Bivalvia

(Class of Phylum Mollusca)

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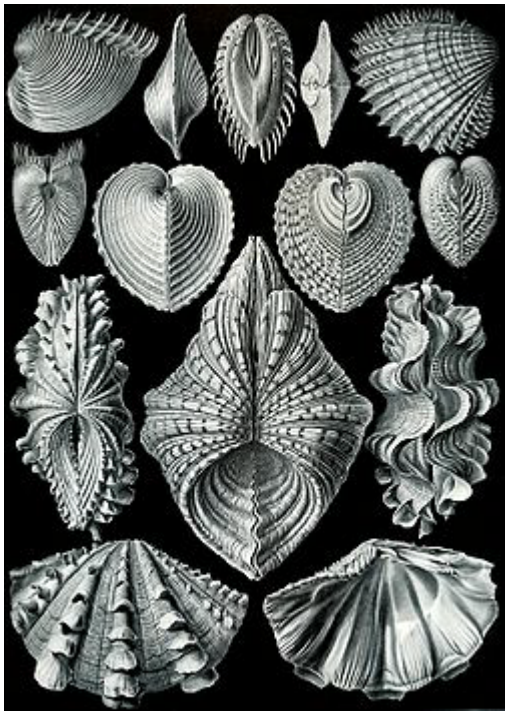
"Acephala", from Ernst Haeckel's *Kunstformen der Natur* (1904)
Scientific classification
Kingdom: Animalia
Phylum: Mollusca
Class: **Bivalvia** Linnaeus, 1758
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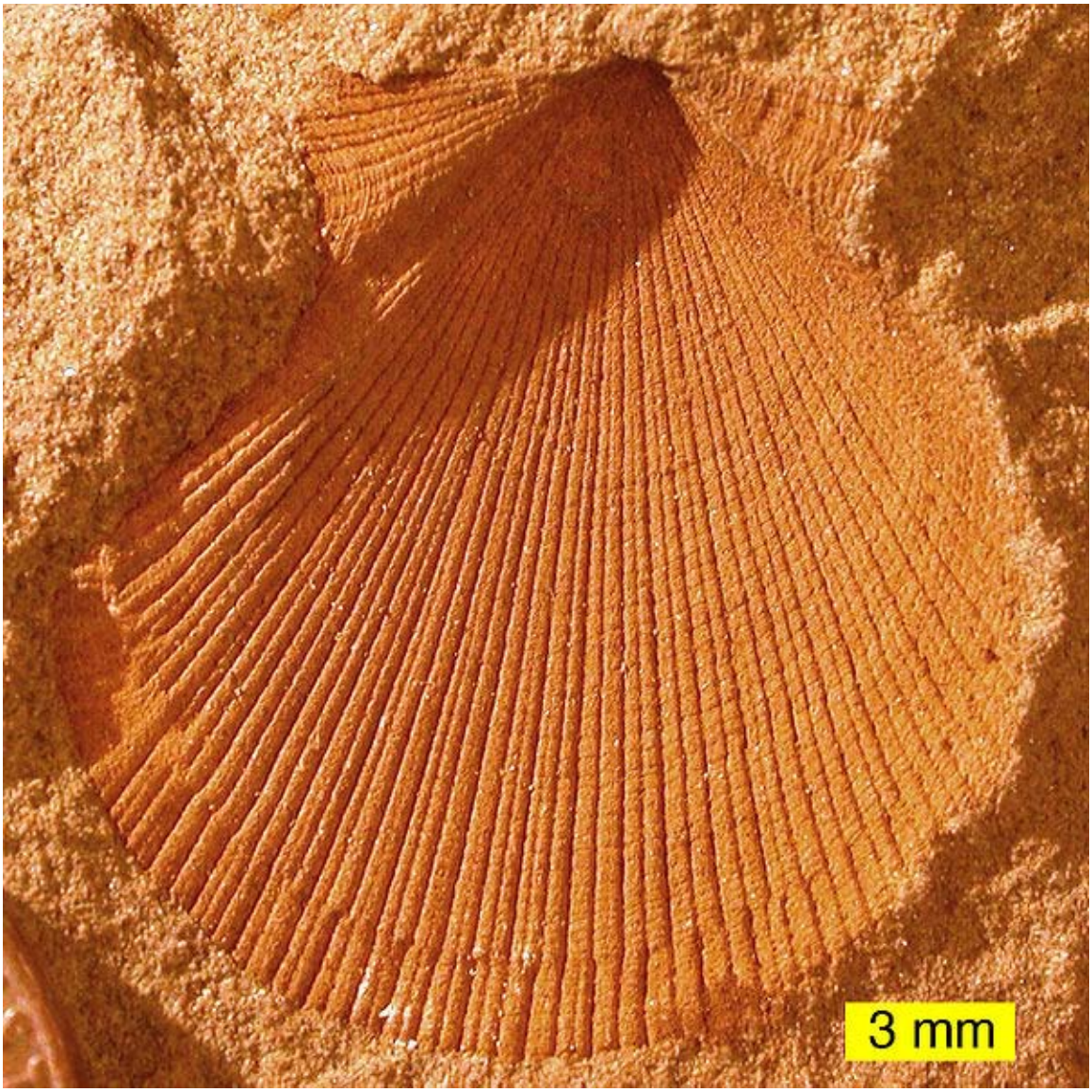
Palaeotaxodonta
Pteriomorphia

Mussels in the intertidal zone in Cornwall, England

Fossil gastropod and attached mytilid bivalves in a Jurassic limestone (Matmor Formation) in southern Israel



Aviculopecten subcardiformis; an extinct pectenoid bivalve from the Logan Formation of Wooster, Ohio (external mold)

Bivalvia is a class of marine and freshwater mollusks known for some time as **Pelecypoda**, but now commonly referred to simply as **bivalves**. As with Gastropoda and Cephalopoda, the term Pelecypoda is in reference to the animal itself while Bivalvia simply describes the shell. Other names for the class include Acephala, Bivalva, and Lamellibranchia. The total number of bivalves currenty amounts to 9,200 species in 1,260 genera and 106 families. The global marine bivalves (including brackish water and estuarine species) contain about 8,000 species, combined in 4 subclasses and 99 families with 1,100 genera. The largest recent families are Veneridae with more than 680 species or Tellinidae and Lucinidae with over 500 species. The freshwater bivalves have 7 additional families, of which the Unionidae contain about 700 species.

Bivalves have a shell consisting of two asymmetrically rounded halves called *valves* that are mirror images of each other, joined at one edge by a flexible ligament called the *hinge*. The shell is typically bilaterally symmetrical, with the hinge lying in the sagittal plane. Recent Bivalves cover a large range of shell sizes from 0.52 mm in *Condylonucula maya* to 1,532 mm in *Kuphus polythalamia*

Bivalves are unique among the molluscs, having lost their odontophore and radula in their transition to filter feeding.

Some bivalves are epifaunal; they attach to surfaces. Others are infaunal; they bury themselves in sediment. These forms typically have a strong digging foot. Some bivalves such as scallops can swim.

The term *bivalve* is derived from the Latin *bis*, meaning 'two', and *valvae*, meaning *leaves of a door* Other bivalved animals include brachiopods, ostracodes, and conchostrachans.

Taxonomy

No consensus exists on bivalve phylogeny. Many conflicts exist due to taxonomies based on single organ systems and conflicting naming schemes. More recent taxonomies use multiple organ systems, fossil records, as well as molecular phylogenetics to draw more robust phylogenies. Due to the numerous fossil lineages, DNA sequence data is of limited use should the subclasses turn out to be paraphyletic.

In his 1935 work *Handbuch der systematischen Weichtierkunde* (Handbook of Systematic Malacology), Johannes Thiele introduced a mollusc taxonomy based upon the 1909 work by Cossmann and Peyrot. Thiele's system divided the bivalves into three orders:

- *Taxodonta* – taxodont dentition
- *Anisomyaria* – either a single adductor muscle or one adductor muscle much larger than the other
- *Eulamellibranchiata* – all forms with lamellibranch ctenidia

The last was divided into four sub-orders: *Schizodonta*, *Heterodonta*, *Adapedonta* and *Anomalodesmata*.

The systematic layout presented here follows Norman D. Newell's 1965 classification based on hinge tooth morphology:

Subclass	Order
Palaeotaxodonta	*Nuculoida
	†Praecardioida
Cryptodonta	
	Solemyoida

	Arcoida (ark shells)
	†Cyrtodontoida
	Limoida (file shells)
Pteriomorphia	Mytiloida (true mussels)
	Ostreoida (oysters, formerly included in Pterioida)
	†Praecardioida
	Pterioida (pearl oysters, pen shells)
	†Trigonioida
Paleoheterodonta	Unionoida (freshwater mussels)
	†Modiomorpha
	†Cycloconchidae
	†Hippuritoida
	†Lyrodesmatidae
Heterodonta	
	Myoida (most "soft shell calms" razor clams)
	†Redoniidae
	Veneroida (most "hard shell calms", cockles, etc)
Anomalodesmata	Pholadomyoida

The monophyly of the Anomalodesmata is disputed, but this is of less consequence as that group does not include higher-level prehistoric taxa. The standard view now is that Anomalodesmata resides within the subclass Heterodonta.

An alternative systematic scheme exists according to gill morphology. This distinguishes between Protobranchia, Filibranchia, and Eulamellibranchia. The first corresponds to Newells Palaeotaxodonta and Cryptodonta, the second to his Pteriomorphia, with the last corresponding to all other groups. In addition, Franc separated the Septibranchia from his eulamellibranchs, but this would seem to make the latter paraphyletic.

In May 2010 a new taxonomy of the Bivalvia was published in the journal Malacologia. In this classification 324 families were recognized as valid, 214 of which are known exclusively as fossils and 110 families occur in the Recent with or without a fossil record. This publication consisted of two parts :

- Nomenclator of Bivalve Names of the Family-Group and above
- Classification of Bivalve Families (under the redaction of Rüdiger Bieler, Joseph G. Carter and Eugene V. Coan)

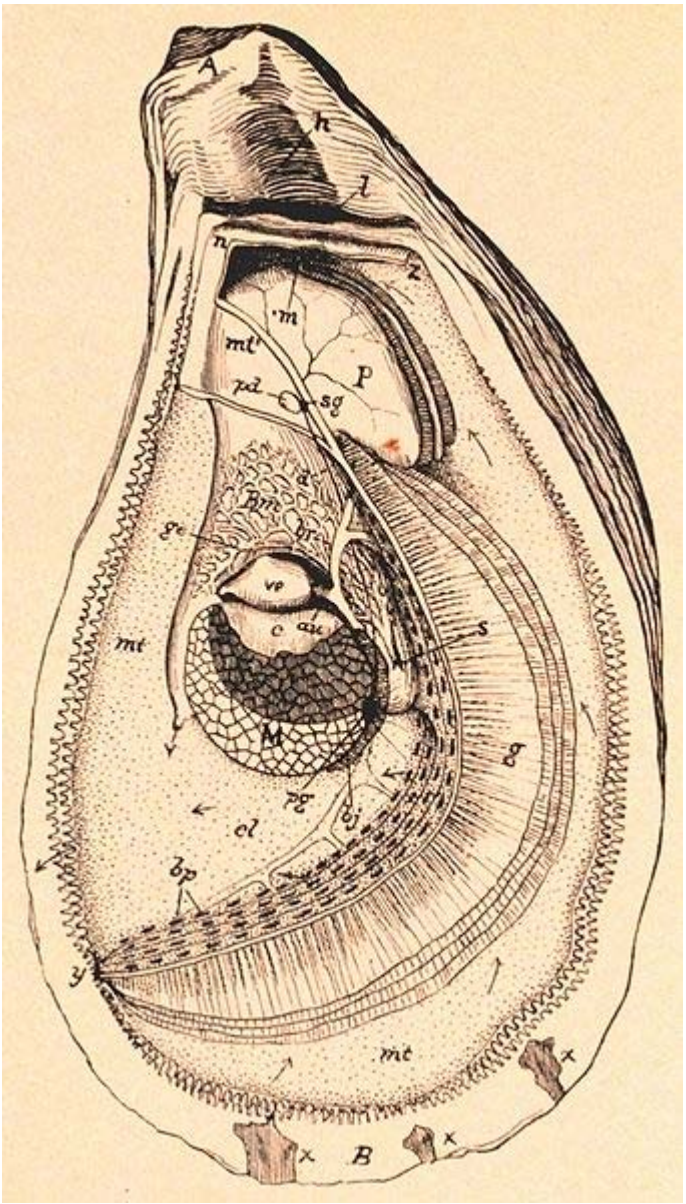
Biodiversity the number of recent bivalves

Huber gives a total number of about 9,200 living bivalves combined in 106 families. He states that the number of 20,000 living species, often encountered in literature, could not be verified and shows the following table.

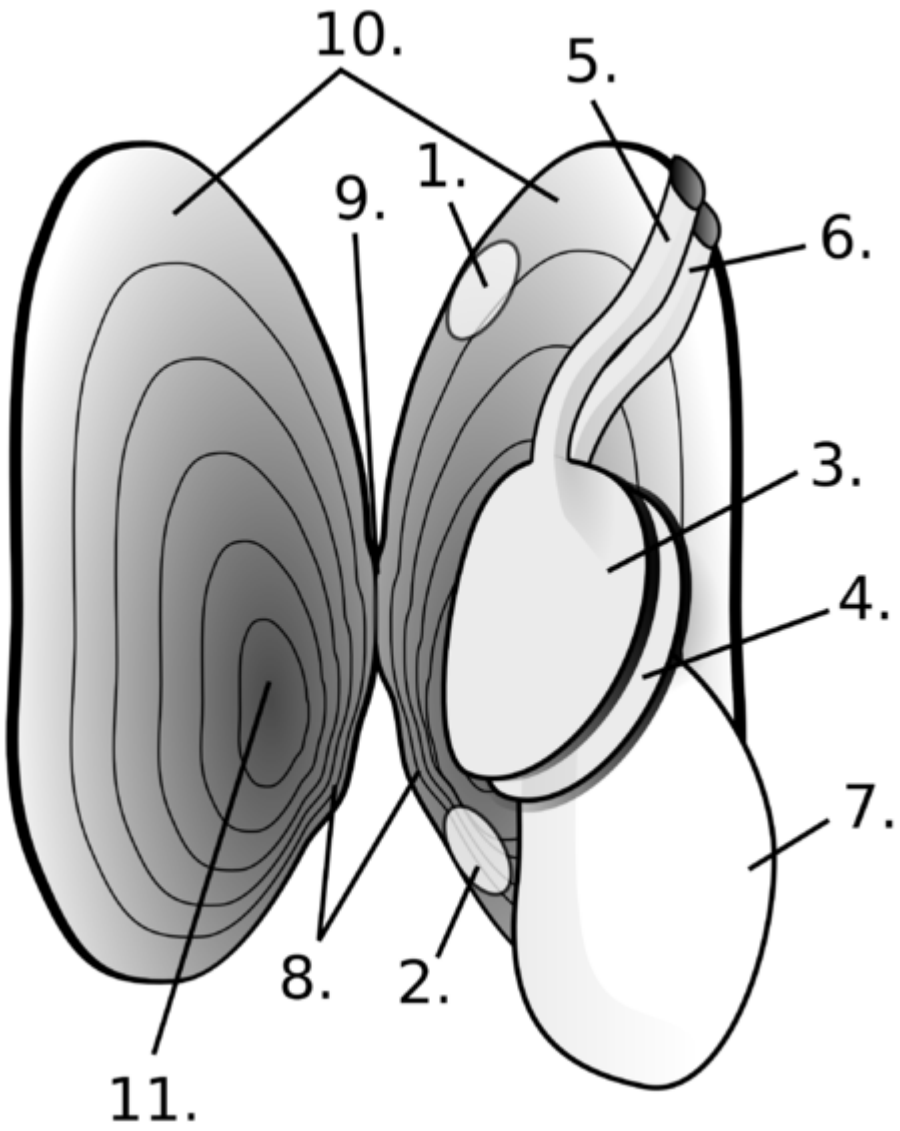
Number of	Families	Genera	Species
PROTOBRANCHIA	**10**	**49**	**700**
Nuculoidea	**1**	**8**	**170**
Sapretoidea	**1**	**ca. 5**	**10**
Solemyoidea	**1**	**2**	**30**
Manzanelloidea	**1**	**2**	**20**
Nuculanoidea	**6**	**32**	**460**
PTERIOMORPHA	**25**	**240 (incl. 2 freshwater)**	**2000 (incl. 11 freshwater)**
Mytiloidea	**1**	**50 (1 freshwater)**	**400 (5 freshwater)**
Arcoidea	**7**	**60 (1 freshwater)**	**570 (6 freshwater)**
Pinnoidea	**1**	**3 (+)**	**50**
Pterioidea	**5**	**9**	**80**
Ostreoidea	**2**	**23**	**80**
Dimyoidea	**1**	**3**	**15**
Anomioidea	**2**	**9**	**30**
Plicatuloidea	**1**	**1**	**20**
Pectinoidea	**4**	**68**	**500**
Limoidea	**1**	**8**	**250**
PALAEOHETERODONTA	**7 (incl. 6 freshwater)**	**171 (incl. 170 freshwater)**	**908 (incl. 900 freshwater)**
Trigonioidea	**1**	**1**	**8**
Unionoidea	**(6 freshwater)**	**(170 freshwater)**	**(900 freshwater)**
HETERODONTA	**64 (incl. 1 freshwater)**	**800 (incl. 16 freshwater)**	**5600 (incl. 270 freshwater)**
Crassatelloidea	**5**	**65**	**420**
Thyasiroidea	**1**	**ca. 12**	**ca. 100**

Lucinoidea	**2**	**ca. 85**	**ca. 500**
Galeommatoidea	**ca. 4**	**ca. 100**	**ca. 500**
Cyamioidea	**3**	**22**	**140**
Solenoidea	**2**	**17 (2 freshwater)**	**130 (4 freshwater)**
Hiatelloidea	**1**	**5**	**25**
Gastrochaenoidea	**1**	**7**	**30**
Chamoidea	**1**	**6**	**70**
Cardioidea	**2**	**38**	**260**
Tellinoidea	**5**	**110 (2 freshwater)**	**900 (15 freshwater)**
Glossoidea	**2**	**20**	**110**
Arcticoidea	**2**	**6**	**13**
Cyrenoidea	**1**	**6 (3 freshwater)**	**60 (30 freshwater)**
Sphaerioidea	**(1 freshwater)**	**(5 freshwater)**	**(200 freshwater)**
Veneroidea	**4**	**104**	**750**
Hemidonacoidea	**1**	**1**	**6**
Cyrenoidoidea	**1**	**1**	**6**
Ungulinoidea	**1**	**16**	**100**
Mactroidea	**4**	**46**	**220**
Dreissenoidea	**1**	**3 (2 freshwater)**	**20 (12 freshwater)**
Myoidea	**3**	**15 (1 freshwater)**	**130 (1 freshwater)**
Pholadoidea	**2**	**34 (1 freshwater)**	**200 (3 freshwater)**
Limoidea	**1**	**8**	**250**
(ANOMALODESMATA)	**(14)**	**(71)**	**(770)**
Pholadomyoidea	**2**	**3**	**20**
Clavagelloidea	**1**	**2**	**20**
Pandoroidea	**7**	**30**	**250**
Verticordioidea	**2**	**16**	**160**
Cuspidarioidea	**2**	**20**	**320**

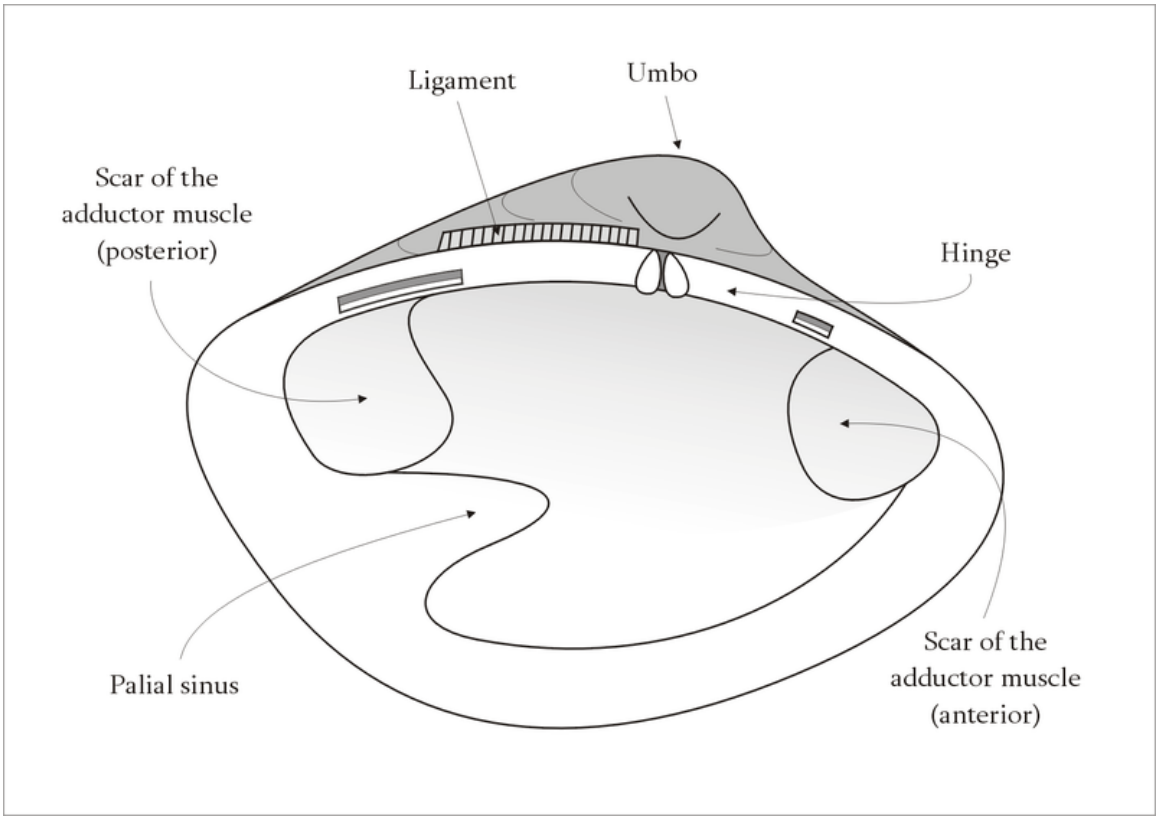
Anatomy



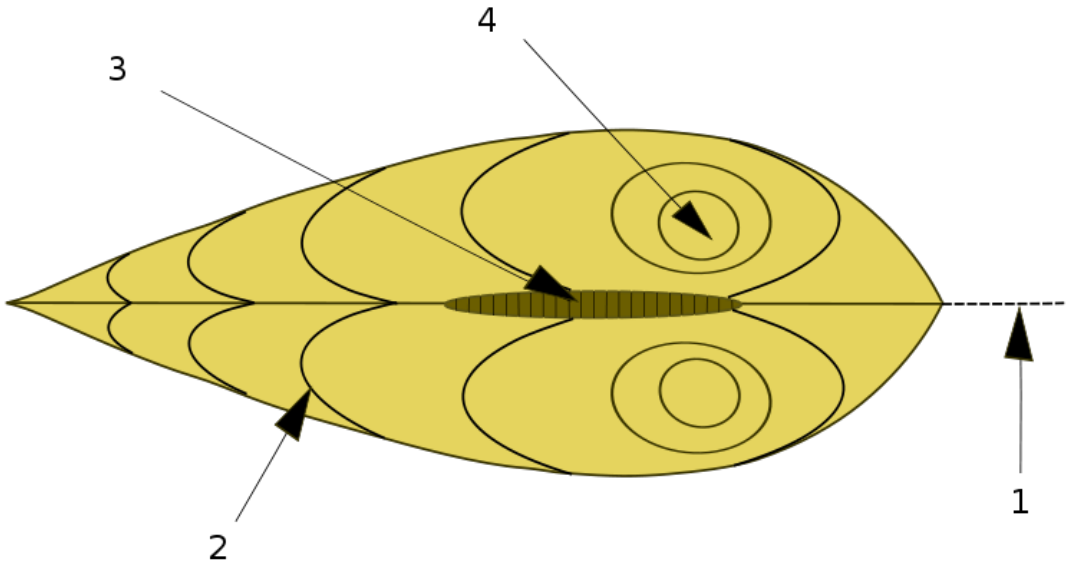
Drawing of oyster anatomy



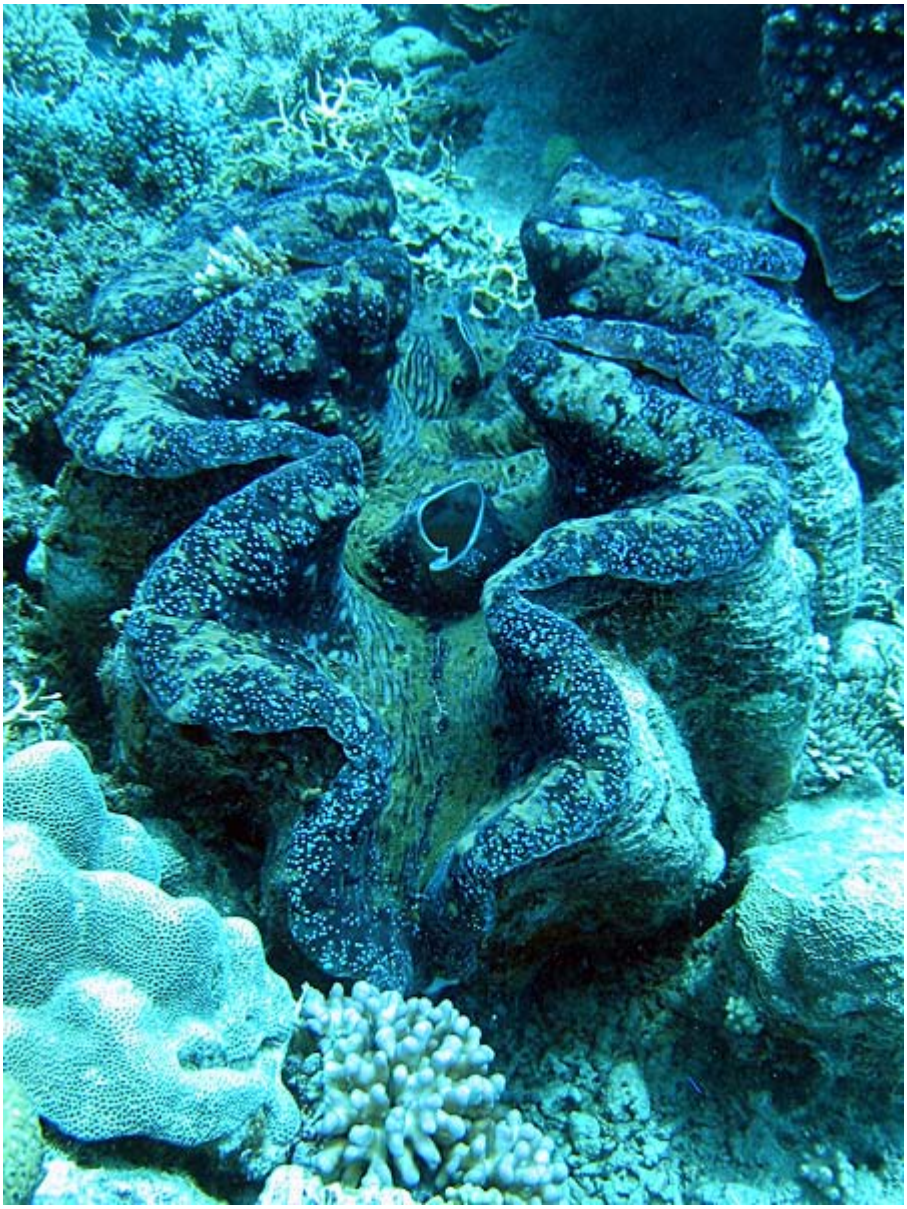
Drawing of anatomy of Freshwater pearl mussel *Margaritifera margaritifera*



A diagram of the internal shell anatomy of the left hand valve of a bivalve such as a venerid



Main parts in the shell of a bivalve: 1: sagittal plane, 2: growth lines, 3: ligament, 4: umbo



Giant clam, *Tridacna gigas*

Bivalve shells vary greatly in shape; some are globular, others flattened, while others are elongated to aid burrowing. The shipworms of the family Teredinidae have greatly elongated bodies, but the shell valves are much reduced and restricted to the anterior end of the body, where they function as burrowing organs that permit the animal to dig tunnels through wood.

Nervous system

The sedentary habit of the bivalves has led to the development of a simpler nervous system than in other molluscs; they have no brain. In all but the simplest forms the neural ganglia are united into two cerebropleural ganglia on either side of the oesophagus. The

pedal ganglia, controlling the foot, are at its base, and the visceral ganglia (which can be quite large in swimming bivalves) under the posterior adductor muscle.[s] These ganglia are both connected to the cerebropleural ganglia by nerve fibres. There may also be siphonal ganglia in bivalves with a long siphon.

Senses

The sensory organs of bivalves are not well developed and are largely a function of the posterior mantle margins. The organs are usually tentacle mechanoreceptors or chemoreceptors.

Scallops have complex eyes with a lens and retina, but most other bivalves have much simpler eyes, if any. There are also light-sensitive cells in all bivalves that can detect a shadow falling over the animal.

Many bivalves possess a number of tentacles, which have chemoreceptor cells to taste the water, as well as being sensitive to touch. These are typically found near the siphons, but in some species may fringe the entire mantle cavity.

Another notable sensory organ found in bivalves is the osphradium, a patch of sensory cells located below the posterior adductor muscle. It may serve to taste the water, or measure its turbidity, but it is probably not homologous with the structure of the same name found in snails and slugs.

In the septibranchs the inhalant siphon is surrounded by vibration-sensitive tentacles for detecting prey.

Statocysts within the organism help the bivalve to sense and correct its orientation.

Muscles

The muscular system is composed of the posterior and anterior adductor muscles, although the anterior muscles may be reduced or even lost in some species.

The paired anterior and posterior pedal retractor muscles operate the animal's foot. In some bivalves, such as oysters and scallops, these retractors are absent.

Circulation and respiration

Bivalves have an open circulatory system that bathes the organs in hemolymph. The heart has three chambers; two auricles receiving blood from the gills, and a single ventricle. The ventricle is muscular and pumps hemolymph into the aorta, and through this to the rest of the body. Many bivalves have only a single aorta, but most also have a second, usually smaller, aorta serving the hind parts of the animal.

Oxygen is absorbed into the hemolymph in the gills, which hang down into the mantle cavity, and also assist in filtering food particles from the water. The wall of the mantle cavity is a secondary respiratory surface, and is well supplied with capillaries. Some species, however, have no gills, with the mantle cavity being the only location of gas exchange. Bivalves adapted to tidal environments can survive for several hours out of water by closing their shells and keeping the mantle cavity filled with water.

The hemolymph usually lacks any respiratory pigment, although some species are known to possess haemoglobin dissolved directly into the serum.

Mantle and shell

The world's largest clam (187 cms), a *Sphenoceramus steenstrupi* fossil from Greenland in the Geological Museum in Copenhagen

In bivalves the mantle forms a thin membrane surrounding the body which secretes the valves, ligament and hinge teeth. The mantle lobes secrete the valves and the mantle crest secretes the ligament and hinge teeth. The mantle is attached to the shell by the mantle retractor muscles at the pallial line. In some bivalves the mantle edges fuse to form siphons, which take in and expel water for suspension feeding.

The shell is composed of two calcareous valves, which are made of either calcite (as with oysters) or both calcite and aragonite, usually with the aragonite forming an inner layer (as with the Pterioida). The outermost layer is the periostracum, composed of a horny organic substance. This forms the familiar coloured layer on the shell.

The shell is added to in two ways; at the open edge and by a gradual thickening throughout the animal's life.

The shell halves are held together at the animal's dorsum by the ligament, which is composed of the tensilium and resilium. The ligament opens the shell.

Digestive system

Modes of feeding

The majority of bivalves are filter feeders, using their gills to capture particulate food from the water. In almost all species, the water current enters the shell from the posterior ventral surface of the animal, and then passes upwards through the gills in a U-shape, so that it exits just above the intake. In burrowing species, there may be elongated siphons stretching from the body to the surface, one each for the inhalant and exhalant streams of water.

The gills of filter-feeding bivalves have become highly modified to increase their ability to capture food. For example, the cilia on the gills, which originally served to remove unwanted sediment, are adapted to capture food particles, and transport them in a steady stream of mucus to the mouth. The filaments of the gills are also much longer than those in more primitive bivalves, and are folded over to create a groove through which food can be transported. The structure of the gills varies considerably, and can serve as a useful means for classifying bivalves into groups.

Some bivalves feed by scraping detritus from the bottom, and this may be the primitive mode of feeding for the group, before the gills became adapted for filter feeding. These primitive bivalves hold onto the substratum with a pair of tentacles at the edge of the mouth, each of which has a single palp, or flap. The tentacles are covered in mucus, which traps the food particles, and transports them back to the palps using cilia. The palps then serve to sort the particles, ejecting those that are too large to be digestible.

A few bivalves, such as *Poromya*, are carnivorous, eating much larger prey than the tiny phytoplankton consumed by the filter feeders. In these animals, the gills are relatively small, and form a perforated barrier separating the main mantle cavity from a smaller

chamber through which the water is exhaled. Muscles pump water through the cavity, sucking in small crustaceans and worms. The prey are then seized in the palps and consumed.

The unusual genus *Entovalva* is parasitic, and lives only in the gut of sea cucumbers.

Digestive tract

The digestive tract of typical bivalves consists of an oesophagus, stomach, and intestine. A number of digestive glands open into the stomach, often via a pair of diverticula; these secrete enzymes to digest food in the stomach, but also include cells that phagocytose food particles, and digest them intracellularly.

In the filter feeding bivalves, an elongated rod of solidified mucus referred to as the **crystalline style** projects into the stomach from an associated sac. Cilia in the sac cause the style to rotate, winding in a stream of food-containing mucus from the mouth, and churning the stomach contents. This constant motion propels food particles into a sorting region at the rear of the stomach, which distributes smaller particles into the digestive glands, and heavier particles into the intestine.

Carnivorous bivalves have a greatly reduced style, and a chitinous gizzard that helps grind up the food before digestion.

Excretory system

Like most other molluscs, the excretory organs of bivalves are nephridia. There are two nephridia, each consisting of a long, glandular tube, which opens into the body cavity just beneath the heart, and a bladder. Waste is voided from the bladders through a pair of openings near the front of the upper part mantle cavity, where it can easily be washed away in the stream of exhalant water.

Reproduction

The sexes are usually separate, but some hermaphroditism is known. Bivalves practice external fertilization. The gonads are located close to the intestines, and either open into the nephridia, or through a separate pore into the mantle cavity.

Typically bivalves start life as a trochophore, later becoming a veliger. Freshwater bivalves of the Unionoida have a different life cycle: they become a glochidium, which attaches to any firm surface to avoid the danger of being swept downsteam. Glochidia can be serious pests of fish if they lodge in the fish gills.

Some of the species in the freshwater mussel family, Unionidae, commonly known as *pocketbook mussels* have evolved a remarkable reproductive strategy. The edge of the female's body that protrudes from the valves of the shell develops into an imitation of a small fish complete with markings and false eyes. This decoy moves in the current and

attracts the attention of real fish. Some fish see the decoy as prey, while others see a conspecific. Whatever they see, they approach for a closer look and the mussel releases huge numbers of larvae from her gills, dousing the inquisitive fish with her tiny, parasitic young. These glochidia larvae are drawn into the fish's gills where they attach and trigger a tissue response that forms a small cyst in which the young mussel resides. It feeds by breaking down and digesting the tissue of the fish within the cyst.

Behaviour

A large number of venerid bivalves with their siphons visible

The radical structure of the bivalves reflects their behaviour in several ways. The most significant is the use of the closely-fitting valves as a defense against predation and, in intertidal species, against desiccation. The entire animal can be contained within the shell, which is held shut by the powerful adductor muscles. This defense is difficult to overcome except by specialist predators such as sea stars and oystercatchers.

Feeding

Most bivalves are filter feeders although some have taken up scavenging and predation. Nephridia remove the waste material. Buried bivalves feed by extending a siphon to the

surface (indicated by the presence of a pallial sinus, the size of which is proportional to the burrowing depth, and represented by their hinge teeth).

Feeding types

There are four feeding types, defined by their gill structure:

- **Protobranchs** use their ctenidia solely for respiration, and the labial palps to feed
- **Septibranchs** possess a septum across the mantle cavity which pumps in food.
- **Filibranchs** and **lamellibranchs** trap food with a mucous coating on the ctenidia; the filibranchs and lamellibranchs are differentiated by the way the ctenidia are joined

Movement

Razor shells can dig themselves into the sand with great speed to escape predation. Scallops, and file clams can swim to escape a predator, clapping their valves together to create a jet of water. Cockles can use their foot to leap from danger. However these methods can quickly exhaust the animal. In the razor shells the siphons can break off only to grow back later.

Defensive secretions

The file shells can produce a noxious secretion when threatened, and the fan shells of the same family have a unique, acid-producing organ.

Comparison with brachiopods

Anadara, a bivalve with taxodont dentition from the Pliocene of Cyprus

Bivalves are superficially similar to brachiopods, but the construction of the shell is completely different in the two groups. In brachiopods, the two valves are on the dorsal and ventral surfaces of the body, while in bivalves, they are on the left and right sides.

Bivalves appeared late in the Cambrian explosion and came to dominate over brachiopods during the Palaeozoic. By the Permian-Triassic extinction event bivalves were undergoing a huge radiation while brachiopods were devastated, losing 95% of their diversity.

It had long been considered that bivalves are better adapted to aquatic life than the brachiopods were, causing brachiopods to be out-competed and relegated to minor niches in later strata. These taxa appeared in textbooks as an example of replacement by competition. Evidence included the use of an energetically-efficient ligament-muscle system for opening valves, requiring less food to subsist. However the prominence of bivalves over brachiopods might instead be due to chance disparities in their response to extinction events.

Chapter 2

Subclass of Bivalvia

Cryptodonta

Cryptodonta	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Bivalvia
Subclass:	**Cryptodonta** Neumayr, 1884
Orders	

- †Praecardioida
- Solemyoida

Cryptodonta is a subclass of the bivalves. It contains a single extant order, Solemyoida, while the Praecardioida are known only from fossils.

The valves of the shell are relatively thin and somewhat elongated. Unlike most other bivalves, species in this group have no hinge teeth on their shells. They have relatively primitive, "protobranchiate", gills.

Taxonomy

- **Cryptodonta**
  - Order †Praecardioida
    - Family †Butovicellidae
      - Genus †*Butovicella*
    - Family †Praecardiidae
      - Genus †*Slava*
      - Genus †*Cardiola*

        - Family †Antipleuridae
            - Genus †*Dualina*
            - Genus †*Hercynella*
    - Order Solemyoida
    - Superfamily Solemyoidea
        - Family Solemyidae (Awning clams)
            - Genus *Acharax*
            - Genus *Solemya*
        - Family Manzanellidae
            - Genus *Huxleyia*
            - Genus *Nucinella*

Heterodonta

Heterodonta

New Zealand cockles
Scientific classification
Kingdom: Animalia
Phylum: Mollusca
Class: Bivalvia
Subclass: **Heterodonta**
Orders
†Cycloconchidae
†Hippuritoida
†Lyrodesmatidae
Myoida
†Redoniidae
Veneroida

Heterodonta is a subclass of bivalve molluscs, including the clams and cockles. They are distinguished by having the two halves of the shell be equally sized, and having a few

cardinal teeth separated from a number of long lateral teeth. Their shells lack a nacreous layer, and the gills are lamellibranch in form. Most species have a siphon.

The subclass contains two living and four extinct orders:

- Order †Cycloconchidae
- Order †Hippuritoida (rudists)
- Order †Lyrodesmatidae
- Order Myoida (soft-shell clams and allies)
- Order †Redoniidae
- Order Veneroida (cockles and allies)

Paleoheterodonta

Paleoheterodonta

Anodonta anatina

Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Bivalvia
Subclass:	**Paleoheterodonta**

Orders
†Trigonioida
Unionoida

Paleoheterodonta is a subclass of bivalve molluscs. It contains the extant order Unionoida (freshwater mussels) and the prehistoric Trigonioida. They are distinguished by having the two halves of the shell be of equal size and shape, but by having the hinge teeth be in a single row, rather than separated into two groups, as they are in the clams and cockles.

Pteriomorphia

Pteriomorphia

Scientific classification
Kingdom: Animalia
Phylum: Mollusca
Class: Bivalvia
Subclass: **Pteriomorphia**
Orders
7, 5 extant

Pteriomorphia is a mollusc subclass of the Bivalvia. Apart from the orders Arcoida, Mytiloida, Ostreoida, and Pterioida, it also contains some extinct and probably basal families, such as the Evyanidae, Colpomyidae, Bakevelliidae, Cassianellidae and Lithiotidae.

Pteriomorpha molluscs have lamellibranch gills and are epibenthic. Some can attach to substrate using a byssus. One foot is reduced. The mantle margins are not fused. Gills are usually large and assist in feeding. This group includes the well known mussels, scallops, pen shells, and oysters.

Orders in the subclass Pteriomorphia

- Arcoida (ark shells)
- Cyrtodontoida†
- Limoida (file shells and allies)
- Mytiloida (saltwater mussels)
- Ostreoida (oysters and scallops)
- Praecardioida†
- Pterioida (winged oysters and allies)

Chapter 3

Bivalve Shell and Razor Shell

Bivalve shell

Live Venerid cockles, *Austrovenus stutchburyi* from New Zealand

A **bivalve shell** is part of the body, the exoskeleton or shell, of a bivalve mollusk. In life, the shell of this class of mollusks is composed of two parts, two valves which are hinged together. Bivalves are very common in many kinds of saltwater habitats, but they are also found in brackish water and in freshwater.

Bivalves are a common part of the marine fauna worldwide (scallops, clams, oysters, mussels, etc). The shells of marine bivalves commonly wash up on beaches (often as separate valves) and the shells of freshwater species can sometimes be found along the flood plains of rivers, and other freshwater habitats.

Bivalves typically have two-part shells, two valves, that are joined by a ligament. The two valves usually articulate with one another using structures known as "teeth" which are situated along the hinge line. In many (but by no means all) bivalve shells, the two valves are symmetrical along the hinge line.

This exoskeleton serves not only for muscle attachment, but also for protection from predators and from mechanical damage. The shell has several layers, and is typically made of calcium carbonate precipitated out into an organic matrix. It is secreted by a part of the molluscan body known as the mantle.

Bivalve shells are collected by professional and amateur conchologists, and are sometimes harvested for commercial sale (the international shell trade), occasionally to the detriment of the local ecology.

Shell anatomy, structure and composition

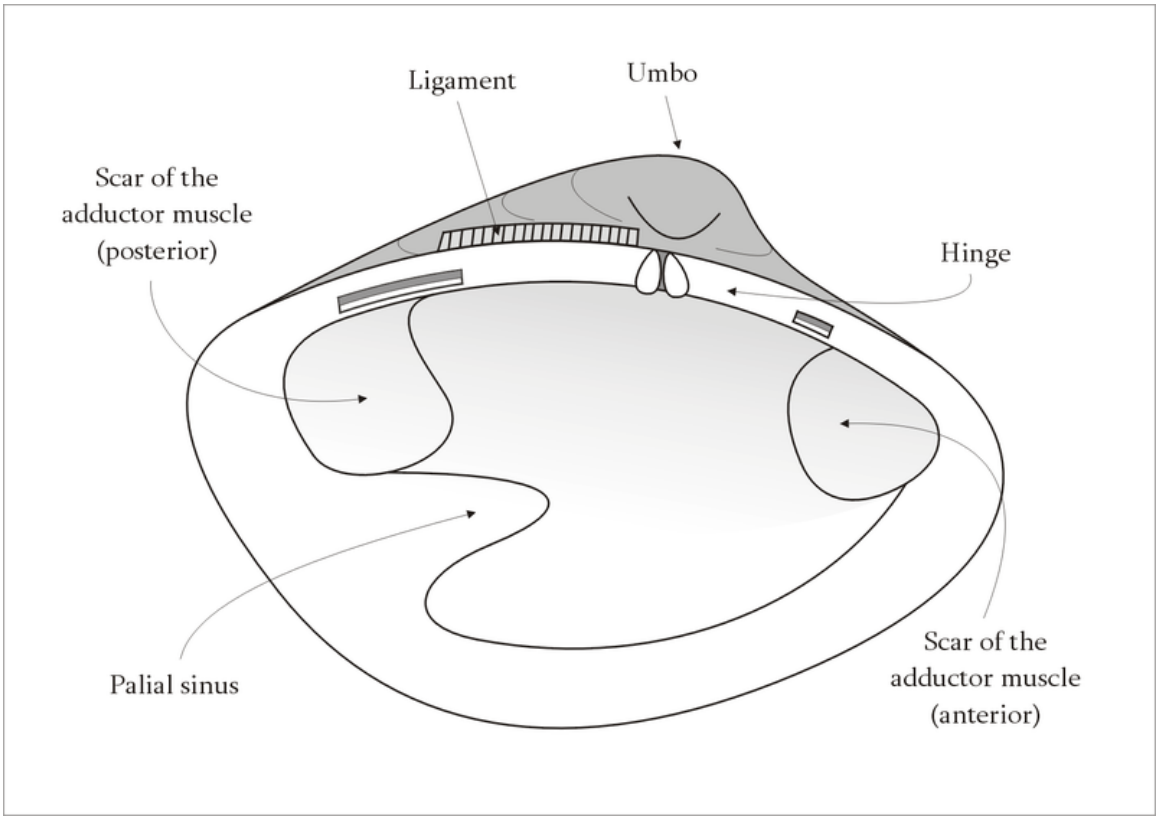
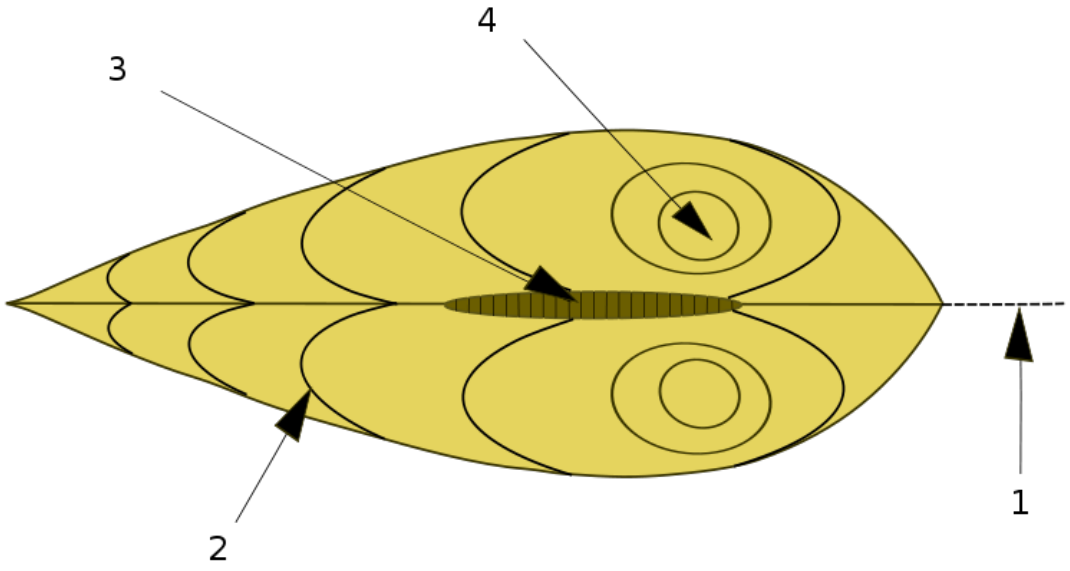
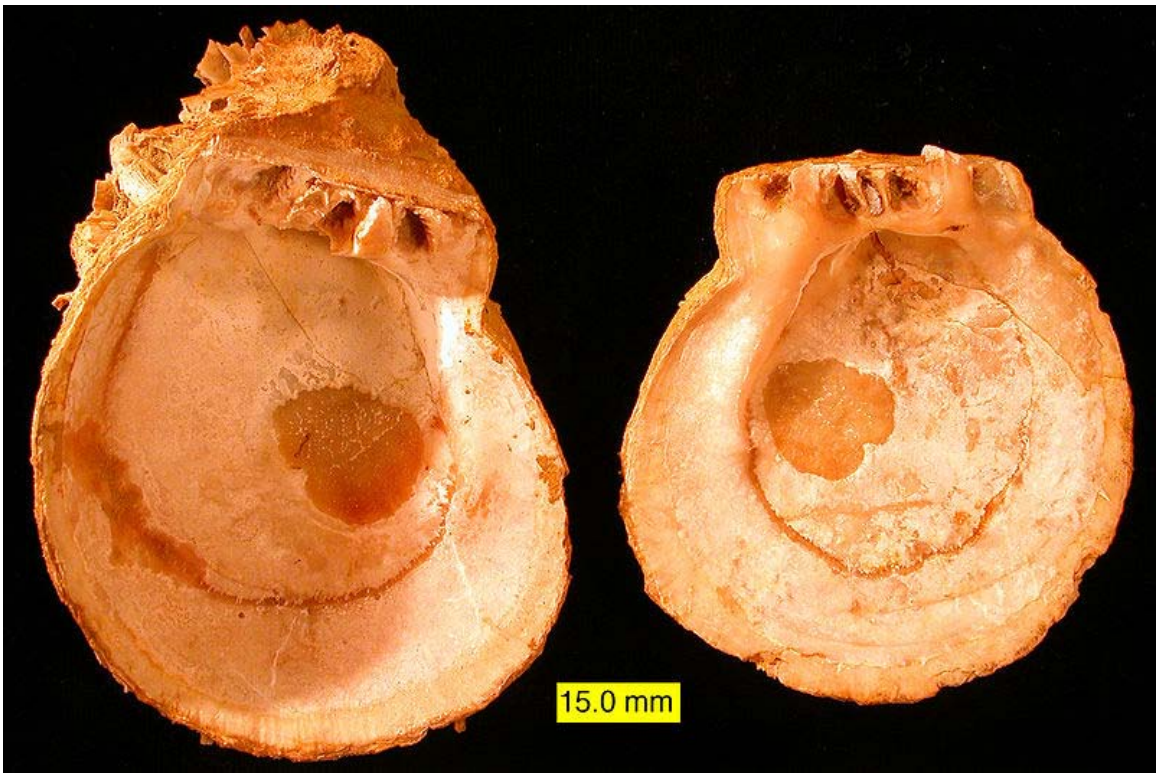


Diagram of the internal shell structure of the left valve of bivalve resembling a venerid



1:Plane of symmetry
2:Growth lines

3:Ligament
4:Umbo



Paired valves of a fossil *Spondylus* shell (a "thorny oyster") showing the isodont, monomyarian, inequivalved condition, from the Pliocene deposits of Cyprus

The bivalve shell is composed of two calcareous valves. The mantle, a thin membrane surrounding the body, secretes the shell valves, ligament and hinge teeth. The mantle lobes secrete the valves, and the mantle crest creates the other parts.

The mantle itself is attached to the shell by numerous small mantle retractor muscles, which are arranged in a narrow line along the length of the interior of the shell. The position of this line is often quite clearly visible on the inside of each valve of a bivalve shell, as a shiny line, the pallial line, which runs along a small distance in from the outer edge of each valve, usually joining the anterior adductor muscle scar to the posterior adductor muscle scar. The two adductor muscles are what allow the bivalve to close the shell tightly.

In some bivalves the mantle edges fuse to form siphons, which take in and expel water during suspension feeding. Species which live buried in sediment usually have long siphons, and when the bivalve needs to close its shell, these siphons retract into a pocket-like space in the mantle. This feature of the internal anatomy of a bivalve is clearly indicated on the interior of the shell surface as a pallial sinus, an indentation in the pallial line.

The valves of the shell are made of either calcite (as with, e.g. oysters) or both calcite and aragonite, usually with the aragonite forming an inner layer, as is the case with the Pterioida which have this layer in the form of nacre or mother of pearl. The outermost layer of the shell is known as the periostracum, which is composed of a horny organic substance. This forms a yellowish or brownish "skin" on the outside of the shell. The periostracum may start to peel off of a shell when it is allowed to dry out for long periods.

The shell is added to, and increases in size, in two ways - by increments added to the open edge of the shell, and by a gradual thickening throughout the animal's life.

The two shell valves are held together at the animal's dorsum by the ligament, which is composed of the tensilium and resilium. The ligament opens the shells.

Razor shell

Razor shell	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Bivalvia
Order:	Veneroida
Family:	Solenidae
Genus:	*Ensis*
Species:	***E. arcuatus***
Binomial name	
Ensis arcuatus (Jeffreys, 1865)	

The **razor shell**, *Ensis arcuatus*, also called **razor clam** or **razor fish**, is a bivalve of the family Solenidae. It is found on sandy beaches in Northern Europe and Eastern Canada, such as Prince Edward Island, where it is most populous in the world. It prefers coarser sand than its relatives *E. ensis* and *E. siliqua*.

Description

It is known for its elongated, rectangular shape, whose similarity to the straight razor gives it its name. The razor shell has been known to reach 23 centimetres (9.1 in) in length. The dorsal margin is straight while the ventral margin is curved. It can easily be confused with the slightly shorter 15 centimetres (5.9 in) and more curved *E. ensis* (in which both front and back are curved in parallel).

Razor shells have a fragile shell, with open ends. The shell is smooth on the outside and whitish in color, with vertical and horizontal reddish-brown or purplish-brown markings separated by a diagonal line. The periostracum is olive-green. The inner surface is white with a purple tinge and the foot is creamy white with brown lines .

Habits

The razor shell lives under the sand, using its powerful foot to dig to a safe depth. Its digging activity comprises six stages, repeated cyclically. A digging cycle involves integration of the muscular foot (which takes up a large part of the body) with the opening and closing of the valve and one end. The foot is inflated hydraulically, extend down into the sand and anchoring the animal. Deflation of the foot then draws the shell down. The razor shell also squirts water down into the sand, removing loose sand from its path. the foot is thought to exert a pressure of 2 kg/cm^2

Its presence is revealed by a keyhole-shaped hole in the sand, made by its siphons during suspension feeding for plankton.

Reproduction

In the razor shell sexual development is highly synchronous. During the summer, they are in the sexual rest stage, and gametogenesis begins at the start of autumn. In winter and spring consecutive spawns take place, interrupted by gonadal restoration periods.

Vulnerability

Many intertidal populations of razor shell have been declined due to overfishing; the species is in decline in many areas.

Razor shells are very sensitive to minor perturbations in, for instance, salinity and temperature. They will emerge from their burrows if salt or brine is poured in.

Disease

Razor shells have been found to be vulnerable to germinoma, a variety of tumour.

Chapter 4

Arcoida and Clam

Arcoida

Arcoida Temporal range: Lower Ordovician–Recent

Anadara from the Pliocene of Cyprus.
Scientific classification

Kingdom:	Animalia
Phylum:	Mollusca
Class:	Bivalvia
Subclass:	Pteriomorpha
Order:	**Arcoida**

The **Arcoida** is an extant order of bivalve molluscs. This order dates back to the lower Ordovician period. They are distinguished from related groups, such as the mussels, by having a straight hinge to the shells, and the adductor muscles being of equal size.

Seven families are currently recognised within the order, including the well-known ark clams or ark shells in the family Arcidae.

Classification

- Superfamily Arcoidea
  - Arcidae
  - Cucullaeidae
  - Noetiidae
  - Parallelodontidae
- Superfamily Limopsoidea
  - Glycymerididae
  - Limopsidae
  - Philobryidae

Clam

Clam

Edible clams in the family Veneridae
Scientific classification
Kingdom: Animalia
Phylum: Mollusca
Class: Pelecypoda

The word "**clam**" can be applied to freshwater mussels, and other freshwater bivalves, as well as marine bivalves.

In the United States, "clam" can be used in several different ways: one, as a general term covering all bivalve molluscs. The word can also be used in a more limited sense, to mean bivalves which burrow in sediment, as opposed to ones which attach themselves to the substrate (for example oysters and mussels), or ones which can swim and are

migratory, like scallops. In addition "clam" can be used in an even more limited sense, to mean one or more species of commonly consumed marine bivalves, as in the phrase clam chowder, meaning shellfish soup usually made using the hard clam. Many edible bivalves have a roughly oval shape; however, the edible razor clam has an elongated, parallel-sided shell, whose shape suggests that of an old-fashioned straight razor.

In the United Kingdom, "clam" is one of the common names of various species of marine bivalve mollusc, but it is not used as a general term to cover edible clams that burrow, and it is not used as a general term for all bivalves.

Numerous edible marine bivalve species live buried in sand or mud, and respire by means of siphons which reach to the surface. In the USA, these clams are collected by "digging for clams" or clam digging.

In October 2007 an *Arctica islandica* clam, caught off the coast of Iceland, was discovered to be at least 405 years old, and was declared the world's oldest living animal by researchers from Bangor University.

In regard to the concept of edible clams, most species of bivalves are at least potentially edible. However some are too small to be useful, and not all species are considered palatable.

The word "clam" has given rise to the metaphor "clamming up", meaning refusing to speak, at least on a certain topic. A "clam shell" is the name given to a plastic container which is hinged, and which consists of two equal halves that lock together.

Anatomy

Littleneck clams, small hard clams, species *Mercenaria mercenaria*

A clam's shell consists of two (usually equal) halves, which are connected by a hinge joint and a ligament which can be external or internal, much like a Venus Flytrap.

In clams, two adductor muscles contract to close the shells. The clam has no head, and usually has no eyes, (scallops are a notable exception), but a clam does have kidneys, a heart, a mouth, and an anus.

Clams, like most molluscs, also have open circulatory systems, which means that their organs are surrounded by watery blood that contains nutrients and oxygen.

Clams feed on plankton by filter feeding. Clams filter feed by drawing in water containing food using an incurrent siphon. The food is then filtered out of the water by the gills and swept toward the mouth on a layer of mucus. The water is then expelled from the animal by an excurrent siphon.

In North America

In culinary use, within the eastern coast of the USA, the term "clam" most often refers to the hard clam *Mercenaria mercenaria*. It may also refer to several other common edible species, such as the soft-shell clam, *Mya arenaria*, and the ocean quahog, *Arctica*

islandica. Another species which is commercially exploited on the Atlantic Coast of the US is the surf clam *Spisula solidissima*.

Clams can be eaten raw, steamed, boiled, baked or fried; the method of preparation depends partly on the size and species of the clam. They can also be made into clam chowder (a popular soup in the U.S. and Canada) or they can be cooked using hot rocks and seaweed in a New England clam bake.

In Italy

In Italy, clams are often an ingredient of mixed seafood dishes, or are eaten together with pasta. The more commonly used varieties of clams in Italian cooking are the **Vongola** *(Venerupis decussata)*, the **Cozza** *(Mytilus galloprovincialis)* and the **Tellina** *(Donax trunculus)*. A variety of mussel called **Dattero di mare** *(Lithophaga lithophaga)* was also once widely popular as seafood. However, since overfishing drove it to the verge of extinction (it takes 15 to 35 years to reach adult size and could only be harvested by smashing the calcarean rocks that form its habitat), it has been declared an endangered species by the Italian government since 1998, and its harvest and sale are forbidden.

In India

In the south western coast of India, also known as the Konkan region, Clams are used to cook curries and side dishes, like Tisaryachi Ekshipi which is clams with one shell on.

In aquaria

Maxima clam, *Tridacna maxima*.

The Maxima clam *Tridacna maxima*, a species of giant clam, is a popular species with saltwater aquarium hobbyists.

In a religious context

Moche clam. 200 A.D. Larco Museum Collection Lima, Peru.

The Moche people of ancient Peru worshipped the sea and its animals. They often depicted clams in their art.

In Jewish tradition all Mollusca are considered non kosher and as such are strictly avoided by observant Jews.

As currency

Some species of clams, particularly Mercenaria mercenaria, were in the past used by the Algonquians of Eastern North America to manufacture wampum, a type of shell money.

Some examples of clams

The world's largest clam (187 cms), a *Sphenoceramus steenstrupi* fossil from Greenland in the Geological Museum in Copenhagen

Edible:

- Grooved carpet shell: *Ruditapes decussatus*
- Hard clam or Northern Quahog: *Mercenaria mercenaria*
- Manila clam: *Venerupis philippinarum*
- Soft clam: *Mya arenaria*
- Atlantic surf clam: *Spisula solidissima*
- Ocean quahog: *Arctica islandica*
- Pacific razor clam: *Siliqua patula*
- Pismo clam: *Tivela stultorum* (8 inch shell on display at the Pismo Beach Chamber of Commerce)
- Geoduck clam: *Panopea abrupta* or *Panope generosa* (largest burrowing clam in the world)
- Atlantic jackknife clam: *Ensis directus*

Not usually considered edible:

- Ark clams, family Arcidae
- Nut clams or pointed nut clams, family Nuculidae
- Duck clams or trough shells, family Mactridae
- Marsh clams, family Corbiculidae
- File clams, family Limidae
- Giant clam: *Tridacna gigas*
- Asian or Asiatic clam: genus *Corbicula*
- Peppery furrow shell: *Scrobicularia plana*

Chapter 5

Freshwater Bivalve and Glochidium

Freshwater bivalve

Freshwater bivalves are freshwater molluscs, bivalves which live in freshwater, as opposed to saltwater. Although the majority of species of bivalve molluscs live in the sea, a number of different families of bivalves live in freshwater (and in some cases in freshwater and brackish water). These families are grouped into two separate lineages which are not closely related.

Habitats for freshwater bivalves vary from very small ditches and ponds, to lakes, canals, and rivers.

One of the largest species of freshwater bivalves is the swan mussel, in the family Unionidae; it can grow to a length of 20 cm, and usually lives in lakes or slow rivers.

Freshwater pearl mussels are well-known as a source of freshwater pearls.

Families of freshwater bivalves

Unionoida

The Unionoida, of worldwide distribution, are the pearly freshwater mussels. All reproduce by means of a larval stage that is parasitic on fish. Many species are utilized as sources of mother-of-pearl.

- Margaritiferidae
- Unionidae
- Hyriidae
- Etheriidae
- Mutelidae
- Mycetopodidae
- Iridinidae

- Order Unionoida: pearly freshwater mussels

Family Margaritiferidae, a shell of *Margaritifera auricularia*

Family Unionidae, *Quadrula metanevra*, the monkeyface mussel

Family Unionidae, *Anodonta cygnea*

Veneroida

The Veneroida is a large group of bivalve "clams", most of which are marine. Several groups have colonized fresh and brackish waters.

- Corbiculidae
- Sphaeriidae
- Dreissenidae

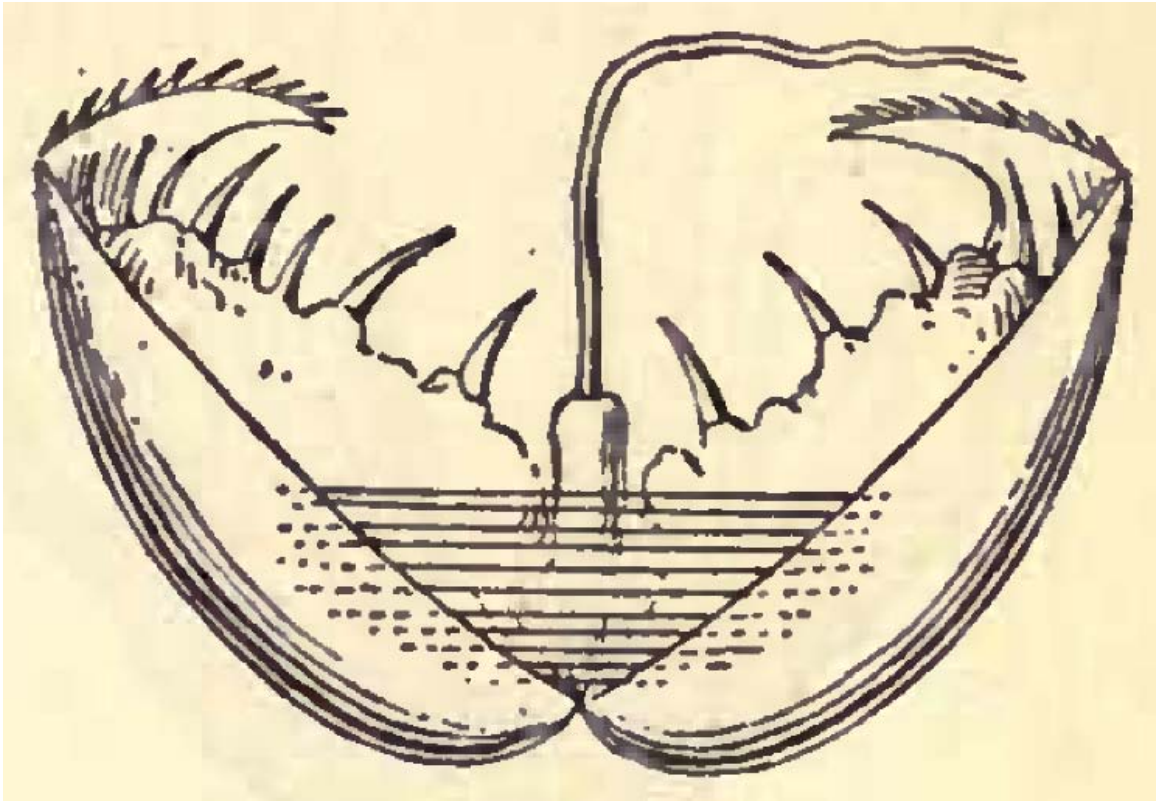
- Order Veneroida

Family Corbiculidae, shell of *Corbicula fluminea*

Family Sphaeriidae, *Sphaerium corneum*, one of the small fingernail clams.

Family Dreissenidae, *Dreissena polymorpha*

Glochidium



A drawing of the glochidium of the swan mussel (*Anodonta cygnea*). The larva is 0.35 mm long

The **glochidium** (plural **glochidia**) is a special microscopic larval stage of larger freshwater mussels, aquatic bivalve mollusks in the families Unionidae and Margaritiferidae, the river mussels and European freshwater pearl mussels.

This larva form has hooks, which enable it to attach itself to fish (for example to the gills of a fish host species) for a period of time before it detaches and falls to the substrate and takes on the typical form of a juvenile mussel. Since a fish is active and free-swimming, this process helps distribute the mussel species to potential areas of habitat that it could not reach any other way.

This larval form used to be described as "parasitic worms" on the fish host, but it is now known that the glochidia do not harm the fish.

Chapter 6

Mussel

Mussel

Blue mussels *Mytilus edulis* in the intertidal zone in Cornwall, England

Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Bivalvia

Subclasses
Pteriomorphia (marine mussels)
Palaeoheterodonta (freshwater mussels)
Heterodonta (zebra mussels)

The common name **mussel** is used for members of several families of clams or bivalvia mollusca, from saltwater and freshwater habitats. These groups have in common a shell whose outline is elongated and asymmetrical compared with other edible clams, which are often more or less rounded or oval.

The word "mussel" is most frequently used to mean the edible bivalves of the marine family Mytilidae, most of which live on exposed shores in the intertidal zone, attached by

means of their strong byssal threads ("beard") to a firm substrate. A few species (in the genus *Bathymodiolus*) have colonised hydrothermal vents associated with deep ocean ridges.

In most marine mussels the shell is longer than it is wide, being wedge-shaped or asymmetrical. The external colour of the shell is often dark blue, blackish, or brown, while the interior is silvery and somewhat nacreous.

The word "mussel" is also used for many freshwater bivalves, including the freshwater pearl mussels. Freshwater mussel species inhabit lakes, ponds, rivers, creeks, canals, grouped in a different subclass, despite some very superficial similarities in appearance.

Freshwater Zebra mussels and their relatives in the family Dreissenidae are not related to previously mentioned groups, even though they resemble many *Mytilus* species in shape, and live attached to rocks and other hard surfaces in a similar manner, using a byssus. They are classified with the Heterodonta, the taxonomic group which includes most of the bivalves commonly referred to as "clams".

General anatomy

Marine blue mussel, *Mytilus edulis*, showing some of the inner anatomy. The white posterior adductor muscle is visible in the upper image, and has been cut in the lower image to allow the valves to open fully.

The mussel's external shell is composed of two hinged halves or "valves". The valves are joined together on the outside by a ligament, and are closed when necessary by strong internal muscles. Mussel shells carry out a variety of functions, including support for soft tissues, protection from predators and protection against desiccation.

The shell has three layers. In the pearly mussels there is an inner iridescent layer of nacre (mother-of-pearl) composed of calcium carbonate, which is continuously secreted by the

mantle; the prismatic layer, a middle layer of chalky white crystals of calcium carbonate in a protein matrix; and the periostracum, an outer pigmented layer resembling a skin. The periostracum is composed of a protein called conchin, and its function is to protect the prismatic layer from abrasion and dissolution by acids (especially important in freshwater forms where the decay of leaf materials produces acids).

Like most bivalves, mussels have a large organ called a foot. In freshwater mussels, the foot is large, muscular, and generally hatchet-shaped. It is used to pull the animal through the substrate (typically sand, gravel, or silt) in which it lies partially buried. It does this by repeatedly advancing the foot through the substrate, expanding the end so it serves as an anchor, and then pulling the rest of the animal with its shell forward. It also serves as a fleshy anchor when the animal is stationary.

In marine mussels, the foot is smaller, tongue-like in shape, with a groove on the ventral surface which is continuous with the byssus pit. In this pit, a viscous secretion is exuded, entering the groove and hardening gradually upon contact with sea water. This forms extremely tough, strong, elastic, byssus threads that secure the mussel to its substrate. The byssus thread is also sometimes used by mussels as a defensive measure, to tether predatory molluscs, such as dog whelks, that invade mussel beds, immobilising them and thus starving them to death.

In cooking, the byssus of the mussel is known as the "beard" and is removed before the mussels are prepared.

Life habits

A *Mytilus* with its byssus clearly showing, at Ocean Beach, San Francisco, California

A starfish consuming a mussel in Northern California

Feeding

Both marine and freshwater mussels are filter feeders; they feed on plankton and other microscopic sea creatures which are free-floating in seawater. A mussel draws water in through its incurrent siphon. The water is then brought into the branchial chamber by the actions of the cilia located on the gills for ciliary-mucus feeding. The wastewater exits through the excurrent siphon. The labial palps finally funnel the food into the mouth, where digestion begins.

Marine mussels are usually found clumping together on wave-washed rocks, each attached to the rock by its byssus. The clumping habit helps hold the mussels firm against the force of the waves. At low tide mussels in the middle of a clump will undergo less water loss because of water capture by the other mussels.

Reproduction

Both marine and freshwater mussels are gonochoristic, with separate male and female individuals. In marine mussels, fertilization occurs outside the body, with a larval stage that drifts for three weeks to six months, before settling on a hard surface as a young

mussel. There, it is capable of moving slowly by means of attaching and detaching byssal threads to attain a better life position.

Freshwater mussels also reproduce sexually. Sperm released by the male directly into the water enters the female via the incurrent siphon. After fertilization, the eggs develop into a larval stage called a glochidium (plural glochidia), which temporarily parasitize fish, attaching themselves to the fish's fins or gills. Prior to their release, the glochidia grow in the gills of the female mussel where they are constantly flushed with oxygen-rich water. In some species, release occurs when a fish attempts to attack the mussel's minnow or other mantle flaps shaped like prey; an example of aggressive mimicry.

Glochidia are generally species-specific, and will only live if they find the correct fish host. Once the larval mussels attach to the fish, the fish body reacts to cover them with cells forming a cyst, where the glochidia remain for two to five weeks (depending on temperature). They grow, break free from the host, and drop to the bottom of the water to begin an independent life.

Predators

Marine mussels are eaten by humans, sea stars, seabirds, and by numerous species of predatory marine gastropods in the family Muricidae, such as the dog whelk, *Nucella lapillus*.

Freshwater mussels are eaten by otters, raccoons, ducks, and geese.

Distribution and habitat

Mussel dredgers

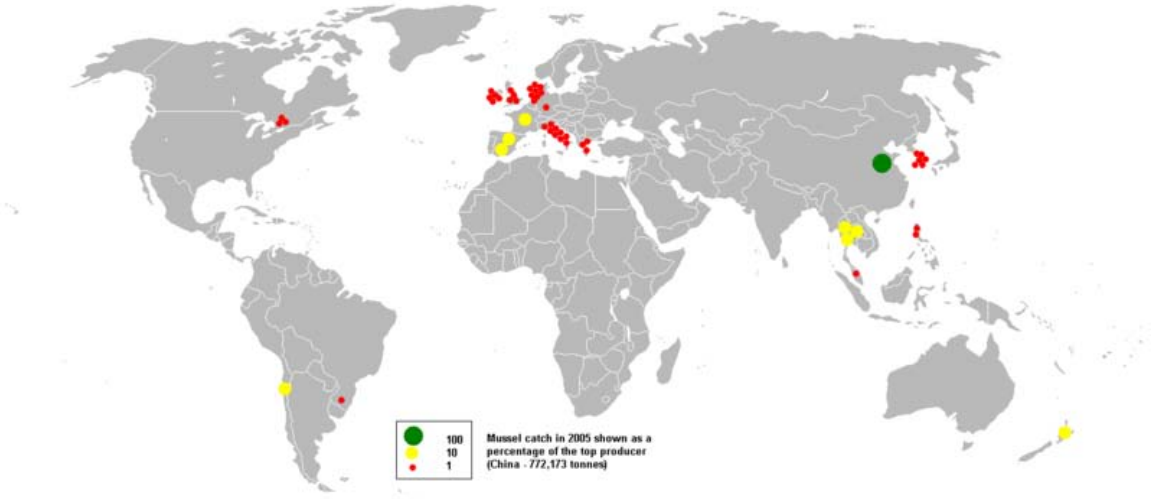
Marine mussels are abundant in the low and mid intertidal zone in temperate seas globally.

Other species of marine mussel live in tropical intertidal areas, but not in the same huge numbers as in temperate zones.

Certain species of marine mussels prefer salt marshes or quiet bays, while others thrive in pounding surf, completely covering wave-washed rocks. Some species have colonized abyssal depths near hydrothermal vents. The South African white mussel exceptionally doesn't bind itself to rocks but burrows into sandy beaches extending two tubes above the sand surface for ingestion of food and water and exhausting wastes.

Freshwater mussels inhabit permanent lakes, rivers, canals and streams throughout the world except in the polar regions. They require a constant source of cool, clean water. They prefer water with a substantial mineral content, using calcium carbonate to build their shells.

Aquaculture



Mussel output in 2005.

Bouchots are marine pilings for growing mussels, here shown at an agricultural fair.

In 2005, China accounted for 40 per cent of the global mussel catch according to a FAO study. Within Europe, Spain remained the industry leader. In North America, 80% of cultured mussels are produced in Prince Edward Island in Canada.

Freshwater mussels are used as host animals for the cultivation of freshwater pearls. Some species of marine mussel, including the Blue Mussel (*Mytilus edulis*) and the New Zealand green-lipped mussel (*Perna canaliculus*), are also cultivated as a source of food.

There are a variety of techniques for growing mussels.

- Intertidal growth technique, or *bouchot* technique: pilings, known in French as *bouchots*, are planted at sea; ropes, on which the mussels grow, are tied in a spiral on the pilings; some mesh netting prevents the mussels from falling away. This method needs an extended tidal zone.
- Mussels are cultivated extensively in New Zealand, where the most common method is to attach mussels to ropes which are hung from a rope back-bone supported by large plastic floats. The most common species cultivated in New Zealand is the New Zealand green-lipped mussel.

Chapter 7

Oyster

Crassostrea gigas from the Marennes-Oléron basin in France

The word **oyster** is used as a common name for a number of distinct groups of bivalve molluscs which live in marine or brackish habitats. The valves are highly calcified.

Some kinds of oyster are commonly consumed by humans, cooked or raw. Other kinds, such as pearl oysters, are not.

Etymology

First attested in English 14th century, the word *oyster* comes from Old French *oistre*, in turn from Latin *ostrea*, the feminine form of *ostreum*, which is the latinisation of the Greek ὄστρεον (*ostreon*), "oyster". Compare ὀστέον (*osteon*), "bone".

Types

True oysters

True oysters are members of the family Ostreidae. This family includes the edible oysters, which mainly belong to the genera *Ostrea*, *Crassostrea*, *Ostreola* and *Saccostrea*. Examples include the Belon oyster, Eastern oyster, Olympia oyster, Pacific oyster, Sydney rock oyster and the Wellfleet oyster.

Pearl oysters

Removing a pearl from an oyster.

Almost all shell-bearing molluscs can secrete pearls, yet most are not very valuable.

Pearl oysters are not closely related to true oysters, being members of a distinct family, the *feathered oysters* (Pteriidae). Both cultured pearls and natural pearls can be obtained from pearl oysters, though other molluscs, such as the freshwater mussels, also yield pearls of commercial value.

The largest pearl-bearing oyster is the marine *Pinctada maxima*, which is roughly the size of a dinner plate. Not all individual oysters produce pearls naturally. In fact, in a harvest of three tons of oysters, only three to four oysters produce perfect pearls.

In nature, pearl oysters produce natural pearls by covering a minute invading parasite with nacre, not by ingesting a grain of sand. Over the years, the irritating object is covered with enough layers of nacre to form what is known as a pearl. There are many different types, colours and shapes of pearl; these qualities depend on the natural pigment of the nacre, and the shape of the original irritant.

Pearl farmers can culture a pearl by placing a nucleus, usually a piece of polished mussel shell, inside the oyster. In three to six years, the oyster can produce a perfect pearl. These pearls are not as valuable as natural pearls, but look exactly the same. In fact, since the beginning of the 20th century, when several researchers discovered how to produce artificial pearls, the cultured pearl market has far outgrown the natural pearl market. Natural pearls have become increasingly scarce, and a necklace with only natural pearls can easily cost several hundred thousand US dollars.

Other types of oysters

A number of bivalve molluscs (other than edible oysters and pearl oysters) also have common names that include the word "oyster", usually because they either taste or look like oysters, or because they yield noticeable pearls. Examples include:

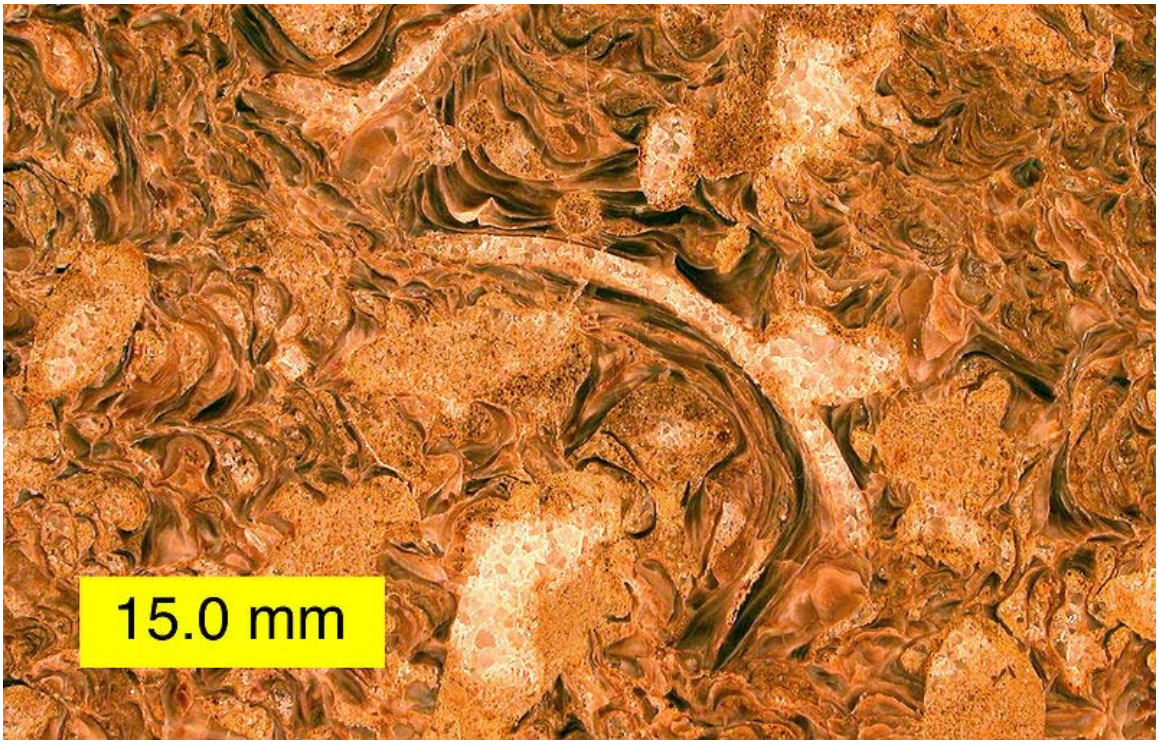
- Thorny oysters (Spondylidae)
- Pilgrim oysters (a kind of scallop)
- Saddle oysters (*Anomia ephippium*)

Crassostrea gigas

Crassostrea gigas, opened

An ostreolith from the Middle Jurassic Carmel Formation of southern Utah.

Exterior of an ostreolith showing it is made up almost entirely of the Jurassic oyster species *Liostrea strigilecula*.



Ostreolith interior showing an aragonitic shell cast as the nucleus and *Gastrochaenolites* borings.

Anatomy

Oysters are filter feeders, drawing water in over their gills through the beating of cilia. Suspended plankton and particles are trapped in the mucus of a gill, and from there are transported to the mouth, where they are eaten, digested and expelled as faeces or pseudofaeces. Oysters feed most actively at temperatures above 10 °C (50 °F). An oyster can filter up to 5 litres (1.3 US gal) of water per hour. Chesapeake Bay's once flourishing oyster population historically filtered excess nutrients from the estuary's entire water volume every three to four days. Today that would take nearly a year. Excess sediment, nutrients, and algae can result in the eutrophication of a body of water. Oyster filtration can mitigate these pollutants.

In addition to their gills, oysters can also exchange gases across their mantle, which is lined with many small, thin-walled blood vessels. A small, three-chambered heart, lying under the adductor muscle, pumps colorless blood to all parts of the body. At the same time, two kidneys, located on the underside of the muscle, remove waste products from the blood.

While some oysters have two sexes (European Oyster & Olympia Oyster), their reproductive organs contain both eggs and sperm. Because of this, it is technically possible for an oyster to fertilize its own egg. The gonads surround the digestive organs, and are made up of sex cells, branching tubules and connective tissue.

Once the female is fertilized, they discharge millions of eggs into the water. The larvae develop in about six hours and swim around for about two to three weeks. After that, they settle on a bed and mature within a year.

Habitat and behaviour

Oyster reef at about mid-tide off fishing pier at Hunting Island State Park, South Carolina

A group of oysters is commonly called a **bed** or **oyster reef**.

The largest oyster-producing body of water is located in Chesapeake Bay, although these beds are starting to lower in numbers due to overfishing and pollution. Large beds of edible oysters are also found in Japan and Australia.

As a keystone species, oysters provide habitat for many marine species. *Crassostrea* and *Saccostrea* live mainly in the intertidal zone, while *Ostrea* are subtidal. The hard surfaces of oyster shells and the nooks between the shells provide places where a host of small animals can live. Hundreds of animals such as sea anemones, barnacles, and hooked mussels inhabit oyster reefs. Many of these animals are prey to larger animals, including fish such as striped bass, black drum and croakers.

An oyster reef can increase the surface area of a flat bottom 50-fold. An oyster's mature shape often depends on the type of bottom to which it is originally attached, but it always

orients itself with its outer, flared shell tilted upward. One valve is cupped and the other is flat.

Oysters usually reach maturity in one year. They are protandric; during their first year they spawn as males by releasing sperm into the water. As they grow over the next two or three years and develop greater energy reserves, they spawn as females by releasing eggs. Bay oysters usually spawn by the end of June. An increase in water temperature prompts a few oysters to spawn. This triggers spawning in the rest, clouding the water with millions of eggs and sperm. A single female oyster can produce up to 100 million eggs annually. The eggs become fertilized in the water and develop into larvae, which eventually find suitable sites, such as another oyster's shell, on which to settle. Attached oyster larvae are called **spat**. Spat are oysters less than 25 millimetres (0.98 in) long. Many species of bivalve, oysters included, seem to be stimulated to settle near adult conspecifics.

Some tropical oysters in the family Isognomonidae grow best on mangrove roots. Low tide can expose them, making them easy to collect. In Trinidad in the West Indies, tourists are often astounded when they are told that in the Caribbean, "oysters grow on trees."

Common oyster predators include crabs, sea birds, sea stars, and humans. Some oysters contain live crabs, known as oyster crabs.

Marine pollution

Oysters consume nitrogen-containing compounds (nitrates and ammonia), removing them from the water. Nitrogen compounds are important phytoplankton nutrients. Phytoplankton increase water turbidity. Limiting the amount of phytoplankton in the water improves water quality and other marine life by reducing competition for dissolved oxygen. Oysters feed on plankton, incidentally consuming nitrogen compounds as well. They then expel solid waste pellets which decompose into the atmosphere as nitrogen. In Maryland, the Chesapeake Bay Program plans to use oysters to reduce the amount of nitrogen compounds entering the Chesapeake Bay by 19,000,000 pounds (8,600,000 kg) per year by 2010.

Human history

The Whaleback Shell Midden in Maine contains the shells from oyster harvesting for food consumption dating to 2200-1000 years ago

Middens testify to the prehistoric importance of oysters as food. In the United Kingdom, the town of Whitstable is noted for oyster farming from beds on the Kentish Flats that have been used since Roman times. The borough of Colchester holds an annual Oyster Feast each October, at which "Colchester Natives" (the native oyster, *Ostrea edulis*) are consumed. The United Kingdom hosts several other annual oyster festivals, for example Woburn Oyster Festival is held in September. Many breweries produce Oyster Stout, a beer intended to be drunk with oysters that sometimes includes oysters in the brewing process.

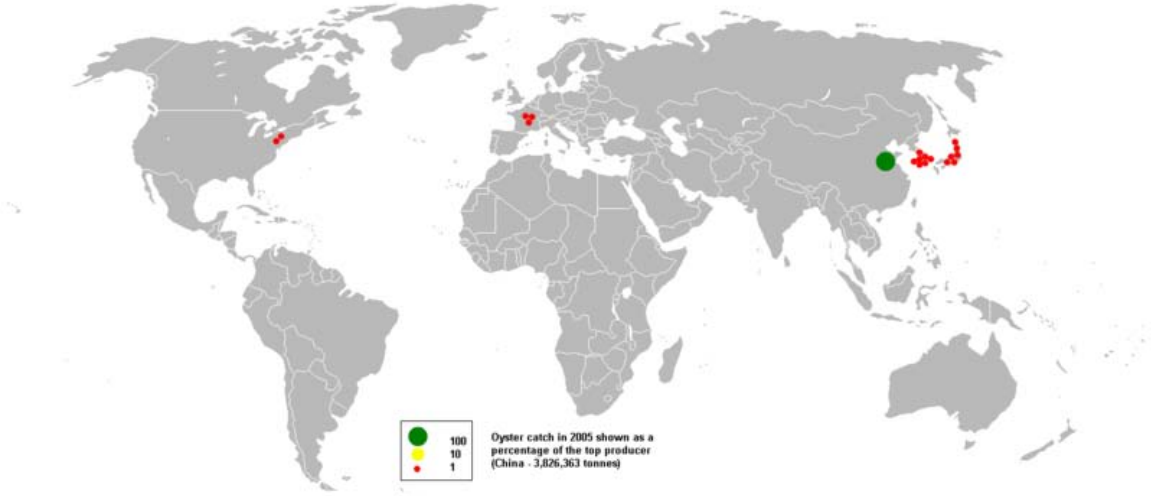
The French seaside resort of Cancale is noted for its oysters, which also date from Roman times. Sergius Orata of the Roman Republic is considered the first major merchant and cultivator of oysters. Using his considerable knowledge of hydraulics, he built a sophisticated cultivation system, including channels and locks, to control the tides. He was so famous for this that the Romans used to say he could breed oysters on the roof of his house.

The world-famous Clarenbridge and Galway Oyster Festivals take place in Galway, Ireland each September. In Ireland it is traditional to eat them live with Guinness and buttered brown soda bread.

In the early 19th century, oysters were cheap and mainly eaten by the working class. Throughout the 19th century, oyster beds in New York harbor became the largest source of oysters worldwide. On any day in the late 19th century, six million oysters could be found on barges tied up along the city's waterfront. Oysters were naturally quite popular in New York City, and helped initiate the city's restaurant trade. New York's oystermen became skilled cultivators of their beds, which provided employment for hundreds of workers and nutritious food for thousands. Eventually, rising demand exhausted many of the beds. To increase production, they introduced foreign species, which brought disease, when combined with effluent and increasing sedimentation from erosion, which destroyed most of the beds by the early 20th century. Oysters' popularity has put an ever-increasing demands on wild oyster stocks. This scarcity increased prices, converting them from their original role as working class food to their current status as an expensive delicacy.

In the United Kingdom, the native variety is still held to be the finest, requiring five years to mature and protected by an Act of Parliament during the May–August spawning season. The current market is dominated by the larger Pacific oyster and rock oyster varieties which are farmed year round.

Commercial fishing



Oyster catch in 2005

Fishing from the wild

Oysters are harvested by simply gathering them from their beds. In very shallow waters they can be gathered by hand or with small rakes. In somewhat deeper water, long-handled rakes or oyster tongs are used to reach the beds. Patent tongs can be lowered on a

line to reach beds that are too deep to reach directly. In all cases the task is the same: the oysterman scrapes oysters into a pile, and then scoops them up with the rake or tongs.

In some areas a scallop dredge is used. This is a toothed bar attached to a chain bag. The dredge is towed through an oyster bed by a boat, picking up the oysters in its path. While dredges collect oysters more quickly, they heavily damage the beds, and their use is highly restricted. Until 1965 Maryland limited dredging to sailboats, and even since that date motor boats can be used only on certain days of the week. These regulations prompted the development of specialized sailboats (the bugeye and later the skipjack) for dredging.

Oysters can also be collected by divers.

In any case, when the oysters are collected, they are sorted to eliminate dead animals, bycatch (unwanted catch), and debris. Then they are taken to market where they are either canned or sold live.

Cultivating oysters

Oyster culture in Belon, France.

Oysters have been cultured for well over a century. Two methods are commonly used, release and bagging. In both cases oysters are cultivated onshore to the size of spat, when they can attach themselves to a substrate. They may be allowed to mature further to form *seed oysters*. In either case they are then placed in the water to mature. The release technique involves distributing the spat throughout existing oyster beds allowing them to mature naturally to be collected like wild oysters. Bagging has the cultivator putting spat in racks or bags and keeping them above the bottom. Harvesting involves simply lifting the bags or rack to the surface and removing the mature oysters. The latter method prevents losses to some predators, but is more expensive.

The Pacific or Japanese oyster, *Crassostrea gigas* has been grown in the outflow of mariculture ponds. When fish or prawn are grown in ponds, it takes, typically 10 kilograms (22 lb) of feed to produce 1 kilogram (2.2 lb) of product (dry-dry basis). The other 9 kilograms (20 lb) goes into the pond and after mineralization, provides food for phytoplankton, which in turn feeds the oyster.

To prevent spawning, sterile oysters are now cultured by crossbreeding tetraploid and diploid oysters. The resulting triploid oyster cannot propagate, which prevents introduced oysters from spreading into unwanted habitats.

Restoration and recovery

In many areas non-native oysters have been introduced in attempts to prop up failing harvests of native varieties. For example, the eastern oyster was introduced to California waters in 1875, while the Pacific oyster was introduced there in 1929. Proposals for further such introductions remain controversial.

The Pacific oyster prospered in Pendrell Sound where the surface water is typically warm enough for spawning in the summer. Over the following years, spat spread out sporadically and populated adjacent areas. Eventually, possibly following adaptation to the local conditions, the Pacific oyster spread up and down the coast and now is the basis of the North American west coast oyster industry. Pendrell Sound is now a reserve that supplies spat for cultivation. Near the mouth of the Great Wicomico River in the Chesapeake Bay, five year-old artificial reefs now harbor more than 180 million native *Crassostrea virginica*. That is still a far cry from the late 1880s, when the Bay's population was in the billions, and watermen harvested about 25 million imperial bushels (910,000 m^3) annually. The 2009 harvest was less than 200,000 imperial bushels (7,300 m^3). Researchers claim that the keys to the project were:

- using waste oyster shells to elevate the reef floor 10–18 inches (0.25–0.46 m) to keep the spat free of bottom sediments
- building larger reefs, ranging up to 20 acres (8.1 ha) in size
- disease resistant broodstock

In 2005, China accounted for 80% of the global oyster harvest. Within Europe, France remained the industry leader.

Ethical considerations

While technically an animal, the oyster is considered by some ethicists to be an appropriate food choice for vegans and vegetarians, arguing it is acceptable to eat oysters, because in the relevant *ethical* terms they are rather closer to plants than animals. Two common ethical objections to the consumption of animals is that they feel pain (and that causing pain is wrong), and that their cultivation is environmentally harmful. On both of these, oysters are significantly closer to plants than animals. Regarding pain, oysters lack a central nervous system, and do not experience pain in the same way as humans do, with them and other bivalves being closer to mobile plants than to plant perception. Regarding environmental impact, 95% of oysters are sustainably farmed and harvested (other bivalves are frequently harvested by harmful dredging), feed on plankton (very low on the food chain), and in fact improve the marine environment by removing toxins. As such, oysters are listed as a "Best Choice" (highest rating) on the Seafood Watch list.

The view that oysters are acceptable to eat, even by strict ethical criteria, has notably been propounded in the seminal 1975 text *Animal Liberation,* by philosopher Peter Singer; while subsequent editions have reversed this position (advocating *against* eating oysters). Singer has stated that he has "gone back and forth on this over the years," and as of 2010 states that "unless some new evidence of a capacity for pain emerges, the doubt is so slight that there is no good reason for avoiding eating sustainably produced oysters.".

Diseases

Oysters are subject to various diseases which can reduce harvests and severely deplete local populations. Disease control focuses on containing infections and breeding resistant strains and is the subject of much ongoing research.

- *Dermo* (*Perkinsus marinus*) is caused by a protozoan parasite. It is a prevalent pathogen, causes massive mortality and poses a significant economic threat to the oyster industry. The disease is not a direct threat to humans consuming infected oysters. Dermo first appeared in the Gulf of Mexico in the 1950s, and until 1978 it was believed to be caused by a fungus. While it is most serious in warmer waters, it has gradually spread up the east coast of the United States.

- *MSX* (Multinucleated Sphere X) is caused by the protozoan *Haplosporidium nelsoni*, generally seen as a multi-nucleated plasmodium. It is infectious and causes heavy mortality in the Eastern Oyster; survivors, however, develop resistance and can help propagate resistant populations. MSX is associated with high salinity and water temperatures. MSX was first noted in Delaware Bay in 1957 and is now found all up and down the east coast of the United States. Evidence suggests that it was brought to the United States when *Crassostrea gigas*, a Japanese oyster variety, was introduced to Delaware Bay.

Chapter 8

Scallop

Scallop

Scientific classification
Kingdom: Animalia
Phylum: Mollusca
Class: Bivalvia
Order: Ostreoida
Suborder: Pectinina
Superfamily: Pectinoidea
Family: **Pectinidae** Rafinesque, 1815

A **scallop** is a marine bivalve mollusc of the family **Pectinidae**. Scallops are a cosmopolitan family, found in all of the world's oceans. Many scallops are highly prized as a food source. The brightly colored, fan-shaped shells of some scallops, with their radiating fluted pattern, are valued by shell collectors.

The name "scallop" is derived from the Old French *escalope*, which means "shell".

Anatomy

Scallops have between 50 and 200 simple eyes

Like the true oysters (family Ostreidae), scallops have a central adductor muscle, and thus the inside of their shells has a characteristic central scar, marking the point of attachment for this muscle. The adductor muscle of scallops is larger and more developed than that of oysters, because they are active swimmers; scallops are in fact the only migratory bivalve. Their shell shape tends to be highly regular, recalling one archetypal form of a seashell, and because of this pleasing geometric shape, the scallop shell is a common decorative motif.

Scallops have between 50 and 200 simple eyes strung around the edges of their mantles like a string of beads. They are reflector eyes with a retina that is more complex than those of other bivalves. Their eyes contain two retina types, one responding to light and the other to abrupt darkness, such as the shadow of a nearby predator. They cannot resolve shapes, but can detect changing patterns of light and motion.

Reflector eyes are an alternative to a lens where the inside of the eye is lined with mirrors which reflect the image to focus at a central point. The nature of these eyes means that if one were to peer into the pupil of an eye, one would see the same image that the organism would see, reflected back out. The scallop *Pecten* has up to 100 millimeter-scale reflector eyes fringing the edge of its shell. It detects moving objects as they pass successive lenses.

Food and digestion

Most scallops are filter feeders, and eat plankton. Coincidentally, the plankton can include scallop larvae. Siphons bring water over a filtering structure, where food becomes trapped in mucus. Next, the cilia on the structure move the food toward the mouth. Then, the food is digested in the stomach and digestive gland. Waste is passed on through the intestine and exits via the anus.

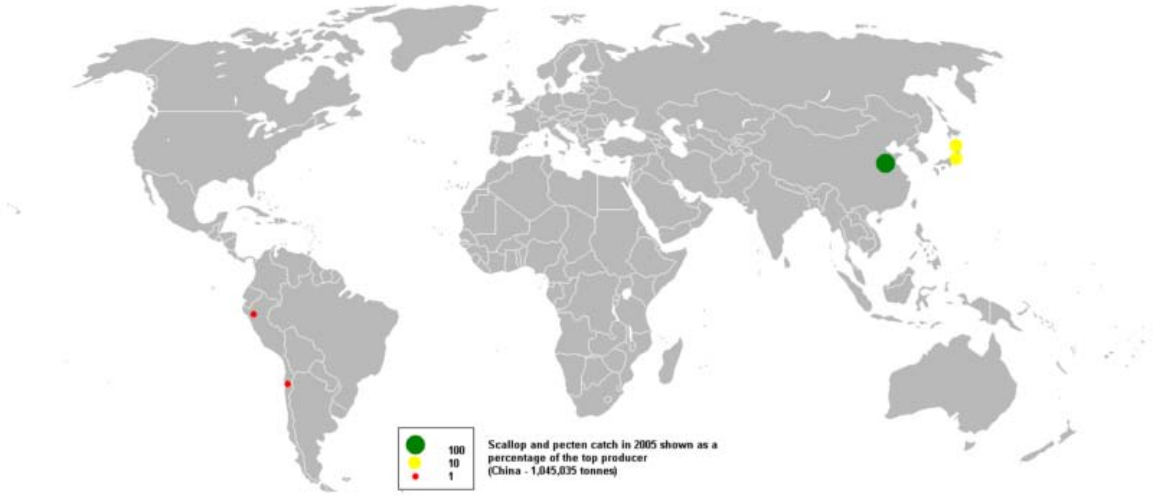
Life habits

Most scallops are free-living, but some species can attach to a substrate by a structure called a byssus, or even be cemented to their substrate as adults (e.g. *Hinnites spp.*). Other scallops can extend a "foot" from between their valves (shell). By then contracting the foot, they can burrow themselves deeper into sand. A free-living scallop can swim, by rapidly opening and closing its shell. This method of locomotion is also a defensive technique, protecting it from threatening predators. Some scallops can make an audible soft popping sound as they flap their shells underwater, leading one seafood vendor to dub them "singing scallops".

Reproductive cycle

The scallop family is unusual in that some members of the family are dioecious (males and females are separate), while other are simultaneous hermaphrodites (both sexes in the same individual) and a few are protoandrous hermaphrodites (males when young then switching to female). Red roe is that of a female, and white, that of a male. Spermatozoa and ova are released freely into the water during mating season and fertilized ova sink to the bottom. After several weeks, the immature scallop hatches and the larvae drift in the plankton until settling to the bottom again to grow, usually attaching by means of byssal threads. Some scallops, such as the Atlantic bay scallop *Argopecten irradians* are short lived, while others can live 20 years or more. Age can often be inferred from annuli, the concentric rings of their shells.

Seafood industry



Scallop and pecten catch in 2005

Wild fisheries

By far the largest wild scallop fishery is for the Atlantic sea scallop (*Placopecten magellanicus*) found off northeastern United States and eastern Canada. Most of the rest of the world's production of scallops is from Japan (wild, enhanced, and aquaculture), and China (mostly cultured Atlantic bay scallops).

Scallops are most commonly harvested using scallop dredges or bottom trawls. Recently, scallops harvested by divers, hand-caught on the ocean floor, have entered the marketplace. In contrast to scallops captured by a dredge across the sea floor, diver scallops tend to be less gritty. They may also be more ecologically friendly, as the harvesting method does not cause damage to undersea flora or fauna. In addition, dredge-harvesting methods often result in delays of up to two weeks before the scallops arrive at market, which can cause the flesh to break down, and results in a much shorter shelf life.

Aquaculture

In 2005, China accounted for 80 percent of the global scallop and pecten catch, according to an FAO study. Within Europe, Russia remained the industry leader.

Sustainability

New Zealand

The Tasman Bay area has been closed to commercial scallop harvesting for the past two years due to a decline in the numbers. Industry-funded research is currently being conducted into scallop harvesting patterns. Forest and Bird list scallops as "Worst Choice" in their Best Fish Guide for sustainable seafood species.

United States

On the east coast of the United States, over the last 100 years, the populations of bay scallops have greatly diminished. This decrease is due to several factors, but probably is mostly due to reduction in sea grasses (to which bay scallop spat attach) due to increased coastal development and concomitant nutrient runoff. Another possible factor is reduction of sharks from overfishing. A variety of sharks used to feed on rays, which are a main predator of bay scallops. With the shark population reduced, in some places almost eliminated, the rays have been free to dine on scallops to the point of greatly decreasing their numbers. By contrast, the Atlantic sea scallop (*Placopecten magellanicus*) is at historically high levels of abundance after recovery from overfishing.

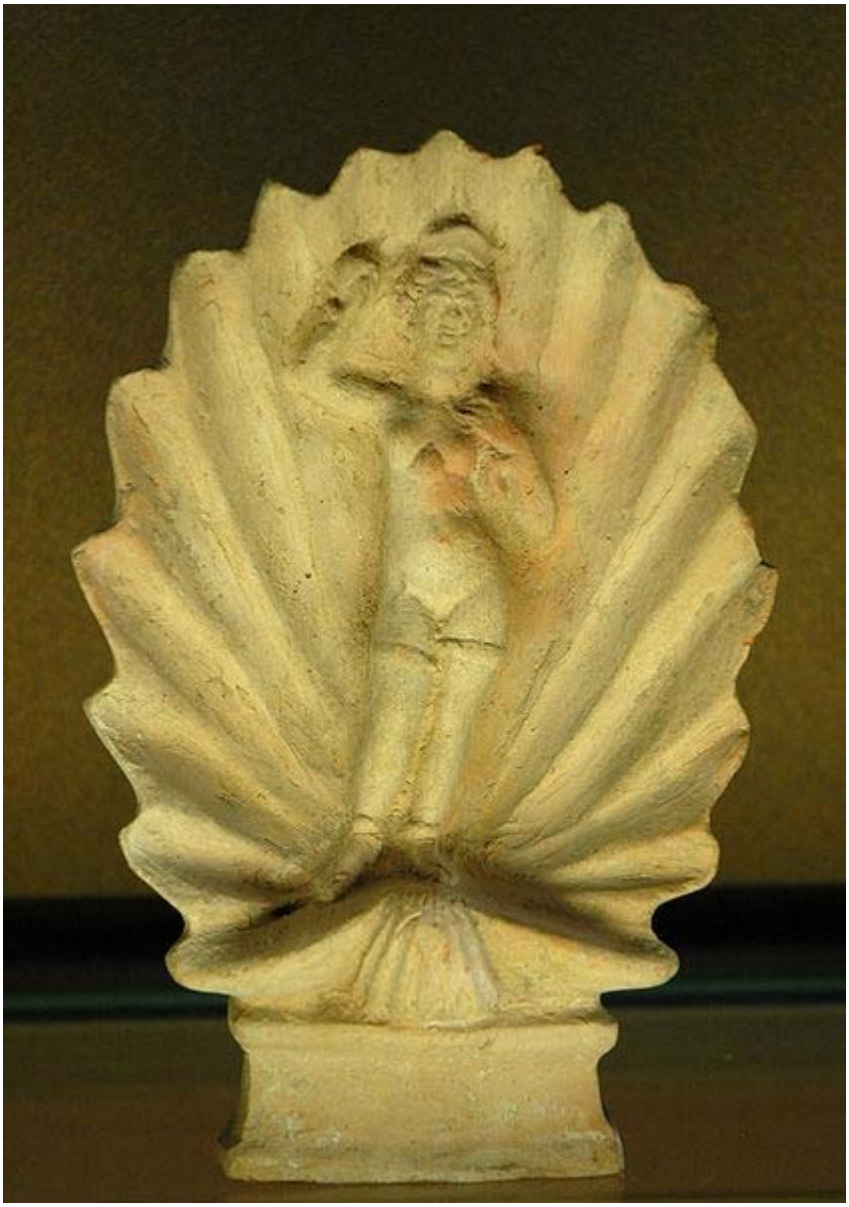
Symbolism

Portrait by Carlo Crivelli, c. 1480

Shell of Saint James

The scallop shell is the traditional emblem of James, son of Zebedee and is popular with pilgrims on the Way of St James to the apostle's shrine at Santiago de Compostela in Spain. Medieval Christians making the pilgrimage to his shrine often wore a scallop shell symbol on their hat or clothes. The pilgrim also carried a scallop shell with him, and would present himself at churches, castles, abbeys etc., where he could expect to be given as much sustenance as he could pick up with one scoop. Probably he would be given oats, barley, and perhaps beer or wine. Thus even the poorest household could give charity without being overburdened. The association of Saint James with the scallop can most likely be traced to the legend that the apostle once rescued a knight covered in scallops. An alternative version of the legend holds that while St. James' remains were being transported to Spain from Jerusalem, the horse of a knight fell into the water, and emerged covered in the shells.

Fertility symbol



Aphrodite in a sea shell, from Amisos, now in the Louvre

Throughout antiquity, scallops and other hinged shells have symbolized the feminine principle. Outwardly the shell can symbolize the protective and nurturing principle, and inwardly the "life-force slumbering within the Earth", an emblem of the vulva.

Many paintings of Venus, the Roman goddess of love and fertility, included a scallop shell in the painting to identify her. This is evident in Botticelli's classically inspired *The Birth of Venus* (also known as *Venus on the half-shell*).

One legend of the Way of St. James holds that the route was seen as a sort of fertility pilgrimage, undertaken when a young couple desired to bear offspring. The scallop shell is believed to have originally been carried therefore by pagans as a symbol of fertility.

Alternatively, the scallop resembles the setting sun, which was the focus of the pre-Christian Celtic rituals of the area. To wit, the pre-Christian roots of the *Way of St. James* was a Celtic death journey westwards towards the setting sun, terminating at the *End of the World* (*Finisterra*) on the "Coast of Death" (Costa da Morte) and the "Sea of Darkness" (i.e., the Abyss of Death, the *Mare Tenebrosum*, Latin for the Atlantic Ocean, itself named after the *Dying Civilization* of Atlantis). The reference to St. James rescuing a "knight covered in scallops" is therefore a reference to St. James healing, or resurrecting, a dying (setting sun) knight. Similarly, the notion of the "Sea of Darkness" (Atlantic Ocean) disgorging St. James' body, so that his relics are (allegedly) buried at Santiago de Compostella on the coast, is itself a metaphor for "rising up out of Death", that is, resurrection.

State shell of New York

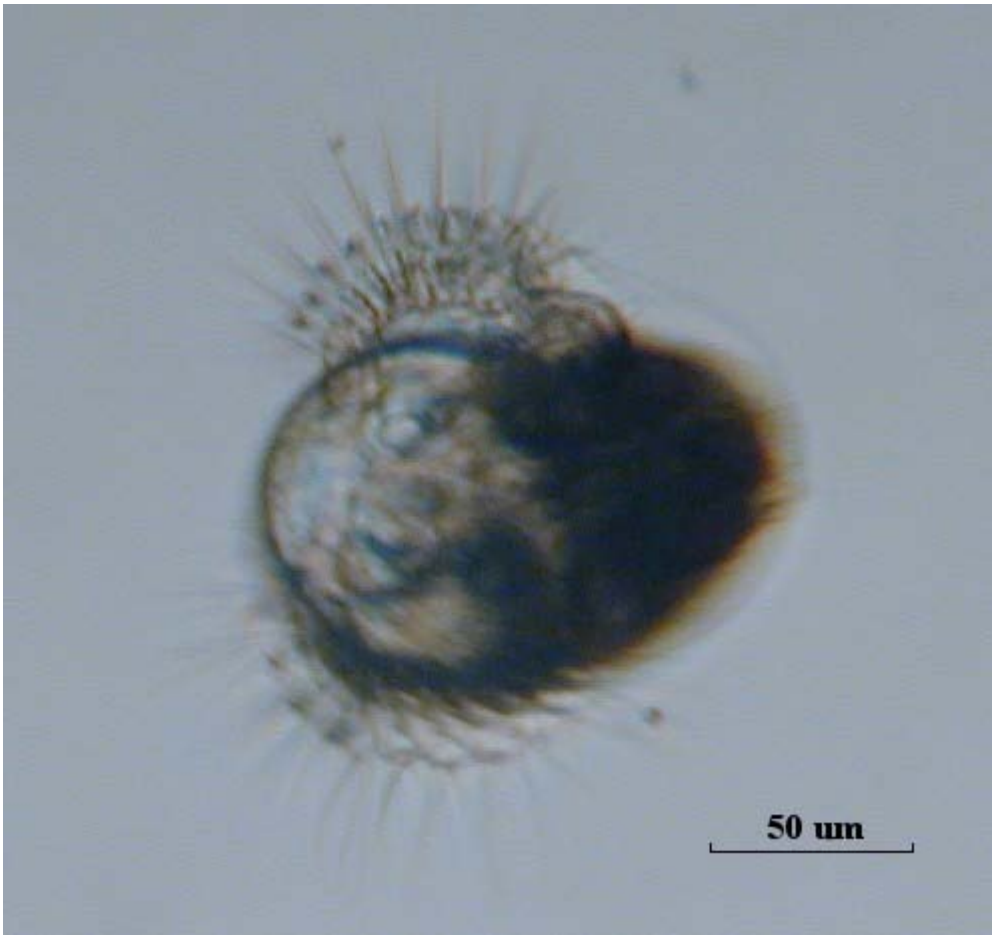
The U.S. state of New York made the Atlantic bay scallop its state shell in 1988.

In design

In design, *scalloped edges* or *ridges* refers to a wavy pattern reminiscent of the edge of a scallop's shell.

Chapter 9

Veliger



Veliger of sea hare *Dolabrifera dolabrifera*, with two rows of cilia visible

A **veliger** is the planktonic larva of many kinds of marine and fresh-water gastropod molluscs, as well as most bivalve mollusks (including the genus *Dreissena*).

Description

The veliger is the characteristic larva of the gastropod, bivalve and scaphopod taxonomic classes that is produced following either the embryonic or trochophore larval stage of development. This stage in the life history of these groups is a free living, planktonic organism that potentially enhances dispersal to new regions far removed from the adult mollusks that produced the larvae. The general structure of the veliger includes a shell that surrounds the visceral organs of the larva (e.g., digestive tract, much of the nervous system, excretory organs) and a ciliated velum that extends beyond the shell as a single or multi-lobed structure that is used for both swimming and particulate food collection. The larva may have or may develop a foot that will be used by the newly settled veliger as it moves about and searches for an appropriate place to metamorphose and subsequently by the juvenile for benthic locomotion. The velum and foot of the veliger may be retracted into the shell for protection of these structures from either predatory or mechanical damage.

Life cycle

Veligers hatch from egg capsules or develop from an earlier trochophore larval stage.

Veligers mature to a point called "competence" where they settle to the substratum and metamorphose to become the juvenile stage. The process of metamorphosis involves losing their velum and undergoing both external and internal changes that produce the juvenile.

Both feeding and non-feeding veligers are possible, depending on the specific species that produced them. In the case of a feeding veliger, the larval stage is, in most cases, relatively “undeveloped” and must feed on phytoplankton for a period of time (weeks to months) in order to develop to the point where it can metamorphose. During this period the veliger grows and also develops the organ systems necessary for the benthic life of a juvenile. "Non-feeding" veligers utilize yolk stored in the egg as an energy source for development. In such cases, the organ systems necessary for juvenile life develop either during the embryonic period or also during a brief larval stage. Non-feeding veliger larvae generally are thought to metamorphose to the juvenile stage in a relatively short period of time; however, in some cases such larvae can feed secondarily and persist in the plankton for long periods.

Metamorphosis of both feeding and non-feeding competent larvae is usually induced by a chemical cue that is characteristic of the proper habitat for the juvenile. In gastropods, this chemical cue is often a substance produced by the juvenile or adult food source. In bivalves, the chemical cue may be produced by bacteria that are specific to the type of biofilm growing in the adult habitat. As a result of this inductive response, the veliger will metamorphose in a habitat where it can successfully feed and grow to adulthood.

Veliger of gastropods

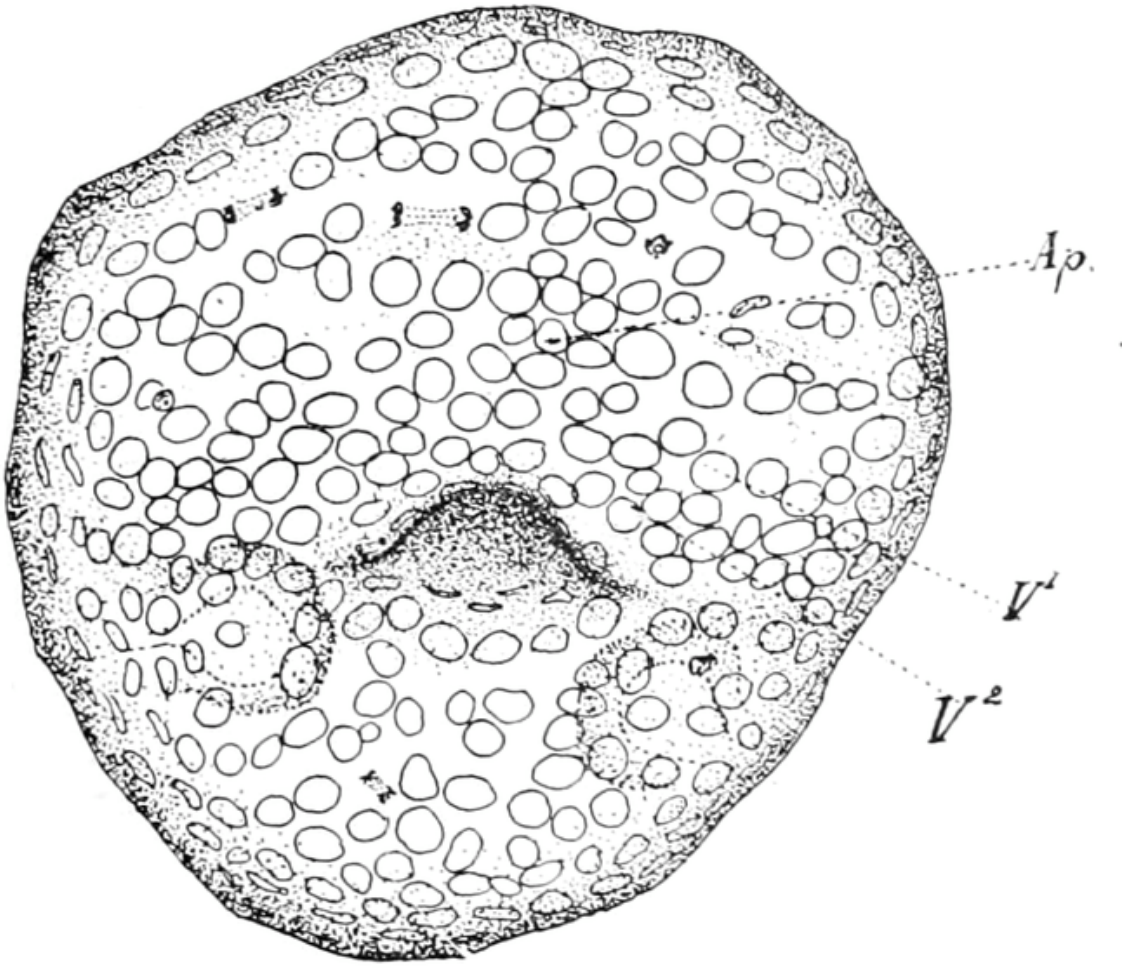
The veliger is the second larval stage in the development of gastropods, following the earlier, trochophore, stage. In some species, including virtually all pulmonates, the veliger stage is passed within the egg capsule and the hatching stage is a juvenile rather than a free-living larva. In species with a larval stage, the veliger is exclusively aquatic. Free-living veliger larvae typically feed on phytoplankton; however, the larvae of some species are lecithotrophic (nourished by yolk from the egg that is retained within their bodies) and do not need to feed. In at least some cases, lecithotrophic veligers can also facultatively feed on phytoplankton.

Unlike the trochophore, the newly hatched veliger may possess or will develop many of the characteristic features of the adult including such structures as a muscular foot, eyes, rhinophores, a fully developed mouth, and a spiral shell (in fact, the veliger of nudibranchs possesses a shell, even though the adult does not). Unlike the adult, however, the veliger possesses two ciliated semi-circular structures resembling fins or wings. These are collectively referred to as the **velum**, and are the larva's main means of propulsion, as well as being used for the collection of food particles from the water.

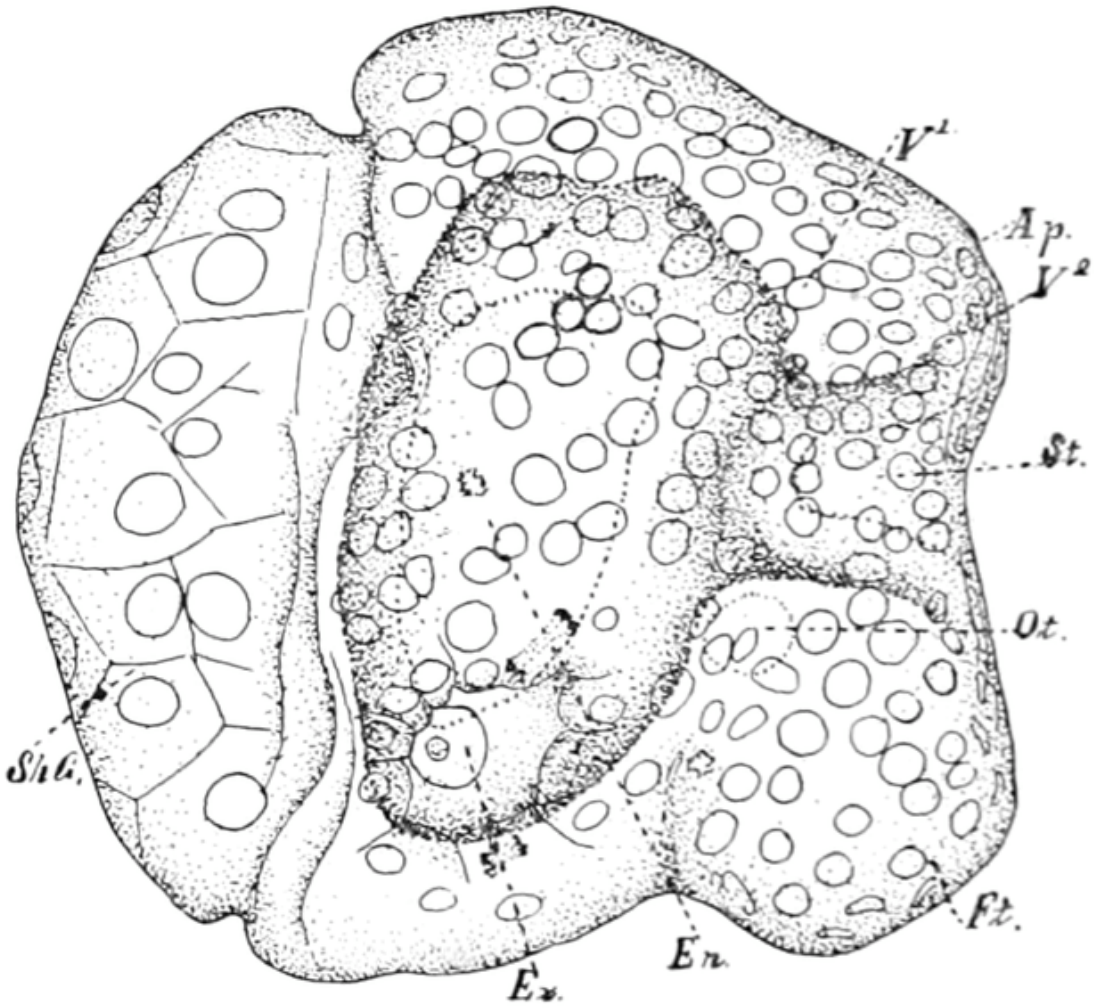
The torsion of the visceral mass so distinctive of many gastropods occurs during the veliger stage. The sudden rotation of the bodily organs relative to the rest of the animal may take anywhere from three minutes to ten days, depending on species.

The actual length of the veliger stage in the natural environment is unknown and undoubtedly variable; however, in the lab, veligers of some species become competent to metamorphose in anywhere from a few days (lecithotrophic larvae) to a month or more after hatching (planktotrophic larvae). The feeding larvae of some species have been cultured for over a year and have still retained the ability to metamorphose. As the veliger stage reaches metamorphic competence, the foot becomes sufficiently developed to allow crawling on the substratum and internal development has established the organ systems necessary for juvenile life. In many species, induction of metamorphosis occurs as a sensory response to a chemical cue indicative of the juvenile and/or adult habitat. Often this cue (the inducer) is a water soluble chemical secreted by the adult food. Induction of metamorphosis results in the larva settling to the substratum. This settlement may be followed by a "searching" phase as the larva apparently looks for an appropriate place to metamorphose. When metamorphosis occurs, the velum is lost, and the newly metamorphosed juvenile adopts its slug-like adult form.

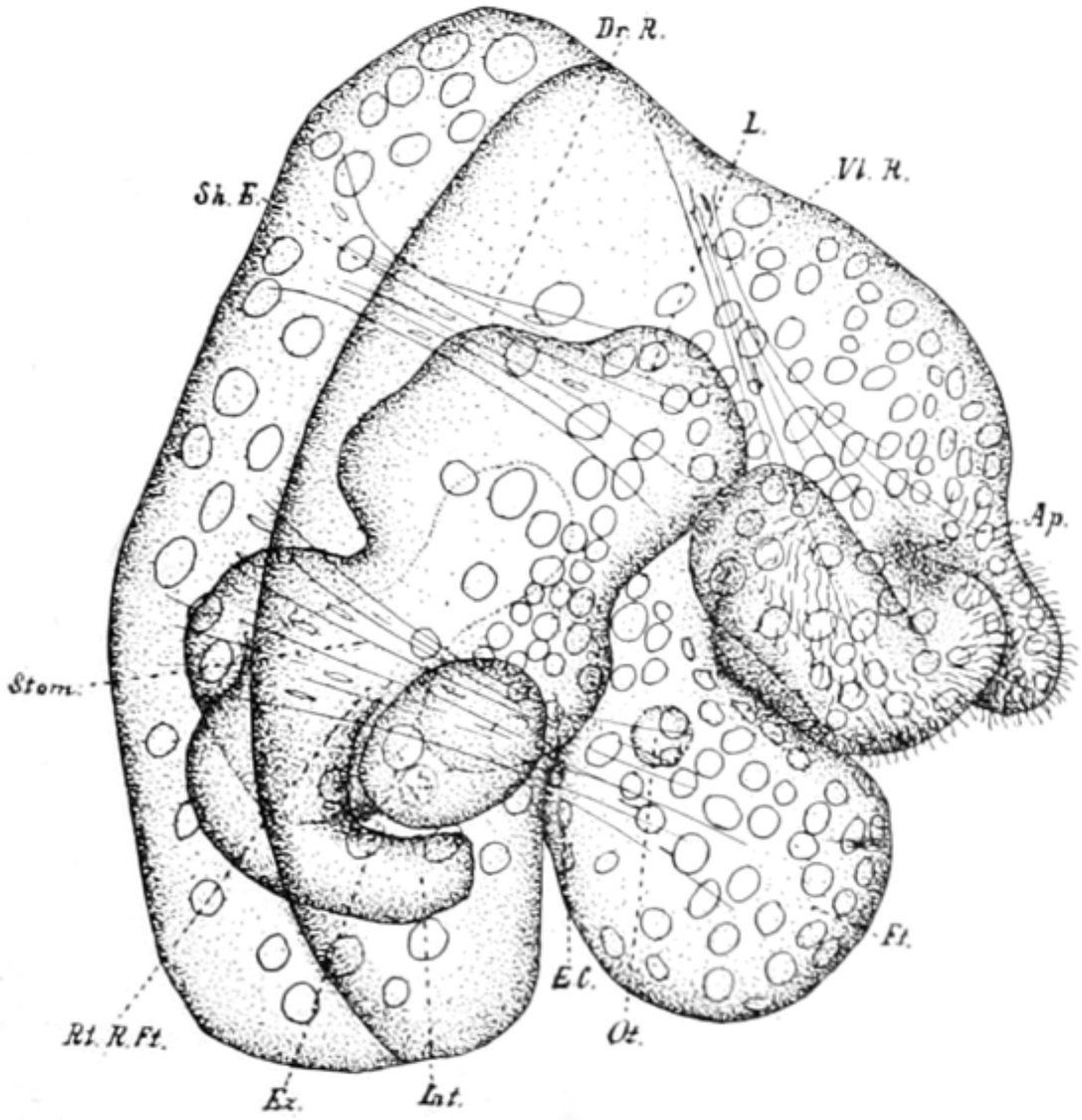
Whole development of veliger of nudibranch *Fiona pinnata*:



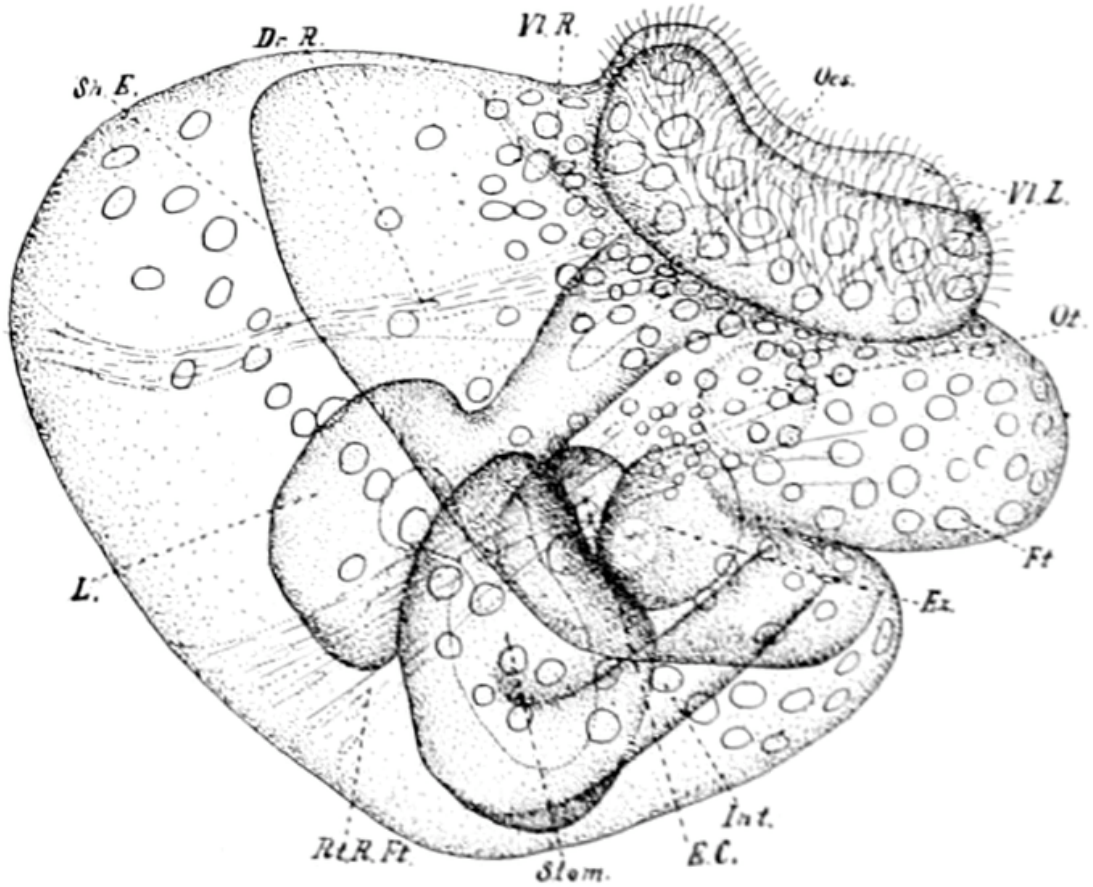
Drawing of anterior view of young veliger of *Fiona pinnata*.



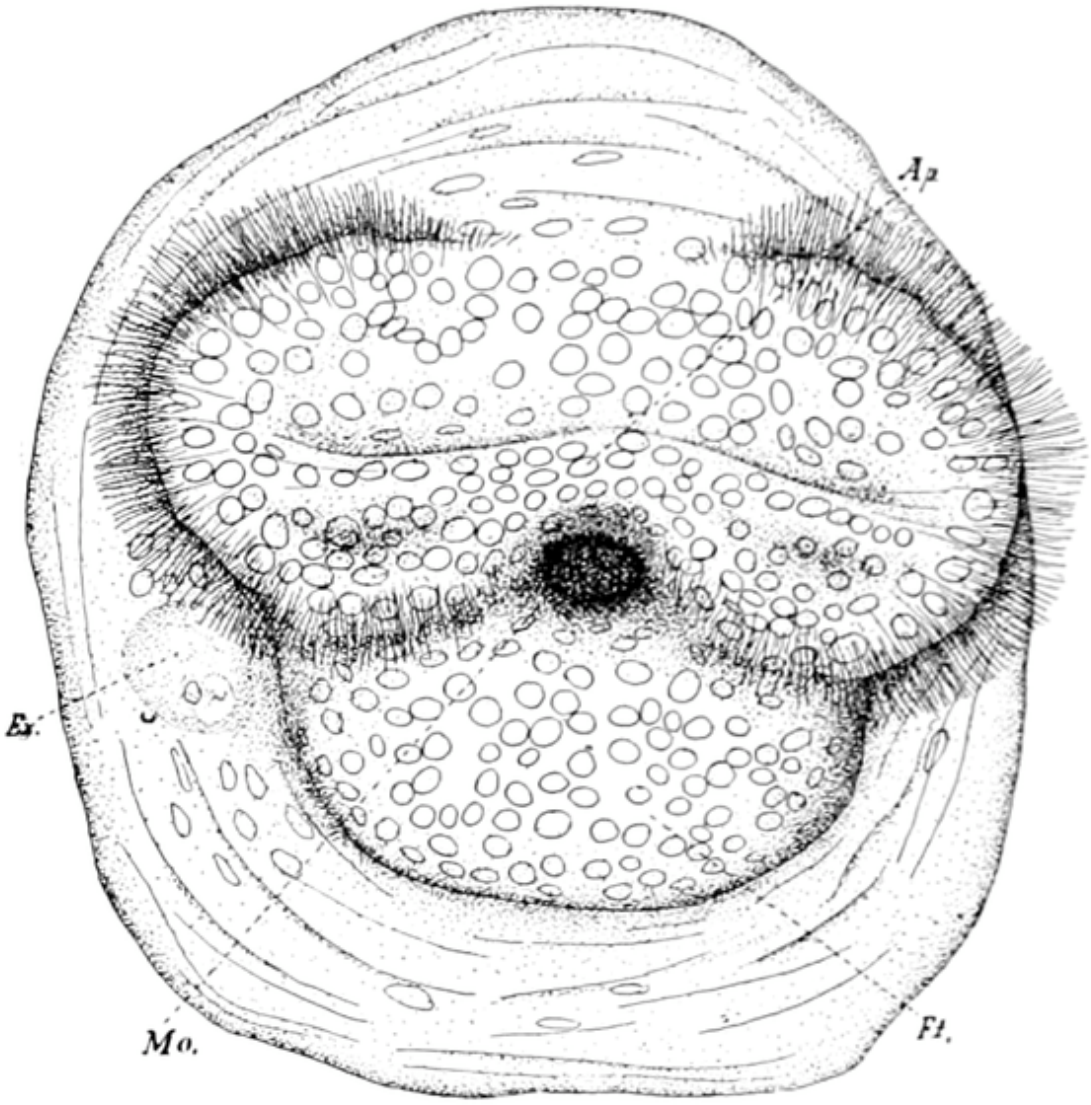
Drawing of right side of young veliger.



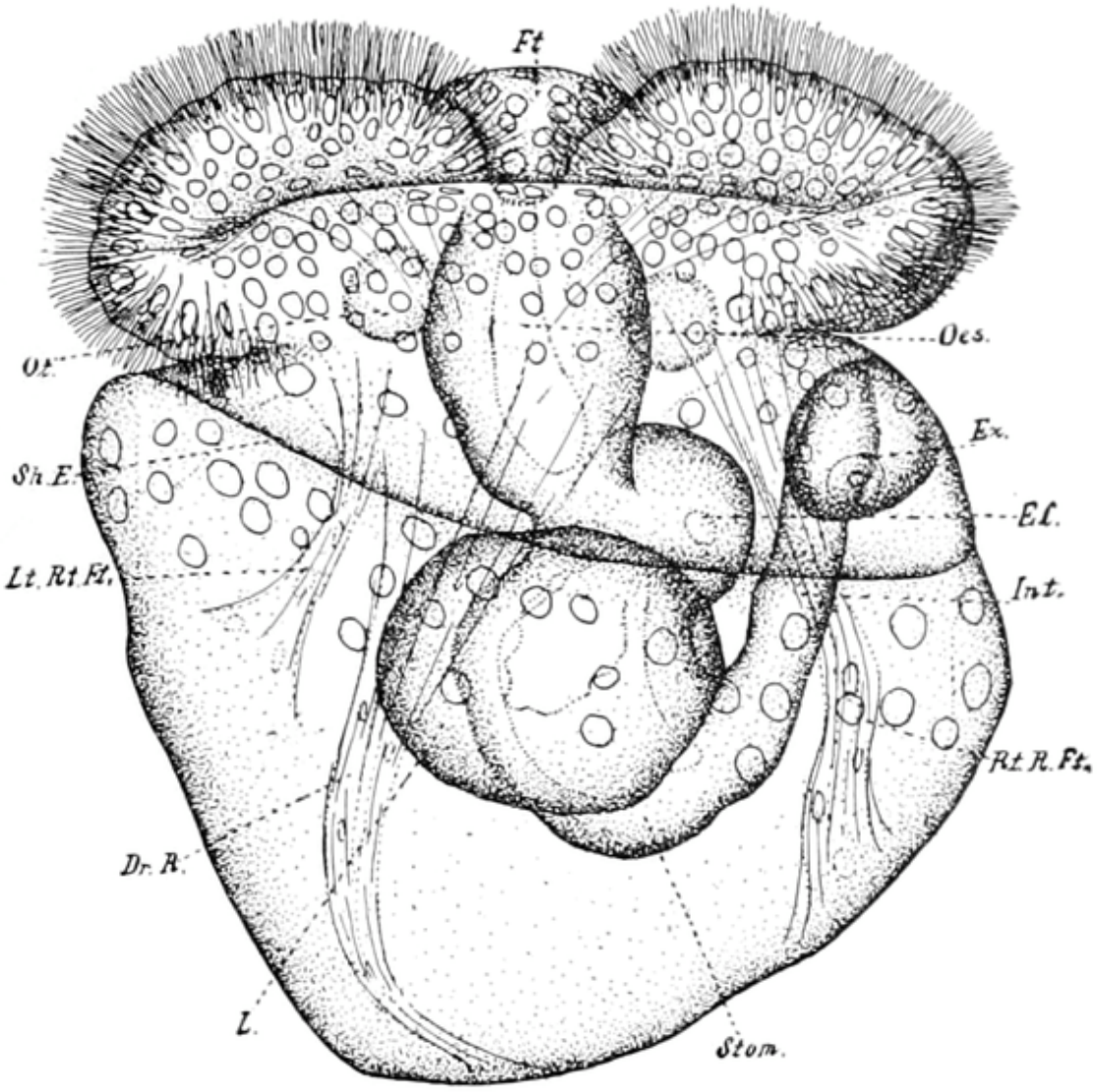
Drawing of right side of veliger.



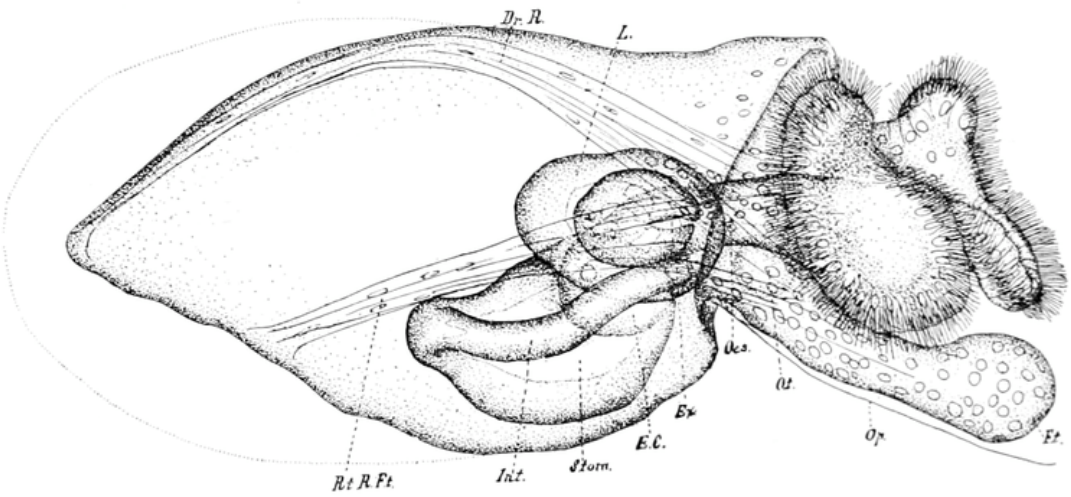
Drawing of right side of veliger.



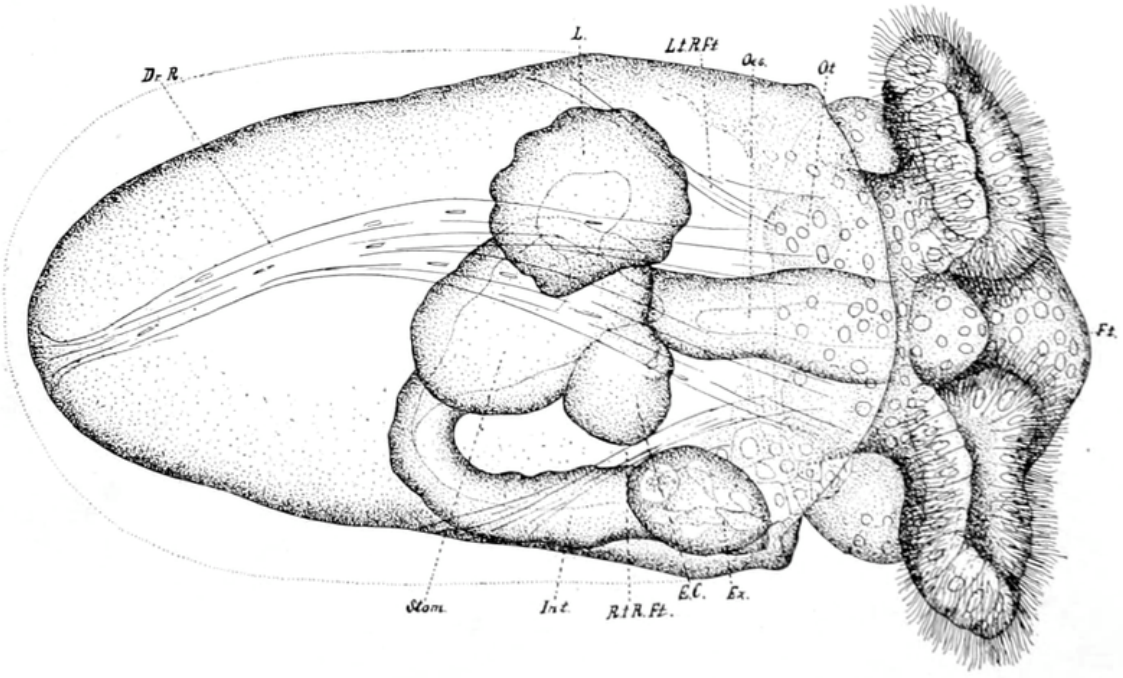
Anterior view of well developed veliger.



Dorsal view of well developed veliger.



Right side of veliger just before hatching.



Dorsal view of veliger just before hatching.

Veliger of bivalves

Like gastropods, the veliger of bivalves typically follows a free-living trochophore stage. Shipworms, however, hatch directly as veligers, with the trochophore being an embryonic stage within the egg capsule. Many freshwater species go further, with the veliger also remaining within the egg capsule, and only hatching after metamorphosing into the adult form.

The shell of a bivalve veliger first appears as a single structure along the dorsal surface of the larva. This grows around the veliger's body, becoming folded into two valves similar to the adult condition. The velum projects from between the valves, in front of the small foot. As in the gastropods, the veligers of bivalves may either feed on phytoplankton or survive off yolk retained from the egg. In plankton feeding veligers, the larva can undergo considerable growth. As this occurs, the shell and structures such as the larval foot, velum and visceral organs increase in size. As is the case for planktotrophic gastropod veligers, the larvae continue to feed and grow until they develop the organs and systems necessary for metamorphosis to the juvenile stage. At this point, the larvae are considered competent (able to metamorphose) and can respond to a chemical cue indicative of the adult habitat. In bivalves, this cue may be released by bacteria in biofilms characteristic of an appropriate adult environment.

During metamorphosis, the veliger sheds its velum and, depending on species, may secrete an attachment structure called a byssus that anchors it to the substratum. Some species spend considerable time searching for an ideal habitat before metamorphosing, but others may settle on the nearest suitable substrate.

Veliger of scaphopods

The scaphopods, or tusk shells, have a veliger larva very similar to that of bivalves, despite the great difference in the appearance of the adults. The shell develops in a similar way, developing a bi-lobed form that surrounds the larval body. However, unlike bivalves, this never splits into two, and, in fact, fuses along the ventral margin, eventually becoming a tube that encloses the length of the body, and is open at both ends.

The scaphopod veliger is free-living, and metamorphosis is marked by a great elongation of the body, in order to assume the adult form.

Chapter 10

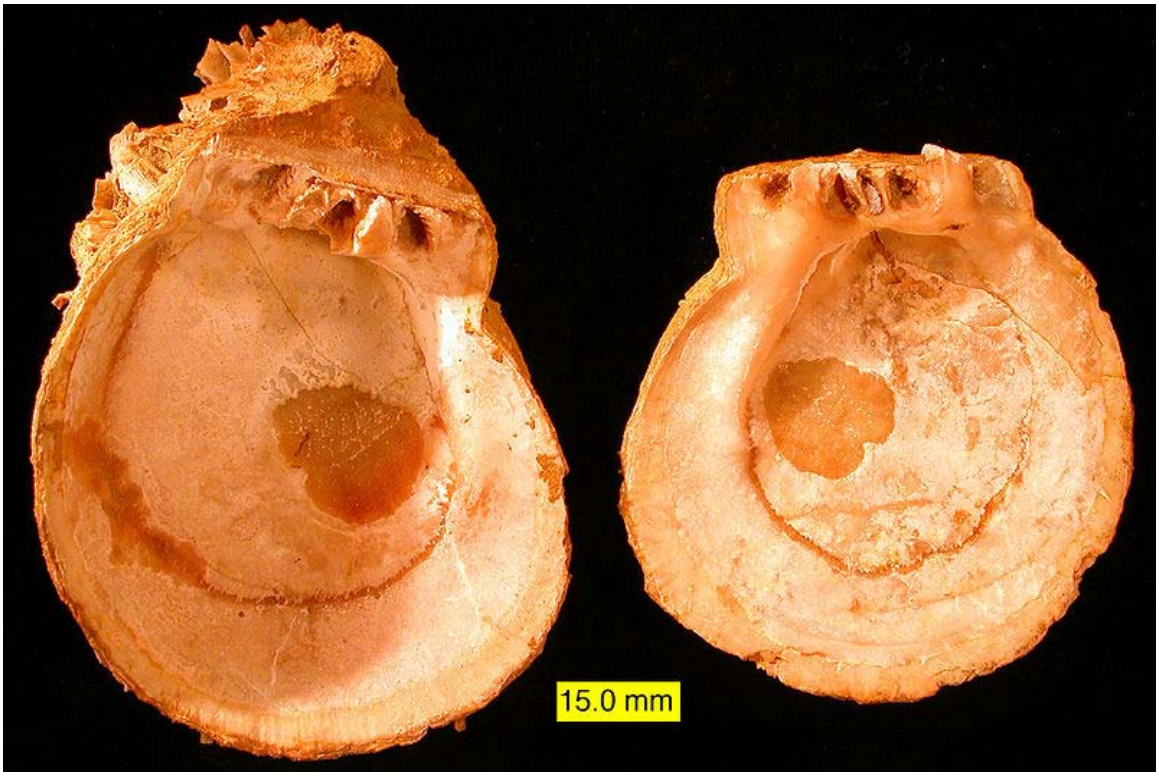
Ostreoida and Nuculanoida

Ostreoida

Ostreoida

Scientific classification
Kingdom: Animalia
Phylum: Mollusca
Class: Bivalvia
Subclass: Pteriomorphia
Order: Ostreoida
Families
Anomiidae Dimyidae Entoliidae Gryphaeidae

Ostreidae
Pectinidae
Placunidae
Plicatulidae
Propeamussiidae
Spondylidae
Syncyclonemidae



Fossil *Spondylus* valve interiors from the Pliocene of Cyprus.

The order **Ostreoida** includes the true oysters and a number of other related families of bivalves.

About eleven families are recognised within it, but suborders, superfamilies and subfamilies are used relatively heavily in this order. The following classification represents a synthesis of different views, reconciled so far as possible. The lists of genera are illustrative rather than complete. There are nearly 100 genera in this order.

Superfamilies, families & important genera

- Suborder Pectinina
  - Superfamily Pectinoidea
    - Family Entoliidae (5 genera total)
      -

        - Genus *Pectinella*
    - Family Pectinidae (scallops) (49 genera total in 11 tribes)
        -
        - Genus *Aequipecten*
        - Genus *Amusium*
        - Genus *Anguipecten*
        - Genus *Annachlamys*
        - Genus *Argopecten*
        - Genus *Bractechlamys*
        - Genus *Chlamys*

- Genus *Coralichlamys*
- Genus *Cryptopecten*
- Genus *Decatopecten*
- Genus *Delectopecten*
- Genus *Equichlamys*
- Genus *Excellichlamys*
- Genus *Flexopecten*
- Genus *Glorichlamys*
- Genus *Gloripallium*
- Genus *Haumea*
- Genus *Hyalopecten*
- Genus *Juxtamusium*
- Genus *Lissopecten*
- Genus *Mesopeplum*
- Genus *Mimachlamys*
- Genus *Minnivola*
- Genus *Mirapecten*

        - Genus *Notochlamys*
        - Genus *Patinopecten*
        - Genus *Pecten*
        - Genus *Pedum*
        - Genus *Pseudohinnites*
        - Genus *Semipallium*
        - Genus *Serratovola*
        - Genus *Somalipecten*
        - Genus *Talochlamys* Iredale, 1935
        - Genus *Veprichlamys*
        - Genus *Volachlamys*
    - Family Propeamussiidae (7 genera total)
    - Family Spondylidae (thorny oysters) (monotypic family)
        -
        - Genus *Spondylus*
    - Family Syncyclonemidae

        -
        - Genus *Cyclochlamys'*
        - Genus *Cyclopecten'*
        - Genus *Parvamussium'*
        - Genus *Propeamussium'*
        - Genus *Similipecten'*
- Superfamily Anomioidea
    - Family Anomiidae (7 genera)
        - Subfamily Anomiinae
            - Genus *Anomia*
            - Genus *Enigmonia*
        - Subfamily Placunanomiinae
            - Genus *Monia*
            - Genus *Patro*
            - Genus *Pododesmus*
    - Family Placunidae (2 genera total)
        -
        - Genus *Placuna*

- Suborder Ostreina

    - Superfamily Dimyoidea (freshwater mussels)
        - Family Dimyidae (3 genera total)
            -
            - Genus *Dimya*

- Superfamily Ostreoidea

    - Family Gryphaeidae (4 extant genera, 2 fossil genera)
        -
            - Genus *Hyotissa*
            - Genus *Neopycnodonte*
            - Genus *Parahyotissa*
            - Genus *Pycnodonte*
    - Family Ostreidae (true oysters) (14 or 15 genera in 3 subfamilies)
        - Subfamily Crassostreinae
            - Genus *Crassostrea*
            - Genus *Saccostrea*
            - Genus *Striostrea*
        - Subfamily Lophinae
            - Genus *Alectryonella*
            - Genus *Anomiostrea*
            - Genus *Dendostrea*
            - Genus *Lopha*
        - Subfamily Ostreinae
            - Genus *Booneostrea*

        - Genus *Nanostrea*
        - Genus *Ostrea*
        - Genus *Planostrea*
        - Genus *Pretostrea*
        - Genus *Pustulostrea*
        - Genus *Tiostrea*

- Superfamily Plicatuloidea
    - Family Plicatulidae (monotypic family)
        -
        - Genus *Plicatula*

Nuculanoida

Nuculanoida

Shells of *Acila cobboldiae*
family Nuculidae

Scientific classification

Kingdom: Animalia
Phylum: Mollusca

Class:	Bivalvia
Subclass:	Protobranchia
Order:	**Nuculanoida**

Nuculanoida is an order of bivalves. It belongs to the subclass Protobranchia. They are distinguished from other bivalves by the presence of relatively primitive, "protobranchiate" gills, with a row of short teeth along the hinge of the shell. The shells are often nacreous.

Families

- Bathyspinulidae Coan & Scott, 1997
- Lametilidae
- Malletiidae H. and A. Adams, 1858
- Neilonellidae Schileyko, 1989
- Nuculanidae Meek, 1864
- Sareptidae Stoliczka, 1871
- Siliculidae Allen and Sanders, 1973
- Tindariidae Verrill and Bush, 1897
- Yoldiidae Habe, 1977

- Praenuculidae Mcalester, 1969
- Pristiglomidae Sanders and Allen, 1973

Chapter 11

Placopecten Magellanicus and Pseudofeces

Placopecten magellanicus

Placopecten magellanicus

Scientific classification
Kingdom: Animalia
Phylum: Mollusca
Class: Bivalvia
Subclass: Pteriomorphia
Order: Ostreoida
Suborder: Pectinina
Superfamily: Pectinoidea
Family: Pectinidae
Genus: *Placopecten*
Species: ***P. magellanicus***
Binomial name
Placopecten magellanicus Gmelin, 1791

Placopecten magellanicus, the Atlantic sea scallop, is a commercially important Pectinid bivalve mollusk native to the western Atlantic Ocean.

Description

The shell has a classic seashell form, with flutes and scalloped edges, size is appropriately 80 mm, with individuals up to 170 mm in diameter. The shell is generally pinkish-red in color, with striped variegation to darker shades appearing in many individuals. The adductor muscle itself is large, often 30-40mm in diameter. Like all scallops, *P. magellanicus* has photoreceptive eyes along the edge of the pinkish mantle.

Range and Habitat

P. magellanicus is found on the continental shelf of the northwest Atlantic from the north shore of the Gulf of St. Lawrence south to Cape Hatteras, North Carolina.

Sea scallops typically occur at depths ranging from 18-110 m, but may also occur in waters as shallow as 2 m in estuaries and embayments along the Maine coast and in Canada. In southern areas, scallops are primarily found at depths between 45-75 m, and are less common in shallower water (25-45 m) due to high temperature. Although sea scallops are not common at depths greater than about 110 m, some populations have been found as deep as 384 m, and deep-water populations at 170-180 m have been reported in the Gulf of Maine Sea scallops often occur in aggregations called beds. Beds may be sporadic (perhaps lasting for a few years) or essentially permanent (e.g., commercial beds supporting the Georges Bank fishery). The highest concentration of many permanent beds appears to correspond to areas of suitable temperatures, food availability, substrate, and where physical oceanographic features such as fronts and gyres may keep larval stages in the vicinity of the spawning population.

Adult sea scallops are generally found on firm sand, gravel, shells and rock. Other invertebrates associated with scallop beds include sponges, hydroids, anemones, bryozoans, polychaetes, mussels, moon snails, whelks, amphipods, crabs, lobsters, sea stars, sea cucumbers, and tunicates.

Sustainability of Fishery

According to NOAA, the Atlantic sea scallop fishery is healthy, and is harvested at sustainable levels. The sea scallop fishery is the largest wild scallop fishery in the world. In 2008, 53.5 million pounds of sea scallop meats worth $370 million were harvested in the United States. Massachusetts and New Jersey are responsible for the majority of the U.S. harvest. The Monterey Bay Aquarium Seafood Watch lists sea scallops as a "Good Alternative," its second best rating.

Pseudofeces

Pseudofeces or **pseudofaeces** are a way that filter-feeding bivalve mollusks (and filter-feeding gastropod mollusks) get rid of suspended particles which have been rejected as unsuitable for food. The rejected particles are wrapped in mucus, and are expelled without having passed through the digestive tract. Thus although they may closely resemble the mollusk's real feces they are not actually feces, hence the name pseudofeces, meaning false feces.

Bivalves which exhibit this behavior are numerous and include Ostreidae oysters (such as *Crassostrea*) and Dreissenidae false mussels (such as *Dreissena*). Gastropods which filter feed are in a minority, but include the mudsnail genus Batillaria and deep sea vent limpets in the family Lepetodrilidae .

Bivalves have two siphons or apertures at the *posterior* edge of their mantle cavity: an inhalant or incurrent siphon, and an exhalant or excurrent siphon or aperture. The water is circulated by the action of the gills. Usually water enters the mantle cavity through the inhalent siphon, moves over the gills, and leaves through the exhalent siphon. The water current is utilized for respiration, but also for feeding, and for reproduction. The mouth of the bivalve is situated *anterior* to the gills. The bivalve needs phytoplankton as its food source, but the water circulating through the bivalve also usually contains other particles such as small grains of sand, detritus, etc.

After moving over the gill margins, particles reach the mouth of the bivalve. Each side of the mouth of the bivalve has an inner and an outer appendage called a palp. The outer palp has a long extensible proboscis, which collects incoming particulate matter. The particles are then sorted by both the inner and outer palps, which have ciliated grooves for collecting organic material. These food grooves sort the particles by both density and size. The inner pair of palps transfers smaller and lighter particles, such as phytoplankton, to the mouth, using ciliary currents. Some material is rejected because it is too large or too dense: this is often pieces of sediment or detritus, but also includes some overly large edible particles. The outer palps send this rejected material into the mantle cavity as a mucus-bound mass. These mucus-bound masses are the pseudofeces.

Pseudofeces accumulate with, and look much like, the actual feces in the bottom of the mantle cavity. The unwanted material is periodically ejected (usually through the inhalant siphon or aperture) by contractions of the adductor muscles, which "clap" the shells together, pushing most of the water out of the mantle cavity and forcibly ejecting both the feces and the pseudofeces.

Planktonic food is not usually in short supply, and therefore accidentally rejecting a few larger edible particles along with the larger or denser inedible ones is a small price to pay in order to optimize the processing of the rest of the food.

Land runoff containing particulate pollutants and excess nutrients can cause problems in estuaries and coastal waters. Bivalves can filter the particulate pollutants, and either eat

them or discharge them as pseudofeces deposits onto the substrate, where they are relatively harmless. Chesapeake Bay's once-flourishing oyster populations historically filtered the estuary's entire water volume of excess nutrients every three or four days.

Chapter 12

Rudists and Myoida

Rudists

Rudists Temporal range: Jurassic–Late Cretaceous

Rudist bivalves from the Cretaceous of the Omani Mountains, United Arab Emirates. Scale bar is 10 mm.
Scientific classification
Kingdom: Animalia
Phylum: Mollusca
Class: Bivalvia
Subclass: Heterodonta
Order: **Hippuritoida**
Families
• Antillocaprinidae • Caprinidae • Caprotinidae • Diceratidae • Dictyoptychidae • Hippuritidae

- Ichthyosarcolitidae
- Plagioptychidae
- Polyconitidae
- Radiolitidae
- Requieniidae

Rudists are a group of box, tube or ring shaped marine heterodont bivalves that arose during the Jurassic, and became so diverse during the Cretaceous that they were major reef-building organisms in the Tethys Ocean.

Shell description

The Jurassic forms were elongate, with both valves being similarly shaped, often pipe or stake-shaped, while the reef-building forms of the Cretaceous had one valve become a flat lid, with the other valve becoming an inverted spike-like cone. The size of these conical forms ranged widely from just a few centimeters to well over a meter in length.

Their "classic" morphology consisted of a lower, roughly conical valve that was attached to the seafloor or to neighboring rudists, and a smaller upper valve that served as a kind of lid for the organism. The small upper valve could take a variety of interesting forms, including: a simple flat lid, a low cone, a spiral, and even a star-shaped form (Johnson, 2002).

Fossil range and extinction

The rudists went extinct at the end of the Cretaceous, apparently as a result of the Cretaceous–Tertiary extinction event. It had been thought that this group began a decline about 2.5 million years earlier which culminated in complete extinction half a million years before the end of the Cretaceous (Johnson, 2002). However, evidence now suggests that rudists survived until the mass extinction event, and perished in it (Steuber et al. 2002).

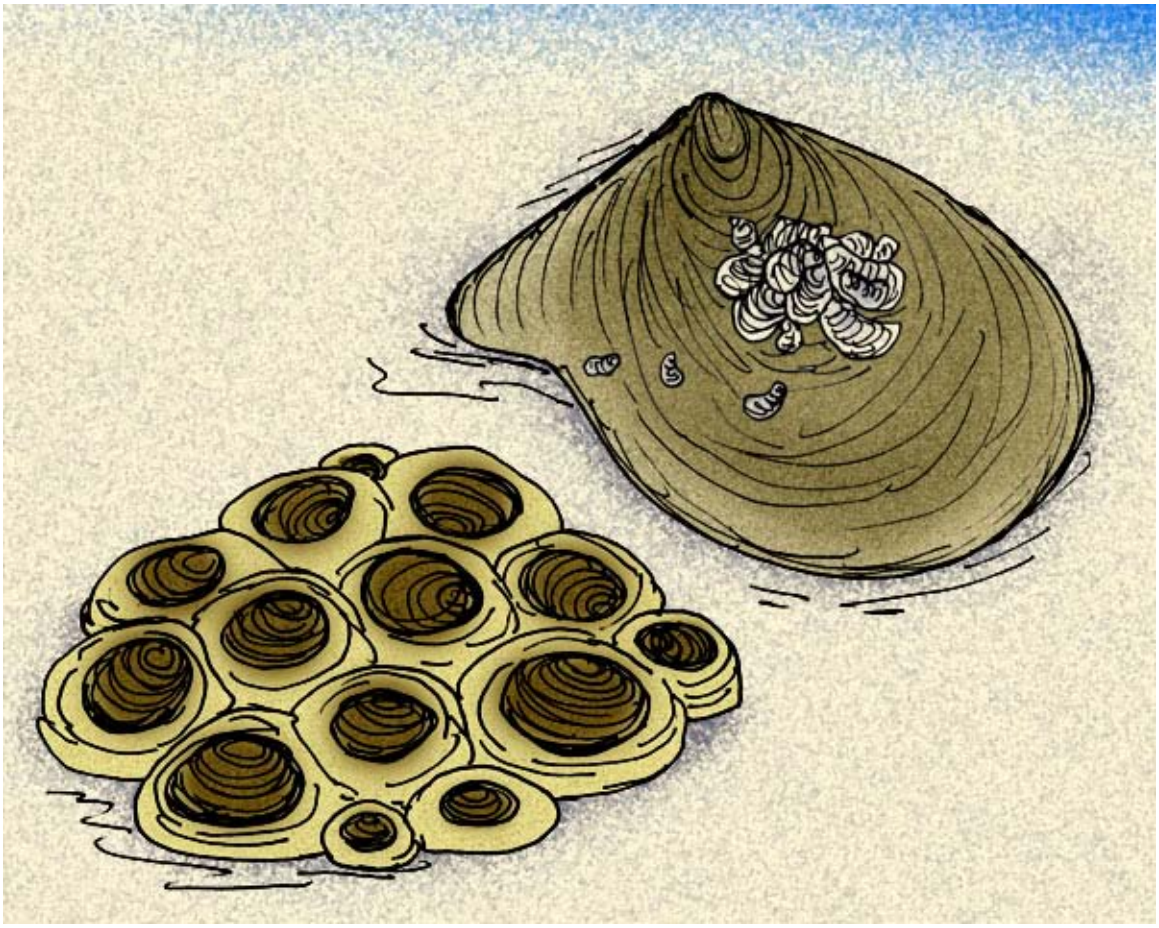
Taxonomy

The rudists are, according to different systematic schemes, placed in the orders **Hippuritoida** or **Rudistes** (sometimes **Rudista**).

Ecology

Their classification as true reef-builders is controversial because they would catch and trap lots of sediment between their lower conical valves, meaning that they are not completely composed of biogenic carbonates as a coral reef would be. However they were one of the most important constituents of reefs during the Cretaceous Period. During the Cretaceous, rudist reefs were so successful that they drove scleractinian corals

out of many tropical environments, including shelves that are today the Caribbean and the Mediterranean. It is likely that their success as reef builders is at least partially due to extreme environment of the Cretaceous. During this period tropical waters were between 6 and 14 C° warmer than today and also more highly saline, and while this may have been a suitable environment for the rudists, it was not nearly so hospitable to corals and other contemporary reef builders (Johnson, 2002). These rudist reefs were sometimes hundreds of meters tall and often ran for hundreds of kilometers on continental shelves, in fact at one point they fringed the North American coast from the Gulf of Mexico to the present-day Maritime Provinces. Because of their high porosity, rudist reefs are highly-favored oil traps.



Comparison of *Volviceramus grandis* and *Durania maxima*

Myoida

Myoida

Soft-shelled clam, *Mya arenaria*
Scientific classification

Kingdom:	Animalia
Phylum:	Mollusca
Class:	Bivalvia
Subclass:	Heterodonta
Order:	**Myoida** Stoliczka, 1870

Myoida is an order of bivalve molluscs. They are burrowing molluscs, with well-developed siphons. The shell is relatively soft, and lacks a nacreous layer. Some species have a single cardinal tooth.

The order includes such molluscs as soft-shell clams, geoducks, and shipworms.

Classification

- Superfamily Anomalodesmacea
- Superfamily Gastrochaenoidea
  - Gastrochaenidae
- Superfamily Hiatelloidea
  - Hiatellidae
- Superfamily Myoidea
  - Myidae
  - Corbulidae
- Superfamily Pholadoidea
  - Pholadidae
    - Teredinidae