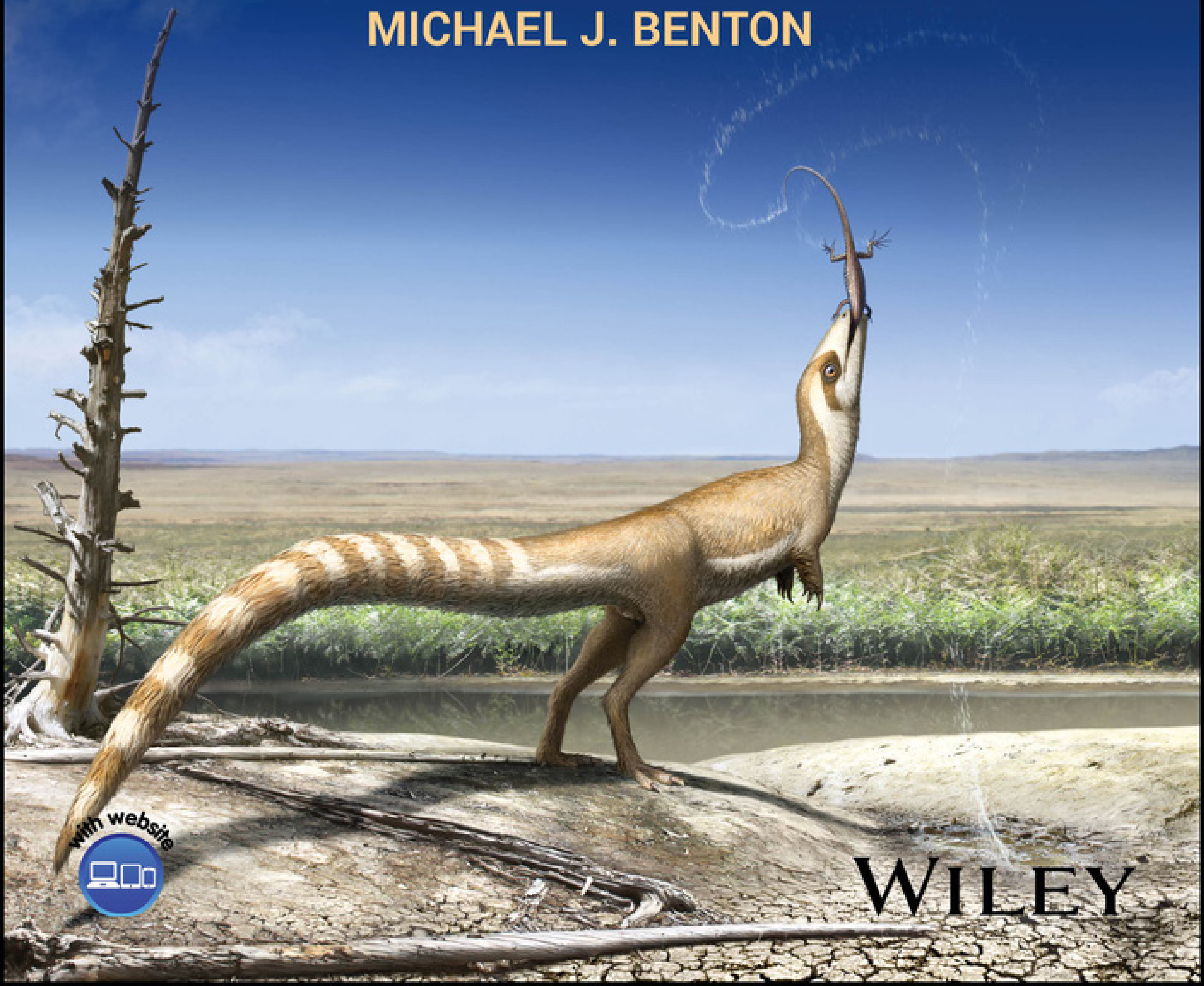
FIFTH EDITION

VERTEBRATE PALAEONTOLOGY

MICHAEL J. BENTON



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Dedicated to Mary, for her good-humoured acceptance of my six months of absent mindedness while I revised this book.

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Preface

Palaeontology in general, and vertebrate palaeontology in particular, is all about finding new fossils. Or is it? If you rely on newspapers and social media for your news, the reports are mainly about the latest dinosaurs or human fossil finds. These discoveries are massively important of course, and we can celebrate that palaeontologists are active in lands that had not been much explored before, such as China and various countries in Africa and South America. The new fossils expand our knowledge of fossil distributions, and of course, many of them offer remarkable new information. But, as any young palaeobiologist knows, the discovery of new species is a minor concern. Much more exciting has been the blossoming of new computational techniques that extend the reach of studies in macroevolution and palaeobiology further than might have been imagined even ten years ago.

When I wrote the first edition of this book in 1989, I felt that there was a need for an up-to-date account of what is known about the history of vertebrates, but also for a thorough phylogenetic framework throughout, then something of a novelty. The first edition was published in 1990. The second edition, substantially modified, appeared in 1997, the third, extensively rewritten in 2005, and the fourth, further updated and enlarged and with a section of colour plates, in 2015. These new editions offered extensive coverage of new discoveries and new interpretations through the previous 25 years. Between 1990 and 2005, the book hopped from publisher to publisher: it was commissioned by Unwin Hyman, who was soon after acquired by Harper Collins, and their science list was in turn acquired by Chapman & Hall, so the first edition appeared under three publishers' logos, in 1990, 1991 and 1995. The second edition appeared with Chapman & Hall, but they were then taken over by Kluwer, and this book was marketed by their Stanley Thornes subsidiary for a while, before passing to Blackwell Science in 2000, which is now part of John Wiley & Sons. I hope these wandering days are now over.

The first edition appeared in Spanish in 1995 (*Paleontología y evolución de los vertebrados*, Edition Perfils, Lleida), the second in Italian in 2000 (*Paleontologia dei Vertebrati*, Franco Lucisano Editore, Milano), the third in German in 2007 (*Paläontologie der Wirbeltiere*, Dr Friedrich Pfeil, München), and the fourth in Chinese (*Gǔ jǐchuí dòngwù* xué [*Vertebrate Palaeontology*], Science Press, Beijing, 2017). This is a measure of the international appeal of vertebrate palaeontology and the demand from students and instructors for up-to-date information.

Presenting this new, fifth, edition to the public is hugely exciting for me, for three reasons. First, this marks 35 years in print – ever since 1990 – and I am still beavering on. Second, it is a chance to share an astonishing array of remarkable new research across the field, from the first fossil chordates in the Cambrian to fossil hominids. Third, it is all in colour. Publishing has advanced in leaps and bounds since the last edition, in 2015, and colour is the norm in scientific papers. Young authors take great care in designing the images in their papers, so they are as graphic and informative as possible. This massively helps the textbook writer and reader.

The story of the evolution of the vertebrates, the animals with backbones, is fascinating. There is currently an explosion of new research ideas in the field concerning all the major evolutionary transitions, the origin of the vertebrates, dramatic new fish specimens unlike anything now living, adaptations to life on land, the Triassic revolution when life recovered from the profound end-Permian mass extinction, the origin and radiation of dinosaurs, the evolution and palaeobiology of dinosaurs, the origin and diversification of birds, the earliest mammals, ecology and mammalian diversification, the Paleogene radiation of modern mammalian clades, reconciling morphological and molecular evidence on bird and mammal evolution, and the origins and evolution of human beings.

I have five aims in writing this book. The first aim is to present **a readable narrative of the history of the vertebrates** that is accessible to everyone, with either a professional or an amateur interest in the subject. The book broadly follows the time sequence of major events in the sea and on land so that it can be read as a continuous narrative, or individual chapters may be read on their own. I have tried to show the adaptations of all major extinct groups, both in words and in images.

The second aim is to highlight **major evolutionary anatomical changes** among vertebrate groups. This book is not a classic anatomy text, and there is no space to give a complete account of all aspects of the hard-part and soft-part anatomy of the major groups. However, I have selected certain evolutionary anatomical topics, such as the vertebrate brain, tetrapod vertebral evolution, posture and gait in archosaurs, and endothermy in mammals, to present an overview of current thinking, including evolutionary and developmental aspects, where appropriate.

The third aim is to show **how palaeobiological information is obtained**. It is important to understand the methods and debates, and not simply to assume that all knowledge is fixed and immutable. Further, science is about testing hypotheses against evidence, not about who shouts loudest, and it is important to realize that even historical sciences, such as palaeontology, can work through hypothesis testing. As an introduction, I summarize in Chapter 2 the methods used by vertebrate palaeontologists in collecting and preparing the fossils, in using them to learn about ancient environments, biomechanics and palaeobiology, and as evidence for discovering parts of the great evolutionary tree of life. Then, throughout the text, I present box features that are divided into three categories: tree of life controversies (deuterostome relationships, jawless fishes, osteichthyans, sarcopterygians, basal tetrapods, amniotes, dinosaurs and the origin of birds, molecular information on mammalian phylogeny, hominin relationships), exceptional fossils or faunas (new exceptionally preserved basal chordates from China, a rich fossil deposit of early tetrapods, exceptional fishes and marine reptiles from the Triassic of China, dramatic new discoveries of Cretaceous birds, fossil mammals with hair, new basal humans from Africa, the Flores 'hobbit') and palaeobiology of selected unusual ancient vertebrates (limb mechanics of the first tetrapods, jaw action and diet of dicynodonts, archosaur locomotion, hadrosaur chewing adaptations, flight efficiency in pterosaurs, giant penguins, horse-eating birds, rodents as large as rhinos).

The fourth aim is to survey **the present state of discovery of the tree of life of vertebrates**. The cladograms are set apart from the body of the text, and comprehensive lists of the key diagnostic characters are given. In some cases, there are controversies among palaeontologists, or between the morphological and the molecular results, and these are explored. In many cases, it was a difficult task to represent current views fairly, yet incisively. Some parts of the tree appear to have been relatively stable for ten years or more, whereas others are changing rapidly – these aspects are indicated. The cladograms throughout the book may be linked to provide an overview of the vertebrate tree of life, and this is replicated in the classification (Appendix).

The fifth aim, which has always been embedded in earlier editions, is to highlight **career development for aspiring palaeontologists**. This is done partly by the emphasis on method: the young palaeontologist, progressing through Bachelors, Masters, and Doctoral degrees, must keep an open and enquiring mind. Learning in detail about the occurrence, anatomy, systematics, and function of a particular group of sharks, dinosaurs, or rodents is clearly crucial, as ever, but now the enthusiastic student must also master reasonably advanced computational protocols in phylogenetic, macroevolutionary, palaeoecological, taphonomic, or biomechanical analysis. Interdisciplinarity is key. The message about career development is stressed also by the choice of current research highlights in the box features: many of these are based on recent publications by young researchers.

I am indebted to many people. I thank †Roger Jones and Clem Earle of Unwin Hyman who commissioned the first edition 35 years ago, Ward Cooper of Chapman & Hall who steered the second edition through, and Ian Francis and Delia Sandford who worked hard on the third and fourth editions for Blackwell and Blackwell-Wiley. The following people read parts of earlier editions, or made other valuable contributions: †Dick Aldridge, Phil Anderson, †Peter Andrews, Kenneth Angielczyk, David Archibald, Chris Beard, Roger Benson, Donald Benton, David Berman, Martin Brazeau, Derek Briggs, Steve Brusatte, Richard Butler, †Henri Cappetta, †Bob Carroll, Luis Chiappe, Brian Choo, †Jenny Clack, Mike Coates, Liz Cook, Joel Cracraft, Ted Daeschler, Brian Davis, Eric Delson, †David Dineley, Phil Donoghue, Gareth Dyke, Greg Edgecombe, Andrzej Elzanowski, Susan Evans, Valentin Fischer, Jens Franzen, Nick Fraser, Matt Friedman, Jörg Fröbisch, Keqin Gao, †Brian Gardiner, †Alan Gentry, David Gower, Lance Grande, †Bev Halstead, David Hone, Jim Hopson, Axel Hungerbühler, Christine Janis, Philippe Janvier, †Dick Jefferies, Tom Kemp, †Zofia Kielan-Jaworowska, Gillian King, Jürgen Kriwet, Adrian Lister, Liz Loeffler, Zhexi Luo, John Maisey, Gerald Mayr, Andrew Milner, Sean Modesto, Jingmai O'Connor, Kevin Padian, †Alec Panchen, Mike Parrish, †Colin Patterson, Kevin Peterson, Davide Pisani, Mark Purnell, Emily Rayfield, Jeremy Rayner, Robert Reisz, Olivier Rieppel, Bruce Rubidge, Lauren Sallan, Rob Sansom, †Bob Savage, Rainer Schoch, Paul Sereno, Koen Stein, Glen Storrs, Chris Stringer, Pascal Tassy, Ian Tattersall, Mike Taylor, †Nigel Trewin, David Unwin, Jakob Vinther, †Cyril Walker, †Peter Wellnhofer, Bernard Wood, Feixiang Wu, Xing Xu, and Adam Yates. For the fifth edition, I thank Ken Angielczyk, Steve Brusatte, Emma Dunne, Russell Engelman, Greg Erickson, Dan Field, Anjali Goswami, Susana Gutarra, Joe Keating, Nicole Klein, Melissa Kemp, Dan Ksepka, Tetsuto Miyashita, Giovanni Mussini, Jingmai O'Connor, Jason Pardo, Emily Rayfield, Jason Russell, Lauren Sallan, Martin Sander, Rainer Schoch, Qingyi Tian, and Qi Zhao who read and commented on individual chapters, supplied images, or gave helpful advice. I thank Mike Drummond, Mike Hayes, and Carl Mendelson for pointing out errors in the previous edition.

My special thanks go to three artists: Libby Mulqueeny (Belfast) who drew most of the diagrams for the first edition of the book in a frenzy of work, John Sibbick (Bath) who prepared the chapter openers in earlier editions, and Debbie Maizels (Surrey) for computer-generated artwork in earlier editions. I also thank those people, who are acknowledged separately throughout the book, who supplied photographs and drawings. Finally, thanks to Frank Weinreich at Wiley for commissioning the revision and Indira Kumari and Jamila Niroop for careful work on the text.

Note Concerning the References

Throughout the book, I refer readers to relevant papers. Most of these are recent, but I include a few older, classic works. There are so many papers on some themes, such as the phylogenetic relationships of particular groups or the biomechanics of dinosaurs, that it is impossible to give a comprehensive, or even a fair listing. I have chosen by preference, short and well-illustrated papers and reviews that should be accessible to students. Indeed, I have tried to favour work by young researchers, especially in the box features – this has the additional purpose of showing students how their contemporaries and near-contemporaries are using their skill and enthusiasm to forge professional careers for themselves around the world.

Note: I would appreciate any corrections (e-mail to mike.benton@bristol.ac.uk). More details are available at https://www.bristol.ac.uk/earthsciences/research/palaeobiology/research/benton-lab/.

Michael J. Benton

About the Companion Website

This book is accompanied by a companion website:

www.wiley.com/go/benton/vertebratepalaeontology

The website includes:

- PowerPoints of all figures from the book for downloading

1

Vertebrates Originate

Key Questions in this Chapter

1) What are the closest living relatives of vertebrates? Did vertebrates originate as worms or bag-like beasts?
2) When did deuterostomes and chordates originate?
3) What are the key characteristics of chordates?
4) How do embryology and morphology, combined with new phylogenomic studies, inform us about the evolution of animals and the origin of vertebrates?
5) How do extraordinary new fossil discoveries from China help us understand the ancestry of vertebrates?

Introduction

Did vertebrates begin as worms or bags? This is the question. There are currently two viable hypotheses for the origin of vertebrates, called more properly the vermiform and the sessile hypotheses (Nanglu et al. 2023a). The vermiform hypothesis is that the ancestral vertebrate was like an enteropneust hemichordate, with a simple nervous system and a gill-slit-laden pharynx. The sessile origins hypothesis is that the ancestral vertebrate was a tentaculate animal that lived in a fixed position on the seabed and was perhaps more like a pterobranch hemichordate or a urochordate. We will look at what all this means, examining these close relatives of vertebrates as well as some spectacular fossils, and then summarize between worms and bags at the end of the chapter.

Vertebrates are the animals with backbones, fish, amphibians, reptiles, birds, and mammals. We have always been especially interested in vertebrates because this is the animal group that includes humans. The efforts of generations of vertebrate palaeontologists have been repaid by the discovery of countless spectacular fossils: heavily armoured fishes of the Ordovician and Devonian, seven- and eight-toed Devonian tetrapods, sail-backed synapsids, early birds and dinosaurs with feathers, giant rhinoceroses, rodents with horns, horse-eating flightless birds, and sabre-toothed cats. These fossils tell us where the living vertebrates have come from, and they show us glimpses of different worlds that are bizarre enough to defy the imagination of a science fiction writer. Despite all this information that has accumulated over the past 200 years, the origin of vertebrates is still hotly debated.

One thing is clear from the biology of living animals. Vertebrates are members of a larger group, the Phylum Chordata, which also includes their closest living relatives, marine animals such as the sea squirts and amphioxus (see below). These creatures do not have a skeleton, but they share other features, such as a **notochord**, a flexible, tough rod that runs the length of the body along the back. The notochord in living chordates is generally made from an outer sheath of collagen, a tough fibrous connective tissue that encloses turgid, fluid-filled spaces. Invertebrate chordates also have V-shaped muscle blocks (**myomeres**) along the length of their body. The question about the origin of vertebrates then broadens out to include the origin of chordates.

Looked at more widely, vertebrates are a minor twig among Animalia in the 'Tree of Life' (Figure 1.1). It is common to think of the major divisions of life as being animals, plants, protists, and simple organisms classed broadly as bacteria and viruses. Molecular studies (Williams et al. 2020; McGrath 2022) show that all living things evolved from a single last universal common ancestor (LUCA) perhaps 4000 Ma, and then split into two clades, Bacteria and Archaea. Eukaryota then branched from Archaea perhaps 2200 Ma, with some input from symbiotic bacteria to form fundamental cell organelles. The familiar plants, animals, and fungi are

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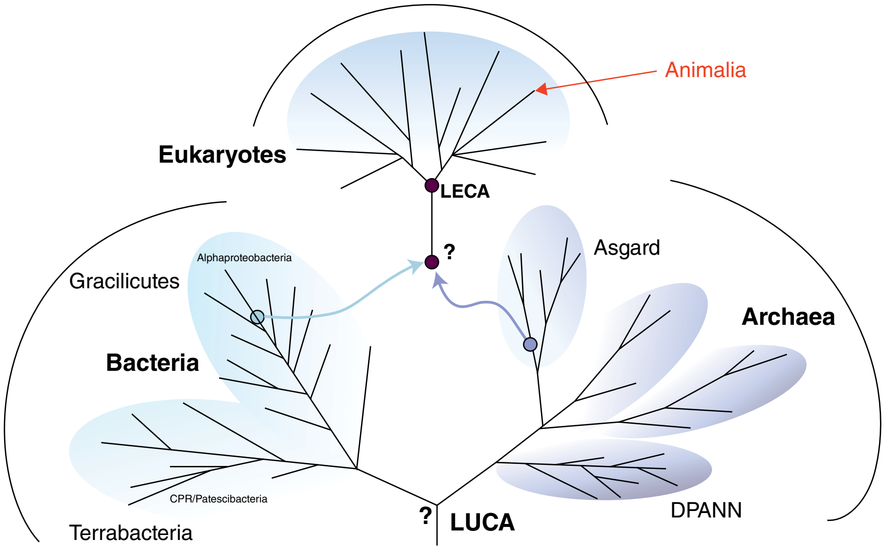

Figure 1.1 The Universal Tree of Life, showing the three main divisions: Eukarya, Archaea, and Eukaryotes. The last universal common ancestor (LUCA) and last eukaryote common ancestor (LECA) are marked. Animals are one of many twigs of the phylogenetic tree. *Source:* From McGrath (2022), reproduced according to CC BY-4.0 licence.

members of Eukaryota, all diagnosed by complex cells with a membrane-bound nucleus and mitochondria. Within Eukaryota are various protist groups, as well as plants, fungi, and animals, and of course, vertebrates are animals. Among animals, it has always been assumed that chordates are closely related to hemichordates (acorn worms and pterobranch worms) and echinoderms (starfish, sea lilies, and sea urchins), and this is now widely confirmed, based on morphological, developmental, and molecular evidence.

The purpose of this chapter is to explore the various lines of evidence that can be used to reconstruct the origin of the vertebrates: the study of modern animals that are vertebrate-like in some features, the study of molecular relationships, and fossils.

1.1 Sea Squirts and the Lancelet

There are two key groups of living non-vertebrate chordates: cephalochordates (amphioxus) and sea squirts. The amphioxus certainly looks superficially fish-like, but adult sea squirts look like rubbery little bottles, and so would hardly seem to be sensible candidates for close relatives of the vertebrates.

1.1.1 Cephalochordata: Amphioxus

The Cephalochordata (or Acraniata) have long been understood to be close relatives of the vertebrates. The clade includes 30–35 species that live generally in shallow seas of temperate to tropical latitudes, the most famous of which is the amphioxus or lancelet, *Branchiostoma*. The adult amphioxus is convincingly chordate-like, being a 50 mm-long paperknife-shaped animal that looks like a young lamprey or eel yet lacking a head (Bertrand and Escriva 2011; Holland 2015; Zhang et al. 2018; d'Aniello et al. 2023). Amphioxus swims freely by undulating its whole body from side to side, and it burrows in the sediment on the sea floor (Figure 1.2a, b).

Amphioxus feeds by filtering food particles out of the seawater. Water is pumped into the mouth and through the pharynx by cilia or the gill slits, and food particles are caught up in a bag of mucus produced by the endostyle, the feeding system seen also in tunicates and in the larvae of the lamprey. The mucus with its contained food particles is pulled into the gut for digestion, whereas the seawater passes through the gill slits into the atrium. Oxygen is also extracted, and the wastewater then exits through the **atriopore**.

The anatomy of amphioxus, with its pharynx, notochord, dorsal nerve cord, myotomes, and endostyle (Figure 1.2c) is typically chordate. Swimming and burrowing are done by means of lateral contractions of the myomeres acting against the stiff rodlike notochord.

1.1.2 Urochordata: Sea Squirts

A typical sea squirt, or tunicate, is *Ciona* (Figure 1.3a), which lives attached to rocks in seas around the world. It is a 100–150 mm-tall bag-shaped organism with a translucent outer skin (the tunic) and two openings, or siphons, at the top. *Ciona intestinalis* is one of about 3000 species of urochordates that mostly live in shallow seas, are generally attached to the seabed, and live either a solitary or colonial existence. But the adult sea squirts do not look much like vertebrates.