri, radii, and ulnae like basilosaurids (Sanders and Barnes 2002b; Boessenecker et al., 2015C), yet possess a locked elbow like other Neoceti; the antebrachium and humerus are of equivalent length, intermediate between basilosaurids (humerus longer) and crown Mysticeti (antebrachium much longer). Eomysticetids possess at least 15 thoracics (Figure 2B) and an unknown number of lumbar and caudal vertebrae (Sanders and Barnes 2002b; Boessenecker and Fordyce 2015c); the lumbars retain somewhat ventrolaterally deflected transverse processes like toothed mysticetes, though they are not as steeply descending as in Basilosauridae. Eomysticetids are large for stem mysticetes, with condylobasal skull length as small as 1.16 metres (*Yamatocetus*) to approximately 2 metres (*Tokarahia* spp., *Micromysticetus*).

New Zealand and Australian eomysticetidae

Six nominal eomysticetids in four genera have been reported from the Oligocene strata of New Zealand, all from the Kokoamu Greensand and Otekaike Limestone of the southern Canterbury Basin in North Otago (Waitaki Valley) and South Canterbury (Hakaramea Valley), except for a single specimen collected from Oligocene limestone within Te Tahi Cave (West Coast).

Matapanui waihao is known from a partial juvenile specimen with an unusually flat and anteroposteriorly broad supraorbital process of the frontal, a rounded anterior margin of the occipital shield, a wide bulla, and a pointed anterior margin of the mandible relative to other New Zealand Eomysticetidae (Figure 1E, L, Q; Boessenecker and Fordyce 2017a). *Matapanui waihao* is known only from the Kokoamu Greensand, though a specimen of *Matapanui* sp., cf. *M. waihao* was reported from Te Tahi Cave, West Coast, either from the Potikohua or Tiropahi Limestone and has uncertain age control. This species was originally named *Matapa waihao* (Boessenecker and Fordyce 2017a) reassigned to *Matapanui* as *Matapa* was preoccupied (Boessenecker and Fordyce 2017c). *Matapanui waihao* is the oldest eomysticetid from New Zealand, corresponding to Whaingaroan correlative beds of the Kokoamu Greensand (lower Chattian).

Tokarahia includes the incompletely known *Tokarahia lophocephalus* and *Tokarahia kauaeroa* (Figure 1A, H-I, M-N; Marples 1956; Boessenecker and Fordyce 2015c); whereas the holotypes of these species are from the Kokoamu Greensand and Otekaike Limestone (respectively), referred specimens of each species indicate that both are found in each stratum and were probably sympatric. *Tokarahia* spp. are the largest eomysticetids from New Zealand (condylobasal length 2 m; estimated body length 6-8 m; Figure 2B).

Tohoraata is represented by *Tohoraata waitakiensis* from the Kokoamu Greensand (Marples 1956) and *Tohoraata raekohao* from the Otekaike Limestone (Boessenecker and Fordyce 2015b). Species of *Tohoraata* have a thickened paroccipital process and a relatively wide and short tympanic bulla with a flat ventral surface; additionally, *Tohoraata raekohao* has numerous diploic foramina in the supraorbital process of the frontal, a relatively low sagittal crest, and a periotic with an unusually long and narrow anterior process and greatly ventrally deflected posterior process (Figure 1F, K, P).

Waharoa ruwhenua is known from several skulls and an isolated juvenile bulla, all from the Oteikaike Limestone (Figure 1B-D, J, O; Boessenecker and Fordyce 2015a). The holotype skull has a condylobasal length of 1.8 m, a long rostrum, diploic foramina in the frontal (like *Tohoraata raekohao*), smaller and more attenuated zygomatic processes, and proportionally small and gracile tympanoperiotics relative to all other New Zealand Eomysticetidae (Figure 1D, J, O). Critically, the hypodigm includes juvenile specimens that indicate that *Waharoa*, and likely other eomysticetids, has a relatively short rostrum as juveniles that rapidly lengthens during postnatal ontogeny (Figure 1B-C). Critically, the nasal bones are also much shorter, further supporting the elongate nasals as synapomorphic of Eomysticetidae. The holotype specimen of *Waharoa ruwhenua* was extensively bioeroded by the bone-eating worm *Osedax*, and traces preserved within the skeleton permitted the first documentation of fish and rays feeding on *Osedax* in the fossil record (Boessenecker and Fordyce 2015d).

More fragmentary specimens include a juvenile specimen of cf. *Yamatocetus* from the basal Otekaike Limestone, indicating that at least some eomysticetid genera had an antitropical distribution (Boessenecker and Fordyce 2017b). A partial skeleton of cf. *Waharoa* sharing a robust, anteroposteriorly thickened atlas vertebra with *Waharoa ruwhenua* from the uppermost Otekaike Limestone and above the Oligoene-Miocene boundary (upper Waitakian; 22.8-22.28 Ma) suggests that eomysticetids may have survived into the early Miocene (Boessenecker and Fordyce 2017b), though this specimen may represent a non-eomysticetid (see Marx et al., this volume). Isolated bullae from the Chattian Jan Juc Marl of Australia, here provisionally identified as cf. *Matapanui*, cf. *Tokarahia*, and cf. *Waharoa*, indicate that eomysticetids inhabited temperate-subtropical waters there as well (Marx et al. 2019).

Additional specimens are now available for study either owing to more recent preparation or collection after the aforementioned studies by Boessenecker and Fordyce (Figure 2C-J). These include a fragmentary specimen from the Duntroonian Kokoamu Greensand of Smite River, mid Canterbury, consisting of fragmentary braincase, mandibular fragments, and nearly complete periotic (OU 22028) identifiable as *Matapanui sp.* (Figure 2I-J). A somewhat more complete specimen (OU 22783) from the Duntroonian lower Otekaike Limestone of the Sisters Stream valley, Hakataramea, with partial braincase, vertex, squamosal, partial rostrum, posterior mandible, atlas vertebra, and periotic is identifiable as *Tokarahia* sp. (Figure 2C-D). Specimen OU 22120 is from a fallen block from the same locality as *Waharoa ruwhenua* specimen OU 22075. Its glauconitic limestone lithology suggests it originates from the transitional Kokoamu – Otekaike beds of Duntroonian age, and the specimen includes a partial rostrum and left supraorbital process of the frontal with associated mandible in a limestone block (Figure 2E-F); this specimen is suspected to be the same individual as isolated periotic OU 22743 *Matapanui waihao*, which was assigned a unique specimen number to reflect this uncertainty as the specimen was found unlabelled in OU collections.

Eomysticetid phylogeny

Eomysticetids are typically resolved as some of the latest-diverging stem mysticetes, diverging after toothed mysticetes (Llanocetidae, Coronodonidae, Mammalodontidae, Aetiocetidae) and sister (or close to) Crown Mysticeti (Marx 2011; Boessenecker and

Fordyce 2015a, 2015C, 2017A; Geisler et al. 2017; Boessenecker et al. 2023). A few fragmentary mysticetes of uncertain relationships may reflect stem mysticetes diverging just crownward of Eomysticetidae (Marx and Fordyce 2015; Tsai and Fordyce 2015, 2016, 2018; Hernández-Cisneros 2018).

The most recent and most comprehensive analysis to include eomysticetids included 130 OTUs and 392 characters (Boessenecker et al. 2023), an updated version of the matrix assembled and analyzed earlier by Boessenecker and Fordyce (2015a, 2015c, 2017a). This analysis supported monophyly of Eomysticetidae with strong support (bootstrap support = 90% under equal weighting, and 70% under implied weighting). Both equal and implied weighting supported a sister taxon relationship (with strong bootstrap support) between *Tokarahia kauaeroa* and *Tokarahia lophocephalus*, as well as a sister taxon relationship between *Waharoa* and *Tohoraata*. In turn, *Tokarahia* was found as sister to the *Waharoa* + *Tohoraata* clade; *Matapanui* was recovered, also with strong support, as sister to this clade. These results strongly support a southern hemisphere radiation of eomysticetids. Northern hemisphere eomysticetids including *Eomysticetus*, *Micromysticetus*, and *Yamatocetus* were recovered as sister to the New Zealand clade – and, for the first time, *Sitsqwayk* and *Maiabalaena* were recovered as eomysticetids.

Despite closely resembling eomysticetids in many respects, *Sitsqwayk* was formerly recovered by Peredo and Uhen (2016) as diverging one node more basally than Eomysticetidae; *Maiabalaena*, likewise, was recovered as sister to *Sitsqwayk* in the same position by Peredo et al. (2018). The diagnoses of these species are themselves taken from the synapomorphy list from their respective analyses, and these mysticetes possess many synapomorphies of Eomysticetidae, including, but not limited to: longitudinally rotated zygomatic processes; zygomatic processes lacking supramastoid crest; zygomatic processes with parallel lateral and medial margins; secondary squamosal fossa present; large squamosal prominence; ventral fossa present on zygomatic apex; zygomatic process medially bowed in dorsal view; and sharp involucral ridge of bulla (Boessenecker et al. 2023). Some of these features were acknowledged by Peredo and Uhen (2016) and Peredo et al. (2018) and otherwise described and coded incorrectly. Characters which likely pulled *Maiabalaena* and *Sitsqwayk* further stemward turned out to be miscodings (Boessenecker et al. 2023); additionally, Peredo and Uhen (2016) coded *Sitsqwayk* for eight characters where regions of the skull are completely missing (e.g. anterior rostrum and palate) or too poorly preserved to evaluate. Re-coding these characters brings these taxa back in line with prior phylogenetic studies of mysticete evolution (Boessenecker et al. 2023). However, as the ‘phylogenetic position of *Maiabalaena* is … critical to the results presented in this study’ (Peredo et al. 2018:e1), these new phylogenetic results have serious implications for our understanding of the teeth-baleen transition in Mysticeti.

Eomysticetid paleobiology, feeding morphology, tooth reduction, and the evolution of baleen

Eomysticetidae have a worldwide distribution during the Oligocene (Sanders and Barnes 2002a; Okazaki 2012; Boessenecker and Fordyce 2017b; Marx et al. 2019) and in some cases, individual eomysticetid genera had antitropical distributions (Boessenecker and Fordyce 2017b) like many extant cetaceans. Analysis of a large sample of mysticete bullae from the Oligocene of Australia and New Zealand indicates that eomysticetid specimens are more common in pelagic sediments and suggestive of offshore distribution (Marx et al. 2019). Low δ13C ratios from tympanic bullae of *Tokarahia* suggest that at least some eomysticetids undertook latitudinal migration (Clementz et al. 2014); in concert with juvenile specimens of *Waharoa ruwhenua* and *Matapanui waihao* (OU 22120; Figure 2E-H), this suggests that the relatively warm continental shelves of Zealandia served as a calving ground for eomysticetids that seasonally migrated further south toward Antarctica to feed during the austral summer (Boessenecker and Fordyce 2015a).

Early studies interpreted Eomysticetidae as the earliest toothless, baleen-bearing mysticetes (Sanders and Barnes 2002b; Boessenecker and Fordyce 2015a, 2015c), though the presence of possible alveoli suggested that vestigial teeth may have been present (Okazaki 2012; Boessenecker and Fordyce 2015a). In this scenario, eomysticetids represent a further stage in the stepwise teeth to baleen transition with the toothed Aetiocetidae possessing functional teeth and rudimentary baleen and Eomysticetidae possessing vestigial teeth and a better developed baleen rack (Deméré et al. 2008; Boessenecker and Fordyce 2015a, 2015c; Ekdale and Deméré 2022; Gatesy et al. 2022). The discovery of a possible tooth in *Tokarahia* sp., cf. *T. lophocephalus* further supported this hypothesis (Boessenecker and Fordyce 2015c).

However, later studies interpreted the mandible of *Sitsqwayk* as lacking teeth (Peredo and Uhen 2016) and that *Maiabalaena* lacked teeth and baleen (Peredo et al. 2018). Moreover, according to the supposedly unique phylogenetic position of *Maiabalaena*, this implied that mysticetes went through a toothless suction feeding stage where they also lacked baleen (Peredo et al. 2017, 2018). However, as outlined in previous studies (Ekdale and Deméré 2022; Gatesy et al. 2022), *Maiabalaena nesbittae* has a poorly preserved palate that was perhaps overinterpreted by Peredo et al. (2018). Moreover, *Maiabalaena* possesses possible alveoli and lateral palatal foramina, acknowledged in the supplemental description (Peredo et al. 2018; Ekdale and Deméré 2022; Gatesy et al. 2022). The long rostrum of *Maiabalaena* lacks suction feeding adaptations (e.g. Boessenecker et al., 2017). Lastly, *Maiabalaena* is quite clearly an eomysticetid (Boessenecker et al. 2023), and owing to its limited preservation, is no more relevant or informative than New Zealand Eomysticetidae towards the question of early feeding morphology in Mysticeti.

The best-preserved specimens of Eomysticetidae, and therefore those most relevant towards the evolution of teeth and baleen in mysticetes, are *Waharoa ruwhenua* and *Tokarahia* spp. from New Zealand, and *Yamatocetus canaliculatus* from Japan. *Waharoa ruwhenua* and *Yamatocetus* both preserve lateral palatal foramina concentrated on the posterior ¾ of the palate, which led Boessenecker and Fordyce (2015a) to propose that baleen was present posteriorly and absent at the tip of the rostrum. In both taxa, the lateral palatal foramina terminate where the alveolar groove begins to possess paired foramina interpreted as maxillary alveoli (Okazaki 2012; Boessenecker and Fordyce 2015a). It is therefore possible that the tooth-bearing part of the rostrum was completely anterior to the baleen-bearing part (Figure 2A; Boessenecker and Fordyce 2015a). The discovery of a possible tooth in *Tokarahia* further suggests the presence of teeth in Eomysticetidae (Boessenecker and Fordyce 2015c). Newly reported specimen OU 22120 includes a well-preserved ventral maxilla that is intensely vascularised, further supporting the identification of eomysticetids as baleen-bearing mysticetes (Figure 2G). Lastly, indirect evidence of filter feeding in Eomysticetidae is provided by carbon isotope analysis of the tympanic bullae of *Tokarahia* (OU 22081), which indicate that these eomysticetids were feeding quite low in the food chain and likely consuming zooplankton (Clementz et al. 2014), which argues quite strongly against suction feeding (contra Peredo et al. 2018). Altogether, Eomysticetidae appear to be broadly transitional between the Aetiocetidae and the earliest crown mysticetes.

Further anatomical structures of fossils from New Zealand provide evidence of feeding behaviour in Eomysticetidae. The rostra of *Waharoa* and *Tokarahia*, like *Eomysticetus*, indicate that the premaxilla-maxilla suture is completely open – but that the nasal and premaxilla are tightly sutured together and in turn, both are tightly sutured to the frontal. This suggests minimal dorsoventral kinesis of the rostrum but substantial longitudinal rotation or flexing of the maxilla (Boessenecker and Fordyce 2015a). The delicate odontocete-like pan bone further suggests that eomysticetids were unlikely to be capable of lunge feeding (Boessenecker and Fordyce 2015a), though this has yet to be borne out by finite element modelling. The large temporal fossa, tall sagittal and nuchal crests speak to considerable jaw closing power, in contrast to the delicate mandible (Boessenecker and Fordyce 2015a). In view of the sum of this information, and possible absence of baleen from the anterior rostrum, a skim-feeding behaviour was proposed, where the voluminous temporalis kept the long mandible oriented at the proper (but shallow) angle as the whale cruised slowly through clouds of planktonic prey (Boessenecker and Fordyce 2015a). Lunge feeding is possible, though requires modelling or analyzing the mechanical properties of the delicate mandible; further, this hypothesis is unlikely if the baleen terminated as far posteriorly as hypothesised by Boessenecker and Fordyce (2015a).

The origin and extinction of eomysticetidae

Fossils of eomysticetids are known only from the Oligocene, and the oldest known eomysticetid, *Micromysticetus*, has a maximum age of 30 Ma (Weems et al. 2016). Eomysticetids co-occur with toothed mysticetes in the North Atlantic (Coronodonidae) and North Pacific (Aetiocetidae), and more derived *Mauicetus*-grade taxa (*Mauicetus*, *Horopeta*, *Toipahautea*) in the western South Pacific. Their occurrence alongside more derived mysticetes immediately outside Crown Mysticeti suggests that eomysticetids were a relict lineage in the late Oligocene (Sanders and Barnes 2002b). However, the co-occurrence of eomysticetids further suggests that toothed mysticetes are also relict lineages; indeed, the Oligocene was a period of unusual radiation of early mysticete lineages (Marx and Fordyce 2015; Hernández-Cisneros and Velez-Juarbe 2021). The divergence of Eomysticetidae, and the clade Chaeomysticeti, likely dates to just before or after the Eocene-Oligocene boundary (mean date 35.5 Ma, Marx and Fordyce 2015). The known range of New Zealand Eomysticetidae extends from the upper Whaingaroan to basal Waitakian local stage (~28-24.2 Ma; see specimen age revisions from Sr isotope dating in Marx et al. in press). Whereas most New Zealand Eomysticetidae date to the Duntroonian stage (27.3-25.2 Ma; early late Oligocene), *Eomysticetus whitmorei* from the slightly younger Chandler Bridge Formation of South Carolina (latest Oligocene) is dated at 24.7-24.5 Ma with a minimum date of 23.5 Ma from the overlying Edisto Formation (Weems et al. 2016). More recent discoveries from New Zealand

and North Carolina (USA) suggest that eomysticetids may have persisted into the Miocene. A fragmentary skeleton with a robust atlas identified as cf. *Waharoa* dates to 23.0-22.8 Ma based on foraminifera and 87Sr/86Sr dates (Boessenecker and Fordyce 2017b), though recent excavations in the same strata at Haughs Quarry, Hakataramea, South Canterbury, have uncovered a prevalence of phenetically-similar robust atlas bones amongst specimens that lack eomysticetid features in their tympanoperiotics (Marx et al. in press). Tympanic bullae from the Oligocene-Miocene Belgrade Formation of North Carolina 25.95-21.12 Ma (Boessenecker 2022), may still suggest persistence to or just past the Oligocene-Miocene boundary. Eomysticetids disappear from the fossil record at approximately the same time as toothed mysticetes (Mammalodontidae, Aetiocetidae, Coronodonidae), late surviving archaeocetes (Kekenodontidae), and a host of archaic odontocetes ('Agorophiidae', Simocetidae, Xenorophidae; Marx et al. 2019; Boessenecker 2022). The following five million years are marked by a period of time where mysticete remains are globally rare and marine mammal assemblages are dominated by diverse odontocete assemblages; perhaps mysticetes were nearly entirely pelagic and low in population during this 'dark age' in mysticete evolution (Marx et al. 2019).

Acknowledgments

First and foremost, we thank the late R.E. Fordyce for his mentorship and unparalleled stewardship of fossil vertebrates from Zealandia. Thanks to S. White and the late A. Grebneff for herculean preparation efforts at OU. This study was permitted by field studies and preparation funding thanks to a doctoral scholarship awarded to RWB and grants to R.E. Fordyce from the National Geographic Society, New Zealand Lottery Board, Natural History New Zealand, U. Otago Research Committee, former New Zealand University Grants Committee, and U. Otago Geology Head of Department and PBRF funds. Thanks to the editors (C. Loch, D. Thomas, J. Robinson) for inviting us to contribute to this volume. Lastly, reviews from E.M.G. Fitzgerald and Y. Tanaka improved this study.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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