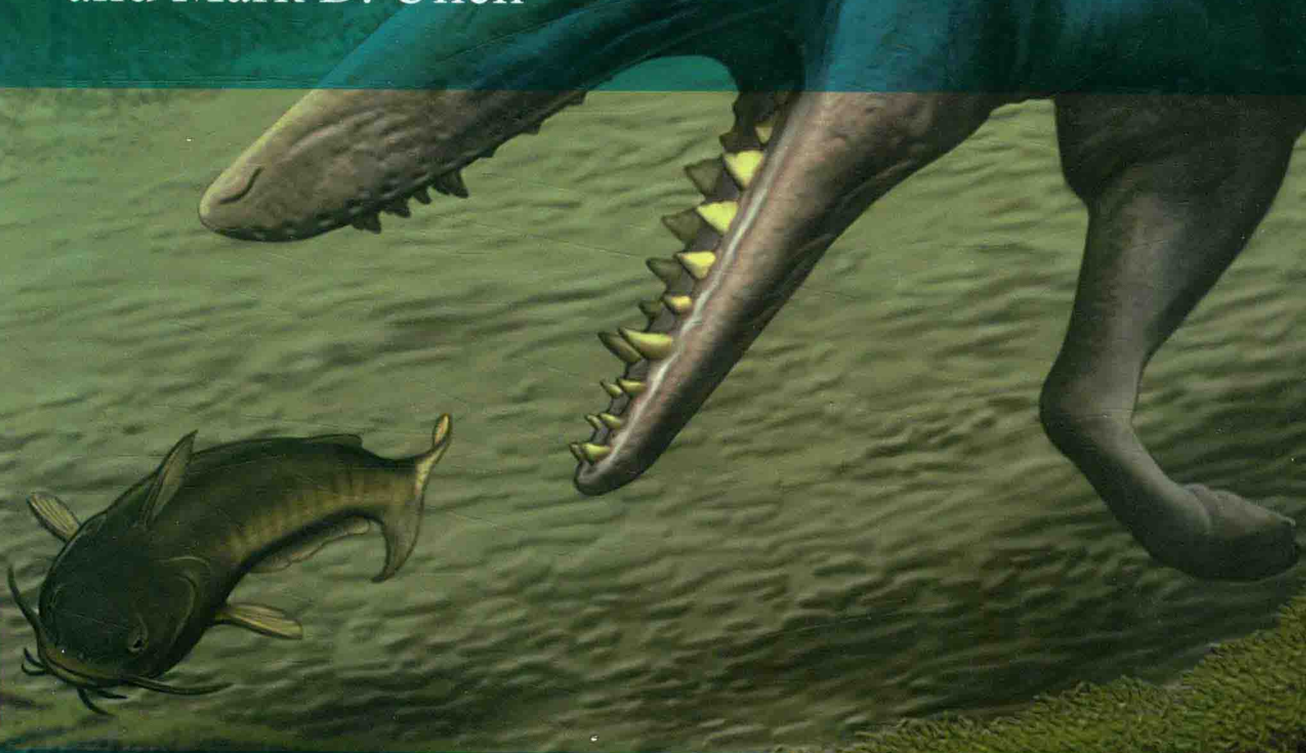
Topics in Paleobiology

Cetacean Paleobiology

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



Series Editor: Professor Michael J. Benton

WILEY Blackwell

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Registered Office
John Wiley & Sons, Ltd, The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK

Editorial Offices
9600 Garsington Road, Oxford, OX4 2DQ, UK
The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK
111 River Street, Hoboken, NJ 07030-5774, USA

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Library of Congress Cataloging-in-Publication Data

Names: Marx, Felix G., author. | Lambert, Olivier, (Paleontologist), author. |
Uhen, Mark D., author.
Title: Cetacean paleobiology / Felix G. Marx, Olivier Lambert and Mark D. Uhen.
Description: Chichester, UK; Hoboken, NJ : John Wiley & Sons, 2016. |
Includes bibliographical references and index.
Identifiers: LCCN 2015047431 (print) | LCCN 2016005795 (ebook) |
ISBN 9781118561270 (cloth : alk. paper) | ISBN 9781118561539 (pbk. : alk. paper) |
ISBN 9781118561362 (Adobe PDF) | ISBN 9781118561553 (ePub)
Subjects: LCSH: Cetacea, Fossil. | Evolutionary paleobiology.
Classification: LCC QE882.C5 M37 2016 (print) | LCC QE882.C5 (ebook) |
DDC 569/.5–dc23
LC record available at http://lccn.loc.gov/2015047431

A catalogue record for this book is available from the British Library.

Wiley also publishes its books in a variety of electronic formats. Some content that appears in print may not be available in electronic books.

Cover image: Courtesy by Carl Buell
Cover design by Design Deluxe

Set in 9/11.5pt Trump Mediaeval by SPi Global, Pondicherry, India

Printed in Singapore by C.O.S. Printers Pte Ltd

1 2016

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.

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

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

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Previously published

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Rainer R. Schoch
ISBN: 978-0-470-67178-8 Paperback; May 2014

Dinosaur Paleobiology
Stephen L. Brusatte
ISBN: 978-0-470-65658-7 Paperback; April 2012

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.

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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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Acknowledgments

Writing a book like this inevitably means to stand on the shoulders of giants. None of us could have begun to conceptualize such a project without being able to draw on the work of our colleagues and predecessors. To all of them, and to the many other people who have been involved in the discovery, preparation, curation, and study of fossil cetaceans, we extend our sincere thanks. Writing this book has been both a joy and a journey—not just for us but also for our families, who patiently endured the many hours we spent on this project. Brian, Catherine, Ikerne, and Matthias: we greatly appreciate your loving support, and dedicate this book to you. Much of what we know we owe to our former mentors and teachers. Our special thanks thus go to Michael J. Benton, R. Ewan Fordyce, Philip D. Gingerich, Pascal Godefroit, James G. Mead, and Christian de Muizon, all of whom have shaped our careers, never ceased to provide advice and help when needed and, more than anything, have become great friends.

Finally, we wish to thank the many people who helped to advance this book indirectly through insightful discussions, or went out of their way to help us out with photographs and information. Their help has been invaluable, and any errors in interpreting their contributions are entirely ours. Many thanks to: Lawrence G. Barnes, Ryan M. Bebej, Annalisa Berta, Giovanni Bianucci, Michelangelo Bisconti, Robert W. Boessenecker, David J. Bohaska, Mark Bosselaers, Mark D. Clementz, Lisa N. Cooper, Thomas A. Deméré, Erich M. G. Fitzgerald, R. Ewan Fordyce, Jonathan H. Geisler, Philip D. Gingerich, Stephen J. Godfrey, Pavel Gol'din, Oliver Hampe, Toshiyuki Kimura, Naoki Kohno, Lori Marino, James G. Mead, Ismael Miján, Christian de Muizon, Maureen A. O'Leary, Mary Parrish, George Phillips, Klaas Post, Nicholas D. Pyenson, Rachel A. Racicot, J. G. M. Thewissen, Mario Urbina, William J. Sanders, Frank D. Whitmore Jr., and Tadasu Yamada. Finally, we wish to thank Michael J. Benton for suggesting that we write this book, and Delia Sandford and Kelvin Matthews for their support and guidance during the writing process.

Contents

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.

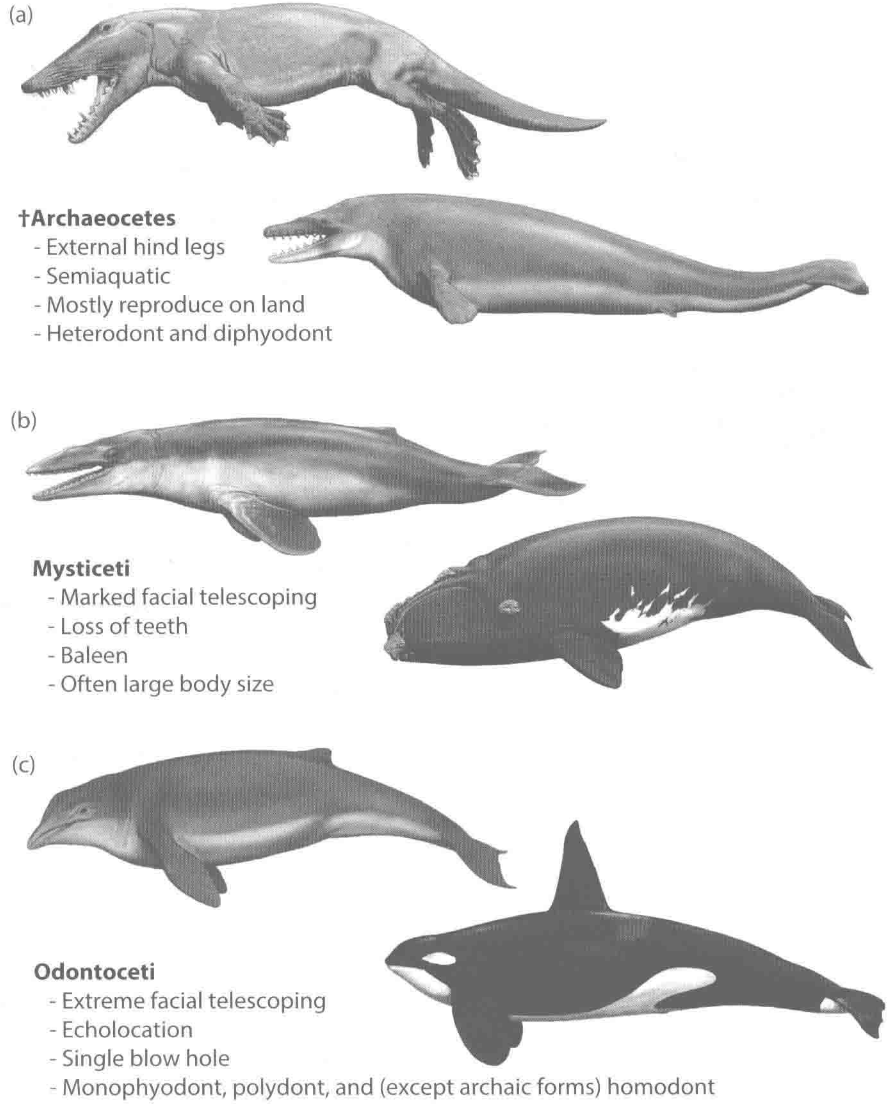
1.2 What is a whale?

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).

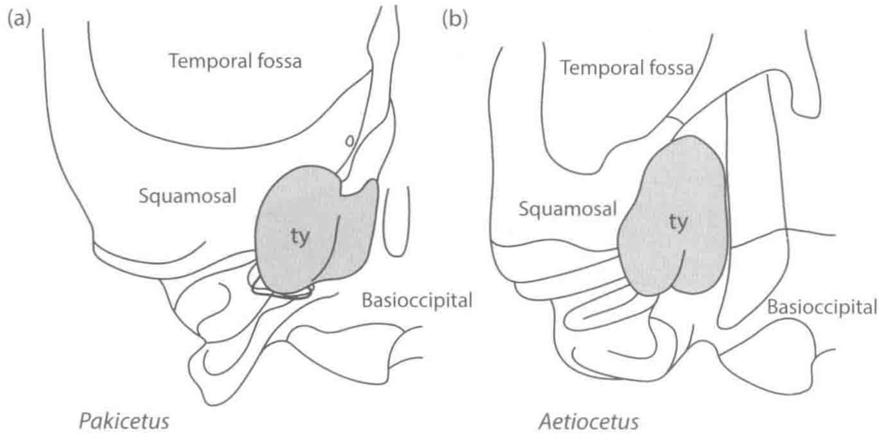
Figure 1.1 Overview of the three main subdivisions of Cetacea: (a) archaeocetes (archaic whales), (b) Mysticeti (baleen whales), and (c) Odontoceti (toothed whales, including dolphins). Life reconstructions © C. Buell.



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

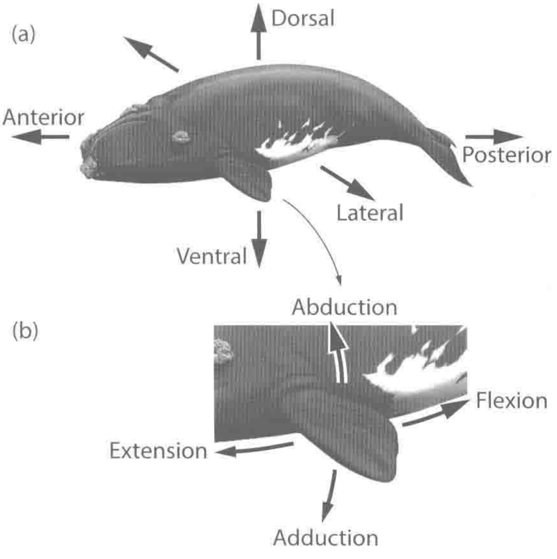


Figure 1.3 Standard anatomical terms of (a) location and (b) motion. Life reconstructions © C. Buell.

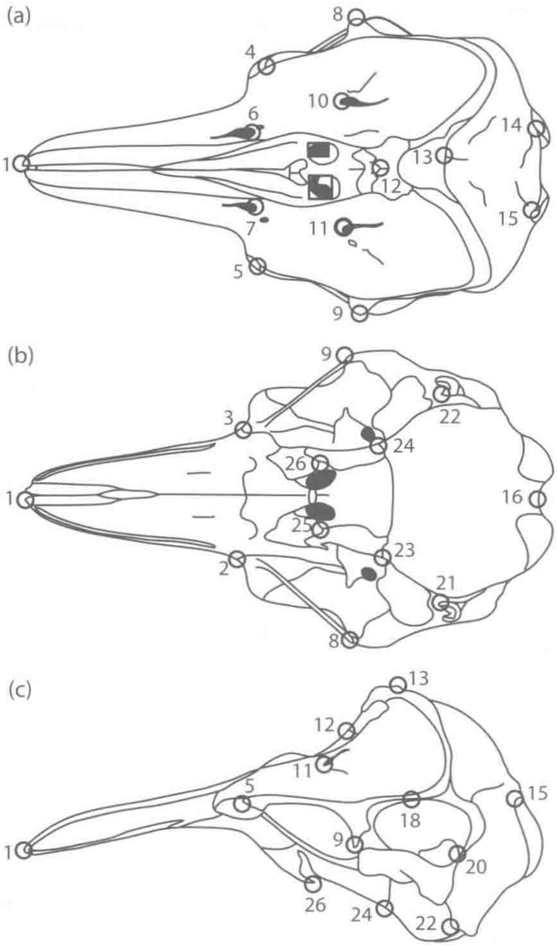


Figure 1.4 Example of a three-dimensional set of landmarks, based on the skull of a porpoise. (a) Dorsal, (b) ventral, and (c) lateral views. Reproduced from Galatius (2010), with permission of the Linnean Society of London.

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