

Like phoenix from the ashes: How modern baleen whales arose from a fossil “dark age”

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The evolution of baleen whales (Mysticeti), the largest animals on Earth, was punctuated by a pivotal turnover event. Following their emergence around 36 million years (Ma), mysticetes diversified into a disparate range of toothed and toothless species until 23 Ma, but then nearly vanished from the global fossil record for the next five million years. Following this early Miocene “dark age”, toothless mysticetes spectacularly reappeared around 18–17 Ma, whereas toothed mysticetes had gone entirely extinct. Here, we suggest that this turnover event reflects a change in mysticete habitat occupancy. Using the well-sampled record of Australasia as a case study, we show that Oligocene pre-“dark age” mysticetes formed distinct coastal and offshore assemblages, dominated by small (2–4 m), ecologically disparate toothed species, and larger (5–6 m) toothless filter feeders, respectively. Environmental change around the Oligocene–Miocene boundary led to the decline of the endemic coastal assemblages, leaving nearshore deposits virtually devoid of mysticetes. Filter feeders persisted offshore and subsequently re-invaded coastal habitats during the mid-Miocene Climatic Optimum, thus establishing the modern, cosmopolitan mysticete fauna.

Key words: Mammalia, Mysticeti, evolution, Oligocene, Miocene, Zealandia, Australia.

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Introduction

Baleen whales (Mysticeti) are the largest animals on Earth. Unlike all other cetaceans, extant mysticetes are completely toothless, and instead rely on a comb-like keratinous filter, baleen, to strain small prey directly from seawater (Pivorunas 1979). Filter feeding enables whales to tap into vast food sources at a relatively low trophic level, and has turned them into major consumers and ecosystem engineers (Roman et al. 2014). In the North Pacific, for example, pre-whaling populations of extant mysticetes consumed as much as 10% of total net primary productivity (Croll et al. 2006).

The evolution of mysticetes from their archaeocete ancestors is becoming increasingly better documented, and reveals a stepwise morphological shift from toothed raptorial feeders to toothless suction and/or filter feeders (Deméré

et al. 2008; Marx et al. 2016a; Geisler et al. 2017). During this transition, lasting from the origin of mysticetes around 36 Ma (Lambert et al. 2017) to the end of the Oligocene (23 Ma), filter feeders were just one of several ecomorphs, and by no means dominant. Instead, mysticetes evolved into a wide range of toothed and toothless forms (Barnes et al. 1995; Fitzgerald 2006, 2010; Tsai and Fordyce 2015; Marx et al. 2016a; Boessenecker and Fordyce 2017a; Geisler et al. 2017), leading to high levels of morphological disparity that have never been matched since (Marx and Fordyce 2015). This disparate golden age of baleen whale evolution was not to last.

Baleen whales abruptly vanish from the fossil record near the Oligocene–Miocene boundary, marking the beginning of an as yet unexplained 5 million-year-long “dark age” in their evolution. During this time, mysticetes are

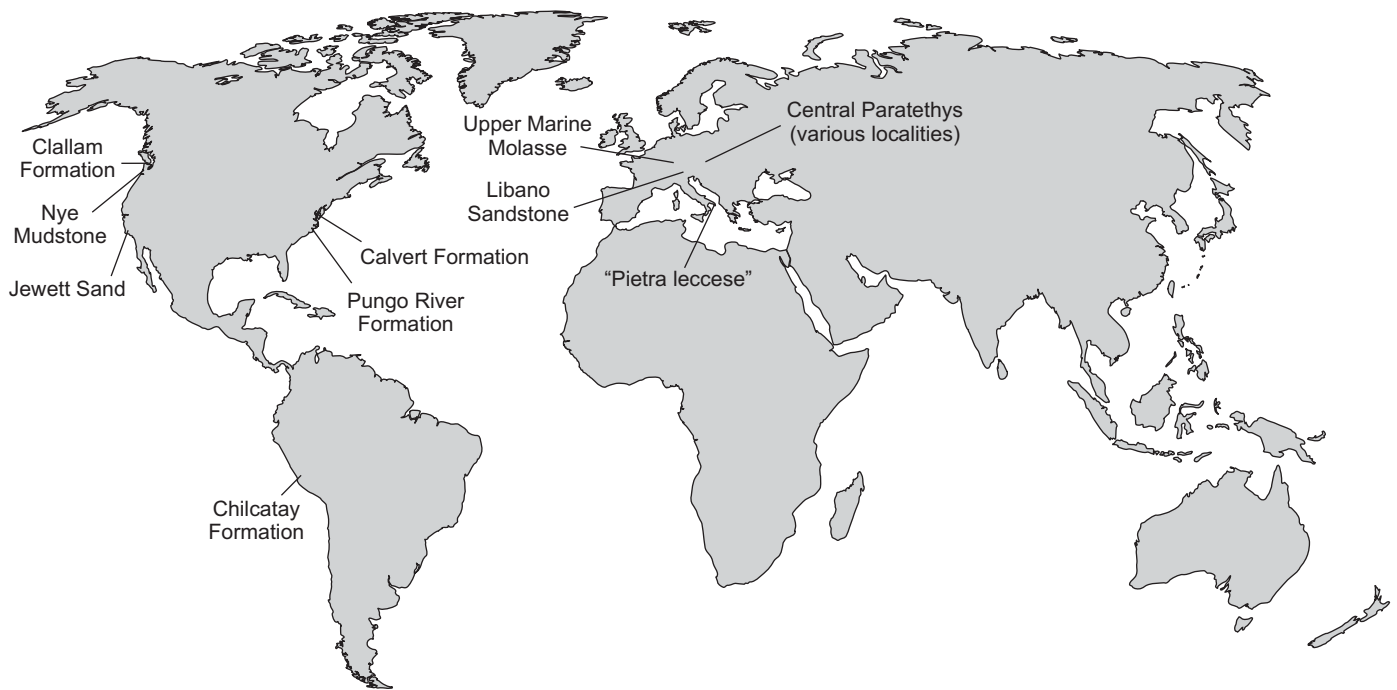


Fig. 1. Location of major formations that have yielded diverse odontocete assemblages, but few or no mysticetes. Sources: Clallam Formation, Nye Mudstone, and Jewett Sand (Barnes 1977; Crowley et al. 1999); Calvert Formation (Gottfried et al. 1994); Pungo River Formation (Whitmore and Kaltenbach 2008); Chilcatay Formation (Bianucci et al. 2018); Upper Marine Molasse (Pilleri 1986a, b); Libano Sandstone and "Pietra leccese" (Bianucci and Landini 2002); Central Paratethys (Grigorescu and Kazár 2006).

virtually absent even from deposits where other cetaceans (Odontoceti) abound, such as (i) the Chilcatay Formation of Peru (Di Celma et al. 2018); (ii) the Pungo River and lower Calvert formations of the United States East Coast (Gottfried et al. 1994; Whitmore and Kaltenbach 2008); and various formations across (iii) the Mediterranean basin (Bianucci and Landini 2002), the (iv) western and central Paratethys (Pilleri 1986a, b; Grigorescu and Kazár 2006); and (v) the western United States (Barnes 1977; Crowley et al. 1999; Goedert et al. 2007) (Fig. 1). This pattern is striking, considering that mysticetes are common in, and sometimes even dominate, Oligocene assemblages (Barnes et al. 1995; Fordyce 2006; Goedert et al. 2007).

Toothless baleen whales (Chaemysticeti) finally re-appeared around 18–17 Ma, in the form of abundant, widespread, and comparatively large taxa that dominate middle Miocene assemblages across the Atlantic and Pacific basins (Gottfried et al. 1994; Otsuka and Ota 2008; Bisconti et al. 2013; Di Celma et al. 2017). Toothed mysticetes, by contrast, had gone entirely extinct. The early Miocene "dark age" thus marks a major turning point in baleen whale evolution: prior to it, mysticetes were relatively small, disparate, and included raptorial, suction and filter feeders; after it, only large, cosmopolitan filter feeders remained—a situation that has remained constant to this day, and defines the modern baleen whale fauna.

Here, we suggest that the early Miocene "dark age", and the ensuing dominance of filter feeders, reflect a concurrent shift in mysticete habitat occupancy. Specifically, we predict that Oligocene toothed mysticetes retained closer ties to

the coast than their toothless cousins, which in turn would have limited their geographical range and increased their susceptibility to environmental perturbations. Selective extinction of nearshore assemblages may explain the temporary absence of baleen whales from the early Miocene fossil record, with pelagic filter feeders persisting, but being poorly represented owing to their remote habitat. Modern mysticetes would ultimately have arisen from this pelagic stock, as reflected in the dominance of filter feeders following the end of the "dark age".

Geological setting

To test the idea that Oligocene toothed mysticetes were primarily coastal, we focus on a globally informative case study: the late Oligocene fossil records of Victoria (Australia) and southern New Zealand. Both regions were located at similar palaeolatitudes, and preserve substantial coeval, well-dated (Graham et al. 2000; McLaren et al. 2009; Tanaka and Fordyce 2016; Korasidis et al. 2018) and richly fossiliferous late Oligocene deposits (Fitzgerald 2004; Boessenecker and Fordyce 2017a; Tsai and Fordyce 2018). The latter primarily include the Jan Juc Marl, Point Addis Limestone, and Waurn Ponds Limestone of Australia (Holdgate and Gallagher 2003; Piper et al. 2006); and the Otekaike Limestone and Kokoamu Greensand of New Zealand (Thompson et al. 2014).

Whereas the Australian strata formed in a relatively warm, restricted bay along a continental margin (Holdgate

and Gallagher 2003), the nearby continental block of Zealandia was largely submerged during the late Oligocene. The remaining archipelago was far removed from any major landmass, and surrounded by cool- to temperate-water carbonate ramps that were broadly exposed to the open ocean (Thompson et al. 2014). This unique situation—extensive sediment accumulation in an offshore setting, now broadly exposed on land—singles out New Zealand from all other coeval cetacean localities globally, every one of which was located close to a major landmass. Taken together, Australia and New Zealand thus permit an unparalleled comparison of nearshore vs. open marine late Oligocene assemblages.

Material and methods

Both southern Victoria and the South Island of New Zealand have been consistently prospected as part of long-term field-work programmes at the University of Otago (OU; Dunedin, New Zealand) and Museums Victoria (NMV; Melbourne, Australia). Both are currently led by two of the authors (REF and EMGF), with a focus on the fossil-rich regions of North Otago, South Canterbury, and coastal Victoria. Tympanic bullae (ear bones), in particular, have always been collected when encountered, irrespective of their association with other elements or state of preservation. Both programmes have amassed a substantial number of specimens, many of which have recently been (re)described (Fitzgerald 2006, 2010; Boessenecker and Fordyce 2015a–c, 2017a; Tsai and Fordyce 2015, 2016, 2018; Fordyce and Marx 2016). Nevertheless, the majority have so far remained unreported, thus preventing a comprehensive species-level assessment of the two assemblages.

We quantified the number of mysticete fossils from both regions by counting the total number of tympanic bullae currently held at public institutions (see SOM: table 1, Supplementary Online Material available at http://app.pan.pl/SOM/app64-Marx_etal_SOM.pdf). We focussed on bullae because of their high diagnostic value and relative abundance. Most of the specimens were isolated finds and counted as a single data point, irrespective of whether they were left or right. This approach maximises the use of available material, but carries the risk of recording individuals twice. Given the considerable time scales and areas involved, however, we judge double-counting to be minimal. Where bullae formed part of articulated specimens, only one side was counted.

To determine assemblage structure, we used diagnostic morphological characters to identify all bullae to one of three higher taxa: (i) Mammalodontidae, a family of small, tooth-bearing raptorial and/or suction feeders with a total body length of around 3 m (Fitzgerald 2010); (ii) Eomysticetidae, a basal clade of toothless suction and/or filter feeders reaching 4–6 m (Boessenecker and Fordyce 2017a); and (iii) other, more crownward chaeomysticetes, all of them likely filter feeders and generally reaching lengths

of 5–7 m (Tsai and Kohno 2016; Slater et al. 2017; Fordyce and Marx 2018). See SOM for details.

Finally we calculated the contribution (in %) of each group to the Australian and New Zealand records, and then tested for differences in the relative counts by means of a two-way chi-square test, using PAST 3.14 (Hammer et al. 2001). This approach focuses solely on proportions, rather than absolute abundance or taxonomic diversity, and should therefore be robust to potential sampling biases. Crucially, the basic nearshore/offshore contrast between New Zealand and Australia persisted throughout the late Oligocene, thus also minimising the effects of time averaging.

Results and discussion

Coastal vs. offshore assemblages.—We counted 67 tympanic bullae from Australia and 48 bullae from New Zealand (SOM: table 1). The Australian late Oligocene record is dominated by mammalodontids, with eomysticetids a distant second, and other chaeomysticetes being barely detectable (Fig. 2). By contrast, chaeomysticetes comprise most of the New Zealand assemblage, with eomysticetids contributing roughly one quarter, and mammalodontids only 4%. This pronounced difference in composition is statistically significant ($\chi^2 = 77.744$, $p < 0.001$), and suggests the presence of distinct regional assemblages.

Given the geographical proximity of Australia and New Zealand, the marked divergence of their late Oligocene mysticete assemblages is best explained by environmental variation, namely, exposure to the open ocean and distance from the nearest major landmass. Specifically, the small-bodied mammalodontids seemingly were restricted to nearshore settings around Australia, where heterogeneous habitats allowed them to diversify into a disparate assemblage of raptorial and suction feeders. By contrast, larger filter feeding chaeomysticetes inhabited pelagic waters, allowing them to range around and beyond the archipelago of Zealandia.

The small number of chaeomysticetes from Australia likely represent occasional visitors, or else carcasses washed in from the open sea. Their low proportion is consistent with extant cetacean stranding records, which are generally dominated by nearshore species. Thus, in the North Pacific, pelagic taxa like balaenopterids and ziphiids constitute $\leq 2\%$ of local death assemblages (Pyenson 2010). Eomysticetids occurred in both coastal and offshore settings, but were more abundant in the latter (15% vs. 23%). Unlike the purely Australasian mammalodontids (but see Bianucci et al. 2011; Shipps et al. 2018), they also enjoyed a global distribution (Boessenecker and Fordyce 2017a). Eomysticetids thus may have been pelagic, albeit somewhat intermediate in terms of their geographical range and habitat preference.

There are no comparable Oligocene offshore records that would allow a similar analysis elsewhere. Nevertheless, assemblages consistent with our Australasian scenario oc-

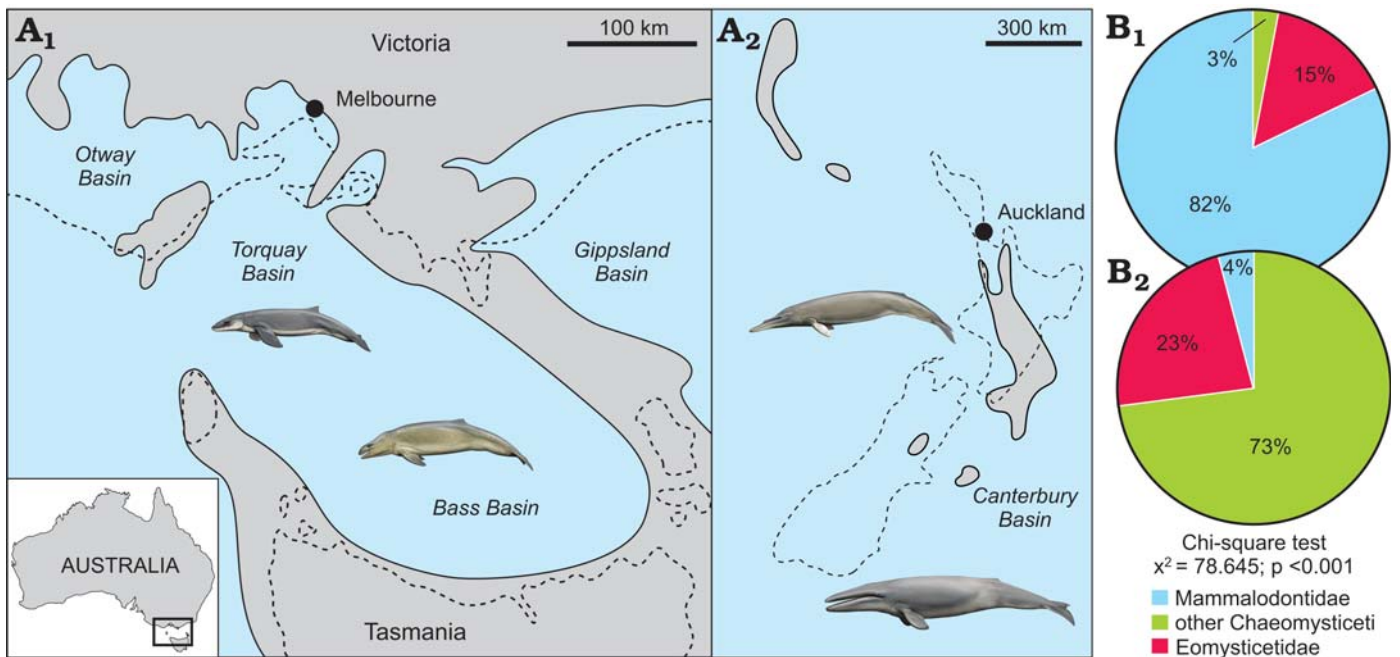


Fig. 2. Comparison of Australasian late Oligocene baleen whale assemblages: south-eastern Australia (A₁, B₁) and New Zealand (A₂, B₂). **A.** Late Oligocene palaeogeographical reconstruction. **B.** Differences in mysticete assemblage composition. Note the widespread inundation of New Zealand. Dashed lines in A delineate the modern coastline without compensating for late Neogene Alpine Fault movement. Palaeogeographical reconstructions are based on King et al. (1999), King (2000), Holdgate and Gallagher (2003). Drawings of whales by Carl Buell.

cur worldwide. Thus, other small toothed mysticetes (aetiocetids and *Coronodon*) inhabited the margins of the major landmasses of Japan (Barnes et al. 1995), western North America (Barnes et al. 1995; Marx et al. 2015), and the United States East Coast (Geisler et al. 2017). Most of these localities have also yielded either eomysticetids (Okazaki 2012; Boessenecker and Fordyce 2017a; Hernández Cisneros et al. 2017), or similar species (e.g., *Maiabalaena*, *Sitsqwayk*, *Tlaxcallicetus*) resembling eomysticetids in their size, archaic morphology, and basal phylogenetic position (Peredo and Uhen 2016; Hernández Cisneros 2018; Peredo et al. 2018). Other, more crownward, chaemysticetes are generally rare. We therefore suggest that marked divisions between coastal and offshore assemblages existed globally, even though the composition of each assemblage varied between ocean basins.

The early Miocene “dark age”.—Around the Oligocene–Miocene boundary (ca. 24–23 Ma), baleen whales seemingly vanish from the global fossil record, heralding a 5-million-year long global “dark age” in their evolution (Bianucci et al. 2018). In the few places where mysticetes do occur, such as the ca. 20 Ma Gaiman Formation (Patagonia, Argentina), only chaemysticetes located crownward of Eomysticetidae are present (Cabrera 1926). The only exception to this pattern is a single, fragmentary eomysticetid from the earliest Miocene of New Zealand (Boessenecker and Fordyce 2017b).

Unlike mysticetes, odontocetes never disappear, which rules out taphonomy as a likely explanation for the “dark

age”. Likewise, a previously suggested decrease in global diatom-based productivity (Bianucci et al. 2018) seemingly occurred too late (ca. 22–21 Ma) to have acted as a trigger (Renaudie 2016). Instead, we suggest that the demise of archaic mysticetes had an abiotic cause, such as the >0.5 shift in $\delta^{18}\text{O}$ coinciding with the Oligocene–Miocene boundary (Zachos et al. 2008), and/or the pronounced 40 m drop in global sea level around 25–24 Ma (Miller et al. 2005) (Fig. 3). The latter seems especially significant, as it reached levels not previously experienced by any cetacean, nor subsequently seen again until the latest Miocene.

Restriction to the coast likely promoted endemism, which, along with foraging at a comparatively higher trophic level (Clementz et al. 2014), limited the population sizes of toothed mysticetes, and increased their susceptibility to environmental perturbations. Loss of shallow-water habitats in response to falling sea levels would furthermore have directly impacted coastal species, and may have been a major factor in their decline. The disappearance of the more pelagic eomysticetids is harder to explain. Their occurrence in coastal waters may hint at a somewhat limited geographical distribution, plausibly increasing their sensitivity to environmental change. Alternatively, their demise may simply have been a result of their relatively low overall abundance (15–23%).

As coastal (toothed) mysticetes declined, vacant niches were filled by a variety of diversifying odontocetes, resulting in marked faunal turnover. Both direct competition and opportunistic replacement may have contributed to this pattern, with echolocation plausibly providing odontocetes

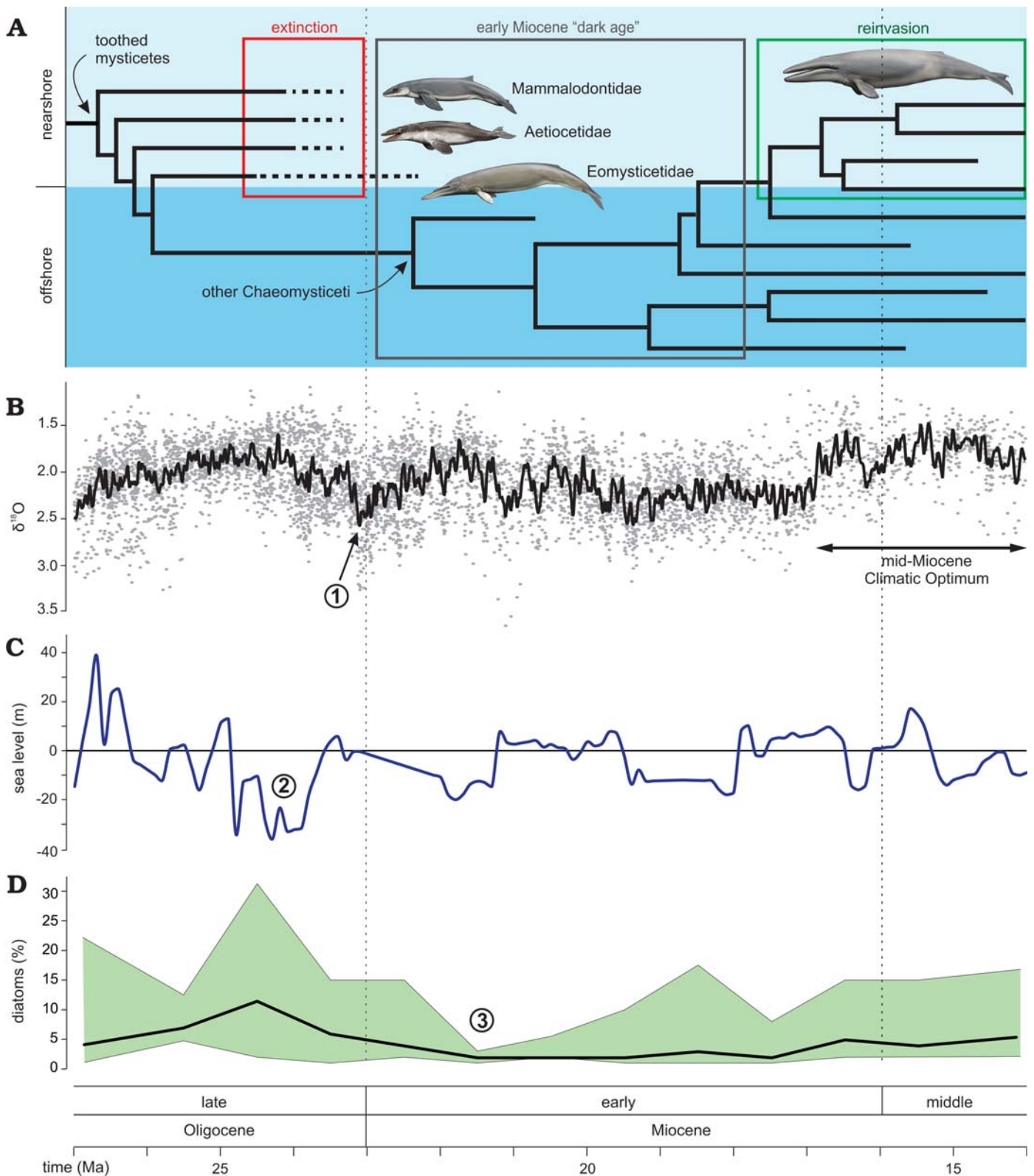


Fig. 3. Patterns and potential drivers of the early Miocene “dark age”. **A**. Extinction of toothed mysticetes and eomysticetids at the beginning of the early Miocene “dark age”, and subsequent reinvansion of coastal habitats by larger, toothless filter feeding mysticetes during the middle Miocene. The occurrence of eomysticetids in the earliest Miocene is based on a single, fragmentary specimen from New Zealand (Boessenecker and Fordyce 2017b). **B**. Global oxygen isotope curve, showing the timing of the mid-Miocene Climatic Optimum (Zachos et al. 2008). **C**. Global sea-level change (Miller et al. 2005). **D**. Global diatom abundance as derived from Deep-Sea Drilling Programme/Ocean Drilling Programme smear slides (Renaudie 2016). Highlighted events potentially relevant to the “dark age”: 1, a 0.5 shift in $\delta^{18}O$; 2, a 40 m sea-level fall; and 3, an early Miocene decrease in global diatom abundance. Reconstructions of mysticetes by Carl Buell.

with a competitive advantage. Nevertheless, we consider opportunistic replacement to be more likely, given that (i) toothed mysticetes and odontocetes had previously existed and diversified alongside each other for some 13 million years (Marx et al. 2016b); (ii) this long period of coexistence was possible despite the early emergence of sophisticated echolocation (Geisler et al. 2014); and (iii) certain odontocete lineages, such as xenorhids, also seemingly disappeared during the “dark age”.

In light of these observations, we suggest that early Miocene environmental change equally affected both mysticetes and odontocetes, with endemic coastal assemblages being under the greatest pressure. Toothed mysticetes were the first to disappear in response, perhaps because they were fewer in number, or less ecologically versatile. By contrast, echolocating odontocetes were diverse and/or adaptable enough to weather the changes, and subsequently (re) invaded the newly vacant regions of nearshore ecospace. Unlike their coastal counterparts, pelagic mysticetes could range more widely, and thus benefitted from access to more varied habitats and scattered, but richly concentrated, prey. They persisted through the early Miocene, but, with few exceptions, are poorly represented in the mostly nearshore sedimentary record. Where they do occur, they seem to be associated with relatively open-water facies, consistent with a more pelagic habitat (Cuitiño et al. 2019).

The origin of the modern mysticete fauna.—Baleen whales spectacularly re-emerge in the fossil record close to the early–middle Miocene boundary, around 18–17 Ma (Gottfried et al. 1994; Kimura and Ozawa 2002; Otsuka and Ota 2008; Bisconti et al. 2013; Di Celma et al. 2017). The abruptness of this reappearance is best seen in locations with sequential early and middle Miocene exposures, such as the Calvert Formation of the eastern United States (Vogt and Parrish 2012; Vogt et al. 2018), and the Chilcatay–Pisco formations of Peru (Di Celma et al. 2017; DeVries and Jud 2018; Bianucci et al. 2018). In both cases, early Miocene strata virtually devoid of mysticetes are followed by middle Miocene beds in which baleen whales are abundant, or even dominant (Gottfried et al. 1994; Di Celma et al. 2017; Bianucci et al. 2018). Crucially, all middle Miocene baleen whales are toothless filter feeders, with no trace of the ecologically disparate coastal assemblages that existed during the Oligocene.

The sudden abundance of middle Miocene mysticetes might be explained by a reinvasion of coastal habitats by pelagic filter feeders, perhaps associated with the onset of the mid-Miocene Climatic Optimum (Zachos et al. 2008). Because of their offshore origins, these new arrivals were not only larger (5–8 m long) than their Oligocene predecessors, but also more uniform in their feeding style and widespread in their distribution. In particular, globally occurring taxa like *Parietobalaena* (Kellogg 1968; Otsuka and Ota 2008; Bisconti et al. 2013) and *Pelocetus* (Kellogg 1965; Kimura et al. 2007; Di Celma et al. 2017) seem to herald the onset of

mysticete cosmopolitanism. Considering the profound ecological impact of extant whales (Roman et al. 2014), it is tempting to speculate that this proliferation of large filter feeders also had a lasting effect on ocean ecology, e.g., in the form of increased prey consumption (Croll et al. 2006), more numerous whale falls (Smith and Baco 2003; Pyenson and Haasl 2007), and elevated rates of vertical nutrient transfer (the “whale pump”) (Roman and McCarthy 2010).

The reinvasion of coastal habitats may have triggered a renewed diversification of mysticetes, perhaps giving rise to the speciose and relatively small-bodied cetotheriids (Gol'din 2018). Nevertheless, baleen whales never again attained the high levels of ecomorphological disparity that existed during the Oligocene (Marx and Fordyce 2015). Instead, the basic characteristics of this new cosmopolitan fauna—obligate filter feeding, comparatively large body size, and wide geographical range—remained largely constant, and continue to define mysticetes to this day. In this light, the early Miocene “dark age” represents a crucial turning point, which marks the rise of the modern mysticete fauna from the ashes of its disparate Oligocene past.

Conclusions

The evolution of baleen whales was punctuated by a major turnover event that resulted in a 5 million-year-long “dark age” in their global fossil record. This turnover event was plausibly driven by environmental change, and led to the disappearance of coastal assemblages composed of small, ecologically disparate species. Offshore assemblages dominated by larger filter feeders persisted, but remain cryptic in the fossil record owing to their remote habitat. Around the time of the mid-Miocene Climatic Optimum, pelagic species reinvaded nearshore waters, thereby establishing the modern, cosmopolitan mysticete fauna.

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