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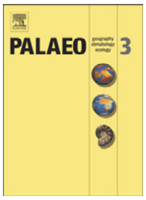

Ancient marine isoscapes and isotopic evidence of bulk-feeding by Oligocene cetaceans

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ABSTRACT

The first appearance and evolution of the crown group Cetacea – Mysticeti (baleen whales) and Odontoceti (toothed whales and dolphins) – from archaeocete ancestors corresponds with major climatic and oceanographic changes shortly before the Eocene–Oligocene boundary (ca. 34.0 Ma). These environmental changes impacted marine productivity and may have sparked the evolution of the distinct bulk-feeding strategy used by mysticete whales today. The movements and feeding habits of living cetaceans can be tracked using the isotopic composition of the structural carbonate within bioapatite of their bones and teeth, which records latitudinal gradients in marine $\delta^{13}C$ and $\delta^{18}O$ values. Here, we exploit this relationship to determine the past movements and feeding habits of late-surviving archaeocetes (kekenodontids) and early odontocetes and mysticetes sampled from Oligocene fossil sites in the USA (latitude: ~30°N) and New Zealand (latitude: ~50°S). Bioapatite $\delta^{13}C$ and $\delta^{18}O$ values for fossilized tooth enamel and bullae from fossil cetaceans were surprisingly similar to those for living cetaceans, which indicates that the feeding habits of these species and the isotopic composition of Oligocene seawater (ca. 28 Ma) were very close to present-day conditions. Values for toothed mysticetes and odontocetes match expectations based on cetacean species feeding at these latitudes today, suggesting these individuals were residents that foraged in close proximity to where their fossils were discovered. In contrast, the extremely low $\delta^{13}C$ and $\delta^{18}O$ values for some edentulous mysticetes from New Zealand are more similar to values observed in extant mysticetes that seasonally migrate to high latitudes, where they bulk-feed on lipid-rich zooplankton. Enamel $\delta^{13}C$ values for kekenodontids showed the greatest range and overlapped with both edentulous mysticetes and resident species; these differences correlate most strongly with tooth type and may reflect an ontogenetic shift in diet associated with the transition from nursing to marine prey. When combined with evidence of increasing morphological disparity, fossil bioapatite $\delta^{13}C$ and $\delta^{18}O$ values support interpretations that the Oligocene was an interval of heightened taxonomic and ecological diversification within Cetacea.

1. Introduction

The emergence of modern cetaceans (whales, dolphins and porpoises) at the close of the Eocene (ca. 34.0 Ma) marks a major advance in the feeding strategies used by marine cetaceans (Fordyce, 2003). Prior to the appearance of crown Cetacea (Neoceti), early cetaceans of the paraphyletic group Archaeoceti were primarily piscivorous (Swift and Barnes, 1996; O'Leary and Uhen, 1999; Thewissen et al., 2007) and captured prey by raptorial snap-feeding, which is an effective method for securing slippery prey. Many modern cetaceans still use this feeding style, but most have developed additional or alternative feeding strategies that are associated with the divergence of modern cetaceans into the Odontoceti (toothed whales, dolphins, porpoises) and Mysticeti (baleen whales) (Fig. 1). Odontocetes maintained the dietary focus of their archaeocete ancestors by favoring individual prey items hunted with the use of echolocation, while mysticetes followed a different path and evolved baleen for efficient bulk filter-feeding on shoals of small, but abundant prey (zooplankton, schooling fish and squid). This feeding style, which involves engulfing large quantities of small prey that are strained from seawater within the oral cavity, is, within Cetacea, unique to the Mysticeti (Croll et al., 2009). Though a few species of pinnipeds and sea birds are known to consume zooplankton as part of their diet (Croll et al., 2009), none are as committed to this diet as the mysticetes, which are suspected to have evolved this method of feeding only once in the past (Deméré et al., 2008).

Along with changes in feeding morphologies, the postcrania of late Eocene and Oligocene cetaceans exhibit increasing modification towards a streamlined fusiform body plan, which aided in more

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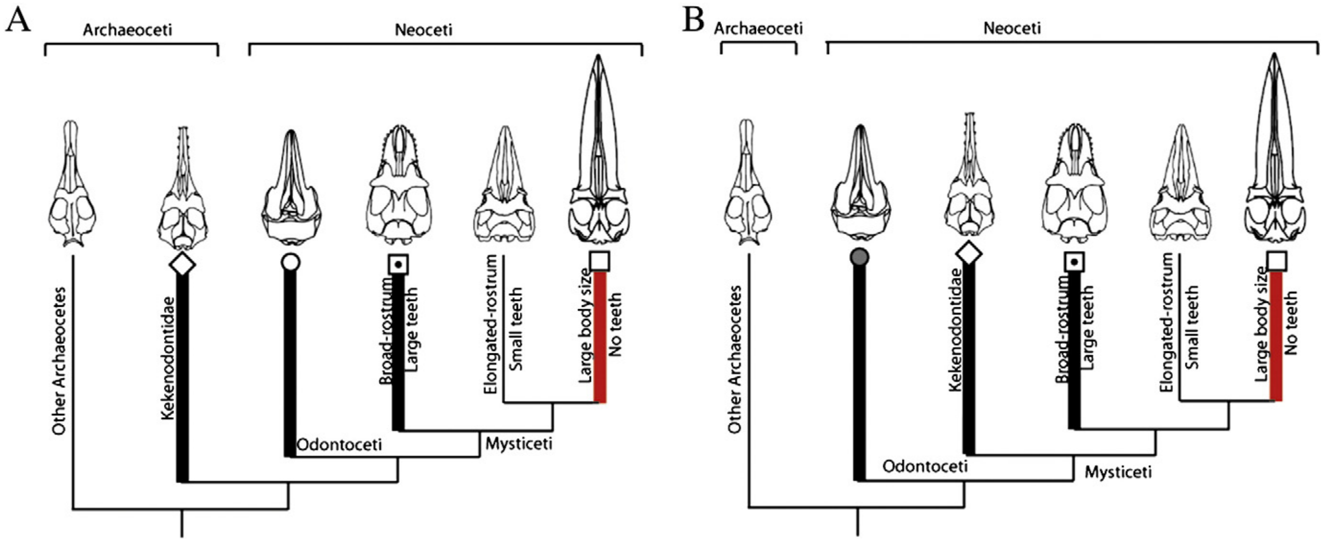

Fig. 1. Two possible phylogenies for the Cetacea that place Kekenodontidae (A) outside or (B) inside Neoceti: Mysticeti. Thick lines indicate groups included in this project and red lines identify groups with isotopic evidence for filter-feeding on zooplankton. Symbols for groups match symbols used in Fig. 7. Phylogenies are modified from those presented in Fitzgerald (2006).

efficient swimming. Of particular note was the neomorphic evolution of tail flukes and vertically-oscillating caudal propulsion by the Pelagiceti (Basilosauridae + Neoceti) (Uhen, 2008a). These modifications allowed cetaceans to become fully aquatic, and to colonize pelagic waters worldwide. Support for this model of functional shift/ geographic spread comes from the spatial distribution of cetacean fossils: from an early Eocene origin in the Indo-Pakistan region, cetaceans spread outward, achieving a southern temperate distribution (Köhler and Fordyce, 1997) and expanding into the tropical eastern Pacific (Uhen et al., 2011) by the late middle Eocene (Bartonian), and then extending to near-polar in the Priabonian (Mitchell, 1989; Uhen, 2010). Fluke-propelled pelagic cetaceans could exploit widely spaced, highly productive areas of upwelling — oceanic features that were, in turn, enhanced as ocean circulation patterns and global climate changed in response to the opening of the Southern Ocean and establishment of permanent ice on Antarctica (Berger, 2007; Pagani et al., 2011). Today, productivity at upwelling zones is often seasonally variable, especially at high latitudes (Bost et al., 2009); accordingly, mysticete whales generally move to temperate waters when productivity declines in the winter (MacKintosh, 1965). Enhanced polar-to-tropical temperature gradients and regions of upwelling were established by the Oligocene (Coxall and Pearson, 2008; Katz et al., 2008) and the morphological adaptations of pelagicetes would have allowed them to take full advantage of the seasonally abundant resources that these conditions produced.

The fossil record and phylogenetic patterns among Cetacea (Fitzgerald, 2006; Uhen, 2010; Marx, 2011) indicate a rapid diversification of Neoceti from the latest Eocene onwards, linked to large-scale changes in productivity (Fordyce, 2003; Lindberg and Pyenson, 2007; Marx and Uhen, 2010) that attest to the importance of physical drivers in Neoceti history. Previously, Neoceti were thought to have exploited the progressively-modernizing Oligocene oceans, with Archaeoceti displaced rapidly by mysticetes and odontocetes (Fordyce and Barnes, 1994). It is now clear, however, that archaeocete-like cetaceans typified by the genus *Kekenodon* Hector, 1881 coexisted with late Oligocene Odontoceti and Mysticeti in New Zealand and probably beyond: thus, archaeocetes were not simply displaced by Neoceti (Fig. 1) early in the Oligocene. Opinions have varied as to the affinities of *Kekenodon* because of the fragmentary nature of the type material for *Kekenodon onamata*. The species has sometimes been considered a basal mysticete (Fordyce and Barnes, 1994; Barnes and Sanders, 1996; Fordyce and de Muizon, 2001), but recently-recognized skulls of *Kekenodon*-like taxa are of archaeocete design, without the apomorphies of Mysticeti or Odontoceti (Fig. 2). Fordyce (2002) placed *Kekenodon*-like cetaceans as a sister clade to Neoceti. Thus, *Kekenodon* and relatives are taken to represent late-surviving archaeocetes (Fordyce, 2002; Uhen, 2008b), and our working hypothesis is that they constitute the taxon Kekenodontidae (on taxonomic rank, see Fordyce and Barnes, 1994).

Regarding morphological characteristics related to feeding ecology, kekenodontids lack the skull modifications sometimes linked with bulk-feeding in early toothed mysticetes (Fig. 2); for example, the posterior of the attenuated rostrum is steep-sided, without a laterally-produced flange of maxilla, the cheek-teeth are vertically inserted and in a row, the palate has embrasure pits, the palate lacks extensive vascular foramina, the rostral bones are firmly sutured, rather than loose, and the mandibular symphysis is elongate. As in late Eocene dorudontine archaeocetes (e.g., *Dorudon*), the

Fig. 2. Well-preserved and nearly complete kekenodontid skull: Tokarahi-Island Cliff skull of *Kekenodon* sp., OU22294 — top: dorsal, middle: left lateral, and bottom: ventral.