

BIVALVES

AN INTRODUCTION TO BIVALVES

What is a bivalve?

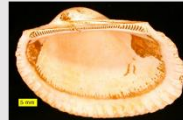
Marine and freshwater Molluscs that have **laterally compressed bodies** enclosed by a shell consisting of **two hinged parts**.

Key Terms:

- **Articulated:** the valves are joined together but can move along the hinge line.
- **Disarticulated:** means that the valves are no longer joined together.
- **Inarticulate:** means the valves may be joined but can't open or close.
- **Equivalve:** the valves are of the same size.
- **Inequivalve:** the valves are of different sizes.
- **Siphons:** soft tissue that takes in fresh water and filters it (inhalant siphon), and removes used water (exhalant siphon). These have evolved to prevent the mixing of fresh and used water supplies, aiding respiration and feeding efficiency.
- **The resting area:** Part of the bivalve in contact with substrate

Bivalves are at ~ **maximum diversity today**, and in the **recent past ~ Tertiary**, making them useful for analyzing **Mesozoic/Cenozoic** environments.

- Bivalves belong to the **phylum Mollusca** and the **class Bivalvia**.
- Mollusca is considered a **major phylum** both today and throughout the **Phanerozoic** (= *collective term for Paleozoic, Mesozoic and Cenozoic*)
- **Geologically widespread**, living in **most aquatic environments**.
- Evolved in the **Cambrian** (just like brachiopods and corals).
- They are **extant** (still living today)
- They utilize two/three part **chitin, calcite and/or aragonite shell** (i.e. a **calcareous shell**).
- Molluscs are very economical, typically known for their **use of the same organ for multiple functions**.
- In bivalves, the **gills both breathe and produce currents** in the water in the **mantle cavity**, important for **excretion and reproduction**.
- Bivalves include **clams, oysters, cockles, mussels, scallops**, and numerous other families living in **saltwater** as well as some in **freshwater**.



HOW DID THEY LIVE?

- Most bivalves bury themselves in sediment (**infaunal**) – they may be **shallow or deep buriers**, where they are **safe from predation**.
- Others lie on the sea floor (**benthonic, epifaunal and free lying**)
- Some **attach** themselves to rocks or other hard surfaces (**sessile**). **Fixed to the substrate** with **cement** or using a **byssus**.
- Some are **Nektonic**, swimmers! E.g. a Scallop
- Bivalves occupy the same/similar modes of life as Brachiopods.



- **Byssus:** a group of thread-like structures made of the protein collagen.
- **A byssus notch:** may be present on a **bivalve's dorsal side**, as a **shallow indentation or hole to prevent interference:** with the opening and closing of the valves.
- **Cement:** is the calcareous substance secreted by the mantle and attaches the left valve to the substrate (sea floor).

*It has been found that one bivalve lives in the deep waters of the **mid-ocean ridge**, near to **black-smokers of hot sulphide-rich water** where **pressures and temperatures are high** but the **light is low**.*

Bivalves have clearly evolved to **exploit most ecological niches due to the variety in the of mode of life**. Some bivalves are found in high-energy waters of the littoral zone or shallow seas, others in the calm waters of the continental shelf.

Feeding:

- The majority are filter feeders using modified gills for feeding and breathing. They **feed using siphons**, extending either to the edge of the shell or some way out of the shell. The inhalant siphon brings in fresh water and the exhalant siphon removes wastewater, preventing their mixing and **improving the efficiency of feeding and respiration**. **Burrowing bivalves require longer siphons** to reach the top of their burrow (reach above sediment).

Opening and closing of the valves:

- To be able **to feed**, the bivalve needs to **open and close** the valves to **let in fresh water** in. Adductor muscles contract to keep the shell sealed. When shellfish like mussels are cooked, they will open as the muscles become damaged and the organism dies, **they disarticulate on death**.
- The valves are opened by a **ligament on the hinge plate**.
- **Muscle scars** remain when the organism dies, marking the position of the muscle attachment. The muscle scars can be found in **fossil specimens** and samples of **disarticulated** bivalves.

Moving

- Some bivalves are **vagrant** and can move around using a **muscular foot**.
- Many bivalves are burrowers, and the foot is used to burrow into the sediment.
- Some bivalves are **sessile** and do not move on or in the sediment.

HOW ARE EPIFAUNAL BIVALVES ADAPTED TO THEIR ENVIRONMENT?

Bivalves show **adaptive radiation**. Meaning they have evolved into a variety of **different shapes and sizes** in **response to** the environment they lived in and the **selection pressures in that environment**. These differences, in shape and size, relate to their **mode of life**. The adaptations in summary are to prevent the organism being **washed away by high-energy** tides and currents and to **exploit different substrates**.

The three genera looked at in this course are **Mytilus**, **Ostrea** and **Gryphaea**.

MYTILUS TYPE – BYSSALLY ATTACHED



A byssus is a structure of **many threads** made of the **protein collagen** that attaches the bivalve to the substrate, **usually a rock**. Some juvenile bivalves used a primitive byssus for stability. Only a few bivalves continue to use them into adulthood. An example today is **Mytilus**, the **common mussel**.



Mytilus type bivalves are moved around by the currents when **the tide is in** so that they can **filter feed**.

Morphological adaptation	Probable function or reason
Byssus	Attachment to a hard substrate (rock), or another shell by the strong and flexible byssus . This allows it to survive in high-energy waters like the littoral zone (beach).
Shell exterior coated in periostracum	This protects the shell from acidic rainwater or river water, preventing dissolution .
Strong shell	Preventing breakage of the shell during exposure (intertidal zone) and during collisions as the tide moves in and out.
Streamlines and unornamented	No sharp edges to damage others in the colony and as protection against strong currents due to the reduced resistance/surface area.
Large adductor muscles	These hold the shell shut during extremely high energy currents, against predators opening the shell when it is exposed above the sea level and to prevent desiccation (drying out of soft tissue).

OSTREA TYPE - CEMENTED

Ostrea is a type of **oyster**. **Modern-day oyster larvae** attach to the sea floor when they find a suitable substrate, by secreting a calcareous cement from their **mantle**. It is always the **left valve** that attaches to the substrate.



Oysters often take on the shape of their substrate so that any **irregularities in the left valve** due to the substrate are **reflected in the right valve** too. The **left valve** is usually **larger** than the right valve in **Ostrea** bivalves so their bilateral symmetry is not perfect/exact as they are **Inequivalve**.

They have a single **large adductor muscle**.

Morphological adaptation	Probable function or reason
Cement	Attachment to the hard substrate (rock).
Strong, thick shell	To withstand high-energy waters and collisions.
Strong adductor muscle	To be able to keep heavy shells closed in high-energy conditions and be able to open them to filter feed (relax muscle).
Right and left valves of different sizes. Uneven with irregularities.	The larger left valve is cemented to the rock and the smaller right valve is like a lid . It enables the valves to close exactly when not feeding. The shell irregularities are often the same shape as the substrate .

GRYPHAEA TYPE – FREE LYING

Gryphaea are a type of **extinct oyster**, so we assume that they had a similar life cycle to modern-day oysters. They were **not attached** to the substrate but **simply rested** on a **convex left valve**. As a result, the left valve was much larger than the right. This gave a **'snowshoe' effect** to the resting area of the bivalve, **preventing it from sinking** into the sediment. These are often found in **mudstones and calcareous mudstones**, which would have been **soft mud** in the paleo environment.



Morphological adaptation	Probable function or reason
Large, curved and rounded left valve	Large resting area , which means that there is a large surface area of the bivalve in contact with the substrate. This prevents the bivalve sinking in the soft sediment. It is not attached but uses the weight to keep it in place. It does NOT live in high energy conditions as the substrate is soft.
Small right valve lid-like	Ensures that the centre of gravity is low for stability, to stop the bivalve being turned in the currents .
Strong, thick shell with lots of growth lines, giving a rough texture.	Growth lines and ribs (ornamentation) act as a rough surface in the soft sediment, this provides traction to withstand abnormal high-energy currents . The curved shape helps keep the feeding edge of the shell clear above the sediment .

HOW ARE **INFAUNAL BIVALVES** ADAPTED TO THEIR ENVIRONMENT?

Burrowing bivalves have evolved shell types and strategies to enable them to live in **shallow, medium and deep** burrows.

They have generally have **elongated valves** – the greater this is shown, the deeper the burrow potential. Bivalves also require **extended siphons** to be able to extend them out of the burrow. Again, the greater the siphon length, the deeper the burrow. This evident in fossils with a **large pallial sinus** (indentation in the pallial line).

The two species we are going to look at as examples are **Cytherea** and **Solen (both extant)**. The same ideas may be applied to fossil/extinct forms.

SHALLOW BURROWERS – E.G. CYTHEREA

Morphological adaptation	Probable function or reason
Ribs or strong growth lines	To help create resistance to grip the sediment when burrowing.
Small pallial sinus and no gape between the shells	Indicates short siphons , which are completely retractable .
Unornamented shell	This enables the bivalve to move easily through the shell. Only some have this feature .
Large adductor muscles (scars)	For attachment of large muscles . This ensure the valve remain firmly closed during high-energy currents – these bivalves typically live in the littoral zone and at shallow depth therefore their burrow only provides them with a little protection against harsh currents .
Ability to completely close the valves	Providing protection against predation and desiccation (drying out) in the littoral zone when the tide is out and they are exposed above sea level.



Cytherea is a **type of clam** that is **benthonic** and commonly lives in **sandy substrates**. It has a **shallow pallial sinus**, indicating **short siphons**. The shell is **rounded** and the shells **close completely** indicating it is a shallow burrower.



DEEP BURROWERS – E.G. SOLEN

Solen is a type of **razor shell** that commonly lives in a **sandy substrate**. It has a **very deep pallial sinus**, indicating **long siphons**. The shell is extremely elongate and the valves **do not close completely**, giving it a **permanent gape** both to the **anterior** and the **posterior**. The **shell is smooth**.

Morphological adaptation	Probable function or reason
Large pallial sinus	Indicates large siphons , needed for a deep burrow .
Unornamented, streamlines, very elongate shell.	To enable the razor shell to move easily through the sediment and move up and down in its burrow to correspond with tidal flow (feeding when the tide is in, so it moves up and going back down when the tide is out).
Small adductor muscle (scars)	No need for large muscles to protect the shell, the burrow acts as additional protection and shields the bivalve for the high energy currents of the littoral zone .
Anterior and posterior gapes	The gapes indicate that the siphons and foot cannot be retracted due to their size (not necessarily an adaptation but rather a consequence of other features). The strong muscular foot moves the razor shell up and down in the burrow. The siphons are for feeding and respiration.



HOW ARE NEKTONIC BIVALVES ADAPTED TO THEIR ENVIRONMENT?



- These are **swimming** bivalves with a single powerful **adductor muscle (monomyarian)** that relaxes and contracts to **expel water and move** the bivalve. The **internal ligament** helps to hold the shell together and works against the adductor muscle so that when the adductor muscle relaxes, this **ligament pulls the shell open**.
- The valves are **flattened on one side and rounded** on the other (like an aeroplane wing), increasing the **efficiency of swimming**.
- The valves may be thin but are **corrugated with ribs**.
- 'Ears' or **extensions around the umbone** act to **direct the water currents**. The specific example we shall observe is **Pecten or Scallop**.

NEKTONIC/SWIMMING TYPE – E.G. PECTEN, SCALLOP

- Pecten **do not swim all the time** and instead use swimming in short bursts to **escape predation**.
- The same morphological ideas can be applied to fossil and extinct forms of nektonic bivalve.
- They are unusual in that they only have a single, **large adductor muscle**, named the **monomyarian adductor**. This is **positioned centrally** to ensure **swimming is stable** and that a large amount of energy can be rapidly generated for **rapid swimming** away from predation.

Morphological feature	Probable function or reason
Ribbed, corrugated thin valves	Corrugated valves give strength while maintain a low weight , like corrugated roofs/cardboard.
One flattened valve and one curved	This gives a hydrofoil effect , helping to generate lift , keeping the animal swimming . The curvature of the left valve will also help keep sediment out of the valve shell when resting on the substrate. Large surface area prevents the valve sinking on the substrate.
Monomyarian adductor muscle	One large central muscle , which is very strong , as it must contract several times rapidly to allow for swimming. An internal ligament opens the valves.
Have 'ears' along a straight hinge line	These ' ears ' direct water currents away from the shell during swimming to improve stability . Movement of the bivalve points towards the umbone .
Numerous tiny eyes in the edge of the mantle among sensory tentacles	Eyes are able to sense shadows or movement so if a predator such as a starfish casts a shadow , the scallop will close the shell or swim away .



Morphological features	Bivalves	Brachiopods
Shell shape and symmetry	Bilateral about the plane passing between left and right valves (the hinge line). Each valve is asymmetrical about a line from the umbo to the ventral margin .	Always bilaterally symmetrical about a plane from the umbo to the anterior margin . Inequivalve with a larger pedicle valve but smaller brachial valve.
Composition of shell	Calcareous and partly organic in 3 layers .	Calcareous
Shell size	A few mm to 1m (giant clam)	Generally 2 – 10cm
Opening and closing mechanisms	A pair of adductor muscles contract to keep the valves closed. They leave a pair of muscle scars at the anterior and posterior margin . When muscles are relaxed, the external ligament acts as a spring, pulling the valves open .	Antagonistic muscle pair : adductor muscles close the shell, diductor muscles pull on the cardinal process to open the shell.
Umbo	First formed part of the shell. Where the most curvature is.	First formed part of the shell. Where the most curvature is.
Growth lines	Concentric lines parallel to the shell edge.	Concentric lines parallel to the shell edge.
Ribs	Radial markings forming from fine lines to coarse ribs and grooves .	Radiating lines from the umbo of the shell.
Foot	Found at the posterior of the shell and is used for digging in infaunal forms. Also used for movement .	None
Pedicle	None	Pedicle attaches to rocks
Orientation of valves in life position	Right and left valves hinged at the dorsal surface .	Ventral (lower) side of the body is the pedicle valve. The dorsal (upper) side of the body is the brachial valve. Pedicle valve is larger than brachial.
Pallial line and sinus	Marks the end of soft parts in the shell. Scars on both valves	Not present
Respiration and feeding	Gills	Lophophore
Teeth and sockets	Dentition – collective term for teeth and sockets all along the hinge plate . Cardinal teeth under the umbo and lateral teeth beyond the umbo or many similar teeth and sockets along the hinge plate .	Two teeth within the hinge apparatus of the pedicle valve. Socket – this is where the teeth fit into two sockets in the brachial valve .
Example	 A giant clam (bivalve)	 A Rhynchonellid brachiopod
WARNING ABOUT EVOLUTION	Bivalves and Brachiopods show very similar/same modes of life (habitats, predator-prey relations, environments etc.) . As a result of natural selection , both have developed similar adaptive solutions to the same environmental problems which they face. This is a form of convergent evolution, they are NOT similar because of any genetic relation but instead the fact they face the same selection pressures/challenges and thus have developed similar solutions.	

BIVALVE MORPHOLOGICAL FEATURES

Soft parts on a real bivalve

Light blue circle = adductor muscles

Black line = pallial line (and sinus)

Yellow arrow = Ligament

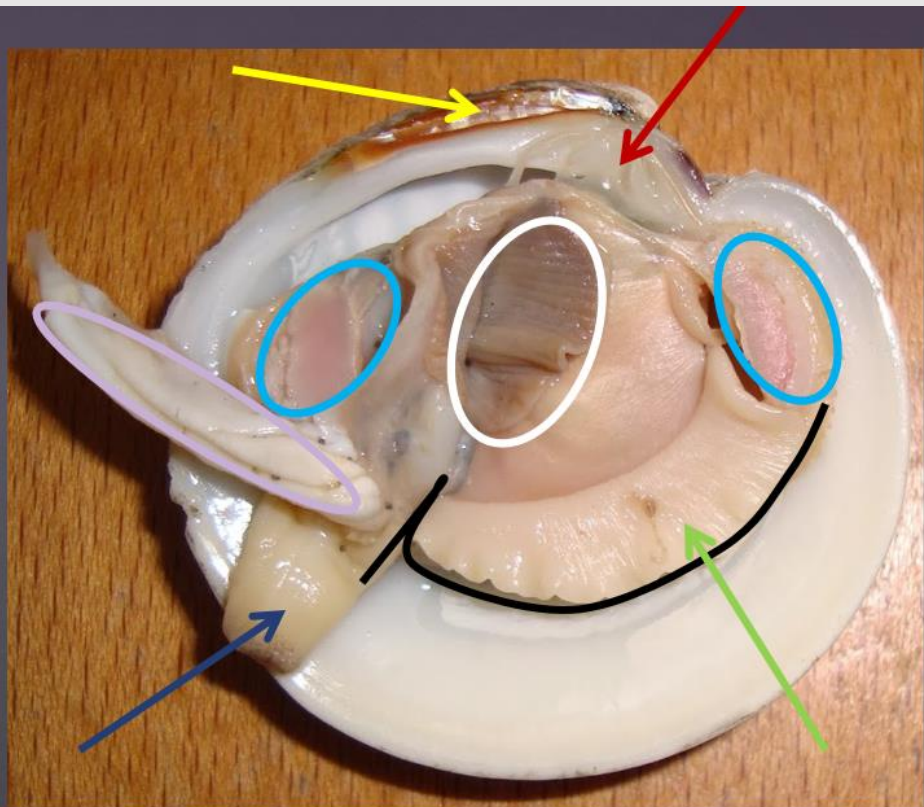
Red arrow = cardinal teeth and sockets in the hinge line.

Light green arrow = mantle

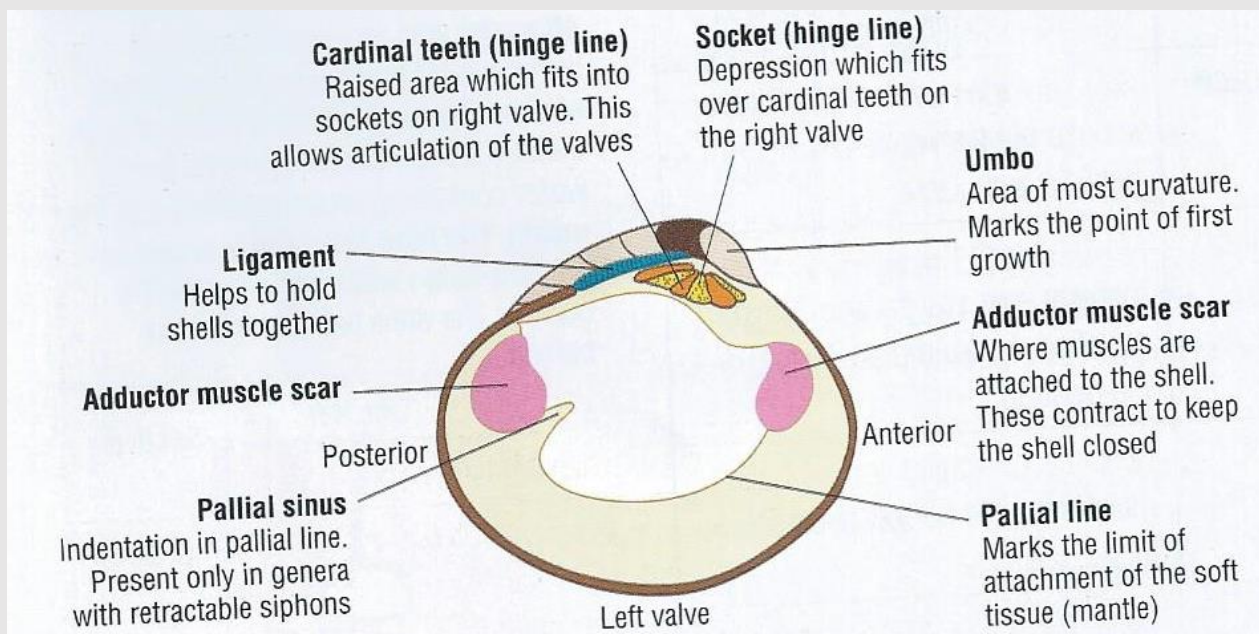
White circle = gills

Lavendar circle – inhalant, exhalant siphons

Purple arrow = foot



- The **anterior end is the mouth end** (usually closer to the umbone) and the **posterior end is the anus end** which is further from the umbone.
- **Most soft parts** are in the **dorsal end**, containing the **main organs and muscles**.
- The **mantle is the fleshy part that extended out toward the edge** of the valves. It **enclosed most of the soft parts** and was also **responsible for the growth** of valves as the mantle wrapped over the edge of the



- valve.
- The **foot is a muscular organ that extends out** of the shell and is used for **movement through/on the sediment**.
- Many **burrowing bivalves did not completely close** and left a small gap (a **gape**) which siphons or foot may **protrude through permanently**.
- Some bivalves had smooth edges to their valves but others had **crenulation (small ridges/grooves)** that **ensure a tighter fit**.