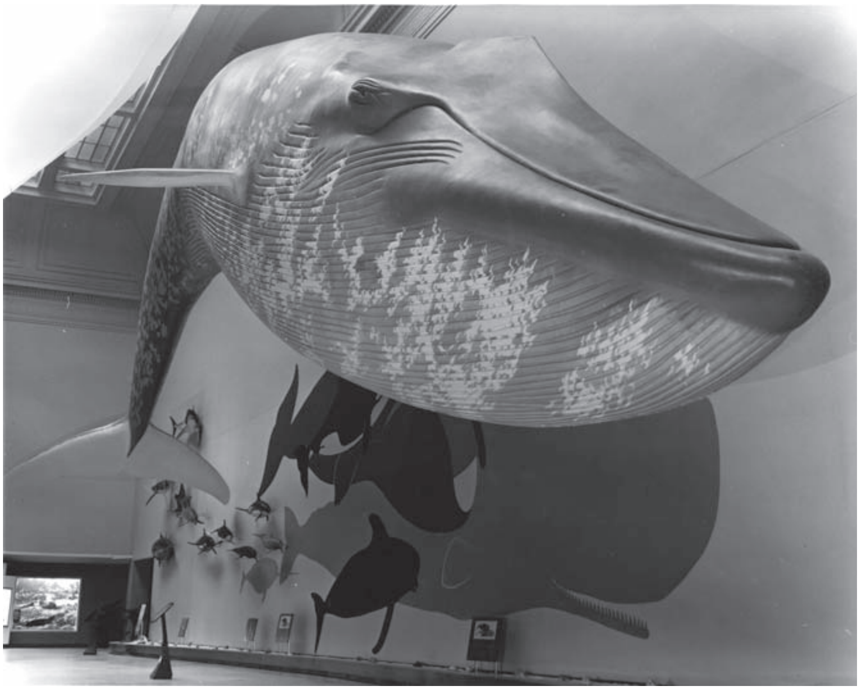

Figure 2 *The full-size model of a blue whale that was mounted at the National Museum of Natural History in Washington, DC.*

References

Conover, A. (1996). The object at hand. *Smithsonian* **27**(7), 28, 30, 31.

Dalebout, M. L., van Helden, A., van Waerebeek, K., and Baker, C. S. (1998). Molecular genetic identification of southern henmisphere beaked whales (Cetacea: Ziphiidae). *Mol. Ecol.* **7**, 687–694.

Fraser, F. C. (1974). "Report on Cetacea Stranded on the British Coasts from 1948 to 1966." British Museum (Natural History), London.

Mysticetes, Evolution

Annalisa Berta and Thomas A. Deméré

I. Introduction

The fossil record of mysticete cetaceans is rapidly improving and the origin and diversification of this highly specialized mammalian group is coming into focus. Crown mysticetes (i.e., extant baleen whales of the families Balaenidae, Neobalaenidae, Balaenopteridae, and Eschrichtiidae) are edentulous as adults, but possess deciduous teeth that are resorbed prior to birth. This ontogenetic pattern reflects an ancestral ontogeny in which fully formed teeth were retained into adulthood. Archaic baleen whales include stem mysticetes, both toothed and toothless, that do not belong to extant families. Toothed mysticetes first evolved in the late Eocene or earliest Oligocene, diversified in the late Oligocene, and appear to have been extinct before the Miocene began. They do not constitute a monophyletic group. Stem edentulous mysticetes are first reported from the late Oligocene coincident with the radiation of toothed forms, but are not diverse until the Miocene. Although contested, it is likely that most, if not all, archaic mysticetes possessed some form of baleen in the upper jaw. This key filter feeding innovation permitted exploitation of a new niche and heralded the evolution of modern baleen whales, the largest animals on Earth.

II. Toothed Mysticetes

As currently understood, toothed mysticetes are grouped into four families: Llanocetidae, Mammalodontidae, and Janjucetidae from the Southern Ocean and Aetiocetidae, from the North Pacific. To date no toothed mysticetes are known from the Atlantic region. The retention of an adult dentition in toothed mysticetes is the primitive condition seen in basilosaurid "archaeocetes" and stem odontocetes. The degree of telescoping of the skull is also primitive with little interdigitation of rostral and cranial elements. Consequently, there is a long intertemporal exposure of the frontal and parietal on the cranial vertex. In addition, the supraorbital processes of the frontals retain an elevated position on the cranium, and the external narial opening ("blowhole") is only midway between the tip of the rostrum and the orbit. Derived features of toothed and later mysticetes include transverse expansion of the descending process of the maxilla to form an edentulous infraorbital plate, loss of a bony mandibular symphysis, and thin lateral margins of the maxillae.

The geologically oldest purported mysticete is *Llanocetus denticrenatus* from the late Eocene or early Oligocene of the Antarctic Peninsula. Although only a portion of the mandible and an endocranial cast have been described, the holotype also includes a nearly complete skull and partial skeleton under study by Ewan Fordyce. Despite its antiquity, *Llanocetus* was a large whale with a skull length

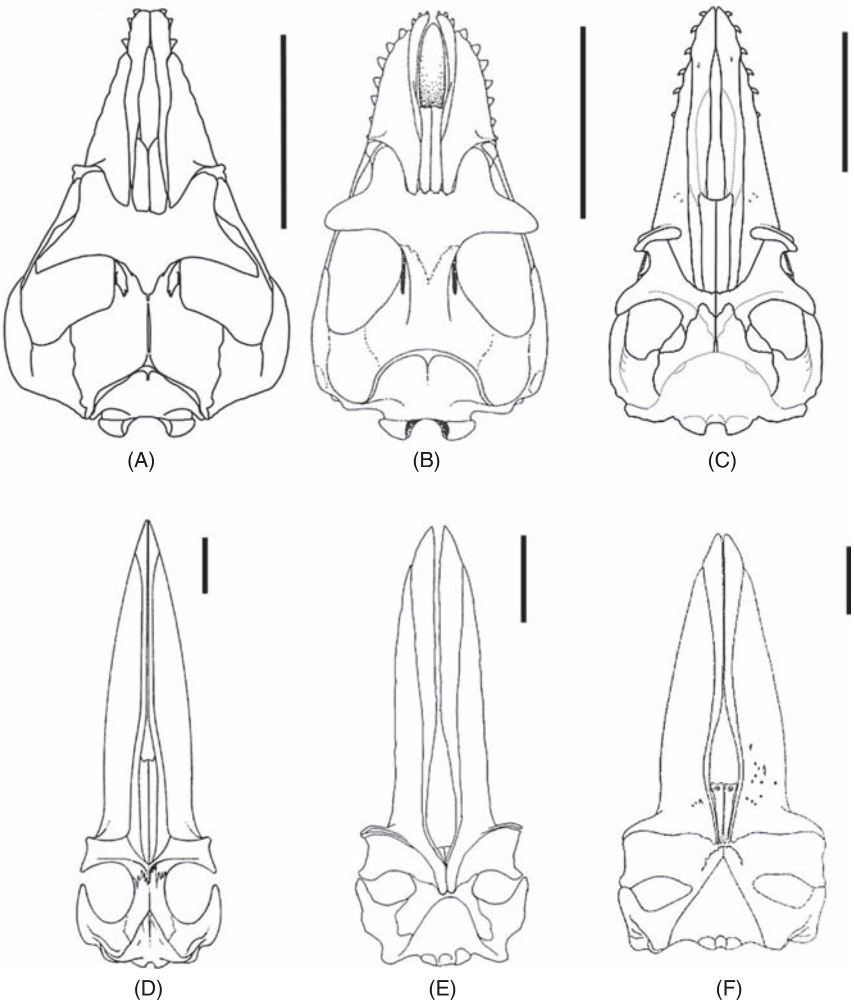

Figure 1 *Archaic mysticete skulls: (A)* Janjucetus hunderi *(from Fitzgerald, 2006); (B)* Mammalodon collivieri *(from Fordyce and Muizon, 2001); (C).* Aetiocetus weltoni *(from Deméré and Berta, 2008); (D)* Eomysticetus whitmorei *(from Sanders and Barnes, 2002); (E)* Piscobalaena nana *(from Bouetel and Muizon, 2006); (F)* Aglaocetus patulus *(from Kellogg, 1968). Scale bars equal 20 cm.*

of about 2 m. The distinctly heterodont dentition of *Llanocetus* consisted of widely spaced molariform postcanine teeth with crowns characterized by roughened enamel and large, palmate denticles. Functional comparisons have been made with the palamate teeth of the modern filter-feeding crabeater seal, *Lobodon carcinophagus*.

Janjucetus hunderi and *Mammalodon collivieri* from the late Oligocene of Victoria, Australia (Fitzgerald, 2000), were smaller, short-faced toothed mysticetes with closely spaced, heterodont dentitions (Fig. 1). Crown morphology of the postcanine teeth is poorly known for *M. colliveri*, but for *J. hunderi* consists of roughened enamel and moderately sized, closely appressed denticles. The orbits of *J. hunderi* are large relative to skull length (~46 cm), suggesting acute vision. Although both taxa have been assigned to separate monotypic families, character support for this distinction is weak and they eventually may be shown to be sister taxa.

Aetiocetids represent the most diverse clade of toothed mysticetes and include seven nominal species grouped into 3–4 genera. *Aetiocetus* is the most speciose genus, followed by *Chonecetus* and *Morawanocetus*. Overall, aetiocetids were small-bodied cetaceans with skull lengths of about 60–70 cm and an estimated total body length of 2–3 m. Unlike species of *Mammalodon* and *Janjucetus*, aetiocetids had a relatively long rostrum (Fig. 1). Little is known of their postcranial skeleton except that they had elongated necks and relatively long arms with rigid elbow joints. The aetiocetid skull retained numerous primitive features inherited from their archaeocete ancestors (e.g., anteriorly positioned "blowhole," elevated supraorbital processes of the frontals, long intertemporal constriction, large mandibular coronoid process, and large mandibular foramen). However, as mosaic stem mysticetes, aetiocetids also possessed important advanced features (e.g., broad rostrum, vascularized palate, and

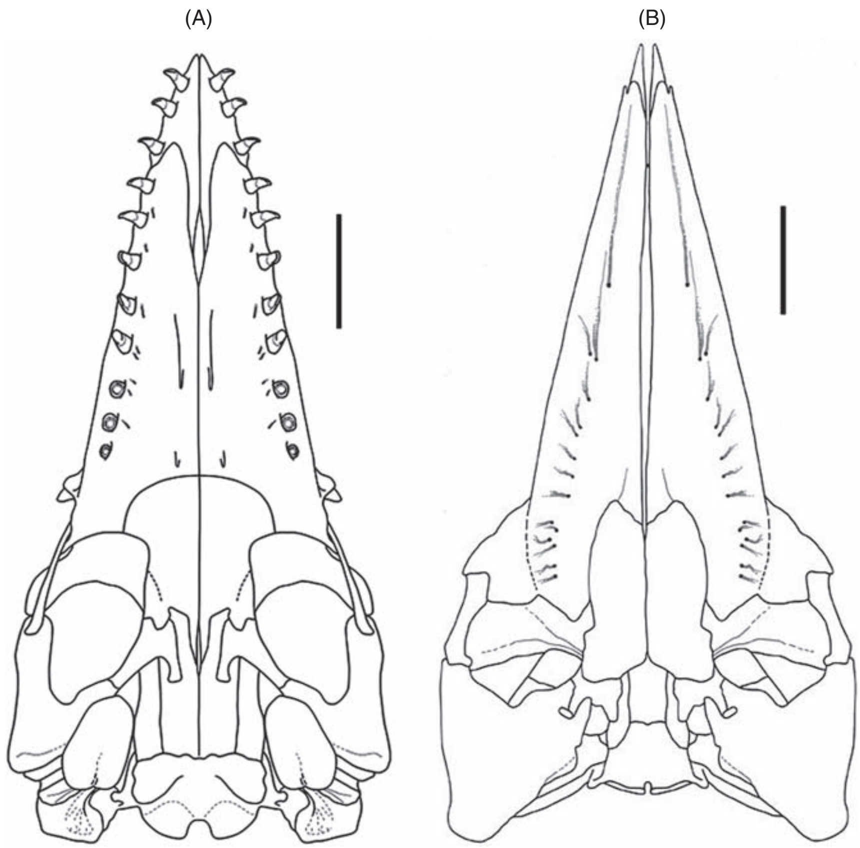

Figure 2 *Mysticete palates showing lateral foramina and sulci: (A) Toothed mysticete (*Aetiocetus weltoni *~28–25 million years old; scale bar equals 10 cm); (B) Edentulous mysticete (*Balaenoptera acutorostrata*; scale bar equals 20 cm). From Deméré and Berta (2008) and Deméré et al (2008).*

outwardly bowed mandible with prominent groove for the fibrocartilaginous symphysis) that portend the later diversification of fully edentulous baleen whales. Dental morphology varied within the group with *Morawanocetus* possessing a distinctly heterodont dentition and postcanine crowns with roughened enamel and moderately sized denticles. In contrast species of *Aetiocetus* had a more weakly heterodont dentition with postcanine crowns with lightly roughened enamel and diminutive denticles. The teeth were widely spaced and eastern North Pacific species (*A. cotylaveus* and *A. weltoni*) show a tendency toward polydonty, while one western North Pacific species (*A. polydentatus*) was distinctly polydont.

III. Origin of Baleen

Baleen is a unique mammalian structure consisting of keratinized tubules typically organized into transverse cornified plates suspended from epithelial tissues of the roof of the mouth. The frayed tubules on the medial margin of each plate overlap those of adjacent plates to produce a sieve that entraps prey within the oral cavity. The origin of baleen, although still poorly documented by fossils, appears to have been a stepwise transition from an ancestor with teeth only, to an intermediate state with functional teeth and baleen, to the derived condition with baleen only. Because baleen rarely fossilizes, morphologic evidence for its presence (or absence) must rely on correlated osteological features. Extant mysticetes have a highly vascularized palate with distinct foramina and associated sulci concentrated along the medial portion of each maxilla (Fig. 2). The blood supply and innervation of the developing baleen apparatus pass through these openings. Thus, the presence of lateral palatal foramina and sulci in fossil mysticetes serves as indirect evidence for the presence of baleen (Figs. 2,3). Importantly, such structures have been reported in some toothed mysticetes.

IV. Edentulous Mysticetes

Archaic edentulous mysticetes are grouped into two families, Eomysticetidae and "Cetotheriidae." Described eomysteicetids include *Eomysticetus whitmorei* and. *E. carolinensis* from the late Oligocene (30–28 Ma) of South Carolina, USA (Sanders and Barnes, 2002). These earliest edentulous baleen whales were of medium size (skull length ~1.5 m) and possessed a mosaic of primitive (e.g., elongated intertemporal region with long parietal and frontal exposures on the cranial vertex, anteriorly placed "blowholes," elongated nasals, large mandibular coronoid processes, and large mandibular foramina) and derived (e.g., loss of adult dentition, flattened rostrum, and laterally bowed mandibles) features. Other probable eomysticetids include species of *Mauicetus* from the late Oligocene of New Zealand

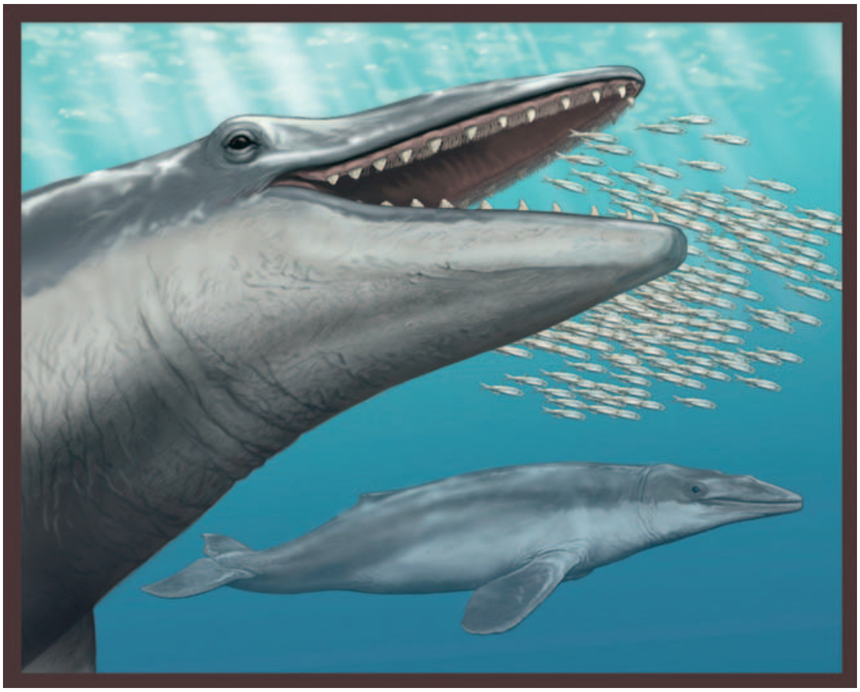

Figure 3 *Reconstruction of* Aetiocetus weltoni *by Carl Buell (Deméré* et al., 2008*).*

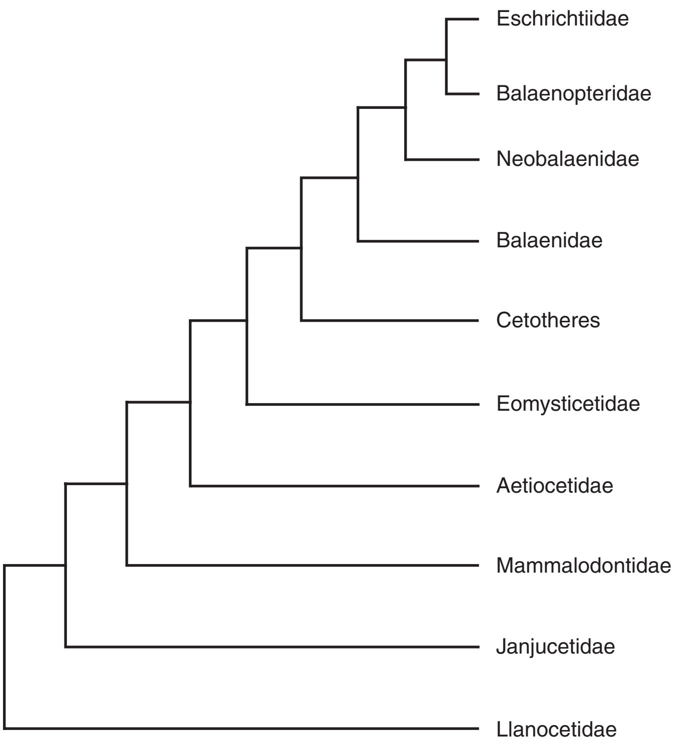

Figure 4 *Phylogeny of mysticetes based on Deméré* et al, *accepted.* (2008).

and undescribed specimens from the late Oligocene of Japan; Baja California, Mexico; and California and Washington, USA.

"Cetotheriidae" is a large, diverse, nonmonophyletic assemblage of extinct small-to-medium-sized toothless mysticetes that traditionally have been grouped together primarily based on their lack of synapomorphies of crown mysticetes. "Cetotheres" comprise the greatest taxonomic and morphologic diversity among fossil mysticetes with over 45 described species divided among more than 30 genera. Nominal "cetotheres" range in age from the late Oligocene to the late Pliocene of North and South America, Europe, Japan, Australia, and New Zealand. Monophyly of the "Cetotheriidae" has been questioned since at least the 1920s and the group currently is recognized as paraphyletic or possibly polyphyletic (Bouetel and Muizon, 2006). Several recent cladistic studies have utilized a small number of "cetotheres" to investigate mysticete phylogeny and in the process have recognized two alternative topologies: either "cetotheres" lie outside of crown mysticetes or they are positioned within crown Mysticeti (Fig. 4). With the current increased interest in mysticete paleontology and the description of critical new fossils, it is likely that greater phylogenetic resolution will emerge for "cetotheres." It is also likely that this greater resolution will allow recognition of distinct groups of "cetotheres" that are implicated in the origin of specific crown mysticete clades.

References

Bouetel, V., and de Muizon, C. (2006). The anatomy and relationships of *Piscobalaena nana* (Cetacea, Mysticeti), a Cetotheriidae *s.s.* from the early Pliocene of Peru. *Geodiversitas* **28**, 319–395.

Deméré, T. A., and A. Berta (2008). Skull anatomy of the Oligocene toothed mysticete *Aetiocetus weltoni* (Mammalia: Cetacea): implications for mysticete evolution and functional anatomy. *Zool. Jour. Linn. Soc.*, 154(2): 308–352.

Deméré, T. A., McGowen, M. R., Berta A., and Gatesy, J. (2008) Morphological and molecular evidence for a stepwise evolutionary transition from teeth to baleen in mysticete cetaceans. *Syst. Biol.* **57**, 15–37.

Fitzgerald, E. M. (2006). A bizarre new toothed mysticete (Cetacea) from Australia and the early evolution of baleen whales. *Proc. R. Soc. B. London*.

Fordyce, R. E., and Muizon, C.de. (2001). Evolutionary history of cetaceans: A review. *In* "Secondary Adaptation of Tetrapods to Life in Water" (J.-M. Mazin, and V. deBuffrenil, eds), pp. 169–233. Verlag Dr. Frederich Pfeil, Munchen.

Kellogg, A. R. (1968). Fossil marine mammals from the Miocene Calvert Formation of Maryland and Virginia, Part 7: A sharp-nosed cetothere from the Miocene Calvert. Bull. *US Natl. Mus.* **247**, 163–173.

Sanders, A. E., and Barnes, L. G. (2002). Paleontology of the Late Oligocene Ashley and Chandler Bridge Formations of South Carolina, 3: Eomysticetidae, a new family of primitive mysticetes (Mammalia: Cetacea). *Smithsonian Contrib. Paleobiol* **93**, 313–356.