CARLETON UNIVERSITY

Brachiopods and Bivalves

A theory on the morphology

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Brachiopods and Bivalves are superficially similar, but are rather distantly related. Both are twin-valved and are filter-feeders. That said, what caused these morphological convergences or possibly divergences? What similarities are there? What distinguishes them from one to another?

Abstract

The *Brachiopoda* phylum is compared to the *Bivalvia* class. An attempt is made at explaining what could have influenced their morphology as well as to explore what similarities and differences these two groups exhibit. They are commonly confused due to their similar external shells. Both of these are organisms with "valves" (somewhat symmetrical), but many differences that exist between the two: these might not seem quite as obvious at first sight. The most common way of differentiating them is using the symmetry content these two groups expose and express differently. *Brachiopoda* have their plane of symmetry perpendicular to the hinge of the valves. In contrast, *bivalvia* (with exceptions from scallops and oysters) have a plane of symmetry parallel to this hinge. The morphological changes are assumed to be the direct result of natural selection. However, organisms are known to able to change morphologically during their lifespan. It has been concluded that the superficial resemblance is from the same ancestors rather than a result of convergent evolution. Both of them are found to occupy similar niches but exhibit a few differences. Brachiopods mainly focus on simply keeping a single location that is stable and have developed many different apparatus in order to achieve this goal. Bivalves are more flexible in that are mobile. Both are able to burrow down into the sediment, but bivalves are able to go much deeper or change their lateral location altogether if necessary. Knowing the significant advantages that bivalves have over brachiopods and that they can share similar lifestyles, it is somewhat surprising that both still coexist to this day. This is most likely due to the slightly different environments that these two can occupy.

Introduction

Brachiopoda and Bivalvia are often confused by their similar exterior, but have some differences in live styles and internal anatomy. Although the two are not closely related, their morphology of a twin-valved shell is possibly due to similarities in their ecological niches. That being said, it is most likely that they originated in a similar niche and became divergent more internally then externally as they evolved with time. They have can have similar lifestyles but have come to different adaptations to arising external or environmental pressures such as salinity, competition, temperature changes, substrate type, etc.

Brachiopod Morphology

The term ‘Brachiopoda’ comes from Ancient Greek, the prefix *brachio–* meaning something that is related to an arm and the suffix *–pod* meaning foot. Brachiopods, commonly known as lampshells, are amongst the most successful invertebrate phyla. Their first appearance datum is within the Early Cambrian which collides with the well-known and so-called “Cambrian Life Explosion”. They have ever since evolved, diversified and lived on throughout the Paleozoic dominating low-level benthic suspension feeding. They are mainly composed of a pedicle (resembling an “arm” or “lamp stand”) and a shell with two valves (resembling a “foot” or “lamp”). From the outside, they might seem almost the same as bivalves. However, their feeding methods, life styles and internal structures (such as soft tissues) are quite definitely different from one another (see Figure 1).

Brachiopods are sessile (non-mobile): most remain permanently attached to the substrate via their external stalk-like appendage known as the pedicle: it essentially allows them to maintain or “anchor” their position in the water column. As with most suspension feeders, they tend to remain in a local area and extract food from the water around them. They are able to do this using a structure known as a lophophore: this organ can be used for both feeding and respiration. These are mainly rings or crowns with fine tentacles. These tentacles are covered with fine little “hairs” known as cilia. These are also responsible for generating the “feeding current”: a current of water with food particles that flows towards the mouth or the gape. That being said, there is mucus found on these cilia which essentially enable them to create adhesion with the food particles to filter them out from the indrawn water. The lophophore is supported by the brachium. This can be a calcareous structure in some species, otherwise known as a brachidium. Common types of this support structure include brachiophores (a pair of prong-like extensions), spiralia (a pair of spiral-like or coiled structures) and “loops” (hoop-like structures). The mentioned examples are all attached to the brachial valve (described later).

The two valves of the shell are different: one ventral and one dorsal. One of the valves is termed the pedicle valve where the stalk-like appendage is attached: this can be the ventral or dorsal valve depending on the species. Dorsal and ventral are terms used in relation to the internal morphological features (soft-body parts) of the organism. Bearing this in mind, brachiopods generally have their pedicle exiting from the ventral valve. The currently living *Magellania* is an example of this. The other valve is referred to as the brachial valve where it contains supports for the lophophores. Following with our last example, this would be the upper or dorsal valve. Evidently, the pedicle valve is larger than the brachial valve due to the pedicle opening. Some extinct brachiopods have evolved and lost their pedicles: a free-living mode. However, they were still benthic, lying idle on or partially buried in the seafloor. Even though brachiopods tend to have shells with different size valves, all of them exhibit bilateral symmetry. The plane of symmetry is perpendicular to the hinge line. In other words, this plane cuts perpendicularly through both valves of the shell.

The umbo or beak is the initial point where the valve starts growing (or secreting). Valves with radial ornamentation generally point towards this origin. Opposite to the posterior or apex (where the beak and hinge is located) is the opening of the valves: this is the anterior. The margin or trace between this “opening” is termed the commissure. In one species this can be a relatively straight feature whereas in another, this can be sinuous. For example, *Waconella wacoensis* has a relatively linear commissure whereas the *Zygospira modesta* has a zig-zag trace. Most brachiopod shells today have a mineral composition of calcium phosphate and chitin (a complex, long-chain polymer). This is usually easily recognisable by its enamel-like lustre. Others have calcitic or calcium carbonate shells like many marine organisms.

Brachiopods use a system of muscles to open and close their valves. As with most fossils, soft tissue parts such as these muscles are not commonly preserved. However, the impressions or scars are usually still visible. The adductor scars are where the closing muscles were attached. Its opposite, the diductor scars, is where the opening muscles were attached.

Some brachiopods exhibit dentition and were archaically grouped under two classes: Inacticulata (no teeth or sockets) and Articulata (those with both teeth and sockets). These teeth are knob-like protrusion located on the hinge of the pedicle valve. Sockets are small depressions on the hinge of the brachial valve. The teeth fit into the sockets to assure the appropriate opening and closing of the valves. That being said, brachiopod dentition is nowhere near as complex as bivalvian dentition (discussed later).

Brachiopoda - Life Environments and Modes

Naturally, these bottom dwellers are all exclusive to a marine environment. However, various species can inhabit different depths and regions of the ocean. Brachiopods are typically oriented vertically to the substrate during their life time. That said, they can be inclined and even horizontal. Additionally, vertically oriented ones tend to have shells with valves that are equally biconvex whereas inclined or horizontal ones will have unequal valve shapes such as concavo-convex or plano-convex. Brachiopods vary greatly in shapes and sizes from a few microns to tens of centimetres in length. Considering their general morphology, they have not changed all that much compared to other phyla such as Chordata or even Mollusca. There are only about 120 genera of them. These bottom dwellers have always essentially been twin-valved filter-feeding shellfish, opening and closing their shells, waving around lophophores. Despite the tough competition from the Bivalvia, brachiopods are still around. They live in many different conditions from near-shore or intertidal environments to very deep basins over 6 kilometres below sea level. The larger species tend to live in these deeper environments. Note that the larger size is more likely to be the consequence rather than the cause of living in such an environment. Possible reasons could be due rarer competition (as not many organisms can tolerate such depths or pressures), relatively more (or rather less divided) food supply, most particles fall and land on the seafloor.

Brachiopod life styles can be classified based on its relation with the substrate. When the animal lives completely buried within the seafloor, it is known as Infaunal. Those that do live this way commonly have their posterior oriented downward and can stabilize themselves by projecting their pedicle further downwards. For those that are only partially buried are known as Semi Infaunal and are not necessarily attached to the substrate by their pedicle. Those that are Epifaunal essentially live on or above the substrate rather than in it. They are generally attached to the seafloor or other objects (such as marine plants) by their pedicle (discussed later). Reclining or free-living brachiopods (essentially an unattached lifestyle) are those that are horizontally floating on (or partial in) the substrate (not to be confused with epifaunal). These will generally have a plano-convex or concavo-convex shell shape. Some of them are modified to have spines or larger surface area to help float atop the sediment. Additionally, some of these have no pedicle opening, but will expose attachment point for those with external spines.

Although brachiopods are sessile, they have developed many different adaptations (see Figure 2 for following morphologies). Some cement themselves to rocks or other hard-shell animals such as *Craniops* or *Schuchertella*. Others such as *Craniids* or *Disciniids* live together by encrusting hard surfaces (similarly to barnacles). Some species have *clasping spines* can attach and cling on to other marine lifeforms and feed from there instead of on the substrate acting as an epibiont such as *Linoproductus* and

Tenaspinus. The *Chonetes* is example of a reclining brachiopod that essentially supports itself on top of the substrate by having its weight divided due to its large surface area shell. A similar case is the *Waagenoconcha*, which accomplishes the same task using many external spines. However, this morphology can be more advantageous since it does not need the surface to be flat and can adjust its anterior at different angles relative to the substrate. Finally, the "Mobile" brachiopods subdivide into the previously discussed Infaunal and Semi-Infaunal lifestyles. Note that "mobile" is mentioned in the sense that can move vertically but not necessarily laterally: their movement is limited to burrowing. The Linguloids (resembling to *Lingula*) are commonly infaunal. *Camerisma* and *Magadina* are examples of the semi-faunal type.

Brachiopods seem to be able to change their shell shape and life mode during ontogeny (from birth to maturity). A study from the San Juan Islands, show the shells to be more lopsided and asymmetric with increasing hydroenergy. (Schumann, 1991)[1] This strongly suggests that morphologic changes not only occur as a result of evolution but also as a result of ecology.

Bivalve Morphology

The term 'Bivalvia' quite evidently comes from prefix bi- meaning two and valve, and that is quite frankly what they look like. In contrast to Brachiopoda, Bivalvia is a class, not a phylum. From a taxonomic and ecological standpoint, they are far more diverse: a taxonomically lower rank expressing more heterogeneity. Like brachiopods, bivalves (with exceptions from scallops and oysters) are also bilaterally symmetrical with a twin-valve shelly exoskeleton (see Figure 3). Bivalves first appeared in the Early Cambrian and started out as burrowers. Their diversity was originally fairly limited. It was not until the Mesozoic that radiated becoming very successful burrowers and the now second largest class within the Mollusca phylum. The section is slightly briefer as many parts found in bivalves are analogous to those of brachiopods.

In contrast to brachiopods, bivalves do not have diductor muscles to open their shells. Instead, they have a ligament that automatically opens the valves because of its elasticity. This ligament can be internal like in oysters or mussels, but it may also be external in others. To close the valves or rather to hold them shut, bivalves usually have two adductor muscles: contracting one of them accomplishes this task. Most bivalves have mirrored valves and are referred to as left and right valves instead. When this is the case, it is said they are equivalved. Asymmetrically valved ones are said to inequivalved. Similar to its distant cousins (Brachipoda), these organisms also have an umbo where the first parts of the shell are secreted. The composition of the shell is biomineralized calcium carbonate such as calcite, aragonite (in higher temperatures) or even vaterite.

[1] From Introduction to Paleobiology and the Fossil Record

However, some bivalves produce nacre (discussed later). In addition, the valves are attached together by a toothed hinge (somewhat analogous to interlocking door hinges). This structure ensures the valves close correctly without misalignment. There are eight different types of teeth that can be observed with bivalves: desmodont (reduced to absent), dysodont (small, simple teeth near the edge of the valve), taxodont (multiple teeth, subequal, subparallel), actinodont (multiple, radially fanning out towards the umbo), isodont (large teeth located on both side of the ligament's depression), schizodont (large, diverging, sometimes grooved), pachyodont (rather large, blunt) and heterodont (cardinal, very large, lateral).

In contrast to brachipods, bivalves have a muscular foot instead of a pedicle. This structure is use for attachment to the substrate, or to further burrow down into the seafloor. This foot generally protrudes from the opening of the shell (anterior). Bivalves use siphons to feed which located near the pallial sinus (similar to gape in Brachiopoda). One of them, the inhalant siphon, is to drawn in water towards the internal cavity. The other, known as the exhalant siphon, brings the water back out and away from the internal cavity. When the water is drawn in, it passes through ciliated gills. These gills are essentially able to filter out food particles and oxygen. There are four main types (not explained here): protobranch, filibranch, eulamellibranch, septibranch.

Bivalvia - Life Environments and Modes

As with brachiopods, Bivalvia can also be classified by its relations to the substrate (see Figure 4). The Infaunal bivalves can be subdivided into Shallow Infaunal and Deep Infaunal. The shallow type commonly lives in the substrate of a river or sea. Most have a height to length close to 1:1. They typically have a smooth and streamlined shell which renders burrowing a much simpler task. They may have spines to firmly attach themselves to the substrate so that they are not so easily removed by predators. The deep type will live submerged with the substrate and their length is usually twice its height. Burial is achieved by opening the valves and pushing the muscular foot downwards into the sediment. This foot can also be used for locomotion. This is however a relatively much younger lifestyle dating back to roughly 2 million years ago. Since living and burrowing at such depths is difficult, it took longer to evolve fused siphons (inhalant and exhalent) to accommodate this mode.

There are also Epifaunal bivalves. Instead of a pedicle to hold their ground, they have the ability (that all bivalves have) to secrete byssal threads. These are sticky threads that are typical used during infancy for when additional stabilization is needed. That being said, there are some that use this ability during adulthood. The *Mytilus* is example of this. They are known as epibyssate bivalves because they use these threads (that reach down in the substrate) for stability and maintain this life style. This is somewhat analogous to spider webs. Semi Infaunal or Endobyssates are similar but are partially in the sediment: they combine the substrate and these thread for even more stability. These typically have a pointed anterior. Given these points, bivalves that employ byssal threads during their adulthood are typically found in high current environments. Next, cementing and reclining bivalves are commonly inequivalved. Just like reclining brachiopods, reclining bivalves can also have spines to help with stabilization. Unique to bivalve is swimming. This offers a huge advantage over brachiopods. Swimming bivalves are usually equilateral but they are inequivalved. The lower valve is usually larger. They typically exhibit a wider umbonal angle (greater to 105°) and have a single, large, centrally located adductor muscle.

Although most bivalves have shells that are primarily composed of calcium carbonate, some can produce a different material known as nacre (such as *Pinctada* also known as the “pearl oyster”). Calcareous shells are hard, robust and provide generally good protection. However, it is very susceptible to chemical weathering and is relative brittle. Chitin (complex, long-chain polymer) is quite resilient and pliable (so not very brittle). With this in mind, nacre has the advantage of both calcium carbonate and chitin. This biomaterial (organic-inorganic) composite consist of multilayered structures of calcium carbonate and an elastic biopolymer such as chitin. More precisely, it is comprised of micro aragonite tablets that usually have a rectangular, hexagonal or rounded shape. This combination gives it a tough, hard structure that will rather deform that shatter. Nacre has even been used in the material science industry to produce tougher materials. It is considered to be almost as resilient as silicon. An interesting fact is that pearls are the result of an autoimmune reaction known as “Nacrezation”: when foreign material such as an irritant (such as sand) or a parasite, the host will secrete nacre around it. Sometimes it is incorporated and creates bump within the animal. Otherwise, the irritant essentially become the nucleus of a pearl. The goal of this behaviour to isolate the irritant or to the very least creates a smoother surface. This seems to be the next big step in their evolution to have a greater tolerance towards both mechanical and chemical weathering.

Conclusion

To summarize, lophopores are too complex and distinctive of a structure for it to be implicated in convergent evolution. A twin-valved exoskeleton currently seems to primarily involve the specific lifestyle of filter feeding. Species that have this morphology are more likely to be from one common point of origin: *Lophotrochozoa*. Both Bivalvia and Brachiopoda are members of this superphylum. However, Bivalvia use siphons for feeding whereas Brachiopoda use lophophores. This is one of the most important distinctions between the two. Both of them have a shell that can be composed of calcium carbonate. However, brachiopods tend to have a more phosphoritic composition (such as chitin which is less susceptible to chemical deterioration). And bivalve shells are primarily calcareous. That being said, the shell can provide protection against predators and desiccation. Both have adopted similar forms of burrowing lifestyles and tend to remain near the substrate. For filter feeding, brachiopods use lophophores whereas bivalves use siphons. Both started to appear in the early Cambrian: bivalves already had toothed hinges, but articulate brachiopods only started to appear in the late Cambrian. Bivalves seem to have taken this evolution step much sooner. The Jurassic involved losses of both brachiopods and bivalves, but free swimming animals were not affected. This is most likely due to other lifeforms starting to also take advantage of the substrate disturbing pre-existing life. It is possible that many of the brachiopods were tipped over and bivalves were completely submerged by “sediment-bulldozing” organisms, ultimately leading to the extinction of some species. Bivalves can live in anywhere from freshwater to brackish waters. With this in mind, they are commonly found in the shallower subtidal environments whereas brachiopods will prefer deeper, calmer ocean waters. Both exhibit similar external morphology but their internal anatomies are quite different. Brachiopods have developed many different complex structures to achieve stability such as clasping spines and various shell shapes. In contrast, bivalves have adopted different life modes such as swimming or moving to different areas using their muscular foot. The concluded distinction is brachiopods changed morphologically to maintain a lifestyle whereas bivalves changed morphologically to adopt new lifestyles. That said, both are well adapted to their environments and have been generally very successful.

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Appendix

Figure 1

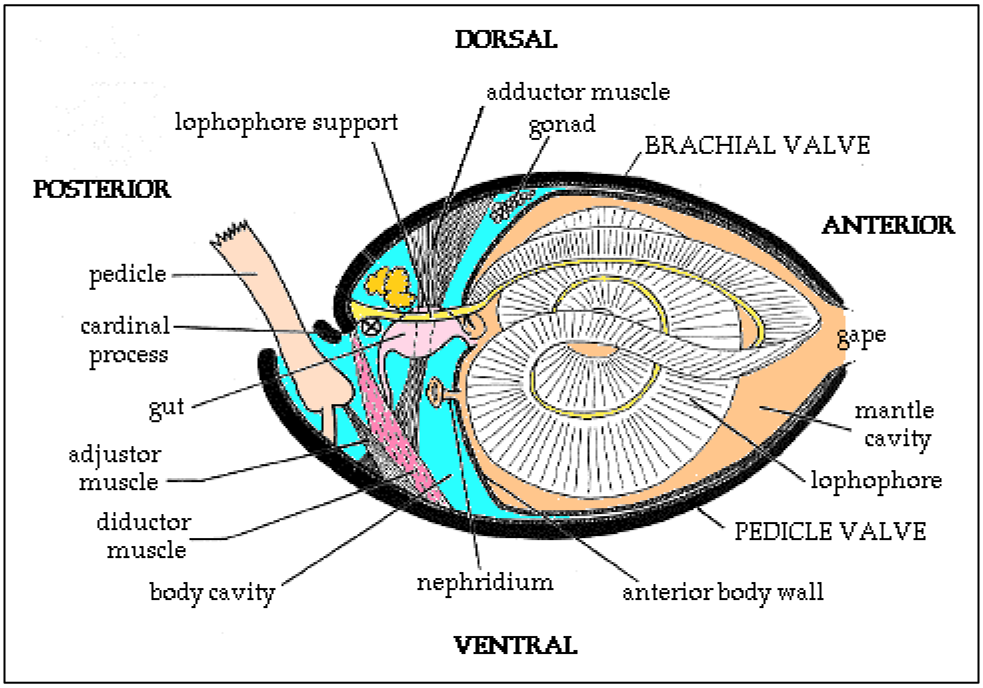

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Figure 2

LIFESTYLE	BRACHIOPOD TAXA	ADAPTATIONS
Attached by pedicle Epifaunal – hard substrate (1) (plenipedunculate)	Orthides, rhynchonellides, spiriferides and terabratulides	
Epifaunal – soft substrate (2) (rhizopedunculate)	*Chlidonophora* and *Cryptopora*	
Cryptic	*Argyrotheca* and *Terebratulina*	
Interstitial	*Acrotretides* and *Gwynia*	
Cemented	*Craniops* and *Schuchertella*	
Encrusting (3)	Craniids and disciniids	
Clasping spines (4)	*Linoproductus* and *Tenaspinus*	
Mantle fibers	Orthotetoids	
Unattached Cosupportive (5)	Pentamerids and trimerellids	
Coral-like (6)	Gemmellaroids and richthofeniids	
Recumbent	Strophomenides	
Pseudofaunal (7) and inverted (8)	*Waagenoconcha* and *Marginifera*	
Free-living (9, 10)	*Cyrtia, Chonetes, Neothyris* and *Terebratella*	
Mobile Infaunal (11)	Linguloids	
Semi-infaunal (12)	*Camerisma* and *Magadina*	

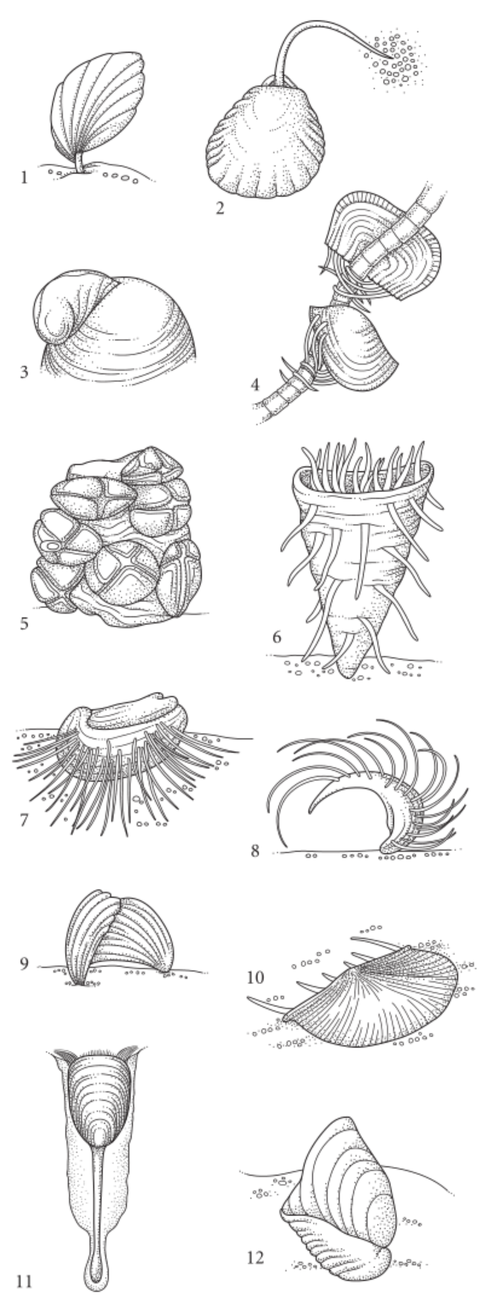

Figure 12.9 Brachiopod lifestyles. (Courtesy of David Harper and Roisin Moran.)

Retrieved (March 2017) from:"Brachipoda", Michael J. Benton and David A.T. Harper, "Introduction to Paleobiology and the Fossil Record", 2009, http://www.blackwellpublishing.com/paleobiology/figure.asp?chap=12&fig=Fig12-9&img=c12f009

Figure 3

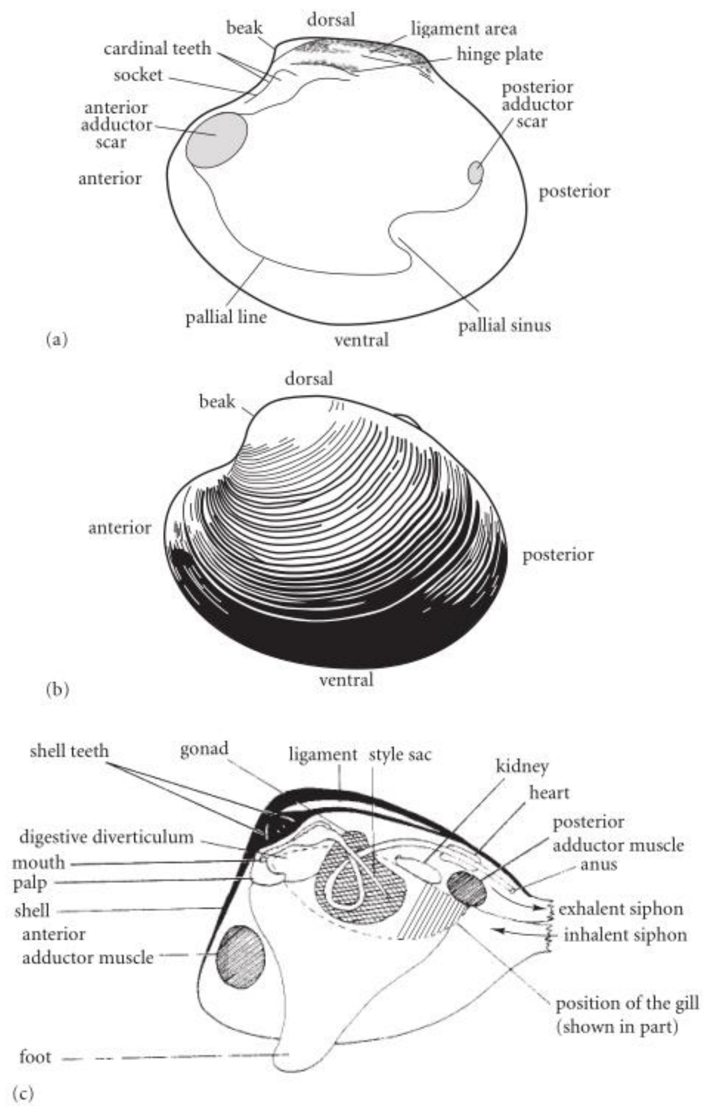

Figure 13.5 Bivalve morphology based on a living bivalve: (a) internal features of the right valve, (b) external features of the left valve, and (c) reconstruction of the internal structures attached to the right valve. (Based on *Treatise on Invertebrate Paleontology*, Part N. Geol. Soc. Am. and Univ. Kansas.)

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Figure 4

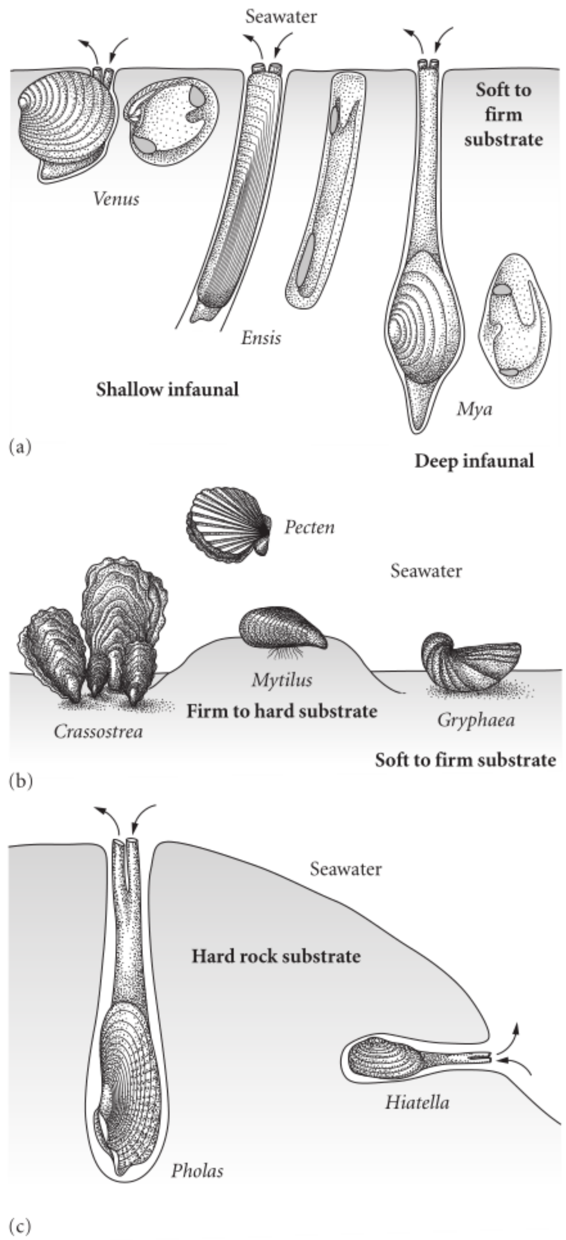

Figure 13.9 Life modes of bivalve mollusks: (a) shallow and deep burrowers into soft to firm substrates, (b) epifaunal swimming, attached or resting on soft to firm substrates, and (c) boring into hard substrates. (From Milsom & Rigby 2004.)

Retrieved (March 2017) from: "Bivalvia", Michael J. Benton and David A.T. Harper, "Introduction to Paleobiology and the Fossil Record", 2009, http://www.blackwellpublishing.com/paleobiology/figure.asp?chap=13&fig=Fig13-9&img=c13f009