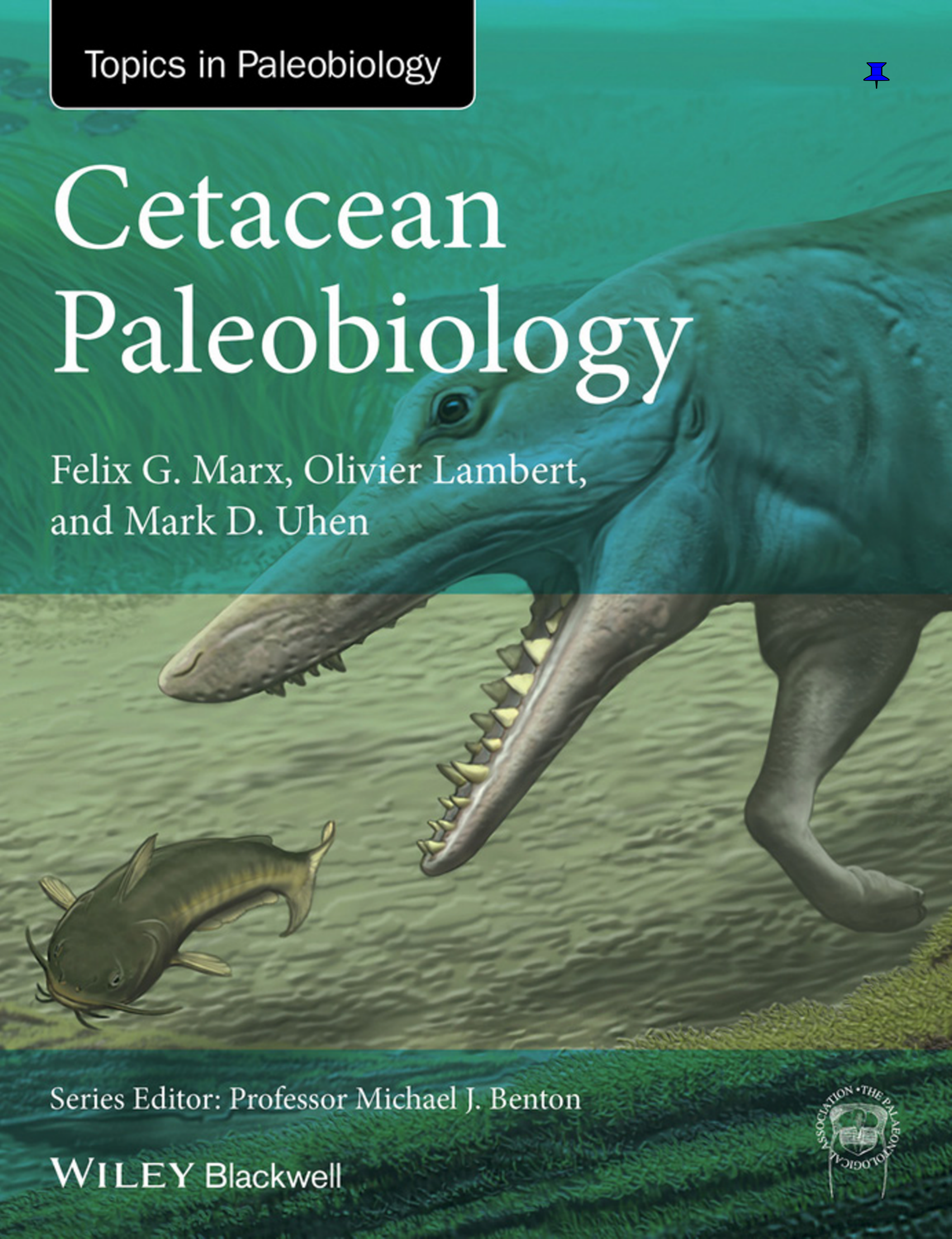

Topics in Paleobiology

# Cetacean Paleobiology

Felix G. Marx, Olivier Lambert,
and Mark D. Uhen

Series Editor: Professor Michael J. Benton

WILEY Blackwell

# Cetacean Paleobiology

Books in the **Topics in Paleobiology** series will feature key fossil groups, key events, and analytical methods, with emphasis on paleobiology, large-scale macroevolutionary studies, and the latest phylogenetic debates.

The books will provide a summary of the current state of knowledge and a trusted route into the primary literature, and will act as pointers for future directions for research. As well as volumes on individual groups, the Series will also deal with topics that have a cross-cutting relevance, such as the evolution of significant ecosystems, particular key times and events in the history of life, climate change, and the application of new techniques such as molecular paleontology.

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The Series Editor is *Mike Benton*, Professor of Vertebrate Palaeontology in the School of Earth Sciences, University of Bristol.

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# Contents

# Series Editor's Preface

*Paleobiology* is a vibrant discipline that addresses current concerns about biodiversity and about global change. Furthermore, paleobiology opens unimagined universes of past life, allowing us to explore times when the world was entirely different and when some organisms could do things that are not achieved by anything now living.

Much current work on biodiversity addresses questions of origins, distributions and future conservation. Phylogenetic trees based on extant organisms can give hints about the origins of clades and help answer questions about why one clade might be more species-rich ('successful') than another. The addition of fossils to such phylogenies can enrich them immeasurably, thereby giving a fuller impression of early clade histories, and so expanding our understanding of the deep origins of biodiversity.

In the field of global change, paleobiologists have access to the fossil record, and this gives accurate information on the coming and going of major groups of organisms through time. Such detailed paleobiological histories can be matched to evidence of changes in the physical environment, such as varying temperatures and sea levels, episodes of midocean ridge activity, mountain building, volcanism, continental positions and the impacts of extraterrestrial bodies. Studies of the influence of such events and processes on the evolution of life address core questions about the nature of evolutionary processes on the large scale.

As examples of unimagined universes, one need only think of the life of the Burgess Shale or the times of the dinosaurs. The extraordinary arthropods and other animals of the Cambrian sites of exceptional preservation sometimes seem more bizarre than the wildest imaginings of a science fiction author. During the Mesozoic, the sauropod dinosaurs solved basic physiological problems that allowed them to reach body masses 10 times larger than those of the largest elephants today. Furthermore, the giant pterosaur *Quetzalcoatlus* was larger than any flying bird, and so challenges fundamental assumptions in biomechanics.

Books in the Topics in Paleobiology series will feature key fossil groups, key events and analytical methods, with emphasis on paleobiology, large-scale macroevolutionary studies and the latest phylogenetic debates.

The books will provide a summary of the current state of knowledge and a trusted route into the primary literature, and will act as pointers for future directions for research. As well as volumes on individual groups, the Series will also deal with topics that have a cross-cutting relevance, such as the evolution of significant ecosystems, particular key times and events in the history of life, climate change and the application of new techniques such as molecular paleontology.

The books are written by leading international experts and have been pitched at a level suitable for advanced undergraduates, postgraduates and researchers in both the paleontological and biological sciences.

Michael Benton
Bristol
November 2011

# Preface

> All the fossil whales hitherto discovered belong to the Tertiary period, which is the last preceding the superficial formations. And though none of them precisely answer to any known species of the present time, they are yet sufficiently akin to them in general respects, to justify their taking rank as Cetacean fossils.
>
> Detached broken fossils of pre-adamite whales, fragments of their bones and skeletons, have within thirty years past, at various intervals, been found at the base of the Alps, in Lombardy, in France, in England, in Scotland, and in the States of Louisiana, Mississippi, and Alabama. Among the more curious of such remains is part of a skull, which in the year 1779 was disinterred in the Rue Dauphine in Paris, a short street opening almost directly upon the palace of the Tuileries; and bones disinterred in excavating the great docks of Antwerp, in Napoleon's time. Cuvier pronounced these fragments to have belonged to some utterly unknown Leviathanic species.
>
> But by far the most wonderful of all Cetacean relics was the almost complete vast skeleton of an extinct monster, found in the year 1842, on the plantation of Judge Creagh, in Alabama. The awe-stricken credulous slaves in the vicinity took it for the bones of one of the fallen angels. The Alabama doctors declared it a huge reptile, and bestowed upon it the name of *Basilosaurus*. But some specimen bones of it being taken across the sea to Owen, the English Anatomist, it turned out that this alleged reptile was a whale, though of a departed species. A significant illustration of the fact, again and again repeated in this book, that the skeleton of the whale furnishes but little clue to the shape of his fully invested body. So Owen rechristened the monster *Zeuglodon*; and in his paper read before the London Geological Society, pronounced it, in substance, one of the most extraordinary creatures which the mutations of the globe have blotted out of existence.
>
> When I stand among these mighty Leviathan skeletons, skulls, tusks, jaws, ribs, and vertebrae, all characterized by partial resemblances to the existing breeds of sea-monsters; but at the same time bearing on the other hand similar affinities to the annihilated antichronical Leviathans, their incalculable seniors; I am, by a flood, borne back to that wondrous period, ere time itself can be said to have begun.
>
> —Herman Melville's account of the cetacean fossil record, from "The Fossil Whale," *Moby Dick*

In what is maybe his most famous novel, Herman Melville provides an excellent account of the state of the cetacean fossil record in the mid-19th century. When *Moby Dick* was published in 1851, just a few years before Darwin's *On the Origin of Species*, whales were still among the most mysterious of all animals. How had a group of air-breathing, warm-blooded mammals come to live in the sea? As we shall see in the book, surprisingly little changed following Melville's early account. As late as 1945, great paleontologists like George Gaylord Simpson were still baffled by the origins of these seemingly "peculiar and aberrant" creatures. Since then, however, new finds and scientific approaches have led to a series of breakthroughs, and increased our knowledge of whale evolution to the point where it can no longer simply be summarized in a few paragraphs. Our goal here is to introduce our readers to this fascinating subject, and hopefully spark further interest in different areas of fossil cetacean research. Each chapter includes an extensive bibliography from which we have drawn the facts and hypotheses presented, as well as a list of suggested readings. We sincerely hope that you find the evolution of whales as interesting as we do, and that you will enjoy reading about it in this book. Afterward, be sure to keep your eye out for further developments in the field, as new information is unearthed around the globe in the future.

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# 1

# Cetaceans, Past and Present

## 1.1 Introduction and scope of the book

Cetaceans (whales, dolphins, and porpoises) are some of the most iconic inhabitants of the modern ocean. They are, however, also one of its most unlikely. This point was beautifully made by the famous paleontologist George Gaylord Simpson when he described cetaceans as "on the whole, the most peculiar and aberrant of mammals" (Simpson, 1945: p. 213). Living cetaceans are the result of more than 50 million years of evolution, which transformed a group of small, four-legged landlubbers into the ocean-going leviathans of today. As far back as the fourth century BC, the Greek philosopher Aristotle recognized in his *Historia Animalium* that whales and dolphins breathe air, give birth to live offspring, show parental care, and suckle their young. Along with their warm-bloodedness, these traits betray the terrestrial mammalian ancestry of cetaceans, and often present them with a considerable challenge. Put into water, most land mammals would struggle to swim for any length of time, breathe, cope with ingested saltwater, or maintain their body temperature. Yet cetaceans have managed to clear all of these hurdles, alongside many others. They can find prey even in murky water where eyes cannot see. Their air-breathing calves are born underwater, yet do not drown. They move around fast in three dimensions, yet avoid becoming dizzy. They dive deep beneath the surface, yet do not suffer from the bends.

For a long time, the story of how cetaceans managed to leave behind the shore and adapt so completely to life in the sea remained largely in the dark. Fossils of ancient cetaceans have been known since the early 19th century, but most of them were too fragmentary, or too similar to the living forms, to illuminate the morphological and ecological transition back into the water. This all changed in the early 1990s, when the first of a string of spectacular new fossil finds started to rewrite our understanding of how, when, and where the first cetaceans evolved. Over the following 25 years, further discoveries coincided with the emergence of an ever-more sophisticated array of analysis techniques, such as molecular phylogenetics, stable isotope analysis, **computed tomography** (CT) scanning, and molecular divergence time estimation. Together, these developments allowed unprecedented insights into not only the origin and evolutionary relationships of cetaceans, but also their ecology and functional biology.

In this book, we aim to provide an overview of the study of cetacean evolution from their first appearance to the present day. We start with a description of basic principles, including a brief summary of the ecology of living whales and dolphins, cetacean taxonomy, and an explanation of the main techniques and

*Cetacean Paleobiology*, First Edition. Felix G. Marx, Olivier Lambert, and Mark D. Uhen.

concepts used to study extinct species (Chapter 1). This is followed by more detailed summaries of the cetacean fossil record (Chapter 2) and a description of their anatomy, phylogenetic relationships, and diversity (Chapters 3 and 4). Finally, Chapters 5–8 are devoted to particular topics and case studies of cetacean paleoecology, functional biology, development, and macroevolution.

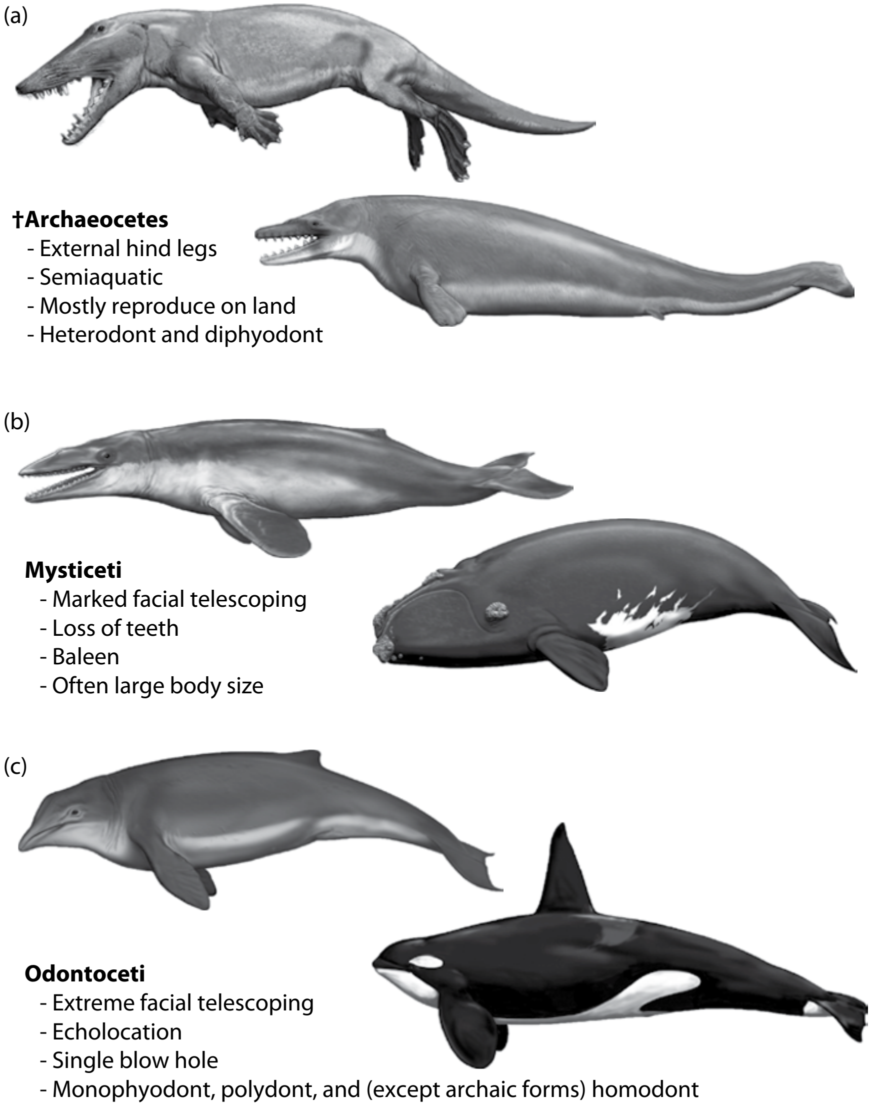
## 1.2 What is a whale?

Whales and dolphins are the only mammals besides sea cows (sirenians) that have completely adapted to life in the ocean. Unlike the other major group of marine mammals, the pinnipeds (seals, sea lions, and walruses), cetaceans sleep, mate, give birth, and suckle their young in the water. Instead of hair, they rely on a thick layer of insulating blubber to maintain their body temperature. Their overall shape is extremely streamlined, with no external projections such as ears or genitals that could produce drag. Their forelimbs have turned into flippers and, having all but lost their original function in locomotion, are merely used for steering. To propel themselves through the water, they instead rhythmically beat their massive tail, which ends in a pair of characteristic horizontal flukes.

Given their distinctive anatomy, the question of how to define a cetacean may seem obvious to the modern observer. However, the issue becomes more vexed when fossils are taken into account. Taxonomically, cetaceans fall into three major groups: ancient whales (**archaeocetes**), baleen whales (**Mysticeti**), and toothed whales (**Odontoceti**), each of which comprises a range of families (Chapter 4). Broadly speaking, archaeocetes are defined by their retention of archaic morphologies, such as (1) well-developed hind limbs; (2) a small number of morphologically differentiated (heterodont) teeth, which are replaced once during life (diphyodonty); and (3) relatively close ties to land (e.g., to rest or give birth) (Figure 1.1). By contrast, mysticetes and odontocetes are completely aquatic, with no trace of an external hind limb, and they are unable to move or support their weight on land. Both groups furthermore underwent a pronounced reorganization of their facial bones—a process commonly known as **telescoping**—to facilitate breathing (section 3.2). Besides these shared features, modern odontocetes in particular are recognizable by (1) having a single blowhole; (2) having a variable but often large number of greatly simplified, conical teeth (i.e., they are both polydont and homodont); and (3) their ability to **echolochate** (i.e., use sound to navigate and detect prey). In contrast, mysticetes (1) are often extremely large, (2) have lost any trace of teeth as adults, and (3) possess a series of keratinous, sieve-like **baleen** plates suspended in two rows from their upper jaw (section 5.2.1). Incidentally, note that the term *whale* carries little biological meaning in this context, except when understood to mean *all cetaceans*. In common parlance, the word is usually applied only to large-sized species and their (presumed) relatives—including, ironically, some members of the dolphin family (e.g., the killer whale, *Orcinus orca*).

The morphological similarity of the oldest whales to terrestrial mammals can make it difficult to recognize their true evolutionary affinities. Potentially diagnostic features mostly relate to details of the morphology of the skull, such as incipient telescoping and the shape and arrangement of the teeth—in particular, the anteroposterior alignment of the tooth row and the absence of crushing basins on the check teeth (Thewissen *et al.*, 2007; Uhen, 2010). However, many of these are difficult to recognize across Cetacea as a whole or also occur in other, non-cetacean mammals. The clearest trait uniting all cetaceans is a marked increase in the thickness and density (**pachyosteosclerosis**) of the medial wall of the **tympanic bulla**, one of the two main ear bones located at the base of the skull (Figure 1.2) (section 3.2.5). A pachyosteosclerotic bulla was long thought to be unique to cetaceans, until a similar morphology was described for a group of extinct artiodactyls (even-toed ungulates) known as raoellids (Thewissen *et al.*, 2007). This wider distribution is, however, largely unproblematic, since raoellids are now known to be more closely related to cetaceans than to any other extant or extinct artiodactyls and, although never formalized as such, could therefore be seen as de facto cetaceans (sections 4.1 and 5.1.1) (Geisler and Theodor, 2009; Thewissen *et al.*, 2007).

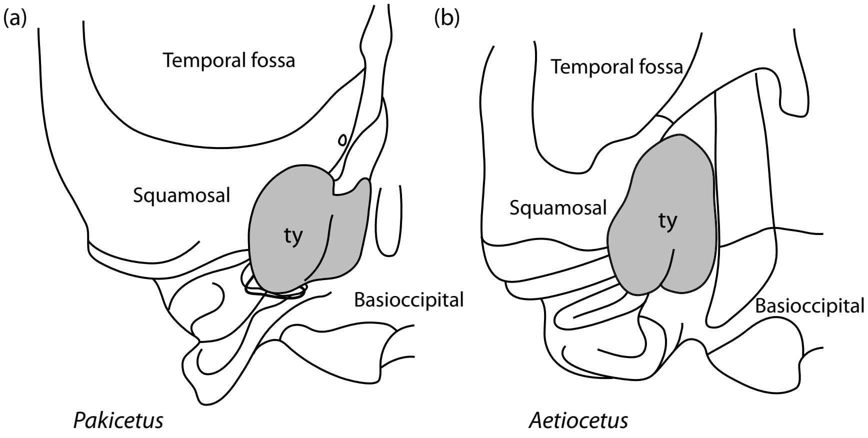
**Figure 1.1** Overview of the three main subdivisions of Cetacea: (a) archaeocetes (archaic whales), (b) Mysticeti (baleen whales), and (c) Odontoceti (toothed whales, including dolphins). Life reconstructions © C. Buell.



## 1.3 Diversity, distribution, and ecology of modern cetaceans

Modern whales and dolphins form an essential part of the ocean ecosystem as **top predators**, as large-scale **nutrient distributors**, and as a **food source** for many deep-sea organisms (Croll *et al.*, 2006; Nicol *et al.*, 2010; Smith and Baco, 2003; Willis, 2014; Wing *et al.*, 2014). Their ranks include the holders of several world records, most of which are related to their often gigantic size: the blue whale *Balaenoptera musculus*, which at up to 190 tonnes is the Earth's heaviest animal (Tomilin, 1957)—and at least one-third again as heavy as the largest known dinosaur (Carpenter, 2006); the sperm whale *Physeter macrocephalus*, owner of

**Figure 1.2** The pachyosteosclerotic tympanic bulla (highlighted in gray) characteristic of all cetaceans, as developed in (a) the early archaeocete *Pakicetus* and (b) the archaic mysticete *Aetiocetus*. Drawing of *Pakicetus* adapted from Gingerich *et al.* (1983) and Luo and Gingerich (1999).



the world's largest brain (up to 8 kg) (Marino, 2009); the right whales of the genus *Eubalaena*, which possess the more dubious accolade of having the world's largest testes (approximating 1 tonne) (Brownell and Ralls, 1986); and the longest lived of all mammals, the bowhead whale *Balaena mysticetus*, which may reach a venerable age of more than 200 years (George *et al.*, 1999).

All extant species are either mysticetes or odontocetes, with archaeocetes having become extinct around 25 Ma (section 4.2). The Society of Marine Mammalogy currently recognizes 90 living species, 84% of which are odontocetes (Committee on Taxonomy, 2014). On the whole, the modern cetacean fauna is heavily biased toward three families in particular: the **rorquals** (Balaenopteridae), representing around 60% of all living mysticetes; and the **oceanic dolphins** (Delphinidae) and **beaked whales** (Ziphiidae), accounting for roughly 50% and 30% of all living odontocetes, respectively. Even more strikingly, nearly all balaenopterids and roughly two-thirds of all ziphiids each belong to a single genus (*Balaenoptera* and *Mesoplodon*). This skewed taxonomic distribution is probably an indicator of relatively recent radiations, possibly driven by the evolution of enlarged brains or particular feeding and mating strategies (sections 6.1, 6.5, and 7.5). Cetacean taxonomy remains in flux, and discoveries of new species (even large-sized ones) are still relatively frequent. Thus, a new beaked whale was reported as recently as 2014, and at least one new rorqual is currently awaiting formal description (Dalebout *et al.*, 2014; Sasaki *et al.*, 2006).

Living cetaceans range in size from about 1 m to more than 30 m, and they inhabit all parts of the world's oceans and seas. Geographically, modern diversity is highest at intermediate latitudes and sea surface temperatures of roughly 21 °C (Whitehead *et al.*, 2008). Mysticetes undergo long-distance migrations between low-latitude breeding and high-latitude feeding areas (Stern, 2009). Cetacean feeding strategies can broadly be divided into (1) **filter feeding**, which targets vast quantities of small-sized prey en masse and is characteristic of mysticetes; and (2) the targeting of individual prey items via **suction**, **raptorial feeding**, or a combination of the two, as seen in odontocetes (section 6.1) (Pivorunas, 1979; Werth, 2000). For their diet, most species rely on fish and cephalopods. Exceptions are the mysticetes, which also feed on tiny crustaceans (mostly copepods and krill), and the killer whale *Orcinus*, which regularly preys on other marine mammals and, occasionally, even turtles and sea birds. The false and pygmy killer whales, *Pseudorca* and *Feresa*, may also target other marine mammals, but tend to do so much less frequently (Werth, 2000). Feeding takes places at a range of depths. Sperm whales and beaked whales dive both the deepest (more than 2.9 km in the case of *Ziphius*) and the longest, with routine dives lasting 40–70 minutes (Aoki *et al.*, 2007; Hooker and Baird, 1999; Schorr *et al.*, 2014). By contrast, shorter (up to 10 min) and shallower (100–150 m) dives are characteristic of many dolphins and porpoises, as well as mysticetes (Stewart, 2009).

Nearly all living odontocetes are highly **gregarious**. Some species, such as the sperm, killer, and pilot whales, form matrilineal family groupings, whereas others are organized in less stable fission–fusion societies. Living in groups may help to guard against predators (e.g., in the case of sperm whales), facilitate cooperative feeding and serve mating purposes (Trillmich, 2009). Older killer and pilot whale females experience menopause, which may free them to support their descendants through day-to-day assistance and/or allomaternal care (Foster *et al.*, 2012; Marsh and Kasuya, 1986). In contrast to their tooth-bearing cousins, mysticetes are comparatively solitary creatures, but they aggregate during migration, in breeding areas and to engage in cooperative feeding (Brown and Corkeron, 1995; Weinrich, 1991). Relatively large groups of pygmy right whales have been observed at sea (Matsuoka *et al.*, 1996), and there is evidence of individual humpbacks forming long-term associations across several feeding seasons (Ramp *et al.*, 2010). Both mysticetes and odontocetes show signs of **culture** and engage in **complex social interactions**. These require flexible communication and sophisticated cognitive abilities, and likely explain both the intricate vocalizations of some taxa (May-Collado *et al.*, 2007) and the **enlarged cetacean brain** (sections 3.4.4 and 7.5) (Marino *et al.*, 2007; Rendell and Whitehead, 2001).

## 1.4 How to study extinct cetaceans

### 1.4.1 Comparative and functional anatomy

Anatomical observation has long been the mainstay of paleobiological inquiry, and it still plays a major role in (1) defining and classifying species; (2) establishing evolutionary relationships and certain measures of biological diversity (Slater *et al.*, 2010; Wiens, 2004; Wills *et al.*, 1994); (3) determining stages of physical maturity (Walsh and Berta, 2011); (4) gaining insights into developmental processes, such as heterochrony and vertebral patterning (Buchholtz, 2007; Galatius, 2010); and (5) reconstructing the feeding strategies, brain size, reproduction, sensory capabilities, and modes of locomotion of extinct taxa (Deméré *et al.*, 2008; Ekdale and Racicot, 2015; Montgomery *et al.*, 2013; Racicot *et al.*, 2014). **Anatomical descriptions** rely on specialized terminology relating to particular structures, locations, and motions (Figure 1.3). The sheer bulk of anatomical vocabulary may sometimes appear overwhelming, but it is hard to avoid given the complexity of biological systems and the need to ensure consistency. Luckily, there are some excellent summaries that help to navigate the jungle of jargon, especially with regards to the highly modified body of cetaceans (e.g., Mead and Fordyce, 2009).

Descriptive osteology forms the basis for phylogenetic analyses (section 1.4.2) and can be used to assess morphological disparity, or variation in body shape, through time (section 7.3). In addition, functionally relevant observations, such as the range of motion allowed by a particular

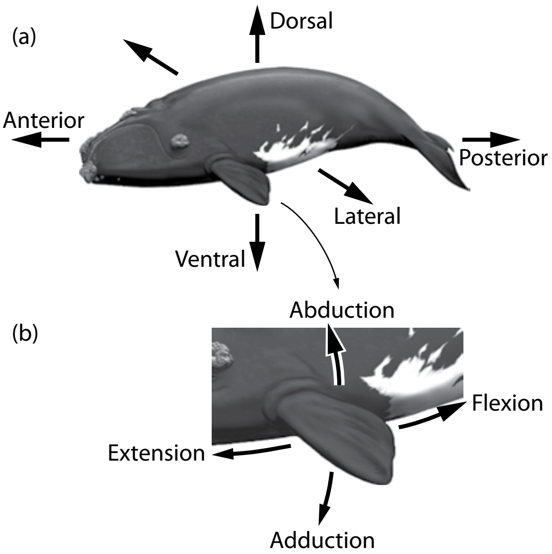


**Figure 1.3** Standard anatomical terms of (a) location and (b) motion. Life reconstructions © C. Buell.

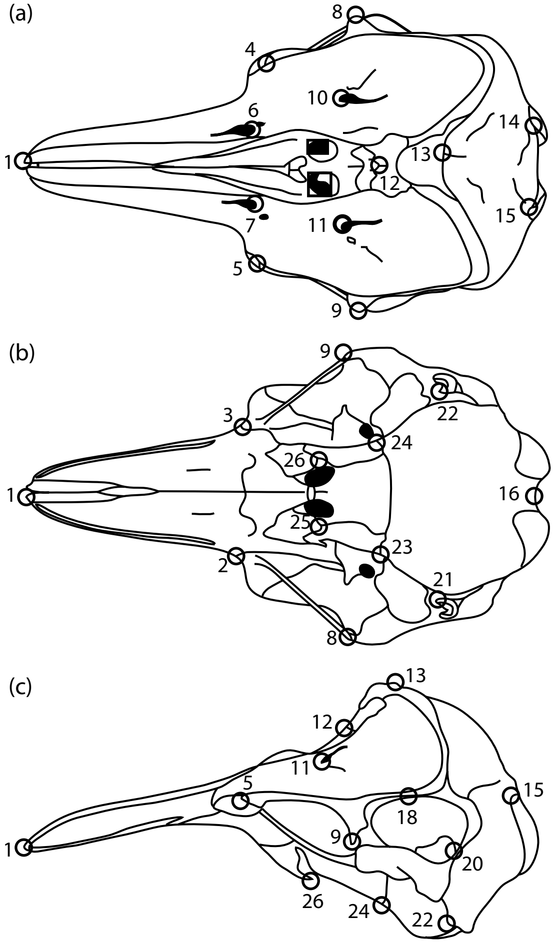


**Figure 1.4** Example of a three-dimensional set of landmarks, based on the skull of a porpoise. (a) Dorsal, (b) ventral, and (c) lateral views. Reproduced from Galatius (2010), with permission of the Linnean Society of London.

joint, help to reconstruct locomotor and feeding abilities (Deméré *et al.*, 2008; Gingerich *et al.*, 1994; Gutstein *et al.*, 2014). Similar insights can be gained from **morphometrics**, which involves the quantification of direct measurements or anatomical **landmarks** (homologous points) based on two- or three-dimensional osteological models (Figure 1.4) (Galatius, 2010; Hampe and Baszio, 2010). This approach has the advantage of suffering less from subjective assessments and individual scoring error than purely descriptive character data, but usually it can only be applied to largely complete, undistorted fossil specimens. Besides quantifying shape, direct measurements of particular parts of the skeleton are used to estimate the total body size of incompletely preserved fossil specimens (Lambert *et al.*, 2010; Pyenson and Sponberg, 2011).

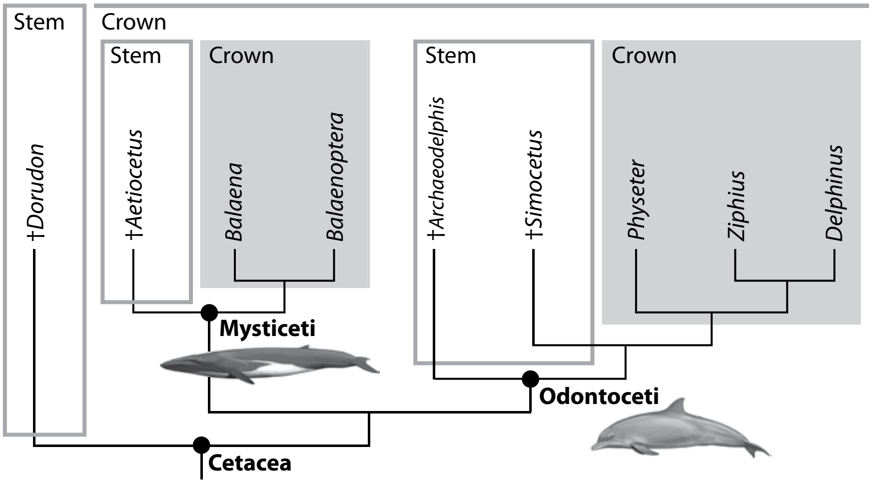
**Soft tissues** are also a rich source of information on evolutionary relationships, ecology, life history, and functional anatomy, but, unlike bones, they are prone to rapid decay following death. With very few exceptions, details on the external anatomy, musculature, and inner organs of fossil organisms are thus invariably lost. Sometimes, however, soft tissues leave tell-tell traces (**osteological correlates**) on the bones themselves, which can be used to reconstruct their appearance and function in life. Such traces may take the form of distinctive muscle scars, hollow spaces for the reception of air-filled sacs, vascular structures associated with particular tissue types, and, in some cases, even the complete outline of an entire organ. The latter particularly applies to the shape of the brain, the inner ear, and the organ of balance, whose shapes can be reconstructed and measured using CT scans (sections 3.4.4 and 7.5) (Ekdale and Racicot, 2015; Marino *et al.*, 2003; Spoor *et al.*, 2002).

### 1.4.2 Evolutionary relationships

Understanding the evolutionary relationships between species helps to clarify their origins, and provides the fundamental framework underlying most paleobiological inquiry. Modern techniques to reconstruct cetacean interrelationships (their **phylogeny**) are also able to determine when two related species first diverged. Together with ongoing refinements in the dating of individual fossils, phylogenies thus can answer such important questions as: What other mammals are whales related to? When did they first evolve? When, and how quickly, did they diversify? And does their evolution follow any particular trends?

By convention, evolutionary relationships are depicted in the form of a **tree**, which may include both living and extinct species. A tree consists of terminal and internal **branches**, all of which connect at **nodes**. Internal branches, and the nodes

**Figure 1.5** Illustration of cetacean, mysticete, and odontocete crown and stem groups. Life reconstructions © C. Buell.



they lead to, are sometimes also interpreted as **hypothetical ancestors**. Related species (i.e., those deriving from a single ancestor) form a **clade**. Both clades and individual species can be referred to as **taxa**. A clade is said to be **monophyletic** if it includes all of its ancestor's descendants, and **paraphyletic** if a particular, usually highly distinctive subgroup of its members has been deliberately excluded. Mammals and birds are examples of monophyletic clades, whereas non-avian dinosaurs (all dinosaurs minus birds) are paraphyletic. Proposed groups that contain members of different clades—say, a group including birds and mammals—are **polyphyletic**, and taxonomically untenable. A related concept is that of the crown and stem group. A **crown group** is a clade defined by all of the extant representatives of a particular taxonomic group (e.g., all extant cetaceans), and it comprises them, their last common ancestor and all those extinct taxa that are descended from the latter. In most cases, a crown group is associated with a **stem group**, which includes all those extinct taxa that fall outside of the crown group, yet are more closely related to it than to any other major clade. Stem groups are often, though not necessarily, paraphyletic (Figure 1.5).

Phylogenetic analyses can be based on two basic types of data: (1) **molecular** sequences, including DNA and, less commonly, proteins; and (2) **morphological** observations. With the exception of extremely young (i.e., Pleistocene) material, fossils do not preserve any usable DNA. Likewise, protein sequences have never been reported from any truly ancient cetacean fossil, although it is possible that some limited information may be preserved under ideal conditions. Reconstructing the evolutionary relationships of fossil taxa must therefore rely solely on morphological data, although molecular sequences still play an important role in the placement of extant species—and thus, by proxy, also that of their close fossil relatives (Wiens, 2009). At the basis of morphological phylogenetics lies anatomical observation (as discussed in this chapter). For the purpose of phylogenetic reconstruction, descriptive morphological data are usually broken down into **discrete characters**, each of which can take two or more **states** (Figure 1.6). For example, a simple character may record the presence (state 0) or absence (state 1) of an external hind limb. The characters are then collated into a **matrix** and analyzed according to cladistic principles.

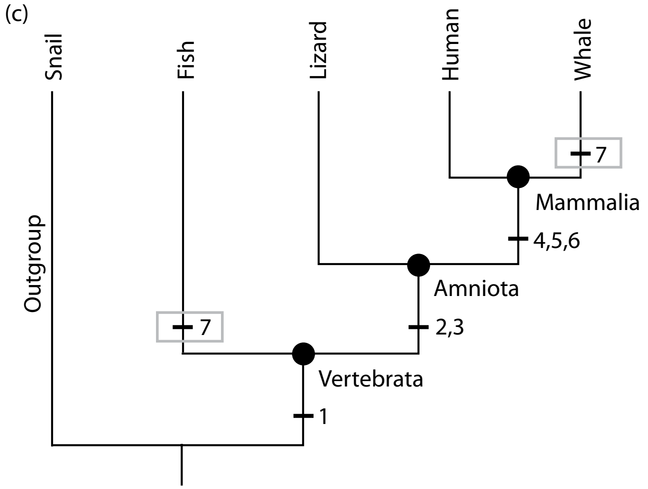
Cladistics was first proposed by the German entomologist Willi Hennig (Hennig, 1965), who proposed that two species should only be considered as related to each other if they are united by one or more derived characters. In other words, evolutionary relatedness must be demonstrated by the possession of **shared, homologous features** demonstrating an evolutionary change from a primitive state (**plesiomorphy**) to a derived state (**apomorphy**). Each character has therefore a **polarity** (primitive to derived), which is usually reflected in the numbering of states within a cladistic matrix; by convention, 0 denotes the primitive condition. Imposing character polarities naturally raises the question of how the primitive state can be recognized. The most commonly used option is to define an external point of reference, usually in the form of an additional species (**outgroup**), that clearly falls outside the group of interest and therefore is likely to show the primitive state for all of the analyzed characters.

Figure 1.6 provides an example of a simple cladistic analysis. The matrix shown in Figure 1.6a contains five taxa scored for seven characters (Figure 1.6b). The snail represents the outgroup and accordingly shows the primitive state (0) for all characters. All of the other taxa possess a certain number of derived features (synapomorphies; state 1). Whales and humans share most of these derived characters (e.g., possession of hair, constant body temperature, and suckling of young), followed by lizards and, finally, fishes. The matrix therefore suggests a ladder-shaped cladistic hypothesis, or **cladogram**, in which whales and humans form a clade (in this case, Mammalia) to the exclusion of all other taxa in the analysis. Together, mammals are most closely related to lizards, with which they form a clade known as Amniota—animals producing eggs with a protective membrane. Finally, all amniotes share a common ancestor with fishes.

The scenario shown here is the most likely given the available data, but note that there are other possibilities. As shown by character 7 in Figure 1.6, whales and fishes share an aquatic lifestyle, which could be interpreted as evidence for a

(a)

| | Character number | | | | | | |
|---|---|---|---|---|---|---|---|
| Taxon | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| Snail | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Fish | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| Lizard | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| Human | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| Whale | 1 | 1 | 1 | 1 | 1 | 1 | 1 |



(b)

1) Vertebral column: 0, absent; 1, present
2) Embryo covered by protective membrane: 0, absent; 1, present
3) Four limbs with five fingers each: 0, absent; 1, present
4) Hair: 0, absent; 1, present
5) Constant body temperature: 0, absent; 1, present
6) Suckling of young: 0, absent; 1, present
7) Aquatic lifestyle: 0, absent; 1, present

**Figure 1.6** Example of a simple cladistic analysis. (a) Data matrix comprising five taxa (the snail is the outgroup) and seven characters, described in (b). Analysis of the data matrix would result in the cladogram shown in (c). In (c), numbers refer to characters supporting a particular branch. Characters 1–6 are synapomorphies, whereas character 7 is homoplastic and an autapomorphy of fishes and whales, respectively.

close relationship of these two taxa to the exclusion of humans and lizards. If this were true, however, then hair, a constant body temperature and suckling would have had to evolve twice—once in whales, and once in humans. Similarly, a protective egg membrane would have had to arise twice, or else be lost convergently in fishes. More evidence thus speaks for the tree shown in Figure 1.6c, which is more **parsimonious** than the alternative arrangement that allies whales and fishes. In the context of this analysis, being aquatic is thus a **homoplasy** (i.e., a derived feature that is shared but not homologous, having instead arisen via **convergent evolution**). Because an aquatic existence now only characterizes single branches (whales and fishes, respectively), rather than a clade, it is also known as an **autapomorphy**.

This example is a simple demonstration of the principle of **maximum parsimony**, which seeks to minimize the number of transitions between different states. The tree, or trees, with the smallest number of **steps** are considered optimal, and preferred over alternative, less parsimonious arrangements. In computerized form, parsimony analysis has long been one of the most important cladistic tools, and is still widely used to analyze morphological data. Alternative approaches include **maximum likelihood** and **Bayesian** methods, which have largely replaced maximum parsimony in the context of molecular phylogenetics, and are increasingly being adopted by morphologists as well. Unlike parsimony, these approaches include assumptions about how often and how easily changes between certain states can occur. Such models are particularly relevant with regards to molecular data, since it is known that certain mutations are less likely to occur than others. In addition, Bayesian methods offer the advantage of greater control by allowing the inclusion of (well-justified) *a priori* assumptions about tree shape and other analysis parameters.

Recent trends also include the combination of molecular and morphological data into **total evidence** analyses (Deméré *et al.*, 2008; Geisler *et al.*, 2011), and a realization that both data types can be used to estimate the time at which two taxa diverged (section 4.5) (Pyron, 2011; Ronquist *et al.*, 2012). To do so, the total amount of molecular and/or morphological change that occurred along a particular branch is calculated and calibrated against the fossil record, often based on a series of predetermined fossil taxa of known age. This calibration effectively turns the rate of change into a **molecular/morphological clock**, which can either be held constant throughout the tree (**strict clock**) or be allowed to vary across lineages (**relaxed clock**). The latter is often a more likely scenario, since changes in generation times, population sizes, protein functions, species-specific physiological mechanisms, and the strength of natural selection likely conspire to render a universal, strict clock inapplicable (Ayala, 1999).

Once a tree has been constructed, it can be used to reconstruct the combination of morphological character states or molecular sequences that would have been present at each of its internal nodes. **Ancestral state reconstruction** can be carried out within a parsimony, likelihood or Bayesian framework, and is often employed to infer unknown traits for a particular taxon (e.g., soft tissue characters) based on its position in the phylogeny itself—a process also known as **phylogenetic bracketing** (Witmer, 1995). In addition, ancestral state reconstruction can be used to trace the evolution of a particular character over time, or to estimate the morphology of a hypothetical ancestor. Such reconstructions therefore create predictions about particular morphologies that have not yet been found as actual specimens, but are likely to have occurred based on the existing fossil record. One recent example of this approach is the reconstruction of the hypothetical ancestor of all placental mammals, based on a large phylogenetic analysis comprising all major mammalian clades (O'Leary *et al.*, 2013).

### 1.4.3 Habitat and feeding preferences

The habitat preference of a particular fossil species can often be reconstructed from associated **stratigraphic** and **sedimentological** data. However, such information can be confounded by postmortem transportation of the carcass, and it does not record movement during life. Thus, for example, an archaic whale could well have been at home both in the water and on land, even if its remains are only preserved in marine rocks. Tooth morphology, **wear**, **microwear**, and **tooth marks** can provide data on diet and, by proxy, habitat (section 6.1)

(Fahlke, 2012; Fahlke *et al.*, 2013; Thewissen *et al.*, 2011). However, the study of these features relies on the presence of teeth, which are absent, reduced, or highly simplified in many cetaceans, and thus often fails to distinguish clearly between different habitat and prey types. Other observations related to functional anatomy, such as the ability to rotate the jaw or the estimation of muscle function and maximum bite force via **Finite Element Analysis** (Snively *et al.*, 2015), can offer insights into particular feeding strategies, but generally do not distinguish habitats.

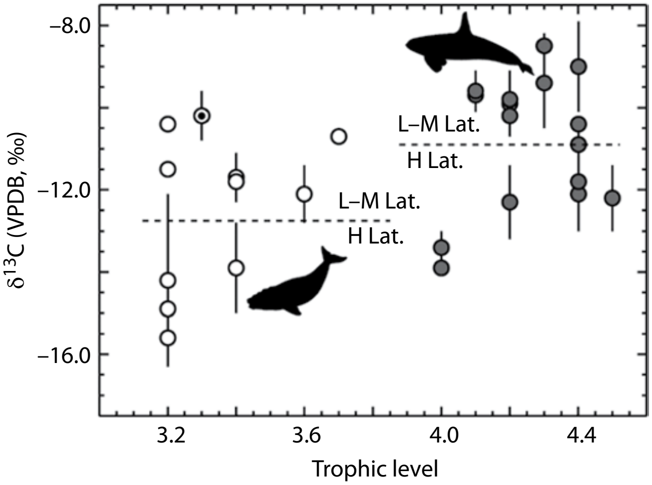
A fourth option is the interpretation of **stable isotope ratios**, particularly those of oxygen and carbon (Clementz *et al.*, 2006; Roe *et al.*, 1998). Oxygen and carbon are both essential components of body tissues, the isotopic composition of which is determined by body and ambient water, as well as an animal's diet. Because of their different physical properties, isotopes vary in the rate at which they take part in environmental and biological processes, such as evaporation, condensation, and tissue formation. Ultimately, this leads to differences in the isotopic compositions of various substances, which can be recorded in the form of stable isotope ratios ($^{18}O/^{16}O$ and $^{13}C/^{12}C$, respectively) and are usually expressed as deviations ($\delta$) from an international standard. Recorded in bone or teeth, such isotopic signals can become "fossilized" along with the remains of the animal itself.

To distinguish marine, freshwater, and terrestrial species (sections 5.1 and 6.1), it is important to consider both the actual value and the variability of their oxygen isotopic signal (Clementz and Koch, 2001; Clementz *et al.*, 2006). $^{16}O$ isotopes evaporate more easily than $^{18}O$, which causes vapor formed over the ocean to be enriched in $^{16}O$. As the vapor moves inland, it condenses and falls as rain, which builds up to form freshwater. This process results in a distinct isotopic difference (typically 3‰) between marine and freshwater environments (Roe *et al.*, 1998). In fully aquatic animals, such as modern cetaceans, this isotopic signal ($\delta^{18}O$) is incorporated into body tissues via direct exchange of water through the skin and ingestion of water during feeding (Costa, 2009; Hui, 1981). Because aquatic environments are relatively homogeneous, variations in the isotopic signal tend to be low—with the exception of some highly variable freshwater systems, such as estuaries. Thus, both freshwater and marine species are characterized by a narrow range of oxygen isotope values (Clementz and Koch, 2001), with freshwater taxa generally scoring lower (Clementz *et al.*, 2006; Thewissen *et al.*, 1996). By contrast, the tissues of terrestrial animals mainly reflect the isotopic composition of dietary and drinking water, the composition of which varies from place to place and over time as a result of evaporation, distance from the sea and differences in elevation. In addition, species-specific physiological processes introduce further variation, which leads to terrestrial species having much more variable $\delta^{18}O$ values than marine animals (Clementz *et al.*, 2006).

Carbon isotope ($\delta^{13}C$) values record the type of primary producer sustaining a particular food web, as well as the trophic level at which an animal feeds. The former is mainly related to the photosynthetic pathway (C3, C4, or CAM) employed by the primary producer and the environmental conditions in which the latter grows. Together, these variables result in a broad range of $\delta^{13}C$ values that distinguish terrestrial from aquatic environments (Thewissen *et al.*, 2011), as well as freshwater and marine offshore habitats (low $\delta^{13}C$) from nearshore habitats (high $\delta^{13}C$) (Clementz *et al.*, 2006). **Trophic fractionation** occurs each time one organism is being fed on by another, and results in a slight enrichment in $^{13}C$ in the tissues of the consumer (Vander Zanden and Rasmussen, 2001). Cumulatively, this enrichment results in markedly higher $\delta^{13}C$ values in consumers feeding at a high trophic level relative to those feeding at a low one (Figure 1.7) (Clementz *et al.*, 2014). Isotope fractionation also occurs to a different degree in herbivores versus carnivores, and can thus be used to distinguish feeding strategies (Clementz *et al.*, 2006; Thewissen *et al.*, 2011).

In addition to reflecting habitat type and feeding, both oxygen and carbon isotopes correlate negatively with latitude as a result of different temperatures, salinities, and levels of productivity. This spatial variation, which seems to have existed since at least the Eocene, results in greater than expected isotopic variance in migratory species (Clementz and Sewall, 2011; Roe *et al.*, 1998). Because the exact relationship between isotopic composition

**Figure 1.7** Graph showing the effect of latitude and trophic level on the stable isotope composition of carbon incorporated in mysticete (white circles) and odontocete (gray circles) teeth and bones. Higher trophic levels reflect longer food chains leading up to the final consumer. The white circle marked by a dot marks an exception: the gray whale, *Eschrichtius robustus*, which differs from other mysticetes in feeding on benthic invertebrates at high latitudes. H Lat., high latitude; L–M Lat., low–mid latitude. Reproduced from Clementz *et al.* (2014), with permission of Elsevier.



and latitude differs between hemispheres and ocean basins, it can be used to identify consumers foraging in particular geographic areas, as well as to create a map of isotopic composition (isoscape) to track the movements of marine consumers (Clementz *et al.*, 2014; Graham *et al.*, 2010).

### 1.4.4 Macroevolutionary dynamics

**Macroevolution** is the study of major, supraspecific evolutionary patterns, such as **adaptive radiations**, evolutionary **trends**, major **turnover events**, and **convergent evolution**, usually over timescales of millions of years (sections 7.1–7.5 and 7.7). To place macroevolutionary events in a temporal context, relevant fossils first need to be dated. Sometimes, this can be done more or less directly by determining the age of fossil-bearing rocks absolutely via **radiometric dating**. Where the latter is impossible—which it often is—rocks are instead dated in a relative fashion by correlating them with units of known age based on their lithology, magnetic profile, chemical composition, or fossil content (**biostratigraphy**). To facilitate comparisons across wide geographical areas, time periods characterized by the occurrence of particular organisms or magnetic profiles are grouped into biozones and chrons, respectively, and correlated with the global **geological time scale**. The latter groups all of Earth's history into a series of hierarchical units, which, in descending order, comprise eons, eras, periods, epochs, and stages. Cetaceans are only known from the most recent eon (the Phanaerozoic, or time of "visible life") and era (the Caenozoic, or time of "new life"), but span both the Paleogene and Neogene periods, as well as several epochs (Figure 1.8).

Once fossils have been dated, their occurrence can be correlated with other paleontological and paleoenvironmental data to identify potential biotic or physical factors that may have acted as **evolutionary drivers**. In the case of cetaceans, potential candidates may range from **competition** to **key innovations** (e.g., baleen and echolocation), ocean restructuring and changes in climate, sea level and food abundance (Fordyce, 1980; Marx and Uhen, 2010; Pyenson *et al.*, 2014b). To investigate whether any of these phenomena played a role in cetacean evolution, there first needs to be an estimate of past biological diversity (Marx and Uhen, 2010; Slater *et al.*, 2010; Steeman *et al.*, 2009). The

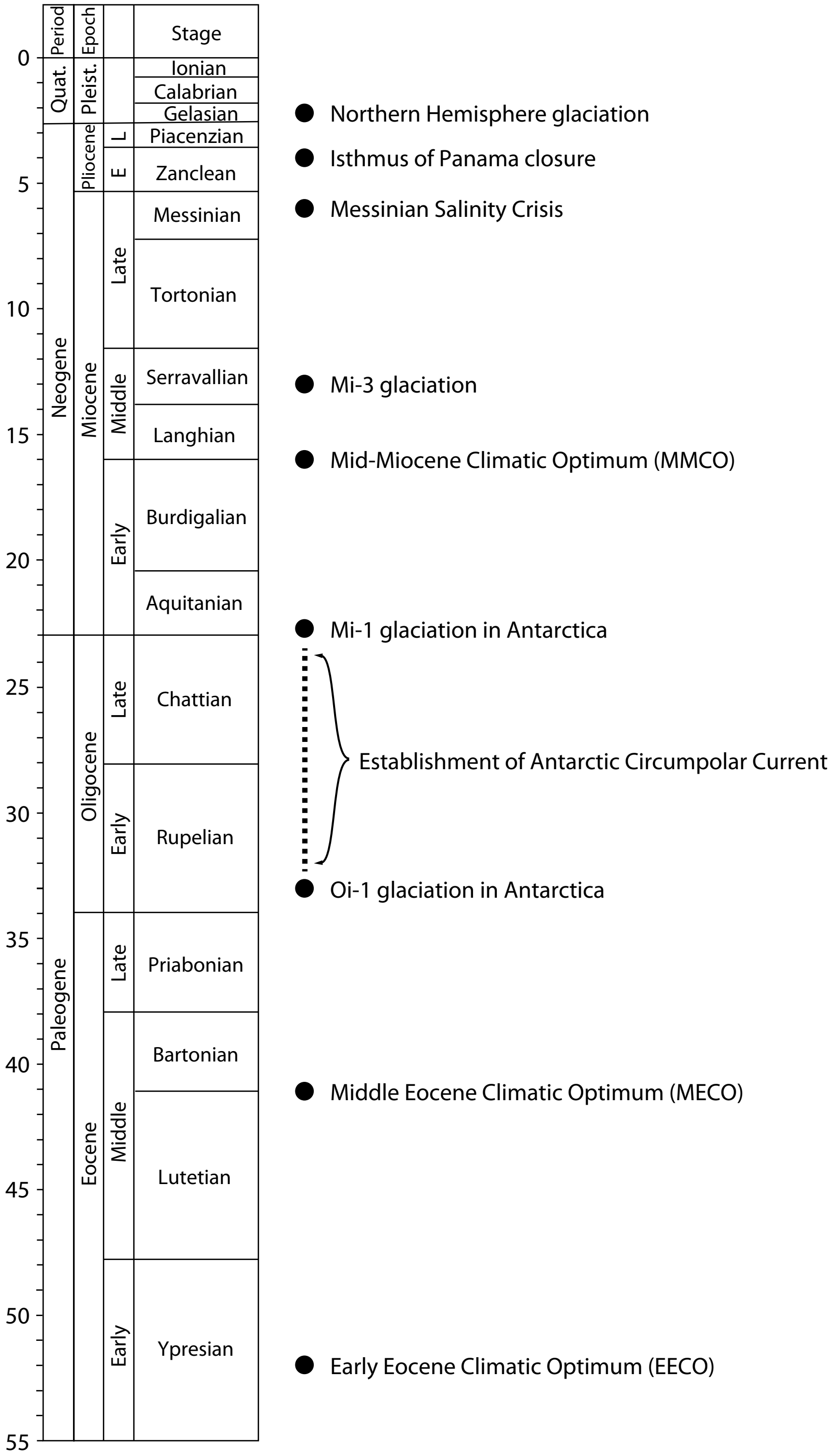


**Figure 1.8** Geological time scale with significant earth history events.

latter is a rather inclusive concept comprising aspects of taxonomy, ecology, and morphology, and accordingly can be quantified in a number of ways.

**Taxonomic diversity** measures the total number of species (or higher ranking taxa) that existed at a particular point in time, as judged from their stratigraphic occurrence (section 7.1). This is the most direct measure of biological diversity, and forms the basis for assessments of lineage **diversification** and **extinction**. However, taxonomic diversity can also be strongly biased, for example, by variable amounts of rock that can be searched for fossils (Smith, 2007; Uhen and Pyenson, 2007). Rather than numbers of taxa, morphological diversity (**disparity**) measures among-species variation in overall body shape (section 7.3) (Foote, 1991). A simple way to think about disparity is to compare an African elephant with an Indian elephant on the one hand, and an elephant with an ant on the other. In both cases, taxonomic diversity is the same (two species), yet it is perfectly obvious even to the non-biologist that the African and Indian elephants look much more similar to each other (i.e., they are less disparate) than either does to the ant. Disparity can be quantified either with regards to overall body shape (Wills *et al.*, 1994) or by focusing on a particular phenotypic trait, such as body or brain size (Lambert *et al.*, 2010; Montgomery *et al.*, 2013; Slater *et al.*, 2010). Finally, **ecological** and **functional disparity** measure variation in life habits, such as diets, feeding styles, or modes of locomotion (Slater *et al.*, 2010).

Although not entirely reliant on it, macroevolutionary analyses greatly benefit from the inclusion of phylogenetic data. Crucially, phylogenies (1) allow the integration of molecular data; (2) provide an alternative way to date lineage divergences (based on molecular/morphological clocks; section 1.4.2), and thus the timing of macroevolutionary events; and (3) provide a framework within which diversity and disparity changes can be analyzed statistically. Phylogeny-dependent analyses include calculating rates of phenotypic and genomic change (Lee *et al.*, 2013), the tempo of lineage diversification, disparification, and extinction (Rabosky, 2014; Thomas and Freckleton, 2012), and the detailed dynamics of evolutionary trends (sections 7.1 and 7.4) (Montgomery *et al.*, 2013). Recent work has even attempted to estimate past taxonomic diversity from molecular-based phylogenies of extant taxa alone, with potentially promising results (Morlon *et al.*, 2011).

### 1.4.5 Other methodologies

Beyond the fields of study detailed in this chapter, insights on cetacean evolution have also come from **bone histology**, **pathology**, and **taphonomy**. Thus, increased bone density has been interpreted as ballast enabling early cetaceans to stay underwater (de Buffrénil *et al.*, 1990; Gray *et al.*, 2007; Thewissen *et al.*, 2007); the presence of well-developed columns of spongy bone in the limb bones as providing support for terrestrial locomotion (Madar, 1998); bone fractures in the lower jaw as evidence of benthic feeding (Beatty and Dooley, 2009); bony outgrowths along tooth sockets as a clue to raptorial feeding (Lambert *et al.*, 2014); and localized breakdown of bone as a proxy for diving-related decompression syndrome, commonly known as the "bends" (Beatty and Rothschild, 2008). By contrast, taphonomy generally does not provide insights into cetacean biology itself, but may elucidate causes of past mass strandings, such as toxic algal blooms (Pyenson *et al.*, 2014a).

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