Second Edition

Marine Bivalve Molluscs




Elizabeth Gosling

WILEY Blackwell

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Preface

The phylum Mollusca is one of the largest, most diverse and important groups in the animal kingdom. There are at least 50 000 described species, and about 30 000 of these are found in the sea. The class Bivalvia is one of the eight classes of molluscs and comprises animals enclosed in two shell valves. Examples are mussels, oysters, scallops and clams. Although this class contains a relatively small number of species, about 10 000, it elicits substantial interest chiefly because these species are widely consumed by people. In 2011, production of marine bivalves from fisheries and aquaculture was almost 14 million metric tonnes worldwide with more than 90% of this figure coming from aquaculture.

Some years ago while teaching a course on bivalve biology to aquaculture students, I realized that although the students could access much relevant information from several texts, a single book covering all aspects of the biology, ecology and culture of bivalve molluscs did not exist. Thus the idea to write such a book was conceived. What started off as a small undertaking very quickly snowballed into a substantial task, which took several years to complete, primarily due to my having to read and digest the wealth of published information. The first edition of *Bivalve Molluscs*, published in 2003, was very well received by reviewers, did well in terms of sales, and in 2011 Wiley-Blackwell invited me to prepare a second edition.

In the intervening years, there have been many significant advances, along with the emergence of new areas of research, one reason being the range of new techniques being applied in bivalve biology and ecology. For example, DNA genetic markers play an increasingly important role in disease diagnosis (Chapter 11), identification and tagging of larvae (Chapters 5 and 10), in detecting different strains of pathogenic bacteria (Chapter 12), and in the completely new area of bivalve genomics (Chapter 10). Also, isotope ratios and fatty acid signatures are being used to identify dietary food sources in bivalves (Chapter 4), while measurements of stable oxygen isotopes in fossil and contemporary bivalve shells are allowing reconstruction of past sea surface temperatures. Trace elemental fingerprinting, based on naturally occurring elements in bivalve shells, is being used to assess larval origins and trajectories, while fluorescence *in situ* hybridization (FISH) combined with cell sorting can identify and rapidly count and sort larvae of several bivalve species in diverse plankton samples (Chapter 5). Immunosensors – devices that use specific biochemical reactions mediated by antibodies to detect chemical compounds – may soon replace liquid chromatography, which has long been the official method for detection and quantification of algal toxins in shellfish (Chapter 12).

Another significant development has been the increasing use of sophisticated mathematical models to describe and predict growth and bioenergetics of individual animals (Chapters 4 and 6), to track larval movement and recruitment (Chapter 5) and to predict geographic range of species in global warming scenarios (Chapter 3). Models are also being employed to simulate disease and forecast outbreaks (Chapters 11 and 12), to describe carrying capacity and environmental effects in aquaculture areas (Chapter 9). Also, several model-based approaches are in use to assess fisheries stocks (Chapter 8).

Another area that has changed is the management of bivalve fisheries and aquaculture systems, where the emphasis is now more on the use of legislation and control measures, particularly in Europe, North America, Australia and New Zealand (Chapters 8 and 9). This also pertains to the control of diseases in oysters and clams (Chapter 11) and to hygiene standards for shellfish and shellfish waters (Chapter 12).

The focus of the book, like the first edition, is on marine bivalves of commercial importance, and while the book is written primarily for undergraduate students, it will be of value to graduate students, investigators engaged in bivalve research, and fishery management and aquaculture personnel. This second edition has been extensively revised and updated; it now has more than 2500 references, of which more than 70% is new, and 250 figures and tables, of which 50% is new. Chapter 1 covers the phylogeny and evolution of Bivalvia – one of the hottest topics in bivalve biology in the past 10 years. Chapter 2 provides a detailed description of external and internal anatomy, while Chapter 3 describes global and local distribution patterns, and the physical and biological factors influencing distribution and abundance, with a new section on climate change and the actual and potential impacts of global warming, ocean acidification and hypoxia on bivalves. Factors influencing filter feeding, together with dietary components and assimilation efficiency are covered in Chapter 4; new material is presented on the influence of bivalves in marine ecosystems. Chapter 5 deals with reproduction, larval development and settlement, and has new sections on sperm–egg interaction, larval dispersal, connectivity, identification and abundance estimates. Chapter 6 covers methods of measuring growth and the various factors influencing growth; new sections deal with the use of the bivalve shell as a marine archive and endogenous modulators of growth. The processes of circulation, respiration, excretion and osmoregulation are described in Chapter 7. The fishery assessment and management methods that are used in commercial fisheries of mussels, oysters, scallops and clams are covered in Chapter 8, with new material on legislation and enforcement measures. The fundamentals of bivalve aquaculture are dealt with in Chapter 9, focusing on a number of key species for detailed treatment. New material deals with larval nutrition, spawning, cryopreservation, and the effects of bivalve culture on the environment, with a new, large section on facilitating sustainable aquaculture development. Chapter 10 describes the application of genetic methods, with new sections dealing with global breeding programmes and the relatively new area of bivalve genomics. Chapter 11 deals with diseases and parasites, with a large amount of new information on diagnostic methods and the diverse defense mechanisms utilized by bivalves. Finally, Chapter 12 deals with the role of bivalves in disease transmission to humans, with new sections on production and processing controls, regulation of monitoring and quality control, including the HACCP system.

Acknowledgements

I would like to express my gratitude to the wide range of people who, in helping me throughout the project, made this greatly revised and extended second edition of *Marine Bivalve Molluscs* possible. A book like this is, in many ways, as good as its illustrations, and I thank those who provided figures and photographs; each is duly acknowledged in the appropriate figure caption.

Helping with accuracy and relevance, the following provided invaluable advice and information, particularly for Bivalve Culture (Chapter 9), Fisheries and Management (Chapter 8), and Public Health (Chapter 12): Joel Bader, Peter Beninger, Mark Camara, Steven Carr, Grete Dinesen, Daniel Hennen, Vic Kennedy, David Kingsley, Judy Kleindinst, John Kraeuter, Per Sand Kristensen, Ian Laing, James Lowther, Vicky Lyons, Enrique Navarro, Shaun Nicholson, Hans Ulrik Riisgård, Stephen Smith, Gemma Watterson and Bob Ward.

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1 Phylogeny and evolution of bivalve molluscs

The phylum Mollusca is one of the largest, most diverse and important groups in the animal kingdom, with at least 50 000 described species and probably as many as 200 000 living species, most of which are marine. The phylum has a remarkable fossil record going back to the Early Cambrian some 540 million years ago (Ponder & Lindberg 2008). Molluscs are soft-bodied animals but most have a hard protective shell. Inside the shell is a heavy fold of tissue called the mantle. The mantle encloses the internal organs of the animal. Another feature of the phylum is a large muscular foot that is generally used for locomotion.

Although most molluscs share this basic body plan the group is characterised by a great diversity of form and habit. As Morton (1967) aptly puts it:

> *Molluscs range from limpets clinging to rocks, to snails which crawl or dig or swim, to bivalves which anchor or burrow or bore, to cephalopods which torpedo through the water or lurk watchfully on the bottom. They penetrate all habitats: the abysses of the sea, coral reefs, mudflats, deserts, and forests, rivers, lakes and under ground. They may become hidden as parasites in the interior of other animals. They feed on every possible food and vary in size from giant squids and clams to little snails a millimetre long.*

Phylogeny of the Mollusca

Eight classes of molluscs are recognized (Figure 1.1), mostly based on cladistic[1] (phylogenetic) analysis of morphological characters in extant and fossil taxa (Haszprunar *et al.* 2008). Aplacophora contains two classes: Solenogastres (~250 species) and Caudofoveata (~150 species). These are worm-shaped, deep-water animals lacking a shell but covered by a cuticle and aragonite spicules. Polyplacophora (~100 species), often referred to as chitons, inhabit hard substrates on rocky shores, and are characterized by eight dorsal shell plates. Aplacophora and Polyplacophora are grouped in Aculifera, which is regarded as monophyletic, that is all taxa in this group share a common ancestor (Sigwart & Sutton 2007). There are only 30 or so species in the class Monoplacophora (not shown in Figure 1.1)

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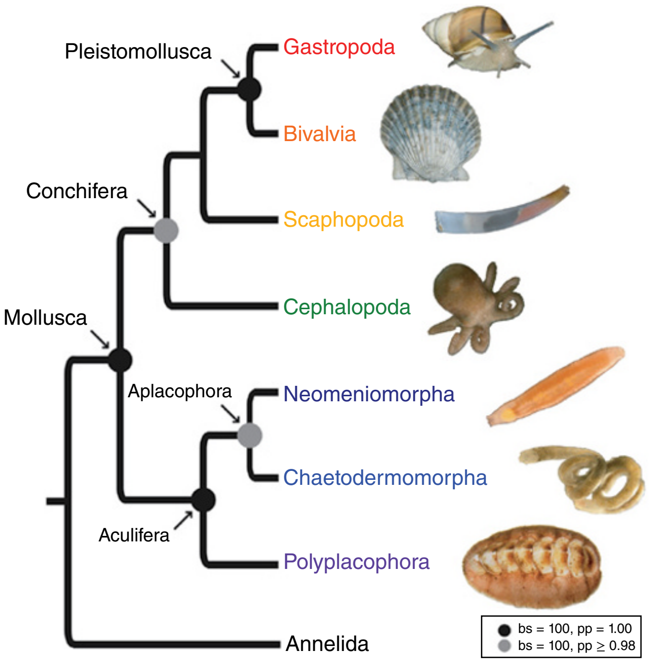

Figure 1.1 Molluscan phylogenetic tree based on transcriptome and genome data from all major lineages, except the Monoplacophora. Black circles represent nodes with bootstrap support (bs) = 100 and posterior probabilities (pp) = 1.00. Grey circles represent nodes with bs = 100 and pp ≥ 0.98. Bootstrapping is used to assess the stability of taxon groupings in a phylogenetic tree; posterior probability measures the likelihood that an event will occur given that a related event has already occurred. Photos of the major lineages are not to scale. Neomeniomorpha = Solenogastres; Chaetodermomorpha = Caudofoveata.
From Kocot *et al.* (2011). Reproduced with permission of Nature Publishing Group.

and all live in deep waters, and are small and limpet-like with a single cap-like shell. Scaphopoda (~600 species), commonly known as tusk shells because of their conical and slightly curved shell, live in marine mud and sediments. The class Gastropoda is the largest (>100 000 species) and most diverse, containing spirally coiled snails, flat-shelled limpets, shell-less sea slugs and terrestrial snails and slugs. The class Bivalvia with about 9200 species (Huber 2010) includes laterally compressed animals enclosed in two shell valves, such as mussels, oysters, scallops and clams. Octopus, squid and cuttlefish are in the class Cephalopoda. There are about 1000 species in this class and they represent the largest, most organised and specialised of all the molluscs. These four shelled classes are grouped as Conchifera, which is regarded as a monophyletic group. The Monoplacophora are generally accepted as the earliest extant offshoot of the Conchifera.

The hypothetical ancestral mollusc (HAM) is believed to have been either an advanced flatworm or a reduced annelid. It is envisioned as a small (1–3 mm) shelled animal that lived in shallow, pre-Cambrian seas, and crept over the substrate on a large foot, scraping algae off the rocks with its specialised mouthparts. At the posterior of the animal was a pair of ciliated filamentous ctenidia (gills), which functioned solely as respiratory organs (see Haszprunar *et al.* (2008) and references therein). Whether such a creature really existed is a moot point. Lindberg and Ghiselin (2003) regard it as ‘a pest preserved in a textbook refugium’ and made a strong case for its ‘extinction’, on the basis that it has hindered rather than helped evolutionary biologists and palaeontologists in solving problems.

Until relatively recently morphological data were the only source used to deduce phylogenetic relationships within the Mollusca. In the 1980s the application of molecular methods was seen as a potentially important advance towards elucidating relationships of this major taxon. Most analyses have focused on single nuclear genes, for example small 18S ribosomal subunit (SSU) and large 28S ribosomal subunit (LSU). However, fundamental questions in mollusc evolution remain largely unanswered by the morphological and molecular data, which often give non-congruent results. Examples of such questions are whether the worm-like Aplacophora diverged before the Conchifera or lost their shells secondarily; whether the Polyplacpophora is a sister group to Conchifera, or Monoplacophora; and what are the interrelationships of conchiferan groups (Smith *et al.* 2011). Recently, researchers have adopted a multigene approach in an attempt to answer these questions. This approach uses sequences derived from genome and transcriptome data (Chapter 10) that allow numerous orthologous[2] protein-coding genes to be identified and employed in phylogeny reconstruction. Kocot *et al.* (2011) identified more than 300 orthologous genes, which they used in a phylogenetic study on 42 taxa from all major lineages within the Mollusca, except the Monoplacophera (Figure 1.1). Their results strongly supported two major clades[3]: Aculifera, which included a monophyletic Aplacophora sister to Polyplacophora, and Conchifera, which supported a sister–taxon relationship between Gastropoda and Bivalvia. They proposed the name Pleistomollusca for this grouping, which contains greater than 95% of all molluscan species (Figure 1.1). Scaphopoda was sister to Pleistomollusca, albeit with only moderate support, and Cephalopoda was found to be the sister taxon of all other Conchifera. Smith *et al.* (2011), using a similar approach but this time including Monoplacophra, also found strong support for the same two major clades, but within the Conchifera, Monoplacophora was not the sister group to all other Conchifera, as has been suggested by most authors, but was instead the sister group to Cephalopoda. They also found support for a clade comprising Bivalvia, Scaphopoda and Gastropoda, with the last two as sister groups. Just to highlight the complexity of deducing molluscan phylogeny, Vinther *et al.* (2012), using seven nuclear genes, found support for Cephalopoda as a sister group to Aculifera.

Because this book is concerned with bivalve molluscs, attention will now be fully focused on the class Bivalvia.

Phylogeny and evolution of Bivalvia

Classification and phylogeny

Bivalves are the second largest class within the Mollusca. Over evolutionary time they have become flattened side to side. Two mantle lobes cover the body organs and secrete the two shell valves that are hinged dorsally (Figure 1.2 and Chapter 2). Extant bivalves are an important component of marine and freshwater ecosystems, with more than 80% of species living in ocean habitats, and exhibiting varied ecologies. Sessile epifaunal bivalves, such as oysters and mussels, attach themselves to hard surfaces using cement or byssal threads, while infaunal burrowers bury themselves to different depths in sand or sediment on the seafloor or in riverbeds. Other sessile forms bore into hard sediments, coral or wood. Some species such as scallops are free-living and can move through the water by clapping the two shell valves together, or can dig into the sediment using their muscular foot. Although some bivalves are deposit feeders, the majority use greatly enlarged gill surfaces to filter food particles from the surrounding water (Chapter 4). Some species obtain all or part of their food through symbiosis with bacteria or zooxanthellae. Because bivalves are rich in

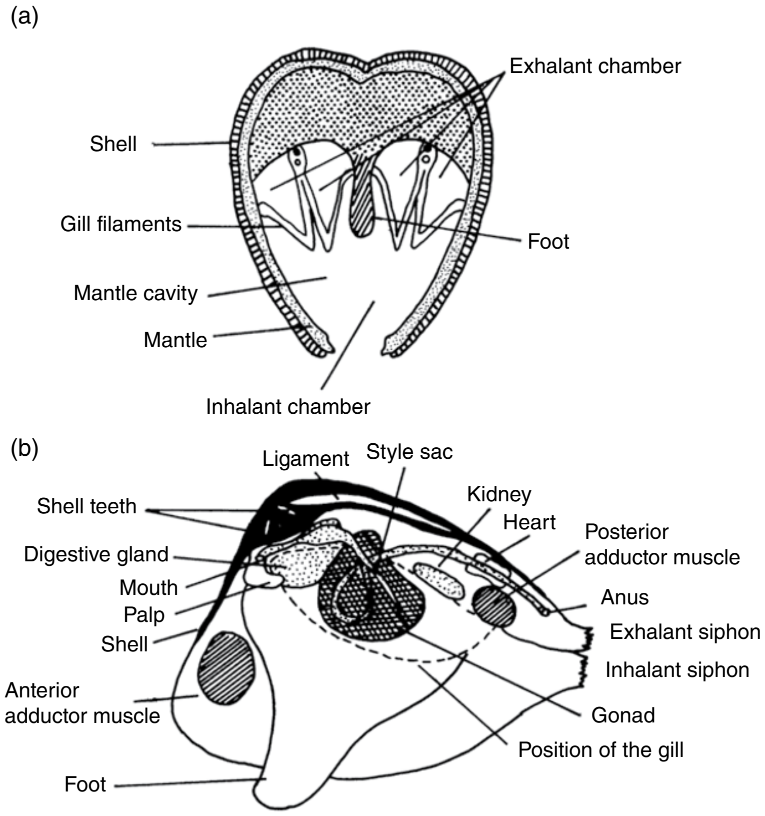

Figure 1.2 (a) Transverse section through a bivalve illustrating lateral compression and the position of the mantle, foot and gills. (b) Longitudinal section showing the major organs; gill omitted for clarity. Adapted from Barnes *et al.* (1993).
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protein they form the basis of valuable fisheries and aquaculture industries worldwide (Chapters 8 and 9). However, because of their mode of feeding they pump large volumes of water and thus have the potential to accumulate contaminants, bacteria, viruses and toxins, frequently posing significant public health risks (Chapter 12).

Despite the fact that bivalves, because of their strong shells, provide one of the most complete fossil record of any animal group, their systematics,[4] until recent times, lagged behind that of other animal groups. However, this situation has changed with researchers becoming increasingly involved in large-scale phylogenetic analyses using combinations of morphological, palaeontological and molecular data sources (Bieler & Mikkelsen 2006). Historically, there was a heavy reliance on single-character systems, for example shell hinge teeth, shell ligament, gill structure, gill ciliation, stomach morphology, mantle edge fusion and shell microstructure. This changed in the 1970s with the development of numerical systematics based on simultaneous analysis of multiple character systems. From the early 1990s gene sequence data became available and over the past two decades this data source has made a significant contribution in systematic studies, encompassing all Bivalvia as well as major groups within the class (Giribet 2008 and references therein; Plazzi & Passamonti 2010; Plazzi *et al.* 2011; Tsubaki *et al.* 2011; Sharma *et al.* 2012; Yuan *et al.* 2012).

Traditionally, bivalves were divided into five extant subclasses (Protobranchia, Pteriomorpha, Palaeoheterodonta, Heterodonta and Anomalodesmata), established mainly on the basis of shell structure and anatomy. However, a new classification was recently

Table 1.1 Classification of Bivalvia after Bieler *et al.* (2010).

Class Bivalvia	
Subclass Protobranchia	
Order	Nuculida
	Superfamily Nuculoidea
Order	Solemyida
	Superfamily Manzanelloidea
	Superfamily Solemyoidea
Order	Nuculanida
	Superfamily Nuculanoidea
Subclass Autobranchia	
Superorder Pteriomorphia	
Order	Arcida
	Superfamily Arcoidea
	Superfamily Limopsoidea
Order	Limida
	Superfamily Limoidea
Order	Mytilida
	Superfamily Mytiloidea
Order	Ostreida
	Superfamily Ostreoidea
Order	Pectinida
	Superfamily Anomioidea
	Superfamily Dimyoidea
	Superfamily Pectinoidea
	Superfamily Plicatuloidea
Order	Pteriida
	Superfamily Pinnoidea
	Superfamily Pterioidea
Superorder Heteroconchia	
Clade Palaeoheterodonta	
Order	Trigoniida
	Superfamily Trigonioidea
Order	Unionida
	Superfamily Etherioidea
	Superfamily Hyrioidea
	Superfamily Unionoidea
Clade Heterodonta	
Order	Lucinida
	Superfamily Lucinoidea
	Superfamily Thyasiroidea
Order	Carditida
	Superfamily Carditoidea
	Superfamily Crassatelloidea
Order	Venerida
	Superfamily Arcticoidea
	Superfamily Cardioidea
	Superfamily Chamoidea
	Superfamily Cyamioidea
	Superfamily Cyrenoidea
	Superfamily Cyrenoidoidea
	Superfamily Dreissenoidea
	Superfamily Gaimardiodea
	Superfamily Galeommatoidea
	Superfamily Glossoidea
	Superfamily Mactroidea

(*Continued*)

Table 1.1 (Continued)

Class Bivalvia	
	Superfamily Sphaerioidea
	Superfamily Tellinoidea
	Superfamily Ungulinoidea
	Superfamily Veneroidea
Order	Myida
	Superfamily Myoidea
	Superfamily Pholadoidea
Order	Uncertain
	Superfamily Hiatelloidea
	Superfamily Solenoidea
Order	Uncertain
	Superfamily Gastrochaenoidea
Order	Pholadomyida (=Anomalodesmata)
	Superfamily Ceratomyoidea
	Superfamily Clavagelloidea
	Superfamily Cuspidarioidea
	Superfamily Myochamoidea
	Superfamily Pandoroidea
	Superfamily Pholadomyoidea
	Superfamily Poromyoidea
	Superfamily Thracioidea
	Superfamily Verticordioidea

Adapted from Bieler *et al.* (2010). © BioOne.
Only extant taxa have been included.

proposed and adopted by the World Register of Marine Species (WoRMS; Bieler *et al.* 2010). The authors used a variety of phylogenetic information including molecular analysis, anatomical analysis, shell morphology and microstructure, as well as biogeographic, paleobiogeographic and geological information. This new classification of Bivalvia has been used for the following section.

Protobranchia are primitive, marine, infaunal bivalves that use their large labial palps in deposit feeding, the ctenidia being used solely for respiration, in contrast to other subclasses within Bivalvia. Protobranchs belong to the orders Solemyida, Nuculida and Nuculanida (Table 1.1). There is general agreement that Protobranchia is the first emerging lineage of Bivalvia and although most morphological studies have shown the subclass to be monophyletic, this has been questioned in more recent studies using molecular data (Giribet 2008 and references therein; Sharma *et al.* 2013). The subclass Autobranchia is divided into the superorders Pteriomorphia and Hereroconchia and includes all bivalves that have their ctenidia modified for filter feeding. Pteriomorphia contain entirely marine, mostly byssate and infaunal forms, such as many familiar and commercially important bivalves, for example mussels, oysters, arks and scallops. There are 11 superfamilies in this group (Bieler *et al.* 2010). The Heteroconchia comprise the clades Paleoheterodonta and Heterodonta (Table 1.1). Palaeoheterodonta contains two very distinct orders: the marine Trigoniida, remnants of a once diverse group, and the diverse freshwater Unionida (freshwater mussels and pearl mussels). This clade is regarded as basal to the remaining Autobranchia (Plazzi *et al.* 2011). Heterodonta, which now includes Anomalodesmata, is the largest, most widely distributed and most diverse of all bivalve clades, and includes the majority of familiar burrowing bivalves (cockles and clams), some of which live in freshwater, notably the invasive zebra mussel. Bieler *et al.* (2010) list 33 superfamilies in this clade (but see Giribet 2008).

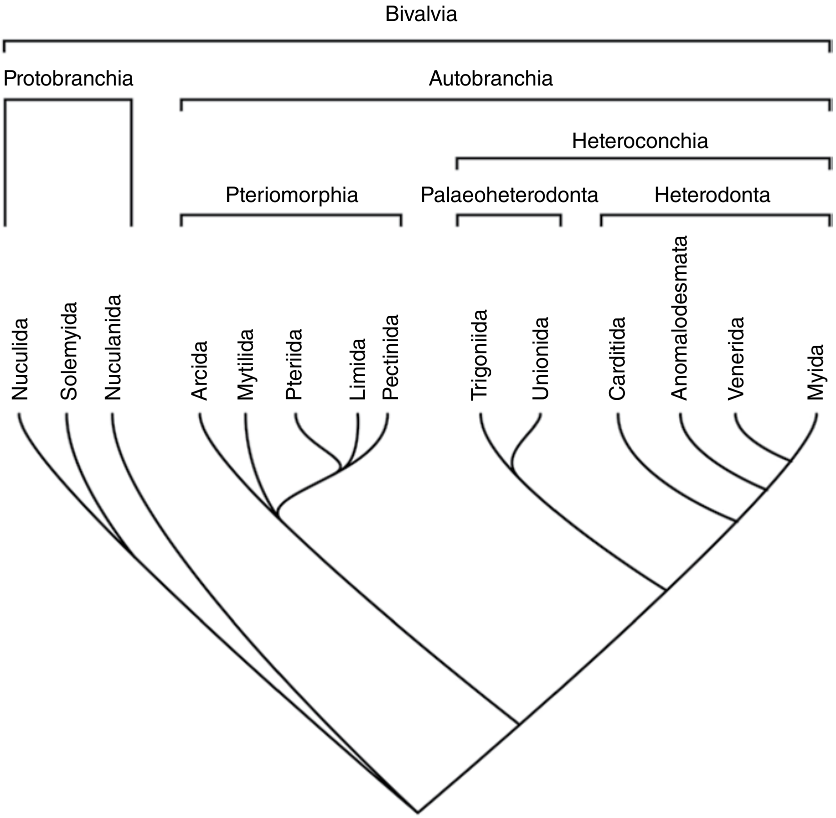

Figure 1.3 Phylogenetic diagram showing hypothesized relationships between the major clades recognized for the living members of the class Bivalvia. Note that the order Ostreida in the superorder Pteriomorphia and the order Lucinida in the clade Heterodonta (as per Table 1.1) are not included in the figure.
From Bieler and Mikkelsen (2006). Reproduced with permission of John Wiley & Sons.

Results from the combined analysis of morphological and molecular data sets support the monophyly of Autobranchia, Pteriomorphia, Heteroconchia, Palaeoheterodonta and Heterodonta (see Giribet 2008 for details). Those wishing to further explore relationships within and between different bivalve groups should consult Johnson and Haggart (1998); Harper *et al.* (2000); Bieler (2006); Taylor *et al.* (2007) and Ponder and Lindberg (2008). Figure 1.3 illustrates the hypothesized phylogenetic relationships between some of the major clades recognized for extant members of the class Bivalvia.

Evolution and adaptive radiation in Bivalvia

It is generally agreed that the early bivalves were shallow burrowers in soft substrates. They belonged to the Protobranchia and are represented today by fossil forms that date back to the Cambrian era of the Paleozoic period (500 mya), and also by some living forms such as the little nut shells, genus *Nucula*. These lie just barely covered in muddy sand, with the anterior end directed downward and the posterior end directed towards the soil–water interface. *Nucula* is a typical isomyarian bivalve, that is anterior and posterior adductor muscles are about the same size. Unlike most other bivalves the flow of water into the animal is from anterior and posterior directions (see Figure 1.4a and b). *Nucula* feeds on surface deposits by means of palps, long fleshy extensions of the mouth. Therefore, the ctenidia are primarily respiratory organs. The development of labial palps was perhaps a necessary stage in the evolution of filter feeding, making it possible for the mouth to be lifted off the substrate. There is no doubt that study of this group makes it easier to understand the transition from the primitive mollusc to more modern bivalves.

One of the most important developments in the evolution of modern bivalves was moving the site of water intake to the posterior of the animal (Figure 1.4b and d). This made it possible for bivalves to penetrate sand or mud 'head first' with the posterior end in free communication with the water above. Extensions of the mantle to form siphons at the posterior enabled the animals to live deeper and deeper under the surface. As bivalves evolved, plankton in the incoming current was increasingly adopted as a source of food, the ctenidia replacing the palp processes as the feeding organs. The chief modification of the ctenidia for filtering was the lengthening and folding of individual gill filaments.

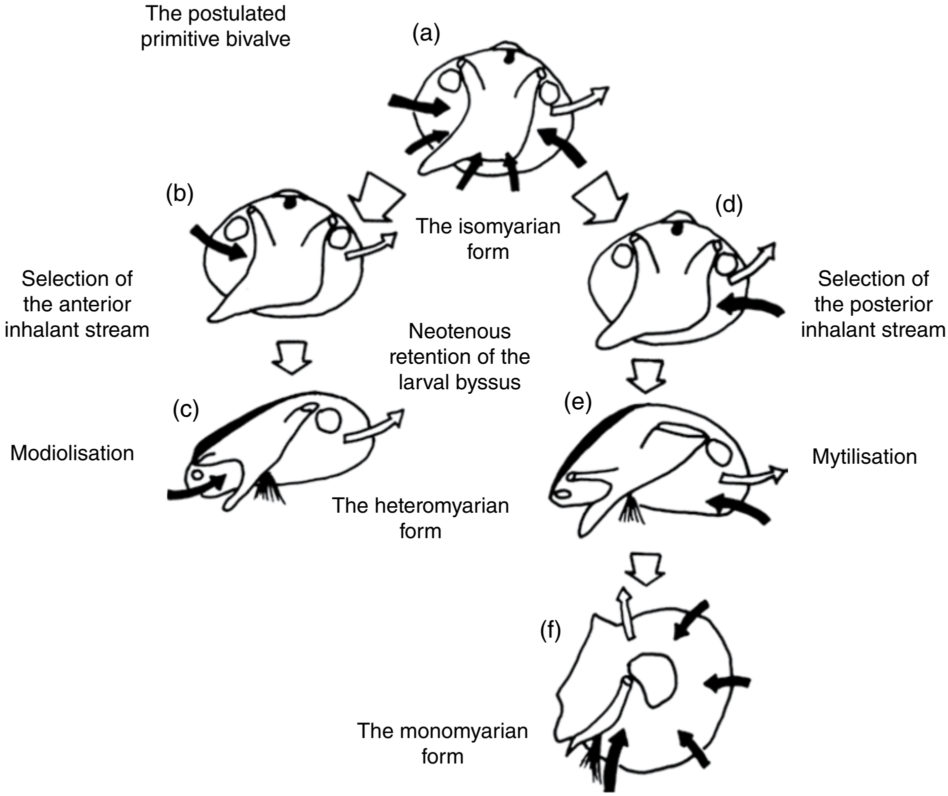

Figure 1.4 The evolution of the heteromyarian form, and ultimately monomyarian form, from an isomyarian ancestor. (a) Postulated primitive isomyarian bivalve such as *Nucula* or *Glycymeris* with water capable of entering the mantle from anterior and posterior directions. (b) Selection of the anterior inhalant stream by representatives of such groups as the Lucinoidea (shallow burrowers in tropical mud) can only result in the process of heteromyarianisation leading to (c) a modioliform shell found in ark shells, *Arca*. (d) Selection of the posterior inhalant stream can result in full expression of the heteromyarian form (e), for example in the mussel, *Mytilus*, and ultimately, the monomyarian form (f), in oyster and scallop species.
From Morton (1992). Reproduced with permission of Elsevier.

In addition, many extra filaments were added so that they extended as far forward as the labial palps. Both of these modifications greatly increased the surface area of the ctenidia. It is believed that the triangular-shaped filaments of the primitive bivalve gill progressively changed over evolutionary time to the W-shaped filaments of the modern bivalve gill (see Cannuel *et al.* 2009). A notch at the bottom of each side of the W lines up with similar notches on adjacent filaments to form a food groove that extends the length of the underside of the ctenidia. Yonge (1941) suggested that since the food groove was necessary for nutrition these notches probably preceded folding of the gill filaments. Changes in both ciliation and water circulation followed. The exploitation of filter feeding led to the first increase in bivalve diversity and body plan disparity so that by the Ordovician period of the Paleozoic era (~450 mya) all extant higher lineages and feeding types were present and had colonised a wide variety of habitats that had hitherto been inaccessible to their protobranch ancestors (Giribet 2008 and references therein).

An important factor in this diversification was the development of a larval byssal apparatus in the basal Autobranchia, which was absent in Protobranchia, and which was later retained in some adult forms (Morton 1996). Byssus threads fixed one valve to the substrate, thus providing attachment. Consequently, individuals could exploit a variety of hard substrates, allowing them to adopt an epibenthic lifestyle in new adaptive niches (Giribet 2008). The byssal apparatus is seen as a persistent post-larval structure that evolved for temporary attachment of the animal to the substrate during the vulnerable stage of metamorphosis. In most species of oysters, clams and scallops the byssal apparatus is subsequently lost. However, in mussels it persists into adult life (Figure 1.4c and e), allowing them to anchor themselves and live in more wave-exposed habitats (Morton 1996). In byssally attached forms there has been a tendency for the anterior (head) end of the animal to become smaller with a corresponding enlargement of the posterior end. Accompanying this change there has also been a reduction of the anterior adductor muscle and an increase in the size of the posterior adductor muscle. The evolution of this heteromyarian form led to the development of a pronounced triangular shape (Figure 1.4c). This is very marked in mussels in the order Mytilidae (see Figure 1.4e) and is believed to be an adaptation to living in clusters, expansion of the posterior shell allowing free access, posteriorly, to the water above (Morton 1992). The heteromyarian condition has been seen as a stepping-stone towards the monomyarian form and the adoption of a horizontal posture (Figure 1.4f). Monomyarian bivalves, such as scallops and oysters, have largely circular shells, all trace of the anterior adductor muscle is lost, and the body has been reorganised around the enlarged and more or less centrally placed posterior muscle. Water enters around two-thirds or more of the rounded margins of the shell. Shell attachment has led to varying degrees of inequality in the size of the two shell valves. In scallops the shell valves are circular but both can be concave and similar, or the left (uppermost) valve may be flat. Like oysters they also lie in a horizontal position on the substrate. However, scallops far from being fixed are active, swimming bivalves. In early life they use byssus threads for attachment to algae, but before they attain a size of 15 mm the majority of species have detached themselves to take up a free-living existence on the seabed.

Cementation also evolved during the Paleozoic era. This adaptation arose independently in several marine pteriomorphians, heterodonts and anomalodesmatans, as well as in freshwater unionids, peaking in the Late Triassic and Jurassic periods of the Mesozoic era (150–220 mya) as a possible response to the appearance of many predatory groups (Vermeij 1977; Harper 1991). During the Triassic another important development occurred when an ancestral unionid (Paleoheterodonta) colonised freshwater environments. Giribet (2008) suggests that this move might have been triggered by evolution of a novel mode of development using microscopic glochidia larvae with fish as intermediate hosts.

Burrowing into the substrate is the habit most extensively exploited by bivalves. Contact is maintained with the surface by way of siphons that extend from the posterior end of the animal. During the Cenozoic era (up to 60 mya) soft, nutrient-rich sediments on continental margins allowed diversification of shallow burrowing, globular, strongly ribbed forms and deep burrowers with smooth, blade-like shells (Giribet 2008). Cockles (e.g. *Cardium* spp.) are shallow burrowers, while many clam species, for example razor clams (*Siliqua*, *Ensis*), burrow as deep as 60 cm. The geoducks (*Panopea*) on the West Coast of the United States are among the deepest burrowers, digging down to a depth of over a metre, aided by a streamlined shell for fast burrowing and fusion of the mantle edges (apart from a small gape for the large muscular foot) to prevent entry of sediment into the mantle cavity. Geoduck siphons are so large that they can no longer be retracted into the shell. Many bivalves that burrow deeply (>30 cm) live in permanent burrows, moving deeper as they grow larger. This lifestyle is brought to an extreme by bivalves that bore into hard substrates such as shell, coral, wood and rock and are permanently locked in their burrows and are, therefore, inevitably dependent on outside sources of food. However, in wood-boring bivalves excavated 'sawdust' is the principal food source and phytoplankton is only used to supply the nitrogen and vitamins missing from an all-wood diet.

While the number of species of bivalve molluscs is only about 10% of that documented for gastropods, there is substantial interest in this group chiefly because so many of its members are eaten by humans in large amounts. In the following chapters attention will be focused only on bivalves of commercial importance: mussels, oysters, scallops and clams. Although the general term 'shellfish' will sometimes be used to refer to this group, the author is well aware that for many people the term has a wider meaning and incorporates many other non-bivalve molluscs not dealt with in this book, such as abalone, periwinkles, whelks and even crustaceans such as crabs, prawns and shrimp.

Notes

1 A system of classification based on the phylogenetic relationships and evolutionary history of groups of organisms, rather than on purely shared features.
2 Orthologs are genes whose encoded proteins fulfill similar roles in different species.
3 A clade is a monophyletic group.
4 The classification of organisms and the evolutionary relationships among them.

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2 Morphology of bivalves

Introduction

In this chapter the approach is to use much studied, representative species from each group of mussels, oysters, scallops and clams rather than to attempt an exhaustive description of the morphology of all bivalve species. So the following species have been chosen: for mussels the genus *Mytilus*, for oysters *Ostrea* and *Crassostrea*, for scallops *Pecten maximus* and for clams *Mercenaria mercenaria*.

The general morphology and functions of the shell, mantle, foot, gill, alimentary canal, gonad, heart, kidney and nervous tissue are described in the following sections. Additional information on their particular roles in feeding, reproduction, and circulation, excretion and osmoregulation, is presented in Chapters 4, 5 and 7, respectively.

Shell

Bivalves have two shell valves that are hinged dorsally and connected by an elastic ligament. Adductor muscles hold the valves together, and relaxation of the ligament and contraction of these muscles open and close the shell, respectively. A series of interlocking teeth and sockets along the hinge line prevent the valves from sliding against one another. The shell has several functions: it acts as a skeleton for the attachment of muscles, it protects against predators, and in burrowing species it helps to keep mud and sand out of the mantle cavity.

The main component of the shell is calcium carbonate, formed by the deposition of crystals of this salt in an organic matrix, which is composed of the polysaccharide β-chitin, a hydrophobic silk protein and a complex assemblage of hydrophilic proteins, many rich in aspartic acid (Addadi *et al.* 2006). The mineral component represents more than 95% of the shell weight, while 1–5% represents the organic matrix. Three layers make up the shell: (1) a thin outer periostracum of horny conchiolin, a fibrous insoluble protein, often much reduced due to mechanical abrasion, fouling organisms, parasites or disease; (2) a middle prismatic layer of aragonite or calcite, crystalline forms of calcium carbonate and

Marine Bivalve Molluscs, Second Edition. Elizabeth Gosling.

(3) an inner nacreous layer composed of tablets of aragonite arranged in layers that are separated by sheets of organic matrix composed of elastic biopolymers of chitin and silk-like proteins; nacre is either of dull texture or iridescent mother-of-pearl, depending on the species.

Techniques such as scanning electron microscopy (SEM), transmission electron microscopy (TEM) and X-ray and electron diffraction patterns have played an important role in clarifying shell microstructure (Weiner *et al.* 1983; Levi–Kalisman *et al.* 2001; Nudelman *et al.* 2008), while analytical methods such as secondary ion mass spectrometry (SIMS; Shirai *et al.* 2008), electron probe microanalysis (EPMA; Jacob *et al.* 2008) and laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS; Jacob *et al.* 2008) have been used to elucidate the chemical composition of the shell in several species. To date, more than 10 morphological types of shell structure are discriminated among bivalves (Kobayashi & Samata 2006).

The construction of the shell begins very early in larval development. An area of ectodermal cells in the dorsal region of the developing embryo secretes the first larval shell. The secretion of a second larval shell by the mantle, rather than the shell gland, follows soon after. After metamorphosis the secretion of the adult shell begins. This is more heavily calcified, has different pigmentation and more conspicuous sculpturing than the larval shell. Growth takes place at the edge of the shell in a small fluid-filled space sealed by the periostracum and the epithelial cells of the mantle. Into this space these cells release all the precursors for mineralization: mineral ions actively extruded from the cytoplasm, and organic components of the shell matrix that are secreted by exocytosis (Marin & Luquet 2005). The outer mantle fold secretes the periostracum and prismatic layers, while the inner nacreous layer is secreted by the general mantle surface (see later). Shell matrix proteins play a key role in the mineralization process (see Marin & Luquet 2004 for a review), and recently several genes that code for nacreous and prismatic layer proteins in bivalves have been identified (Inoue *et al.* 2010; Jackson *et al.* 2010).

The shell grows in circumference by the addition of material from the edge of the mantle, and grows in thickness by deposition from the general mantle surface. Calcium for shell growth is obtained from the diet or taken up from seawater. Carbonate is derived from the CO_2/bicarbonate pool in the animal's tissues. The energy required for shell growth is not an insignificant portion of a bivalve's total energy budget (Hawkins & Bayne 1992).

The colour, shape and markings on the shell vary considerably between the different groups of bivalves. Not surprisingly, therefore, shell characters are consistently used in species identification (Table 2.1).

Mussels

In mussels the two shell valves are similar in size, and are roughly triangular in shape (Figure 2.1a and b). The valves are hinged together at the anterior by means of a ligament. This area of the shell is called the umbo. The interior of the shell is white with a broad border of purple or dark blue. This is called the pallial line and is the part of the shell along which the mantle is attached when empty shells are examined. On the inside of each valve are two muscle scars, the attachment points for the large posterior adductor muscle and the much-reduced anterior adductor muscle. In *Perna* species the anterior adductor scar in absent. Anterior and posterior retractor muscles are also attached to the shell; these control the movement of the foot (see later). The foot in turn secretes a byssus, a bundle of tough threads of tanned protein. These threads emerge through the ventral part of the shell and serve as mooring lines for attachment of the mussel to the substrate, and to other mussels.

Table 2.1 The major shell characters used in species identification.

Character	**Variations**
Shell shape	Oval, circular, triangular, elongate, quadrate
Shell valves	Similar (equivalve), or dissimilar (inequivalve)
Colour	Shell exterior: background/surface patterns; shell interior: white, pearly, etc.
Ribs	Number, width, prominence (distinct, flattened)
Sculpturing	Concentric lines, ridges, grooves
Ligament	Shape, position (internal, external), structure
Umbo	Position (anterior, terminal, subterminal)
Adductor scars	Number, size, position
Hinge line	Straight or curved, presence of 'ears' (size, shape)
Hinge teeth	Number, type
Pallial line	With or without a sinus
Pallial sinus	Size
Shell microstructure	Mineral composition and structure of shell layers

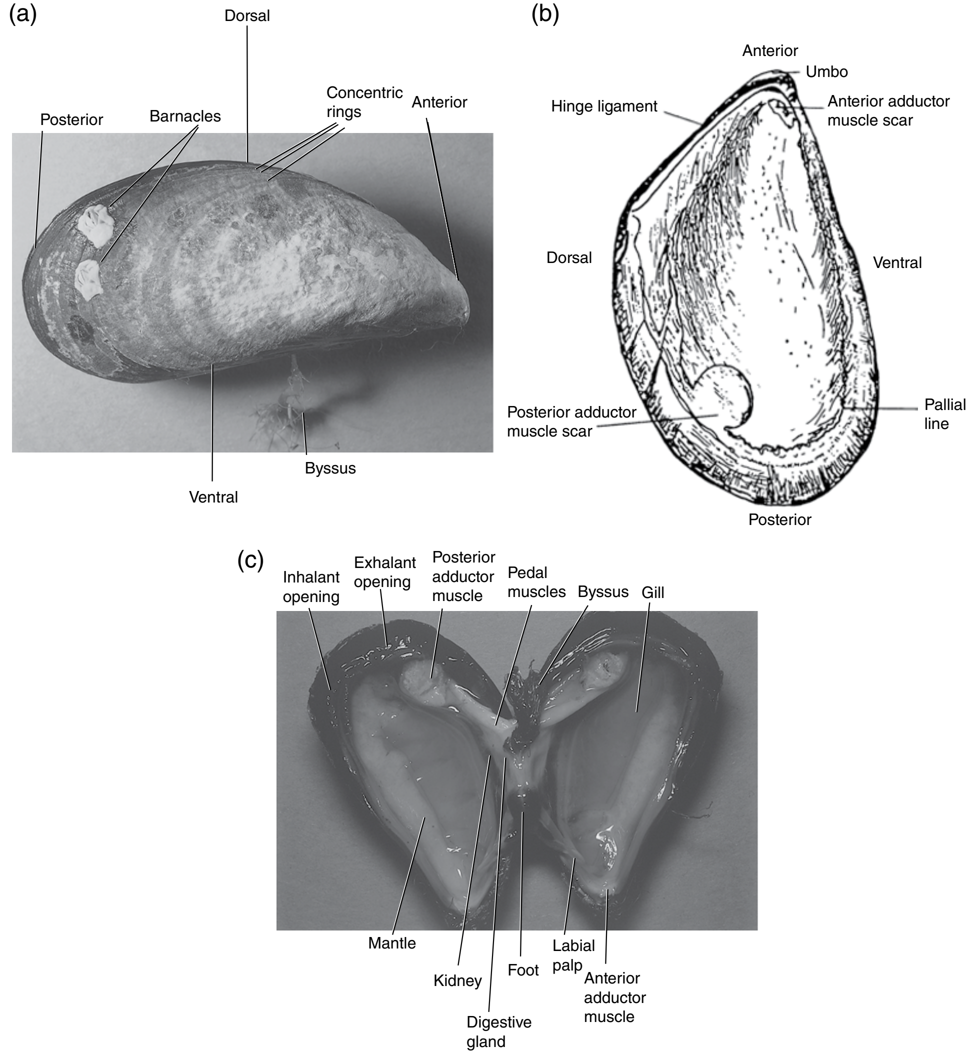

Figure 2.1 The (a) external, (b) internal shell and (c) internal features of the mussel *Mytilus edulis*. Photograph and permission to reproduce by Craig Burton.

The colour of mussel shells is controlled by several genes (Innes & Haley 1977; Newkirk 1980) and also varies depending on the age and location of the animal (Mitton 1977). In the intertidal zone the blue mussel *Mytilus edulis* has a blue-black and heavy shell, while in the sublittoral region, where mussels are continuously submerged, the shell is thin and brown with dark brown to purple radial markings. In the rock mussel *Perna perna* the shell is red-maroon with irregular patches of light brown and green. Juvenile green mussels, *Perna viridis*, have bright green or blue-green shells, but older individuals tend to have more brown in the shell (Siddall 1980).

The presence of concentric rings on bivalve shells has been extensively used to estimates their age. In many species of scallops and clams these rings have been shown to be annual in origin and therefore can be used as a reliable estimate of age. However, in mussels there are few geographic locations where the rings provide an accurate estimate of age (Lutz 1976). One must therefore resort to shell sectioning for age determination. When longitudinal sections are examined microscopically distinct growth bands in the inner nacreous layer are clearly seen (see Figures 6.8 and 6.9 in Chapter 6). These are formed at a rate of 1 year^{-1} during spring (Lutz 1976). In addition, in the middle prismatic layer there are micro-growth bands, which have a tidal periodicity (Richardson 1989). These bands, together with the annual bands, can thus be used to track individual short-term and long-term variations in growth rates, respectively.

Figure 2.2 illustrates the convention used for the principal shell parameters. Height is the distance from the hinge line to the shell margin. Length is the widest part across the shell at 90° to the height. The width is measured at the thickest part of the two shell valves (Dore 1991).

Under optimal conditions, such as in the sublittoral zone, *M. edulis* and the Mediterranean mussel *Mytilus galloprovincialis* attain a shell length of 100–130 mm, whereas in marginal conditions, for example the high intertidal zone on an exposed shore, mussels may measure as little as 20–30 mm, even after 15–20 years (Seed 1976). This is not, however, a universal pattern. In South Africa the native mussel *P. perna* is largest on more exposed shores,

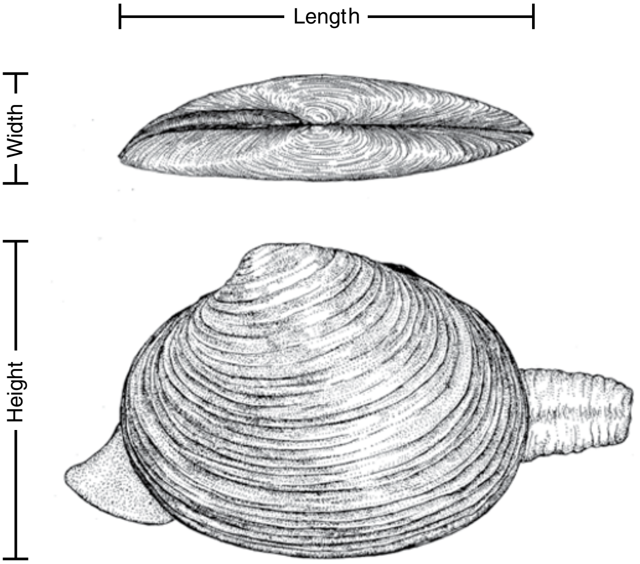

Figure 2.2 The convention used for the main shell measurements in bivalves. © Sandra Noel http://www.noeldesigninterp.com. Reproduced with permission.

whereas the invasive mussel *M. galloprovincialis* is largest at intermediate levels of shore exposure (McQuaid *et al.* 2000; Hammond & Griffiths 2004). Shell shape is also very variable in mussel species. The shells of densely packed mussels have higher length-to-height ratios than those from less crowded conditions. This is most extreme in older mussels and ensures that they can more readily exploit posterior feeding currents, as they are effectively elevated above younger mussels in the same clump (Seed & Suchanek 1992). Shell morphology can also be correlated with wave exposure; on the west coast of Canada both juvenile and adult *Mytilus trossulus* at wave-exposed sites show a lower shell height-to-shell width ratio, and a thicker shell than mussels from sheltered locations (Akester & Martel 2000). Shell shape has also been used in taxonomic studies to differentiate both within and between various *Mytilus* taxa (Innes & Bates 1999; Krapivka *et al.* 2007; Gardner & Thompson 2009).

Mussels have been extensively used to assess environmental contamination. Radionucleotides and metals such as uranium, vanadium, silver, cadmium, cobalt, zinc and lead are highly concentrated in the shell (Livingstone & Pipe 1992; Widdows & Donkin 1992; Fisher *et al.* 1996; Boisson *et al.* 1998). Antifouling agents, for example tributyl tin (TBT), cause shell deformities, characterised by the production of cavities within the shell, in both mussels and oysters.

Oysters

In the European flat oyster *Ostrea edulis*, the shell valves are approximately circular and are hinged together on the dorsal side by a horny ligament (Figure 2.3a(i)). The right valve is flat while the left is cupped (Figure 2.3a(ii)). At rest on the sea bottom the flat valve is uppermost and the cupped valve is cemented to the substrate. The American Eastern oyster *Crassostrea virginica* also has dissimilar valves, but the general shell shape is more elongated and the left valve is more deeply cupped than in *Ostrea* (Figure 2.3b(i) and b (ii)). In both oyster species the shell colour is off-white, yellowish or cream but often with purple or brown radial markings in *C. virginica*. The inside of the shell valves is pearly-white and there is a single large adductor scar. The shell in both oyster groups is thick and solid and both valves have distinct concentric sculpturing, with the surface of the cupped valve more raised and frilled in *Crassostrea*. The concentric markings cannot be used to determine the age of oysters, and one must resort to sectioning of the hinge plate for an accurate estimate (Kraeuter *et al.* 2007). In general, *O. edulis* has a maximum shell height of 100 mm, while *C. virginica* grows as large as 350 mm; *Saccostrea* species tend to be smaller, with a maximum shell height of 60 mm. For a very comprehensive account of larval and adult shell structure in *C. virginica* see Carriker (1996).

Scallops

Scallops more than any other group of bivalves have attracted the interest of naturalists and collectors for centuries. ‘In appearance no other molluscan shells have so pleasing a design and range of colours as pecten shells’ (Cox 1957). In the king scallop *P. maximus*, the left valve is flat and is slightly overlapped by the right one, which is convex (Figure 2.4a). Adults recess in the substrate with the flat valve uppermost. The two valves, which are roughly circular, are held together along the hinge line by a rubbery internal ligament (see Kitagawa & Li 2004 for details). Typically, there are 15–16 ribs radiating from the hinge. These alternate with grooves and give the scallop its distinct comb-like appearance. There are two projecting ‘ears’ or auricles on either side of the umbo; these vary in size and shape and are used, along with other shell characters, to differentiate one species of scallop from

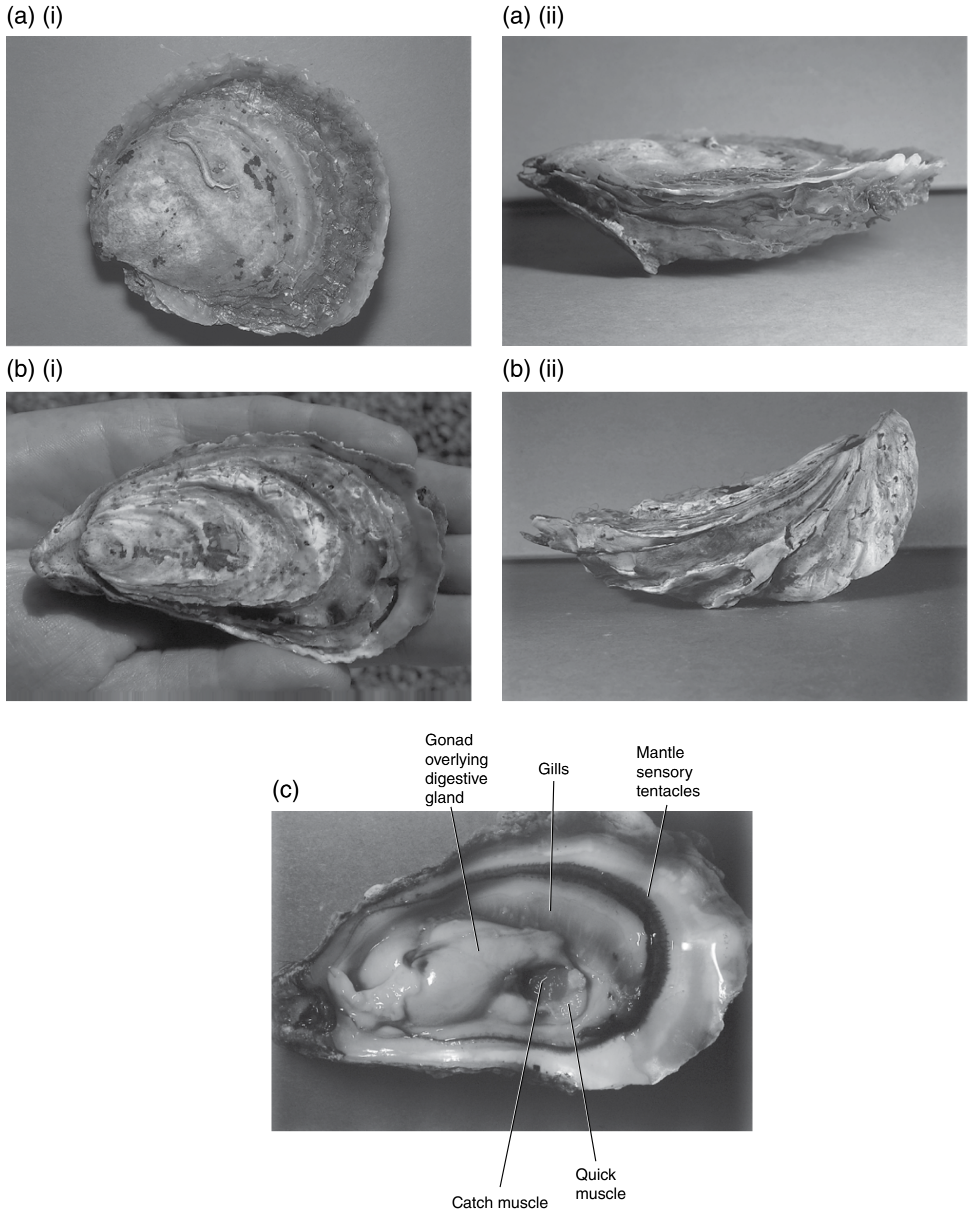

Figure 2.3 External shell of (a) *Ostrea edulis* (i) & (ii) and (b) *Crassostrea gigas* (i) & (ii). (c) Internal features of *C. gigas*.
Photograph and permission to reproduce by Craig Burton.

the next (see Table 2.1 for shell characters used in species identification). There is a large, centrally placed, adductor muscle, a standard seafood commodity that is widely traded and universally available. Distinct annual rings on the shell make ageing of scallops a relatively easy task, compared to mussels and oysters. Shell size in scallops varies quite a bit depending in the species: *P. maximus* can be up to 150 mm in length, while the sea scallop *Placopecten magellanicus* and the yesso scallop *Placopecten (=Mizuhopecten) yessoensis* can reach a size of 200–230 mm. Other species such as the queen scallop *Aequipecten (Chlamys)*

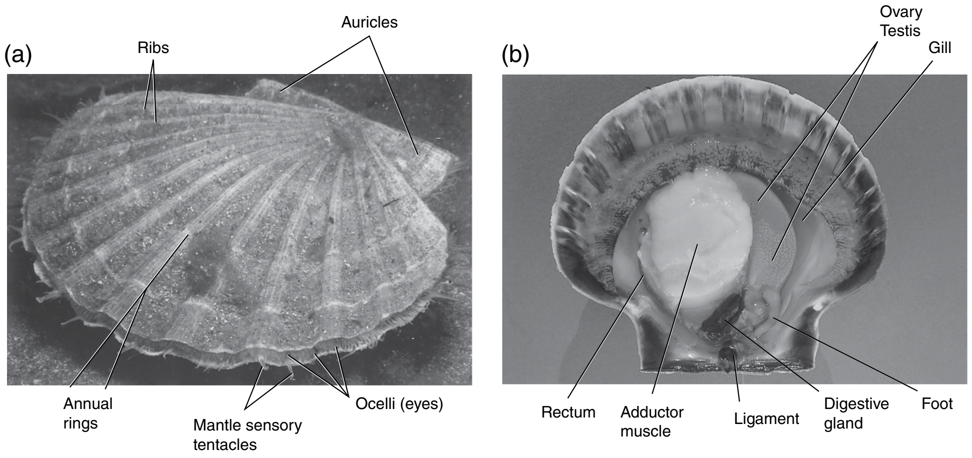

Figure 2.4 (a) External shell and (b) internal anatomy of the scallop, *Pecten maximus*. Photograph and permission to reproduce by Craig Burton.

opercularis, the Icelandic scallop *C. islandica* and the bay scallop *Argopecten irradians* seldom grow larger than 100 mm.

The beautiful colours that are a feature of scallop shells are laid down when the shell is being formed. In *P. maximus* the colours range from off-white to yellow to light brown, often overlaid with bands or spots of darker pigment. In *A. irradians*, background colour of the shell and overlying pigment distribution is coded by one gene locus (Adamkewicz & Castagna 1988), which has recently been mapped (Qin *et al.* 2006). In the Chilean scallop *Argopecten purpuratus*, there are at least three separate loci controlling shell colour (Winkler *et al.* 2001), which aside from their particular phenotypic effects have been associated with differences in growth and survival (Wolff & Garrido 1991).

The scallop shell, as well as the digestive gland, kidney and gills, accumulate trace elements, such as cobalt, manganese and zinc, from their environment, as well as natural and anthropogenic radionuclides (see Metian *et al.* 2011 for references).

Clams

Clams are a very diverse group of bivalves in that there is notable variation in the shape, size, thickness, colour and degree of sculpturing of the shell from one species to the next. The one feature that all clams have in common is that they burrow into the seabed. Consequently, both shell and body (see later) display modifications necessary for this type of existence. The quahog clam *M. mercenaria* has a thick, triangular shell (Figure 2.2). It is grey or brown with a sculpturing of numerous shallow concentric rings that run around the shell, parallel to the hinge. Annual rings are clearly visible on the shell exterior and thus ageing in this species, and indeed in many of the other commercially important clam species, is an easy task. The inside of the shell is glossy white, often with bluish-purple tints. It was this feature that made them valued as currency in earlier times (Dore 1991). There are three conspicuous teeth on each valve and each tooth fits into a corresponding socket on the opposing valve (Figure 2.5). This ensures an intimate fit when the valves are closed. The shell interior is marked by an anterior and posterior adductor muscle scar, a distinct pallial line and a short pallial sinus – the indentation indicating the position of the retracted siphons in the closed shell (see later). The depth of the pallial sinus is a very reliable indicator of the length of the siphons, and thus the burrowing depth of a particular clam species.