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# 1 Phylogeny and evolution of bivalve molluscs

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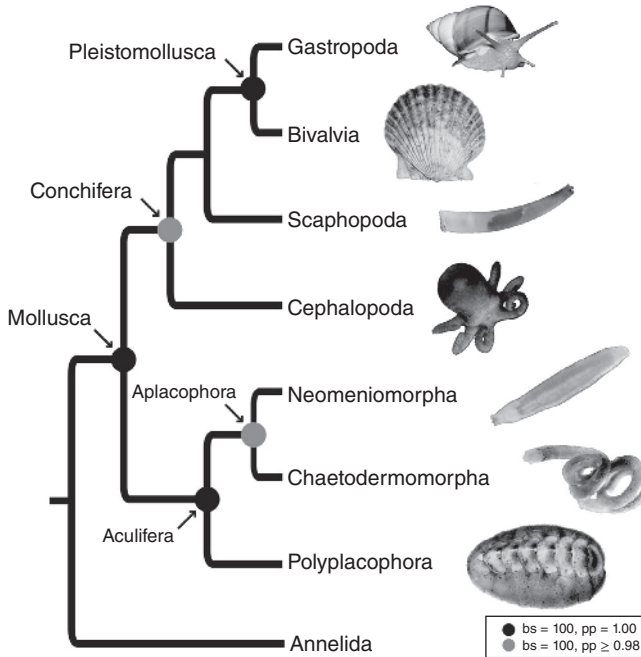
The phylum Mollusca is one of the largest, most diverse and important groups in the animal kingdom, with at least 50 000 described species and probably as many as 200 000 living species, most of which are marine. The phylum has a remarkable fossil record going back to the Early Cambrian some 540 million 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<sup>1</sup> (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)



**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.

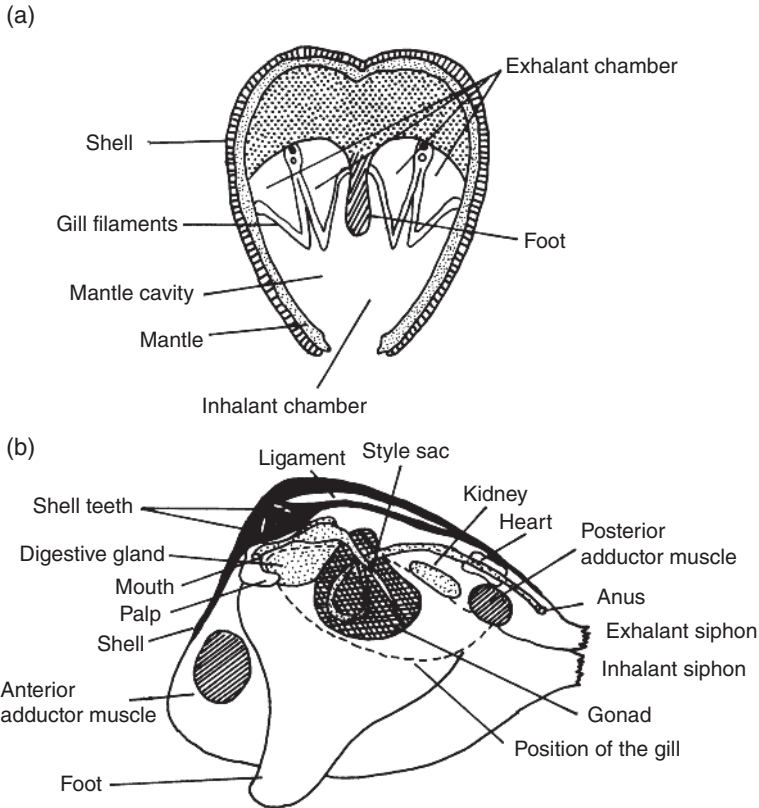
Until relatively recently morphological data were the only source used to deduce phylogenetic relationships within the Mollusca. In the 1980s the application of molecular methods was seen as a potentially important advance towards elucidating relationships of this major taxon. Most analyses have focused 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 Polyplacophora 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<sup>2</sup> 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 Monoplacophora (Figure 1.1). Their results strongly supported two major clades<sup>3</sup>: 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 Monoplacophora, 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). Reproduced with permission of John Wiley & Sons.

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,<sup>4</sup> 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 Pteriomorpha	
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 Cyrenoideoidea
	Superfamily Dreissenoida
	Superfamily Gaimardioida
	Superfamily Galeommatoidea
	Superfamily Glossoidea
	Superfamily Mactroidea

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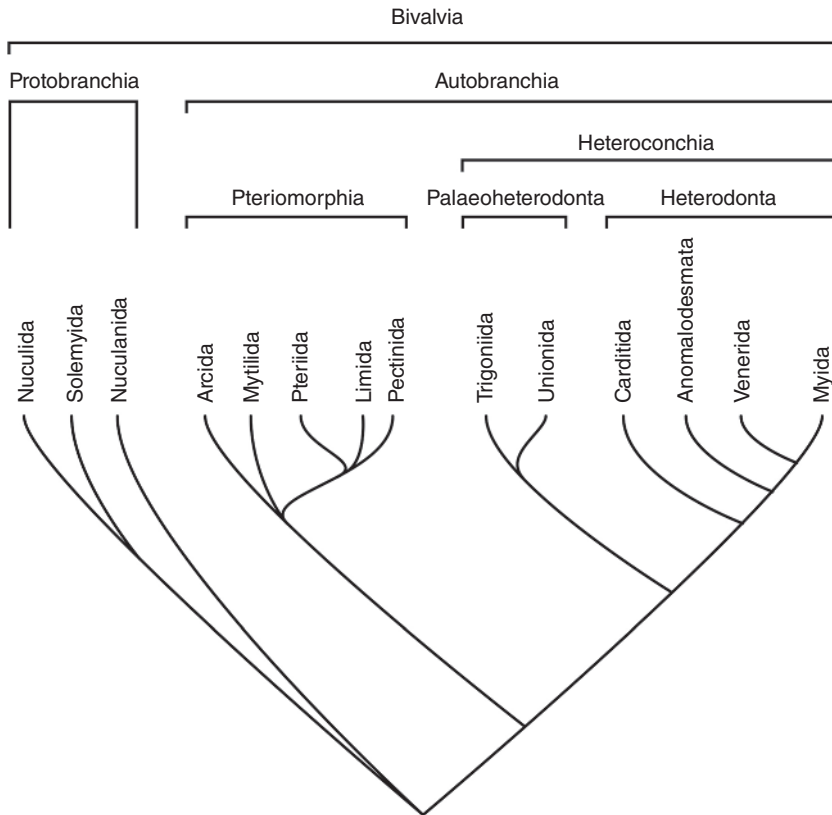
**Table 1.1** (Continued)

<b>Class Bivalvia</b>	
	Superfamily Sphaerioidea
	Superfamily Tellinoidea
	Superfamily Ungulinoidea
	Superfamily Veneroidea
Order	Myida
	Superfamily Myoidea
	Superfamily Pholadoidea
Order	Uncertain
	Superfamily Hiattelloidea
	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 Pteriomorpha and Heteroconchia and includes all bivalves that have their ctenidia modified for filter feeding. Pteriomorpha 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 Pteriomorpha 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.

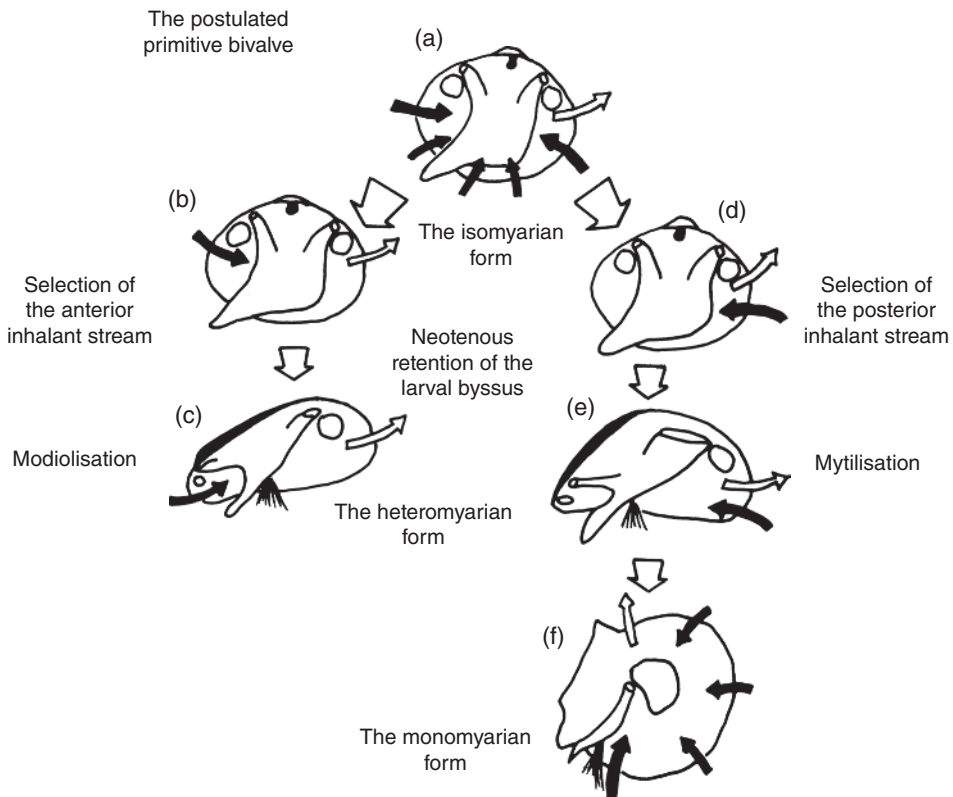
Results from the combined analysis of morphological and molecular data sets support the monophyly of Autobranchia, Pteriomorpha, Heteroconchia, Palaeoheterodonta and Heterodonta (see Giribet 2008 for details). Those wishing to further explore relationships within and between different bivalve groups 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 modioliiform 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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