CHAPTER

2

Fossil record

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Introduction

Balaenids are an ancient lineage of baleen whales (Mysticeti), which today only survives in the form of two genera: *Balaena*, or bowhead whales; and three species of *Eubalaena*, which—like the family itself—are commonly referred to as right whales. Bowhead whales today occur exclusively in northern polar waters, and have gained fame as the Methuselah among mysticetes: some individuals are thought to be over 200 years old (George et al., 1999; Chapter 7; *Balaena* also holds the distinction of being the only mysticete genus named by Linnaeus (1758). Because of this long history, numerous species were referred to it over the past 250 years, but nearly all have since been reidentified or relegated to the status of nomen dubium (see McLeod et al., 1993 for a detailed review).

Mysticetes descend from toothed ancestors, as exemplified by the small but ferocious *Janjucetus hunderi*, which inhabited Australian waters 26.5–23 Ma (million years ago; Fig. 2.1) (Fitzgerald, 2006). By contrast, living mysticetes are toothless, and instead rely on a set of comb-like keratinous plates (baleen) to filter tiny prey directly from seawater (Pivorunas, 1979; Chapter 14). Compared to other mysticetes, balaenids are bulky and adapted for slow cruising rather than speed (Woodward et al., 2006). When foraging, they swim forwards with the mouth partially open, taking in prey-laden water at the front while simultaneously expelling excess water at the back of the mouth. This form of continuous "skim feeding" benefits from a large filtration area, which in turn has caused the baleen plates to become extremely elongate: in the case of bowheads, up to 4 m (Werth and Potvin, 2016; Chapter 14).

To accommodate the enormous baleen racks, the rostrum of right whales is narrow and notably arched (Fig. 2.2). This arrangement makes the skull appear remarkably tall, and is matched by both an equally tall lower lip and a large supraoccipital bone for the attachment of strong neck muscles. Other typical balaenid features include broad, paddle-like flippers with five fingers; the lack of a dorsal fin; hypertrophy of the periotic, which

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FIGURE 2.1 Skull of the archaic toothed mysticete *Janjucetus hunderi* (Museums Victoria, Melbourne, Australia, specimen P216929) from Australia. *Janjucetus* occurred around 26.5–23 Ma and, just like many other early mysticetes, had teeth but no baleen. *Source: Photograph by Erich M. G. Fitzgerald.*

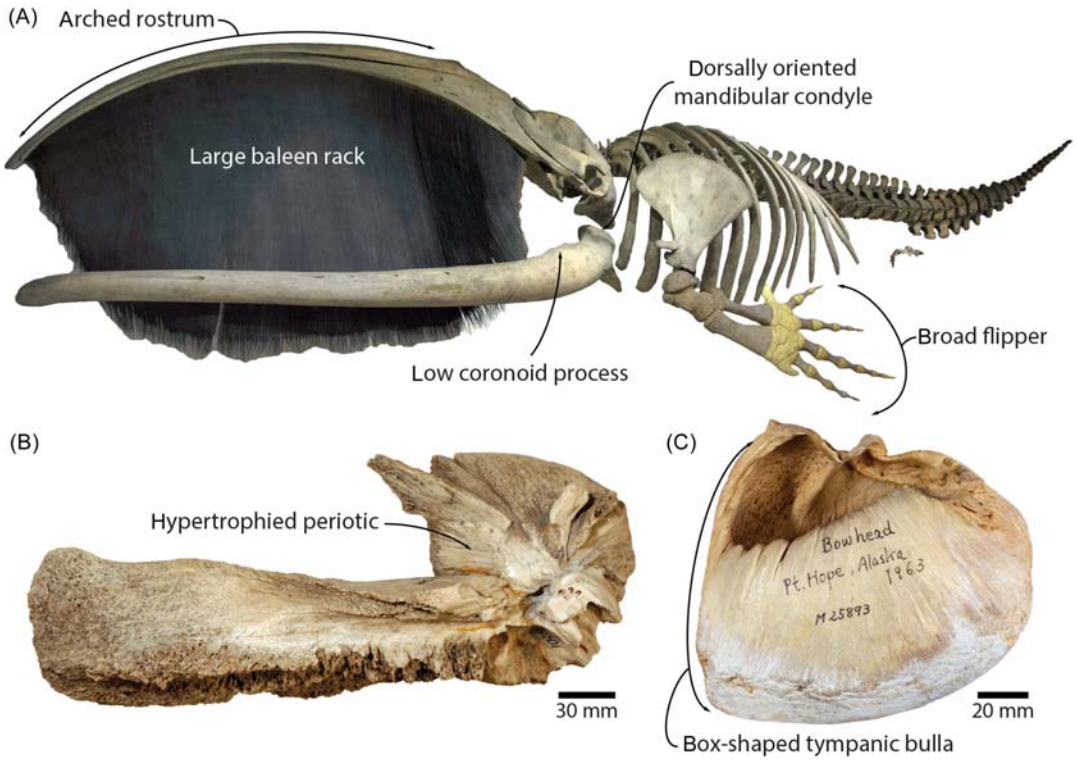

FIGURE 2.2 Skeleton of the bowhead whale (*Balaena mysticetus*). (A) The skeleton (Zoological Museum of the University of Copenhagen, Denmark, specimen CN1). (B) The right periotic (National Museum of Natural History, Smithsonian Institution, Washington, DC, USA, specimen 63301). (C) The right tympanic bulla (National Museum of Nature and Science, Tokyo, Japan, specimen M25893).

houses the organs of hearing and balance; box-shaped, posteriorly diverging tympanic bullae; a well-defined glenoid fossa housing the synovial craniomandibular joint; a robust mandible with a twisted symphyseal portion, a low coronoid process, a dorsally oriented articular condyle, and a well-developed mylohyoid sulcus; fused neck vertebrae; and, primitively, the retention of a comparatively well-developed hind limb comprising the pelvis, femur, and cartilaginous tibia.

In bowhead whales, the rostrum and neurocranium form a continuous arc, with the nasal bones being elevated above the level of the supraoccipital (Chapter 9). By contrast, *Eubalaena* has a more irregular skull outline, and a dome-like vertex that rises above the level of the rostrum. Bowhead whales further differ in having a straighter frontoparietal suture (in lateral view), and more slender forelimb bones that retain both the olecranon process on the ulna and the coracoid process on the scapula (Bisconti, 2000; Churchill et al., 2012; Westgate and Whitmore, 2002). Externally, the two genera appear relatively similar, but bowhead whales lack the callosities (patches of roughened skin infested by whale lice) characterizing *Eubalaena* and are somewhat larger, with a maximum body length of about 19 m.

Balaenid origins and the Miocene gap

The distinctive bauplan of balaenids has ancient origins, and fundamentally has remained almost unchanged since their first appearance in the fossil record. Within its scope, however, right whales once attained a far greater diversity of shapes and sizes than is apparent in the living species.

Right whales are generally considered to be basal to all other extant mysticetes (including the pygmy right whale, *Caperea marginata*), and may have evolved as early as 28 Ma (Fordyce, 2002; Marx and Fordyce, 2015; McGowen et al., 2009; Chapter 1); however, fossils from that time have not yet been unambiguously identified. The earliest definitive balaenid is *Morenocetus parvus* from the lower Miocene of Argentina (Fig. 2.3), which at an age of 20–18 Ma is by far the oldest member of any of the extant baleen whale families (Cabrera, 1926). *Morenocetus* was smaller (about 5–6 m) than its living relatives, but already had the tall skull and hypertrophied periotic typical of modern balaenids (Buono et al., 2017).

The second-oldest balaenid, dating to about 16–15 Ma, is *Peripolocetus vexillifer* from the middle Miocene of California, USA. The holotype of this species is fragmentary, and was only recognized as a right whale following the discovery of a more complete specimen from the same locality (Deméré and Pyenson, 2015). Together with *Morenocetus*, it is often considered basal to all other balaenids (Buono et al., 2017; Duboys de Lavigerie et al., 2020; Gol'din and Steeman, 2015), but the phylogenetic position of these early species remains in flux (e.g., Bisconti, 2005; Bisconti et al., 2017).

After *Peripolocetus*, there is a large gap in the balaenid fossil record lasting until about 7–6 Ma. Why this is so remains an enduring and largely underappreciated mystery (Buono et al., 2017; Deméré and Pyenson, 2015). Curiously, there are several Miocene rock formations across the globe that are rich in cetacean remains, yet have never yielded a right whale fossil. Pertinent examples include the Chesapeake Group of the eastern United States (Gottfried et al., 1994); the Pisco Formation of southern Peru (Di Celma et al., 2017); and the Bihoku Group of southern Japan (Otsuka and Ota, 2008).

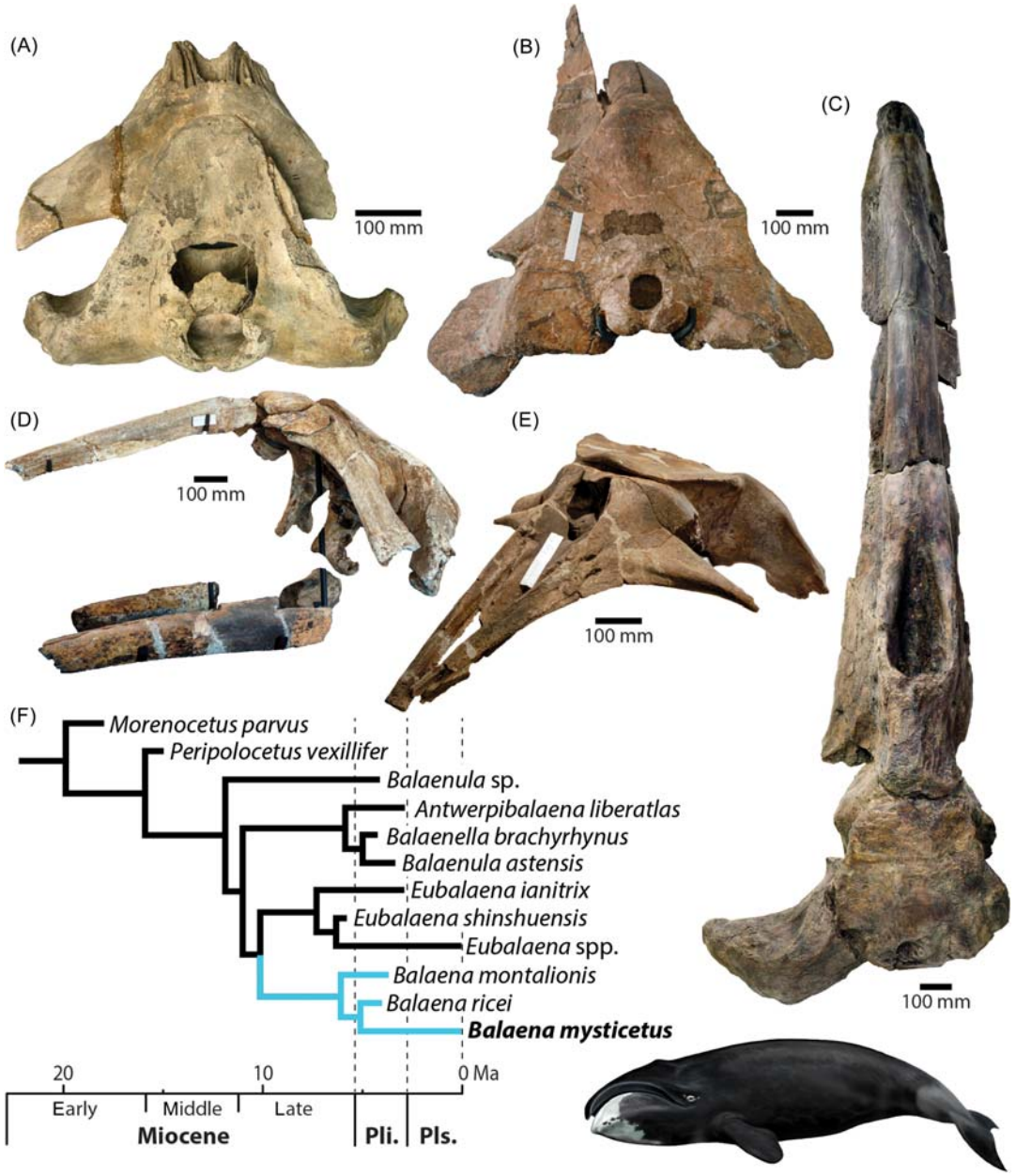

FIGURE 2.3 Overview of extinct balaenids. (A) *Morenocetus parvus* (Museo de La Plata, La Plata, Argentina, specimen 5–11). (B) *Balaena montalionis* (Museo di Storia Naturale e del Territorio/MSNTUP, Università di Pisa, Pisa, Italy, specimen I12357). (C) *Eubalaena shinshuensis* (Shinshushinmachi Fossil Museum, Shinshushinmachi, Japan, specimen CV0024). (D) *Balaenula astensis* (MSNTUP I12555). (E) *Balaenella brachyrhynus* (Natuurmuseum Brabant, Tilburg, The Netherlands, specimen 42001). (F) Time-calibrated phylogeny of living and extinct right whales, following Duboys de Lavigerie et al. (2020); bowhead whales are shown in blue. Drawing of *Balaena mysticetus* by Carl Buell. *Pli.*, Pliocene; *Pls.*, Pleistocene.

Given the worldwide distribution of these localities, there seems to be no obvious biogeographical explanation for the "balaenid gap." Perhaps early right whales were relatively rare and/or restricted to habitats not captured by the Miocene fossil localities explored to date. Alternatively, most of them may have been limited to the Southern Hemisphere, large swathes of which remain underexplored. Support for this idea comes from as yet undescribed specimens from Argentina dating to 12–9 Ma (Buono et al., 2009).

Late Neogene diversification and the emergence of bowheads

About 7–6 Ma, a new wave of right whale fossils abruptly appears across the globe. Oldest amongst them is *Eubalaena shinshuensis* from Japan (Kimura, 2009), which at an estimated length of 12–13 m was twice as large as all of its predecessors (Buono et al., 2009, 2017). Its appearance heralded a short-lived phase, lasting until about 3 Ma, during which balaenids diversified into a variety of species and body sizes: from the diminutive (6–8 m long) *Balaenella brachyrhynus*, *Balaenotus insignis*, *Balaenula balaenopsis*, and *Balaenula astensis*, to the medium-sized (9–10 m) *Antwerpibalaena liberatlas*, and the relatively large (>10 m) *Balaena ricei* and *Eubalaena ianitrix* (Bisconti, 2000, 2005; Bisconti et al., 2017; Duboys de Lavigerie et al., 2020; Trevisan, 1941; Van Beneden, 1880; Westgate and Whitmore, 2002).

The phylogenetic relationships of most of these species remain poorly resolved. Some analyses variously intersperse them with living right whales (Bisconti, 2005; Bisconti et al., 2017; Churchill et al., 2012), whereas others support a closely knit crown group comprising only *Balaena* and *Eubalaena* (Buono et al., 2017; Duboys de Lavigerie et al., 2020). All studies agree, however, that bowhead whales emerged as part of this late Neogene "explosion" in balaenid diversity, giving rise to a lineage with at least three species: *Balaena montalionis*, *B. ricei*, and the extant *Balaena mysticetus*. Of these, *B. ricei* is the oldest (c. 4.9–4.4 Ma), which is notably younger than some recent molecular estimates (10.6 Ma) for the split between *Balaena* and *Eubalaena* (Chapter 1). Initially, *Balaena* occurred as far south as 35°N–37°N and broadly overlapped with *Eubalaena* in its geographic range (Field et al., 2017).

About 3 Ma, small balaenids, along with most other small mysticetes, disappear from the fossil record in tandem with the onset of Northern Hemisphere glaciation and more patchy prey distributions (Marx and Fordyce, 2015; Slater et al., 2017). *Balaena* and *Eubalaena* survived, perhaps because of their relatively large size, and eventually started to separate geographically into their modern polar vs temperate habitats (Foote et al., 2013).

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