

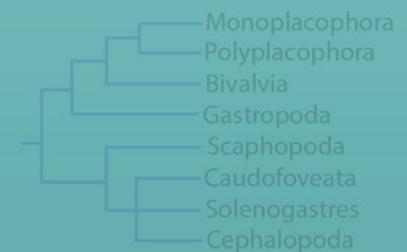
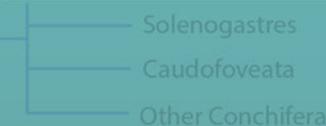
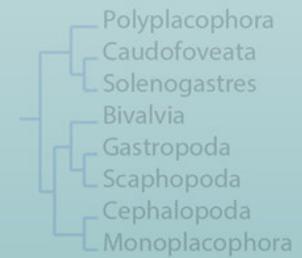
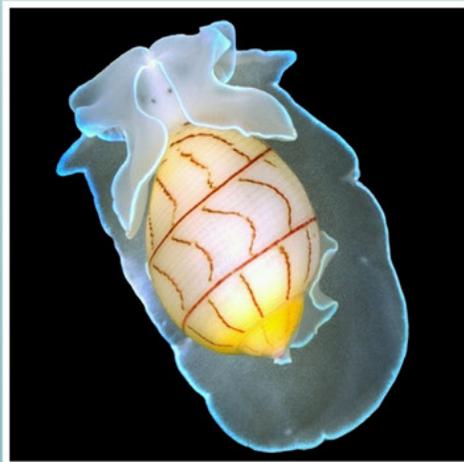
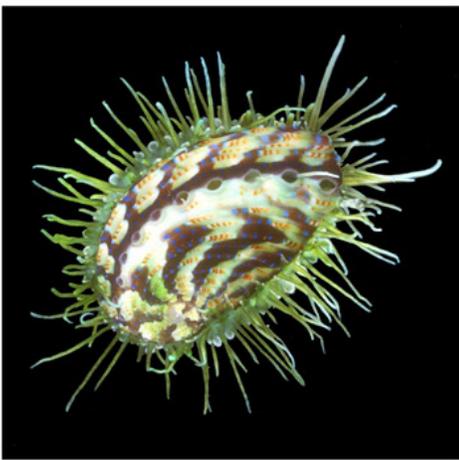
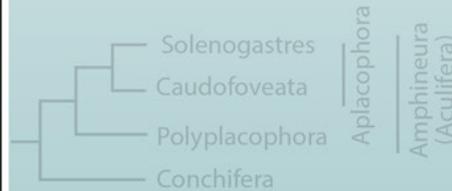
Biology and Evolution of the Mollusca

VOLUME TWO

Winston F. Ponder

David R. Lindberg

Illustrations by **Juliet M. Ponder**



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Volume Two

Winston F. Ponder
David R. Lindberg
Juliet M. Ponder



CRC Press

Taylor & Francis Group
Boca Raton London New York

CRC Press is an imprint of the
Taylor & Francis Group, an **informa** business

CRC Press
Taylor & Francis Group
6000 Broken Sound Parkway NW, Suite 300
Boca Raton, FL 33487-2742

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Printed on acid-free paper

International Standard Book Number-13: 978-0-8153-6184-8 (Hardback)

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Winston F. Ponder MSc, PhD, DSc is a Senior Fellow at the Australian Museum (Sydney), and an Honorary Associate at the University of Sydney. Before retirement in 2005 he was a Principal Research Scientist at the Australian Museum, where he worked in the malacology section for 37 years and was instrumental in organising and building up the extensive collection. While at the museum he also held several hon-

orary positions at a number of Australian universities. In addition to pursuing research programs, he has also been active in transferring expertise to new generations of young zoologists by way of training research students, hosting overseas collaborators, running workshops and organising a number of conferences. It was when running an intensive mollusc course at the University of Wollongong over several years, that the idea for this book dawned. Winston's research extends broadly across marine and freshwater molluscs and includes observations of living animals, microanatomy, biometrics, cladistics and molecular analysis. He, like his collaborator David Lindberg, has been involved in the revolution in molluscan phylogenetics that has taken place over the last 20 years. His publications include 250 peer-reviewed papers and book chapters and two edited books on molluscs and one on invertebrate conservation. Recently he produced (with two others) an online interactive key and information system of Australian freshwater molluscs, has been involved with the molluscan part of the online Australian faunal directory, and was editor of the journal *Molluscan Research* for 14 years. He organised or co-organised 12 national or international meetings and presented papers at many more. He has undertaken study trips and field work in various parts of the world over more than 40 years but field studies have mainly focused on Australian marine and freshwater habitats. His awards include the Hamilton Prize (Royal Society of N.Z., 1968), Fellow of the Royal Zoological Society, NSW, Silver Jubilee award, Australian Marine Sciences Association (2008), and the Clarke Medal, Royal Society of NSW (2010).



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Juliet M. Ponder MA Grad Dip Ed has spent 55 years married to the senior author of this book and developing a variety of interests. She excelled at school and began studying science at Auckland University where she met Winston. She was blown away by his passion for molluscs and decided that, if such dedication was required to be a scientist, she didn't have it. However, she was happy to support his work and to this end began developing competence in scientific writing and illustrating and even scuba diving. She and Winston have two children and, while rearing them, Juliet acquired qualifications in fine art, community welfare and education. She worked part-time for 10 years painting lifelike models in the Australian Museum but, as her children grew older, she moved into full time community work and then teaching for 15 years. Retirement from paid work in 2004 gave her the opportunity to learn computer graphics and develop a method of colour coding illustrations to clarify similarities and differences between groups of animals. The drawings in this book combine her love of art, science and education.



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Introduction to Volume Two

This two-volume work is devoted to the Mollusca, one of the most diverse and important groups of animals. It provides an overview of the diversity, utility, physiology, and functional morphology of molluscs, as well as their evolutionary history and relationships. Also, we highlight some current areas of research and flag some areas urgently in need of work.

The first volume provides general introductory material on molluscs and overviews of the history of malacology, molluscan physiology and genomics, and the structure and function of each of the body systems and processes. It also includes a chapter on natural history that gives a general account of various aspects of molluscan biology not otherwise covered elsewhere in the book. There is also a chapter on the significance of molluscs to, and their interactions with, humans, and the last chapter covers aspects of current and future research relevant to the topics covered in the volume.

In this second volume we discuss the relationships of molluscs to other invertebrates and to each other, review their early fossil history, and provide comprehensive overviews of each of the major molluscan groups. Where necessary, the chapters dealing with the major groups include a brief summary of the information covered in the system chapters, and additional detail is often provided about some systems that are particularly significant. Lastly, we discuss aspects of current and future research relevant to the areas covered in this volume and some more general aspects relevant to the future of malacology.

The Appendix provides a summary of the classification of all major extant classes (i.e., those that contain at least some living representatives) to the family level, with both living and fossil taxa included. Extinct major groups (classes) are reviewed in Chapter 13.

The bulk of this volume comprises the chapters dealing with the extant classes of molluscs. We have tried to present the most up-to-date information on these groups, including their phylogenetic relationships. This information is, however, far from static, and readers should be aware that phylogenies and classifications can quickly change. We recommend that names and classifications provided in the chapters and in the Appendix be checked for changes using online databases such as the World Register of Marine Species (WoRMS).

We do not provide a glossary, but most terms used are explained in the text, and many of these can be located using the comprehensive index. Most information provided is extensively referenced, and all cited references are listed in the bibliography associated with each volume.

The extraordinary range of body form and function exhibited by molluscs has been addressed in part in the first volume by way of the chapters dealing with the shells and external body and those reviewing the individual organ systems. In this volume we examine molluscan fossil history, focusing on their early evolution in the Paleozoic. From humble beginnings, they have evolved into the remarkable array of modern

molluscs which range from minute spicule worms, to chitons, tusk shells, clams, limpets, snails, slugs, octopuses, and squid. In the chapters dealing with these groups, we outline their classification and review their external morphology, organ systems, habits, biology, ecology, fossil history, and human uses.

From the beginning, ordering the incredible molluscan diversity into a classification has been a preoccupation of those who have studied molluscs. Until recently shells and anatomy were the main tools used to build those classifications; then molecular studies came to the fore. The latter are often seen as a panacea, but they are not necessarily, especially when it comes to understanding divergences in deep time. One has only to look at the molecular phylogenies produced in recent years to see the often-considerable disagreements in branching patterns in different studies. We hope that the data provided in this book will encourage those engaged in phylogenetic studies to look for congruence between their branching patterns and the plausibility of gains and losses in morphological features and physiological attributes.

None of this work would have been possible without the huge body of research on which it draws heavily. Our role has been to attempt to distil this work, but in so doing it has been impossible to be comprehensive as even though thousands of references are listed, these are but a fraction of the available works. So, dear colleagues, we apologise in advance if we have not cited a particular paper or book you favour.

Once again we acknowledge the huge help from volunteers Doris Shearman and Rosemary Coucouvinis (see introduction to Volume One). Both have been invaluable in checking references, organising the bibliographic database, and proof reading. Doris also greatly assisted with editing and checking the manuscript.

Figures incorporating colour photographs of living animals are provided in the taxon chapters and were largely from three sources. A large number were kindly provided via Philippe Bouchet of the Muséum national d'Histoire naturelle (MNHN) and mostly selected and sent by Philippe Maestrati. These photographs were taken by several photographers who are identified by the museum acronym following their name in the captions. Other photographers who generously provided multiple photographs for this volume were Dr Terry Gosliner, Denis Riek (www.roboastra.com/), and Ria Tan (www.wildsingapore.com/). Photographs were also provided by Julia Sigwart, Ron Schimek, John Buckland-Nicks, Nina T. Mikkelsen, Emanuel Redl, Carmen Cobo, Kevin Kocot, John Walker, Steven Smith, Peter Middelfart, Cristine Huffard, Jenna Judge, Gerald and Buff Corsi, Jann Vendetti, Julian Finn, Monterey Bay Aquarium Research Institute (MBARI), Roy Caldwell, D. Chowderly, Alison Miller, Edie Widder (NOAA), Gary MacDonald, Peter Batson and Janet Voight, Chong Chen, Scott Johnson, Jeanette Johnson, Yuki Tatara, Hiroshi Fukuda, S. Groves, Stijn Ghesquiere, Tomoki

Kase, Prof. Brian Eversham, Clay Bryce, Ian F. Smith, Hugh Jones, Barbara Buge, Katja Peijnenburg, Keith Hiscock, Rüdiger Bieler, Masanori Taru, Gustav Paulay, Bastian Brenzinger, Mat Nimbs, Rosemary Golding, Lars Peters, N. Yotarou, Barry Roth, David Lochlin, David G. Robinson, and Vince Kessner.

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Appendix—the following sections were reviewed: Scaphopoda, G. Steiner; Bivalvia, J. Taylor, J. Cope; Gastropoda, P. Bouchet; Neogastropoda, A. Fesodov.

12 Molluscan Relationships

Detailed treatments of the early history of molluscan classification and other studies are given by Simroth (1892–1894), Lameere (1936), and Hyman (1967) and so are not repeated in detail here. Although molluscs were used and eaten by humans in prehistoric and historic times, an understanding of their place among other animals and their classification did not come to anything approaching a modern concept of the group until Cuvier (1795).

Aristotle (384–322 BCE¹) recognised two groups of molluscs: Ostrachodermata for those with shells and Malachia for the cephalopods. Although the Polish scholar J. Jonston (or Jonstonus) (1603–1675) first coined the name Mollusca in 1650 (to include cephalopods and barnacles), the name did not come into general usage until it was used and redefined by the great Swedish naturalist Carl von Linné (e.g., Linnaeus 1758). Linnaeus included all ‘invertebrates’, other than insects, as Vermes, which he divided into several groups, one of which was Mollusca, and in which he included soft-bodied animals such as slugs, coleoid cephalopods, and pteropods that we still recognise as molluscs, but also some non-molluscs including certain cnidarians, tunicates, polychaetes, and echinoderms. Most shelled molluscs were included in another group, Testacea (including chitons, snails, limpets, bivalves, and *Nautilus* but also barnacles and the serpulid polychaetes). In contrast, Cuvier (1795) devised a concept of molluscs (mollusques) which included the subgroups Céphalopodes (including Foraminifera), Gastéropodes (including slugs and snails and also parasitic copepods) and Acéphales (bivalves, tunicates, brachiopods, and barnacles). This scheme was modified a little by Duméril (1806) and later again by Cuvier (1817); both included the pteropods (as Ptéropodes) as a separate group, although non-molluscan groups were still included in the Mollusca². For example, barnacles were thought to be related to chitons and grouped as the Nematopoda, but by the 1830s barnacles were recognised as crustaceans and foraminiferans were excluded from cephalopods. Tunicates were removed in the mid-1860s, but brachiopods remained with the molluscs until close to the end of the 19th century.

12.1 THE HYPOTHETICAL ANCESTRAL MOLLUSC

‘In the post-Hennig world, cladograms have replaced HAMs and exposed our ignorance’ (Runnegar 1996, p. 78).

Many treatments of molluscan phylogeny have used archetypes, *Baupläne*, or other images of reconstructed common ancestors to postulate what the first mollusc looked like. These figures are known as *hypothetical ancestral molluscs* (HAMs), with over

40 different examples in the literature. The first was proposed by the great evolutionary biologist Thomas H. Huxley (Huxley 1853), and they continue to appear in many invertebrate textbooks today. The HAM is also known as the Archimollusc (Salvini-Plawen 1972, 1981) or ‘archaeomollusk’ (Yochelson 1978), and there have been several concepts over the years (Figure 12.1). Because the HAM is a device to convey features that the molluscan ancestor might have possessed, HAM concepts have evolved according to prevailing ideas about molluscan evolution (Lindberg & Ghiselin 2003). One trend in the evolving HAM concept was the expansion and enlargement of the posterior mantle cavity and its structures, making these supposed common ancestors of all molluscs much more gastropod like. In other renditions, there was a substantial loss of organs and other features, particularly the radula and gonads, or the organs appear in the juvenile condition, although the animal is represented as an adult. Overall, the classical textbook version of HAM might serve better as a hypothetical conchiferan ancestor rather than a common ancestor of all molluscs. Lindberg and Ghiselin (2003) noted that major discoveries were slow to impact on these images in standard textbooks, and they recommended the extinction of the HAM concept.

Haszprunar (1992a) proposed a new HAM concept based on the idea that aplacophorans are ‘basal’ molluscs (e.g., Salvini-Plawen 1972, 1985a, 2003). In this concept, the ancestral mollusc was small, rather worm-like, and covered with spicules instead of a shell.

Attempts to define the molluscan ancestor also depended on ideas about what the sister taxon of the Mollusca is (see Section 12.2.2). Concepts of ancestral molluscs thus included designs based on shared ancestry with turbellarian flatworms, reduced annelids, or even entoprocts (see Ghiselin 1988; Haszprunar 1996 for reviews).

None of the HAM ideas discussed above are likely to be an accurate approximation of the first mollusc. Indeed, the molluscan ancestor may have been larger than the small, worm-like ancestor favoured by some and perhaps more like a chiton as suggested by some ancient fossils (see Chapter 8).

12.2 HYPOTHESES OF PHYLOGENETIC RELATIONSHIPS OF THE MAJOR MOLLUSCAN GROUPS

The grouping of molluscan classes into higher taxon groups has been a popular pastime among molluscan workers, with several names proposed for those groupings (see Box 12.1 and Figure 12.2). For example, polyplacophorans and aplacophorans are often grouped as the Aculifera, with the remaining classes contained within the Conchifera in recent phylogenies (e.g., Haszprunar et al. 2008; Kocot et al. 2011; Smith et al. 2011; Vinther et al. 2011).

¹ Before Common Era, an alternative to BC.

² Blainville (1825) changed Mollusca to Malacozoa, from which the term malacology is derived.

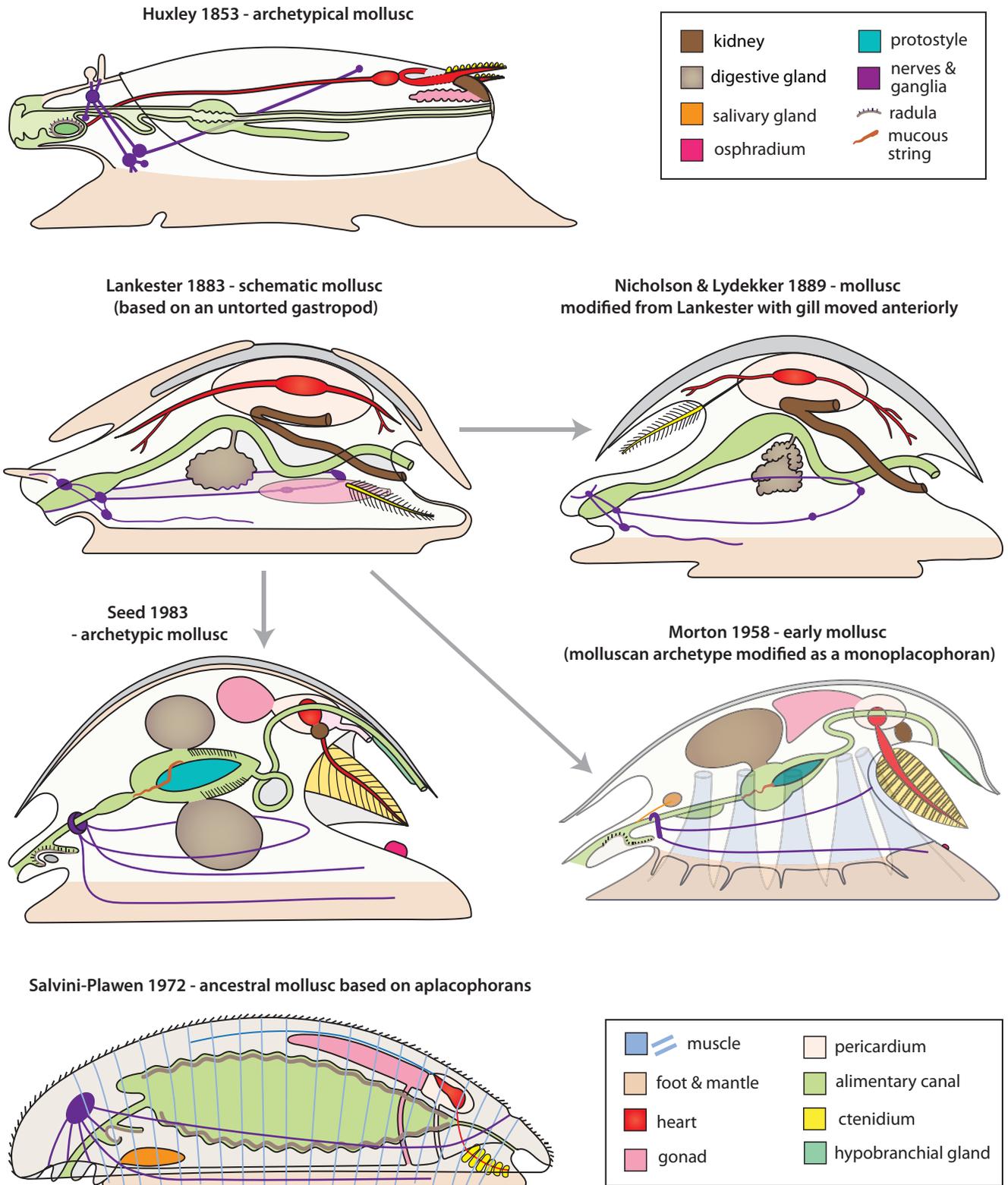


FIGURE 12.1 Examples of the changing concepts of the hypothetical ancestral mollusc (HAM). The arrows indicate changes in HAM thinking based on new findings and theories when they were proposed. The illustrations are redrawn and modified from the authors mentioned in the figure. See text for explanation and Lindberg and Ghiselin (2003) for more details.

**BOX 12.1 SOME NAMES PROPOSED
FOR GROUPINGS OF MOLLUSCS
ABOVE THE CLASS LEVEL**

Below we list many of the names used to group the molluscan classes. The list includes the reference in which the term was first proposed and the taxa included in the original concept. For some names, the concepts have been changed since their original introduction with more or fewer taxa included, but these modified usages are mainly not detailed below (see Runnegar & Pojeta 1974; Salvini-Plawen 1980, 1981; Ax 2000; Kocot et al. 2011; Kocot 2013; Giribet 2014). This list is not comprehensive but includes most of the names used in recent literature.

- Adenopoda** – all living groups of molluscs other than Caudofoveata (Salvini-Plawen 1972).
- Aculifera** – Polyplacophora + Aplacophora (Hatschek in Blumrich 1891), although Stasek (1972) included only Aplacophora. This proposed grouping was based on shared characters of the nervous system, the presence of sclerites and epidermal papillae (see Scheltema 1993), and also supported by ciliary ultrastructure (Lundin et al. 2009). Several extinct taxa are also assignable to this grade or group (see Chapter 9). Equivalent to Amphineura.
- Amphineura** – Aplacophora + Polyplacophora (Ihering 1876a). Equivalent to, and predates, Aculifera.
- Ancyropoda** – Scaphopoda + Bivalvia (Hennig 1979). Equivalent to, and predates, Loboconcha.
- Aplacophora** – Solenogastres + Caudofoveata (Ihering 1876a).
- Cephalomalacia** – Cephalopoda + Gastropoda + Scaphopoda (Keferstein 1862).
- Conchifera** – Mollusca excluding Aculifera (i.e., Monoplacophora, Cephalopoda, Bivalvia, Scaphopoda, and Gastropoda) (Gegenbauer 1878).
- Cyrtosoma** – Monoplacophora + Gastropoda + Cephalopoda (Runnegar & Pojeta 1974).
- Diasoma** – Rostroconchia + Bivalvia + Scaphopoda (Runnegar & Pojeta 1974). Not equivalent to Loboconcha which does not include the rostroconchs.
- Dorsoconcha** – Polyplacophora, Monoplacophora, Gastropoda, and Bivalvia (Stöger et al. 2013).
- Eumollusca** – all molluscs other than Aplacophora. Originally introduced by Roule (1891) and subsequently by Ax (1999). Equivalent to, and predates, Testaria.
- Galeoconcha** – Tryblidiida (i.e., Monoplacophora) + Bellerophonitida (Salvini-Plawen 1980).
- Ganglioneura** – all Conchifera other than Monoplacophora (Hennig 1979).
- Hepagastralia** – all molluscs other than Solenogastres (Salvini-Plawen & Steiner 1996; Haszprunar 2000).
- Heterotecta** – Solenogastres + Polyplacophora (Salvini-Plawen 1980).

- Loboconcha** – Scaphopoda + Bivalvia (Salvini-Plawen 1980). Equivalent to Ancyropoda.
- Mollusca** – originally included several non-molluscan groups including brachiopods, ascidians, and barnacles (Cuvier 1798).
- Placophora** – proposed as a class for the chitons. Equivalent to the earlier name Polyplacophora (Ihering 1876a).
- Pleistomollusca** – Gastropoda + Bivalvia (Kocot et al. 2011).
- Rhacopoda** – Gastropoda + Cephalopoda (Hennig 1979).
- Scutopoda** – introduced as a ‘subphylum’ for Caudofoveata only (Salvini-Plawen 1978).
- Serialia** – Polyplacophora + Monoplacophora (Giribet et al. 2006).
- Testaria** – Conchifera + Polyplacophora (Salvini-Plawen 1972). Equivalent to Eumollusca.
- Variopoda** – Scaphopoda, Cephalopoda, and the two aplacophoran classes (Stöger et al. 2013).
- Visceroconcha** – Gastropoda + Bellerophonitida + Cephalopoda (Salvini-Plawen 1985a) – originally as Vesceroconcha but emended by Haszprunar (1988f).

There have been several alternative hypotheses of the relationships of the major molluscan groups (classes) to one another that have been derived from recent analyses involving morphological, molecular, developmental, and fossil data. The main competing ideas involve the relationships of (1) the aplacophoran groups, (2) the Monoplacophora, (3) the Scaphopoda, and (4) the Cephalopoda.

The aplacophoran taxa (Solenogastres and Caudofoveata) and Polyplacophora are of particular interest because they are often considered to represent the sister taxon (Aculifera) of the Conchifera. There are several hypotheses regarding the relationships of the aplacophoran groups. Until recently the main ones were: (1) they are a paraphyletic grade with the Caudofoveata the sister taxon to other molluscs (Testaria) (Salvini-Plawen 1972, 1980, 1981; Haszprunar 2000; Salvini-Plawen 2003; Haszprunar et al. 2008; Todt et al. 2008b) and (2) they form a monophyletic group (Aplacophora) that is sister to the Testaria (e.g., Hyman 1967; Scheltema 1993). More recent molecular phylogenies (Kocot et al. 2011; Smith et al. 2011; Vinther et al. 2011; Smith et al. 2012) have placed the aplacophoran taxa as a monophyletic group with the polyplacophorans in the Aculifera and sister to the Conchifera. Other molecular data (Wilson et al. 2010) suggested that the Caudofoveata were derived, possibly paedomorphic, and sister to the cephalopods, while the solenogastres were grouped outside the molluscs with the Sipuncula (Annelida).

The Monoplacophora has traditionally been included in the Conchifera and the chitons in the Aculifera (see Section 12.2.1 and Figure 12.2), although two molecular studies using Sanger-based approaches have shown monoplacophorans and chitons form a clade named Serialia (Giribet et al. 2006;

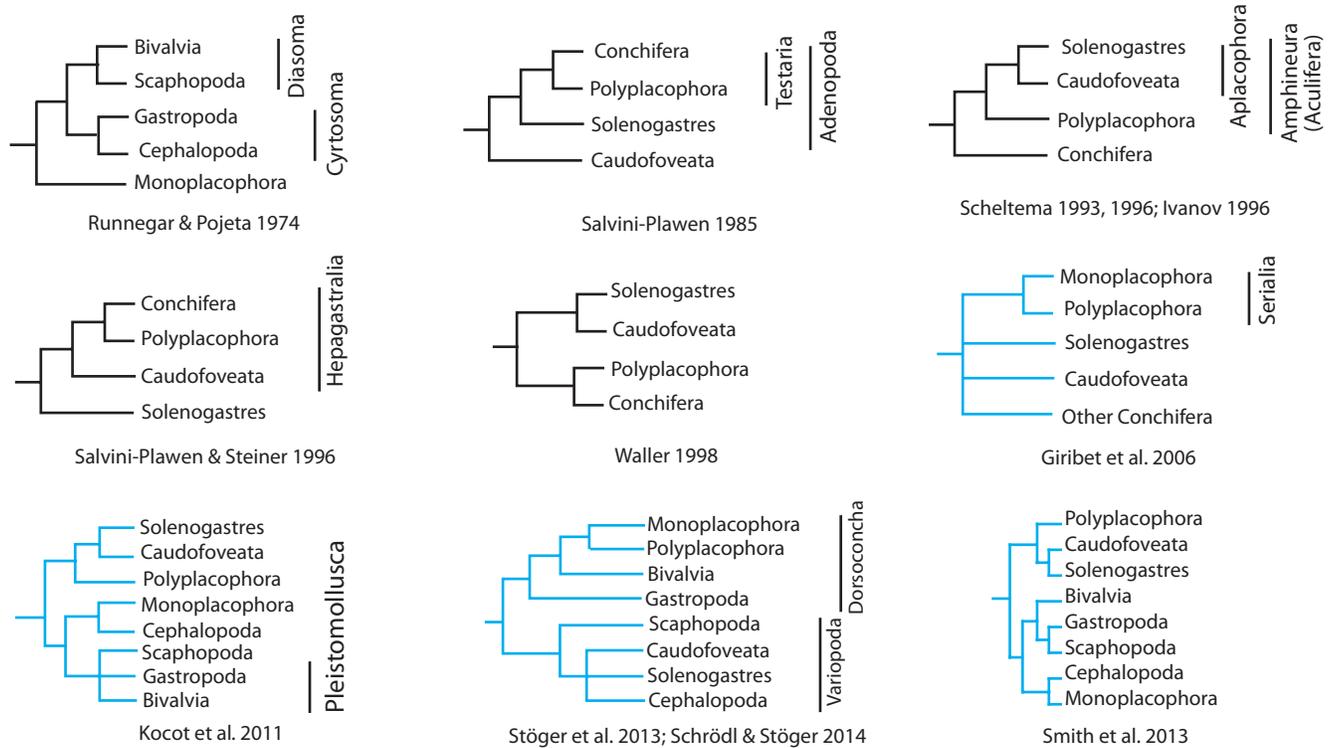


FIGURE 12.2 Some of the alternative hypothesised relationships among the Mollusca, with molecular analyses in blue.

Wilson et al. 2010) (see Section 12.2.1 and Figure 12.2). In contrast to these results, the only other phylogenomic analyses incorporating monoplacophorans (Smith et al. 2011, 2012) favoured a sister taxon relationship with cephalopods.

Traditionally, Polyplacophora and Aplacophora were combined into Amphineura based on similarities in their nervous systems (Ihering 1876a, b; Spengel 1881; Hoffmann 1929–1930), and the same group was named Aculifera, characterised by having a mantle with cuticle-bearing spicules (see Scheltema 1988a; Ivanov 1996; Scheltema 1996). In schemes with paraphyletic aplacophorans at the base of the molluscan tree, the remaining molluscs form a clade Testaria, with Polyplacophora the sister group to Conchifera (e.g., Salvini-Plawen 1980, 1985a, 1990, 2003; Wingstrand 1985; Salvini-Plawen & Steiner 1996). More recently Haszprunar (2000) proposed Hepagastralia for all molluscs other than Solenogastres, based mainly on gut morphology.

The idea that bivalves and scaphopods were related was previously popular and is indicated by the grouping Diasoma (as a subphylum), along with the extinct Rostroconchia (Runnegar & Pojeta 1974). These classes all have a shell primitively open at both ends with flow-through ventilation and possess a relatively straight gut. Runnegar and Pojeta (1974) also proposed another subphylum, Cyrtosoma, to include the Monoplacophora, Gastropoda, and Cephalopoda (Figure 12.2). A morphological analysis of molluscan relationships by Waller (1998) showed that scaphopods were not related to bivalves (and rostroconchs) and should be included in the Cyrtosoma and that Monoplacophora should be excluded from that group (Figure 12.2). These latter

conclusions relating to scaphopods have been supported by other more recent analyses using molecular data.

12.2.1 ACULIFERA – CONCHIFERA, TESTARIA, AND SERIALIA HYPOTHESES

As seen from the previous section and Figure 12.2, the phylogenetic relationships of the molluscs have been expressed as three competing hypotheses:

- The Aculifera (chitons + aplacophorans) + Conchifera (all other classes) hypothesis
- The Testaria (or Eumollusca) (chitons + all other classes) hypothesis (with aplacophorans basal)
- The Serialia (chitons + monoplacophorans) hypothesis, with all other molluscs forming a separate clade

Today, most workers consider living molluscs to be divisible into two groups, the Aculifera and the Conchifera. The Aculifera includes the Caudofoveata and Solenogastres (considered by some to be sister taxa comprising the clade Aplacophora) and the Polyplacophora (chitons). The conchiferan taxa are the Monoplacophora, Bivalvia, Scaphopoda, Cephalopoda, and Gastropoda. The primary distinction between aculiferan and conchiferan molluscs is the formation of single or paired calcified structure(s) (i.e., the shell) that cover the dorsal surface of their bodies. Both aplacophorans and chitons produce calcium carbonate spicules, and chitons produce eight shell plates. In the aplacophorans, these spicules cover the body surface while in chitons they are

restricted to an epidermal band (the girdle), which surrounds the eight dorsal shell plates. Other characters that unite the Aculifera are epidermal papillae (extensions of the mantle into the body cuticle, thought to be secretory in function) and a suprarectal commissure in the nervous system (Scheltema 1993; Scheltema et al. 1994; Ivanov 1996).

Other controversies regarding the Aculifera are (1) whether the Caudofoveata and Solenogastres represent a grade or clade and (2) whether the Caudofoveata and Solenogastres are closer to the base of the molluscan tree than the polyplacophorans (Figure 12.2). Those that argued for Caudofoveata and Solenogastres being a basal grade (e.g., Salvini-Plawen 1980; Salvini-Plawen & Steiner 1996) placed the Caudofoveata as the most basal extant group (i.e., they are the sister to all remaining molluscs, the Hepagastralia, Salvini-Plawen 1996; Haszprunar 2000), followed by the Solenogastres, Polyplacophora, and lastly, the Conchifera. This hypothesis renders the Aculifera paraphyletic, and for this reason, Salvini-Plawen (1980) argued against that name. In contrast, Scheltema (1993) and Ivanov (1996) thought that aplacophorans were monophyletic and were the sister taxon to the Polyplacophora and together (as the Aculifera) were the sister taxon to the Conchifera. Lastly, Waller (1998), like Scheltema and Ivanov, argued for a monophyletic Aplacophora but considered the Polyplacophora to be the sister taxon of the Conchifera, thereby making the Aculifera biphyetic.

Regardless as to whether the Caudofoveata and Solenogastres represent a grade or clade, many molluscan morphologists have erroneously considered these two groups to represent the earliest molluscan 'bauplan' and to lie near the base of the molluscan tree simply because they are worm-like (Todt et al. 2008b). Yochelson (1978) suggested that the worm-like morphology of the aplacophorans was secondarily simplified rather than primitive, although he continued to regard the Polyplacophora as a primitive group. Lindberg and Ponder (1996) made a similar argument and suggested that the Caudofoveata and Solenogastres represented separate lineages, derived through paedomorphosis, from extinct or living molluscan lineages. These matters are discussed further in Chapter 13.

A relationship between the Monoplacophora and Polyplacophora was first noted by Knight and Yochelson (1958). The shell muscles have a similar configuration in both taxa with eight-fold shell-attachment muscle groups, so some have suggested that this configuration was a feature of their common ancestor (Wingstrand 1985), although just what that ancestor looked like is still open to speculation (e.g., Eernisse & Reynolds 1994). Assuming a common ancestor, various hypotheses have been proposed to explain the origin of the very different shells of monoplacophorans and chitons. Suggestions include independent derivations (e.g., Scheltema 1988a), that the single shell of monoplacophorans resulted from the fusion of multiple valves (Haas 1981), or that chiton valves were derived from the segmenting of a single shell (Runnegar & Pojeta 1974).

In a molecular analysis based on two mitochondrial genes and three nuclear genes, with a single (18S rRNA) monoplacophoran sequence included, the Monoplacophora were placed within the Polyplacophora, and the aplacophorans were located among the other 'Conchifera' (Giribet et al. 2006). Solenogastres was the sister taxon to Patellogastropoda, and the Caudofoveata to the Cephalopoda, although these groupings were poorly supported. Based on this analysis, Giribet et al. (2006) proposed a new taxon, the Serialia, to include the Monoplacophora and Polyplacophora – taxa with serially repeated gills and eight pairs of pedal retractor muscles. In a subsequent paper, Wilson et al. (2010) included additional sequence data for several gene fragments for a second monoplacophoran species. In this second analysis, the Serialia were again recovered, but the monoplacophorans were positioned as the sister taxon of the Polyplacophora rather than being nested among them, and statistical support for the Serialia was strong. The Caudofoveata were once again identified as the sister taxon of the Cephalopoda, still with weak support, while the Solenogastres were placed outside the Mollusca as part of a clade that included Sipuncula and Annelida. So far only two studies have sequenced multiple monoplacophoran taxa. Kano et al. (2012) used sequences from three monoplacophoran taxa and recovered a well-supported Serialia clade in their 18S, 18S+28S, and five-gene (18S, 28S, 16S, H3, COI) analyses. Stöger et al. (2013) also recovered a Serialia clade in their Maximum Likelihood and Bayesian analyses of the same molecular markers for six monoplacophoran taxa. In a follow-up analysis including gene order and sequence data from three complete monoplacophoran mitochondrial genomes, Stöger et al. (2016) recovered Serialia in some analyses, but their results were inconclusive because of sensitivity to taxon sampling.

Kocot et al. (2011) used transcriptome³ data and obtained a very different result with the two aplacophoran taxa grouping together (Aplacophora) as sister to the Polyplacophora (i.e., they recovered Aculifera and Conchifera); however they did not have a monoplacophoran in their analysis. A more recent phylogenomic study (Kocot et al. 2017) did include a single monoplacophoran. A strongly supported Aculifera was recovered in every analysis, and in one of these (Kocot 2017, Fig. 7), the monoplacophoran taxon was recovered as the sister taxon of the Aculifera. In the remaining analyses, the monoplacophoran was sister to the remaining conchiferan taxa in three of them, sister to the gastropods, or sister to the cephalopods (in one analysis each).

Not only has there been debate about the relationship of molluscan classes, but also ideas regarding relationships within the classes have changed considerably over the last few decades, as discussed in the appropriate chapters.

³ The transcriptome is the RNA molecules in a cell or tissue and may include just mitochondrial RNA (mRNA) or all RNA.

12.2.2 THE SEARCH FOR THE MOLLUSCAN SISTER GROUP

Phylogenetic studies based on either morphological or molecular data vary in their conclusions as to the sister taxon of molluscs. While it has been suggested that this may result from the burst of rapid evolution in the Cambrian, our current analytical methods and the datasets employed also need to be improved to uncover these ancient relationships.

The molluscs, along with several other phyla, are included in the Lophotrochozoa (Figure 12.3). Although not supported by the most recent molecular analyses, lophotrochozoans have previously been divided into subgroups with the molluscs placed in the Trochozoa (molluscs, annelids, brachiopods, phoronids, and nemerteans) and then in the Eutrochozoa (molluscs, annelids, and nemerteans) (see Box 12.2). Potential candidates for the molluscan sister taxon include several of these phyla, as detailed below.

BOX 12.2 SOME HIGHER GROUPINGS OF ANIMALS

Bilateria can be divided into three main groups, Lophotrochozoa, Ecdysozoa, and Deuterostomia (Figure 12.3):

Xenacoelomorpha – Acoel flatworms (**Acoela**) and xenoturbellidans.

Deuterostomia – the blastopore⁴ gives rise to the anus – includes echinoderms, hemichordates, cephalochordates, urochordates, and vertebrates (or craniates).

Protostomia – the blastopore gives rise to the mouth – includes molluscs and the remaining animals. The protostomes can be divided into three unresolved taxa: the **Spiralia**, **Ecdysozoa**, and **Chaetognatha** (or arrow worms). The Ecdysozoa includes arthropods, tardigrades, nematodes, priapulidans, etc. They have a modified spiral cleavage and moult. Arrow worms are predatory, dart-shaped animals with tripartite bodies.

Spiralia – are recognised as having spiral cleavage, and the mesoderm is derived from the 4d cell. Relationships are unresolved among the spiralian clades Cycliophora, Dicyemida, Orthonectida, Gnathifera, and Platytrchozoa. The Platytrchozoa consists of two clades – Rousphozoa (Platyhelminthes + Gastrotricha) and Lophotrochozoa.

Lophotrochozoa includes brachiopods, phoronids, bryozoans, entoprocts, nemerteans, molluscs, and annelids. Previously proposed subgroups within Lophotrochozoa are *Platyzoa* (Rousphozoa, Gnathifera), *Polyzoa* (Entoprocta, Cycliophora, Bryozoa), *Lophophorata* (Brachiopoda, Bryozoa,

Phoronida), *Brachiozoa* (Brachiopoda and Phoronida), *Eutrochozoa* (Mollusca, Annelida, Nemertea, Orthonectida, and Rhombozoa, although it has been used in a wider sense), and *Trochozoa* (Polyzoa, Brachiozoa, Eutrochozoa), unified by the possession of a trochophore larva and, in many adults, the possession of lophophore feeding tentacles.

(For further details see Halanych et al. 1995; Giribet 2002; Giribet 2008b; Helmkamp et al. 2008; Edgecombe et al. 2011; Dunn et al. 2014; Giribet 2016b).

Proposed sister taxa include turbellarian flatworms (e.g., Salvini-Plawen 1972), reduced annelids (see Ghiselin 1988; Haszprunar 1996 for reviews) and, based on supposed similarities in their larvae, entoprocts (Wanninger et al. 2007; Haszprunar & Wanninger 2008) and sipunculans (Scheltema 1993). Brachiopods have also been suggested, based on both mitochondrial, nuclear, and genomic data (Stechmann & Schlegel 1999; Paps et al. 2009; Luo et al. 2015) and nemerteans based on mitochondrial genomic data (Podsiadlowski et al. 2009). One outgroup suggestion even included cnidarians, this idea being born through the observation of apparent strobilation in *Clio*, a thecosome pteropod (van der Spoel 1973) (see Chapter 8). This led to speculation that molluscs might be related to cnidarians through their vague similarity to Conulata, an extinct group often included in the Cnidaria (Pafort-van Iersel & van der Spoel 1979).

A distinct anterior head and ventral foot are features that set many molluscs apart from other animals. Superficially similar features in sipunculan and entoproct larvae have been identified and have fuelled debates about the relationships of those groups with molluscs (e.g., Haszprunar 1996; Scheltema 1996; Haszprunar & Wanninger 2008), but a closer examination of these supposedly homologous characters discounts these putative relationships. In the ectoprocts, the larval ‘foot’ is derived from the central region of the neurotroch, and the anus is located at the terminal end (Nielsen 1979). Molluscan trochophores lack a neurotroch (Rouse 1999), and the molluscan foot is derived from an ectodermal thickening that forms behind the mouth (Raven 1964). The location of the anus on the terminal end of the ‘foot’ is even more problematic as in the Mollusca the anus is always situated above and independent of the foot. Even in the footless, worm-like Caudofoveata, the anus lies above the pedal nerves which innervate the foot of all other molluscs. The molluscan foot is also distinctive in having regular dorsoventral pedal muscles.

It is now generally agreed that molluscs are lophotrochozoans (Figure 12.3), but which lophotrochozoan ancestor is most closely related to molluscs remains uncertain, although a growing body of evidence (morphological, molecular, fossil) is focusing on the Brachiozoa (see also Chapter 13).

A mineralised shell is not a unique molluscan character as shells are produced by brachiopods (Figure 12.4), some crustaceans (barnacles), and some tube-living annelids.

⁴ The fate of the blastopore is more variable than the protostome/deuterostome dichotomy suggests. In some protostome taxa the blastopore gives rise to the anus or ultimately closes and the openings are *de novo* structures (Martín-Durán et al. 2016).

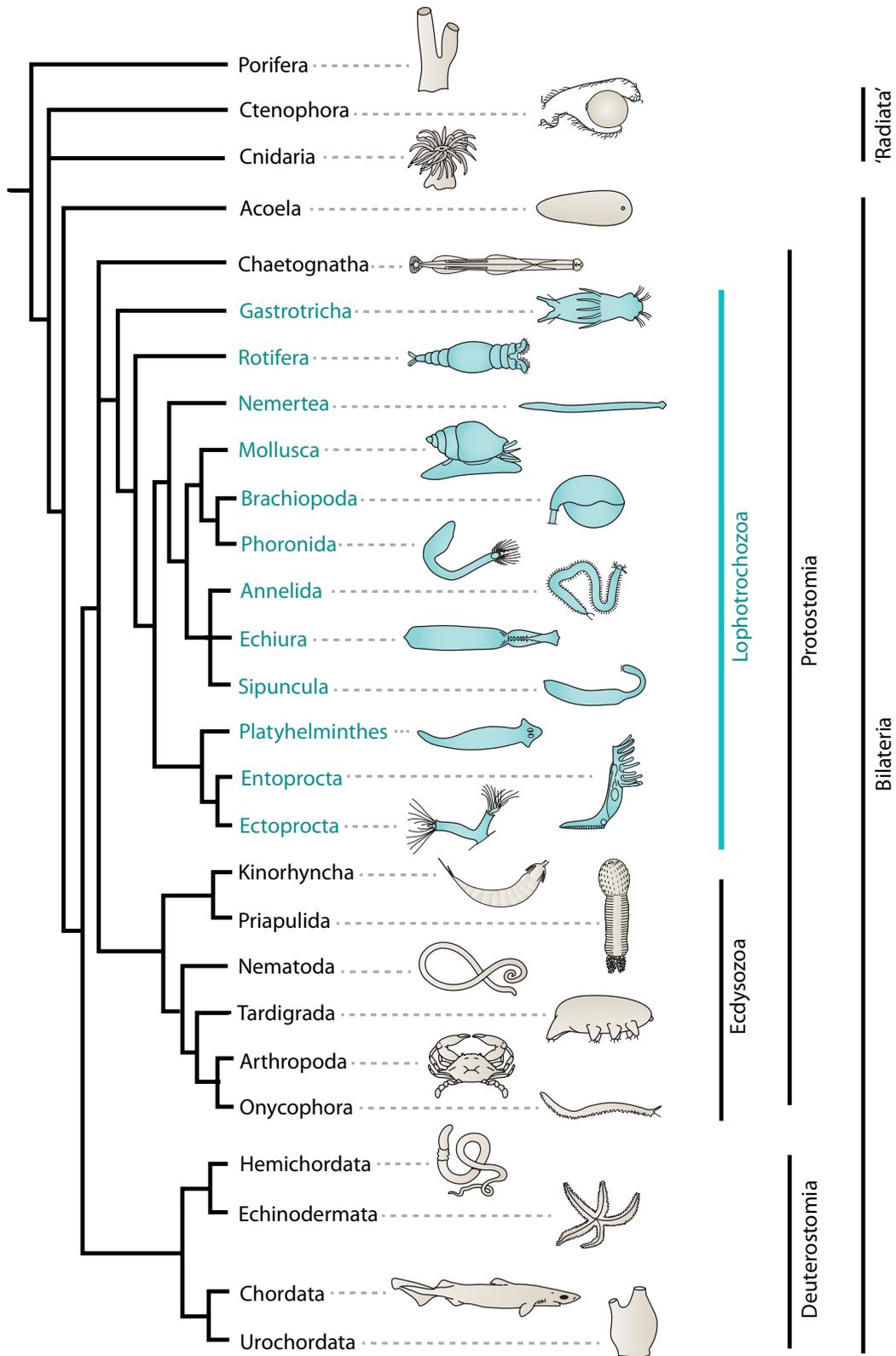


FIGURE 12.3 A hypothesis of relationships of animal phyla. Lophotrochozoans are shaded in blue. Relationships based largely on analyses of nuclear ribosomal genes by Paps et al. (2009).

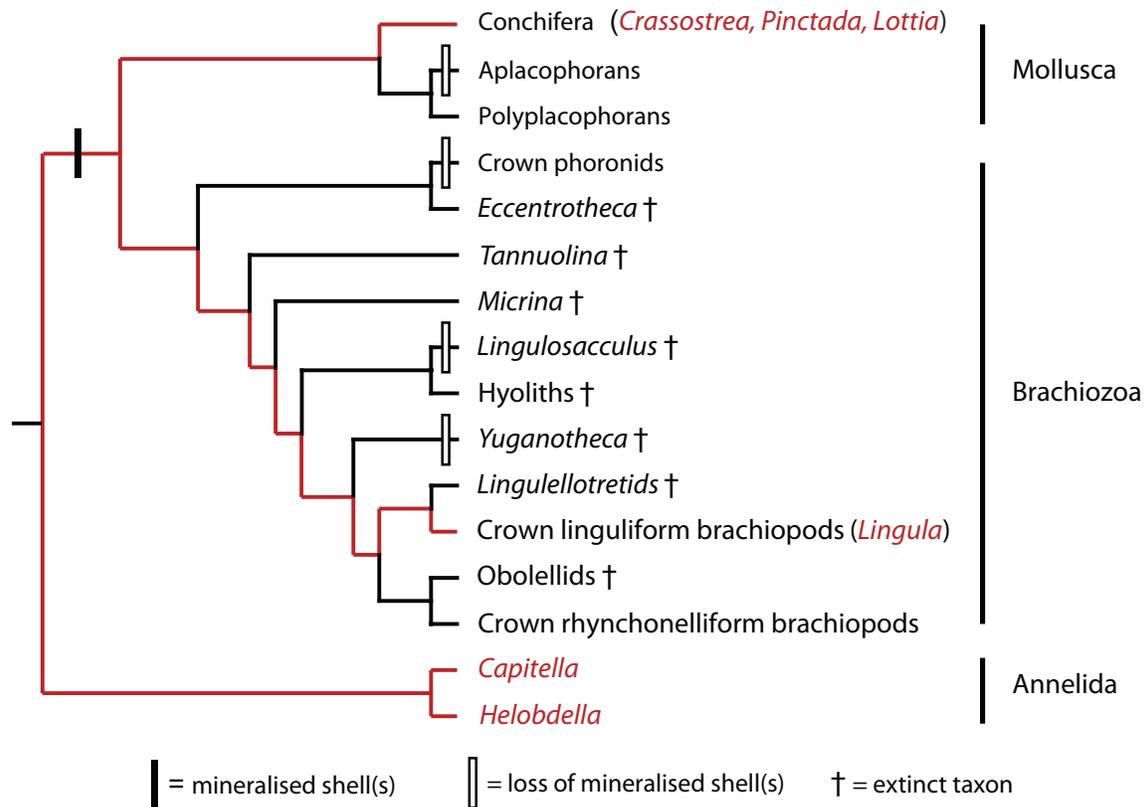


FIGURE 12.4 Mineralised shell(s) in major molluscan and brachiozoan clades. Mineralised shell(s) would have occurred in the common ancestor of molluscs and brachiozoans and were later lost at least four times. In molluscs, mineralised shell loss would have occurred at least once (or possibly twice) in the aplacophorans and on three occasions in the brachiozoans, once in the phoronids and twice in the putative stem brachiopods *Lingulosacculus* and *Yuganotheca*. Lophotrochozoan relationships (red lines and taxa) from phylogenomic analyses in Luo, Y.J. et al., *Nat. Commun.*, 6, 9301, 2015, brachiozoan phylogeny from Moysiuk, J. et al., *Nature*, 541, 394–397, 2017. See Chapter 13 for information on some of the extinct groups.

The homology of the molluscan coelom is also important when considering molluscan relationships. The plesiomorphic molluscan coelom is a *gononephrocoel* – that is, a coelomic space within both the gonad and kidney – but its homology with the coeloms of other phyla is not clear, as it is uncertain if it independently evolved or is a plesiomorphic condition (see Haszprunar 1992b for discussion; Bartolomaeus 1997) (see Chapters 7 and 8 for more information on the molluscan coelom).

The radula is often cited as a uniquely molluscan character, but bilaterally symmetrical, mineralised buccal structures also occur in other spiralian taxa including Annelida and Gnathifera and several extinct putative taxa (e.g., some halkieriids) (see Chapter 13). Each of these structures is characteristic of their respective lineages with some shared similarity (Chapter 13, Figure 13.10) suggesting both convergence as well as the possibility of plesiomorphic buccal structures in some lineages.

Summaries of earlier studies relating to the search for the molluscan sister group can be found in Haszprunar (1996), Lindberg et al. (2004), and Haszprunar et al. (2008). The search is, of course, ongoing with recent molecular analyses reconstructing the annelids, phoronids and brachiopods, or nemertean (or various combinations of these) as potential molluscan sister taxa (Table 12.1).

Three main trends have occurred independently in two or more major groups of molluscs with fundamental effects on more than one organ system of the body. These are briefly outlined below.

12.3 REPETITION OF ORGANS

Multiple pairs of organs are found in some molluscs, a phenomenon known as *serial repetition*. It includes shell muscles in chitons, monoplacophorans, protobranch bivalves, and *Nautilus*; ctenidia and auricles in *Nautilus* and monoplacophorans; ctenidia alone in chitons; kidneys in monoplacophorans and *Nautilus*; and gonads in monoplacophorans. *Nautilus* has two pairs of pedal retractors, kidneys, gills, and atria, but the numbers of repeated organs in monoplacophorans do not correspond, with zero to two pairs of auricles, three to six pairs of ctenidia, three to seven pairs of kidneys, and one to three pairs of gonads. In chitons, only the shell muscles and ctenidia are serially repeated, but these two systems do not correspond to each other.

There have been two main theories to account for organ repetition in molluscs. It has been thought to be a primitive feature indicating metamerism (e.g., Naef 1926; Lemche & Wingstrand 1959; Wingstrand 1985) or that the repetition is

TABLE 12.1
Sister Taxon Relationships Suggested by Selected Molecular Analyses of Molluscan Relationships over the Last Ten Years

Authority	Sister Taxa
Dunn et al. (2008, figure 1)	Annelida (Phoronida (Brachiopoda, Nemertea))
Dunn et al. (2008, figure 2)	Annelida (Brachiozoa, Nemertea)
Giribet et al. (2009, figure 6.1)	Entoprocta
Paps et al. (2009, figure 1)	Brachiozoa
Edgecombe et al. (2011, figure 1)	Annelida, Brachiozoa, Nemertea
Smith et al. (2011, figures S2, S3, S4, S5, S6)	Brachiopoda, Nemertea
Smith et al. (2011, figures S7, S9)	Nemertea (Annelida, Brachiopoda)
Kocot et al. (2011, figure 2)	Annelida
Laumer et al. (2015, figure 1)	Nemertea (Brachiozoa, Annelida)
Kocot et al. (2017, figures 1, 3, 5, 6)	Brachiozoa (Annelida, Nemertea)
Kocot et al. (2017, figures 4, 7)	Brachiozoa

Note: Brachiozoa includes Brachiopoda and Phoronida

due to secondary duplication (e.g., Morton & Yonge 1964; Haszprunar & Schaefer 1996), as there is no support for segmentation due to the lack of correspondence of the repeated organs and no evidence of segmentation in the nervous system.

In the 1950s, the discovery of a living monoplacophoran (*Neopilina*) (Lemche 1957; Lemche & Wingstrand 1959) that possessed several gills, shell muscles, and kidneys gave rise to the notion that molluscs were primitively segmented and rekindled the idea that annelids might be the molluscan sister taxon.

Serial repetition of shell muscles may be a primitive feature of molluscs (Haszprunar & Wanninger 2000), with a reduction in the number of these muscles having occurred independently in different molluscan groups, as shown in the fossil record. This is notably the case for cephalopods (Kröger & Mutvei 2005) (see Chapter 17) and protobranch bivalves (e.g., Driscoll 1964).

Based on outgroups, the lack of segmentation is plesiomorphic in the Lophotrochozoa as only Annelida are segmented. Serial replication of organs also occurs in the gonads of Nemertea, the proglottids of the Cestoda, and in the muscle systems of some bryozoans and brachiopods (Bulman 1939; Jebram 1986; Giribet 2016a).

12.4 ANO-PEDAL FLEXURE AND A CHANGE IN BODY ORIENTATION

This topic has been covered in Chapters 1, 3, 5, and 8, but the main points of this important aspect of molluscan evolution are repeated here for convenience.

Chitons, living monoplacophorans, and aplacophorans have the anteroposterior axes (as determined by the position of the mouth and anus) coinciding with their body orientation (i.e., the main body axis), and they have a linear alimentary system. Because of this body configuration, their dorsoventral axes are shorter than their anteroposterior axes. The other

major groups (classes) exhibit ano-pedal (or anal-pedal) flexure, with the gut curved into a U-shape, although it is less marked in bivalves than in other groups. This resulted in the anteroposterior axis becoming shorter and the dorsoventral axis longer, so the latter became the longest body axis in gastropods, scaphopods, and cephalopods. The consequences of this change were profound, resulting in greater lateral compaction of the viscera and dorsoventral elongation. In bivalves, this enabled shortening of the body and its enclosure in a two-valved shell, while in gastropods and cephalopods a single conical or coiled shell was developed and in scaphopods a tube.

12.5 REDUCTION AND PAEDOMORPHOSIS

Paedomorphosis occurs when juvenile or larval traits are retained in adults, and such events are thought to have played an important role in molluscan evolution. There are two ways paedomorphosis can occur. The first is by *progenesis* where sexual maturation occurs earlier relative to the rest of development, and the other is by *neoteny* (or juvenilisation) where somatic development is retarded relative to reproductive maturity. These processes often result in simplification or reduction in organs and are two of the developmental changes termed *heterochrony* that involve changes in the timing of developmental events (see Chapter 8).

Today, most workers consider living molluscs to be divisible into two groups, the Aculifera and the Conchifera. Relationships within these two clades continue to be investigated, but consensus on a single hypothesis of relationships within these groups remains elusive (Sigwart & Lindberg 2015). In addition, our current understanding of the Aculifera and Conchifera does little to elucidate the morphology of the earliest mollusc. Assuming they were worms because there are worm-like aplacophorans in the Aculifera is without merit. Only a well-supported outgroup or an extraordinary

fossil occurrence is likely to assist in resolving this issue. In the former case, molecular data appears to be homing in on three taxa, Brachiozoa, Nemertea, and Annelida. Of these three, the fossil record is likely to be useful only with the Brachiozoa, but care must also be exercised here to guard against overly broad diagnoses of character state homology and the 'shoe-horning' (Gould 1989) of inimitable fossil taxa into living taxa.

13 Early History and Extinct Groups

13.1 INTRODUCTION

Molluscan fossils have been involved in every aspect of the development of the fields of palaeontology, palaeobiology, evolution, and phylogeny. Fossils are the remains and traces of once-living organisms, but in the past naturalistic and supernaturalistic explanations were given for their existence. Over 300 years ago, the term ‘fossil’ referred to any object found buried in the earth and included geological objects such as crystals and concretions, archaeological items, and the remains of dead organisms. The latter category was especially problematic because many of the molluscan fossils strongly resembled living taxa, suggesting an organic origin for these remains. Others were more fragmentary or were the remains of extinct taxa such as ammonites (which at one time were thought to be representations of decapitated snakes). Such strange objects suggested a non-organic origin of fossils, one such explanation being that they had grown spontaneously within the rock. Extensive beds of fossil molluscs found at high elevations in mountains, far from the ocean, also prompted the notion that they had spontaneously appeared there.

The idea of the spontaneous generation of molluscs and other fossils within solid rock traces its origins to Aristotle (384–322 BCE¹) and his writings on animal reproduction and generation. Aristotle thought that molluscs reproduced exclusively by spontaneous generation and that they would suddenly appear where and whenever conditions were suitable for their lifestyle. For example, when mountainous areas with briny soils and abundant limestone were inundated by water, conditions became appropriate for molluscs, and they would spontaneously generate, live out their lives, and then die, remaining embedded in the rocks in which they had first appeared. This view was commonly held until Nicolaus Steno (1638–1686) established the foundations of palaeontology. Steno made observations of conditions surrounding living organisms and used these observations to test the idea that fossils had actually grown within the rocks in which they were found. Many of his arguments involved molluscan fossils. For example, he noted that tree roots in softer soils were relatively straight and regular in their growth pattern while the roots of trees growing in harder soils were contorted and irregular. He pointed out this was not the case for fossil molluscs which were often similar to one another regardless of the hardness of the rock in which they had supposedly grown. He also noted that their growth within the rock should have, but did not, crack the rocks. The observations and arguments by Steno established fossils as the remains of once-living organisms. It was not until about 200 years later that molluscs again played a major role in the next advances in the

study of fossils. From the time of Steno, there remained the question as to why extensive fossil beds of marine snails were found at high elevations in mountains far from marine habitats. Catastrophic flood stories, prominent in many religious traditions, were often invoked to account for their distribution. During the Renaissance, Leonardo da Vinci (1452–1519) argued that the fossil molluscs in the mountains did not represent a death assemblage from a single event but rather the different beds comprised different taxa, which in turn represented events at different times.

Charles Lyell (1830) observed that younger strata had a higher percentage of fossils of living mollusc species than those in the older strata, which had few, if any, living taxa present (Stanley et al. 1980). Lyell later inferred from this pattern that over time, extinction removed older taxa, while the ‘origination of fresh species’ gave rise to a greater abundance of living taxa in younger strata (Lyell 1881 p. 5). The percentage of extinct to living taxa was the first basis for the recognition of the Pliocene, Miocene, and Eocene time periods.

Charles Darwin, a friend of Lyell, made extensive geological observations in South America during his global circumnavigation aboard the *Beagle* between 1831 and 1836. Darwin (1838–1843) noted elevated shell beds in Argentina, along the coast of Tierra del Fuego, and along the coast and in the mountains of Chile. His experience of strong earthquakes and observations of the extent to which they caused parts of the coast to be uplifted led him to propose an earthquake-driven uplift mechanism for the origin of these elevated beds.

Today molluscs provide one of the most important datasets in palaeobiological research and are crucial for understanding and analysing factors and patterns in the evolutionary history of life on Earth. The molluscan fossil record also plays a critical and unique role in advancing our understanding and reconstruction of the evolutionary relationships within molluscs and between the molluscs and other lophotrochozoan taxa. This is driven primarily by the evolution of the molluscan exoskeleton (shell and/or spicules), which has ensured that the Mollusca are well represented in the metazoan fossil record. Only the aplacophoran taxon Caudofoveata remains unrecognised in the fossil record, although the supposed occurrence of putative Solenogastres in the Silurian remains debatable (see Section 13.3.4.1.3). Techniques for reconstructing soft tissue morphology (Sutton 2008) and recovering microfossils and other microscopic skeletal elements are rapidly improving. Within the last thirteen years, even putative developing lophotrochozoan embryos have been discovered from the Cambrian of China, and putative molluscan-like radulae from the early Cambrian of Canada have been reported (Butterfield 2006, 2008). Thus, the potential to discover aplacophoran spicules and other molluscan elements and microfossils

¹ Before Common Era, an alternative to BC.

remains high, and it is likely that our knowledge in these areas will continue to increase.

13.1.1 THE FIRST MOLLUSCS?

The first appearance of molluscs in the fossil record is controversial. According to Parkhaev and Demidenko (2010), the first known molluscs (*Purella*) appeared in the uppermost zone of the Nemakit-Daldynian (542–534 Ma).² Beginning with the Tommotian (534–530 Ma) putative molluscs, thought to have been prominent in Cambrian ‘small shelly fossil’ assemblages, have been identified as Polyplacophora, Monoplacophora, Bivalvia, and Gastropoda. In contrast to the aplacophoran groups, these four groups and the remaining molluscan taxa can be followed through the fossil record. For some taxa, the affinities and relationships between the fossils and living taxa appear straightforward. For example, bivalves, most gastropods, cephalopods, and monoplacophorans are recognised and allocated to extinct and living groups. As one goes deeper in time, the interpretation and affinities become more difficult – especially when extinct stem groups are involved.

Determining taxon affinities in the earliest portions of the fossil record is fraught with potential difficulties. For Cambrian ‘molluscs’, typically only a shell is available for comparison with the six extant molluscan morphologies – cephalopods (shell with septa), gastropods (limpet or coiled shell), bivalves (bivalved shell), scaphopods (tusk-like shell), polyplacophorans (multiple shell plates), and monoplacophorans (limpet shell); living aplacophoran molluscs have spicules but lack shells. Besides gross shell morphology, several other characters may be resolvable, including shell microstructure, muscle attachment areas, and external and internal sculpture.

The presence of other shelled taxa in the Cambrian such as brachiopods, hyoliths, tentaculitans, and some arthropods further complicates accurate allocation. In these situations, extra caution must be exercised to avoid ‘shoe-horning’ specimens into more familiar taxa. Gould (1989) highlighted this phenomenon with another Cambrian group, the Burgess Shale arthropods. In this example, diverse morphologies of arthropods were originally identified as trilobites or as members of extant taxa, rather than understood for the unique lineages they represented. Numerous potential ‘shoe-horning’ opportunities exist in Cambrian shells, especially with groups such as the siphonoconchs, helcionellidans, pelagiellidans, and sachtidans.

Recent palaeontological and molecular work in one of the putative molluscan sister taxa, the Brachiozoa, is illustrative here. The Brachiozoa (brachiopods + phoronids) were once thought to be a relatively low disparity group. Brachiopods were well known and delimited, bivalved animals with a lophophore and, typically, a peduncle; the group first appeared at the Nemakit-Daldynian boundary (542.0 Ma). In contrast,

phoronids are shell-less, tubular animals³ with U-shaped guts and a lophophore. The U-shaped gut necessitates that both groups undergo a folding similar to ano-pedal flexure in some molluscs (see Chapters 8 and 12). Over the last 20 years, brachiozoan morphological disparity has been substantially increased by proposals to include additional groups in the phylum. Tommotiidans, hyoliths, and tentaculitans are all tubular animals living in shells (blind tubes) with hypothesised U-shaped guts, and were formerly placed in the Mollusca as well as in other lophotrochozoan groups. Other recently discovered ‘brachiozoan’ taxa, such as *Lingulosacculus* and *Yuganotheca*, are more brachiopod-like but lack shells or have agglutinated shells (Balthasar & Butterfield 2009; Moysiuk et al. 2017).

Based on a morphological analysis, Vinn and Zatoń (2012) concluded that tentaculitans clustered with the Brachiozoa rather than Mollusca or Bryozoa, while the re-examination of hyoliths from the Burgess Shale by Moysiuk et al. (2017) reported a putative lophophore in this taxon, again suggesting brachiozoan rather than molluscan affinities. Tommotiidans have long been problematic, and reconstructions before the discovery of partial, tubular scleritomes (Skovsted et al. 2008) often featured the individual sclerites arranged in a similar way to the plates of polyplacophorans (e.g., Evans & Rowell 1990). In addition, the discovery of a bivalved larval shell in some tommotiids suggests further brachiozoan affinities. While not all workers accept these new interpretations and alternative relationships, these data and the hypotheses they support require a re-examination of other putative early molluscs, especially given molecular analyses of lophotrochozoan relationships which place the brachiozoans as the sister taxon of the Mollusca rather than the Annelida (Paps et al. 2009; Luo et al. 2015).

Allocation of Cambrian taxa to the Mollusca was initially straightforward with few controversies (Runnegar & Pojeta 1974a), although both new specimens and the re-examination of existing data have sometimes been in conflict with traditional concepts. For example, Dzik (2010) made a cautionary call regarding putative early Cambrian monoplacophoran-like limpets which, based on the muscle attachment patterns, may actually represent brachiopod valves and not the ancestors of cephalopods, and Butterfield (2006) cogently argued that the Burgess Shale taxa *Odontogriphus omalus* and *Wiwaxia corrugata* are not stem group molluscs but rather jawed, segmented worms which could represent two phyla. Last, the startling discovery by Roger Thomas and colleagues (Thomas et al. 2010; Thomas & Vinther 2012) of pelagiellidans with paired clusters of chaetae calls into question the recognition of this spirally coiled, septate shell as a mollusc. Dzik and Mazurek (2013) reported similar structures in *Aldanella* and suggested the transfer of the pelagiellidans to the Hyolitha rather than them representing one of the earliest occurrences of the Gastropoda (see Section 13.3.2.2.7). If correct, this assignment would also substantially increase the disparity

² Nemakit Daldynian ‘molluscs’ were initially thought to be latest Ediacaran, although they are now considered to be Terreneuvian (Cambrian) by most workers.

³ We regard animals with U-shaped guts as ‘tubular’ rather than worm-like or vermiform because of their lack of a posterior anus.

of the brachiozoan taxa by including spirally coiled shells in the group. An alternative view was presented by Vendrasco and Checa (2015) who noted that many helcionelloids also had shell pores, which are more typical of brachiopods than of molluscs, and suggested that chaetae and shell pores might be plesiomorphic character states shared by Mollusca, Brachiopoda, Bryozoa, and Annelida, which were subsequently lost in crown molluscs. Many of the aforementioned debates centre on the homology (and envisioned importance) of specific structures, often unconstrained by outgroups or using imaginary cartoon creatures to reconstruct the correspondence of the molluscan body plan in ancient conchs (Lindberg & Ghiselin 2003b). This is especially inappropriate when the cartoon represents, among other features, a gastropod with a detached head (Figure 13.1).

The potential position of a morphologically diverse brachiozoan clade as sister to the Mollusca necessitates a careful reconsideration of character states – what is a mollusc and what is something else? For example, if sister taxa, several calcareous shell microstructures become potentially plesiomorphic within the ancestor of the two groups and not diagnostic of either (Carter 1985, Figure 26; Malakhovskaya 2008; Li et al. 2017b). Moreover, a diverse array of extinct body plans also provides additional considerations for the last common ancestor of molluscs and brachiozoans. Although focused on the Burgess Shale Cambrian arthropod disparity, the conclusions of Briggs et al. (1992) are illustrative of this problem (Figure 13.2). If only the extant morphologies are considered, taxa (body plans and their associated character states) are reduced by more than half (20 versus 46 taxa). Extinction rates in the three surviving clades ranged between 0% and 87.5% (Figure 13.2), and the disparity is reduced (Briggs et al. 1992). Extinction applies similar sampling constraints on molecular data which exists only for a small subset of living taxa.

The above discussion highlights the difficulties of determining what constitutes a mollusc, much less a definitive origin(s) of the phylum. Therefore, we have taken a conservative approach and consider alternative narratives for the Cambrian appearance of the Mollusca.

13.1.2 SHELL MORPHOLOGY

Palaeontologists have searched for diagnostic shell morphologies by which to recognise molluscs in the fossil record. Molluscan shells are predominately the product of accretionary growth processes that add calcium carbonate in a protein matrix to the growing edge of the shell. Some molluscs such as polyplacophorans and aplacophorans also secrete intracellular spicules and scales. Definitions of hard part structures (e.g., spicule, scale, plate, conch) are given in Table 13.4. A multitude of morphologies are produced by variation in the rates of shell secretion around the edge of the shell. Through this relatively simple process, molluscs have generated an amazingly diverse range of morphologies both between and within different groups and lineages. These morphologies included coiled shells, limpets, tubes, and bivalves. The shell has also been lost numerous times in gastropods and more than once in coleoid cephalopods. Unfortunately, the early forms are not unique to individual molluscan clades or even to molluscs themselves, and this has resulted in many difficulties in interpreting their early history. For example, Smith and Caron (2010) proposed that the Burgess Shale animal *Nectocaris* was an early, shell-less, stem cephalopod although previous workers had identified it as either an arthropod or chordate, and obvious molluscan synapomorphies are absent (see Mazurek & Zaton 2011). Scaphopods and the multivalved Polyplacophora are unique in having a limited morphological diversity compared to the other major molluscan groups. Simple morphologies, such as the often unsculptured tubes of scaphopods, also present problems for palaeontologists because of their lack of diagnostic characters and potential confusion with calcified tubes of other living and extinct lophotrochozoan taxa (e.g., some polychaetes).

The most recognisable putative molluscan form in the fossil record is the single bilaterally symmetrical shell or conch. This ancestral shell is thought to have been subsequently decalcified along the dorsal midline during development to produce the pair of valves of the Bivalvia, each with a prodissoconch. While rostroconchs might appear to be intermediate in this sequence, they have a single protoconch associated

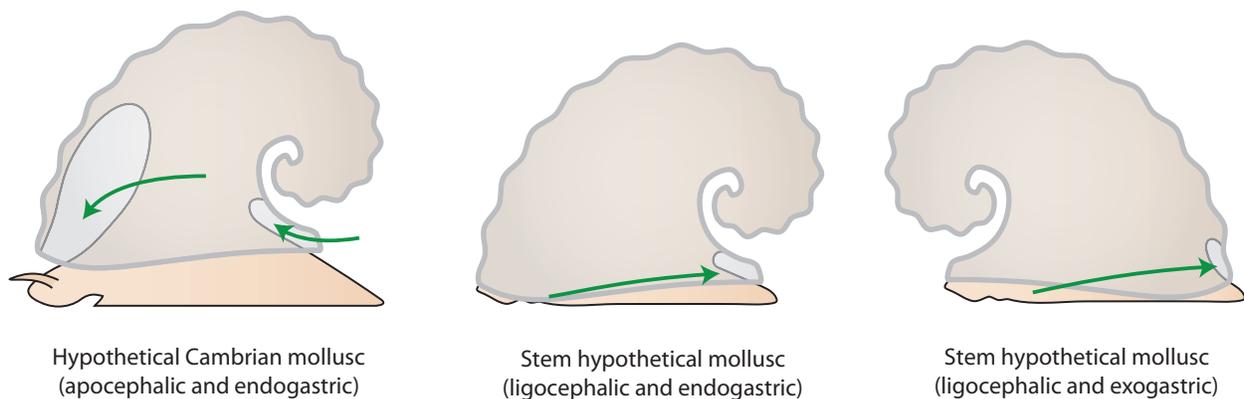


FIGURE 13.1 Left: Hypothetical ancestral mollusc cartoon commonly used to reconstruct anatomical features and functions; note free head (apocephalic), proposed water currents, and large anterior and small posterior mantle cavities. Middle and right figures reconstructed with the plesiomorphic attached head (ligocephalic), estimated extent of posterior and lateral mantle cavities and hypothesised water currents.

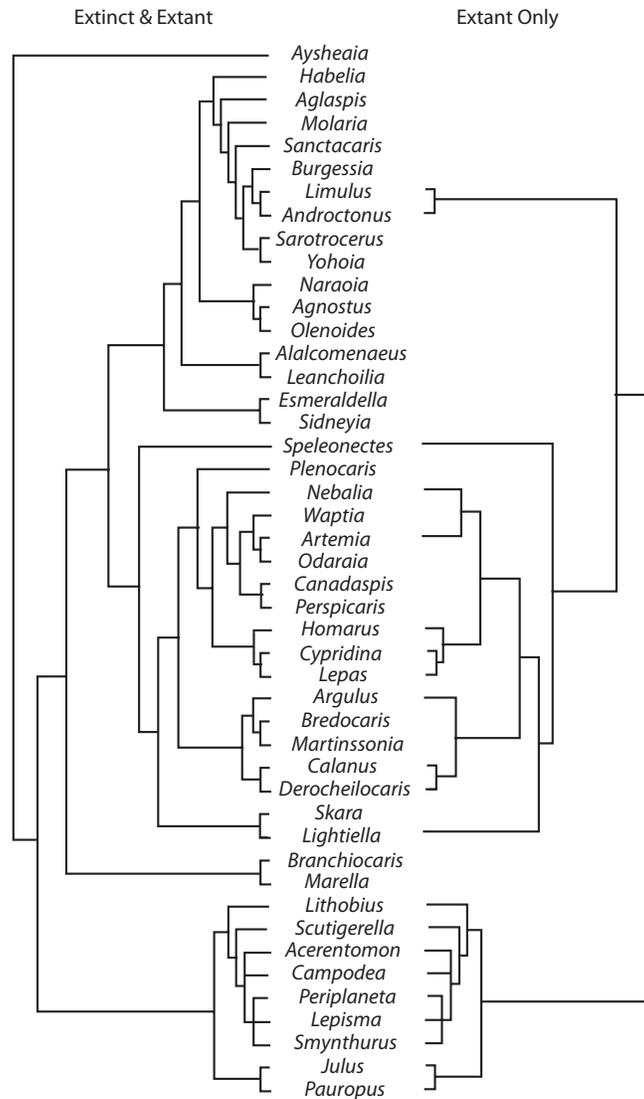


FIGURE 13.2 Unrooted phylogeny of Cambrian and living arthropods based on morphology. Modified from Briggs, D.E. et al., *Science*, 256, 1670–1673, 1992.

with one valve and a calcified groove joining the two valves. Polyplacophorans are unique among the molluscs in having exoskeletons that consist of multiple valves, although in the fossil record, the disarticulated valves of what are assumed to be early chitons can be difficult to recognise as molluscan or envisioned in life position. Therefore, the rare discovery of whole specimens (the scleritome) is critical in recognising these disarticulated bits as being part of a single animal. Once the overall pattern is recognised, the ratio of head and tail-like valves to mid-valves in bulk samples can be very informative for estimating both the diversity and abundance of fossil chitons.

Because molluscan palaeontologists have to rely to a large degree on shell morphology, this limited character set has produced a proliferation of higher taxon names because supposed differences in shell morphology are the sole determinant of many extinct higher taxa. The limitations of this approach in understanding the diversity and relationships of

fossil molluscs are readily apparent when one considers the degree of morphological disparity that can occur in both small and large clades, e.g., Neritimorpha (~450 species) and Caenogastropoda (~75,000 species). At the other end of the spectrum is rampant morphological convergence such as seen in the limpet-like morphologies that have independently evolved in living Mollusca over 54 times (Vermeij 2016). As previously noted, this convergence is particularly problematic when trying to interpret molluscan relationships in the Cambrian where limpet morphologies dominate (also see Section 13.3.2).

13.1.2.1 Beyond Shell Morphology

Aware of the problems that convergent shell morphologies present, many palaeontologists have sought and described non-traditional morphological characters from fossils, including shell microstructure, anatomical impressions from muscles, and even some soft anatomy features and structures.

By the mid-20th century, palaeontologists had recognised that phosphatic casts of the internal surface of bivalve shells contained impressions that allowed the identification of the type of shell microstructure (Runnegar 1983, 1985) (see Chapter 3). Both phosphatic and fine-grained sediments such as silt, mudstones, and clays can preserve these structures, including nacre, prismatic, and crossed lamellar, as far back as the Cambrian (Kouchinsky 2000; Feng et al. 2003; Feng & Sun 2003). While exceptional preservation of the original shell structure components is more common in Mesozoic and Cenozoic fossils, original shell structure has been found in some early Paleozoic specimens (i.e., Ordovician bellerophonians and bivalves). Sometimes, combinations of certain shell microstructures, such as crossed lamellar and nacre, have been documented in extinct taxa although this combination is unknown in living bivalves. Phosphatic and fine-grained sediments can also preserve anatomical impressions such as muscle attachment surfaces (muscle scars – see below and Chapter 3), pallial lines, radula, veins, digestive systems, and even gills. Typically, the most illuminating fossil characters come from the exceptional preservation of anatomy, such as found in the *Lagerstätten* deposits. These are thought to occur where anoxic conditions suppress bacterial decomposition, and impressions or traces of the body parts are incorporated into the fossil via the presence of rapidly accumulating fine sediment. Unfortunately, *Lagerstätten* that provide insights into molluscan ancestry and relationships are rare.

The Precambrian Ediacara Hills (700 Ma) in South Australia, Doushantuo Formation (600–555 Ma) in Guizhou Province, China, and other localities worldwide are well known for the preservation of numerous strange, soft-bodied organisms. When these fossils have been referred to extant phyla, the vast majorities are assigned to the Cnidaria, but putative annelids have also been identified (Bottjer 2002) as well as a putative mollusc – *Kimberella* (see Section 13.3.1). Alternatively, Seilacher (1984a) and others have argued that the Ediacaran faunas represented an early experiment in metazoan diversification that largely underwent extinction at the Cambrian explosion (Hoyal Cuthill & Han 2018).

Cambrian *Lagerstätten* have been problematic. These localities include the Chengjiang (525 Ma) in Yunnan Province, China, the Emu Bay shale (525 Ma) in South Australia, the Sirius Passet Formation (518 Ma) in Greenland, and the Burgess Shale (505 Ma) in British Columbia, Canada. Skeletonised body fossils such as brachiopods and trilobites are present in the Chengjiang formation, but the only supposed molluscs found in abundance are hyoliths, which are now considered putative brachiopods. The well-known Burgess Shale fauna, popularised by Stephen J. Gould in *Wonderful Life* (1989), is also rich in skeletonised body fossils including brachiopods, arthropods, and echinoderms (Hagadorn 2002a). Again, the only putative molluscs occurring here are hyoliths (Briggs et al. 1994). A similar absence of unequivocal molluscs also occurs in the Emu Bay shale (525 Ma) in southern Australia and in the Sirius Passet Formation in Greenland,

although the latter yielded the controversial *Halkieria* (see below).⁴

The absence of unequivocal molluscs from Cambrian *Lagerstätten* is puzzling. Helcionelloidans, gastropods, and bivalves are known from numerous non-*Lagerstätten* localities around the world from the early Cambrian on (Parkhaev 2008); however, they are virtually non-existent in *Lagerstätten* faunas. Whether their absence is due to ecological or taphonomic factors, or a combination of these and other factors, is not known. However, P. Wagner (pers. comm., Feb. 2019) has pointed out that the fact that aragonitic hyolithid shells are present argues against mineralogy-based taphonomy, but there could have been a size-based taphonomic filter. Lastly, although hyolithids often occur with molluscs, they also occur without them, suggesting that they had a broader tolerance for Cambrian environments.

Molluscs are known from subsequent *Lagerstätten*, of which the Silurian Herefordshire *Lagerstätten* of England (426.2–422 Ma) is perhaps the most important to date. This locality has provided fossilised gastropod soft tissue and organ morphology (Sutton et al. 2006) as well as *Acaenoplax hayae* – a possible early shelled solenogaster (Sutton et al. 2004) (see Chapter 14). The Herefordshire specimens are preserved as three-dimensional fossils within calcareous nodules, and the fossils are computer-reconstructed from serial images recorded as the specimens are literally ground out of the matrix (Sutton et al. 2001a).

Soft-body structures of cephalopods are abundant at several Carboniferous localities, including the Mississippian Bear Gulch beds of central Montana, USA (339.4–318.1 Ma) and the Pennsylvanian Mazon Creek material of northern Illinois, USA (309.2–302.0 Ma). Cephalopods from Mazon Creek are so well preserved that using a scanning electron microscope (SEM) it has been possible to compare the ultrastructure of fossil ink from these specimens with that from living specimens (Doguzhaeva et al. 2007a).

The Mesozoic Posidonia Oil Shale of southwestern Germany (Lower Jurassic 183–175 Ma) is the earliest *Lagerstätten* to preserve the belemnite animal; aspects of ammonite and coleoid anatomy and bivalves with colour patterns are also present (Etter & Tang 2002). The Middle Jurassic La Voulte-sur-Rhône (164.7–161.2 Ma) formation in southern France contains some of the best-known fossil cephalopod anatomy (Etter 2002a) (Figure 13.3).

Another Jurassic locality is the Oxford Clay of central England (164.7–161.2 Ma), which has revealed over 50 species of bivalves (Tang 2002) and gastropods; scaphopods are also abundant but not diverse. Cephalopods are again especially well preserved and include ammonites, nautiliforms, belemnites, squid and sepiids. Lastly, there is Solnhofen in southern Germany (150.8–145.5 Ma). Best known for the fossil feathered bird *Archaeopteryx*, molluscs from Solnhofen include bivalves, gastropods, ammonites, belemnites, nautiliforms, and sepidans – many still in association with their substrata and habitats (Etter 2002b).

⁴ If hyoliths are in fact brachiopods, the pattern of molluscan absence in these communities is strengthened.



FIGURE 13.3 *Vampyronassa rhodanica*. A pyritised coleoid from the Middle Jurassic (Callovian) (164.7–161.2 Ma). Voulte-sur-Rhône, France. Public Domain. Photograph by William Stoddar (<https://commons.wikimedia.org/wiki/File:Vampylarge.JPG>).

These, and other exceptionally preserved molluscan fossil localities, provide important morphological and palaeoecological insights into diverse groups of extinct putative molluscs. In addition, co-occurring taxa at these localities provide insights into ecological interactions with molluscs and other organisms, including bivalve/algal associations in the Mississippian Bear Gulch beds (Hagadorn 2002b) and the distinctive hypothesised feeding techniques of ichthyosaurs on belemnites in the Jurassic seas of Germany (Wiesenauer 1976). With the possible exception of the Silurian Herefordshire Lagerstätten, these amazingly resolved glimpses into the past have failed to produce uncontested stem taxa that would facilitate the connection of the disparate morphologies that define the living molluscan groups (Lindberg & Ponder 1996). This markedly contrasts with some other groups where Lagerstätten have been crucial in contributing to our understanding of the relationships of the crown taxa, as for example with the aforementioned Burgess Shale Arthropoda (Briggs & Fortey 1989).

Some physiological traits can be inferred both from hard parts and exceptionally well-preserved fossils. For example, hypothesised water flow patterns into and out of the mantle cavity have been used to test alternative shell orientations for Cambrian and other extinct taxa (Knight 1952; Lindberg & Ghiselin 2003b) (Figure 13.1). If the shell is altered in such a way that it has the potential to direct water, the remaining and more difficult question is – in which direction did it flow? In crown molluscs outflow control is plesiomorphic (Lindberg & Ponder 2001). Altered surfaces include grooves, holes, trains, folds, and notches. The attempts to link living taxa to Paleozoic fossils carry with them inferences about anatomy. Examples include the hot vent limpet-like *Neomphalus* being linked with euomphaloideans (McLean 1981a, b), fissurelids linked with euphemitid bellerophonians based on shell microstructural similarities (MacClintock 1967; McLean 1984b), or patellogastropods linked to platyceratoideans (Ponder & Lindberg 1997). Protoconch characters have also been used extensively in gastropods (Bandel & Frýda 1998; Frýda et al. 2008a; Frýda et al. 2009; Nützel 2014) and provide both characters and inferences of reproductive mode (Shuto 1974; Jablonski & Lutz 1983). In very rare cases soft

tissue can be preserved, giving insights into the anatomy of long extinct taxa. Anatomical characters from a supposed Silurian platyceratoidean led Sutton et al. (2006) to link them with patellogastropods, and fossilised intestinal tracts in the bellerophoniform ‘monoplacophoran’ *Cyrtodiscus nitidus* demonstrate the potential presence of torsion in that taxon (Horný 1998), which suggests bellerophonian rather than monoplacophoran affinities.

13.1.2.2 Muscle Scars

Muscles in living molluscs are discussed in Chapter 3. Two main groups of muscles concern us here because they leave distinctive scars on the shell – the dorsoventral and oblique foot retractor muscles (or shell muscles) and the buccal muscles. The latter are the main retractor muscles associated with the buccal mass and are typically involved in the retraction of the odontophore, and hence the radula, where present.

Horný (1965) recognised two putative apex/muscle scar relationships in molluscs. In the tergomyan condition the shell apex is located outside the ‘muscle ring’, and within it in the cyclomyan state. This dichotomy was questioned by Peel (1991a) and examined by Schaefer and Haszprunar (1996), who concluded there is no major difference in the position of the apex relative to the muscle ring between the two states. These terms do usefully demarcate two distinct muscle organisation character states (see below), which are defined in Table 13.1.

Not all shells with dorsal serial muscle scars are molluscs, as similar muscle scar patterns are also found in Cambrian inarticulate brachiopods (Dzik 2010) with some, including *Lenaella*, *Moyerokania*, *Scenella*, and *Kirengella* being previously treated as monoplacophorans. Some brachiopod taxa may be distinguished from monoplacophorans by a medial pair, or pairs, of muscle scars (e.g., as in *Craniops*), although in some fossil shells, a single pair of anterior medial scars could be mistaken for buccal musculature.

There are three major patterns in molluscan musculature: (1) multiple right and left retractor muscles (e.g., polyplacophorans, monoplacophorans, protobranch bivalves, and solenogasters, albeit greatly reduced). This pattern results in the bilateral presence of muscle units and is non-homologous

TABLE 13.1**Some Terms Used to Describe the Relationship of the Shell, Musculature, and Body Relative to the Shell in Molluscs**

Tergomyan	Foot musculature of paired dorsoventral retractors with paired oblique muscles. Buccal muscle scars often present.	Polyplacophora, Monoplacophora, Protobranchia, Solenogastres
Cyclomyan	Foot musculature of paired dorsoventral retractors often fused into horseshoe-shaped muscle band; paired oblique muscles absent. Putative buccal muscle scars often present.	Helcionelloida, Cyrtolites, Rostroconchia
Both these terms have been used as ordinal names (Tergomya, Cyclomya). Here they are used as descriptors of muscle scar patterns found in both stem and crown molluscs.		
We introduce two new terms here:		
Ligocephalic	Head region dorsally attached to the shell. Buccal muscle scars often present.	Monoplacophora, Polyplacophora, Bivalvia, Rostroconchia?
Apocephalic	Head region not attached to the shell. Buccal muscle scars absent except those integrated with shell muscle(s).	Cephalopoda, Scaphopoda, Gastropoda
The two terms below describe coiling direction relative to the head of the mollusc. They were first used in fossil cephalopod descriptions before being extended to gastropods and to early Cambrian molluscs.		
Endogastric	Earliest shell whorls positioned over the posterior region of the body. This coiling direction supposedly enables the head to withdraw before the foot.	
Exogastric	Earliest shell whorls positioned over the anterior region of the body. This coiling direction supposedly requires the foot to withdraw before the head.	

with ‘muscle bundles’ in gastropods (see below). (2) In addition to the plesiomorphic dorsoventral retractor muscles, oblique retractor muscles are present in polyplacophorans, monoplacophorans, solenogastres, and protobranch bivalves. These muscles are combined into distinct bundles in polyplacophorans and monoplacophorans and are both bundled and separate in the protobranchs and solenogastres. The dorsoventral pedal muscles are lost in heterodont bivalves, leaving the oblique pedal retractors and protractors and the autapomorphic adductor muscles. Muscle proliferation in the ancestor(s) of these groups probably increased functionality and control of foot movement giving great mobility over diverse surfaces and, in ancestral protobranchs, some burrowing capability. In crown molluscs, increasing motility is often associated with shell reduction or sometimes either loss or replacement with spicules or multiple shell plates, an apparent parallel theme within Sachtida as well (see Section 13.3.2.2.1). (3) In stem gastropod and cephalopods, a paired retractor muscle configuration is typically present. In both fossil and living taxa, these paired muscles can expand posteriorly on each side of the shell, forming either a partial or complete horseshoe-shaped muscle band (e.g., Archinacelloidea, Hipponicidae). The muscle band may be traversed by blood sinuses suggesting separate muscles (e.g., Patellogastropoda), but these are not to be confused with duplications of retractor muscles as in polyplacophorans, monoplacophorans, protobranch bivalves, and solenogastres. Instead, the divisions between bundles are superficial and only deep enough to allow venous blood to move from the central visceral mass to the mantle edge for oxygenation. Such muscle scar morphology is: (1) probably homoplastic in numerous Cambrian lineages, especially

among limpet-shaped groups, (2) unlikely to reflect either a torted or non-torted state of the former occupant, and (3) while it can assist in the difficult task of identifying early ‘Monoplacophora’, it is much less useful in assisting with the identification of possible ancestors of the various conchiferan groups. In several early coiled lineages there was a subsequent reduction of the right retractor muscle and its eventual loss so that, as in gastropods, only the left retractor muscle remains.

Besides the pedal retractor muscles, multiple paired buccal muscles that manipulate the mouth and radula often terminate on the shells of the shelled groups. These muscles and their size appear to be correlated with the robustness of the radular apparatus (e.g., Polyplacophora and ‘Aplacophora’), and they may be closely associated with the dorsoventral retractor muscle scars. The similarity of the placement of the buccal muscle attachment scars in various groups of molluscs is surprising given the vast differences in morphology. In polyplacophorans, monoplacophorans, both aplacophoran groups, and bivalves the head region is not detached from the shell, but rather it is continuous with it, providing attachment surfaces directly above the head region. In scaphopods, gastropods, and cephalopods the head is detached from the calcareous shell and is connected to the body by a short peduncle (neck), and attachment of buccal muscles to the shell must be done through this ‘neck’. In these groups, the buccal musculature extends posteriorly to attach to the shell.

In the ‘aplacophoran’ groups, the radular retractor muscles terminate near the third and fourth pair of dorsal-ventral retractors, while in chitons and monoplacophorans the posterior components of the mouth muscles terminate with the first pair of dorsal-ventral retractors (see Chapter 14). The radula

is absent in all bivalves, but buccal muscles are present in at least some protobranchs and still attach to the dorsal surface of the shell between the oblique anterior retractors and dorso-ventral retractors (Heath 1937). In scaphopods, cephalopods, and gastropods the posterior retractor muscles extend through the ‘neck’ to the foot region where they integrate with the pedal retractor muscles and then attach to the shell.

While detached heads do not inform us as to whether the mollusc was torted or not, their distribution in crown taxa and consideration of other lophotrochozoans suggests that the earliest molluscs had head regions attached to the shell, which prohibits the presence of a primarily anterior mantle cavity. A detached head and anterior mantle space are sometimes featured in hypothetical ancestral mollusc reconstructions, as shown in Chapter 12 and Lindberg and Ghiselin (2003b). Detached heads are correlated with the presence of ano-pedal flexure in the molluscan body plan.

Life in a narrow tube is difficult without a detached head and foot complex capable of extending and retracting beyond the confines of the aperture. And unlike most tube-dwelling lophotrochozoans, the secretory relationship between the body surface (mantle) and the shell prevents the organism from moving independently within the tube.

13.1.3 PHYLOGENETICS AND FOSSILS

Numerous studies have shown the importance of including fossils in phylogenetic analyses (Wagner 1999, 2001; Giribet 2002; Waller 2006), but such analyses are uncommon (Neige et al. 2007), and full molluscan group analyses including fossil taxa are rare (Runnegar 1996; Sigwart & Lindberg 2015). Instead, most have focused on individual taxa and include: cephalopods (Landman 1989; Monks 1999; Moyne & Neige 2004; Sutton et al. 2015), placophorans⁵ (Vendrasco et al. 2004; Sigwart & Sutton 2007a), rostroconchs (Wagner 1997), bivalves (Waller 1998; Carter et al. 2000; Harper et al. 2000), and gastropods (Wagner 1999, 2002). As discussed above, the limits of shell characters and the rarity of exceptionally well-preserved fossils which could expand the character matrix have undoubtedly placed limits on analyses for some groups. As demonstrated by Wagner (2000), morphological character space may become exhausted through geological time. Wagner’s result implies that biases in character selection are not at fault for the lack of characters but suggests biological factors, such as ecological restrictions, internal constraints, or long-term selective pressures, reduce the number of character states.

Working with ancient faunas affects how monophyletic groups are identified, as what is a monophyletic group in the past is not necessarily a monophyletic group in living taxa. For example, in the hypothetical cladogram in Figure 13.4, the ‘Archaeogastropoda’ was once a clade composed of the Eogastropoda, Vetigastropoda, and stem Neritimorpha. This

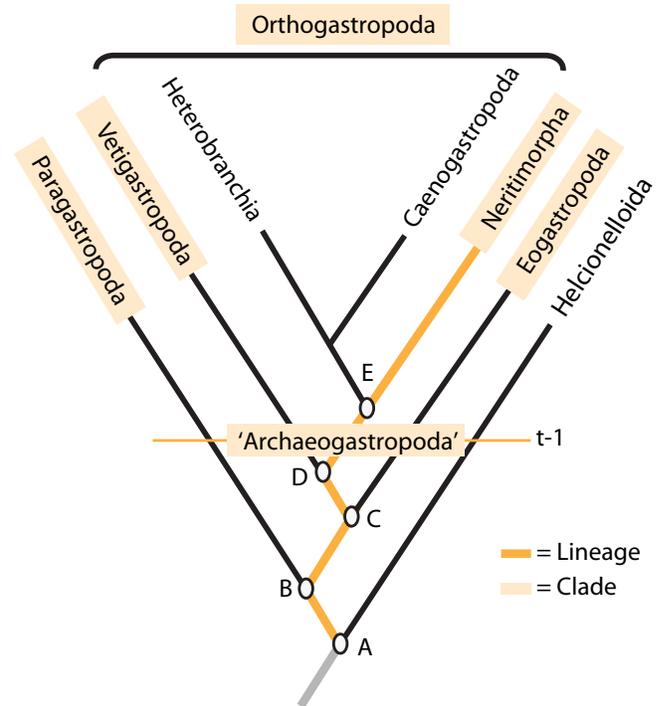


FIGURE 13.4 Hypothetical cladogram illustrating changing clade definitions through time and showing one example of a lineage. A-E = ancestral nodes, t-1 = an arbitrary time in the past.

remained true until the divergence of the lineage that gave rise to the heterobranchs and caenogastropods, which resulted in a paraphyletic ‘Archaeogastropoda’. This origination did not change the character states that diagnosed the former clade, and while this name is now no longer used in gastropod classification, this former ‘primitive order’ remains important in discussions of the ‘archaeogastropod’ level of organisation or grade within the Orthogastropoda (Graham 1985; Haszprunar 1993). Monophyletic status can also depend on how monophyly is defined. Clades are defined as containing all and only the descendants of a common ancestor. For example, in Figure 13.4 the Orthogastropoda contains C and all of its descendants, and in the past, the clade Archaeogastropoda contained B and all of its descendants. Monophyletic clades are a synchronic concept, a snapshot of a lineage at a single time slice (e.g., t-1 in Figure 13.4). Lineages, which are also monophyletic, connect an ancestor with its descendants and extend through time rather than being defined only at a particular slice of time, for example, the neritimorph lineage (A → Neritimorpha) in Figure 13.4. Thus, a lineage is a diachronic concept; a series of connected replicators through time. See Mishler (2010) for further discussion of the synchronic and diachronic concepts.

13.2 ORIGINATIONS, EXTINCTIONS, AND RECOVERIES

Molluscan diversity is typically estimated using taxonomic ranks, with the family and genus-level being the most commonly used indicators when looking across large expanses of time. Changes in molluscan diversity patterns occur because

⁵ We use the term ‘placophoran’ informally to refer to the Solenogastres, Polyplacophora, Caudofoveata, and Monoplacophora, which likely share plesiomorphic character states. The formal taxon name Placophora is a synonym of Polyplacophora.

of the interaction between origination and extinction rates although these rates vary in different molluscan groups (Sepkoski et al. 2002). For example, ammonites had high turnover rates, speciating rapidly and going extinct quickly. This volatility may have contributed to this highly diverse clade almost going extinct at the Permian/Triassic boundary and its final appearance at the end of the Cretaceous. In contrast, the Neogastropoda began a spectacular diversification in the Lower Cretaceous and continued unfettered into the Cenozoic. Whatever the factor(s) were that contributed to the extinction of the ammonites, they apparently had relatively little effect on neogastropod extinction rates.

Rather high rates of molluscan origination occurred during the Upper Cambrian–Lower Ordovician, the Middle Triassic, Paleocene, and Pliocene (Sepkoski et al. 2002), but if periods of high origination rates were accompanied by high rates of extinction, such as possibly occurred during the Lower Cambrian, the overall increase in diversity was minimal. Although such events are less common, there have also been periods (e.g., Oligocene) when both the relative origination and extinction rates dropped, and here again, a corresponding change in overall diversity may not be evident. Thus, in understanding diversification and extinction patterns, it is important to examine the relative relationship between origination and extinction rates by epoch.

Origination rates have exceeded extinction rates in 21 of the 30 Phanerozoic epochs, making the Mollusca one of the most diverse and abundant groups on Earth today. During the Paleozoic period, overall molluscan origination and extinction rates were about equal, however during seven of the 16 Paleozoic epochs, extinction rates exceeded origination rates, albeit only slightly. During the Mesozoic, origination rates were about 1.5 times that of extinction rates, and in only two of eight epochs did extinction rates exceed origination rates. During the Cenozoic, origination rates increased to more than twice the extinction rate, and overall, extinction rates never exceeded origination rates (see Table 13.2). The high diversity of the Cenozoic may be an artefact of sampling methods and an effect called the ‘pull of the Recent’ because of the more

comprehensive sampling of living taxa (Raup 1977; Jablonski et al. 2003). The stratigraphic ranges of living taxa are typically extended from their first occurrences to the modern day, including intervals in which they are not known in the fossil record. This increases taxon richness for living taxa in these intervals but not for extinct ones, resulting in artificially low diversity in intervals without living taxa. Correcting for the ‘pull of the Recent’ with standardised sampling and more robust counting methods reveals only a modest rise in diversity after the Mid-Cretaceous. During the Neogene, taxon diversity was twice as high as it was during the Mid-Paleozoic (see Table 13.2). This pattern exists at both global and local scales as well as at high and low latitudes, suggesting that the ratio of global to local taxon richness has changed little, and a latitudinal diversity gradient was present in the early Paleozoic (Alroy et al. 2008).

The greatest origination rate was during the Lower Silurian when it was over four times the extinction rate and during the Lower Triassic and Paleocene when origination rates were over three times the extinction rates. Most of the Cenozoic also saw origination rates in excess of twice the extinction rates (see Table 13.2).

Extinction events are typically divided into two categories – background extinction and mass extinctions. Background extinctions are thought to represent the ‘normal’ winnowing of taxa that occurs over geological time. Mass extinctions are significant increases in background extinction rates and typically occur on much shorter timescales. Some mass extinctions appear to have been caused by extra-terrestrial impact events such as the Cretaceous–Paleogene (K–Pg) mass extinction, while others are thought to be driven by large-scale tectonic events, volcanism, climate change, and oceanographic changes. While over 15 mass extinction events have been proposed, the most spectacular of these are often called the ‘Big Five’ mass extinctions – Ordovician–Silurian (444 Ma), Upper Devonian (385–359 Ma), Permian (251 Ma), Upper Triassic (228–199 Ma), and the K–Pg (66 Ma). The molluscs show mixed responses to the Big Five events, and only the Upper Devonian, Permian, and Upper Triassic events show marked decreases in molluscan diversity. The Permian event has long been recognised as a major molluscan extinction horizon marking the final occurrence of the Rostroconchia, most Bellerophonchia and ammonites, and numerous other molluscan groups.

In addition to three of the Big Five events, relatively high rates of molluscan extinctions occurred during the Lower Cambrian, Upper Silurian, Eocene, and Pliocene. With the Lower Cambrian, Upper Silurian, and Pliocene, these periods also show relatively high origination rates as well, and therefore there is no marked decrease in overall molluscan diversity. In contrast to the eight epochs where molluscan originations exceeded extinction rates by more than a factor of two, extinction rates have exceeded origination rates by more than a factor of two on only three occasions, and these are all associated with mass extinctions (see Table 13.2).

Increased rates of origination immediately followed mass extinctions. These recovery events are often called diversity

TABLE 13.2

Epochs Where Molluscan Origination and Extinction Rates Exceed One Another by at Least a Factor of Two

Origination Rate > Extinction Rate (n = 21 epochs)	Extinction Rate > Origination Rate (n = 9 epochs)
Silurian (l) 4.5x	Permian (u) 3.7x
Paleocene 3.8x	Devonian (u) 2.8x
Triassic (l) 3.6x	Triassic (u) 2.2x
Triassic (m) 2.2x	
Miocene 2.2x	
Oligocene 2.0x	
Eocene 2.0x	
Carboniferous (m) 2.0x	

Data are from Sepkoski (1998). l = Lower, m = Middle, u = Upper.

rebounds and are thought to represent increased diversification of surviving lineages as they move into habitats and niches recently vacated by unsuccessful lineages. Two of the three highest rates of origination relative to extinction in the Mollusca occur following mass extinctions – in the Lower Triassic following the Permian mass extinction and in the Paleocene following the K–Pg mass extinction.

13.3 THE MOLLUSCAN FOSSIL RECORD

The following overview of the early history of the Mollusca covers their putative origin and early history up to the Permian–Triassic extinction event and the establishment of the ‘Modern Evolutionary Fauna’ (Sepkoski 1981). Brief reviews of fossil (and crown) taxa in each class through the Mesozoic and Cenozoic are presented in Chapters 14–20. Estimates of first occurrences and stratigraphic ranges of the taxa discussed here have been gleaned from the Paleobiology Database (www.paleobiodb.org/) and the compendium of fossil marine animal genera by Sepkoski et al. (2002). We have also updated the dates used here from the primary literature when ranges were extended or reduced, although our search was not comprehensive for every group and should be viewed accordingly. Stratigraphic stages follow the ICS International Chronostratigraphic Chart 2018-08 (Cohen et al. 2013; updated) unless we could not confidently resolve regional faunal stages, and then we report the original text of the author.

The literature on early molluscan history is extensive and diverse, and our overview is, of necessity, superficial. As discussed in Section 13.1.1 we have attempted to review the early history of molluscs from traditional, current, and alternative perspectives and to present and synthesise our own views on early molluscan morphology, origins, and relationships. While also being informed by molecular studies of surviving taxa, we have relied primarily on stratigraphy to verify morphological character distributions and to propose alternative scenarios of relationships and affinities. Our assignment of various taxa to the Mollusca, and to one of the surviving classes, has been cautious. Lastly, we relied on outgroups, mostly living and often outside the Mollusca, from which to determine putative shared characters in early taxa. While we have included some new interpretations and ideas for discussion in this review, we echo Erwin and Valentine (2013) who concluded their treatment of lophotrochozoan origins with the promise that we have yet to hear the final word on the relationships of these intriguing animals.

Because of the origination and diversification of the ‘modern evolutionary fauna’ following the Permian extinction (Sepkoski 1981), we only treat Paleozoic molluscan palaeontology in this chapter (i.e., the Cambrian and Paleozoic faunas). Discussions of taxa comprising the modern fauna may be found in Chapters 14–20.

13.3.1 EDIACARAN

Many Russian workers consider that the earliest molluscs are from the latest Ediacaran (635–542 Ma) of Siberia in Russia. These small (<5 mm) bilaterally symmetrical shells are

initially partially coiled but rapidly open into an expanded, limpet-like aperture. The number of whorls rarely exceeds 1.5, and these minute specimens, along with a variety of sclerites and plates, are commonly called ‘small shelly fossils’ (SSF). Their occurrence is associated with the sudden appearance of composite mineralised skeletons, including those of many of the major groups extant today such as echinoderms, brachiopods, arthropods, etc., as well as putative molluscs. Several hypotheses for this event include increasing levels of calcium carbonate in seawater, increasing body sizes, and the evolution of skeletons as responses to increased predation pressure. Regardless of the factor or factors responsible for the appearance of mineralised skeletons, the ancestors of the skeletonised organisms were already present in the Ediacaran, although identifying them has been problematic as most of the multicellular organisms from that period bear little resemblance to the taxa of the Cambrian explosion. Even so, the origins of the Mollusca are somewhere there, and one suggested possible stem mollusc is *Kimberella*.

Kimberella (Figures 13.5 and 13.6) was first collected from the Ediacaran of South Australia and originally identified as a ‘problematic fossil possibly belonging to the Siphonophora’ (Glaessner & Daily 1959). It was formally described by Glaessner and Wade (1966) and compared to the cnidarian taxon Cubozoa (box jellyfish) and the Hydrozoa (medusae) (Figure 13.6). Additional (>800), better-preserved specimens from the Ediacaran of the White Sea region of Russia (555.3 ± 0.3 Ma) became available in the early 1990s. These new specimens revealed a bilaterally symmetrical animal with rigid parts, and the fine sediments in which they were preserved revealed details of the external morphology and internal anatomy as well as the mode of locomotion and feeding traces. The presumptive shell of *Kimberella* was not mineralised, and although rigid it remained flexible, as demonstrated by its deformation in numerous fossils. The ventral portion of the body bore a fringed foot-like structure that extended beyond the putative shell. *Kimberella* also appeared to have had dorsoventral musculature arranged in a segmented pattern and weaker transverse ventral musculature. Examination of this additional material led to a reinterpretation of the taxon by Fedonkin and Waggoner (1997) who considered it a benthic bilaterian, possibly related to molluscs. Follow-up studies by Ivantsov and Fedonkin (2001) described and illustrated specimens with internal anatomy, the putative dorsal shell, and additional trace fossils that purported to show both its path on the substratum and feeding marks (Figure 13.5, right). A second species of *Kimberella*, *K. persii*, has been described from the Ediacaran of Iran (Vaziri et al. 2018).

These characteristics and the Precambrian occurrence of the fossils led some palaeontologists and malacologists to accept *Kimberella* as the first mollusc (Fendonkin & Waggoner 1997). It has been argued that *Kimberella* shares many features with monoplacophoran molluscs such as the segmented musculature, a ventral foot surrounded by respiratory structures – ctenidia in monoplacophorans and the foot fringe in *Kimberella* – while the fan-shaped rasp marks near

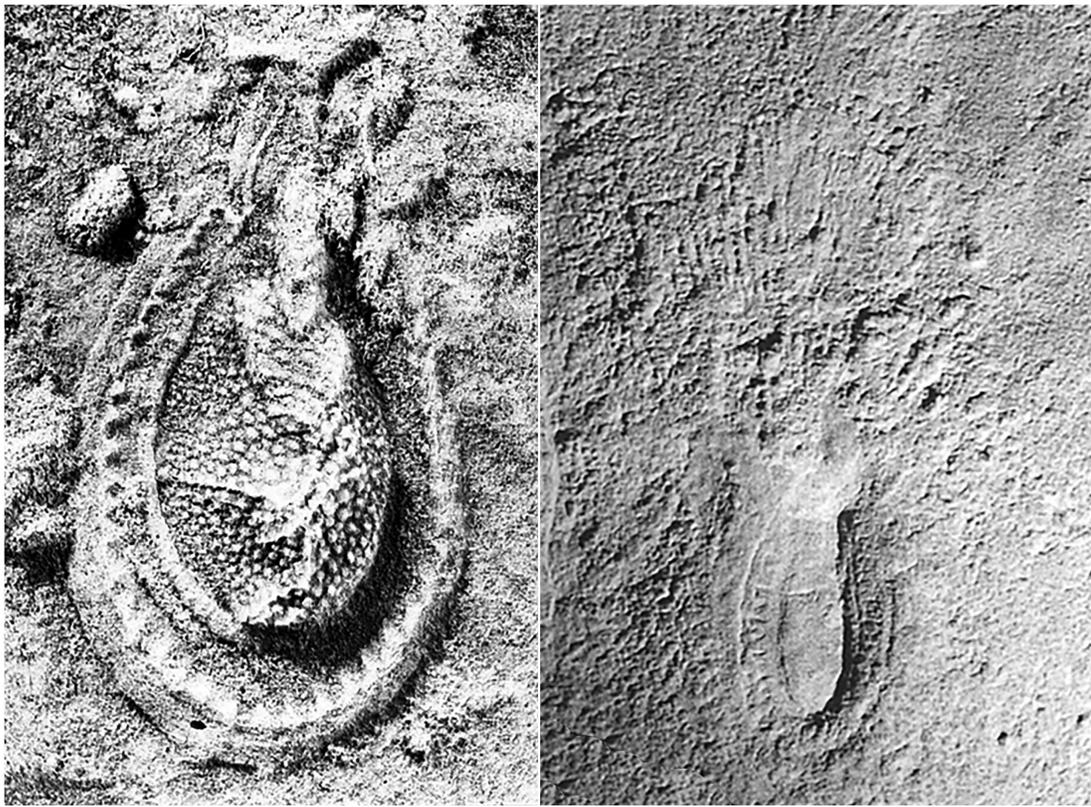


FIGURE 13.5 *Kimberella quadrata* from the White Sea Region of Russia. The figure on the right shows possible feeding traces. (Courtesy of M. Fedonkin.)

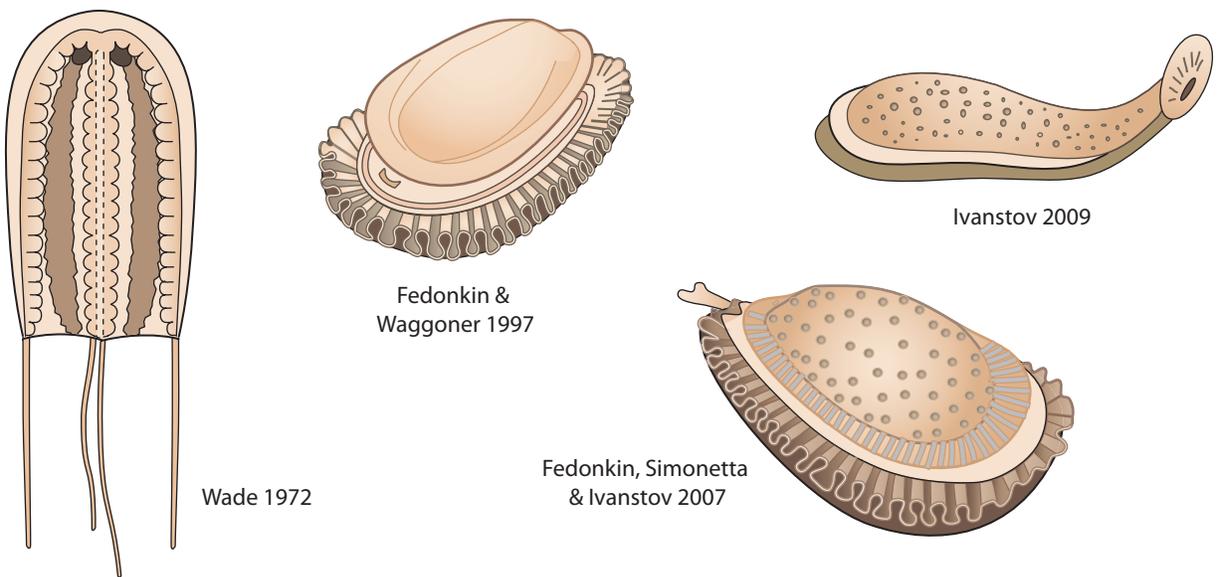


FIGURE 13.6 Some reconstructions of the Ediacaran taxon *Kimberella*. Originally it was reconstructed as a cnidarian (Wade 1972), before being reinterpreted as a mollusc 25 years later (Fedonkin & Waggoner 1997). Additional specimens initially refined the molluscan reconstruction (Fedonkin et al. 2007), but this was called into question when specimens with an elongated, worm-like body and a compressible head (Ivanstov 2009) were found. Today it is regarded as a possibly distantly related lophotrochozoan lineage.

Kimberella trails were considered as evidence it possessed a radular-like structure, although none has been yet reported in the hundreds of specimens examined, and the rasping marks extended in front of the supposed feeding swath of the animal,

not behind it as in feeding molluscs. In the early 2000s, additional specimens became available that showed an elongated, worm-like body with a compressible head region (Ivanstov 2009). These new specimens necessitated the re-examination

of the putative molluscan relationships of *Kimberella*, leading Ivantsov (2010, 2012) to conclude that *Kimberella* was not a mollusc but may have been a related lophotrochozoan lineage appearing between 558 and 555 Ma (see Erwin et al. 2011).

Whether putative molluscs such as helcionelloidans first appeared in the Ediacaran or Cambrian is determined by the preferred age assignment of the Nemakit-Daldynian (542–534 Ma), which is based on trace fossil occurrences and the beginning of a negative carbon isotope excursion. Russian workers typically regard this period as the latest Vendian (Rozanov et al. 2008), whereas other workers consider it to represent the first stage of the Cambrian (Budd 2003; Gradstein et al. 2004).

TABLE 13.3
Cambrian Chronostratigraphy

System/Period	Series/Epoch*	Stage/Age*	Beginning
Cambrian	Furongian	Stage 10	490 Ma
		Jiangshanian	494 Ma
		Paibian	497 Ma
	Miaolingian	Guzhangian	501 Ma
		Drumian	505 Ma
		Wuliuan	509 Ma
		Series 2	Stage 4
	Terreneuvian	Stage 3	521 Ma
		Stage 2	529 Ma
		Fortunian	541 Ma

* Some Epochs and Stages have yet to receive formal names.

Based on International Chronostratigraphy Chart (2018-08) [www.stratigraphy.org/ICSchart/ChronostratChart2018-08.pdf]

13.3.2 CAMBRIAN

The first supposed occurrences of the earliest crown Mollusca are found during the Cambrian, but recognition of these taxa is complicated by a plethora of other skeletonised SSF (Matthews & Missarzhevsky 1975; Dzik 1994; Maloof et al. 2010; Erwin & Valentine 2013). Besides putative molluscs, these assemblages include poriferan (sponge) spicules, pieces of archaeocyathan⁶ walls, putative annelid tubes, stem brachiozoans, hyoliths (see Section 13.3.2.2.1), and a vast morphological array of sclerites including shelly plates. Complete or partial scleritomes (see Table 13.4) are rarely preserved but provide insights into both the arrangement and complexity of the armour of these early animals which include cancellorids, halkieriids, wiwaxiids, and tommotiids (Conway Morris & Caron 2007; Skovsted et al. 2009). The vast majority of the SSF are calcareous, although many are secondarily phosphatised and some phosphatic tubes, valves, and spicules also occur (Bengtson & Runnegar 1992; Kouchinsky et al. 2012). As noted above, the first SSFs appear in the latest Ediacaran or earliest Cambrian, depending on the chosen time scale, and disappear during the Middle Cambrian (Erwin & Valentine 2013) (see Table 13.3).

Regardless of whether the SSFs first appear in the latest Ediacaran or earliest Cambrian, they are the first component of the Nemakit-Daldynian skeletonisation event (Fortunian), a relatively short period of time (approximately 10 million years) in which most stem and crown taxa of most living skeletonised phyla appeared (Cloud 1948; Stanley 1976; Budd & Jensen 2000; Budd 2003). This period saw major events in the history of metazoan biomineralisation, including the

⁶ The Archaeocyatha was an extinct group of sessile, reef-building organisms that lived during the early Cambrian.

TABLE 13.4
Exoskeleton Terminology

Term	Definition	Composition	Morphology	Examples
Scleritome	The complete set of hard parts (sclerites) which make up the exoskeleton of an organism	Phosphatic, calcium carbonate, chitinous	Varied	Mollusca, Brachiopoda, Arthropoda, Annelida, Hyolitha, Bryozoa, Kinorhyncha
Sclerites	A component of an exoskeleton. Sclerites may occur individually or aggregated; aggregated sclerites may be articulated or unarticulated	Phosphatic, calcium carbonate, chitinous	Often with internal shell pores	Mollusca, Brachiopoda, Arthropoda, Annelida, Hyolitha, Bryozoa
<i>Molluscan-specific terminology</i>				
Spicules	Typically small needle-like structures	Calcium carbonate; typically aragonitic	Solid or partially hollow; intracellular growth	Aplacophorans, Polyplacophora
Scales	Small plate-like structures	Calcium carbonate; typically aragonitic	Solid; intracellular growth	Aplacophorans, Polyplacophora
Conch	A single (univalve) shell	Calcium carbonate; aragonitic and calcitic	Accretionary growth; often with internal shell pores	Monoplacophora, Scaphopoda, Cephalopoda, and Gastropoda
Plates and valves	Multiple sclerites, often articulated	Calcium carbonate; aragonitic and calcitic	Accretionary growth, often with internal shell pores	Polyplacophora (plates or valves), Bivalvia (valves)

appearance of the primary skeletal minerals (phosphate, carbonate, silica), a diverse array of microstructures (fibrous, granular, nacreous, prismatic and crossed lamellar structures), and morphological forms including spicules, tubes, conchs, and sclerites (Runnegar 1989; Bengtson & Conway Morris 1992; Feng et al. 2003) (see Table 13.4).

The exoskeleton structures are typically derived from ectodermal tissues but may not be homologous between groups. For example, the absence of chitin in the polyplacophoran spicule matrix suggests that spicule biomineralisation differs substantially from the biomineralisation of chiton shell plates where, as in most molluscs, chitin provides the scaffolding for shell formation (Levi-Kalisman et al. 2001; Treves et al. 2003).

The ‘sudden’ appearance of skeletonised bodies in the fossil record has been attributed to multiple biological, geophysical, and geochemical mechanisms (Marshall 2006; Maloof et al. 2010; Peters & Gaines 2012). These include the crossing of an oxygen threshold which supported larger animals and their more complex physiologies, changes and innovation in developmental pathways, environmental perturbations associated with global changes in climate (e.g., Gaskiers glaciation), and changes to the geophysical setting of the Earth (Marshall 2006; Erwin & Valentine 2013) (Figure 13.7). The treatment by Marshall of the so-called ‘Cambrian explosion’ examined whether potential factors and drivers were both necessary and sufficient to account for different aspects (disparity, diversity, timing, duration, etc.) of the event and found only the origin of predation to be both

necessary and sufficient to explain an increase in diversity. Some have argued that, correlated with this selection pressure, the evolution of body armour or skeletonisation marked the beginning of an arms race between predator and prey (Stanley 1973; Vermeij 1987; 1989; Bengtson 2002). The appearance of all these metazoan taxa undoubtedly produced significant changes in the marine trophic food webs of the Cambrian which may have been partially sustained by parallel increases in diversity of planktonic microfossils (e.g., acritarchs) during Stage 3 of the Cambrian (see Table 13.3) (Nowak et al. 2015). Acritarchs are also thought to have had a significant role in the Great Ordovician Biodiversification Event (see Section 13.3.3).

As with most major events in the history of life, it is probable that multiple drivers (both biotic and abiotic), and the complex interactions which they engender, were responsible for the ‘Cambrian explosion’. For example, along with the formation of enormous evaporite basins during the late Neoproterozoic (~1000–~541 Ma), glaciations cooled the oceans and salinity fell. The coincidence of falling temperatures and salinity may have led to significant increases in dissolved oxygen, thus allowing for metazoan respiration in calcite- and silica-saturated oceans (Knauth 2005). This and other events triggered scenarios suggesting that before the Cambrian oceans were low in calcium, but as concentrations rose calcium was initially secreted as a waste product resulting in the availability and potential use of calcium carbonate as a skeletal material (Vermeij 1989). A parallel pattern in calcification intensity in the early Cambrian is also seen in Cyanobacteria (Riding

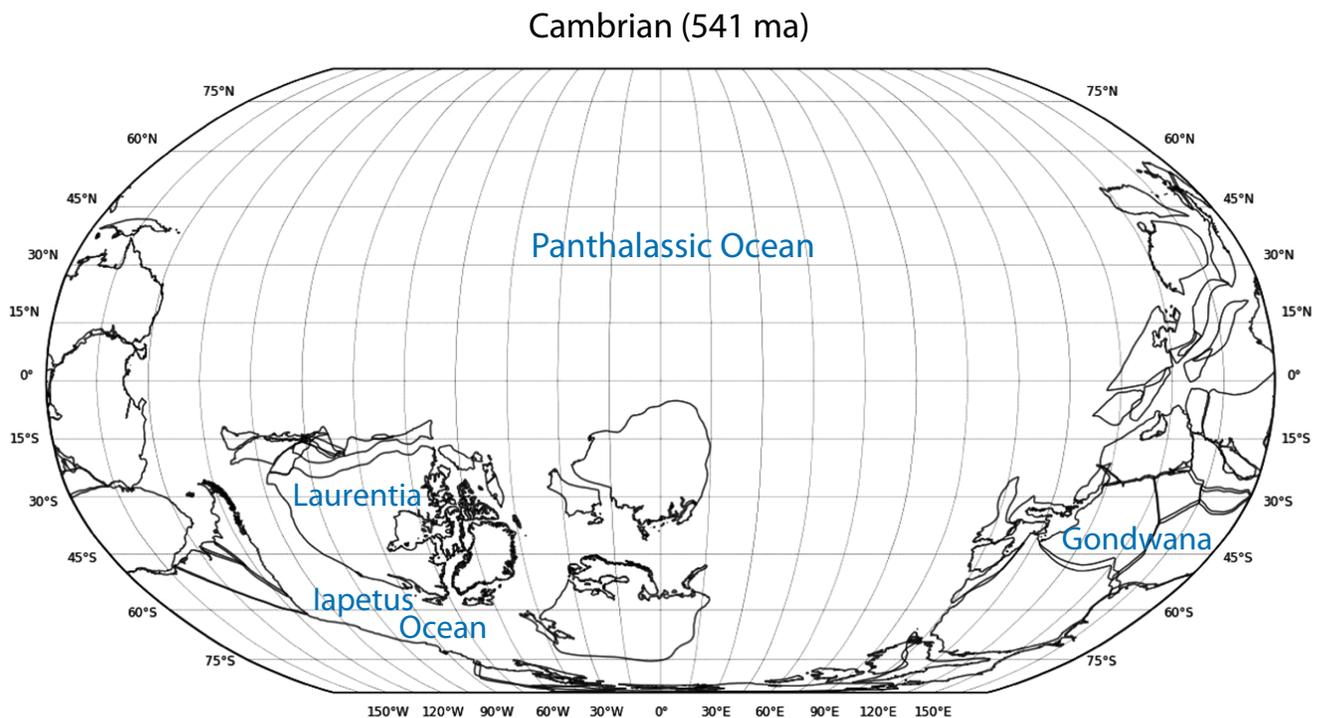


FIGURE 13.7 Palaeogeographic reconstruction of tectonic plate positions during the Cambrian (Terreneuvian) period.¹

¹ Palaeogeographical reconstructions in this and subsequent maps were made with GPlates 2.0 (<http://www.gplates.org/>). Outlines represent plate boundaries and not necessarily coastlines; epeiric sea (or epicontinental seas) covered areas of some plates as well.

2006a, 2006b). The importance of geochemical and physical environmental perturbations during the Neoproterozoic has also been argued by Peters and Gaines (2012) who suggested that the Great Unconformity, which stratigraphically precedes the ‘Cambrian explosion’, is causally linked to the evolution of biomineralisation. They hypothesise that chemical weathering and reworking of continental crust during the Ediacaran and early Cambrian increased oceanic alkalinity during a period of intense expansion of shallow marine habitats.

13.3.2.1 Biomineralisation

Some of the Cambrian groups (e.g., Sachtida) have taxa with sclerites and shell plates. These are easily envisioned to fuse, giving rise to solid shells and fused sclerites in *Maikhanella*, and their apparent transition into solid shells in *Purella* has been argued to support this transformation (Bengtson 1992, 1993). Moreover, the presence of both plates and spicules in the Polyplacophora suggests the possibility that an intermediate step of this transformation sequence is preserved today in a group that originated in the Cambrian (Pojeta 1980; Salvini-Plawen 1985a; Eernisse & Reynolds 1994; Vinther 2009).

These scenarios for the formation of the molluscan shell date from the late 1800s, but it is the seminal paper on the evolution of calcareous hard parts in primitive molluscs by Winfried Haas (1981) that serves as the benchmark for this discussion (see Chapter 3 for details of shell formation). After a detailed study and review of spicule and plate formation in Polyplacophora and spicule and scale formation in the Solenogastres and Caudofoveata, Haas concluded that spicule formation was plesiomorphic in molluscs (with no outgroups) and that chiton shell plates and conchiferan shells were derived from the same cellular organisation that originally produced spicules. The evolutionary scenario required that individual invaginated epithelial cells that had secreted spines deep within the epithelium remained at the surface of the epithelium in plate formation and that a cuticle layer sealed these cells off from the environment. This allowed for the precipitation of calcium carbonate under the cuticle – the general mechanism by which both plates and conchs are formed in chitons and conchiferans, respectively. This conclusion is not unanticipated, as Haas found no independent assessment of the evolutionary direction or the polarity of the calcification characters he studied. With their spicule-covered bodies, solenogastres and Caudofoveata were assumed to represent the most primitive living molluscs, and the transformation into chiton plates and ultimately into the shells of conchiferans was predetermined to a large extent by the phylogeny he followed. Thus, the scenario was more an explanation of what was assumed to have happened, rather than an independent test of calcification patterns in molluscs.

Haas’s scenario for the transformation from spicule to plate secretion did not address another important step required in this conversion. Solenogastres and Caudofoveata are covered by spicules, which correspond to the individual secretory cells densely distributed over the dorsal epithelium. Chiton plates are also dorsal, but like conchs, their growth depends on the ability to add material to the shell

edge – accretionary growth. Because calcification is an intracellular process, it must be isolated from the environment and requires a shielding layer (cuticle or periostracal) and shell-secreting cells that line the growing edge of the mantle. Thickness is added by shell-secreting cells in the dorsal mantle surface. Accretionary growth from calcification centres isolated by cuticle also occurs in brachiopods (a potential sister taxon), bryozoans, serpulid and sabellid polychaete worms, and barnacles (Bourget & Crisp 1975; Mukai et al. 1997; Williams 1997). While the Haas scenario adequately explains what occurs early in the ontogeny of chiton and conchiferan shell formation, it does not address the required reorganisation of the individual spicule calcification centres and the evolution of these specialised tissues along the mantle edge.

If spicule formation was secondary, not primary, the evolution of molluscan hard parts is more parsimonious with the fossil record and outgroup comparison. If the common ancestor of molluscs secreted a dorsal cuticle, the addition of the calcified layer or shell required only the proliferation of cells capable of calcium secretion between the epithelium and cuticle at the edge of the dorsum. Away from the shell margins, the role of the cuticle in sealing the crystallisation chamber for shell formation was no longer necessary, and additional shell material could be ventrally added as required in the controlled environment between the existing shell and epithelium. Loss of these marginal calcification centres may have been associated with becoming worm-like, a morphology that enables much greater mobility and range of movement than possible in a body covered with fixed plates or valves. A spiculate body covering might result if elongation was accompanied by strong selection to increase the number of dorsal calcification centres, thereby reducing their size.

This alternative hypothesis is supported by the Paleozoic fossil record with the first occurrence of unequivocal molluscs being shell-bearing taxa – rostroconchs, bivalves, and then gastropods – rather than the supposedly more primitive sclerite-bearing taxa (Figure 13.8).

Furthermore, the putative stem molluscan taxa such as *Odontogriphus* (see Section 13.3.2.2.2) lack spicules, and the sclerites of *Wiwaxia* and halkieriids differ markedly from molluscan spicules both in their formation and composition (see Section 13.3.2.2.2). Therefore, calcium carbonate spicules must have evolved later in an aplacophoran or polyplacophoran lineage. Indeed, the earliest aplacophoran-like animal does not appear until the Silurian, 120 Ma after the appearance of conch and plate-bearing molluscs.

While a later appearance of unequivocal stem molluscs is better supported by the fossil record, are there additional data that can be considered? In the Haas scenario, only the calcification processes within molluscs are considered and examined, but for the hypothesis to be tested, insights are required into calcification mechanisms in lophotrochozoan outgroups.

In the Lophotrochozoa three non-molluscan groups produce calcified shells – Brachiopoda, Bryozoa, and Annelida. At various times, based on different datasets and analyses, all three have been considered as possible molluscan sister

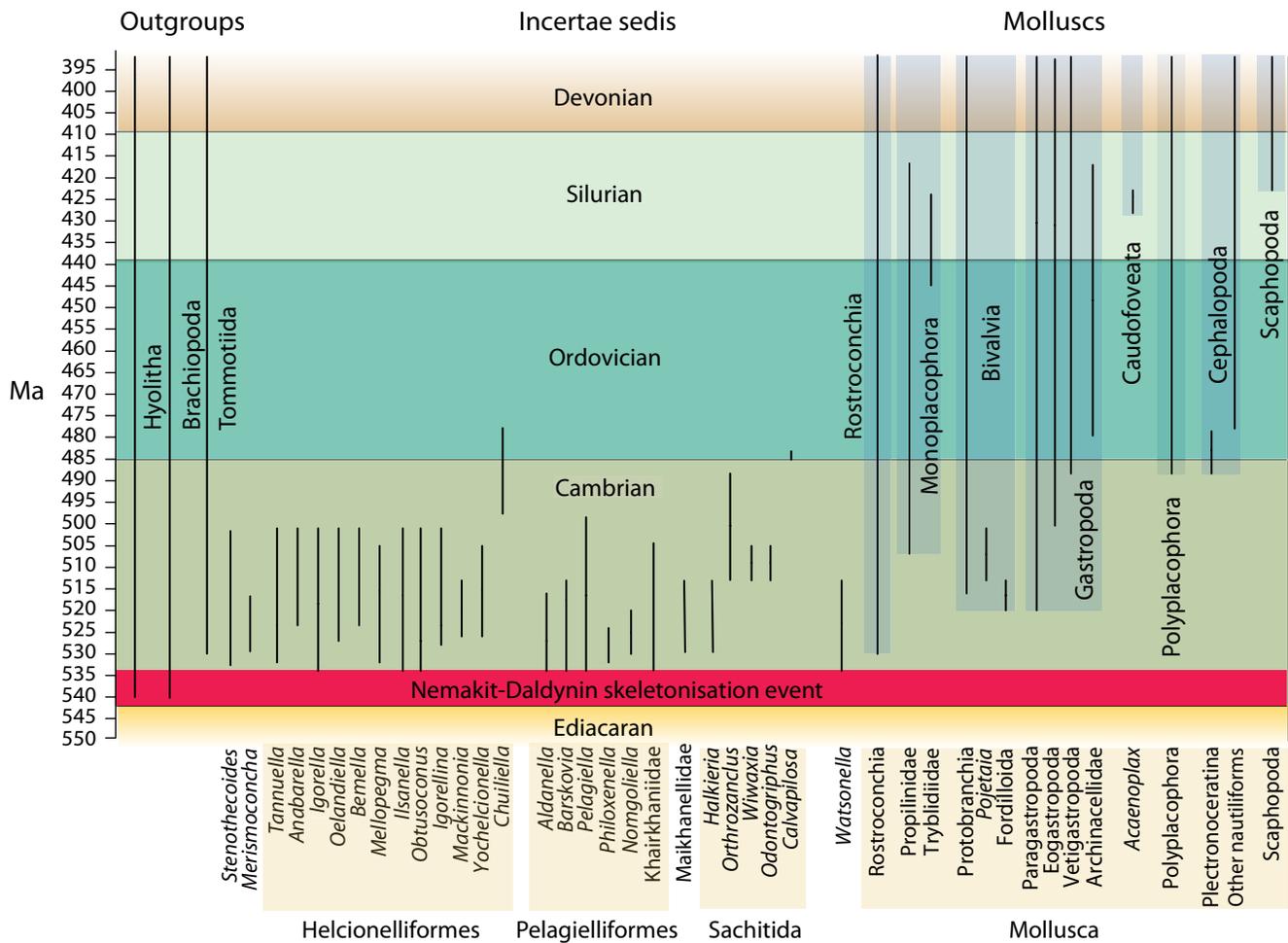


FIGURE 13.8 Early Paleozoic stratigraphic occurrences of small shelly fossils, outgroups, and crown group molluscs. Modified and updated from Maloof, A.C. et al., *Geol. Soc. Am. Bull.*, 122, 1731–1774, 2010.

taxa. All produce plate-like structures, not spicules, and enlarge these structures through accretionary growth, like the majority of molluscs. Studies of the calcification process that produces annelid worm tubes are few, but the calcification processes that produce the brachiopod shell and bryozoan test are well documented. In the Brachiopoda and Bryozoa, the calcium carbonate is laid down between a cuticle and the epithelium by specialised secretory cells found at the growing margins (Mukai et al. 1997; Williams 1997). This is the same basic organisational pattern seen in the production of chiton plates and conchiferan shells and in most non-molluscan groups examined, except for some annelid tubes which are produced from compacted and moulded granular secretions (Simkiss & Wilbur 1989; Taylor et al. 2010). For example, in the polychaete genus *Pomatoceros* (Serpulidae), calcareous granules are formed in intracellular vesicles or calcium-secreting glands. They are then expelled into an acid mucopolysaccharide matrix, which is moulded around the body of the worm and solidifies on contact with sea-water (Simkiss & Wilbur 1989). This type of calcification has not been reported in other lophotrochozoan phyla. A second secretion process, also found in serpulids, more

closely resembles that found in molluscs; the calcareous tube is formed by extracellular mineralisation mediated by an organic matrix secreted by a secretory epithelium. This calcification mechanism is also inferred for some Mesozoic and living Sabellidae (Vinn et al. 2008).

Thus, based on outgroup comparisons, spicules in molluscs would appear to be secondarily derived and not primitive. In order to continue to advocate the Haas scenario, it must be argued that the plesiomorphic state of calcification in the Lophotrochozoa was lost in the lineage leading to molluscs and replaced by spicule production. It would then have to be re-acquired in the common ancestor of the chitons and conchiferans, and spicule production subsequently lost in the conchiferan ancestor (see also Chapter 12).

13.3.2.2 Taxa

Many of the earliest putative crown molluscs in the Cambrian record are morphologically similar to extant gastropods and bivalves (Runnegar & Pojeta 1974b; Dzik 1994; Parkhaev 2007, 2008; Maloof et al. 2010; Erwin & Valentine 2013). As it is highly improbable that gastropods and bivalves arose *de novo* from a lophotrochozoan ancestor in the earliest

Cambrian, the search for and identification of molluscan stem groups have been intensely debated for over 20 years. The following is a review of these groups of putative molluscs.

13.3.2.2.1 *Hyolitha*

Hyoliths are cone-shaped shells with a flattened side and a circular to triangular aperture in cross-section; septa are present in some taxa, and accretionary growth lines are present on both the shell and ‘operculum’. Shell microstructure is crossed lamellar. Musculature has been reconstructed to include five bilaterally symmetrical longitudinal muscles and paired dorsoventral muscles with multiple insertions arranged serially along the shell (Runnegar et al. 1975). Several specimens have been recovered with gut morphology preserved by sediment infilling; gut looping consists of two distinct morphologies. The first is a relatively straight section, and the second is highly folded and accordion-like. The transition between these two morphologies occurs at the apex of the U-shaped bend. The straight dorsal section has been interpreted as a rectum leading back to the aperture.

Hyoliths are commonly placed in two groups, the Hyolithida and Orthothecida (see Table 13.5), based on shell

morphology. Hyolithida have irregular apertures and a pair of apertural projections called *helens* that curve over the dorsal surface of the shell. The helens articulate in sockets on the operculum, and their function is not known. The interior surface of the Hyolithida operculum has raised dorsal (and sometimes ventral) opercular processes. In the Orthothecida the aperture is planar, sometimes with indentations, and the interior surface of the operculum lacks processes.

Hyoliths range from the earliest Cambrian to the Permian and occur globally. Both orders obtain their greatest diversity in the Cambrian and Ordovician. The Orthothecida became extinct in the Middle Devonian, while the Hyolithida became extinct at the end of the Permian. Dzik (1978) identified two kinds of larval shells in hyoliths, a smooth globose form which he thought hatched from an egg (Orthothecida) and a pointed form with growth lines which he felt developed in the plankton (Hyolithida). He compared these structures with similar larval structures seen in Paleozoic and living gastropods. Hyoliths are generally considered sessile, benthic, epifaunal organisms (but see below), and range in length from about 10–40 mm. Taxonomically they have been variously considered to be pteropods, gastropods, cephalopods, or operculate worms

TABLE 13.5
Classification of the Hyolitha

Brachiozoa

Brachiozoa includes the brachiopods and phoronids, and the hyoliths were placed there based on well-preserved material in the Burgess Shale (Moysiuk et al. 2017).

(Class) *Hyolitha*

(= Hyolithomorpha, Orthothecimorpha)

Cambrian (Terreneuvian)–Permian (Lopingian) (530–252 Ma)

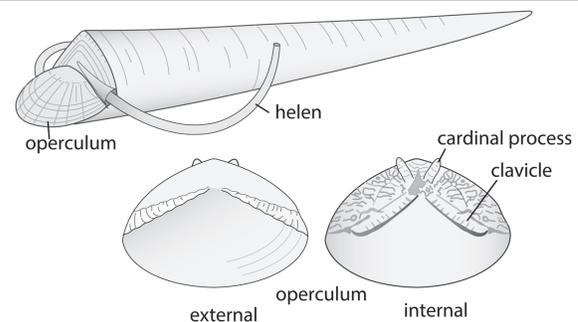
Cone-shaped conchs with distinctive larval shell and an operculum. Septa and apertural spines (helens) present in some taxa.

(Order) *Hyolithida*

Cambrian (Terreneuvian)–Permian (Lopingian) (530–252 Ma)

Conch oval to subtriangular in cross-section; dorsal re-entrant present in some taxa; with external ‘operculum’ resting on a ventral extension of the aperture (ligula); apertural spines (helens) present.

Families include Hyolithidae, Angusticornidae, Aimitidae, Australothecidae, Carinolithidae, Crestjahitidae, Doliutidae, Nelegerocornidae, Pauxillitidae, Parakorilithidae, Sulcavitidae, and Similothecidae.



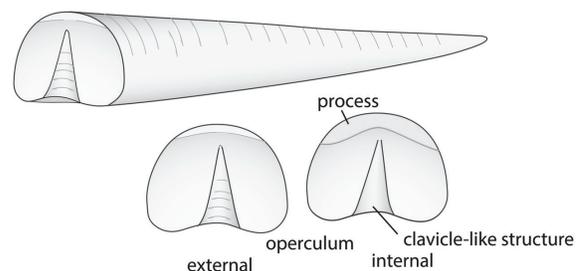
Joachimilites, redrawn and modified from Devaere et al. (2014).

(Order) *Orthothecida* (?= Tetrathecida)

Cambrian (Terreneuvian)–Devonian (Middle) (530–388 Ma)

Conch cross-section highly variable ranging from circular to triangular, with or without a longitudinal furrow on the ventral surface producing a heart- or kidney-shaped cross-section; lacks the ventral ligula and helens; has a retractable ‘operculum’.

Families include Orthothecidae, Allathecidae, Circothecidae, Gracilithecidae, Spinulithecidae, Turcuthecidae, and Tetrathecidae.



Nephrotheca, redrawn and modified from Devaere et al. (2014).

(Fisher 1962). Hyoliths have often been treated as an extinct class of molluscs (Downie et al. 1967; Marek & Yochelson 1976), while Runnegar et al. (1975) placed them in a separate phylum. A recent analysis of Burgess and Spence Shale hyoliths by Moysiuk et al. (2017) revealed soft tissue structures suggestive of a lophophore and a deep ventral visceral cavity. These and other features led the authors to conclude taxonomic affinities with brachiopods, phoronids, tommotiids, and other lophophorate taxa. The gut morphology in material from Noire, France, has also been described (Devaere et al. 2014).

Landing and Kröger (2012) suggested the possibility that small juveniles of the Cambrian taxon '*Allatheca degeeri*' may have been nekctic/planktic while both hatchlings and larger individuals (>17 mm) were negatively buoyant and benthic. More recently, Martí Mus et al. (2014) have reconstructed hyoliths as relatively mobile organisms. Their study of the muscle insertion patterns on conchs, helens, and 'opercula' (Martí Mus & Bergström 2005) suggests an articulated skeleton capable of functioning as oars to move the organism over the substratum, as well as operating as stabilisers and struts to lift the anterior end off the substratum. The location of epibionts on the hyolith shell further supports this interpretation (Galle & Parsley 2005).

13.3.2.2.2 *Coeloscleritophora and Sachitida*

Sclerite-bearing Cambrian lophotrochozoans have been known for over 100 years (Walcott 1911), but a name for these taxa was first proposed by Bengtson and Missarzhevsky (1981). They grouped the *Wiwaxiidae*, *Halkieriidae*, *Sachitidae*, *Siphonochitidae*, and *Chancelloriidae* in the globally distributed taxon *Coeloscleritophora* (see Table 13.6). This was based on these taxa having tissue-filled, hollow sclerites which lacked accretionary growth lines. Grouping the bilateral halkieriids with the sponge-like chancelloriids was controversial but has been supported by the more recent detailed microstructure studies of Porter (2008). At that time *Wiwaxia* was the only supposedly benthic, bilateral member of the group with a complete scleritome, albeit, unlike the other coeloscleritophorans, it was unmineralised. Bengtson (1992) later described cap-shaped shells formed from merged sclerites in the Cambrian fossil *Maikhanella*, which was also allocated to the *Coeloscleritophora*.

The discovery of the complete scleritome of *Halkieria evangelista* (Conway Morris & Peel 1990, 1995) provided additional insights into the complexity of coeloscleritophoran animals and revealed a diverse pattern of sclerite morphology as well as the presence of anterior and posterior plates with accretionary growth leading to consideration of a possible relationship with the Mollusca (Conway Morris & Peel 1995). More recently, Vinther and Nielsen (2005) compared sclerite morphology and scleritome patterns in *Halkieria* with girdle scales and spicules in chitons, concluding there was sufficient similarity to declare *Halkieria* a mollusc, and Vinther (2009) compared the aesthete pores of polyplacophorans with the pores in the sclerites of the halkieriid *Sinosachites*.

Conway Morris and Caron (2007) united the halkieriids and wiwaxiids based on the discovery of *Orthrozanclus*, a

Burgess Shale fossil which possessed an anterior plate, as in the halkieriids, combined with *Wiwaxia*-like sclerites. They combined these two groups in the stem group 'Halwaxiida'. Conway Morris and Caron (2007) also proposed two alternative hypotheses for placing *Orthrozanclus* in early lophotrochozoan phylogeny. In the first hypothesis, *Odontogriphus* and the Ediacaran *Kimberella* were considered stem group molluscs and the sachitidans their sister group. In the second hypothesis, sachitidans were monophyletic, and *Odontogriphus* and *Kimberella* were treated as stem group lophotrochozoans; stem group molluscs were not identified in the second hypothesis.

The Burgess Shale *Odontogriphus* has figured prominently in discussions and scenarios of molluscan evolution. Originally described only as a lophophorate (Conway Morris 1976), the discovery of additional, better-preserved specimens led to the reinterpretation of this taxon as a stem group mollusc (Caron et al. 2006). Despite the lack of sclerites and a shell, structures suggesting a radula, ctenidia, muscular foot, and possible salivary glands were identified. Butterfield (2006) criticised this placement, in particular critiquing the identification of two primary molluscan characters – the putative radula and ctenidia (but see the response by Caron et al. 2007). Butterfield concluded that *Odontogriphus* represented a stem group lophotrochozoan, while *Wiwaxia*, which shared a similar, possibly plesiomorphic, feeding apparatus was a stem group polychaete. This view was, however, disputed by Eibye-Jacobsen (2004), who concluded that *Wiwaxia* was not closely related to Annelida.

Vinther et al. (2017) extended the Sachitida into the Ordovician with the description of *Calvapilosa kroegeri* from the Fezouata biota of Morocco.

13.3.2.2.2.1 Scleritome Reduction

Conway Morris and Caron (2007) produced a partial outline of lophotrochozoan phylogeny that featured relationships between Halwaxiida (i.e., Sachitida), Mollusca, Annelida, and Brachiopoda. In their first hypothesis (Figure 13.9A), the 'halwaxiids' were placed as the sister taxon of the Mollusca and formed a lophotrochozoan grade with the Annelida and Brachiopoda, respectively. In the second hypothesis (Figure 13.9B), the 'halwaxiids' were placed between the molluscs and annelids. In both hypotheses, the unarmoured *Kimberella* and *Odontogriphus* are outgroups to both the clade (hypothesis 1) and grade (hypothesis 2) of 'halwaxiids' and molluscs. A comparison of the genomes of molluscs, annelids, and brachiopods by Paps et al. (2009) and Luo et al. (2015) (Figure 13.9C) necessitates a re-examination of outgroup relationships in the hypotheses of Conway Morris and Caron. Placing brachiopods as the sister taxa of molluscs (Figure 13.9D) suggests that mineralisation of body armour would be present in their last common ancestor⁷ and calls into question the placement of *Kimberella* and *Odontogriphus* as non-mineralised molluscan ancestors.

⁷ Luo et al. (2015) reported that although *Lingula* builds its shell from calcium phosphate and molluscs from calcium carbonate, they share shell formation-related genes and mechanisms.

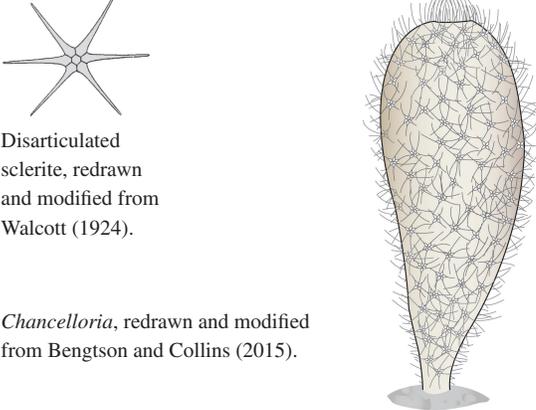
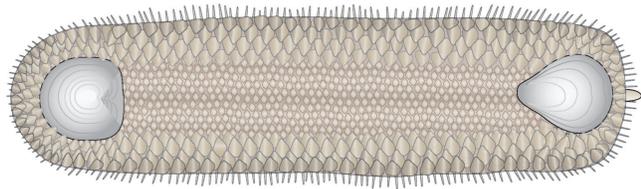
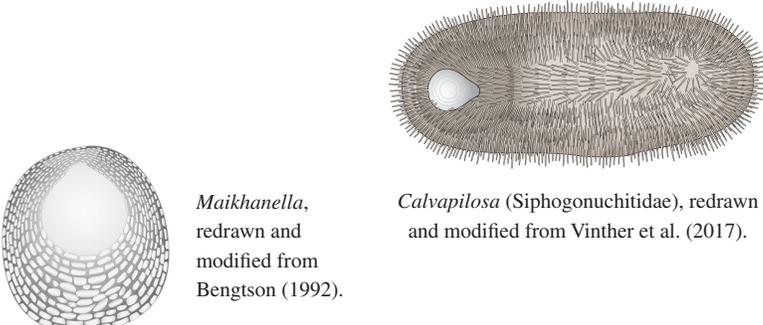
TABLE 13.6

Classification of the Coeloscleritophora

Lophotrochozoa

(Class) Coeloscleritophora

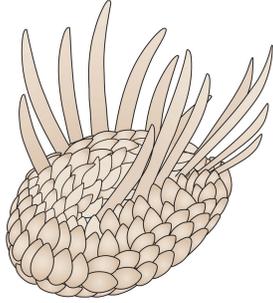
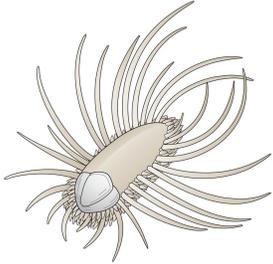
Taxa with hollow sclerites that have a microstructure consisting of a thin, possibly organic, outer layer overlying a single layer of aragonite fibres oriented parallel to the long axis of the sclerites; fibre bundles inclined, producing a scaly upper surface of the sclerite; scale-forming projections absent from the lower surface (Porter 2008). There are two very different body forms of Coeloscleritophora – the sac-like Chancelloriida and the slug-like Sachitida. If this relationship is correct, the diversity of body form is similar to living Tunicata, which includes the sac-like, sessile Ascidiacea and the motile, bilaterally symmetrical Larvacea. Complete scleritomes are rare; many of the taxa are known only from disarticulated sclerites and are a substantial part of the Cambrian small shelly fossil fauna.

<p>(Order) Chancelloriida Cambrian (Terreneuvian)–Cambrian (Furongian) (541–487 Ma) These sac-like animals were somewhat similar to sponges and tunicates. The chancelloriids are not considered further here. See Bengtson and Collins (2015) and Porter (2008) for further treatment.</p>	 <p>Disarticulated sclerite, redrawn and modified from Walcott (1924).</p> <p><i>Chancelloria</i>, redrawn and modified from Bengtson and Collins (2015).</p>
<p>(Order) Sachitida (= Thambetolepida; Diplacophora, 'Halwaxiida') Cambrian (Terreneuvian)–Cambrian (Miaolingian) (530–505 Ma) The Sachitida are bilaterally symmetrical, seemingly motile, slug-like animals typically covered by sclerites and one or more plates; when present, two or three forms of sclerites make up the scleritome; plates, when present, typically enlarged by marginal accretion; early accretionary growth replaced by fused sclerites in some taxa (<i>Maikhanella</i>). Sclerites appear to have been shed and replaced by larger ones during ontogeny. Mineralised mouthparts occurred in some taxa. These slug-like creatures have been considered molluscs by some workers. The classification below is largely inspired by the phylogeny of Vinther et al. (2017).</p> <p>(Superfamily) Halkierioidea Cambrian (Terreneuvian)–Cambrian (Series 2) (530–513 Ma) Typically three forms of mineralised sclerites; with two plates. Family Halkieriida</p>	 <p><i>Halkieria</i>, redrawn and modified from Vinther and Nielsen (2005).</p>
<p>(Superfamily) Siphogonuchitoidea Cambrian (Terreneuvian)–Ordovician (Lower) (530–478 Ma) Simple mineralised scleritome generally with two sclerite forms. Plates sometimes composed of fused sclerites after initial accretionary shell. Mineralised(?) mouthparts present in some taxa. Disarticulated sclerite plates have been referred to the Cambrian limpet taxon Maikhanellidae, which was treated as a monoplacophoran by Bouchet et al. (2017). Families Siphogonuchitidae and Maikhanellidae (= Purellidae).</p>	 <p><i>Maikhanella</i>, redrawn and modified from Bengtson (1992).</p> <p><i>Calvapilosa</i> (Siphogonuchitidae), redrawn and modified from Vinther et al. (2017).</p>

(Continued)

TABLE 13.6 (CONTINUED)

Classification of the Coeloscleritophora

<p>(Superfamily) Wiwaxioidea new name Cambrian (Series 2)–Cambrian (Miaolingian) (513–505 Ma) Sclerites demineralised; without plate; mineralised mouthparts present. Family Wiwaxiidae</p>	<p><i>Wiwaxia</i>, redrawn and modified from Briggs et al. (1994).</p> 
<p>(Superfamily) Orthrozancloidea new name Cambrian (513–488.3 Ma) With a single anterior plate and long lateral sclerites. Family Orthrozanclidae</p>	<p><i>Orthrozanclus</i>, redrawn and modified from Conway Morris and Caron (2007).</p> 
<p>(Superfamily) Odontogriphoidea new name Cambrian (Series 2)–Cambrian (Miaolingian) (513–505 Ma) Lacks plates and sclerites; mineralised mouth parts present. Molluscan affinities have been suggested (see text). Family Odontogriphidae</p>	<p><i>Odontogriphus</i>, redrawn and modified from Briggs et al. (1994).</p> 

While a hypothesis with the sachitidans and molluscs as sister taxa (Figure 13.9D) is not falsified by placing brachiozoans as the living sister taxa of the molluscs, we suggest that the polarity of biomineralisation within the sachitidans is not one of increasing mineralisation, as required by the placement of *Kimberella* and *Odontogriphus* as putative outgroups, but rather one of scleritome reduction. Scleritome reduction and loss is an omnipresent trend in molluscs and other groups (see Chapter 3) and should be considered as a potential trend in sachitidans as well, rather than assuming the traditional mineralisation scenario for the group as discussed in Section 13.3.2.1.

Thus, within the sachitidans, there would have been a demineralisation of sclerites along with plate reduction and/or loss (*Orthrozanclus*, *Wiwaxia*) and lastly, complete sclerite loss in *Odontogriphus* (Figure 13.9D). These possible losses suggest to us increasing motility of the sachitidans. In addition, this topology better fits the stratigraphic appearances of sachitidan taxa. Stem molluscs may also have undergone sclerite loss, while mineralised plates and valves, which are plesiomorphic and shared with brachiozoans, diversified within the phylum. In contrast to the sachitidans, the siphogonuchitids do not appear to have been part of the trend for increasing motility and are instead cap-shaped with a single solid valve present in the early apical region while the later shell is composed of sclerites (Bengtson 1992). For this reason, we treat any relationship of the siphogonuchitids with the

sachitidans as uncertain. Additional molluscan apomorphies would include the radula (see Chapter 5), a chambered heart (see Chapter 6), and the mantle cavity (see Chapter 4).

The work of Bengtson, Conway Morris, Caron, Peel, Vinther, and their colleagues has brought new views and data to our consideration of possible molluscan origins. Some reviews imply that the identity and relationships of the molluscan stem groups are now known and stable (Telford & Budd 2011; Vinther 2015), but there remain numerous issues in the interpretation, stratigraphy, and comparisons of these taxa and their traits. Placing these taxa as stem molluscs primarily rests on two traits – the presence of a radular-like structure in a ‘pharynx’ and a shell and/or scleritome. Significant conjecture remains as to the method of formation of the scleritome of these groups, whether or not they were mineralised, and the homology of molluscan shells and spicules with those of the sachitidans (Conway Morris & Caron 2007); the absence of spicules or plates in *Odontogriphus* is also problematic. As discussed by Todt et al. (2008b), the molluscan radula has particular significance in scenarios of molluscan evolution, but it is critical to distinguish special similarity (apomorphies) from overall or functional similarity when comparing the feeding apparatus of various lophotrochozoans (Sober 1991).

Chitinous and mineralised feeding structures are common in the Lophotrochozoa, including the Mollusca, Annelida, Rotifera, and Gnathostomulida (Brusca et al. 2016), and although separated by over half a billion years of evolution,

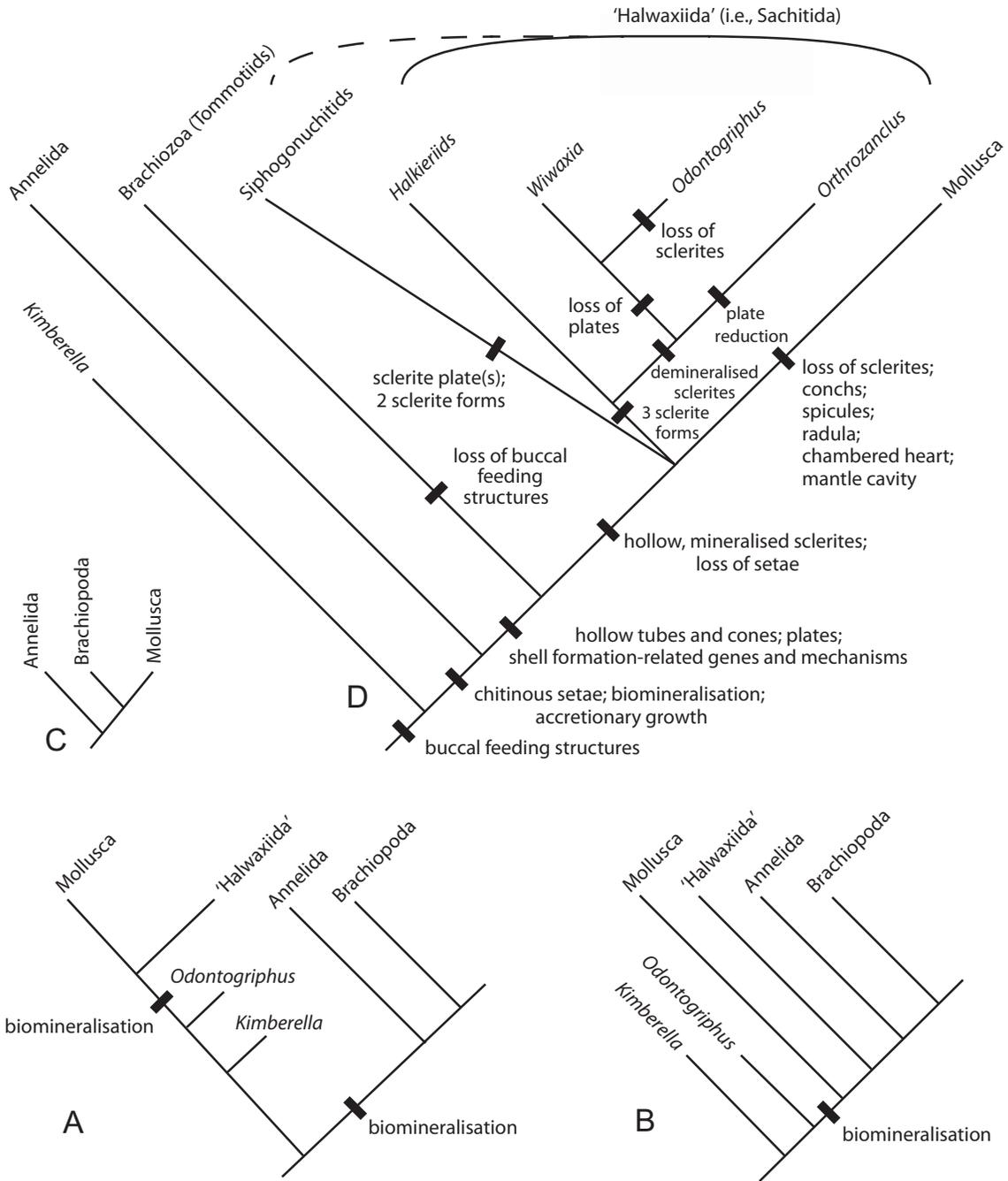


FIGURE 13.9 Outline of a partial lophotrochozoan phylogeny based on Conway Morris, S. and Caron, J.-B., *Science*, 315, 1255–1258, 2007. (a) Hypothesis 1. (b) Hypothesis 2. (c) The relationship among molluscs, annelids, and brachiopods used in the construction of hypothesis 3. (d) Alternative hypothesis 3; modified from hypothesis 1 with brachiozoans (e.g., tommotiids) as the sister taxon of the Mollusca. (a) and (b) redrawn from Conway Morris, S. and Caron, J.-B., *Science*, 315, 1255–1258, 2007 (c) redrawn from Luo, Y.J. et al., *Nat. Commun.*, 6, 9301, 2015.

they can often be surprisingly similar in these different phyla (Figure 13.8). As argued by Butterfield (2006) and Todt et al. (2008b), the putative radula of *Odontogriphus* and *Wiwaxia* is considered well outside the bauplan of the molluscan radula, which is considerably broad to begin with (see Chapter 5). As pointed out by Conway Morris (2006) and others, many comparisons of the shell, sclerites, and radular structures of the Cambrian taxa are often made with apparently unrelated

taxa that are substantially younger. Smith (2012) has recently argued for potential homologies between the molluscan radula and the feeding structures found in *Odontogriphus* and *Wiwaxia*, but there remain substantial differences such as the lack of wear on the anterior-most ‘teeth’ of *Odontogriphus* and *Wiwaxia* and questionable comparisons with living taxa with highly derived tooth morphologies (Figure 13.10).

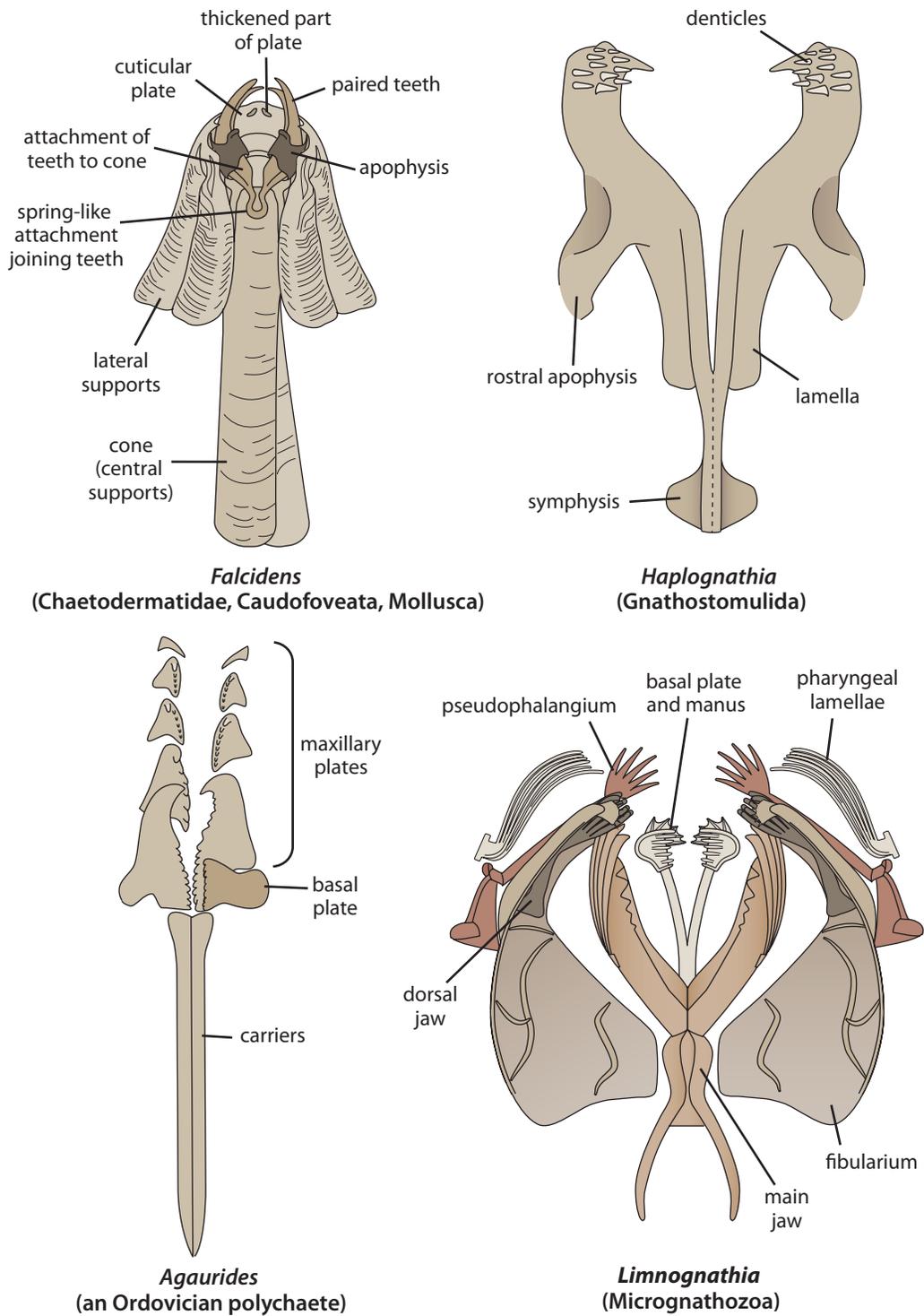


FIGURE 13.10 Examples of chitinous and mineralised feeding structures in lophotrochozoan taxa. Redrawn and modified from the following sources: *Falcidens* (Schander, C. et al., *Mar. Biol. Res.*, 1, 79–83, 2006), *Haplognathia* (Sørensen, M.V. and Sterrer, W., *J. Morphol.*, 253, 310–334, 2002), *Agaurides* (Kielan-Jaworowska, Z., *Acta Palaeontol. Pol.*, 7, 291–332, 1962), *Limnognathia* (Sørensen, M.V., *J. Morphol.*, 255, 131–145, 2003).

While these putative ‘stem group’ taxa appear to fulfil the early molluscan evolutionary scenario which envisions an ancestral dorsoventrally flattened animal with a broad, ciliated ventral foot for locomotion, a ventral mouth with a radula for feeding and dorsally covered by a cuticle, with the shell and/or sclerites making up a scleritome (e.g., *Halkieria*, *Wiwaxia*, *Odontogriphus*) (Vinther & Nielsen 2005; Caron et al. 2006; Telford & Budd 2011; Vinther 2015), their stratigraphic occurrences are typically after the appearance of more likely molluscan morphologies (Figure 13.8). For example, while the coeloscleritophoran sclerites are present in the Cambrian record approximately 5 Ma before the helcionelloidans, the first occurrences of the supposed stem group molluscs (*Wiwaxia*, *Odontogriphus*) are almost 20 Ma later. If these scleritic animals are members of ancestral lineages leading to molluscs, one would expect them to occur earlier in the fossil record than the supposed descendant lineages. There are several possible explanations for this gap. Perhaps conditions for preservation in different habitats or at different times favoured conchs while excluding sclerites, or vice versa. The lack of univalve and bivalve stem group molluscs from the Middle Cambrian Burgess Shale Formation in Canada suggests that taphonomic biases may have occurred, although it could equally well be due to molluscs avoiding the area because of their ecological preferences. Also, the relatively short period of phosphatic preservation (521–542 Ma) may have contributed to the differential occurrence of groups during the early Cambrian. Thus, perhaps these and other stem group taxa were present but were not preserved. Alternatively, if the fossil record, while not complete, does accurately reflect the sequence of the origin of molluscan stem group taxa, the univalve and bivalve taxa are the earliest molluscan stem groups and the sclerite-bearing animals a more distant lophotrochozoan lineage (Lindberg & Ponder 1996; Benton et al. 2000).

13.3.2.2.3 Univalves and Bivalves

Many of the earliest ‘molluscs’ in the Cambrian record have shells morphologically similar to crown gastropods and bivalves, being either limpet-like (e.g., *Anabarella*, *Barskovia*, *Bemella*, *Igorella*, *Oelandiella*, *Purella*), coiled (e.g., *Aldanella*, *Latouchella*, *Pelagiella*), or consisting of two valves (e.g., *Fordilla*, *Pojetaia*) (Runnegar & Pojeta 1974b; Dzik 1994; Parkhaev 2007, 2008; Maloof et al. 2010; Erwin & Valentine 2013). In contrast to the sachtidians, most of these shells are small (less than 5 mm in length) (Runnegar 1983), although a few exceed 1 cm in length (Martí Mus et al. 2008). While some of these early conchs and valves may be components of a large scleritome, others may represent lophotrochozoan or other taxa. The appearance of bivalves and rostroconchs also marked diversification events from the plesiomorphic epifaunal state into infaunal habitats.

13.3.2.2.3.1 Helcionelloida

The earliest limpet-like ‘molluscs’ include the Helcionelloida which date from the Nemakit-Daldynian age/stage of the Cambrian (534 Ma) (Peel 1991b; Gubanov 1998; Gubanov et

al. 1999; Gubanov & Peel 2000; Parkhaev 2008), and while most of these taxa were extinct by 501 Ma, *Chuiliiella* survived until the Lower Ordovician (Tremadocian) (477 Ma) (Gubanov & Peel 2001). Helcionelloidans had a worldwide distribution and are bilaterally symmetrical cap- and horn-shaped shells. They include the Helcionellidae, Coreospiridae, Securiconidae, Stenothecidae, and Yochelcionellidae. Most workers assume them to be the ancestors of living conchiferans, although Parkhaev (2006b, 2007, 2008) considered them to be stem gastropods (Figure 13.11).

Helcionelloidan morphology is variable and includes limpets and loosely symmetrically coiled conchs, typically with less than three-quarters of a whorl. One exception is the Coreospiridae where coiling typically exceeds a single whorl. Shell sculpture consists primarily of raised axial ridges (costae), which in some taxa can be quite well developed (e.g., *Igorella*, *Obtusoconus*, and some Securiconidae). While many groups have broad oval apertures, members of the Securiconidae, Stenothecidae, and Yochelcionellidae show lateral compression and narrowing of the aperture (Pojeta & Runnegar 1985; Gubanov 1998). For example, in most helcionelloids, apertural length is less than twice apertural width, while in stenothecids apertural length is three to five times apertural width (Waller 1998). Parietal trains⁸ and emarginations are also common in these taxa (Peel 1991c; Parkhaev 2001). In Yochelcionellidae the train may become closed ventrally with growth producing a snorkel-like structure (see Table 13.7).

It has also been suggested that some helcionelloidans may actually be ‘protoconchs’ of larger (>5 mm) taxa. Martí Mus et al. (2008) reported 2–3 cm specimens from the Lower Cambrian Rio Huso group in the Montes de Toledo region of central Spain, which resembled *Scenella* but had a coarsely sculptured helcionelloidan-like conch affixed at the apex. The larger and extremely thin shells continued the earlier concentric costate sculpture over the presumptive dorsal surface. More recently, similar specimens have been reported from the Lower Cambrian Hawker Group of the Flinders Ranges in South Australia by Jacquet and Brock (2015), further suggesting the possibility that not all helcionelloidans were small. While the size and position of these possible ‘protoconchs’ are suggestive, further work is needed. Questions remain, including how a protoconch, which typically reflects egg shape and size (especially in lecithotrophic taxa), would become laterally compressed – a feature of many helcionelloidan taxa – and the discrepancy between *Scenella* and helcionelloidan muscle scar patterns.

Pores are found in the shells of many Cambrian helcionelloidan taxa, including *Auriculaspira*, *Auricullina*, *Postacanthella*, *Tuberoconus*, *Igorella*, and *Daedalia* (Feng & Sun 2006; Parkhaev 2006a). In some taxa such as *Auricullina*, the exterior surface of the pore is marked by a raised ridge encircling the pore, forming small tubercles (Kouchinsky 2000). Shell pores in the helcionelloidans differ markedly from the canal systems found in halkieriid sclerites (Vinther 2009) and polyplacophoran plates (see Chapter 14).

⁸ A vaulted posterior projection of the aperture.

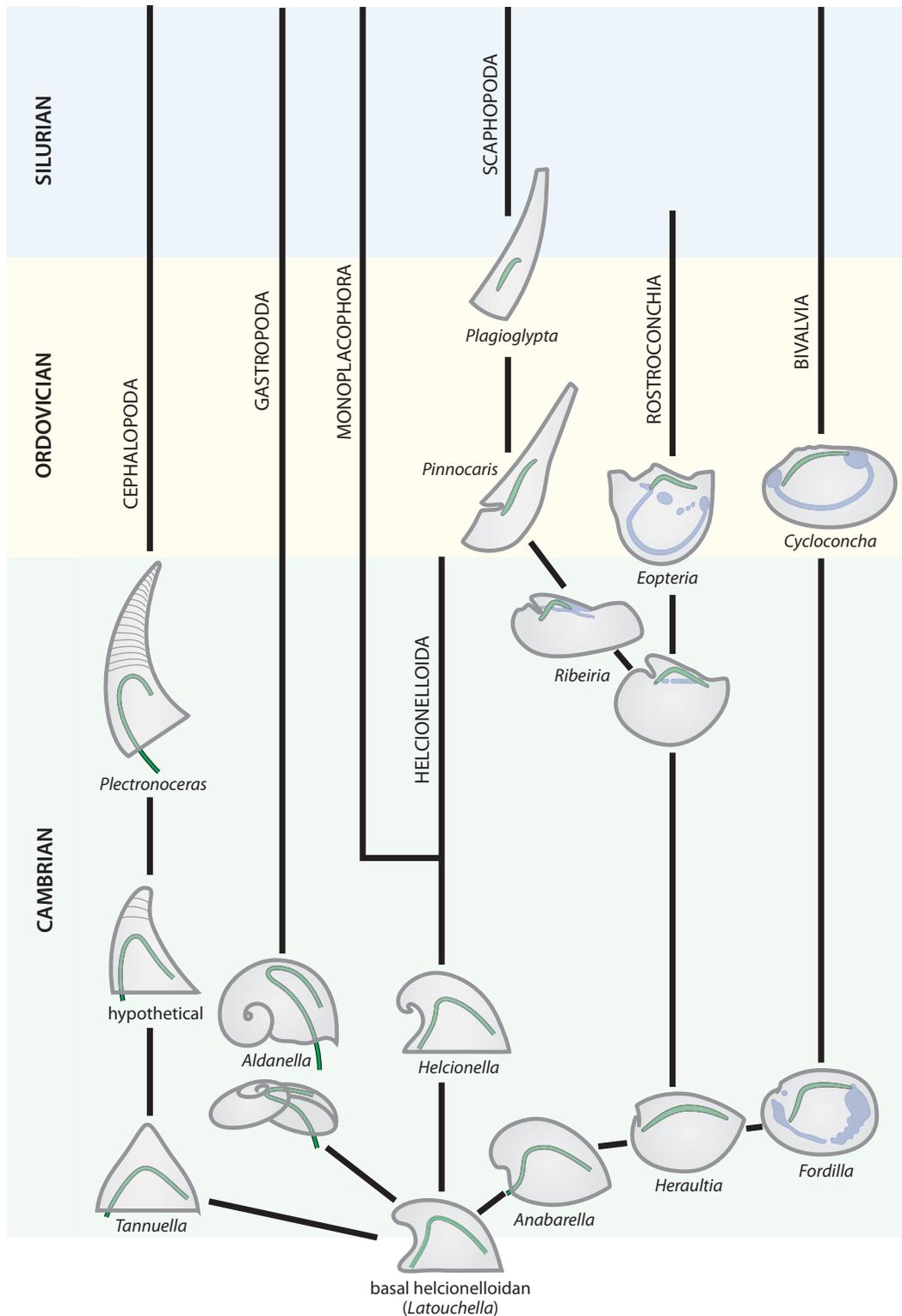


FIGURE 13.11 One view of the phylogeny of the early Paleozoic molluscs, showing their hypothetical derivation from a helcionelloidan ancestor and showing muscle scars and pallial lines. Based in part on Runnegar, B.N. and Pojeta, J., *Science*, 186, 311–317, 1974b. Note: It is now thought that the early Cambrian genus *Aldanella*, shown in this figure as an early gastropod, is not a mollusc (see text).

In most helcionelloidan shells where shell microstructure is preserved, it is in the form of phosphatic replicated and replaced microstructures visible in exfoliated and broken sections of the shell (Runnegar 1985; Kouchinsky 2000). Even if the shell in the fossil is not preserved, the shell

microstructures that make up the shell can be determined by their distinctive morphologies on the internal moulds or steinkerns (MacClintock 1967; Runnegar 1985). Of the six major shell structure groups (I–VI) recognised by Carter (1985) (see Chapter 3), only two, prismatic and laminar, are

TABLE 13.7

Classification of the Helcionelloida, a Group of Putative Molluscs Often Considered to Be an Extinct Early Class

(Class) **Helcionelloida**

(= Helcionellida)

Cambrian (Terreneuvian)–Ordovician (Lower) (530–478 Ma)

Small cap-shaped to planispiral conchs, some with strong growth(?) increments or costae. Some limpet-like forms may be plate-like sclerites from sachtids (see above) or polyplacophoran valves (e.g., Carinopeltidae).

This group is treated as an order of the ‘subclass Archaeobranchia’ (in Gastropoda) by Bouchet et al. (2017).

(Order) **Helcionellida**

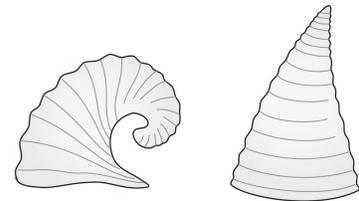
(= Helcionelliformes)

(Superfamily) **Helcionelloidea**

Cambrian (Terreneuvian)–Ordovician (Lower) (530–478 Ma)

Aperture ovoid, simple, and complete.

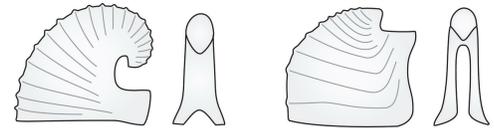
Families Helcionellidae, Carinopeltidae (= Igarkiellidae), and Coreospiridae (= Archaeospiridae, Yangtzespirinae, and Latouchellidae)

Latouchella (left) and
Helcionella (right)*Mackinnonia* (left) and
Helcionella (right)(Superfamily) **Yochelcionelloidea**

Cambrian (Terreneuvian)–Ordovician (Lower) (530–478 Ma)

Substantial lateral apertural narrowing accompanied by a posterior groove or train and its modification into a snorkel in some taxa.

Families Yochelcionellidae, Stenothecidae, and Securiconidae (= Rugaeconidae, Trenellidae)

‘*Latouchella*’ (left) and
Eotebenna (right)*Yochelcionella*

Images redrawn and modified from Peel (1991c)

known from putative Cambrian molluscs. A prismatic outer layer has been reported in stenothecids, trenellids, coreospirids, and helcionellids while in yochelcionellids there is an internal prismatic layer (Vendrasco et al. 2010). Inner lamellar layers include semi-nacreous (stenothecids), lamellofibrillar (onychochilids), and foliated (rostronchs); in yochelcionellids the laminar layer is on the outside of the shell. Unspecified laminar structures are also present in the trenellids, coreospirids, and helcionellids. Crossed structures, the dominant form of shell structures in living molluscs, have not been reported in these putative stem molluscs, but lamellofibrillar is very similar to crossed structures (e.g., crossed lamellar). Lamellofibrillar structures are the first to appear in the earliest Cambrian of Yunnan, China (Feng et al. 2003; Feng & Sun 2003; Vendrasco et al. 2010) while nacreous structures appear later in the record, being reported in *Anabarella* and *Watsonella* (Runnegar 1983, 1985; Carter 2001). Most of these microstructures are inferred to have been originally aragonitic, but calcitic shell structures are known from *Eotebenna*, *Mellopegma*, *Ribeiria*, and *Anabarella* and may have been common during the calcitic seas of the Middle Cambrian (Vendrasco et al. 2011b).

Putative muscle scars have been reported in a variety of helcionelloidans (Wen 1979; Geyer 1994; Parkhaev 2002b, 2004; Parkhaev 2014). While muscle scars are important characters in molluscan palaeontology, they are often weakly distinguished and difficult to locate in many fossil taxa and especially on steinkerns. They are typically recognised by changes in shell texture or slightly depressed areas on the internal surface of the conch or elevated areas on internal moulds. A single pair of symmetrical muscles has been reported in several limpet-like genera of ‘Yangtzeconiaacea’ by Wen (1979), although their strap-like morphology and apical position make a functional interpretation difficult. Parkhaev (2014) described single pairs of symmetrical muscles in the helcionelloidans *Bemella*, *Oelandiella*, *Anabarella*, and *Anhuiconus*; Vendrasco et al. (2010) reported and illustrated a single pair of muscle attachment scars near the apex of *Yochelcionella*, although three pairs of muscles were reported for *Bemella communis* (Parkhaev 2014, 2017). This limited sample suggests that helcionelloidans did not have multiple dorsoventral retractor muscles as seen in monoplacophorans but rather only a single pair. The attachment points of these muscles on the shell vary widely (apex, ‘columella’, overhead region), and

this variability far exceeds the variation seen across conchiferans. Moreover, there is evidence of surprising convergence within molluscs and even between phyla. For example, Dzik (2010) illustrated remarkably similar muscle scar patterns in Cambrian ‘monoplacophorans’ and brachiopod valves.

Helcionelloidans have been considered to be gastropods (Knight & Yochelson 1958; Golikov & Starobogatov 1975; Parkhaev 2000, 2001; Parkhaev 2008), monoplacophorans (Knight 1952; Runnegar & Pojeta 1974b; Pojeta & Runnegar 1976; Wen 1981; Runnegar & Pojeta 1985), or to represent a separate molluscan class (Yochelson 1978; Wen 1984; Peel 1991b; Geyer 1994; Gubanov & Peel 2000). We consider helcionelloidans to represent an extinct paraphyletic class of either molluscs or of unknown affinities. Within its ranks are lineages which range from limpet-like to coiled and tubular taxa (see Section 13.3.2.2.8 and Figure 13.11). One strong trend in the group is the lateral compression of the conchs. This compression was typically accompanied by the formation of a train or tube on the narrow side of the conch, which began after a period of uniform aperture expansion. While train formation requires the partial folding of the accretionary tissue, formation of a tube would appear to have required both extension and folding and subsequent fusion as the conch again returned to uniform apertural expansion. The formation of the tube gave these taxa two apertures, one dorsal and one ventral.

13.3.2.2.3.1.1 Endo- and Exo-Gastric Coiling

Categorising conchs as either endo- or exogastric has featured in both helcionelloidan and cephalopod systematics and palaeobiology (see Chapter 17). In helcionelloidans endo- and exogastric morphologies are used to infer putative water flow patterns

around and through shells, especially those with holes, slits, and sinuses (Pojeta & Runnegar 1976; Peel 1991b; Parkhaev 2008). All crown molluscan groups with coiled shells are endogastric except Cephalopoda, in which both coiling directions are present (Figure 13.12), although endogastric shells are often hypothesised for the cephalopod ancestor (see Chapter 17).

Both exo- and endogastric shells occur in the Nautilida (e.g., exogastric *Nautilus*, while some Discosorida are endogastric [see Chapter 17]). Among coleoids, *Spirula* is endogastric, while most ammonites have been reconstructed as exogastric. Coiling preference in nautiliforms and ammonites is thought to be partly related to shell hydrodynamics and performance in the water column. For example, Stridsberg (1985) suggested that endogastric shells were mechanically better for swimming than the exogastric shells in oncoceratid cephalopods. In curved nautiliforms and ammonites which lack coiling, shells are considered exogastric if the anterior side is convex and endogastric if the posterior side is convex (see Chapter 17, Figure 17.5). For example, the curved tubes of baculitid ammonites have been reconstructed as exogastric according to Klug and Lehmann (2015).

13.3.2.2.3.1.2 Scaphopodisation

One of the key features of the scaphopodisation scenario by Peel (2006) was the formation of anterior and posterior apertures on conchs (see Chapter 16). He used the shell ontogeny of living scaphopods as a model for the formation of these tubular shells. In scaphopods, the developing shell envelops the larvae laterally and ultimately fuses along the ventral margin, forming a cylinder around the organism and leaving a small posterior opening (Wanninger & Haszprunar 2001)

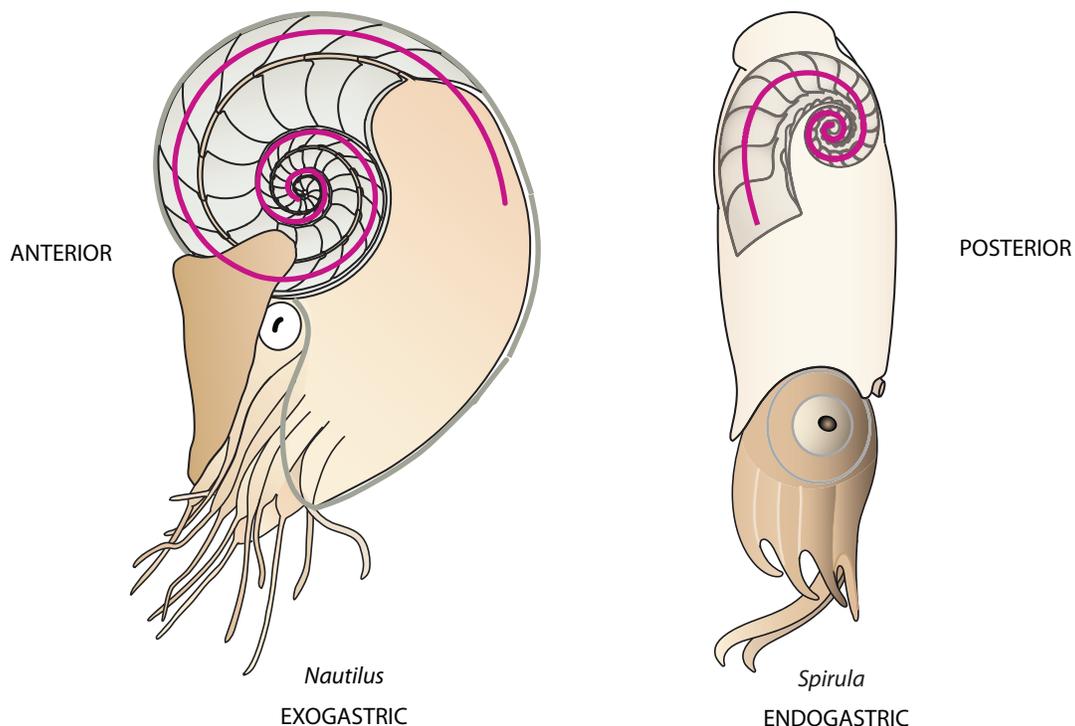


FIGURE 13.12 Examples of exogastric and endogastric coiling in cephalopods. Figures reconstructed from various sources.

(see also Chapter 8). Subsequent accretion of the adult shell or teleoconch then occurs along the anterior margin of the fused cylinder. The lateral expansion of the mantle epidermis and its subsequent ventral fusion as it envelops the larva coincides with ano-pedal flexure. This changes the orientation of the anus by about 90°, and the foot extends anteriorly rather than ventrally relative to the original embryo axes. The anus is now in the anterior third of the shell even though the posterior portion of the mantle never fuses (see also Chapter 8). This developmental pattern is identical to that seen in gastropods except for the complete enveloping of the posterior portion of the gastropod embryo (see Chapter 8, Figure 8.33). Even the fusion of the developing lateral and posterior shell margins and the transition to apertural accretionary growth are alike.

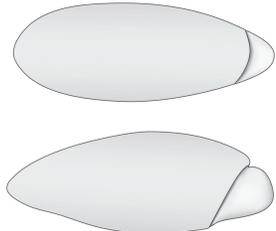
While the helcionelloidans *Yochelcionella* and *Eotebenna* appear to share similar shell ontogeny with the Rostroconchia, there is no evidence for ventral fusion of the lateral shell edges, although both taxa express strong lateral compression of the teleoconch. Instead, the helcionelloidans appear to undergo scaphopodisation by shell elongation along the dorsoventral axis combined with a temporary enfolding of a portion of the posterior secretory epidermis near the apex during shell accretion, thereby forming a tube. The foot is assumed to remain in its ventral position relative to both the larval and adult axes.

Determining possible shell ontogeny associations of the taxa *Janospira*, *Jinonicella*, and *Rhytidentalium* is more difficult because of the lack of living taxa with similar morphologies. Based on gross morphology they probably underwent ventral fusion similar to living scaphopods, although later in their ontogeny, thereby generating a longer (or more coiled) early shell. Regardless of the affinities of *Janospira*, *Jinonicella*, and *Rhytidentalium*, if these are burrowing morphologies, the convergent shell forms of the taxa identified by Peel suggest multiple incursions into the sediment by several molluscan lineages during the early Paleozoic. The elongate tubular shells of these taxa appear to be derived through different growth trajectories, and the ventral mantle fusion of scaphopods may have had its earliest inception in one of these possible stem groups. Scaphopodisation must also have produced significant changes in internal anatomy in these and other lineages, as it did in the scaphopods (see Chapters 4, 5, and 16).

13.3.2.2.3.2 Merismoconchia

The Merismoconchia was erected by Wen (1979) for small cap-shaped shells with apparent tripartite morphology. A transverse ridge divides the shell into two (not three parts as originally thought), a small anterior rostrate segment and a much larger body segment (Wen 2008; Devaere et al. 2013) (see Table 13.8). Wen also mapped internal organs, including muscle scars, gut pattern, and nephridia on the interior surface of the second and body segments, but these are thought more likely to be preservation artefacts (Devaere et al. 2013). Merismoconchs are known from the Meishucunian (= Nemakit-Daldynian, in part) (542.0–516.0 Ma) of China, and Tommotian (530.0–516.0 Ma) of southern France, and

TABLE 13.8
Classification of Merismoconchia

<p>Merismoconchia Cap-shaped shells with two (initially reported as three) distinct body segments. Cambrian (Terreneuvian) – Cambrian (Series 2) (530–516 Ma) Family Merismoconchidae</p>	 <p><i>Merismoconcha</i>, redrawn and modified from Devaere et al. (2013).</p>
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possibly the Lower Cambrian of Siberia and Mongolia (Wen 2008; Devaere et al. 2013).

Wen (2008) compared the merismoconchs to polyplacophorans, noting that whereas each of the eight polyplacophoran valves has two pairs of muscles, in merismoconchs dorsoventral muscles were reportedly attached to the two ‘valves’. The multiple ‘organs’ and circular gut Wen identified (but see above) also drew comparisons with the Monoplacophora and led Wen to propose plate reductions in the chitons that gave rise to the merismoconchs, with further plate fusions producing the monoplacophoran lineage.

Material from the Cambrian of France examined by Kerber (1988) and Devaere et al. (2013) showed no trace of muscle scars and imprints of organs although they were better preserved than the original Chinese material. As noted above, only two shell segments were present in the French specimens (and in several Chinese specimens), and Devaere et al. (2013) concluded that the third putative segment was an artefact. They suggested that the anterior chamber might be homologous with the molluscan protoconch. There is a resemblance of the anterior segment of the Merismoconchia to the distinct, thickened, anterior portion of the conch of the Silurian *Tryblidium reticulatum* illustrated by Lindström (1884), but this anterior enlargement is absent in the apparently closely related *Tryblidium unguis*, also described by Lindström from the Silurian of Götland.

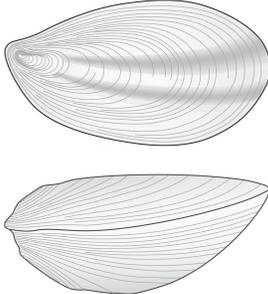
While the Merismoconchia may represent a molluscan lineage, we are uncertain of their affinities within the phylum.

13.3.2.2.3.3 Stenothecoida

Stenothecoidans⁹ are bivalve organisms that range from the Terreneuvian to the Miaolingian of the Cambrian (Kouchinsky 2001). The shells are asymmetric with inequivalve valves, and a simple tooth and socket have been reported in two taxa – *Cambridium* and *Serioides* (Pelman 1985) (see Table 13.9). Putative muscle scars have also been reported (Yochelson 1969), but these are loop-like and more closely resemble intestinal loops of orthothecid hyoliths (Rozanov & Zhuravlev 1992).

⁹ Not to be confused with the helcionelloidan family Stenothecidae.

TABLE 13.9
Classification of Stenothecoida

<p>Stenothecoida (= Probivalvia) (Superfamily) Cambridioidea Bivalved, asymmetric shells with inequivalve valves and a simple tooth and socket; loop-like muscle scars have also been reported in some taxa. Cambrian (Series 2) – Cambrian (Miaolingian) (516–501 Ma) Families Stenothecidae and Cambridiidae</p>	<div style="text-align: center;">  <p><i>Stenothecoides</i>, redrawn from Yochelson (1969).</p> </div> <div style="text-align: center;">  <p><i>Cambridium</i>, redrawn from Knight and Yochelson (1960).</p> </div>
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Rasetti (1954), Aksarina (1968), and Yochelson (1969) considered stenothecoidans to be an independent, extinct molluscan class, although Rozov (1984) considered them to be closer to brachiopods than to molluscs and proposed a separate phylum Stenothecata. Runnegar and Pojeta (1974b) suggested that stenothecoidans might be bivalved monoplacophorans, while Waller (1998) considered Stenothecoida to represent the sister taxon of the Rostroconchia + Bivalvia.

Dzik (1981a) argued that stenothecoidans were inarticulate brachiopods with calcareous shells and characters that unequivocally indicated molluscan affinities could not be identified. Thus, the stenothecoidans are problematic lophotrochozoans, located outside the current concept of Mollusca (Waller 1998).

13.3.2.2.4 Monoplacophora

Early Paleozoic monoplacophorans are the subject of much conjecture. Historically, the group has been an assortment of various supposedly untorted limpets and some planispirally coiled conchs. Pojeta and Runnegar (1976) and Peel (1991c) consider most Cambrian cap-shaped taxa, the coiled Helcionelloida, and some, if not all, of the bellerophonian taxa, to be monoplacophorans. Other workers, including Knight and Yochelson (1960), Starobogatov and Moskalev (1987), and Parkhaev (2002a), limited the diagnosis of Monoplacophora to cap-shaped taxa and considered the remaining Helcionelloida and bellerophonian taxa to be torted gastropods. Because these positions are based on the interpretations of a small suite of muscle insertion characters, it is difficult to test either view.

Limpet-like shells are common in Cambrian and Ordovician deposits. Based on muscle scar morphology, many of these have been assigned to the Monoplacophora, but in a revision of putative monoplacophoran ancestors of cephalopods, Dzik (2010) has argued that many supposed tergomyan taxon are probably stem brachiopods rather than molluscs. These include genera placed in four monoplacophoran families, including *Kirengella* (Kirengellidae), *Hypseloconus* (Hypseloconidae) and *Pygmaeoconus* (Pygmaeoconidae), and *Lenaella*, *Nyuella*, *Romaniella*, and *Moyerokania* (Scenellidae). These taxa are characterised by a putative posterior to central apex, multiple pairs of muscle scars (sometimes showing the fusion of several attachment points), and a pair of medial muscle scars. Here we agree with Dzik and regard this distinctive muscle scar pattern as brachiopod rather than molluscan.

Another problematic group of limpets, the Archinacelloidea, have also been included in the monoplacophorans by different workers (Peel & Horný 1999). As in helcionelloidans, the muscle scar morphologies of assigned taxa are highly diverse and include a single pair of small apical muscles (*Barrandicella*), horseshoe-shaped muscle scars with or without medial muscle scar (*Archinacellopsis*), complete muscle circles (*Archinacella*, *Archinacellina*), and strap-like lateral muscles (*Archaeopruga*). Unlike monoplacophorans, distinct muscle attachment points associated with muscle segments are absent. Also absent are blood sinuses through the muscle bands as found in patellogastropods. The number of types of muscle patterns far exceeds that seen in fossil and living patellogastropods. We agree with Peel and Horný (1999) and consider the Archinacellida to represent one or

more independent secondary flattenings within eogastropod lineage(s). The Archinacellida (families Archinacellidae and Archaeopragidae) range from the Furongian (Cambrian) to Pridoli (Silurian) (492.5–418 Ma).

Because we are uncertain of the phyletic relationships of the cap-shaped helcionelloidans with molluscs, we restrict the monoplacophorans to those molluscan taxa with distinct bilateral, serial muscle segments attached to the dorsal surface of the conch. The number of serial pairs of muscles in the Monoplacophora varies between four and eight. This interpretation is similar to that of Geyer (1994) and Vendrasco (2012).

In Monoplacophora, two superfamilies are recognised, namely Tryblidioidea and Neopilinoidea (see Appendix for details of classification). The Cyrtonelloidea are sometimes included in the Monoplacophora (e.g., Bouchet et al. 2017) but are here treated as bellerophonians within the Gastropoda (see Appendix). In the tryblidioidians, the anterior-most pairs of muscles are often fused on either side of the shell, and there are prominent buccal muscle scars and a diaphragm scar. The latter originates from the anterior-most muscle bundles and extends towards the centre of the shell; it is absent in Neopilinoidea. While known only from fossil monoplacophorans, similar scars are formed from the attachment of a coelomic partition on the anterior plates of the Polyplacophora (Plate 1897; Lemche & Wingstrand 1959). In chitons, this partition isolates a blood sinus around the radula into which the aorta empties (Plate 1897). A similar partition is found in the aplacophoran *Limifossor* (Heath 1905a), and according to Heath, they occur in aplacophoran taxa with a well-developed radula. We infer from these observations of living ‘placophoran’ taxa that the tryblidiid monoplacophorans (*Pilina*, *Tryblidium*, *Archaeophiala*) had more massive radulae than seen in Neopilinoidea. These putative diaphragm scars are also correlated with the large radular attachment muscle scars seen in tryblidiid taxa. Based on the change in habitats documented over geological time, Stuber and Lindberg (1989) suggested that monoplacophorans had more robust radulae in the Paleozoic, concluding that the morphology of the radulae of living monoplacophorans would probably be inefficient in Paleozoic near-shore habitats. Living neopilinids have substantially reduced radular muscle attachment areas. The earliest monoplacophoran, *Pilina*, first appeared in the Upper Cambrian (483 Ma), and the group reached its greatest diversity between the Ordovician and Silurian. Associated fauna include cephalopods, rostroconchs, gastropods, trilobites, and brachiopods (Wen & Yochelson 1999).

13.3.2.2.5 Polyplacophora

The polyplacophorans first appear in the late Cambrian (*Preacanthochiton*, *Chelodes*, *Matthevia*) (Bergenhayn 1960; Runnegar et al. 1979; Pojeta et al. 2010b) but the polyplacophoran affinities of some of these fossils are disputed by Sirenko (1997). In contrast, Wen (2001) proposed that the Terreneuvian (Cambrian) appearance of *Paracarinachites* represents the first polyplacophorans. Conway Morris and Peel (2009) have allocated *Paracarinachites* to the Cambroclaves – a group

of enigmatic, phosphatised, hollow spine-shaped sclerites thought to represent palaeoscolecidan worms.

Early undisputed chitons belong to the Paleoloricata, their shell valves lacking an articulamentum layer and therefore also lacking both insertion plates and sutural laminae which articulate adjoining valves in modern chitons. The articulamentum shell layer and its associated valve components first appeared in the Devonian Multiplacophorida (Vendrasco et al. 2004). It is also present in the eight-valved Neoloricata (crown group chitons) which first appeared in the Lower Carboniferous (Dinantian 359–326 Ma) (Sirenko 2006).

The late Cambrian–Ordovician fossil record is rich with putative polyplacophoran plates (Vendrasco & Runnegar 2004; Pojeta et al. 2010b), but demonstrating clear polyplacophoran affinities of these individual plates is difficult. Such assignments have been bolstered by the discovery of articulated specimens, ratios of different valve morphotypes, and valve microstructure (absence of the articulamentum layer) (e.g., Runnegar et al. 1979; Pojeta et al. 2003; Sutton & Sigwart 2012). In addition, Pojeta et al. (2010) demonstrated that aesthete pores are present in the shell plates of the earliest paleoloricates. Even if restricted to these better-characterised taxa, the overall morphological variation of the Paleoloricata is surprisingly diverse given the relatively conservative morphology of living Neoloricata (see Chapter 14). For example, the Paleoloricata include taxa with triangular, upright, sharply pointed plates (Mattheviidae) (Figure 13.13), rectangular plates (Septemchitonidae), and more typical chevron-shaped plates as seen in living neoloricates (*Echinochiton*) (Pojeta & Dufoue 2008). Most paleoloricates are reconstructed with a narrow girdle surrounding the plates, but in *Echinochiton* the valves are also surrounded by large hollow valve spines, similar to those found in some Multiplacophorida (Vendrasco et al. 2004b). In transverse section, individual intermediate plates vary from inverted V-shapes to inverted U-shape and approach semi-circular in some Septemchitonidae, if reconstructions by Dzik (1994) are accurate (Figure 13.22). These encircling valves suggest a greatly reduced or absent foot.

Vendrasco et al. (2009) skilfully combined three Chinese Cambrian small shelly taxa (*Ocruranus*, *Eohalobia*, and another probably incorrectly assigned to the Ordovician *Gotlandochiton*) as a possible stem polyplacophoran. The shell microstructure layers of *Ocruranus* are similar to those found in *Pelagiella* (see Section 13.3.2.2.7), but if the plate reconstruction is correct, the order of the layers is reversed. In

Matthevia, stem aculiferan

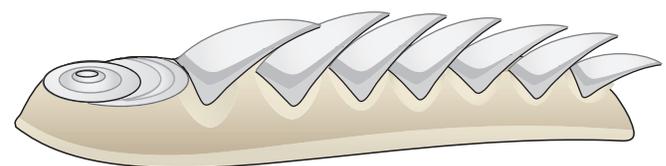


FIGURE 13.13 A reconstruction of the Paleozoic paleoloricate *Matthevia*. Redrawn and modified from Vinther, J., *J. Nat. Hist.*, 48, 2805–2823, 2014.

addition, the morphologies of these Cambrian valves (especially the putative head [*Eohalobia*] and tail [*Ocruranus*] valves) differ from the valves of any known putative fossil or living chiton. *Ocruranus* and *Eohalobia* have been considered possible brachiopods or halkieriids (Liu 1979; Conway Morris & Caron 2007) (see below), and *Ocruranus/Eohalobia* may represent sclerites of another plated brachiozoan.

Unlike most Cambrian molluscan taxa, the Polyplacophora have been subject to several phylogenetic analyses (Cherns 2004; Sigwart & Sutton 2007a; Pojeta et al. 2010b; Sutton et al. 2012). Most recover monophyletic Polyplacophora, Neoloricata, and Multiplacophorida. The Paleoloricata are often paraphyletic or polyphyletic and placed among aplacophoran taxa (e.g., Sigwart & Sutton 2007b; Sutton et al. 2012). Stratigraphically the groups are distinct, with the Paleoloricata in the early Paleozoic, followed by the multiplacophoridans (Neoloricata) with crown Neoloricata appearing in the Upper Paleozoic (Cherns 2004).

It has been suggested that the most likely Cambrian ancestor of Polyplacophora is *Wiwaxia* or *Halkieria*. Sirenko (1997 p. 16) argued that the shell plates were probably derived from spicules like those of *Wiwaxia*, as shown by the similarity of the shape of the plates in the ‘most primitive Ordovician Chelodidae ... but also by several characters of anatomy of chitons and some features of their ontogenesis’. The shell microstructure of the Paleozoic paleoloricate, *Matthevia variabilis*, was reported as differing greatly from that of living chitons, showing a vesicular structure (Runnegar et al. 1979; Carter & Hall 1990), but this was later reinterpreted as oblique sections of aesthete pores (Pojeta et al. 2010a). There are no other reports of shell microstructure in Paleozoic or Mesozoic chitons. Reported calcium phosphatic shell structure in the Paleozoic chiton *Cobcrephora* (Bischoff 1981) – the so-called Phosphatoloricata – may be the result of secondary replacement (Carter & Hall 1990), or they are doubtful polyplacophorans (Hoare 2000; Pojeta et al. 2010a). No other mollusc has this type of shell structure.

The confusion surrounding the early Paleozoic ‘placophorans’ has resulted in different classifications being proposed. Smith and Hoare (1987) recognised three subclasses – Paleoloricata, Phosphatoloricata, and Neoloricata – but the former two were combined into a single subclass (Paleoloricata) by Sirenko (1997), as had been proposed earlier (Bergenhayn 1955; Van Belle 1983). All living chitons are classified in Neoloricata, and fossils range back into the Lower Devonian, but all Paleoloricata are from the Paleozoic. The latter group is quite diverse, with Sirenko (1997) listing 14 families arranged in four orders and five suborders, but these were substantially reduced by Pojeta et al. (2010a).

The classification of polyplacophorans is provided in the Appendix.

13.3.2.2.6 Cephalopoda

As also discussed in Chapter 17, the earliest known cephalopod taxon is *Plectronoceras*, from the Furongian (Cambrian) of China (493–491 Ma) (Chen & Teichert 1983b). The conchs are relatively large compared to earlier Cambrian shelled

taxa, approximately 1.5 cm in length, slightly curved endogastrically, and with a siphuncle along the posterior edge of the shell. The aperture is oval in section due to lateral compression of the shell. The septa are thin and closely spaced and the body chamber about a quarter to a third of the length of the shell. In addition to China, they are known from West Antarctica and North America (Landing & Kröger 2009). The first cephalopods are associated with tropical, shallow-water carbonate platforms (stromatolitic and oolitic limestones), as well as with deeper water/lower energy, massive limestones (Landing & Kröger 2009). Chen and Teichert (1983a p. 650) characterised the shallow water setting as both well-oxygenated and turbulent. Other early cephalopods were thought to be nektonic, living above an anoxic benthos.

According to Landing and Kröger (2009), the entire history of stem Cephalopoda in the Cambrian is confined to the final two million years. Chen and Teichert (1983a) thought they arose only shortly before their first occurrence as fossils, while others have hypothesised hyolith, helcioneloidan, or monoplacophoran ancestors from the early or mid-Cambrian (e.g., Flower 1954; Yochelson et al. 1973; Dzik 1981b; Kobayashi 1987; Kröger 2007; Kröger et al. 2011) (also see Chapter 17 for further discussion). Most current evolutionary scenarios derive cephalopods from a benthic monoplacophoran-like mollusc with a high conical shell and septa (e.g., Kröger et al. 2011). Putative ancestors were found in taxa often attributed to Hypseloconidae, including *Tannuella* (530–518 Ma), *Knighthoconus* (501–497 Ma), and *Shelbyoceras* (493–488 Ma). Stinchcomb and Echols (1966) questioned the affinities of some of these hypseloconids (*Tannuella* and *Shelbyoceras* spp.) in cephalopod phylogeny, and we have argued above that some at least are better treated as brachiopods (see Section 13.3.2.2.4). Another Cambrian septate taxon was the coiled *Aldanella* (Aldanellidae) (Parkhaev 2008), which is also probably not a mollusc (see Section 13.3.2.2.7).

The development of septa is typically discussed in terms of the evolution of buoyancy control in cephalopods (Boyle & Rodhouse 2005), however the septa in the taxa suggested as cephalopod ancestors (*Tannuella*, *Knighthoconus*, *Shelbyoceras*) are not pierced by a siphuncle with which to control the movement of liquid between chambers to affect buoyancy (see Chapter 17). Thus, when septa first appeared in the cephalopod ancestor, they may not have been associated with buoyancy. At least two alternatives exist. In most gastropods, a single septum forms to seal off the adult teleoconch from the protoconch after metamorphosis (e.g., Smith 1935). Some living and fossil taxa (see Cook et al. 2015) create additional septa, often in response to wear or loss of the early whorls. These include a few fissurelloideans, some of the tube-like caenogastropod vermetids (e.g., Savazzi 1996), the coralliophiline muricid *Magilus*, a Miocene melongenid, a species of *Melongena* (Vermeij & Raven 2009), and a few turrillids (Andrews 1974; Waite & Allmon 2013). Several freshwater (Simone et al. 2012) and terrestrial (Gude 1905; Pilsbry 1909) heterobranchs also produce septa (see Chapter 3). Septate gastropods are also widely distributed in the fossil

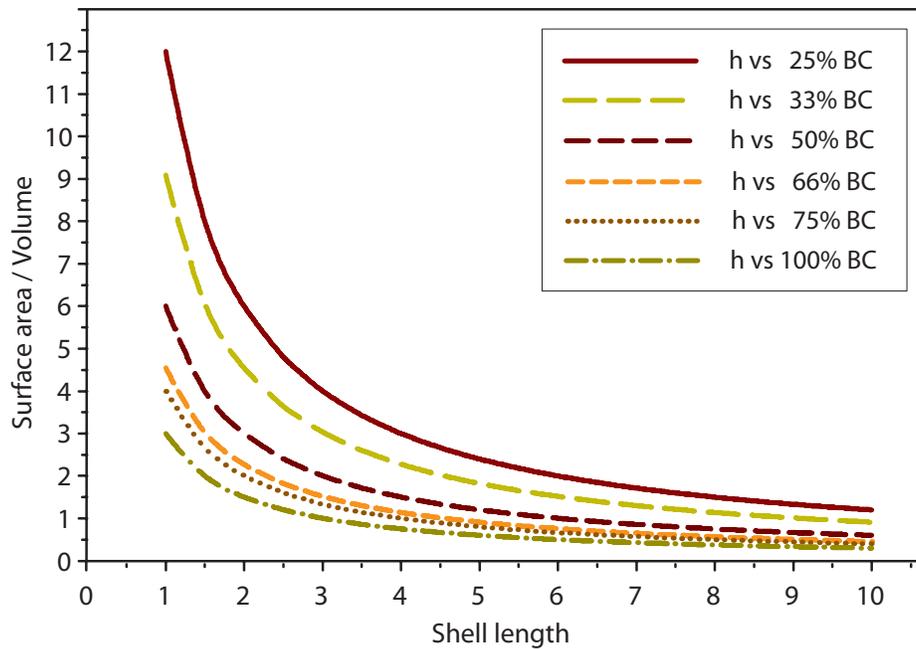


FIGURE 13.14 Relationships between apertural surface area and body volume in conical shells, with variation in body cavity sizes due to the presence of septa. h = height of conical shell, BC = body cavity volume.

record (Yochelson 1971; Gubanov et al. 1995; Cook et al. 2015); Wagner (2002) found septation to be a plesiomorphic character in gastropods.

Another related feature of septa is their ability to increase the surface-area-to-volume ratio in tubular shells. Because only the final body chamber is occupied, the body mass can be substantially reduced relative to the potential respiratory surfaces exposed at the aperture (Figure 13.14). This advantage decreases with increasing shell size but provides a four- to six-fold increase in apertural-area-to-body-volume ratios at smaller sizes, especially for shells where 50% or less of the total volume makes up the body chamber. For example, a conch 4.4 units in height with a body chamber occupying 33% of the total shell volume has the same potential respiratory area to body mass volume as a conch 1.5 units high with the entire shell occupied by the animal. How much these and other factors contributed to the Cambrian appearance of solid septa in the cephalopod ancestor cannot be known, but the functionality of intermediate states needs to be considered and explored.

While the scenario of a monoplacophoran with a tall conic shell developing septa and then a siphuncle is appealing, other anatomical issues accompanying this choice of taxon must be considered, some of which have been obscured by the continued use of hypothetical ancestral cephalopod cartoons (see Chapter 17, Figure 17.45 for examples). Because HAM¹⁰ cartoons typically represent an ancestral gastropod rather than an ancestral mollusc (Lindberg & Ghiselin 2003a), the hypothesised anatomical configurations can become morphological chimeras when crammed into fossil shells. For example,

reconstructions of the cephalopod ancestor generally feature multiple segmented muscles, an anterior mantle cavity, a distinct, free head, and sometimes even gastropod-like cephalic tentacles (Yochelson et al. 1973; Dzik 1981b; Teichert 1988; Kröger 2007) or an operculum (Dzik 1981b), none of which would be found in a monoplacophoran-like ancestor.

While muscle scars are unknown for the putative ancestral taxa *Tannuella*, *Knightoconus*, and *Shelbyoceras*, other ‘hypseloconids’ show a continuous ring-like muscle scar not broken into separate muscle bundles as in monoplacophorans. The head region of monoplacophorans is attached to the anterior region of the shell. Without a detached head region, extension and retraction beyond the anterior region of the shell are impossible, and an anterior dorsal mantle cavity cannot exist. Thus, the proposed simple transition from a tall, septate monoplacophoran to a buoyant, tentaculate cephalopod requires substantial anatomical modifications either preceding, or concordant with, the evolution of the first cephalopod. The detachment of the head alone requires the reorganisation of some of the buccal and mouth musculature and modification of anterior blood sinuses. In addition, jet propulsion is only possible in shelled cephalopods (such as *Nautilus*), with a detached head, with water flowing into the mantle cavity and being forced out through the funnel with piston-like movements of the free head (Chamberlain 1987; Bizikov 2002) (see also Chapter 17).

These constraints and other anatomical ambiguities suggest a reconsideration of ancestral scenarios rather than imaginary monoplacophorans. Tightly coiled taxa may be especially interesting because their shell morphology places potential limits on their internal anatomical arrangements. Tightly coiled conchs suggest motile molluscs capable of extension and retraction of the head-foot complex, requiring detached

¹⁰Hypothetical Ancestral Mollusc – see Chapter 12.

heads, which are found in scaphopods, gastropods, and cephalopods. This character was the basis for a taxon Cephalomacia or headed molluscs (Kopf-Weichthiere) (Keferstein 1862). Here we refer to the condition in which the head region is dorsally attached to the shell as *ligocephalic* and the state where the head region is not attached as *apocephalic* (see Table 13.1). Detached heads are also correlated with ano-pedal flexure which sees the anus displaced ventrally during development (see Chapter 8). Ano-pedal flexure also serves as an exaptation for many features seen in cephalopods.

The detaching of the head was significant in molluscan evolution and presumably occurred independently in different lineages. Both ligocephalic and apocephalic crown groups appear geologically simultaneously in the fossil record, thus providing no suggestion of an ancestral state. Developmentally, the head region forms relatively late in ontogeny; in the veliger phase in gastropods (Buckland-Nicks et al. 2002), during metamorphosis in scaphopods (Wanninger & Haszprunar 2002a), and in middle and late embryos (four–six months) in *Nautilus* (Shigeno et al. 2008), probably indicating that undifferentiated heads are plesiomorphic.

13.3.2.2.7 *Gastropoda*

Coiled gastropod-like conchs are among the earliest small shelly fossils to appear in the Terreneuvian (535 Ma) of the Cambrian (Parkhaev 2008). Most are known as steinkerns and include Pelagiellidae, Aldanellidae, and Khairkhaniidae. All appear near the end of the ‘Nemakit-Daldynian skeletonisation’ event (Maloof et al. 2010) and are contemporary with the helcionelloidans but predate the appearance of the Sachitida. All are multi-coiled, and their overall morphology appears similar to extant gastropod shells. The khairkhaniids are planispiral, dextral, or sinistral, with circular apertures. Aldanellids are typically dextrally coiled with more elliptical apertures and an axial fold sculpture; septa, protoconchs, and muscle scars are known for *Aldanella* (Parkhaev & Karlova 2011). The spiral pelagiellids are low spired and dextral like aldanellids and have elliptical apertures. They also have the greatest variability in whorl expansion rates. These taxa are globally distributed, including Antarctica, Australia, New Zealand, North America, China, Europe, Middle East, Asia, and Siberia, and their distribution and abundance caused Brasier (1989) to suggest a pelagic or epipelagic habit for the group. Many taxa were lost during the End-Botomian extinction event (517 Ma), and none survive after the Dresbachian extinction event (502 Ma).

Pelagiellidae and Aldanellidae were placed in the Orthostrophina in the Paragastropoda by Linsley and Kier (1984) who remarked that the noted Paleozoic gastropod specialist J. Brookes Knight (1952) doubted that they were gastropods. Yochelson (1975) also rejected the molluscan affinities of Aldanellidae, and Linsley and Kier (1984 p. 241) further commented that ‘the long axis of the aperture (*Pelagiella* and *Onychochilus*) is oriented at approximately right angles to elongated apertures of modern gastropods’. The discovery of clusters of chaetae in *Pelagiella* (Thomas et al. 2010; Thomas & Vinther 2012) and *Aldanella* (Dzik & Mazurek

2013) provides further evidence of the non-molluscan affinities of these taxa and led Dzik and Mazurek (2013) to place the Pelagiellida in the Hyolitha (see Section 13.1.1).

The exclusion of both helcionellidans and Pelagiellida from the gastropod fossil record leaves several mimospiridan taxa as the earliest possible gastropods. Wen (1979, 1990) reported representatives of the Onychochilidae and Euomphaliformii from the earliest Cambrian of China. Both were considered hyperstrophic and included in the Paragastropoda by Linsley and Kier (1984). A ‘para-gastropod’ (i.e., ‘resembling’) remains appropriate. Whether these and other early coiled molluscs are gastropods (torted) or not has been the subject of discussion, often accompanied by cartoons of imagined animals (Knight 1952; Horný 1965; Peel 1991c; Parkhaev 2008; Parkhaev & Karlova 2011). Like the cephalopod example above, many of these hypothetical animals are constructed from gastropod parts, including an anterior mantle cavity, a free head, and cephalic tentacles. Typically, the model is rotated in the candidate shell to see if it functions better as a gastropod or monoplacophoran. The assumption of gastropod character states for the ancestral anatomy limits outcomes as character states of monoplacophoran morphology have not been tested. One notable exception is the work of Morris (1991) who used water flow experiments to conclude that some paragastropods were untorted. Consequently, we treat paragastropods as a separate class (see Table 13.10). See the Appendix for gastropod classification.

Paired muscle scars have been argued to provide evidence of torsion (Runnegar 1981; Peel 1991b; Horný 1992). Vendrasco (2012) and others pointed out that torsion, the defining synapomorphy of gastropods (see Chapters 8 and 18), is difficult to convincingly infer without detailed anatomical information, although some general patterns may be deduced from muscle attachment scars and have been used to infer muscle tracts for head and foot retractors (Peel 1991b; Harper & Rollins 2000; Parkhaev 2008). In a few very rare cases, anatomy (such as gut tracts) can be preserved (Horný 1998; Sutton et al. 2006) (see Section 13.3.2.2.7.1).

While torsion remains a difficult character to identify in putative early gastropods, living in closed tubes requires that ano-pedal flexure takes place during ontogeny,¹¹ bringing the larval telotroch (anus) from the apex of the blind tube to the apertural opening (see Chapter 8, Figure 8.33). After this event, the anus would remain in a posterior mantle cavity in juxtaposition with the back of the foot, proximity which may have affected water circulation in and out of the cavity. Torsion brings the anus and mantle cavity to lie dorsally over the detached head in gastropods and would probably enhance water circulation. In cephalopods and scaphopods, the morphological changes related to their unique habitats (water column and burrowing respectively) also provide alternative solutions to a constricted posterior mantle cavity. It is not known if ano-pedal flexure evolved separately in each group or in an ancestor shared by two

¹¹ As noted in Section 13.3.2.2.6, ano-pedal flexure occurs only in apocephalic molluscs.

TABLE 13.10

Classification of Paragastropoda

(Class) **Paragastropoda**

Cambrian (Series 2)–Mississippian (Middle) (513–345 Ma)

Spirally coiled conchs with bulbous protoconchs; coiling geometry includes dextral and sinistral forms, many with moderately high whorl expansion rates.

Withdrawing into the paragastropod shell requires a free head and ano-pedal flexure of the body but not necessarily torsion. Thus, paragastropods as presently constituted are probably paraphyletic and may include both non-torted and torted (i.e., gastropod taxa). This grouping is treated as one of several ‘Paleozoic Basal Taxa that are certainly Gastropoda’ by Bouchet et al. (2017).

(Order) **Mimospirida**

(= Hyperstrophina)

Geological range as in Paragastropoda

Shell hyperstrophic to depressed-orthostrophic, commonly with angulation on the outer part of upper whorl surface marking the possible inhalant or exhalant channel; long axis of aperture converging towards the apex of the depressed spire; shell walls thick, outer layers calcitic, inner layers thick, aragonitic.

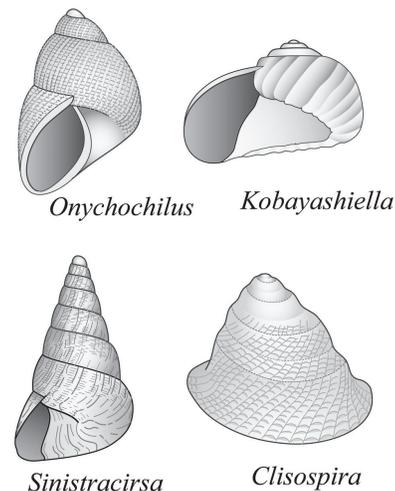
(Superfamily) **Clisospiroidea**

(= Mimospiroidea)

Geological range as in Paragastropoda

Shells hyperstrophic, with highly prosocline tangential apertures. Shell form varying from high spired to moderately low spired. The depressed spire often has a sharp ridge on the upper whorl face.

Families Clisospiridae and Onychochilidae



Examples of Onychochilidae and Clisospiridae (*Clisospira* only).
Redrawn and modified from Knight et al. (1960).

or all three. Waller (1998) considered ano-pedal flexure to be a synapomorphy of gastropods + scaphopods + cephalopods and listed additional possible synapomorphies for the group. He also noted that the pedal retractor muscles of these three taxa all insert in the shell in a single close cluster rather than being dispersed over the shell, although most molecular trees fail to recover such a group (Sigwart & Lindberg 2015).

Frýda et al. (2008a) suggested that the earliest torted gastropods were late Cambrian bellerophontians and euomphali-forms, including *Strepsodiscus* and *Schizopea*. They reached this conclusion primarily based on teleoconch and protoconch morphology of Paleozoic gastropods (Figure 13.15). While teleoconch morphology varies broadly both within and between Paleozoic gastropod taxa just as in living groups, protoconch morphology is much more conservative. While non-gastropod groups have cap-shaped protoconchs, in gastropods the protoconch is more cup-shaped to tubular, with the aperture typically narrower than the length (Ponder & Lindberg 1997). In living taxa, Sasaki (1998) recognised four types: (1) symmetrically uncoiled, (2) paucispiral, (3) multi-spiral, and (4) globular. Globular was restricted to living terrestrial Neritimorpha and will not be considered further here.

A symmetrical, relatively open coiled protoconch with a bulbous initial chamber that slightly constricts with growth is found in Bellerophontia, Macluritida, Perunelomorpha, and Euomphaloidea (Frýda 1999a; Frýda et al. 2006). In patellogastropods the uncoiled protoconch also has a bulbous initial chamber that slightly constricts with growth, but there is no hint of coiling until the teleoconch is formed. A straight to loosely coiled protoconch with a bulbous initial chamber that constricts with growth is a probable synapomorphy of the Eogastropoda (Ponder & Lindberg 1996) (see also Chapter 18). The paucispiral protoconch found in vetigastropods is more tightly coiled (usually less than two whorls), and the chamber continues to enlarge with apertural growth (i.e., there is no constriction). Multispiral protoconchs are found in many caenogastropod groups and are distinguished by having a second growth phase (protoconch II) which results from larval planktotrophy and signals an extended larval life (Jablonski & Lutz 1983). In the ‘cyrtoneritimorphs’, protoconch I is orthoconic and similar to symmetrical open-coiled protoconchs. In addition, protoconch II is distinctive among multispiral groups in having open coiling and in being fish-hook-shaped. This group has been thought to be either ancestral to the Neritimorpha (Frýda et al. 2009) or a separate early

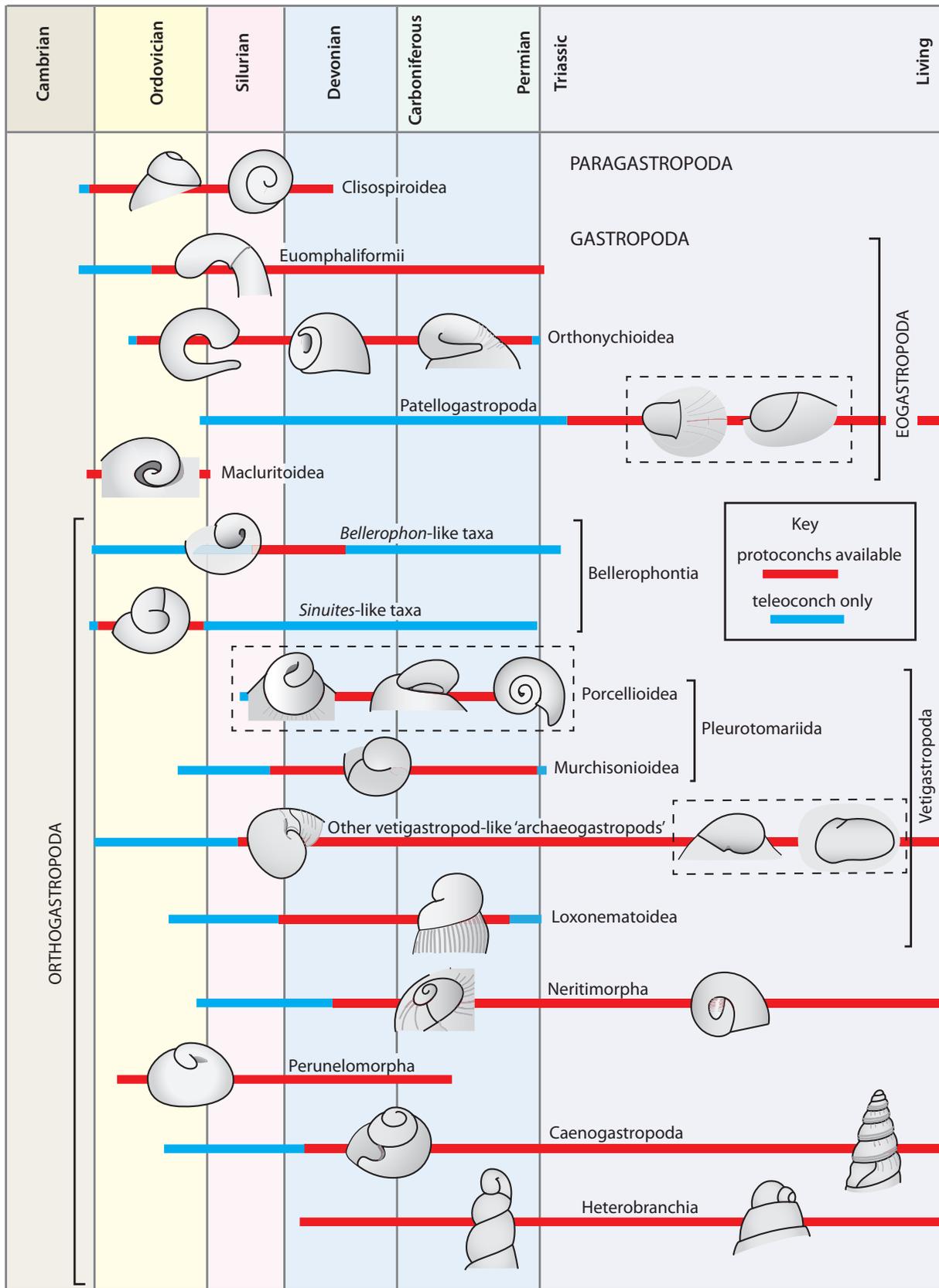


FIGURE 13.15 Paragastropod and gastropod protoconch morphologies through time. Redrawn and modified in part from Frýda J. et al., Paleozoic Gastropoda, pp. 239–270, in Ponder, W.F. and Lindberg, D.R. (eds.), *Phylogeny and Evolution of the Mollusca*, University of California Press, Berkeley, CA, 2008a.

gastropod lineage (Frýda & Heidelberger 2003) (see Section 13.3.5.1.1).

Based on the fossil record, the earliest unambiguous gastropods (Eogastropoda) do not appear until the Miaolingian (Cambrian) (501 Ma) (e.g., *Sinuopea*, *Schizopea*, *Dirhachopea*). Their origins may lie within the paragastropod groups with apertural notches or constrictions suggesting exhalant control of the water flow through the mantle cavity. Other characters probably included a basic docoglossate radular morphology and associated musculature, an openly coiled protoconch, a subradular organ, lateral statocyst position, lack of skeletal support in the ctenidial filaments, and paired foot/head retractors. While there has been little disagreement regarding the gastropod status of the Euomphaliformii, the same cannot be said for the Bellerophontia, and whether all, some, or none of the bellerophontians are torted has been controversial (Wahlman 1985; Peel 1993; Harper & Rollins 2000).

13.3.2.2.7.1 Bellerophontia (= Amphigastropoda)

Bellerophontians first appear in the latest Cambrian (Furongian, 488.3 Ma). They are bilaterally symmetrical (planispiral) shells, sometimes with high whorl expansion rates, and a prominent median sinus, channel, or slit in the outer lip that gives rise to a selenizone. Limited shell structure studies have identified aragonitic shells with complex crossed lamellar microstructure. Nacre, found in many vetigastropod lineages, is not known (MacClintock 1967), although the nature and placement of the apertural flutes and embayments and their placement on the shell are highly suggestive of a bilaterally symmetrical mantle cavity similar to that seen in the vetigastropod Fissurellidae, with exhalant flow control (Lindberg & Ponder 2001) (see also Chapters 4 and 18). In a few taxa this idea is reinforced by the finding of shell structures within the last whorl that divide the internal space into two symmetrical parts (Rohr et al. 2003). Apertures with flutes and channels are also prevalent in both the euomphaliforms and paragastropod onychochilids and continue to crown taxa such as Fissurelloidea and Pleurotomarioidea. In asymmetrically coiled taxa such as Pleurotomarioidea, they are not restricted to the median anterior edge of the aperture as in the bellerophontians but are located more laterally on the aperture. However, a bilaterally symmetrical teleoconch with a median selenizone is present in post-Silurian Porcellidae and is thought to be an apomorphic shell character for that group (Frýda 1997; Frýda et al. 2019). Wagner (2002) provided a phylogenetic analysis of many of these anisostrophically coiled taxa and concluded that the vetigastropod lineage traces its origin to a bellerophontian taxon and that slit-less trochoidean and apogastropod-like morphologies evolve just as frequently as pleurotomarioid-like ones in these stem gastropods.

According to Frýda (1999a), *Bellerophon* has a small, bilaterally symmetrical early shell, indicating a planktotrophic larval stage. There are few other reports of bellerophontian protoconch morphology. Some indicate a protoconch of about half a whorl with an inflated apex region, while others

had two to three complete whorls, and based on these differences Dzik (1981a) suggested that bellerophontians consisted of two groups, a position also held by Frýda (1999c). Wagner (2002) also recognised two groups of bellerophontians based on adult shell characters that coincided with data from the muscle scars, one group having multiple, monoplacophoran-like muscle scars and the other gastropod-like muscle scars. Given the non-correspondence of both muscle scar and protoconch characters, it is not surprising that multiple scenarios for bellerophontian evolution have been proposed (Figure 13.16).

Fossilised intestinal contents have been reported from the Lower Ordovician *Cyrtodiscus nitidus* (Horný 1998). They appear in one or more assumed intestinal loops, some with a terminal 'rectum'. The fossilised gut lies immediately behind the sediment infilling of the last whorl and could indicate that torsion had occurred. The variability of the depth of infilling and its composition caused Horný to caution that the gut was obviously displaced by infilling and did not represent the original position, and therefore any conclusions would be premature. It remains an important find and demonstrates some of the extraordinary detail the fossil record can sometimes provide.

Runnegar (1981) inferred that bellerophontians were untorted but considered them to be a monophyletic group distant from both gastropods and monoplacophorans, and that the gastropod-like columellar muscle scars of some reflected parallelism with gastropods that allowed untorted bellerophontians to retract deep into the shell.

Besides the bilaterally symmetrical muscle scars on the columellar region of the shell, some presumed bellerophontian taxa also have paired central scars over the assumed head region (e.g., *Cyrtolites*, *Sinuilopsis*) (Horný 1965, 1996). These circular scars are far enough back in the body cavity that they would not conflict with the assumption of a detached head and may represent the buccal (i.e., radular) retractor muscle attachment areas seen in other molluscan taxa (Graham 1959, 1964; Lemche & Wingstrand 1959; Wingstrand 1985). The muscle scars of *Cyrtolites nitidus* have been interpreted as monoplacophoran-like because of the three pairs of muscle scars; two pairs are typical of bellerophontian columellar region scars while the third one is centrally located (Horný 1996). While the lateral pairs of muscle scars are typical, the central scars are bifid and unlike either gastropod or monoplacophoran muscle attachment patterns. Alternatively, these channel-like scars in the central area could represent anastomosing vessels and sinuses in the roof of the mantle cavity as seen in patellogastropods and some fissurelloideans (Hickman & Lindberg 1985; Lindberg & Squires 1990). Such an interpretation would also support a torted morphology with anterior auricles.

As noted above, much of the argument as to whether bellerophontians are gastropods or monoplacophorans is based on the muscle scar patterns. There are three hypotheses: (1) bellerophontians are untorted, exogastric monoplacophorans, or (2) are torted, endogastric gastropods, or (3) a mixture of both. See Peel (1991b); Wahlman (1992); Frýda (1999a, 2012); Frýda et al. (2008a) for reviews. The idea that bellerophontians are untorted monoplacophorans is largely based

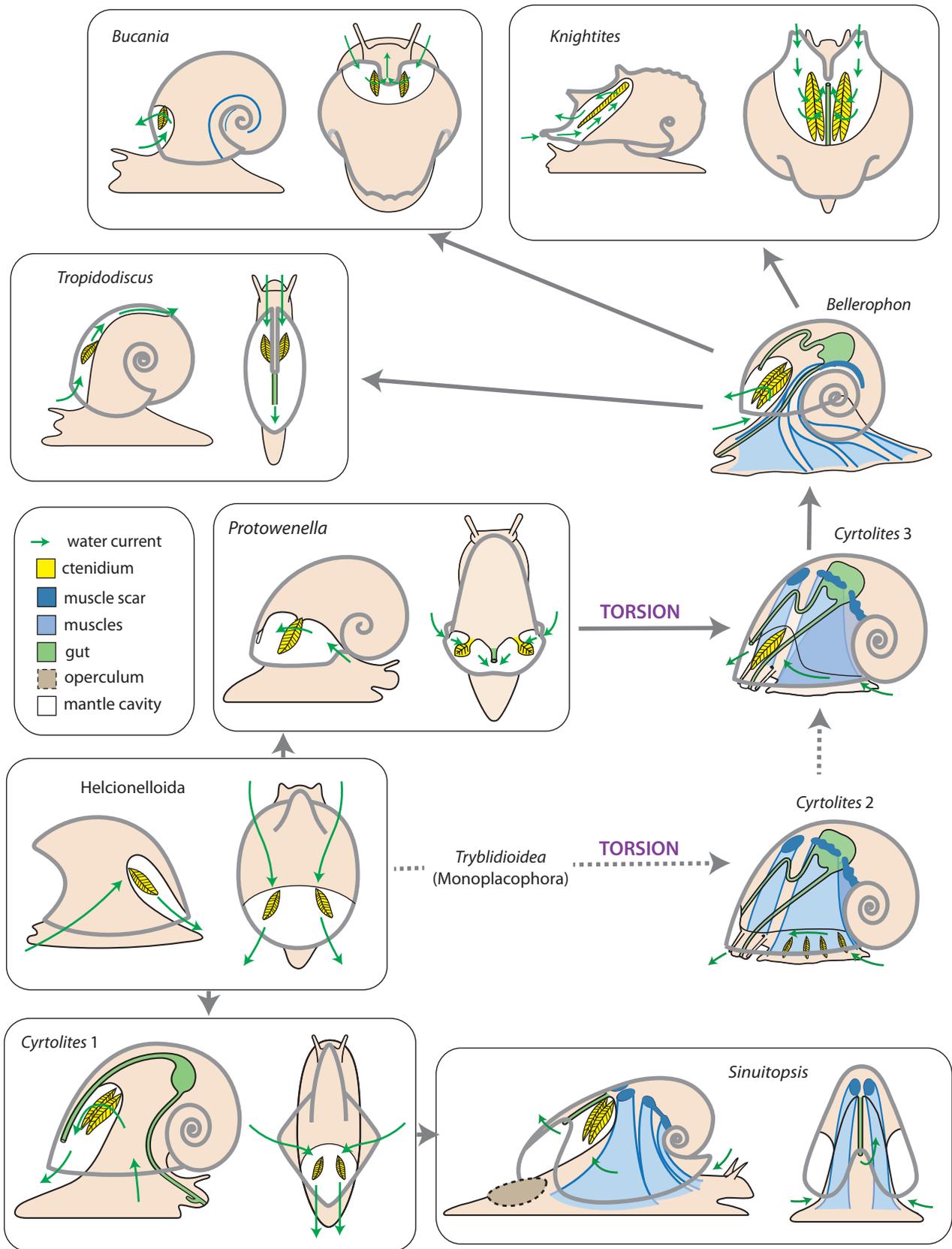


FIGURE 13.16 Some of the alternative reconstructions in the literature of bellerophonian anatomy based on the supposed hypothetical ancestral helcionelloidan. Both torted and untorted models are imagined; for example, see the three different interpretations for *Cyrtolites*. Redrawn and modified from various sources.

on comparisons of the muscle scars of cyrtoneilids with cyrtolimid bellerophonians. The muscle scar patterns are similar (Horný 1965), but the central dorsal muscle scars of the cyrtoneilids are much more anteriorly placed, suggesting an attached head, while the central scars of cyrtolitids are located further back into the last whorl, a position suggestive of a detached head.

In response to the assertion by Wenz (1940) that cyrtoneilid ‘monoplacophorans’ and cyrtolimid bellerophonians were both untorted, Knight (1947) countered that although both shared similar musculature, the similarity was due to convergence and not common ancestry. Knight described bellerophonian muscle scars which fitted his expectations for an anatomically primitive gastropod (such as a vetigastropod). This placement in the Gastropoda was not new but dated from Koninck (1883). Before this, they had been variously thought to be brachiopods, cephalopods, bivalves, or either ‘heteropod’ or ‘pteropod’ gastropods.

Knight (1952) proposed that secondary shell deposits on the ventral parietal surface of the shell indicated their gastropod affinities, although not all workers have agreed with this assessment, and some (e.g., Pojeta & Runnegar 1976; Harper & Rollins 1982) argued there were strong functional arguments to support the non-gastropod hypothesis of Knight (1947). The secondary shell deposits (parietal inductura or callus) are often thick, and similar structures are known only on a few gastropods. It is difficult to imagine how they would function on an untorted coiled snail where the coil was carried over the head. In a torted snail, the parietal inductura would rest on the muscular foot. Frýda and Gutiérrez-Marco (1996) also noted that secondary parietal shell deposits were similar in position, form, and ornamentation in both sinuitid and euphemitid bellerophonians and proposed that their formation indicated that the shell must have been partially enveloped by mantle tissue. More recently, Harper and Rollins (2000) also concluded that bellerophonians are a clade of gastropods.

Within gastropods, Ponder and Lindberg (1997) placed the bellerophonians in the vetigastropods. MacClintock (1967), McLean (1984b), and Golikov and Starobogatov (1975) were even more specific, linking the euphemitid bellerophonians to Fissurellidae based on shell microstructure, external bilateral symmetry, and other shell and anatomical characters. Based in part on the presence of secondary shell deposits on the exterior of the shell, Linsley (1978) and McLean (1984b) reconstructed the bellerophonian genera *Euphemites* and *Retispira*, respectively, with internal shells.

The muscle scar evidence cited for the above competing hypotheses of relationships led to the third hypothesis: that bellerophonians include both monoplacophorans and gastropods, because of parallel evolution of shell form (Yochelson 1967; Wahlman 1992) or because gastropods evolved amid untorted bellerophonians (Knight 1952). The recognition of the differences in head region muscle scars between taxa with attached and detached heads suggests this compromise is no longer necessary (see discussion of cyrtoneilid versus cyrtolimid muscle scars above), and based on this criterion we regard the bellerophonians as stem vetigastropods. The addition of

bellerophonians to the vetigastropods further expands an already impressive range of morphology in the group.

According to Knight et al. (1960), the main groups of what they considered bellerophonians arose in the Upper Cambrian and include: (1) Cyrtoneilidae¹² which continued to the Devonian and had whorls with little overlap and a V-shaped apertural sinus; (2) the Sinuitidae which included tight and looser coiling taxa with a broad, U-shaped sinus, which persisted to the Guadalupian (Permian); and (3) the Bellerophonitidae which had a narrow, median slit and tightly coiled whorls and were extant until the Middle Jurassic (176 Ma). Some bellerophonians had a flared aperture (Bucaniinae); in others (such as *Tremanotus*) the slit is divided into exhalant holes rather like those in abalone shells. Other taxa such as *Chalarostrepsis* and *Temnodiscus* had rapidly expanding whorls, sometimes becoming limpet-like with an internal shelf (as in, for example, *Pterotheca* and *Cycotheca*) similar to that formed in some Neritidae (Neritimorpha) and in the caenogastropod slipper limpets (Calyptraeidae). Sometimes the open coiling is so extreme it is probable these taxa were not very mobile (Rohr et al. 2003).

13.3.2.2.8 Bivalvia

Tiny bivalved molluscs are among the earliest molluscs appearing in the Cambrian record. Both *Fordilla* and *Pojetaia* first appear in the Terreneuvian (529–521 Ma). *Fordilla* is present up to the Botomian extinction event (517 Ma), while *Pojetaia* persists through most of the Miaolingian (~501 Ma). Both taxa are widely distributed with fossil occurrences in North America, China, Greenland, Europe, Siberia, and Turkey; *Pojetaia* also occurs in Australia (Elicki & Gürsu 2009). Other putative Cambrian Miaolingian bivalve taxa include *Tuarangia* of Europe and New Zealand (504–501 Ma) and *Camya* in Europe (509–497 Ma). *Arhouriella* occurs in Epoch 2 of Morocco (521–514 Ma) (Geyer & Streng 1998). While some authors have expressed doubts regarding the bivalve affinities of these latter three taxa (see Runnegar & Pojeta 1992), they are more often accepted as such (e.g., Cope & Kříž 2013). After these first occurrences in the Cambrian Epoch 2 and the Miaolingian, the bivalve fossil record is remarkably depauperate (Cope 2000).

These early bivalves are small, less than 5 mm in length (Cope & Kříž 2013). *Pojetaia* has up to three hinge teeth per valve, similar to some living protobranch taxa, while *Fordilla* has only a single tooth in each valve. Articulated specimens of both *Fordilla* and *Pojetaia* are known, as are their muscle scars, opisthodontic ligament morphology, and shell microstructure, which are generally similar to these features in Devonian nuculoideans (Runnegar & Bentley 1983; Carter 1990; Runnegar & Pojeta 1992; Pojeta 2000). These and other studies have led to general agreement that these taxa represent the earliest stem members of the Bivalvia. Elicki and Gürsu (2009) discussed various Cambrian taxa initially thought to be bivalves and indicated their taxonomic placement.

¹²Treated as Mollusca *incertae sedis* herein.

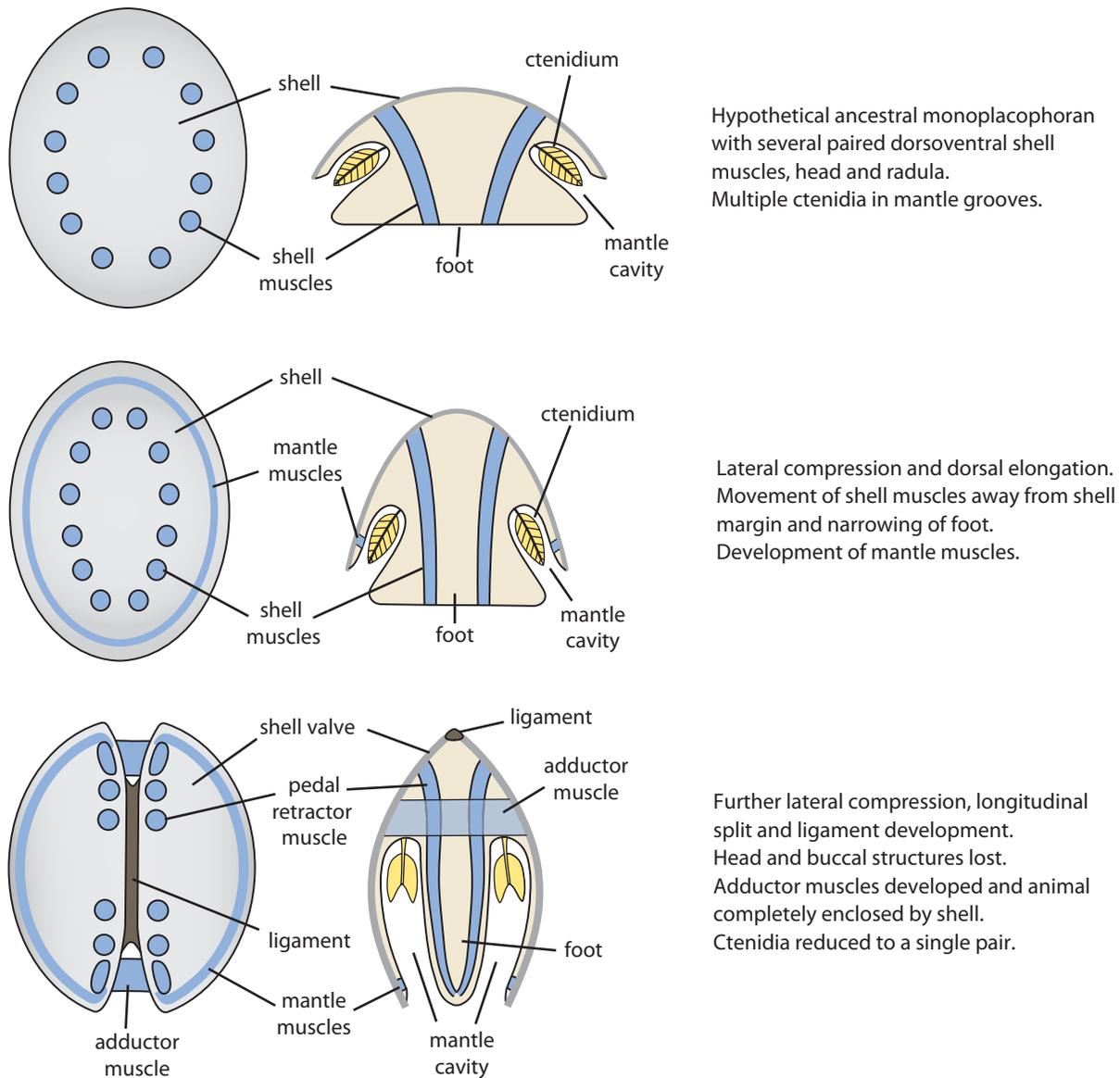
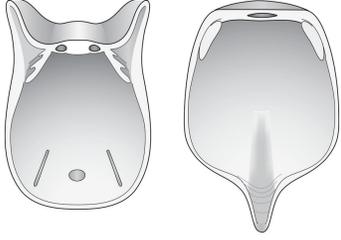


FIGURE 13.17 One scenario of the origin of a bivalve from a monoplacophoran ancestor. Redrawn and modified from various sources.

Geyer and Streng (1998) described two prong-like centrally located hinge teeth in *Arhourietta* in addition to an amphidetic ligament, making it distinct from *Fordilla* and *Pojetaia*. *Tuarangia* is well characterised (e.g., shell and hinge structure, muscle scars, ligament) and based on over 100 specimens, but its placement in the Bivalvia remains controversial. In the original description of *Tuarangia*, MacKinnon (1982) described numerous taxodont-like hinge teeth, an amphidetic ligament, and foliated calcite shell structure, suggesting placement in the Pteriomorphia. Based on similar shell structure, Runnegar and Pojeta (1992) considered *Tuarangia* to be a laterally compressed 'monoplacophoran' closely related to *Pseudomyona*; Wagner (1997) found the same relationship. The latter taxon is often treated as a helcionelloidan, although both Hinz-Schallreuter (1995) and Carter et al. (2000) suggested that *Tuarangia* had a closer affinity with Bivalvia than Monoplacophora; Carter et al. (2011) also treated it as a bivalve.

Owen et al. (1953) proposed that the bivalved shell evolved from a simple, domed univalved shell (such as a helcionelloidan) with a single centre of calcification (Figure 13.17). As also discussed in Chapter 15, the shell became laterally compressed, and the mantle expanded laterally into two lobes, each with its own centre of calcification but narrowly connected dorsally. The shell had a periostracum, and the ostracum (shell) consisted of two layers, with the periostracum extending between the two mantle lobes but with the shell in the middle area 'largely uncalcified'. In this model, the adductor muscles were derived from the cross fusion of mantle muscles with the ligament extending between them on both sides of the umbo of the shell (i.e., an amphidetic ligament). A modification of this theory has bivalves descended from unspecialised ribeiriidan rostroconchs that were posteriorly elongate (Pojeta & Runnegar 1985; Runnegar & Pojeta 1985), with a flexible dorsal margin which evolved into the ligament,

TABLE 13.11
Siphonoconcha, an Extinct Group of Bivalved
Brachiopods that Were Thought to Be a Separate Class
of Molluscs

<p>(Phylum) Brachiopoda Siphonoconcha Cambrian (Series 2) (516–513 Ma) Proposed by Parkhaev (1998) for early Cambrian bivalve- like fossils including <i>Apistoconcha</i>, these are now considered stem brachiopods (Li et al. 2014).</p>	 <p><i>Apistoconcha</i>, redrawn and modified from Parkhaev (1998).</p>
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but both of these models fail to account for the bivalved larval shell that characterises bivalves.

Living molluscan bivalve taxa are often related back to these putative Cambrian ancestors, but it is possible that some Cambrian ‘bivalves’ are separate derivations of the bivalved shell, which is demonstrably homoplastic within the Mollusca, Lophotrochozoa, and Protostomia. ‘Bivalved’ morphologies are present in Brachiopoda, such as the ‘Siphonoconcha’ (see Table 13.11), proposed by Parkhaev (1998) as a class of molluscs for early Cambrian bivalve-like fossils including *Apistoconcha*, but these are now considered stem brachiopods (Li et al. 2014). There are also numerous extinct and living arthropods that are bivalved, including the Cambrian Bradoriida, Phosphatocopida, and Ordovician Leperditicopida (Vannier et al. 2001; Legg et al. 2013) and living Ostracoda, Diplostraca (clam shrimps), and Ascothoracida (parasitic barnacles) (Brusca et al. 2016). Some even have adductor muscles, including the Diplostraca and Ascothoracida. The presence of so many bivalved organisms in the Cambrian fossil record (Briggs 1977; Popov 1992) has contributed to the difficulty in differentiating bivalved molluscs from non-molluscs (Elicki & Gürsu 2009). Bivalve-like forms are also common among the earliest putative molluscs, including the Stenothecoida (see Section 13.3.2.2.10) and the almost bivalve-like *Pseudomyona* and *Eotebenna* (Runnegar & Pojeta 1985; Gubanov et al. 2004) as well as the more recent origin of the bivalve shell in the sacoglossan gastropod group Juliidae (see Chapter 20). Despite these reservations, most workers, and the weight of evidence, suggest that some or perhaps most of the Cambrian taxa usually considered bivalves are indeed members of that class.

Cambrian bivalves are often associated with low-energy, carbonate platforms with reduced sedimentation rates (Cope & Kříž 2013). Both Tevesz and McCall (1979) and Morton (1996) argued these earliest bivalves were epifaunal, while Cope (1996b) considered them only to be able to survive as infauna in fine sediments. Morton (1996) suggested that the earliest bivalves were small, lived on the surface of sediments,

and the inhalant water entered the shell along the anteroventral margins and exited posteriorly. Food collection was done by the foot, and the bivalve was usually oriented on its side. While adult modern nuculoideans are too specialised to be considered models of ancestral bivalves, Morton (1996), following Reid et al. (1992), considered that their surface crawling juveniles would be similar, as these would feed using the foot rather than the derived palp proboscides (see also Chapters 5 and 15).

Over their long history, marine bivalves have experienced periods of elevated extinction and origination, as well as periods of relative evolutionary quiescence. Bivalves exhibit moderate rates of extinction and origination through the Phanerozoic, but these rates decline over time. Prominent peaks in extinction occurred during the late Cambrian, End-Ordovician, late Devonian, End-Permian, End-Triassic, and End-Cretaceous. A similar decline in rates is also observed at broader taxonomic scales (Raup & Sepkoski 1982; Valen 1984; Foote 2003) and may result from losing extinction-prone lineages over time (Roy et al. 2009a). Regions differ little in the severity of extinction experienced by marine bivalves, but they differ markedly in the timing and the processes of recovery (Raup & Jablonski 1993; Jablonski 1998).

The effects of extinction on diversity dynamics have been intensively studied in marine bivalves because of their relatively complete fossil record, the considerable biological variation among taxa, and their diversity and abundance in shallow marine environments today and in the past. These studies have shown that diversity-dependent processes¹³ were most pronounced following mass extinctions but also operated consistently throughout the history of the clade. Geographic range size is the most consistent predictor of bivalve survival, although traits like feeding mode and life habit may also be important but are probably more dependent on the particular context of environmental change. Perhaps surprisingly, bivalve body size is largely decoupled from extinction risk (Harnik & Lockwood 2011).

See Chapter 15 for further information on bivalves and the Appendix for their classification.

13.3.2.2.9 *Rostroconchia*

Rostroconchs look superficially like bivalves but differ in having a single, cap-shaped early shell (Figure 13.18) which subsequently grows laterally, forming extensions or valves on each side of the body. Valve contact along the anterior, ventral, and posterior margins may include a gap or be tightly appressed. In some taxa, the posterior margins may be elongated into a rostrum. Unlike bivalves, there is no dorsal hinge. Instead, some or all of the calcified shell layers are continuous across the dorsal margin. The musculature of bivalves and rostroconchs also differs (Figure 13.20). Rostroconchs are divisible into two groups – the Ribeiriida and Conocardiida. A posteroventrally

¹³ Diversity-dependent processes are outcomes of interspecific competition and are thought to influence the dynamics of both speciation and extinction (Rabosky 2013).

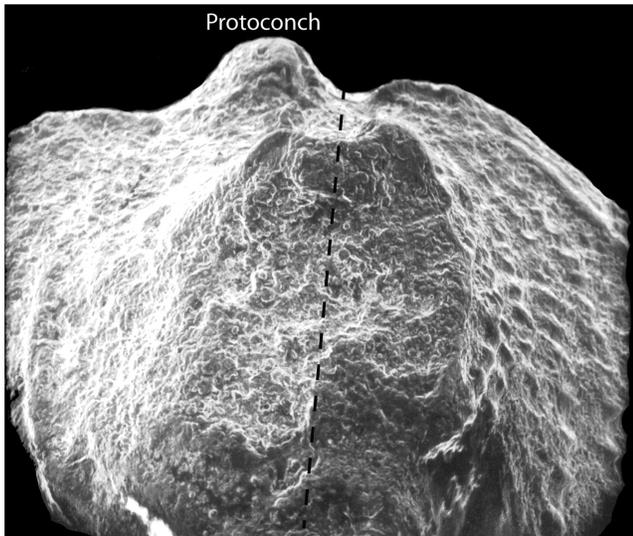


FIGURE 13.18 Posterior view of the protoconch on the left plate of the rostroconch *Pseudoconocardium lanterna* (USNM 209292). Dashed line indicates midline between plates. (Courtesy of B. Runnegar.)

directed transverse shell partition (the *pegma*) extends across the anterior region of most ribeiriidan and conocardioidean rostroconchs (Pojeta & Runnegar 1985) which connects both valves and provides additional muscle attachment points. The *pegma* leaves a characteristic notch in the anterior dorsal margin of internal moulds (Runnegar et al. 1978).

The earliest rostroconchs, if represented by the genus *Watsonella*, are found in Terreneuvian (Cambrian) (~530 Ma) strata in Siberia. The genus *Ribeiria* first appears during the Miaolingian (Cambrian) (498.5 Ma) in Australia. The group diversified during the Lower Ordovician, becoming about equal in abundance to bivalves (Wagner 1997). Members of the Conocardioidea (Figure 13.19) mostly survived the End-Ordovician extinction event although a few ribeirioids continued into the Llandovery (Silurian). All rostroconchs became extinct by the end of the Permian. The classification of rostroconchs is summarised in Table 13.12.

Rostroconch taxa were first described in the early 1800s (Pojeta & Runnegar 1976). While most early workers considered them to be molluscs (typically Bivalvia), they have also been thought to be notostracan crustaceans (Kobayashi 1933). Pojeta et al. (1972) noted the molluscan characters (protoconch, calcified shells with accretionary growth, and prominent muscle scars) of rostroconchs and proposed a new class of bivalved molluscs – the Rostroconchia. Rostroconch shells also reflect the full diversity of molluscan shell structures, with a prismatic outer layer and nacre, foliate, and crossed lamellar layers reported in different taxa (Kouchinsky 1999; Vendrasco et al. 2010). Muscle scar morphology is cyclomyan-like in early rostroconchs such as *Ribeiria* (see Section 13.3.2.2.4). The horseshoe-shaped scar is central on the dorsolateral inner surface of the shell and opens anteriorly; the dorsal portion of the muscle band is the largest and tapers towards the anterior. A single pair

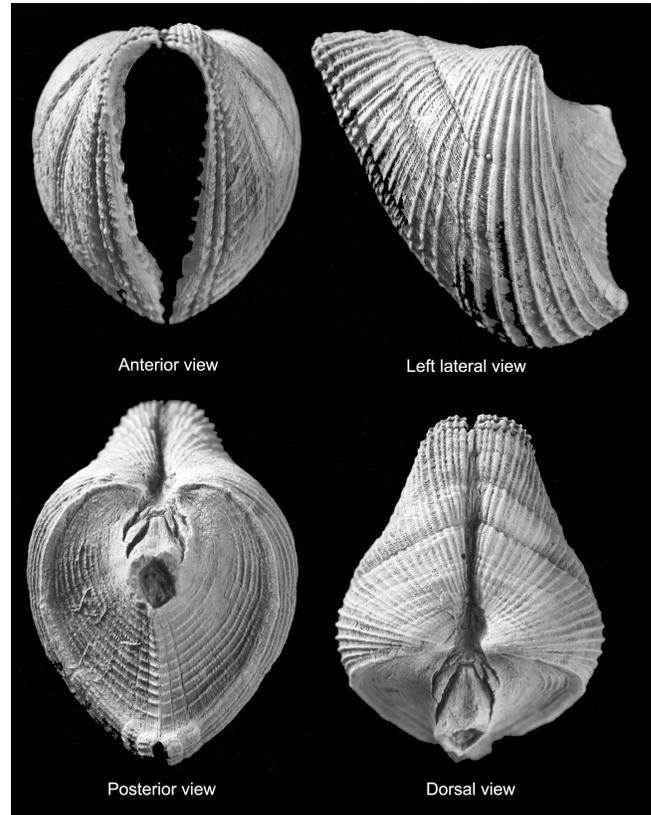


FIGURE 13.19 Four views of the conocardioidean rostroconch *Apotocardium*. (Courtesy of B. Runnegar.)

of muscle attachment areas lies just beyond the anterior ends of the horseshoe-shaped scar on the lateral surface of each plate, and an additional pair of muscle attachment areas occurs on the anterior *pegma* (Pojeta & Runnegar 1976). Muscle scar morphology became more complex in the Conocardioidea, with both band fusion and fragmentation; anterior shell gaps also became more pronounced and ornate. In most Conocardioidea the dorsal margin is also modified by a reduction in the number of shell layers continuous between the shell plates, suggesting greater shell plate flexibility. A small cap-shaped protoconch is found on the left shell plate.

Rostroconchs are thought to have originated within the helcionelloidans (Vendrasco et al. 2011b). Key exaptations within that helcionelloidan lineage were strong lateral compression as seen in the Stenothecidae and Yochelcionellidae, and posterior shell extensions ('trains') which ultimately formed snorkel-like structures, the latter requiring mantle extension, slit-like indentation, and fusion of the mantle tissue. The development of 'snorkels' probably facilitated the formation of the separate, albeit dorsally fused, shell plates in rostroconchs. The supposed earliest rostroconchs (*Watsonella*) lacked anterior *pegma* (Runnegar 1996), and Peel (2004) suggested that ribeirioids and conocardioideans arose from separate helcionelloidan ancestors, but as pointed out by Vendrasco (2012), this scenario would require a stunning amount of morphological convergence. Wagner

TABLE 13.12

Classification of Rostroconchia, an Extinct Class of Molluscs

(Class) **Rostroconchia**

Cambrian (Terreneuvian)–Permian (Lopingian) (530–252 Ma)

Pseudo-bivalves with a single univalved protoconch from which extended two rigidly fixed lateral valves with no functional hinge. The rostrum is prominent.

(Order) **Ribeiriida** (= Ischyriinoida)

Cambrian (Miaolingian)–Silurian (Wenlock) (530–428 Ma)

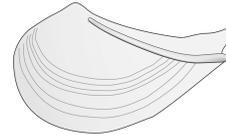
Shell layers continuous across the dorsal margin, with an anterior pegma and dominant posterior growth; anterior and posterior median muscles connected.

(Superfamily) **Ribeiriioidea**

Range as for order.

Ribeiriidans with anterior and posterior shell gapes; lacking radial ornament.

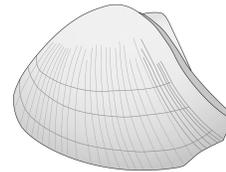
Families Technophoridae and Ribeiriidae

Technophorus, redrawn and modified from Wagner (1997).(Superfamily) **Ischyriinoidea**

Cambrian (Stage 2)–Ordovician (Upper) (530–444 Ma)

Rostroconchs with a dominant anterior growth component resulting in protoconch at centre or posterior on the shell; there are two pegmas and radial ornament.

Family Ischyriiniidae

Ischyrimia, redrawn and modified from Wagner (1997).(Order) **Conocardiida**

Cambrian (Miaolingian)–Permian (Lopingian) (501–252 Ma)

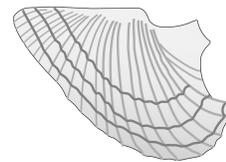
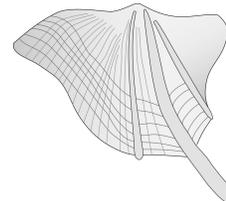
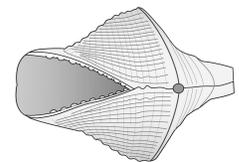
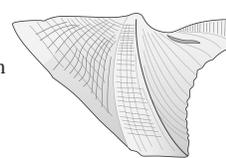
Rostroconchs with external and internal ribs, the latter expressed as marginal denticles on the inside edge of the commissure, and with an anterior gape and dorsal clefts.

(Superfamily) **Conocardiioidea**

Cambrian (Furongian)–Permian (Lopingian) (488–252 Ma)

Anteriorly elongate with shell divided into posterior rostrum, median body, and anterior snout; hood absent.

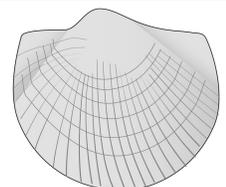
Families Bransoniidae and Conocardiidae

Pseudoconocardium, redrawn and modified from Wagner (1997).*Redstonia*, redrawn and modified from Wagner (1997).*Oxyprora*, redrawn and modified from Mazaev (2015).(Superfamily) **Eopterioidea**

Cambrian (Miaolingian)–Upper Ordovician (501–446 Ma)

Shell posteriorly elongate with anterior or anterior and posterior dorsal clefts; anterior, ventral, and posterior shell gapes continuous; rostrum rudimentary or lacking.

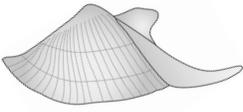
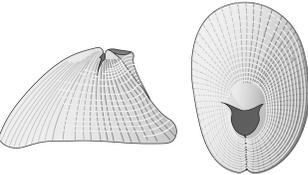
Family Eopteriidae

Eopteria, redrawn and modified from Billings (1865) and Pojeta and Runnegar (1976).

(Continued)

TABLE 13.12 (CONTINUED)

Classification of Rostroconchia, an Extinct Class of Molluscs

<p>(Superfamily) Hippocardioidea Ordovician (Upper)–Permian (Cisuralian) (456–280 Ma) With one or more hoods around the rostral area; hoods consisting of right and left halves. Families Hippocardiidae and Pseudobigaleaidae</p>	<p><i>Hippocardia</i>, redrawn and modified from Wagner (1997).</p> 
<p>(Order) Anetshellida Permian (Cisuralian)–Permian (Guadalupian) (273–268 Ma) Shell cap-shaped, with rostrum positioned posteriorly between the apex and the posterior margin of the aperture; rostral structure separated externally from the apex by a transverse septum. There are multiple paired muscles.</p>	
<p>(Superfamily) Anetshelloidea As for order. Family Anetshellidae</p>	<p><i>Anetshella</i>, redrawn and modified from Mazaev (2012).</p> 

(1997) produced a phylogenetic analysis of rostroconchs which suggested that *Watsonella* and *Heraultipegma* were nested within the *Anabarella*-like helcionelloids and were sister to the earliest bivalves, while the earliest rostroconchs were sister to *Pseudomyona* in a second *Anabarella*-like clade. Perhaps even more surprising is the apparent evolution of a limpet form among the rostroconchs – the Permian Anetshellida (Mazaev 2012).

Pojeta and Runnegar (1976) suggested the possibility of deposit feeding in rostroconchs, and Pojeta (1979) suggested that the loss of rostroconch diversity after the Lower Ordovician was due to competition with bivalves.

Runnegar and Pojeta (1974a) and Pojeta and Runnegar (1976) suggested that rostroconchs gave rise to both bivalves and scaphopods, but more recent studies have discounted these relationships. Based on morphological and molecular data respectively, Waller (1998) and Steiner and Dreyer (2003) argued that scaphopods were more closely related to cephalopods and only distantly related to bivalves. Differences in putative pedal musculature between protobranchs (oblique and dorsoventral retractors) and rostroconchs (cyclomyan-like muscle bands) (Figure 13.20) suggest independent lineages.

13.3.3 ORDOVICIAN

Following the End-Cambrian extinction, the Ordovician Period (Table 13.13 and Figure 13.21) is known as the Great Ordovician Biodiversification Event (GOBE) (Droser & Finnegan 2003; Webby et al. 2004) and has been considered one of the most significant events in the evolutionary history of marine metazoans. During this period, marine familial diversity tripled; the resulting fauna came to dominate and remained relatively unchanged through the rest of the Paleozoic (Droser et al. 1997). The GOBE followed a series of Cambrian–Ordovician extinction events (Sepkoski 1986; Fortey 1989), which saw the extinction of the majority of the Cambrian fauna and, from the

survivors, the rapid diversification of new animals that were primarily suspension feeding and pelagic (Servais et al. 2008, 2010). The GOBE also saw a marked increase in the stacking or tiering of invertebrate taxa above the sediment/water interface and an increase in bioturbation (Ausich & Bottjer 1982; Bottjer & Ausich 1986; Droser & Bottjer 1989) suggesting increased burrowing activity. It is also surmised that there was an increase in water column food resources and increased competition for suspension-feeding space (Signor & Vermeij 1994). Other palaeoecological changes included the appearance of carbonate hardgrounds (Wilson et al. 1992; Taylor & Wilson 2003) and the transition from trilobite- to brachiopod-dominated communities (Droser & Sheehan 1995). Potential drivers of this faunal turnover include tectonic activity which increased provinciality, as well as a warming climate and elevated CO₂ levels which are thought to have increased nutrient levels (Botting & Muir 2008). The Ordovician had some of the highest sea levels seen in the Paleozoic, and there were multiple transgression events. Prior to the End-Ordovician extinctions, both ecological breadth and morphological disparity were similar to the recent fauna (Bambach et al. 2007; Bush & Bambach 2011), although these increases had been neither global nor instantaneous but happened at different times in different regions. Therefore, it is unlikely there was a single cause but rather multiple geological and ecological factors, and their interactions were probably responsible for the diversification (Droser & Finnegan 2003). Just as the GOBE followed the Cambrian–Ordovician extinction event, it ended in another one. The End-Ordovician extinction event was the second largest extinction in the history of metazoans, involving as much as 60% of all marine species (Sepkoski 1981; Sheehan 2001). Global cooling, leading to the glaciation of Gondwana followed by dropping sea level, were probably driving agents for the event.

The Ordovician Period includes the first appearance of scaphopods and impressive diversifications in other molluscan classes, as outlined below.

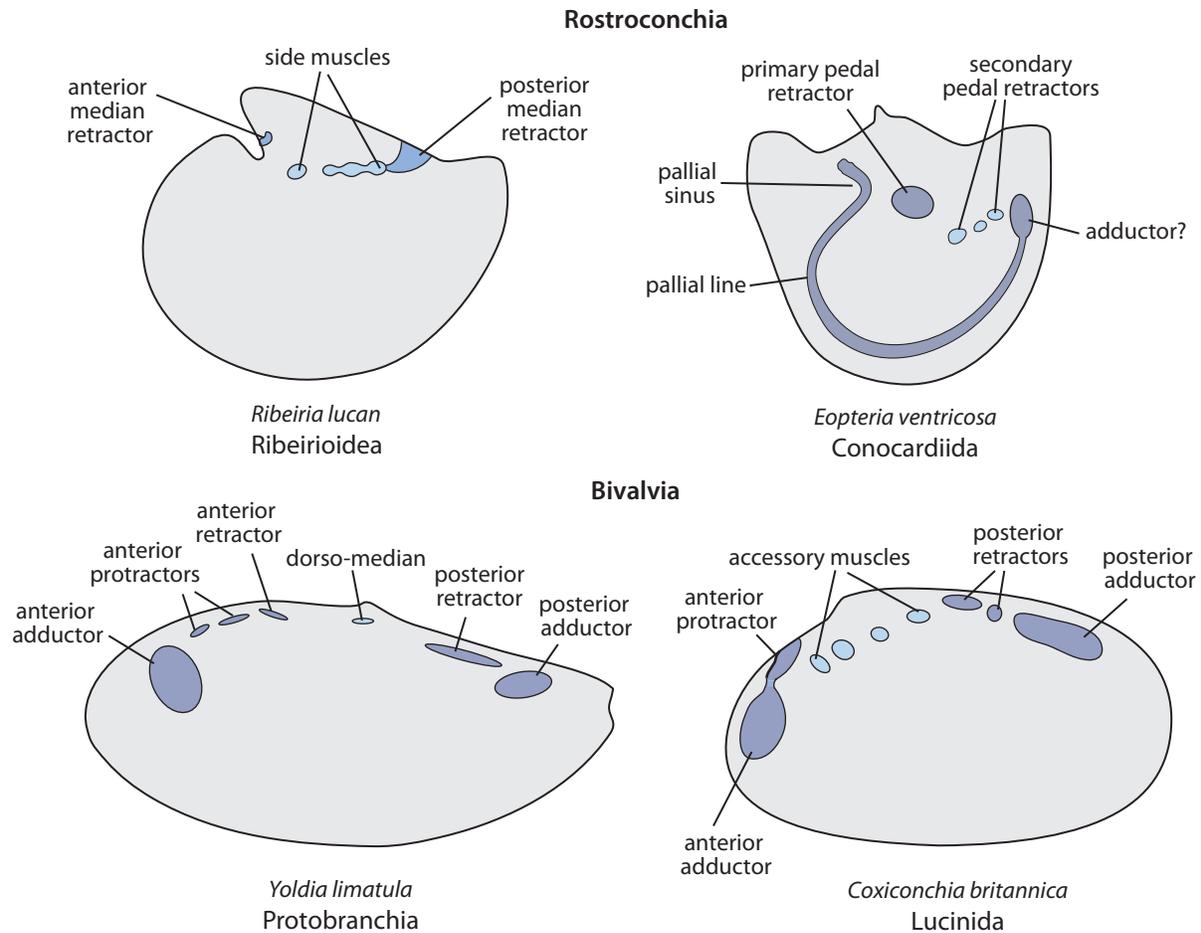


FIGURE 13.20 Comparison of the muscle scar patterns in rostroconchs with two bivalve taxa. Modified from Polechová, M., *Est. J. Earth Sci.*, 64, 84–90, 2015.

TABLE 13.13

Ordovician Chronostratigraphy

System/Period	Series/Epoch	Stage/Age	Beginning
Ordovician	Upper	Hirnantian	445 Ma
		Katian	453 Ma
		Sandbian	458 Ma
	Middle	Darriwilian	467 Ma
		Dapingian	470 Ma
	Lower	Floian	478 Ma
		Tremadocian	485 Ma

Based on International Chronostratigraphy Chart (2018-08) [www.stratigraphy.org/ICSChart/ChronostratChart2018-08.pdf]

13.3.3.1 Taxa

13.3.3.1.1 Gastropoda

Gastropod evolution in the Ordovician shows phases of relative stability separated by periods with high levels of turnover, resulting in diversification (Wagner 1995; Frýda & Rohr 2004). The gastropod groups of the Ordovician are divisible into three major taxa – the Paragastropoda, Eogastropoda,

and Vetigastropoda. Members of the paragastropods include the Onychochilidae and Clisospiridae. They have been considered either hyperstrophic or sinisterly coiled, with a smooth, conical protoconch. The eogastropods include the Euomphaliformii and Macluritoidea. They are characterised by an openly coiled protoconch with a bulbous, initial portion. The open whorl protoconch is shared with the Perunelomorpha which also first appears in the Lower Ordovician (Frýda 2012) and has been considered an early caenogastropod by Frýda and Bandel (1997). The Perunelomorpha differ from the planispiral or low trochispiral shells of the euomphaloides and macluritoideans¹⁴ in having trochispirally rather than planispirally coiled shells. A third group known as the Cyrtoneritimorpha¹⁵ also had a distinctive open coiled protoconch similar to those of the Euomphaloidea, Macluritoidea, Orthonychioidea, and Perunelomorpha. In the cyrtoneritimorph taxa, the initial teleoconch is relatively straight giving the protoconch and initial teleoconch a fishhook-like

¹⁴ Adult *Maclurites* apparently lived more like an epifaunal suspension-feeding bivalve. The apertural morphology underwent significant morphological change probably associated with a switch from grazing when young to suspension feeding (Novack-Gottshall & Burton 2014).

¹⁵ We combine this group with the Orthonychioidea in the Appendix.

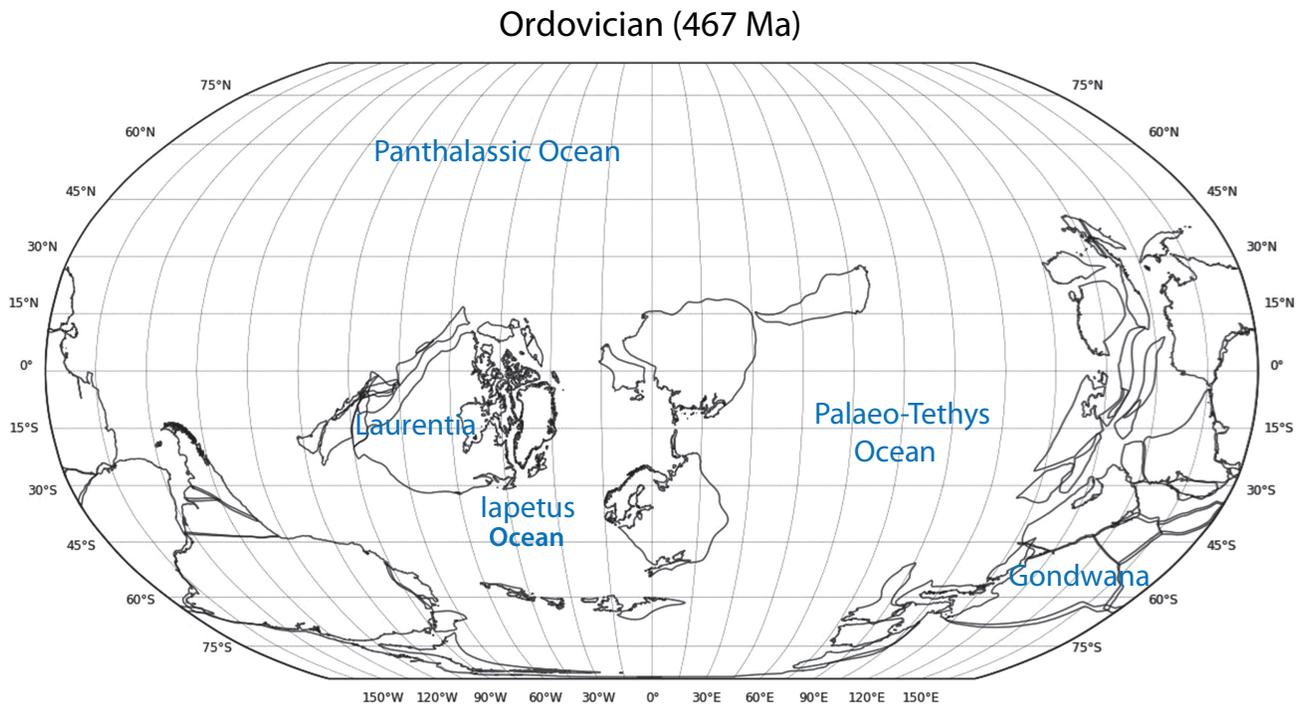


FIGURE 13.21 Palaeogeographic reconstruction of tectonic plate positions during the Middle Ordovician.

appearance (Frýda et al. 2008a). See Appendix and Chapter 18 for further details of stem and crown groups.

Groups such as the euomphaloideans, macluritoideans, and vetigastropods showed the greatest diversity during the first part of the Ordovician. After the drop in both extinction and origination rates in the Darriwilian (467–458 Ma) the euomphaloideans and macluritoideans waned, while the bellerophonians, and especially the vetigastropods (both with and without a selenizone), increased in richness, while the Mimospirina changed little over the period (Frýda & Rohr 2004).

The Ordovician also includes the diversification of the Archinacelloidea – a group of limpet-like shells with a diverse array of muscle patterns, including horseshoe-shaped muscle bands with and without apical muscles, possible buccal muscles, and asymmetric apical attachment areas (Peel & Horný 1999). The Archinacelloidea have been suggested to be the earliest patellogastropods¹⁶ (Yochelson 1988), but there is little evidence for this view except for their limpet morphology. Instead, the diversity of muscle scar patterns within the group suggests that they probably comprise at least three distinct groups – one containing *Archinacellina* and *Archinacellopsis* with cyclomyan-like musculature (horseshoe-shaped muscles with putative buccal muscles), another including *Archinacella* and *Barrandicella* with apical muscles and with or without horseshoe-shaped muscles, and the third containing *Archaeopruga* with its parallel strap-like lateral muscles. Thus, this group appears to include at least three lineages which have independently undergone secondary shell flattening.

After their appearance in the Cambrian, bellerophonian generic diversity remained low until the Middle Ordovician and then reached its zenith in the Upper Ordovician. A move into a wider range of substrata accompanied this diversification, and increased morphological diversification, including secondary flattening (e.g., *Pterotheca*) (Peel 1977; Wahlman 1992).

13.3.3.1.2 *Bivalvia*

It is not known which of the Cambrian bivalve taxa survived the End-Cambrian extinction as there is no evidence of the known lineages having done so. Ordovician originations of new lineages were initially low with those in the Tremadocian having included a limited number of protobranch and autobranch taxa. The protobranchs appeared first, represented by two indeterminate praenuculids, while autobranchs included two cyrtodontoid pteriomorphians (Cyrtodonta, Pharcidoconcha) and the heteroconch *Babinka* (Cope 2004). The Floian saw diversification in the nuculoideans and heteroconchs and the early appearances of the solemyidans, trigoniidans, and afghanodesmatinans. While heteroconch diversity fell in the Upper Ordovician, the remaining taxa showed high origination rates coupled with low extinction rates until the Himantian, when the heterodont anomalodesmatans first appeared (Cope 2004).

13.3.3.1.3 *Rostroconchia*

In contrast to the bivalves, the rostroconchs showed their greatest diversification during the earliest Ordovician (Tremadocian). Most ribeiriidan lineages were extinct by the beginning of the Floian and only a handful of genera (e.g., *Pinnocaris*, *Technophorus*, and possibly *Jinonicella*) continued into the Silurian. The conocardioideans remained at low diversity throughout the Ordovician (Cope 2004).

¹⁶ See Chapter 19 for discussion of patellogastropod origins.

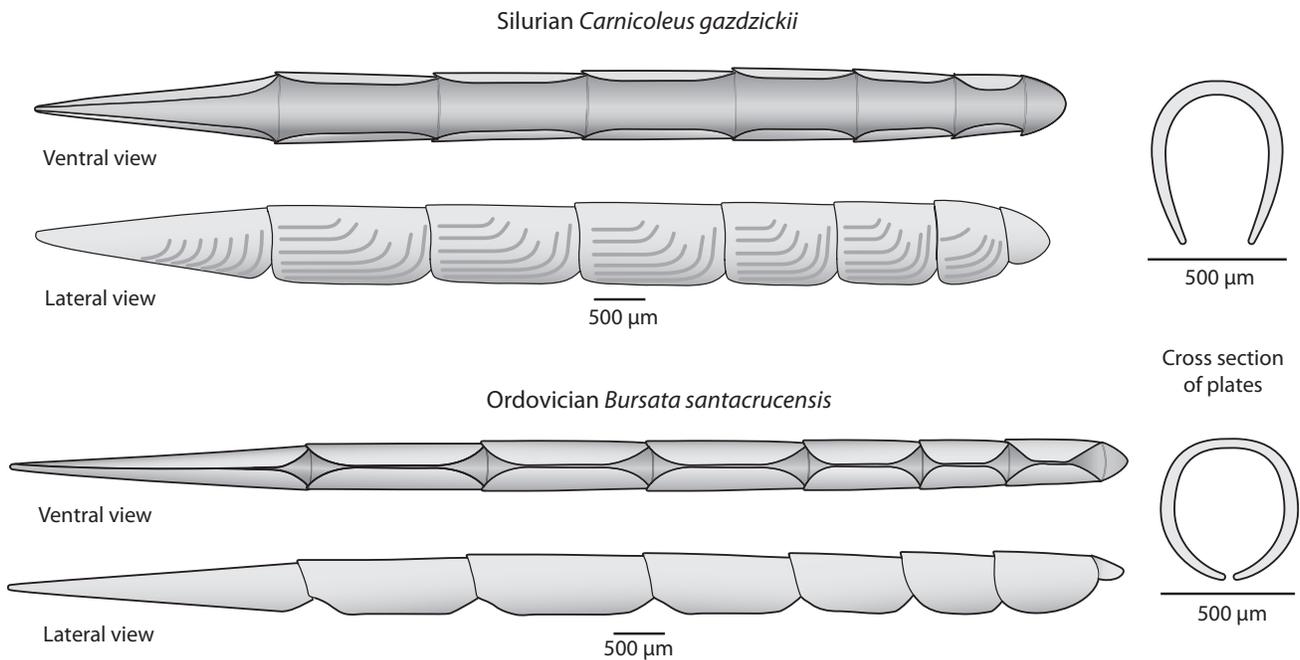


FIGURE 13.22 Reconstruction of shell plates of early Paleozoic solenocaridid Septemchitonina. Redrawn and modified from Dzik, *Acta Palaeont. Pol.*, 39, 247–313, 1994.

13.3.3.1.4 Cephalopoda

The Ordovician Period included the largest radiation of nautiliforms in the fossil record, especially during the Floian (Frey et al. 2004). This radiation included the greatest diversification in morphology ever seen in cephalopods (Teichert 1988), much of which has been linked to buoyancy control (Crick 1988) (see Chapter 17). While globally distributed in a diversity of habitats, nautiliforms were most abundant and reached their maximum diversity and size on shallow marine carbonate platforms deposited at low latitudes in warm climatic conditions (Flower 1976b). The most important Ordovician group in diversity and abundance was the Orthoceratida. They are considered the ancestors of the Bactritida, from which the ammonites and coleoids probably arose. Another Ordovician group, the Endoceratida, included large nautiliforms such as *Endoceras* and *Cameroeras* (>10 m long), although the majority of Ordovician nautiliforms were much smaller (<1 m). The first major extinction of nautiliforms occurred at the end of the Ordovician Period (Himantian), resulting in the extinction of numerous taxa including the Ellesmeroceratida which originated in the Cambrian (see Chapter 17 for further discussion).

13.3.3.1.5 Polyplacophora

Following the first occurrence of *Matthevia* and *Listrochiton* in the Cambrian, the Ordovician saw further diversification of the paleoloricates (Cherns 2004; Cherns et al. 2004). In the Lower Ordovician, this diversification was primarily in the Mattheviidae and Preacanthochitonidae, with additional originations in the Gotlandochitonidae and Helminthochitonidae (Hoare 2000). Originations and extinction rates were low for the remaining Ordovician with additions to the septemchitonids and alastegiids. Only three polyplacophoran lineages

survived the End-Ordovician extinction – the mattheviid genera *Chelodes*, *Gotlandochiton*, and *Helminthochiton*.

The Ordovician also saw the first occurrence of possible footless chitons (Figure 13.22). Based on laterally compressed chiton valves from the Ordovician of Poland and closed valves in the Silurian, Dzik (1994) hypothesised that there was a trend in foot reduction in the septemchitonid paleoloricates. Sigwart and Sutton (2007a) provided more evidence for the origin of this morphology after examining multiple body fossils of ‘*Helminthochiton*’ *thraivensis* from the Upper Ordovician of Scotland. They concluded that the ventral spiculate girdle of this paleoloricate was so expansive there was not enough space for a typically polyplacophoran foot; Sutton and Sigwart (2012) reached a similar conclusion. A paleoloricate genus *Echinochiton*, with large, hollow spines radiating outward from the eight shell plates, also first appeared in the Ordovician.

Lower Ordovician polyplacophoran radiations were centred on the low-latitude Laurentian margin (Cherns et al. 2004), while *Chelodes* was associated with the Gondwanan margin (Runnegar et al. 1979). Palaeoenvironments include stromatolitic, shallow marine carbonates and dolomites (Runnegar et al. 1979; Stinchcomb & Darrough 1995).

13.3.3.1.6 Scaphopoda

The first occurrence of scaphopods in the fossil record is controversial, due largely to their simple and conservative morphology (Yochelson 2004). Proposed first occurrences include the Ordovician (Pojeta & Runnegar 1979), Silurian (Rohr et al. 2006), Devonian (Haas 1972), and even as late as the Mississippian (Yochelson 1978). Peel (2006) argued that scaphopods were probably derived from a helcionelloidan or conocardioidean rostroconch lineage in the late Paleozoic.

Given their occurrence in soft sediments that permit burrowing, their rarity in the fossil record is surprising. The scaphopod fossil record improves after the Mississippian, but it is only in Cenozoic deposits that occasional concentrations are found. The early Paleozoic records represent the Dentaliida, the first occurrence of the Gadilida being in the Permian (Artinskian). Here we regard the report of Pojeta and Runnegar (1979) of *Rhytidentalium* from the Middle Ordovician as representing the first record of a scaphopod. We base this on the overall morphological similarity and range of variation of the Ordovician, Silurian, and Devonian specimens with the undisputed Carboniferous taxa and the origination times of putative sister taxa (gastropods and cephalopods) (Sigwart & Lindberg 2015). This scenario substantially reduces the need for ‘ghost’ taxa spanning 137 Ma (Norell 1992; Cavin & Forey 2007). Scaphopod shell microstructure has been observed in Devonian specimens (Haas 1972). See Chapter 16 and Section 13.3.2.2.3.1.2 for discussion of scaphopodisation.

13.3.3.1.7 *Tentaculita* (= ‘*Tentaculites*’)

Tentaculitans are small (1–30 mm in length), cone-shaped, ringed fossils which first appear in the Lower Ordovician. They reached their greatest diversity and distribution during the Devonian but did not survive the Upper Devonian mass extinction. They were first noted in the late 1700s and formally described in 1820 as crinoid fragments (Bouček 1964). Subsequently, they have been thought to be related to Annelida (Bouček 1964); Bryozoa (Dzik 1993); Phoronida (Vinn & Mutvei 2005); Brachiopoda (Towe 1978); Mollusca – pteropods (Shrock & Twenhofel 1953) or cephalopods (Blind 1969); Cnidaria (Herringshaw et al. 2007); and Hyolitha (Lyashenko 1955). Ljashenko (1957), Lardeux (1969), and Drapatz (2010) suggested that they are an extinct class of Mollusca, but molluscan affinities are unlikely, given their shell morphology and microstructure.

The conical shells are divisible into two regions. The proximal or juvenile region includes the earliest part of the shell and typically differs in sculpture from the distal or adult region of the shell. The proximal section begins with the initial chamber or bulb, which has two distinctive morphologies. Two main groups are recognised (Table 13.14). In the Dacryoconarida an initial bulb-shaped chamber transforms into the proximal section with a slight constriction, while in the Chonioconarida an open hollow tube extends posteriorly from the bulb; in some reconstructions, an apical spine closes and extends from this tube. Shell sculpture includes concentric growth lines, longitudinal ribs, and rings, separately or in combination. Septa are present in the juvenile region of some taxa.

The shell structure of tentaculitans comprises two main layers – an outer secreted by accretion at the aperture and a secondary, inner layer which lines the chambers and forms the septa. Both layers contain multiple sub-layers, and the outer shell layer is penetrated by numerous pores. The inner layer is more compact and non-porous. TEM studies of fractured shells have revealed a calcitic microstructure of ridges and grooves and a cross-bladed fabric otherwise known only from articulate brachiopods (Towe 1978). Vinn and Mutvei

(2009) suggested that tentaculitans, along with problematic tubeworm groups such as the cornulitids, microconchids, trypanoporids, *Anticalyptraea*, and *Tymbochoos*, form a monophyletic group based on their homologous shell microstructure. More recently, Vinn and Zatoń (2012), based on a phenetic analysis, concluded that the tentaculitans were more closely related to the Brachiozoa.

Tentaculite habitats have been reconstructed as both benthic and pelagic. Generally, the heavier shelled taxa (Chonioconarida) are thought to have been benthic but gave rise to the possibly pelagic Dacryoconarida by becoming miniaturised, reducing the shell layers and losing septa. The geological occurrence of these two groups also supports a pelagic habit for this latter group. Organic remains of tentaculitans have been recovered from samples (Filipiak & Jarzynka 2009; Devaere et al. 2014) and may prove important in resolving their phylogenetic relationships. We concur with Yochelson (2000) and others who have argued against their inclusion in the Mollusca and suspect that their affinities are with other shell-forming lophotrochozoans such as the brachiozoans.

13.3.4 SILURIAN

During the Silurian (Table 13.15 and Figure 13.23) the climate stabilised and warmed after the chaotic time of the Himantian glaciation, and the melting glaciers produced a substantial rise in sea level. The transgressive oceans of the Silurian combined with the relatively flat palaeocontinents produced a rich diversity of environmental settings. Coral reefs appeared, as did several major evolutionary events in fish, including the radiation of jawless fish and the diversification of freshwater and jawed fish. It is also during the Silurian that the first evidence of a major diversification of terrestrial life is preserved, including vascular plants and arthropods. These features suggest increased productivity associated with the invasion of terrestrial habitats by plants, thereby making possible the first terrestrially derived eutrophication of the near-shore marine realm. The appearance of armoured fish and the existence of large arthropod predators such as the eurypterids during this period are an indication of increased predation pressure (Signor & Brett 1984; Vermeij 1987).

Molluscs responded to these changing factors in the Silurian in multiple ways but overall were much more stable than in earlier periods. In the cephalopods, the Endoceratida, which contained the giant *Endoceras* and *Cameroceras*, failed to survive the Silurian while other nautiliform orders such as the Tarphyceratida, Discosorida, Oncoceratida, and Orthoceratida slowly decreased in size and diversity although they remained one of the dominant predatory animals in the oceans despite increased competition from jawed fish (Placodermi and Acanthodii) which appeared in the Llandovery (Silurian).

13.3.4.1 Taxa

13.3.4.1.1 *Bivalvia*

Silurian bivalves exhibit little provincialism, with their distributions often cosmopolitan (Cope & Kříž 2013). This pattern was thought to be due to their relatively long pelagic larval life

TABLE 13.14**Classification of Tentaculita – a Group Sometimes Included in Mollusca****Brachiozoa**

Brachiozoa includes the brachiopods and phoronids, and the tentaculitans were placed there based on shell structure and morphology, especially the shared micro-lamellar layers, cross-bladed fabric, and pseudopunctae (Vinn & Zatoň 2012).

(Class) Tentaculita

(= Cricoconarida, 'Tentaculites')

Cambrian (Series 2)–Jurassic (Upper) (513–235 Ma)

Conical fossils with simple, circular apertures; the apex is pointed to bulbous. External sculpture typically composed of strong annulations; conch calcitic with three layers and brachiopod-like microstructure. The 'tubeworms' Microconchida and Cornulitida are sometimes included in Tentaculita.

(Order) Chonioconarida

Silurian (Ludlow)–Devonian (Upper) (426–371 Ma)

Thin conchs with several septa closing off large, cone-shaped embryonic chamber. Includes the genus *Tentaculites*.

Homoctenus, redrawn and modified from Wei et al. (2012) and Bouček (1964).

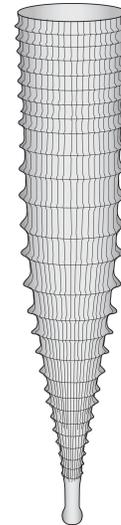
**(Order) Dacryoconarida**

Silurian (Llandovery)–Mississippian (Lower)

(444–354 Ma)

Thin conchs without septa; embryonic chamber bulbous; some taxa lack strong external sculpture.

Nowakia, redrawn and modified from Bouček (1964).



and the relatively small distances between the basins, islands, and continents (Kříž 2011). Silurian bivalves are also characterised by the evolution of numerous new free-burrowing and epibyssate forms from Ordovician infaunal byssate ones. The percentage of non-burrowing attached genera increased rapidly during the Silurian from 6.7% in the Llandovery to 10.6% in the Wenlock, 19.4% in the Ludlow and 24.5% in the Pridoli (Kříž 1984). The Silurian also includes the origin of *Archanodon*, the oldest known genus of freshwater bivalves (Chamberlain et al. 2002), and the discovery of the bivalves

at the oldest known methane seep which hosted a metazoan fauna (Jakubowicz et al. 2017) (see also Chapter 15).

13.3.4.1.2 Gastropoda

Silurian gastropod evolution was not as subdued as in cephalopods and bivalves, and the period was one of increasing diversity in most gastropod clades (Frýda et al. 2008a). While the majority of Silurian gastropods represent bellerophontians, euomphaliforms, murchisonioideans, and porcellioideans, other groups such as the loxonematoideans, perunelomorphs,

and cyrtoneeritiforms also diversified (Frýda et al. 2008a), some possibly representing early crown lineages. For example, some Silurian gastropod genera (*Bucanospira*, *Codonocheilus*, *Craspedostoma*, *Spirina*, *Temnospira*, *Auriptygma*, *Kjerulfonema*, *Morania* and *Stylonema*) include some possible early caenogastropods (Sepkoski et al. 2002). However, the characteristic protoconch II is only present in *Auriptygma* (J. Frýda, pers. comm., 2018). While close-coiled vetigastropod-like protoconchs first occur in the Silurian, definitive crown caenogastropod protoconch morphology is not found until the Devonian (see Section 13.3.5.1.1) (Frýda et al. 2008a).

By the Pridoli (Silurian) two stem pleurotomarioid clades (Eotomarioidea and Trochonematoidea) were present, containing the bulk of vetigastropod morphologies and

representing the first major diversification of slit-bearing gastropods (Wagner 1999). Overall spire height also increased, especially in the loxonematoidean and subulitoidean groups (Frýda et al. 2008a). The earliest unequivocal fossil record for so-called cyrtoneeritiforms is latest Silurian–Devonian (Frýda et al. 2008a), but the putative relationship of this group to later stem and crown neritimorphs (Nützel et al. 2007; Frýda et al. 2009) is not recognised here (see Section 13.3.5.1.1, Chapter 18, and Appendix).

While the actual origin of crown caenogastropod, heterobranch, and neritimorph groups probably occurred later, there is little doubt that the Silurian set the stage for their appearance. The work of Bandel, Frýda, and Nützel has emphasised the evolution of egg size and larval characteristics as determined from protoconch morphology, and the origin of these three taxa also corresponds to the apparent origin of planktotrophic larvae (Jablonski & Lutz 1983; Ponder & Lindberg 1997; Hickman 1999; Frýda 2012; Nützel 2014). Based on the developmental timing of cell fates in gastropod embryos, Lindberg and Guralnick (2003) proposed that nutrient increases in marine systems by a diversifying terrestrial flora, along with changing predation pressure of the Silurian, were possible drivers of the reorganisation of the gastropod developmental pathway that resulted in the evolution of feeding larvae. These are some of the same factors suggested by Vermeij (1995) to correlate with other Phanerozoic macroevolutionary changes.

TABLE 13.15
Silurian Chronostratigraphy

System/Period	Series/Epoch	Stage/Age	Beginning
Silurian	Pridoli		423 Ma
	Ludlow	Ludfordian	426 Ma
		Gorstian	427 Ma
		Homerian	430 Ma
	Wenlock	Sheinwoodian	433 Ma
		Telychian	439 Ma
	Llandovery	Aeronian	441 Ma
		Rhuddanian	444 Ma

Based on International Chronostratigraphy Chart (2018-08) [www.stratigraphy.org/ICSChart/ChronostratChart2018-08.pdf]

13.3.4.1.3 Monoplacophora

A new monoplacophoran morphology appeared in the Silurian. Since their first appearance in the latest Cambrian the monoplacophoran tryblidioids (*Pilina*) had been

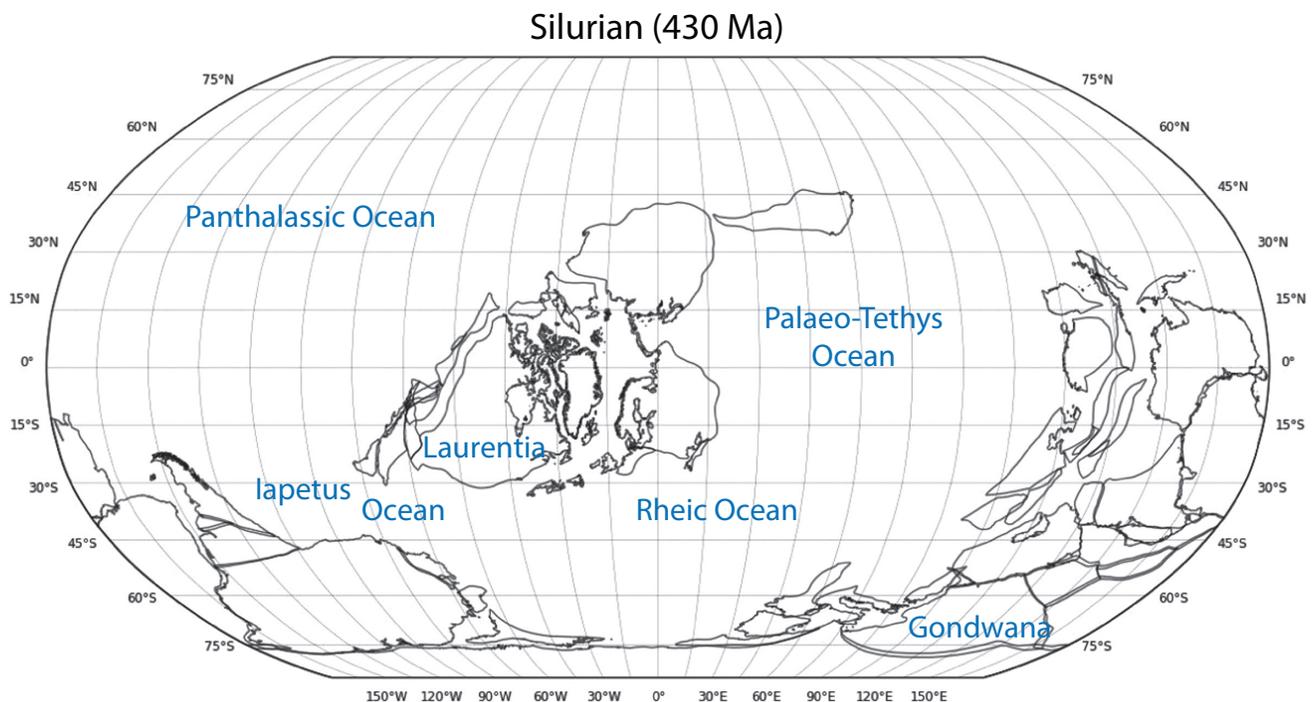


FIGURE 13.23 Palaeogeographic reconstruction of tectonic plate positions during the Silurian (Wenlock).

relatively thin and small, but in the Silurian of Götland, Sweden, they achieved what became the iconic monoplacophoran morphology. Described by Lindström (1884), these large shells (around 50 mm long) had strong growth phases present in the shell and on the outer surface. These relatively massive shells contrasted markedly with early monoplacophorans, but their muscle scars were identical to Cambrian *Pilina*, having paired oblique and dorsoventral retractors and a complex set of buccal muscles.

The Silurian also produced the Drahomiridae with seven sets of dorsal paired muscle scars and several large and small buccal muscle scars. Both adults and juveniles have been reported *in situ* on fragments of orthoconic nautiliform shells (Horný 2005).

13.3.4.1.4 *Aplacophora and Polyplacophora*

The Silurian represents the recovery of the ‘placophorans’ after the End-Ordovician extinction event as well as the first appearance of possible transitional fossils that bridge class-level morphology within molluscs. The first putative aplacophoran fossil, *Acaenoplax hayae* (Figure 13.24), was described from the Herefordshire Lagerstätte of England (425 Ma) (Sutton et al. 2001a). This vermiform fossil was interpreted as an aplacophoran with 18 rows of spicules interspersed among seven dorsal plates and a single posterior ventral plate. Thus, this taxon exhibits characters of both polyplacophoran (dorsal shell plates and spicules) and aplacophoran (spicules and a vermiform body without a foot). Steiner and Salvini-Plawen (2001) pointed out morphological inconsistencies with extant molluscan morphology and suggested *Acaenoplax hayae* was more likely a semi-sessile annelid and noted an overall similarity with some living tube-dwelling annelids. Sutton et al. (2001b) responded, noting that while the ventral surface of *A. hayae* might appear somewhat annelid-like, the aragonitic shell plates, spicules, serial rather than segmented organisation, and the posterior cavity indicated molluscan and not annelid affinities. In a subsequent paper, Sutton et al. (2004) documented the molluscan affinities of *A. hayae*. An additional putative molluscan character is the semi-circular curvature of many of the illustrated fossil remains. This curvature in Solenogastres, Polyplacophora, and Caudofoveata is caused because the longitudinal muscles contract to bend the animal into a semi-circle at death (Scheltema 1992). In chitons, these same muscles enable them to roll up into a ball when dislodged. While annelid worms also have longitudinal muscles,

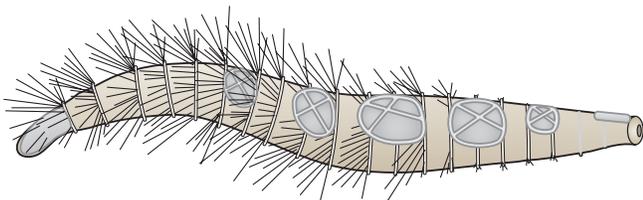


FIGURE 13.24 *Acaenoplax hayae*, which has been suggested to be a possible early aplacophoran. Redrawn and modified from Sutton, M.D. et al., *Nature*, 414, 602, 2001a.

they do not take on this characteristic form in death (Briggs & Kear 1993).

While the mosaic of ‘placophoran’ characters in *Acaenoplax* is confusing from a neontological perspective, they are fascinating from an evolutionary one. Further study of the posterior ‘mantle cavity’ has increased the uniqueness of this animal and provides additional characters for consideration. Dean et al. (2015) reconstructed the posterior mantle cavity of two new specimens of *A. hayae*. Using tomographic analysis of sequential thin sections through the fossils, they reconstructed a mantle cavity unlike that found in any known molluscan taxon (see also Steiner & Salvini-Plawen 2001). Based on Sutton et al. (2001a), the original description of the *Acaenoplax* mantle cavity was unusual because it is underlain by a ventral plate which, with the dorsal plate, encloses the posterior portion of the animal (Dean et al. 2015). These new reconstructions show the putative mantle cavity surrounded by three bilaterally symmetrical structures, which include three pairs of papillate lobes, three pairs of subspheroidal projections above each lobe, and a medial pair of lobes without papillate surfaces. Lastly, there is a single dorsomedial lobe above the central lobes. These lobes extend beyond the edges of the dorsal and ventral plates, and none of these structures can be satisfactorily homologised with those in the mantle cavities of any ‘placophoran’ or other molluscan group. Thus the molluscan affinities of this strange armoured Silurian ‘worm’ remain uncertain (e.g., Vinther & Nielsen 2005; Todt et al. 2008a).

Sutton et al. (2012) described a second ‘placophoran’, *Kulindroplax perissokomos* (Figure 13.25), from the Wenlock Series Lagerstätte fauna of England (also about 425 Ma). *K. perissokomos* has seven valves which resemble those of paleoloricates, and, as in that group, the valves do not articulate on each other, and the head valve is the smallest. Densely packed spicules are present along the broad lateral surface of the body below the plates. Neither a foot nor radula appears to be present; however, there appears to be a posterior mantle cavity extending under the final two valves with four ‘gill elements’, which are neither paired nor resemble ctenidia or caudofoveate respiratory mantle cavity folds. Sutton et al. (2012) consider *K. perissokomos* to be a stem aplacophoran; however, there is little to support this allocation other than the worm-like body plan and lack of a foot, although both Ordovician and Silurian stem polyplacophorans (paleoloricates) are also rather worm-like but not footless (Dzik 1994; Sutton & Sigwart 2012). Whether *K.*

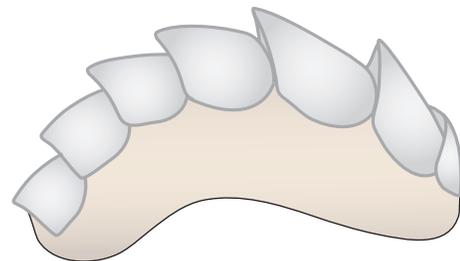


FIGURE 13.25 *Kulindroplax perissokomos*, an apparently footless ‘placophoran’ from the Silurian of England. Drawn from reconstruction in Sutton, M.D. et al., *Nature*, 490, 94–97, 2012.

perissokomos is an aplacophoran or a highly divergent polyplacophoran is uncertain as the boundaries between these two groups appear to be blurred. More of these remarkable finds are needed to resolve the distinction between aplacophorans and possible ‘footless’ chitons.

Silurian ‘placophorans’ were also documented by Cherns et al. (2004), who described a diverse Silurian paleoloricate assemblage from Götland, Sweden, which probably co-occurred with *Acaenoplax*¹⁷ in carbonate shelf environments in shallow, near-shore seas. Cherns (2004) also provided the first cladistic analyses of paleoloricates. Sigwart and Sutton (2007a) also included numerous paleoloricates in their cladistic analysis of the relationships of the Aculifera and related

¹⁷ Cherns et al. (2004) introduced the family name Heloplacidae to include four Silurian plated genera including *Acaenoplax*.

TABLE 13.16
Devonian Chronostratigraphy

System/Period	Series/Epoch	Stage/Age	Beginning
Devonian	Upper	Famennian	372 Ma
		Frasnian	383 Ma
	Middle	Givetian	388 Ma
		Eifelian	393 Ma
	Lower	Emsian	408 Ma
		Pragian	411 Ma
		Lochkovian	419 Ma

Based on International Chronostratigraphy Chart (2018-08) [www.stratigraphy.org/ICSchart/ChronostratChart2018-08.pdf]

taxa, but despite these analyses having multiple shared taxa, their results are quite disparate.

13.3.5 DEVONIAN

In the Devonian (Table 13.16 and Figure 13.26) increases in potential molluscan predators continued with the appearance of both ray-finned (Actinopterygii) and lobe-finned bony fish (Sarcopterygii) which joined the already ecologically diverse placoderms (see Chapter 9). In the Devonian we see additional freshwater bivalves, the first stem neritimorphs, unequivocal caenogastropods, and the first heterobranchs, thus completing the suite of major crown gastropod groups (Frýda et al. 2008a). The Upper Devonian was marked by the Frasnian–Famennian biodiversity crisis which perhaps resulted in the extinction of 31% of Devonian bivalve genera (Bretsky 1973).

It also includes the first freshwater molluscan faunas represented by viviparid-like gastropods and *Modiomorpha*-like clams in the northern hemisphere (Solem & Yochelson 1979). The earliest ammonites also appeared, which, like all coleoids, are thought to have shared a common ancestor with a Devonian Bactritida lineage (see Chapter 17).

13.3.5.1 Taxa

13.3.5.1.1 *Gastropoda*

Based on protoconch morphology, the earliest undoubted caenogastropods are subulitids which appeared in the Lower Devonian (Frýda et al. 2008a). Earlier reports based on teleoconch morphology (high spired and fusiform, with and without siphonal canals) are suspected to relate to convergent morphologies in non-caenogastropod taxa (e.g., Loxonematoidea and Subulitoidea) (Frýda 1999b; Nützel et al. 2000; Wagner

Devonian (393 Ma)

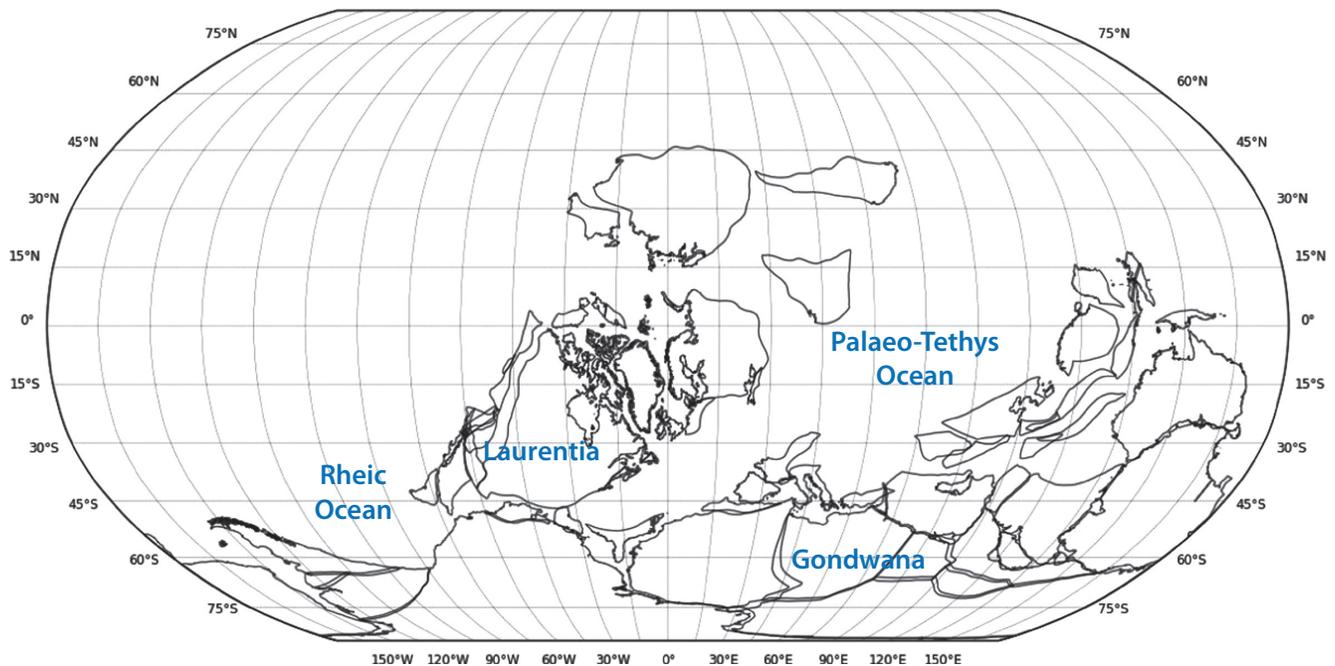


FIGURE 13.26 Palaeogeographic reconstruction of tectonic plate positions during the Middle Devonian.

2002). The origin of heterobranchs was also marked by a heterostrophic protoconch (see Chapters 3 and 20). The earliest stem heterobranchs include the Kuskokwimiidae (Frýda & Blodgett 2001) and Soleniscidae (Bandel & Heidelberger 2002).

The origin of Neritimorpha is more problematic as the earliest distinctive neritimorph protoconchs date only from the Triassic (Bandel & Frýda 1999; Bandel 2000), although with both caenogastropod and heterobranch lineages in Devonian strata, stem neritimorphs must have also been present by this time (given the phylogenetic relationships of these three clades), but their identity remains obscure. Two candidate groups have been identified: the Cycloneritimorpha with a caenogastropod-like protoconch and the Cyrtoneritimorpha with an open fishhook-shaped protoconch (Bandel & Frýda 1999; Frýda 1999a; Frýda et al. 2008a). The Cycloneritimorpha is now considered a synonym of Neritimorpha (see Appendix) and the open whorled protoconch of the older (Ordovician) Cyrtoneritimorpha we treat as a synonym of Orthonychioidea, considered to be an extinct, independent lineage of early gastropods (Frýda et al. 2008b) and which we include in the Eogastropoda (see also Chapter 18).

The platyceratids were allied with cycloneritidans by Bandel (1992). *Platyceras* and its allies first appear in the Silurian of North America, Europe, and China. These limpet-like gastropods have been found attached to the aboral cup or calyx of crinoids where they probably fed on the faecal material of the host. If this reconstruction is correct it is one of the earliest known occurrences of coprophagy in molluscs (Frankenberg & Smith 1967). They appear not to have been obligate coprophages as some species are over 10 cm in length, too large to be epizoid on the co-occurring crinoids and therefore must have had alternative feeding habitats (Bowsher 1955; Morris & Felton 1993; Baumiller & Gahn 2002). Based on protoconch morphology Frýda et al. (2009) suggested that Paleozoic platyceratids were a diphyletic group and the ‘platyceratids’ with tightly coiled protoconchs (that he included in the ‘Cycloneritimorpha’) may have given rise to the neritimorphs. We have (somewhat tentatively) included the platyceratoideans in the Eogastropoda in the Appendix.

13.3.5.1.2 Polyplacophora

The polyplacophorans continued their diversification in the Devonian with the appearance of the Multiplacophorida, and this coincided with the first appearance of the Neoloricata. Whereas most chitons have only eight shell plates, the multiplacophoridans had as many as 17, which appear to be formed by sagittal divisions of the original intermediate plates. This extinct stem group of Neoloricata had the shell plates surrounded by a border of spine-like plates. They occurred during the Devonian–Permian and have been reported from North America and Europe. They were first described in the late 1800s, and the partially articulated and disarticulate valves were thought to represent barnacle plates (Hall & Clarke 1888) and as a result were named accordingly (e.g., *Strobilepis*, *Protobalanus*, and *Hercolepas*), until Name (1926) acquired articulated material of *Protobalanus* and

concluded they were not barnacles. He did, however, reject the Polyplacophora as a placement because the specimen had only seven plates and because of the presence of plate spines. If the intermediate median plates of *Protobalanus* were independent and separated the two lateral sets of intermediate plates, the plate count for *Protobalanus* is 17. Hoare and Mapes (1995) suggested that they were related to chitons, but their partially articulated specimens did not allow for accurate reconstruction of the animal, and their illustrations of the shell plates demonstrated affinities to Neoloricata. Moreover, the large spines surrounding the body appeared to be derived from plate precursors and not girdle spines as they had the same shell morphology as the plates and were hollow and riddled with pores similar to the pores that innervate the aesthetes on the surface of the dorsal plates. Vendrasco et al. (2004) reported the first articulated multiplacophorid and established the arrangement of the plates as well as providing a cladistic analysis and systematic treatment of the group. It appears that this extinct group of chitons is a branch of the Neoloricata that experimented with plate fission and the production of large marginal spines. The plate fission seems analogous to the division of intermediate valves seen in the living *Schizoplax brandtii* (Kaas & Van Belle 1985c). Also, accompanying the fragmentation of the plates was the appearance of the articulamentum shell layer. This layer provides the articulating surfaces between the valves in neoloricates. Similar modified shell plate spines are also found in the eight-plate Ordovician paleoloricate *Echinochiton* (Pojeta et al. 2003). Vendrasco et al. (2004) provide an excellent review of this Devonian to Permian group of chitons.

13.3.5.1.3 Bivalvia

The diversification begun in the Silurian continued into the Lower Devonian (Babin 2000). Kříž (1979) estimated a 59% increase over Silurian generic diversity; some of this origination occurred in early crown taxa giving the bivalve fauna a more modern aspect. Palaeotaxodonts, pteriomorphians, and anomalodesmatans were especially abundant and diverse during the Devonian. The increase in diversity experienced a downturn in the Middle Devonian when extinction rates exceeded origination rates (Sepkoski et al. 2002). The Devonian also saw global dispersal of the earlier, more endemic bivalve faunas, resulting in increased cosmopolitanism (Babin 2000). For example, Rode (2004), in an analysis of *Leptodesma* (Pterineidae), concluded that dispersal in the Middle and Upper Devonian was more likely to be responsible for speciation in this group than vicariance – a pattern also seen in Devonian trilobites and phyllocarid crustaceans. This increase in taxon ranges may have also had a role in ameliorating the impacts of the Upper Devonian biodiversity crisis (Rode 2004).

Bivalve aggregations at methane seeps, first reported in the latest Silurian (Jakubowicz et al. 2017) continued into the Devonian with the Modiomorphidae (Cardiata) being the most abundant taxon. In the Devonian, modiomorphid taxa (e.g., *Ataviaconcha*) formed large aggregations similar to those formed by living cold-seep and hydrothermal vent

bivalves (Hryniewicz et al. 2017); also of note was the observation that the shell morphologies (relatively large elongated shells with allometric growth) of these earliest seep taxa appear convergent with those of other unrelated chemosynthetic bivalve taxa that subsequently came to inhabit these unique environments. Modiomorphid taxa are also unique in combining nacre and crossed lamellar shell microstructures in the same shell, a combination not found in living bivalve taxa (Carter & Michael 1978).

13.3.5.1.4 Cephalopoda

The Devonian saw the origination of the predominately straight-shelled Bactritidae and the coiled ammonites and the migration of these latter cephalopods into the water column during the Devonian Nekton Revolution (Klug et al. 2010, 2015b). This event followed the divergence of stem coleoids from nautiliforms and also mirrored the increase in fish diversity during the same period (Young et al. 1998). The early ammonites were loosely coiled (e.g., *Metabactrites*), but the Devonian history of the group was marked by an increase in coiling, which included both the juvenile and adult shells (Klug et al. 2015b). Increased coiling parameters were also accompanied by an increase in sutural complexity (Ubukata et al. 2014), as well as more variation in internal characters. For example, the Devonian clymeniidan ammonites had a dorsal siphuncle, similar to nautiliforms, rather than the characteristic ventral siphuncle as in other ammonites. De Baets et al. (2012) showed that the size of the ammonite embryonic shells decreased during the Devonian, suggesting a smaller egg and hatching size. Combined with the concurrent increase in adult shell size, De Baets et al. suggested this represented a change in life history strategy in Devonian ammonites; a switch from a K reproductive strategy (a few large eggs) to an R strategy (numerous smaller eggs), the latter requiring less maternal investment and the possibility of earlier feeding by juveniles or paralarvae (see Chapter 8).

Nautiliforms began a precipitous decline during the Middle Devonian, perhaps due to competition with the recently evolved ammonites and predation by durophagous¹⁸ fish. Also, like the ammonites, nautiliform shells became

increasingly more tightly coiled. Signor and Brett (1984) documented a 15% reduction in smooth and finely sculptured nautiliform taxa whereas moderate to strong sculpture increased from 8% to 20%, and very strong sculpture went from non-existent to 11%. Similar changes were also documented in the ammonites (Ward 1981). Lastly, some Devonian nautiliform taxa, which at the beginning of the period appeared to have had relatively low energy buoyancy regulation, became extinct, while subsequent cephalopod morphotypes displayed more energy intensive buoyancy regulation (Kröger 2008a). The Devonian cephalopod record marks an important transition for the group. The appearance of the ammonites, followed by the radiation of durophagous predators, dramatically changed the selective environment for the nautiliforms. Their generic diversity was reduced by about 70% during the End-Devonian extinction event (Sepkoski et al. 2002), but a substantial recovery occurred in the Carboniferous.

See Chapter 17 for further details on the fossil history of cephalopods.

13.3.6 CARBONIFEROUS

The Carboniferous (Table 13.17 and Figure 13.27) was a period of global coal formation derived from the extensive lowland swamps and forests that covered the landscape. Among the molluscs, terrestrial gastropods first appeared among the rich vegetation (and litter) in a warm and humid climate with an atmosphere rich in oxygen (>30%) (Graham, 1995). Freshwater bivalves and gastropods were also present, and the marine Paleozoic molluscan fauna continued its diversification despite the Upper Devonian mass extinction. Shallow, warm seas covered the equatorially located continents, forming numerous shallow basins. Reef-building organisms such as bryozoans and both rugose and tabulate corals were abundant and diverse, while the sea floor was dominated by brachiopods. During the Pennsylvanian, a southern ice sheet formed over Gondwana as the continent moved south and the average global temperature dropped about 12°C (Feulner 2017). Ice sheet formation would also have been accompanied by a drop in sea level, resulting in the loss of many shallow seas.

¹⁸ Shell crushing.

TABLE 13.17
Carboniferous Chronostratigraphy

System/Period		Series/Epoch	Stage/Age	Beginning
Carboniferous	Pennsylvanian	Upper Pennsylvanian	Gzhelian	304 Ma
			Kasimovian	307 Ma
		Middle Pennsylvanian	Moscovian	315 Ma
		Lower Pennsylvanian	Bashkirian	323 Ma
	Mississippian	Upper Mississippian	Serpukhovian	331 Ma
		Middle Mississippian	Viséan	347 Ma
		Lower Mississippian	Tournaisian	359 Ma

Based on International Chronostratigraphy Chart (2018-08) [www.stratigraphy.org/ICSchart/ChronostratChart2018-08.pdf]

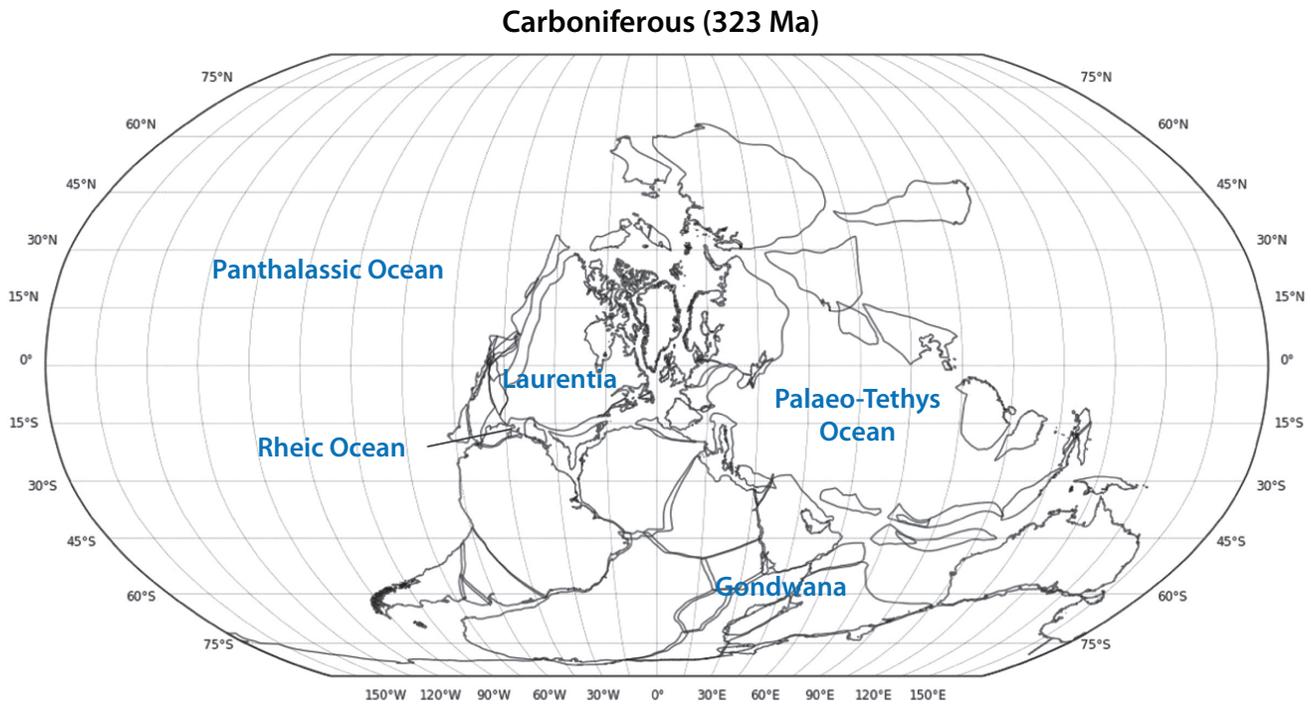


FIGURE 13.27 Palaeogeographic reconstruction of tectonic plate positions during the Lower Pennsylvanian.

13.3.6.1 Taxa

13.3.6.1.1 *Bivalvia*

Diverse bivalves occurred in swampy freshwater habitats which later became coal measures. These included the pteriomorphian group Myalinidae and the heteroconch Amnigeniidae (see Chapter 15). In the marine realm, brachiopods dominated habitats shared with bivalves, which remained subordinate in overall taxonomic diversity. In seep communities, the protobranch solemyids were relatively rare among abundant brachiopods, which were represented by a single rhynchonellid species (Peckmann et al. 2001). After an initial decrease in generic diversity in the early Carboniferous, bivalves increased in numbers and importance while brachiopods decreased over the same period (Babin et al. 1992), but the bivalve dominance was short-lived as the Permian extinction approached. Perhaps more importantly, this diversification in taxa and habitats within major stem marine bivalve clades in the Carboniferous (e.g., the protobranch Nuculida and Solemyida, the pteriomorphian Aviculopectinoidea, Pterioidea, and Mytiloidea, and the heterodont Anthracosioidea) may have facilitated lineage survival across the Paleozoic–Mesozoic boundary. During the Upper Carboniferous diversification geometric mean bivalve size increased by over 20 mm, although mean bivalve size remained stable (Kosnik et al. 2011). In contrast, the geometric mean of gastropod size decreased by about eight mm during the same period.

13.3.6.1.2 *Rostroconchia*

Conocardiid rostroconchs underwent their largest generic diversification event in the Carboniferous. Previous

diversification events had been primarily period-restricted. For example, only three of the ten genera that first appeared in the Silurian remained extant beyond that period, and none of the six genera first recorded in the Devonian survived the End-Devonian mass extinction. Similar to the Silurian diversification, the Carboniferous included first occurrences of 13 genera, four of which remained extant into the Permian. The Carboniferous diversification also included the appearance of minute species in the Silurian genus *Hippocardia* and the Carboniferous *Pseudoconocardium* (Wagner 1997).

13.3.6.1.3 *Cephalopoda*

Carboniferous cephalopods were predominately tightly coiled as the earlier Paleozoic orthoconic and cyrtoconic nautiliform taxa became increasingly rare following the Lower Pennsylvanian extinctions of the Actinoceratia and Oncoceratida. Goniaticid ammonites, which had first appeared in the Devonian, remained dominant during the Carboniferous and were later joined by early representatives of the Ceratitida. Fossils of a supposed octopod body were found in the Pennsylvanian deposits at Mazon Creek, Illinois, USA (Kluessendorf & Doyle 2000), where other soft-bodied cephalopods occur, including *Jeletzkyia*, thought to represent the earliest known crown group squid (Johnson & Richardson 1968; Allison 1987; Doguzhaeva et al. 2007a). Not surprisingly the Carboniferous also records the first ink sacs in cephalopod body fossils (Doguzhaeva et al. 2003, 2004) and the first occurrence of Spirulida (Doguzhaeva et al. 1999). Overall, the Carboniferous is a period of transition for the cephalopods, with the loss of the earlier nautiliform shelled taxa, the increasing diversity of ammonites, and the first

appearance of shell-less cephalopods (Nishiguchi & Mapes 2008) (see Chapter 17 for further details).

13.3.6.1.4 *Polyplacophora*

The Mississippian saw the second largest origination of polyplacophoran genera of the Phanerozoic, being exceeded only in the Miocene; in both cases, origination rates were more than twice that of extinction rates (Sepkoski et al. 2002). This event also marked the first major radiation of the eight-plated Neoloricata. Prior to this, the only known neoloricates were multiplacophoridans (see Section 13.3.5.1.2). Numerous complete articulated chitons have been found in the Carboniferous, including over 100 specimens of *Glaphurochiton concinnus*, some with preserved radulae (Yochelson & Richardson 1979). Hoare and Mapes (1995) described a new Carboniferous (Pennsylvanian) multiplacophoridan genus *Diadeloplax*, and Vendrasco et al. (2004) described an exceptionally well-preserved specimen of another multiplacophoridan, *Polysacos vickersianum*, from the Carboniferous of Indiana, USA, which provided a more accurate reconstruction of the body plan of that group.

13.3.6.1.5 *Scaphopoda*

While earlier reports of scaphopods in the Paleozoic have been controversial (see Section 13.3.3.1.5), the earliest unequivocal appearance of the crown scaphopod taxon *Dentaliida* dates from the Mississippian (Yochelson 1999).

13.3.6.1.6 *Gastropoda*

Marine gastropods showed few changes in diversity at the family rank during the Carboniferous (Erwin 1990b). One significant extinction was the *Perunelomorpha*, an early putative caenogastropod group with an open coiling protoconch (Frýda 1999a). For most gastropods generic and familial diversity was relatively stable, including bellerophontians, Pleurotomarioidea, Murchisonioidea, and Trochoidea, and several groups of uncertain affinities including Lophospiridae (Trochonematoidea), Loxonematoidea, Subulitoidea, and the probable eogastropod Euomphaloidea. Species diversity was also high by Paleozoic standards. For example, the pleurotomarioidian genus *Worthenia* was especially diverse with over 100 species and was one of 30 co-occurring Carboniferous genera (Frýda et al. 2008a). Characteristic vetigastropod characters of crown taxa were prevalent by the Carboniferous, including nacreous shell structure (Batten 1972) and trochoidean protoconch morphology (Bandel et al. 2002). Neritimorphian diversity also appeared stable through the Carboniferous. Because the first occurrence of crown neritimorphs is Mesozoic, the affinities of the Carboniferous *Naticopsis* were questioned, but the analyses of shells and opercula by Kaim and Sztajner (2005) showed its inclusion in the Neritimorpha. A Carboniferous or earlier origination of the group is also suggested by the first occurrences of the putative terrestrial neritimorph taxon *Dawsonella* (Solem & Yochelson 1979) (see below). These patterns appear to be global, and the Carboniferous gastropod faunas were cosmopolitan in their distributions. For example, early Carboniferous gastropods reported by Yoo

(1994) from New South Wales, Australia, include abundant Bellerophontoidea, Euomphaloidea, Vetigastropoda (Pleurotomarioidea, Trochoidea), Neritimorpha (*Naticopsis*), Caenogastropoda (Loxonematoidea, Subulitoidea), and numerous Heterobranchia – a taxonomic diversity similar to early Carboniferous faunas in Europe and North America.

The Carboniferous also marks the first appearance of terrestrial gastropods, with at least two excursions into the lush vegetation of the period – the neritimorph *Dawsonella* (Solem & Yochelson 1979; Kano et al. 2002) and possible Eupulmonata stem lineages (the ellobioidean Carychiinae and early stylommatophorans) (Tracey et al. 1993; Bandel 1997). Mordan and Wade (2008) provided a systematic listing of the earliest fossil occurrence of the various terrestrial heterobranch families and pointed out that the identifications of Carboniferous stylommatophorans by Solem and Yochelson (1979) were in error. Unambiguous stylommatophoran taxa do not appear until the Jurassic–Cretaceous boundary, suggesting morphological convergence by the later-appearing stylommatophorans with the earlier terrestrial groups. Bandel (1997) recognised the Carboniferous terrestrial genera *Anthracopupa*, *Maturipupa*, and *Dendropupa* as ‘carychiids’, although, as with the stylommatophorans, subsequent convergence by the crown taxa is a reasonable alternative hypothesis. This latter scenario is further supported by heterobranch phylogeny (Wägele et al. 2008; Jörger et al. 2010), which requires numerous clades, appearing substantially later in the fossil record, to be present but unpreserved. This includes all ‘lower heterobranchs’, Nudipleura, Euopisthobranchia, Hygrophila, Siphonarioidea, etc., and while many of the taxa in this highly diverse group lack shells, they are present in some, including the stratigraphically useful holoplanktonic pteropods that do not appear in the fossil record until the Cenozoic. These absences from the record suggest that Carboniferous terrestrial taxa bearing similar shells to carychiines (Ellobiidae) are convergent. Whether they belong to a distantly related stem heterobranch group or to another group of gastropods has yet to be determined. These three reported terrestrial taxa are first known from the Pennsylvanian, approximately 50 million years after the establishment of terrestrial plants. The late Paleozoic invasion of land by gastropod molluscs, and perhaps the even later evolution of herbivory, follows a general trend seen in the evolution of herbivory in both terrestrial and marine systems (Labandeira 1998; Vermeij & Lindberg 2000; Labandeira 2002), with a substantial delay between the colonisation of land by plants and the colonisation and evolution of herbivorous organisms. Even after their first appearance in the Pennsylvanian, gastropod grazing patterns on fossil leaves are not known from the late Paleozoic, although insect feeding tracks and other traces on fossil plant material are well documented in the Carboniferous (Labandeira 1998, 2002). This absence suggests that early terrestrial diets were probably based on bacterial and fungal resources, food sources shared with freshwater and marine habitats and still utilised today by many terrestrial gastropods (see Chapters 5 and 20).

The co-occurrence of moist, terrestrial environments (e.g., swampy fern forests) and the high oxygen concentration of

the atmosphere in the Carboniferous may have facilitated the terrestrial invasion by gastropods, the only molluscan class to achieve this habitat transition. Such evolutionary transitions between ecosystems are rare (Vermeij & Dudley 2000) and are thought to occur when low-intensity competition and predation exists in the new ecosystem. The gastropod experiment was not without challenges. An extinction event, the Carboniferous Rainforest Collapse (CRC), occurred during the Upper Pennsylvanian (~305 Ma). This event involved the aridification of the continents and the collapse of the vast tropical rainforests, and where they survived, they were restricted to small relictual patches among new floras and communities (Sahney et al. 2010). Effects on amphibians were particularly

devastating as the hot and humid climate changed to cool and arid (Sahney et al. 2010). Amphibians, slugs, and snails have convergent physiology and habitat requirements, and the CRC was probably also damaging to these early terrestrial gastropod experiments with expatriation, and perhaps extinction, common and widespread.

13.3.7 PERMIAN

The Permian (Table 13.18 and Figure 13.28) marine fauna was similar to that of the Carboniferous. Corals, stromatolites, sponges, bryozoans, brachiopods, and foraminiferans formed reef ecosystems in the warm shallow waters. Cephalopods were common predators, along with a great diversity of fish, including agnathans (jawless fish), chondrichthyans (such as sharks), and many types of bony fish. This collection of marine species represents the last of the Paleozoic evolutionary fauna, which first rose to dominance in the Ordovician, some 200 million years previously.

13.3.7.1 Extinction

The End-Permian mass extinction, approximately 252 Mya, was the largest in the history of multicellular life, with up to 90% of all marine species becoming extinct (Benton 2003; Erwin 2006; Sahney & Benton 2008). This extinction had far-reaching effects on molluscan evolution and marked the transition from the brachiopod-dominated Paleozoic fauna to the mollusc-dominated modern fauna (Gould & Calloway 1980; Sepkoski 1981). Accompanying this change in taxonomic structure was also a change in the ecology of marine ecosystems (Bambach et al. 2002; Bottjer et al. 2008). Prior to the extinction, about two-thirds of marine animals were sessile

TABLE 13.18
Permian Chronostratigraphy

System/Period	Series/Epoch	Stage/Age	Beginning
Permian	Lopingian	Changhsingian	254 Ma
		Wuchiapingian	259 Ma
	Guadalupian	Capitanian	265 Ma
		Wordian	269 Ma
		Roadian	273 Ma
	Cisuralian	Kungurian	284 Ma
		Artinskian	290 Ma
		Sakmarian	295 Ma
		Asselian	299 Ma

Based on International Chronostratigraphy Chart (2018-08) [www.stratigraphy.org/ICSchart/ChronostratChart2018-08.pdf]

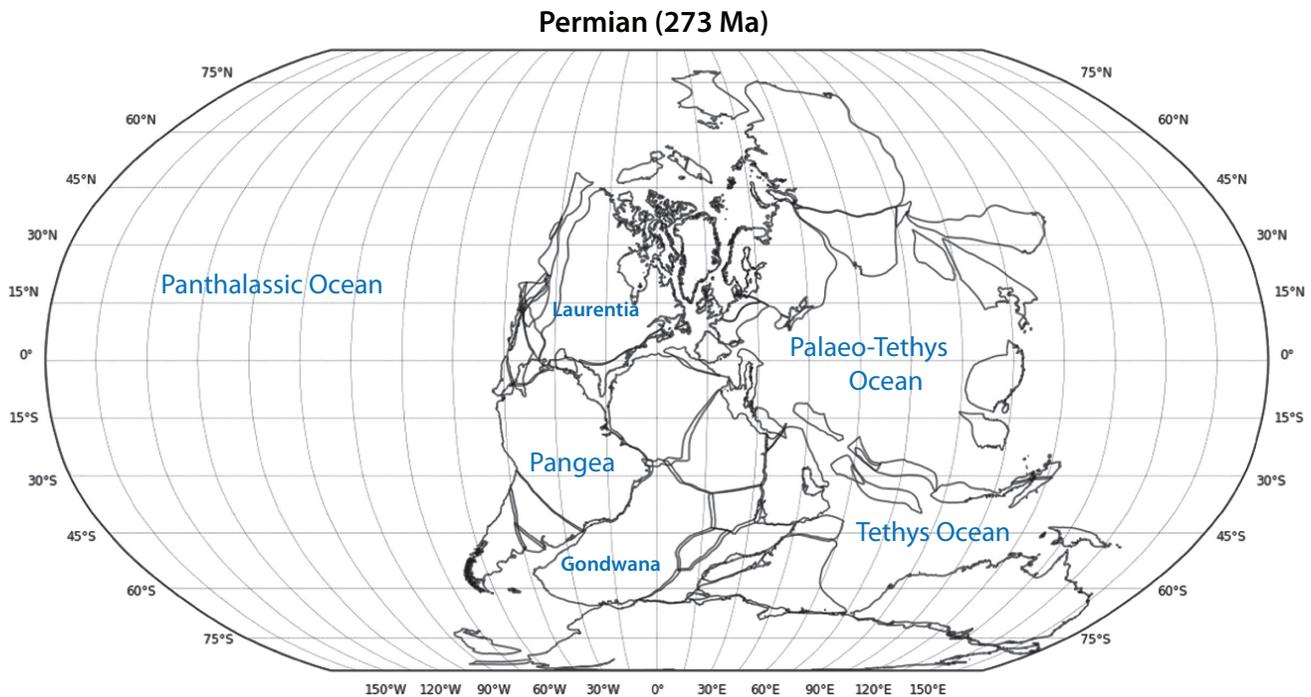


FIGURE 13.28 Palaeogeographic reconstruction of tectonic plate positions during the Permian (Guadalupian).

and attached to the sea floor, but after the extinction, this dropped to 50% as motile invertebrates became just as common, many of which were gastropods (Wagner et al. 2006). Before the End-Permian mass extinction, both complex and simple marine ecosystems were equally common, and following recovery from the extinction, complex communities outnumbered simple communities by three to one (Wagner et al. 2006). This change and the increased levels of predation pressure in these more complex communities may have set the stage for the Mesozoic marine revolution (Vermeij 1977).

Between one and three pulses of extinction have been suggested for the End-Permian (Jin et al. 2000; Sahney & Benton 2008), and an array of causal mechanisms has been proposed (Erwin 1990a; Erwin 2006) (see below). Song et al. (2013) documented two pulses separated by a 180,000-year recovery period. The first pulse occurred in the latest Permian and marked the loss of numerous taxa, but primarily many calcareous algae, all rugose corals, some sponges, all trilobites, most radiolarians, and all fusulinid foraminiferans. The second pulse actually occurred in the earliest Triassic, and smaller foraminiferan, ostracod, brachiopod, bivalve, gastropod, ammonite, and conodont taxa suffered the greatest losses. Gastropods, bivalves, and ammonites also dominated the recovery originations between the two extinction pulses. Stratigraphic resolution of rostroconchs is not sufficient to determine if they also had two staged extinctions. As well, it appears that the second pulse was the one responsible for the collapse of the Paleozoic fauna.

Because the two pulses affected taxa differently, Song et al. (2013) concluded that different environmental causes were probably responsible but did not propose any candidate drivers. Others have linked earlier extinctions in the Guadalupian epoch with gradual environmental change, while the final pulse at the Permian–Triassic boundary is thought to have resulted from a catastrophic event (Ward et al. 2005; Algeo et al. 2012). Several lines of evidence suggest that shallow-water bottom communities were metabolically poisoned, but it remains unclear whether this was due to high carbon dioxide levels (hypercapnia) (Knoll et al. 2007), a severe deficiency of oxygen (anoxia) (Wignall & Twitchett 2002), hydrogen sulphide (euxinia) (Cao et al. 2009), or some combination of these (Clapham & Payne 2011). There is less agreement on what might have caused the toxicity. Possible causes include an impact event, the onset of massive volcanism (e.g., the Siberian Traps), a greenhouse effect triggered by methane hydrate gasification from the deep sea and/or the evolution of a new metabolic pathway in methanogenic microbes (Rothman et al. 2014). These catastrophic events and their short- and long-term effects would have been overlain with ongoing global changes (Kring 2000; Clapham & James 2008), which included glaciations and accompanying sea level changes, ocean acidification, increasing terrestrial aridity, the formation of the Pangaea supercontinent, shifts in ocean circulation, etc.

The End-Permian extinctions were so severe that many of the surviving lineages took 5 Ma, and some as long as 10 Ma, to recover from the decimation and return to pre-extinction

diversity levels (Benton 2003). This slow recovery rate, compared to other mass extinctions, is thought to be due to residual environmental stresses that continued into the Lower Triassic (Woods et al. 1999; Payne et al. 2004), although one surviving ammonite lineage made an extraordinary recovery in only about one million years (see Section 13.3.7.2.3).

13.3.7.2 Taxa

13.3.7.2.1 Bivalvia

Bivalves were one of the most widespread Permian groups and experienced relatively low extinction rates overall (60%) compared to other molluscs. Biakov (2015) recognised three distinctive bivalve faunas in each of the major Permian basins. In the Boreal Superrealm, bivalves were a dominant benthic group although they had relatively low familial diversity. Taxa included the *Inoceramus*-like Kolymiidae (Pterioida) and numerous protobranch Nuculida, while pterinopectinids (Pectinida) and the heterodont Carditida and Lucinida were less common. In the more equatorial Tethyan Superrealm, the bivalve fauna was more diverse, but bivalves were much less dominant in these communities which were dominated by brachiopods. Among the bivalves, pterioideans were again dominant and included Posidoniidae, Alatoconchidae, Myalinidae, Pterineidae, and Isognomoniidae. Other groups included Parallelodontidae (Arcida), Ostreida, numerous Pectinida, including Entoliidae, Annuliconchidae, Pterinopectinidae, and Bakewellidae, and, in the Trigoniida, Schizodidae. Some Alatoconchidae were extremely large and are suspected of being photosymbiotic (Isozaki & Aljinović 2009). In the southern-most Gondwanan Superrealm bivalves again were not very diverse, and there was high endemism, particularly in Pectinida (Eurydesmatidae) and in the Pterioida, the *Inoceramus*-like ambonychiids. Overall, this fauna was most similar to the Boreal Superrealm, and bipolar distributions were not uncommon. The larger epifaunal bivalves also provided hard substrata for other ‘invertebrate’ taxa and communities (Biakov 2015).

Several bivalve taxa have been identified as ‘disaster taxa’ (in the sense of Rodland & Bottjer 2001) following the Permian extinction; these having been characterised as highly abundant, widespread, and ecologically dominant and included the pectinid genera *Claraia* and *Eumorphotis*, the myalinid *Promyalina*, and the trigoniid *Unionites* (Petsios & Bottjer 2013). While the overall extinction rate was low for the class, in some lineages loss was more severe and recovery substantially slower. For example, pectinoideans gradually declined from 23 genera in the Guadalupian to about five genera (a 78% reduction) in the earliest Triassic. After this decline the pectinoideans would not return to their earlier diversity until the Upper Triassic, 35 Ma later (Newell & Boyd 1995).

Bivalves were neither as diverse nor as abundant as brachiopods in Paleozoic faunas but became a major component of the modern fauna following the End-Permian extinction. Rudist bivalves (see Chapter 15) would replace the reef builders (including corals, bryozoans, brachiopods, and echinoderms) lost at the Permian extinction in the Mesozoic (Flügel 1994).

13.3.7.2.2 *Gastropoda*

Like bivalves, gastropods had relatively low extinction rates (66%). Most gastropod clades experienced two extinction pulses. The first, at the end of the Guadalupian, affected all major Permian gastropod clades, including the Bellerophontia, Euomphalina, Pleurotomariina, Trochina, Neritopsina, Loxonematoidea, Subulitoidea, Murchisonioidea, and Heterobranchia (Erwin 1990a). The second pulse, at the End-Lopingian, was not as strong as the first, although all but the Loxonematoidea saw further declines in diversity. In the first pulse, about half of the Permian gastropod genera were lost, and origination rates were low. Extinction rates were lower in the final pulse, but another third of generic diversity was lost, and originations fell to one of the lowest rates seen in the Paleozoic (Erwin 1990a). Bellerophontians survived the End-Permian extinction, but they continued to decline in diversity and were extinct by the Upper Triassic.

Payne (2005) examined gastropod size across the Permian–Triassic boundary. His data suggested that maximum size was relatively stable in the Permian, but minimum adult shell size decreased in both the Cisuralian and Lopingian after a slight recovery in the Guadalupian. Maximum adult size underwent an abrupt, precipitous decline across the Permian–Triassic boundary while minimum adult size had already begun to increase, but Lower Triassic gastropods generally remained small. Both maximum and minimum size gradually increased in the Lower Triassic, and within 10 Ma, gastropod size was once again equivalent with Guadalupian and Lopingian values. Payne (2005) proposed that two scenarios were consistent with the patterns of size decrease across the Permian–Triassic boundary: (1) size-selective extinction at the species level and (2) within-lineage size decrease.

Besides their small size, Lower Triassic gastropod origination rates only slightly exceeded extinction rate, producing a relatively modest rise in diversity (Erwin 1990a). When examined separately, the caenogastropods showed an early and pronounced radiation (Nützel 2005), and within four million years, new originations outnumbered Paleozoic survivors (Pan & Erwin 2002) with most Lower Triassic caenogastropod genera originating after the End-Permian extinction (Nützel & Erwin 2002).

13.3.7.2.3 *Cephalopoda*

Ammonites were reduced by two extinction events in the Permian. The first, in the Guadalupian, reduced the level of

morphological differences in the group. This decline was relatively gradual and was apparently environmentally driven, but the second, the terminal Permian extinction, was non-selective and catastrophic following water column toxicity. Morphological differences in ammonites across the Permian–Triassic boundary declined by almost 60% (McGowan & Smith 2007), and within one million years after the final pulse, the pre-extinction morphospace was reoccupied, but with the divergent shell parameters distributed differently among the new and surviving lineages. This extraordinary recovery occurred due to the diversification of a small surviving lineage of Ceratitida represented by only three genera, one of which would give rise to most Triassic ammonites (Brayard et al. 2007).

At the beginning of the Permian, there were four major clades of ammonites (Saunders et al. 2008; Brayard et al. 2009). After the final extinction pulse, only two remained, the Prolecanitida and the Ceratitida, and unlike other molluscs, this lineage reached its greatest diversity within the Lower Triassic (Brayard et al. 2009). This difference has been explained as the presence of residual toxicity in benthic habitats (gastropods and bivalves) compared to its absence in the water column (ammonites). But as Marshall and Jacobs (2009) pointed out, both *Nautilus* and *Vampyroteuthis*, members of two ancient cephalopod lineages, are low-oxygen specialists. The water column might also have had residual toxicity, and the surviving Ceratitida could have been plesiomorphically adapted to low-oxygen conditions, leading to their more rapid recovery.

13.3.7.2.4 *Other Classes*

Scaphopod species diversity was reduced by 85% across the Permian–Triassic boundary (data from Reynolds 2002). Rostroconchs had already been on the decline, and only the Conocardiida had survived beyond the Ordovician, with the final three genera (*Bransonia*, *Conocardium*, and *Pseudoconocardium*) disappearing at the end of the Permian. The loss of polyplacophoran taxa was continuous through the Permian (Cherns 2004). Almost all paleoloricates were extinct by the end of the Silurian, and the Permian extinction marked the final occurrence of that group. For neoloricates, J. Sigwart (pers. comm., 2016) estimated that generic diversity was reduced by 89% (from 28 to three taxa) by the event, including the loss of the multiplacophoridans. Monoplacophorans are unrecorded in the Permian but obviously survived.

14 Polyplacophora, Monoplacophora, and Aplacophorans

14.1 INTRODUCTION

In this chapter, we introduce the aplacophorans, polyplacophorans, and monoplacophorans, loosely called the ‘placophoran’¹ groups, which have been regarded as the most ‘primitive’ living members of the molluscan tree, although not without controversy (see Chapter 13 for discussion).

Members of this informal level of morphological organisation (or grade) are bilaterally symmetrical and typically have elongate bodies. Monoplacophorans have a single shell and polyplacophorans have eight valves (in some fossils up to 17). Two living groups (‘aplacophorans’) lack shell plates altogether and instead have calcium carbonate spicules, these being the Solenogastres (= Neomeniomorpha) and Caudofoveata (= Chaetodermomorpha).

With the increasing application of molecular systematics, the collection of ‘placophoran’-like fossil taxa, and their supposedly basal position, their relationships with the other molluscan groups has generated considerable controversy, as outlined in Chapters 12 and 13.

Well-preserved Cambrian fossils of *Wiwaxia* and *Odontogriphus* both show a few oral structures that may have been used for grazing on algal mats. These mouthparts have been likened to radulae (e.g., Caron et al. 2006) (see Chapter 13) and used to formulate hypotheses regarding the evolution of early radulae. According to this idea, the early radula comprised a few rows of hardened, wide, denticulate teeth held together with a flexible cuticle, and was used to scrape detritus or larger food items. This is a similar arrangement to the radulae found in some caudofoveates and solenogastres (e.g., Salvini-Plawen 2003; Scheltema et al. 2003; Todt et al. 2008b) and, according to this hypothesis (which we do not support), the specialised radulae seen in modern aplacophorans and chitons evolved from this primitive condition. Specialised offshoots from this early configuration included the pincer-like structures seen in caudofoveates that have evolved to pick up individual foraminiferans and diatoms, and in solenogastres, the development of rows of hooks and other structures suited to carnivorous feeding. In marked contrast, chitons evolved an extremely long radula specialised for scraping hard substrata, with some teeth in each tooth row hardened by metals (Todt et al. 2008b).

14.2 POLYPLACOPHORA (CHITONS, PLACOPHORA, LORICATA, AMPHINEURA IN PART)

14.2.1 INTRODUCTION

Polyplacophorans, or chitons, are small to rather large, entirely marine, dorsoventrally flattened animals that are elongate-oval in shape. Dorsally they have eight articulating shell valves (plates) surrounded by a thick girdle that may be covered with spines, scales, or hairs (Figure 14.1). Ventrally there is a broad, oval, creeping foot. Most chitons are between 5 and 50 mm in length, but some are larger, and one, the ‘gumboot’ chiton, *Cryptochiton stelleri*, which lives on the north west Pacific coast of North America, grows to about 36 cm in length.

Polyplacophorans are ecologically important as they are often abundant in the littoral zone and, from the evolutionary viewpoint, are sometimes considered the most primitive living molluscs. They have a long fossil history from at least the Upper Cambrian (see Section 14.2.5 and Chapter 13).

There have been several accounts of chiton anatomy, the most comprehensive being those of Plate (1897, 1899, 1901), Hyman (1967) and Eernisse and Reynolds (1994) while reviews of aspects of their physiology and biology include those of Boyle (1977) and Pearse (1979).

14.2.2 PHYLOGENY AND CLASSIFICATION

Polyplacophoran monophyly is well established (e.g., Okusu et al. 2003), except for the analysis by Giribet et al. (2006) where a monoplacophoran was nested within the group. Subsequent analyses providing better data (Wilson et al. 2010) have again demonstrated monophyly, with the monoplacophoran being the sister taxon, and together they formed the higher taxon Serialia (see Chapter 12 for discussion).

While extensively studied at the species level, the higher classification of chitons was in flux until recently (e.g., Okusu et al. 2003; Sirenko 2006; Todt et al. 2008b). Today, the phylogenetic relationships of the major chiton clades are still argued, but the membership of species and families within those clades is not in doubt (Sigwart et al. 2013). While their classification incorporates shell, girdle, radular, egg hull, sperm, and neural (aesthete) characters and is in good agreement with molecular phylogeny, earlier classifications were based mainly on features of the shell valves, with other characters such as girdle and radula being mostly utilised at generic or species levels.

The higher-level groups generally recognised in the 20th-century literature on living chitons (Neoloricata or Loricata)

¹ The term ‘placophoran’ is here used informally, as in Chapter 13, and by Lindberg and Ponder (1996), and Parkhaev (2008), as a general term to conveniently encompass all the groups dealt with in this chapter as well as similar fossil taxa. The formal name Placophora has been used, particularly by some European malacologists, for Polyplacophora alone.



FIGURE 14.1 Photos of living chitons. (a) *Leptochiton cascadiensis* (Leptochitonidae) San Juan Island, Washington. Courtesy of J. Sigwart. (b) *Ferreiraella* sp. (Abyssochitonidae), Guadeloupe, French West Indies. Courtesy of L. Charles - MNHN. (c) *Tripoplax regularis* (Ischnochitonidae), Monterey, California (© Gerald and Buff Corsi/Focus on Nature, Inc.). (d) *Stenoplax* sp. (Ischnochitonidae), Panglao, Philippines. Courtesy of P. Maestrati - MNHN. (e) *Tonicia lebruni* (Chitonidae), Falkland Islands. Courtesy of J. Sigwart. (f) *Acanthochitona fascicularis* (Acanthochitonidae), Azores. Courtesy of J. Sigwart. (g) *Cryptoplax lavaeformis* (Cryptoplacidae), Papua New Guinea. Courtesy of P. Maestrati - MNHN. (h) *Cryptochiton stelleri* (Mopaliidae), Vancouver, BC, Canada. Courtesy of J. Sigwart.

were the ‘suborders’ *Lepidopleurina*, *Acanthochitonina*, and *Ischnochitonina*, the latter being the most diverse. An additional monotypic suborder, *Choriplacina*, is recognised for *Choriplax* (Gowlett-Holmes 1987; Kaas & Van Belle 1994; Kaas et al. 1998). The almost exclusive use of valve morphology for higher classification (e.g., Kaas & Van Belle 1994; Kaas et al. 1998) was because it was the only character-set available for fossil chitons. The higher taxon *Chitonida* was introduced for chitons with elaborate extracellular hull processes surrounding their eggs (Sirenko 1993), and this grouping includes most of the living chitons. Egg hull morphology, gill placement and morphology (e.g., Russell-Hunter 1988; Sirenko 1993), and sperm ultrastructure (Buckland-Nicks 1995) have been found to correlate rather well with classifications based on shell morphology (Todt et al. 2008b). Based on all these characters living chitons were found to form two main lineages (Sirenko 1993; Buckland-Nicks 1995; Sirenko 2006). These two lineages were recognised as orders by Sirenko (1997, 2006), namely the *Lepidopleurida* and *Chitonida*, the latter having two suborders, *Chitonina* and *Acanthochitonina*. Within *Acanthochitonina*, two groups were recognised – *Mopalioida* and *Cryptoplacoida* – and two groups also within *Chitonina* – *Chitonoidea* and *Schizochitonoidea*. This classification was largely corroborated by the first molecular analysis of polyplacophorans (Okusu et al. 2003). This analysis recovered the two main groups, *Lepidopleurida* and *Chitonida*, and generally supported *Chitonina*, but some classical higher taxonomic groups, such as *Ischnochitonina* and *Acanthochitonina* and several families, were not monophyletic. The analysis supported the monophyly of *Chitonida*. *Lepidopleurida* were basal, and *Chitonida* formed three lineages:

1. Those with egg hulls having rounded to weakly hexagonal cupules, abanal gills, and type I sperm (clade A of Okusu et al. 2003)
2. Those with egg hulls having strongly hexagonal cupules with flaps, abanal gills, and type I sperm (clade B of Okusu et al. 2003)
3. Those with spiny egg hulls of various shapes, adanal gills, and type II sperm (clade C of Okusu et al. 2003), equivalent to *Chitonoidea* of Sirenko (1997)

Sirenko (2006) revised his earlier classifications (Sirenko 1993, 1997) and recognised four orders – *Chelodida*, *Septemchitonida*, *Lepidopleurida*, and *Chitonida*.

BOX 14.1 HIGHER CLASSIFICATION OF POLYPLACOPHORA

(Class) **Polyplacophora** (= Placophora)
 (Subclass) **Paleoloricata**†
 (Order) **Chelodida**†
 (Suborder) **Septemchitonina**†
 (Subclass) **Neoloricata**
 (Order) **Multiplacophorida**†

(Order) **Lepidopleurida**
 (Suborder) **Cymatochitonina**†
 (Suborder) **Lepidopleurina**
 (Order) **Chitonida**
 (Suborder) **Chitonina**
 (Suborder) **Acanthochitonina**

(† = extinct taxa)

See Appendix for detailed classification.

14.2.2.1 Sister Group Relationships

Despite attempts to resolve molluscan phylogeny using morphological and molecular data, there is no consensus view regarding the position of Polyplacophora within the molluscan tree (see Chapters 12 and 13), in part due to poor sampling for basal taxa (particularly aplacophorans and monoplacophorans) and the considerable extinction that has occurred. Three main ideas about sister group relationships of polyplacophorans have emerged: (1) they are the sister to aplacophorans, forming the *Aculifera* (= *Amphineura*), synapomorphies being the elongate body form and girdle spicules (Scheltema 1996); (2) aplacophorans are paraphyletic, and the remaining molluscs (*Testaria*) contain polyplacophorans as the basal taxon (e.g., Salvini-Plawen 1969; Wingstrand 1985; Haszprunar 2000); (3) Polyplacophora is the sister to all the extant molluscs, with aplacophorans derived and either monophyletic or diphyletic. This latter hypothesis is rarely suggested (e.g., Lindberg & Ponder 1996) but is supported by the *Serialia* concept (see Chapter 12).

The possibility that stem aplacophorans may have had plate-like structures similar to those of polyplacophoran valves was supported by the discovery of foot-less chitons (*Kulindroplax* and *Phthipodoichiton*) (Sigwart & Sutton 2007; Sutton & Sigwart 2012). In addition there is also a putative fossil aplacophoran, the Silurian *Acaenoplax hayae* (Sutton et al. 2001a, 2004), which has both spicules and plates (see Chapter 13), and a putative aplacophoran larva with seven transverse dorsal spaces lacking spicules has been described (Scheltema & Ivanov 2002). The molluscan affinities of both the larva (G. Rouse in Nielsen et al. 2007) and Silurian fossil have been disputed (Steiner & Salvini-Plawen 2001). If stem aplacophorans did have plates and spicules, as some evidence seems to suggest, then these structures are plesiomorphic and shared with extinct ‘placophoran’ lineages as proposed by Lindberg and Ponder (1996).

14.2.3 MORPHOLOGY

Works on the general morphology of Polyplacophora, as well as those detailing anatomy and histology, include the historical accounts of Plate (1897, 1899, 1901), Wingstrand (1985), and the synopses of Hyman (1967) and Eernisse and Reynolds (1994). For details of many features involved in chiton taxonomy see Kaas and Van Belle (1985a, 1985b, 1985c) and Sirenko (1993, 1997, 2006).