Porifera, Ctenophora and Bryozoa

(Animal Phylum)

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First Edition, 2012

ISBN 978-81-323-4214-4

Published by:
White Word Publications
4735/22 Prakashdeep Bldg,
Ansari Road, Darya Ganj,
Delhi - 110002
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Table of Contents

Chapter 1 - Sponge

Chapter 2 - Calcareous Sponge and Hexactinellid

Chapter 3 - Demosponge

Chapter 4 - Archaeocyatha and Cliona celata

Chapter 5 - Halichondria Panicea and Hexasterophora

Chapter 6 - Spongilla and Spongilla Argyrosperma

Chapter 7 - Ctenophora

Chapter 8 - Bryozoa

Chapter 1

Sponge

Sponge
Temporal range: Ediacaran–Recent

Scientific classification [e]

Kingdom:	Animalia
Subkingdom:	Parazoa
Phylum*:	**"Porifera"** Grant in Todd, 1836

Included groups

Calcarea
Demospongea
Demospongiae
Hexactinellida

Sponges are animals of the phylum **Porifera** .Their bodies consist of jelly-like mesohyl sandwiched between two thin layers of cells. While all animals have unspecialized cells that can transform into specialized cells, sponges are unique in having some specialized cells that can transform into other types, often migrating between the main cell layers and the mesohyl in the process. Sponges do not have nervous, digestive or circulatory systems. Instead, most rely on maintaining a constant water flow through their bodies to obtain food and oxygen and to remove wastes, and the shapes of their bodies are adapted to maximize the efficiency of the water flow. All are sessile aquatic animals and, although there are freshwater species, the great majority are marine (salt water) species, ranging from tidal zones to depths exceeding 8,800 metres (5.5 mi).

While most of the approximately 5,000–10,000 known species feed on bacteria and other food particles in the water, some host photosynthesizing micro-organisms as endosymbionts and these alliances often produce more food and oxygen than they consume. A few species of sponge that live in food-poor environments have become carnivores that prey mainly on small crustaceans.

Most species use sexual reproduction, releasing sperm cells into the water to fertilize ova that in some species are released and in others are retained by the "mother". The fertilized eggs form larvae which swim off in search of places to settle. Sponges are known for regenerating from fragments that are broken off, although this only works if the fragments include the right types of cells. A few species reproduce by budding. When conditions deteriorate, for example as temperatures drop, many freshwater species and a few marine ones produce gemmules, "survival pods" of unspecialized cells that remain dormant until conditions improve and then either form completely new sponges or re-colonize the skeletons of their parents.

The mesohyl functions as an endoskeleton in most sponges, and is the only skeleton in soft sponges that encrust hard surfaces such as rocks. More commonly the mesohyl is stiffened by mineral spicules, by spongin fibers or both. Demosponges use spongin, and in many species silica spicules and in some species calcium carbonate exoskeletons. Demosponges constitute about 90% of all known sponge species, including all freshwater ones, and have the widest range of habitats. Calcareous sponges, which have calcium carbonate spicules and in some species calcium carbonate exoskeletons, are restricted to relatively shallow marine waters where production of calcium carbonate is easiest. The fragile glass sponges, with "scaffolding" of silica spicules, are restricted to polar regions and the ocean depths where predators are rare. Fossils of all of these types have been found in rocks dated from 580 million years ago. In addition Archaeocyathids, whose fossils are common in rocks from 530 to 490 million years ago, are now regarded as a type of sponge.

It is generally thought that the sponge's closest single-celled relatives are choanoflagellates, which strongly resemble the cells that sponges use to drive their water flow systems and capture most of their food. It is also generally agreed that sponges do not form a monophyletic group, in other words do not include *all and only* the descendants of a common ancestor, because it is thought that Eumetazoa (more complex animals) are descendants of a sub-group of sponges. However it is uncertain which group of sponges is closest to Eumetazoa, as both calcareous sponges and a sub-group of demosponges called Homoscleromorpha have been nominated by different researchers. In addition a study in 2008 suggested that the earliest animals may have been similar to modern comb jellies.

The few species of demosponge that have entirely soft fibrous skeletons with no hard elements have been used by humans over thousands of years for several purposes, including as padding and as cleaning tools. However by the 1950s these had been over-fished so heavily that the industry almost collapsed, and most sponge-like materials are now synthetic. Sponges and their microscopic endosymbionts are now being researched as possible sources of medicines for treating a wide range of diseases. Dolphins have been observed using sponges as tools while foraging.

Distinguishing features

Sponges constitute the phylum Porifera, and have been defined as sessile metazoans (multi-celled animals) that have water intake and outlet openings connected by chambers lined with choanocytes, cells with whip-like flagella. However, a few carnivorous sponges have lost these water flow systems and the choanocytes. All known living sponges can remold their bodies, as most types of their cells can move within their bodies and a few can change from one type to another.

Like cnidarians (jellyfish, etc.) and ctenophores (comb jellies), and unlike all other known metazoans, sponges' bodies consist of a non-living jelly-like mass sandwiched between two main layers of cells. Cnidarians and ctenophores have simple nervous systems, and their cell layers are bound by internal connections and by being mounted on a basement membrane (thin fibrous mat, also known as "basal lamina"). Sponges have no nervous systems, their middle jelly-like layers have large and varied populations of cells, and some types of cell in their outer layers may move into the middle layer and change their functions.

	Sponges	**Cnidarians and ctenophores**
Nervous system	No	Yes, simple
Cells in each layer bound together	No , except that Homoscleromorpha have basement membranes.	Yes: inter-cell connections; basement membranes
Number of cells in middle "jelly" layer	Many	Few
Cells in outer layers can move inwards and change functions	Yes	No

Basic structure

Cell types

A sponge's body is hollow and is held in shape by the mesohyl, a jelly-like substance made mainly of collagen and reinforced by a dense network of fibers also made of collagen. The inner surface is covered with choanocytes, cells with cylindrical or conical collars surrounding one flagellum per choanocyte. The wave-like motion of the whip-like flagella drives water through the sponge's body. All sponges have ostia, channels leading to the interior through the mesohyl, and in most sponges these are controlled by tube-like porocytes that form closable inlet valves. Pinacocytes, plate-like cells, form a single-layered external skin over all other parts of the mesohyl that are not covered by choanocytes, and the pinacocytes also digest food particles that are too large to enter the ostia, while those at the base of the animal are responsible for anchoring it.

Other types of cell live and move within the mesohyl:

- Lophocytes are amoeba-like cells that move slowly through the mesohyl and secrete collagen fibres.
- Collencytes are another type of collagen-producing cell.
- Rhabdiferous cells secrete polysaccharides that also form part of the mesohyl.
- Oocytes and spermatocytes are reproductive cells.
- Sclerocytes secrete the mineralized spicules ("little spines") that form the skeletons of many sponges and in some species provide some defense against predators.
- In addition to or instead of sclerocytes, demosponges have spongocytes that secrete a form of collagen that polymerizes into spongin, a thick fibrous material that stiffens the mesohyl.
- Myocytes ("muscle cells") conduct signals and cause parts of the animal to contract.
- "Grey cells" act as sponges' equivalent of an immune system.
- Archaeocytes (or amoebocytes) are amoeba-like cells that are totipotent, in other words each is capable of transformation into any other type of cell. They also have important roles in feeding and in clearing debris that block the ostia.

Glass sponges' syncytia

Glass sponges present a distinctive variation on this basic plan. Their spicules, which are made of silica, form a scaffolding-like framework between whose rods the living tissue is suspended like a cobweb that contains most of the cell types. This tissue is a syncytium that in some ways behaves like many cells that share a single external membrane, and in others like a single cell with multiple nuclei. The mesohyl is absent or minimal. The syncytium's cytoplasm, the soupy fluid that fills the interiors of cells, is organised into "rivers" that transport nuclei, organelles ("organs" within cells) and other substances. Instead of choanocytes they have further syncytia, known as choanosyncytia, which form bell-shaped chambers which water enters via perforations. The insides of these chambers are lined with "collar bodies", each consisting of a collar and flagellum but without a nucleus of its own. The motion of the flagella sucks water through passages in the "cobweb" and expels it via the open ends of the bell-shaped chambers.

Some types of cells have a single nucleus and membrane each, but are connected to other single-nucleus cells and to the main syncytium by "bridges" made of cytoplasm. The sclerocytes that build spicules have multiple nuclei, and in glass sponge larvae they are connected to other tissues by cytoplasm bridges; such connections between sclerocytes have not so far been found in adults, but this may simply reflect the difficulty of investigating such small-scale features. The bridges are controlled by "plugged junctions" that apparently permit some substances to pass while blocking others.

Water flow and body structures

Most sponges work rather like chimneys: they take in water at the bottom and eject it from the osculum ("little mouth") at the top. Since ambient currents are faster at the top, the suction effect that they produce does some of the work for free. Sponges can control the water flow by various combinations of wholly or partially closing the osculum and ostia (the intake pores) and varying the beat of the flagella, and may shut it down if there is a lot of sand or silt in the water.

Although the layers of pinacocytes and choanocytes resemble the epithelia of more complex animals, they are not bound tightly by cell-to-cell connections or a basal lamina (thin fibrous sheet underneath). The flexibility of these layers and re-modeling of the mesohyl by lophocytes allow the animals to adjust their shapes throughout their lives to take maximum advantage of local water currents.

The simplest body structure in sponges is a tube or vase shape known as "asconoid", but this severely limits the size of the animal. If it is simply scaled up, the ratio of its volume to surface area increases, because surface increases as the square of length or width while volume increases proportionally to the cube. The amount of tissue that needs food and oxygen is determined by the volume, but the pumping capacity that supplies food and oxygen depends on the area covered by choanocytes. Asconoid sponges seldom exceed 1 millimetre (0.039 in) in diameter.

Some sponges overcome this limitation by adopting the "syconoid" structure, in which the body wall is pleated. The inner pockets of the pleats are lined with choanocytes, which connect to the outer pockets of the pleats by ostia. This increase in the number of choanocytes and hence in pumping capacity enables syconoid sponges to grow up to a few centimeters in diameter. The "leuconid" pattern boosts pumping capacity further by filling the interior almost completely with mesohyl that contains a network of chambers lined with choanocytes and connected to each other and to the water intakes and outlet by tubes. Leuconid sponges grow to over 1 metre (3.3 ft) in diameter, and the fact that growth in any direction increases the number of choanocyte chambers enables them to take a wider range of forms, for example "encrusting" sponges whose shapes follow those of the surfaces to which they attach. All freshwater and most shallow-water marine sponges have leuconid bodies. The networks of water passages in glass sponges are similar to the leuconid structure. In all three types of structure the cross-section area of the choanocyte-lined regions is much greater than that of the intake and outlet channels. This makes the flow slower near the choanocytes and thus makes it easier for them to trap food particles. For example in *Leuconia*, a small leuconoid sponge about 10 centimetres (3.9 in) tall and 1 centimetre (0.39 in) in diameter, water enters each of more than 80,000 intake canals at 6 cm per *minute*. However, because *Leuconia* has more than 2 million flagellated chambers whose combined diameter is much greater than that of the canals, water flow through chambers slows to 3.6 cm per *hour*, making it easy for choanocytes to capture food. All the water is expelled through a single osculum at about 8.5 cm per *second*, fast enough to carry waste products some distance away.

Skeleton

In zoology a skeleton is any fairly rigid structure of an animal, irrespective of whether it has joints and irrespective of whether it is biomineralized. The mesohyl functions as an endoskeleton in most sponges, and is the only skeleton in soft sponges that encrust hard surfaces such as rocks. More commonly the mesohyl is stiffened by mineral spicules, by spongin fibers or both. Spicules may be made of silica or calcium carbonate, and vary in shape from simple rods to three-dimensional "stars" with up to six rays. Spicules are produced by sclerocyte cells, and may be separate, connected by joints, or fused.

Some sponges also secrete exoskeletons that lie completely outside their organic components. For example sclerosponges ("hard sponges") have massive calcium carbonate exoskeletons over which the organic matter forms a thin layer with choanocyte chambers in pits in the mineral. These exoskeletons are secreted by the pinacocytes that form the animals' skins.

Classes

Sponges are divided into classes mainly according to the composition of their skeletons:

	Type of cells	Spicules	Spongin fibers	Massive exoskeleton	Body form
Calcarea	Single nucleus, single external membrane	Calcite May be individual or large masses	Never	Common. Made of calcite if present.	Asconoid, syconoid or leuconoid
Glass sponges	Mostly syncytia in all species	Silica May be individual or fused	Never	Never	Leuconoid
Demosponges	Single nucleus, single external membrane	Silica	In many species	In some species. Made of aragonite if present.	Leuconoid

Vital functions

Spongia officinalis, "the kitchen sponge", is dark grey when alive

Movement

Although adult sponges are fundamentally sessile animals, some marine and freshwater species can move across the bottom at speeds of 1–4 millimetres (0.039–0.16 in) per day, as a result of amoeba-like movements of pinacocytes and other cells. A few species can contract their whole bodies, and many can close their oscula and ostia.

Respiration, feeding and excretion

Sponges do not have distinct circulatory, respiratory, digestive, and excretory systems – instead the water flow system supports all these functions. They filter food particles out of the water flowing through them. Particles larger than 50 micrometers cannot enter the ostia and pinacocytes consume them by phagocytosis (engulfing and internal digestion). Particles from 0.5 µm to 50 µm are trapped in the ostia, which taper from the outer to inner ends. These particles are consumed by pinacocytes or by archaeocytes which partially extrude themselves through the walls of the ostia. Bacteria-sized particles, below 0.5 micrometers, pass through the ostia and are caught and consumed by choanocytes. Since the smallest particles are by far the most common, choanocytes typically capture 80% of a sponge's food supply. Archaeocytes transport food packaged in vesicles from cells that directly digest food to those that do not. At least one species of sponge has internal fibers that function as tracks for use by nutrient-carrying archaeocytes, and these tracks also move inert objects.

It used to be claimed that glass sponges could live on nutrients dissolved in sea water and were very averse to silt. However a study in 2007 found no evidence of this and concluded that they extract bacteria and other micro-organisms from water very efficiently (about 79%) and process suspended sediment grains to extract such prey. Collar bodies digest food and distribute it wrapped in vesicles that are transported by dynein "motor" molecules along bundles of microtubules that run throughout the syncytium.

Sponges' cells absorb oxygen by diffusion from the water flow system, into which carbon dioxide and other soluble waste products such as ammonia also diffuse. Archeocytes remove mineral particles that threaten to block the ostia, transport them through the mesohyl and generally dump them into the outgoing water current, although some species incorporate them into their skeletons.

Carnivorous sponges

A few species that live in waters where the supply of food particles is very poor prey on crustaceans and other small animals. Most belong to the family Cladorhizidae, but a few members of the Guitarridae and Esperiopsidae are also carnivores. In most cases little is known about how they actually capture prey, although some species are thought to use either sticky threads or hooked spicules. Most carnivorous sponges live in deep waters, up to 8,840 metres (5.49 mi), and the development of deep-ocean exploration techniques is expected to lead to the discovery of several more. However one species has been found in Mediterranean caves at depths of 17–23 metres (56–75 ft), alongside the more usual filter feeding sponges. The cave-dwelling predators capture crustaceans under 1 millimetre (0.039 in) long by entangling them with fine threads, digest them by enveloping them with further threads over the course of a few days, and then return to their normal shape; there is no evidence that they use venom.

Most known carnivorous sponges have completely lost the water flow system and choanocytes. However the genus *Chondrocladia* uses a highly modified water flow system to inflate balloon-like structures that are used for capturing prey.

Endosymbionts

Freshwater sponges often host green algae as endosymbionts within archaeocytes and other cells, and benefit from nutrients produced by the algae. Many marine species host other photosynthesizing organisms, most commonly cyanobacteria but in some cases dinoflagellates. Symbiotic cyanobacteria may form a third of the total mass of living tissue in some sponges, and some sponges gain 48% to 80% of their energy supply from these micro-organisms. In 2008 a University of Stuttgart team reported that spicules made of silica conduct light into the mesohyl, where the photosynthesizing endosymbionts live. Sponges that host photosynthesizing organisms are most common in waters with relatively poor supplies of food particles, and often have leafy shapes that maximize the amount of sunlight they collect.

A recently-discovered carnivorous sponge that lives near hydrothermal vents hosts methane-eating bacteria, and digests some of them.

"Immune" system

Sponges do not have the complex immune systems of most other animals. However they reject grafts from other species but accept them from other members of their own species. In a few marine species, gray cells play the leading role in rejection of foreign material.

When invaded, they produce a chemical that stops movement of other cells in the affected area, thus preventing the intruder from using the sponge's internal transport systems. If the intrusion persists, the grey cells concentrate in the area and release toxins that kill all cells in the area. The "immune" system can stay in this activated state for up to three weeks.

Reproduction

Asexual

The freshwater sponge *Spongilla lacustris*

Sponges have three asexual methods of reproduction: after fragmentation; by budding; and by producing gemmules. Fragments of sponges may be detached by currents or waves, and perhaps by predators. They use the mobility of their pinacocytes and choanocytes and reshaping of the mesohyl to re-attach themselves to a suitable surface and then rebuild themselves as small but functional sponges over the course of several days. The same capabilities enable sponges that have been squeezed through a fine cloth to regenerate. A sponge fragment can only regenerate if it contains both collencytes to produce mesohyl and archeocytes to produce all the other cell types. A very few species reproduce by budding.

Gemmules are "survival pods" which a few marine sponges and many freshwater species produce by the thousands when dying and which some, mainly freshwater species, regularly produce in autumn. Spongocytes make gemmules by wrapping shells of spongin, often reinforced with spicules, round clusters of archeocytes that are full of nutrients. Freshwater gemmules may also include phytosynthesizing symbionts. The gemmules then become dormant, and in this state can survive cold, drying out, lack of oxygen and extreme variations in salinity. Freshwater gemmules often do not revive until the temperature drops, stays cold for a few months and then reaches a near-"normal" level. When a gemmule germinates, the archeocytes round the outside of the cluster transform into pinacocytes, a membrane over a pore in the shell bursts, the cluster of cells slowly emerges, and most of the remaining archeocytes transform into other cell types needed to make a functioning sponge. Gemmules from the same species but different individuals can join forces to form one sponge. Some gemmules are retained within the parent sponge, and in spring it can be difficult to tell whether an old sponge has revived or been "recolonized" by its own gemmules.

Sexual

Most sponges are hermaphrodites (function as both sexes simultaneously), although sponges have no gonads (reproductive organs). Sperm are produced by choanocytes or entire choanocyte chambers that sink into the mesohyl and form spermatic cysts while eggs are formed by transformation of archeocytes, or of choanocytes in some species. Each egg generally acquires a yolk by consuming "nurse cells". During spawning, sperm burst out of their cysts and are expelled via the osculum. If they contact another sponge of the same species, the water flow carries them to choanocytes that engulf them but, instead of digesting them, metamorphose to an ameboid form and carry the sperm through the mesohyl to eggs, which in most cases engulf the carrier and its cargo.

A few species release fertilized eggs into the water, but most retain the eggs until they hatch. There are four types of larvae, but all are balls of cells with an outer layer of cells whose flagellae or cilia enable the larvae to move. After swimming for a few days the larvae sink and crawl until they find a place to settle. Most of the cells transform into archeocytes and then into the types appropriate for their locations in a miniature adult sponge.

Glass sponge embryos start by dividing into separate cells, but once 32 cells have formed they rapidly transform into larvae that externally are ovoid with a band of cilia round the middle that they use for movement, but internally have the typical glass sponge structure of spicules with a cobweb-like main syncitium draped around and between them and choanosyncytia with multiple collar bodies in the center. The larvae then leave their parents' bodies.

Life cycle

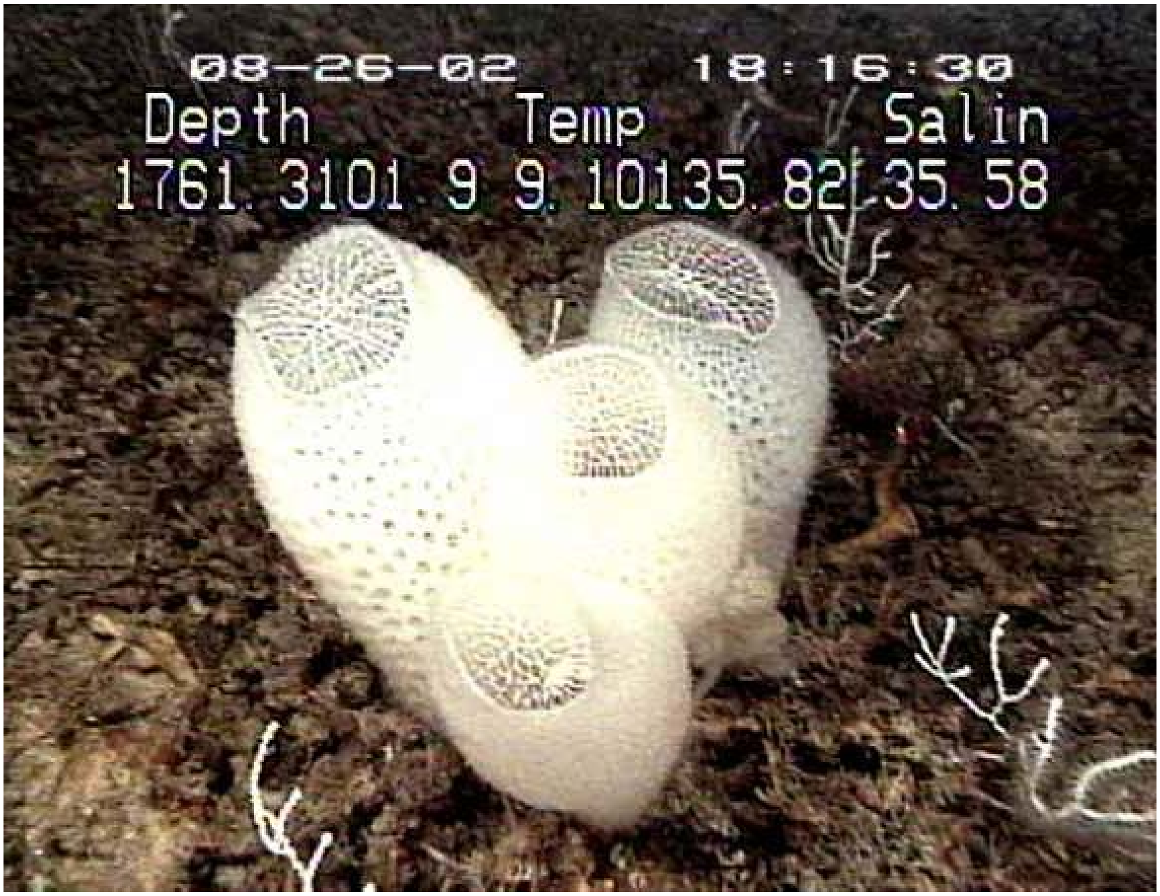
Sponges in temperate regions live for at most a few years, but some tropical species and perhaps some deep-ocean ones may live for 200 years or more. Some calcified demosponges grow by only 0.2 millimetres (0.0079 in) per year and, if that rate is constant, specimens 1 metre (3.3 ft) wide must be about 5,000 years old. Some sponges start sexual reproduction when only a few weeks old, while others wait until they are several years old.

Coordination of activities

Adult sponges lack neurons or any other kind of nervous tissue. However most species have the ability to perform movements that are coordinated all over their bodies, mainly contractions of the pinacocytes, squeezing the water channels and thus expelling excess sediment and other substances that may cause blockages. Some species can contract the osculum independently of the rest of the body. Sponges may also contract in order to reduce the area that is vulnerable to attack by predators. In cases where two sponges are fused, for example if there is a large but still unseparated bud, these contraction waves slowly become coordinated in both of the "Siamese twins". The coordinating mechanism is unknown, but may involve chemicals similar to neurotransmitters. However glass sponges rapidly transmit electrical impulses through all parts of the syncytium, and use this to halt the motion of their flagella if the incoming water contains toxins or excessive sediment. Myocytes are thought to be responsible for closing the osculum and for transmitting signals between different parts of the body.

Sponges contain genes very similar to those that contain the "recipe" for the post-synaptic density, an important signal-receiving structure in the neurons of all other animals. However in sponges these genes are only activated in "flask cells" that appear only in larvae and may provide some sensory capability while the larvae are swimming. This raises questions about whether flask cells represent the predecessors of true neurons or are evidence that sponges' ancestors had true neurons but lost them as they adapted to a sessile lifestyle.

Ecology



Euplectella aspergillum, a glass sponge known as "Venus' Flower Basket"

Habitats

Sponges are worldwide in their distribution, from the polar regions to the tropics. Most live in quiet, clear waters, because sediment stirred up by waves or currents would block their pores, making it difficult for them to feed and breathe. The greatest numbers of sponges are usually found on firm surfaces such as rocks, but some sponges can attach themselves to soft sediment by means of a root-like base.

Sponges are more abundant but less diverse in temperate waters than in tropical waters, possibly because organisms that prey on sponges are more abundant in tropical waters. Glass sponges are the most common in polar waters and in the depths of temperate and tropical seas, as their very porous construction enables them to extract food from these resource-poor waters with the minimum of effort. Demosponges and calcareous sponges are abundant and diverse in shallower non-polar waters.

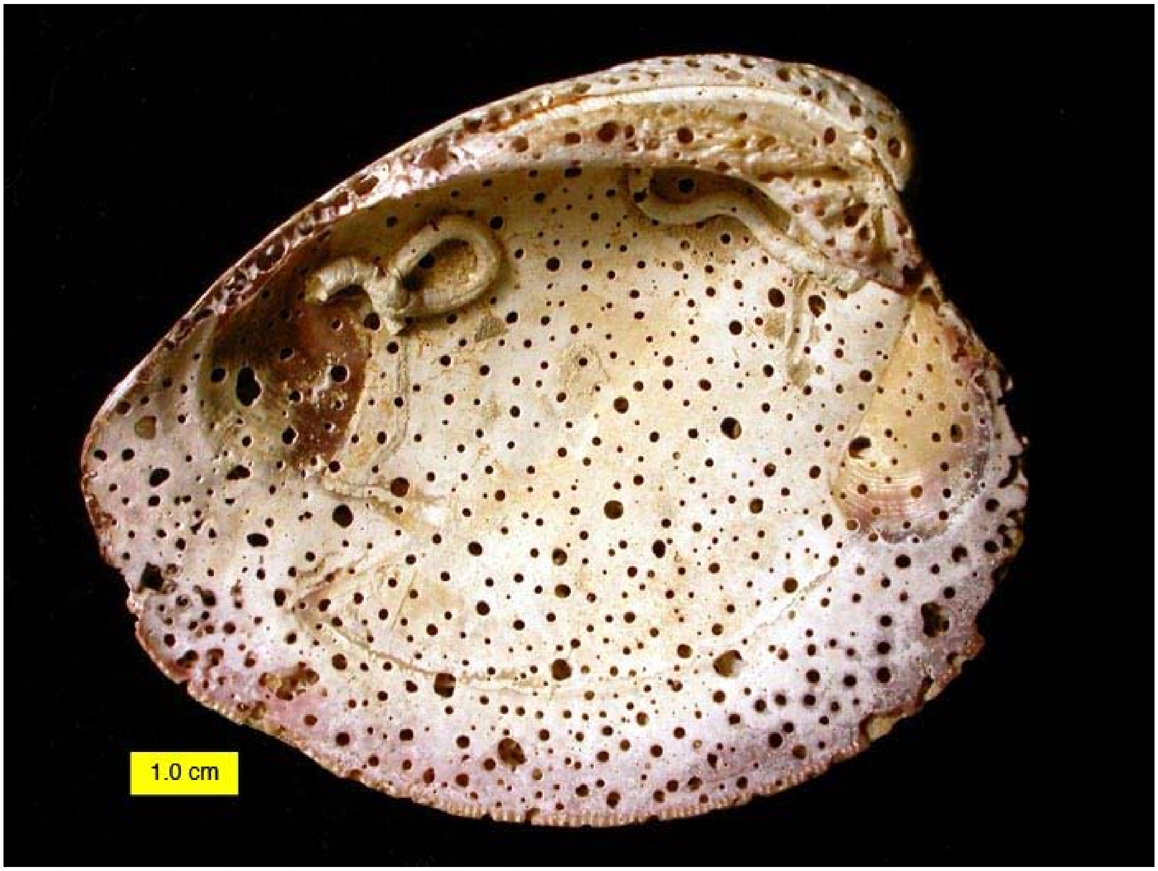
The different classes of sponge live in different ranges of habitat:

	Water type	Depth	Type of surface
Calcarea	Marine	less than 100 metres (330 ft)	Hard
Glass sponges	Marine	Deep	Soft or firm sediment
Demosponges	Marine, brackish; and about 150 freshwater species	Inter-tidal to abyssal; a carnivorous demosponge has been found at 8,840 metres (5.49 mi)	Any

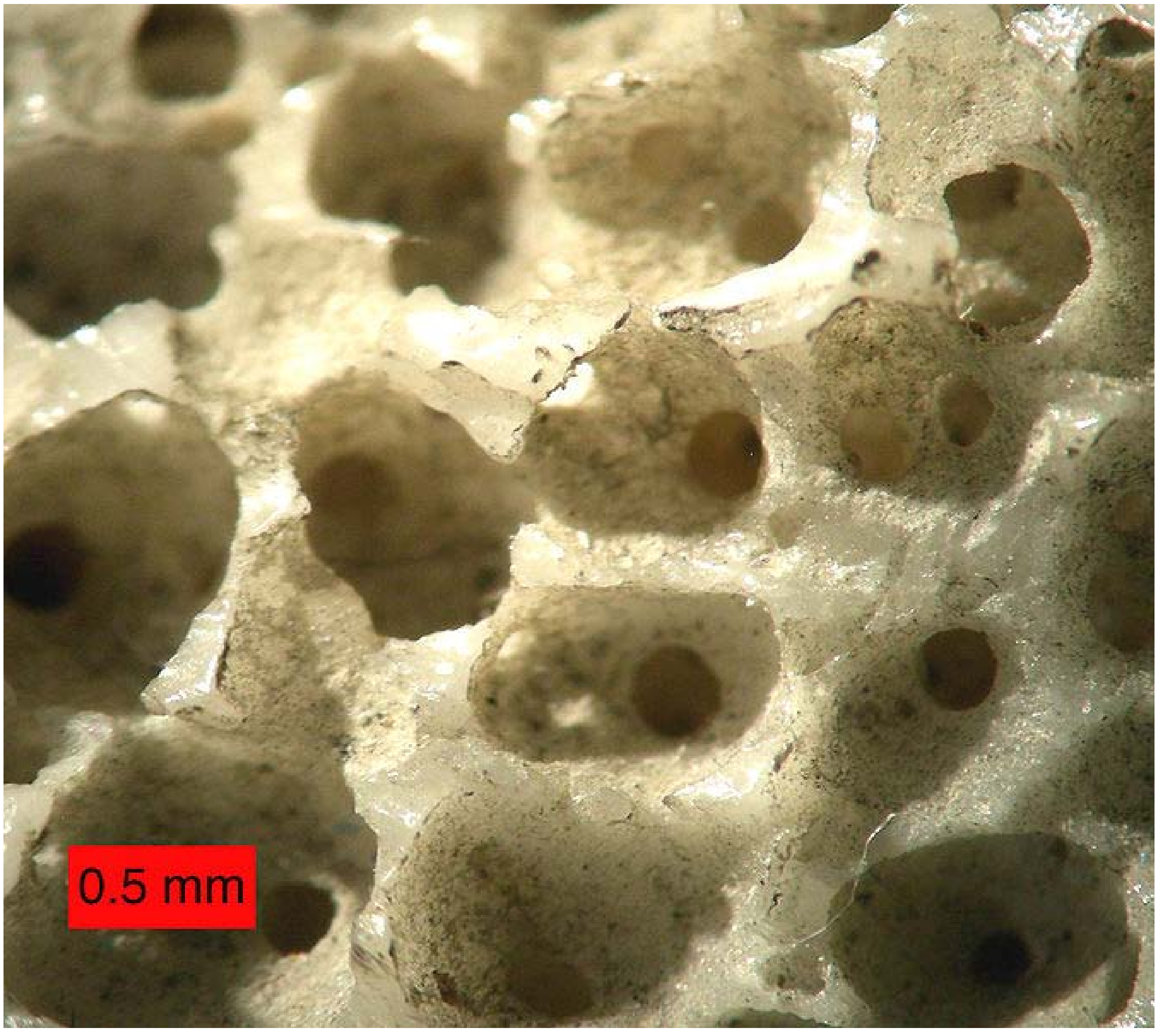
As primary producers

Sponges with photosynthesizing endosymbionts produce up to three times more oxygen than they consume, as well as more organic matter than they consume. Such contributions to their habitats' resources are significant along Australia 's Great Barrier Reef but relatively minor in the Caribbean.

Defenses



Holes made by clionaid sponge (producing the trace *Entobia*) after the death of a modern bivalve shell of species *Mercenaria mercenaria*, from North Carolina



Close-up of the sponge boring *Entobia* in a modern oyster valve. Note the chambers which are connected by short tunnels.

Many sponges shed spicules, forming a dense carpet several meters deep that keeps away echinoderms which would otherwise prey on the sponges. They also produce toxins that prevent other sessile organisms such as bryozoans or sea squirts from growing on or near them, making sponges very effective competitors for living space.

A few species, such as the Caribbean fire sponge *Tedania ignis*, cause a severe rash in humans who handle them. Turtles and some fish feed mainly on sponges. It is often said that sponges produce chemical defenses against such predators. However an experiment showed that there is no relationship between the toxicity of chemicals produced by sponges and how they taste to fish, which would diminish the usefulness of chemical defenses as deterrents. Predation by fish may even help to spread sponges by detaching fragments.

Glass sponges produce no toxic chemicals, and live in very deep water where predators are rare.

Predation

Sponge flies, also known as spongilla-flies (Neuroptera, Sisyridae), are specialist predators of freshwater sponges. The female lays her eggs on vegetation overhanging water. The larvae hatch and drop into the water where they seek out sponges to feed on. They use their elongated mouthparts to pierce the sponge and suck the fluids within. The larvae of some species cling to the surface of the sponge while others take refuge in the sponge's internal cavities. The fully grown larvae leave the water and spin a cocoon in which to pupate.

Bioerosion

The Caribbean chicken-liver sponge *Chondrilla nucula* secretes toxins that kill coral polyps, allowing the sponges to grow over the coral skeletons. Others, especially in the family Clionaidae, use corrosive substances secreted by their archeocytes to tunnel into rocks, corals and the shells of dead molluscs. Sponges may remove up to 1 metre (3.3 ft) per year from reefs, creating visible notches just below low-tide level.

Diseases

Caribbean sponges of the genus *Aplysina* suffer from Aplysina red band syndrome. This causes *Aplysina* to develop one or more rust-colored bands, sometimes with adjacent bands of necrotic tissue (dead). These lesions may completely encircle branches of the sponge. The disease appears to be contagious (spread by physical contact). The rust-colored bands are caused by a cyanobacterium, but it is unknown whether this organism actually causes the disease.

Collaboration with other organisms

In addition to hosting photosynthesizing endosymbionts, sponges are noted for their wide range of collaborations with other organisms. The relatively large encrusting sponge *Lissodendoryx colombiensis* is most common on rocky surfaces, but has extended its range into seagrass meadows by letting itself be surrounded or overgrown by seagrass sponges, which are distasteful to the local starfish and therefore protect *Lissodendoryx* against them; in return the seagrass sponges get higher positions away from the sea-floor sediment.

Shrimps of the genus *Synalpheus* form colonies in sponges, and each shrimp species inhabits a different sponge species, making *Synalpheus* one of the most diverse crustacean genera.

Evolutionary history

Fossil record

Fossil sponge *Raphidonema faringdonense* from Cretaceous rocks in England

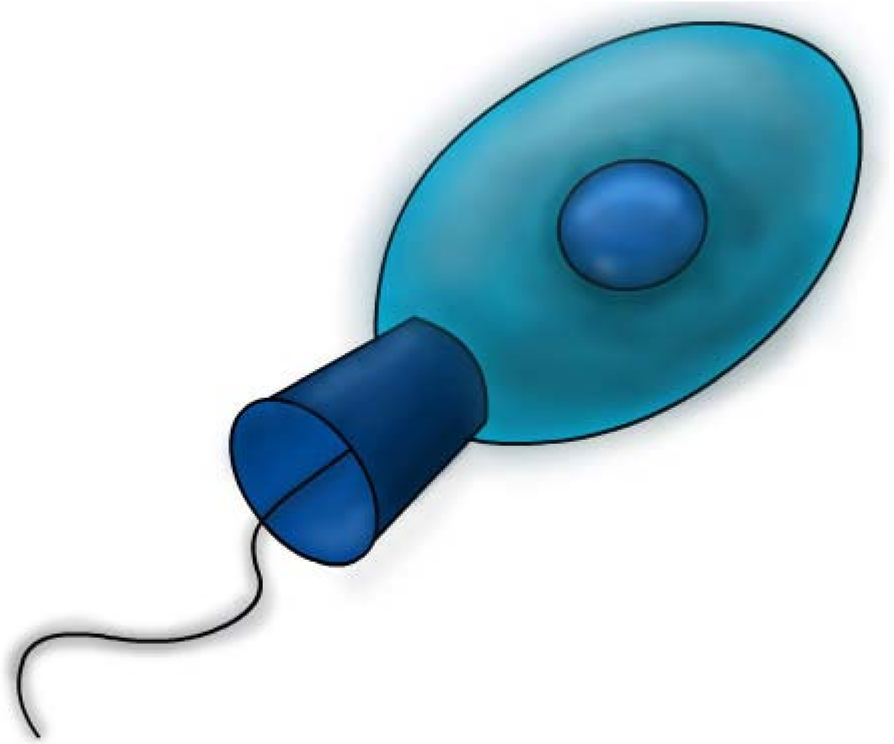
Traces of the chemical 24-isopropylcholestane have been found in rocks formed 1,800 million years ago. This is a stable derivative of 24-isopropylcholesterol, which is thought to be produced by demosponges but not by eumetazoans ("true animals", i.e. cnidarians and bilaterians). Since choanoflagellates are thought to be animals' closest single-celled relatives, a team of scientists examined the biochemistry and genes of one choanoflagellate species. They concluded that this species could not produce 24-isopropylcholesterol but that investigation of a wider range of choanoflagellates would be necessary in order to prove that the fossil 24-isopropylcholestane could only have been produced by demosponges.

Silica spicules like those of demosponges have been reported from Nevada in rocks dated around 750 million years ago. Well-preserved fossil sponges from about 580 million years ago in the Ediacaran period have been found in the Doushantuo Formation. These fossils, which include spicules, pinacocytes, porocytes, archeocytes, sclerocytes and the internal cavity, have been classified as demosponges. Fossils of glass sponges have been found from around 540 million years ago in rocks in Australia, China and Mongolia.

Calcium carbonate spicules of calcareous sponges have been found in Early Cambrian rocks from about 530 to 523 million years ago in Australia. Other probable demosponges have been found in the Early Cambrian Chengjiang fauna, from 525 to 520 million years ago. Freshwater sponges appear to be much younger, as the earliest known fossils date from the Mid-Eocene period about 48 to 40 million years ago. Although about 90% of modern sponges are demosponges, fossilized remains of this type are less common than those of other types because their skeletons are composed of relatively soft spongin that does not fossilize well.

Archaeocyathids, which some classify as a type of coralline sponge, are common in the Cambrian period from about 530 million years ago, but apparently died out by the end of the Cambrian 490 million years ago.

Family tree

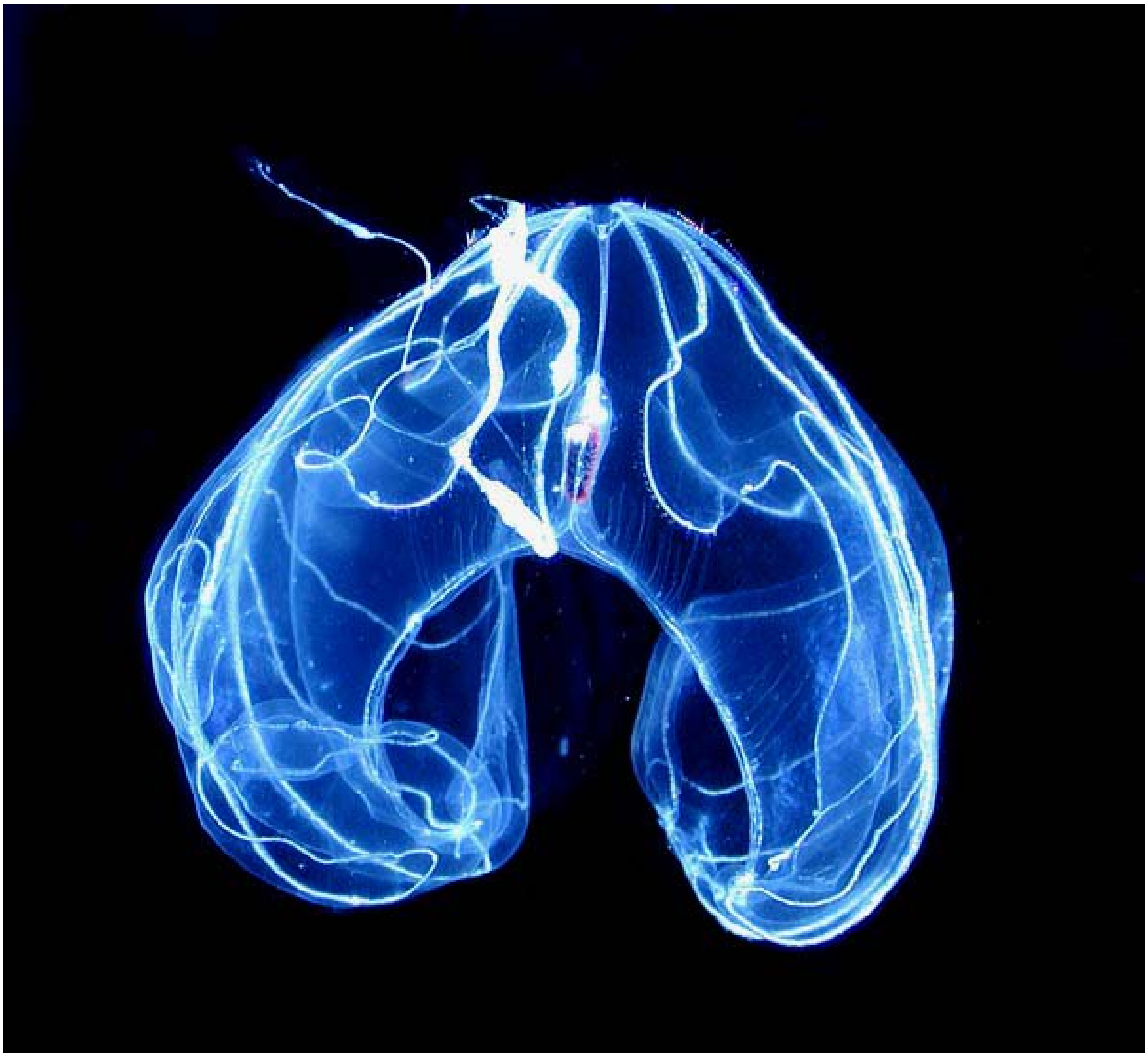


A choanoflagellate

In the 1990s sponges were widely regarded as a monophyletic group, in other words all of them descended from a common ancestor that was itself a sponge, and as the "sister-group" to all other metazoans (multi-celled animals), which themselves form a monophyletic group. On the other hand some 1990s analyses also revived the idea that animals' nearest evolutionary relatives are choanoflagellates, single-celled organisms very similar to sponges' choanocytes – which would imply that most Metazoa evolved from very sponge-like ancestors and therefore that sponges may not be monophyletic, as the same sponge-like ancestors may have given rise both to modern sponges and to non-sponge members of Metazoa.

Analyses since 2001 have concluded that Eumetazoa (more complex than sponges) are more closely related to particular groups of sponges than to the rest of the sponges. Such conclusions imply that sponges are not monophyletic, because the last common ancestor of all sponges would also be a direct ancestor of the Eumetazoa, which are not sponges. A study in 2001 based on comparisons of ribosome DNA concluded that the most fundamental division within sponges was between glass sponges and the rest, and that Eumetazoa are more closely related to Calcareous sponges, those with calcium carbonate spicules, than to other types of sponge. In 2007 one analysis based on comparisons of RNA and another based mainly on comparison of spicules concluded that demosponges and glass sponges are more closely related to each other than either is to calcareous sponges, which in turn are more closely related to Eumetazoa.

Other anatomical and biochemical evidence links the Eumetazoa with Homoscleromorpha, a sub-group of demosponges. A comparison in 2007 of nuclear DNA, excluding glass sponges and comb jellies, concluded that: Homoscleromorpha are most closely related to Eumetazoa; calcareous sponges are the next closest; the other demosponges are evolutionary "aunts" of these groups; and the chancelloriids, bag-like animals whose fossils are found in Cambrian rocks, may be sponges. The sperm of Homoscleromorpha share with those of Eumetazoa features that those of other sponges lack. In both Homoscleromorpha and Eumetazoa layers of cells are bound together by attachment to a carpet-like basal membrane composed mainly of "type IV" collagen, a form of collagen not found in other sponges – although the spongin fibers that reinforce the mesohyl of all demosponges is similar to "type IV" collagen.



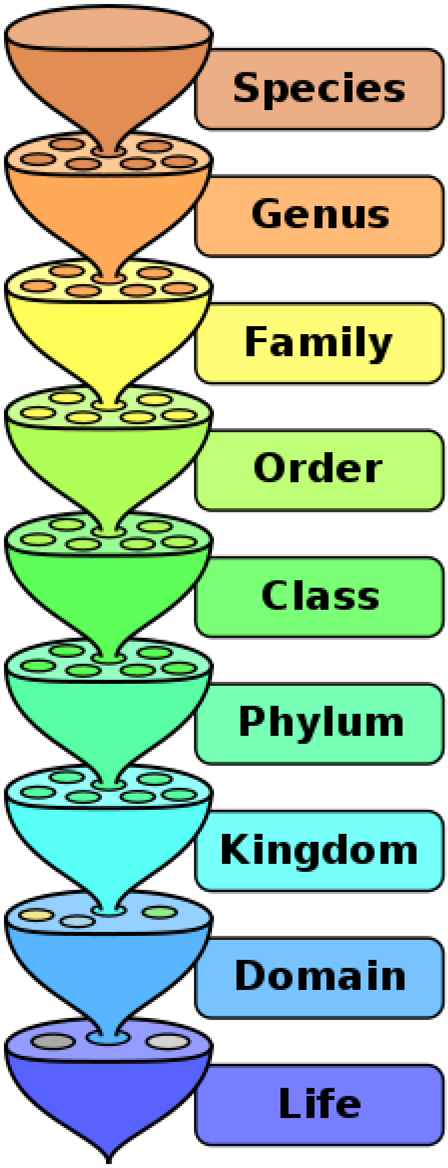
A comb jelly

The analyses described above concluded that sponges are closest to the ancestors of all Metazoa, in other words of all multi-celled animals including both sponges and more complex groups. However, another comparison in 2008 of 150 genes in each of 21 genera, ranging from fungi to humans but including only two species of sponge, suggested that comb jellies (ctenophora) are the most basal lineage of the Metazoa included in the sample. If this is correct, either modern comb jellies developed their complex structures independently of other Metazoa, or sponges' ancestors were more complex and all known sponges are drastically simplified forms. The study recommended further analyses using a wider range of sponges and other simple Metazoa such as Placozoa. The results of such an analysis, published in 2009, suggest that a return to the previous view may be warranted. 'Family trees' constructed using a combination of all available data - morphological, developmental and molecular - concluded that the sponges are in fact a monophyletic group, and with the cnidarians form the sister group to the bilaterians.

Archaeocyathids are very common fossils in rocks from the Early Cambrian about 530 to 520 million years ago but are not found after the Late Cambrian. It has been suggested that they were produced by: sponges; cnidarians; algae; foraminiferans; a completely separate phylum of animals, Archaeocyatha; or even a completely separate kingdom of life, labelled Archaeata or Inferibionta. Since the 1990s archaeocyathids have been regarded as a distinctive group of sponges.

It is difficult to fit chancelloriids into classifications of sponges or more complex animals. An analysis in 1996 concluded that they were closely related to sponges on the grounds that the detailed structure of chancellorid sclerites ("armor plates") is similar to that of fibers of spongin, a collagen protein, in modern keratose (horny) demosponges such as *Darwinella*. However another analysis in 2002 concluded that chancelloriids are not sponges and may be intermediate between sponges and more complex animals, among other reasons because their skins were thicker and more tightly-connected than those of sponges. In 2008 a detailed analysis of chancelloriids' sclerites concluded that they were very similar to those of halkieriids, mobile bilaterian animals that looked like slugs in chain mail and whose fossils are found in rocks from the very Early Cambrian to the Mid Cambrian. If this is correct, it would create a dilemma, as it is extremely unlikely that totally unrelated organisms could have developed such similar sclerites independently, but the huge difference in the structures of their bodies makes it hard to see how they could be closely related.

Taxonomy



Levels in the Linnean taxonomy.

For a long time sponges were assigned to a separate subkingdom, Parazoa ("beside the animals"), separate from the Eumetazoa which formed the rest of the kingdom Animalia. They are now classified as a phylum within Animalia, and divided into classes mainly according to the composition of their skeletons:

- Hexactinellida (glass sponges) have silicate spicules, the largest of which have six rays and may be individual or fused. The main components of their bodies are syncytia in which large numbers of cell share a single external membrane.

- Calcarea have skeletons made of calcite, a form of calcium carbonate, which may form separate spicules or large masses. All the cells have a single nucleus and membrane.
- Most Demospongiae have silicate spicules or spongin fibers or both within their soft tissues. However a few also have massive external skeletons made of aragonite, another form of calcium carbonate. All the cells have a single nucleus and membrane.
- Archeocyatha are known only as fossils from the Cambrian period.

In the 1970s sponges with massive calcium carbonate skeletons were assigned to a separate class, Sclerospongiae, otherwise known as "coralline sponges". However in the 1980s it was found that these were all members of either the Calcarea or the Demospongiae.

So far scientific publications have identified about 9,000 poriferan species, of which: about 400 are glass sponges; about 500 are calcareous species; and the rest are demosponges. However some types of habitat, such as vertical rock and cave walls and galleries in rock and coral boulders, have been investigated very little, even in shallow seas.

Use

By dolphins

A report in 1997 described use of sponges as a tool by bottlenose dolphins in Shark Bay. A dolphin will attach a marine sponge to its rostrum, which is presumably then used to protect it when searching for food in the sandy sea bottom. The behaviour, known as *sponging*, has only been observed in this bay, and is almost exclusively shown by females. A study in 2005 concluded that mothers teach the behaviour to their daughters, and that all the sponge-users are closely related, suggesting that it is a fairly recent innovation.

Chapter 2

Calcareous Sponge and Hexactinellid

Calcareous sponge

Calcareous sponges

"Calcispongiae" from Ernst Haeckel's *Kunstformen der Natur*, 1904

Scientific classification [e]

Kingdom:	Animalia
Phylum*:	"Porifera"

Class:	**Calcarea** Bowerbank, 1817

Subclasses

Calcinea
Calcaronea

The **calcareous sponges** of class **Calcarea** are members of the animal phylum Porifera, the cellular sponges. They are characterized by spicules made out of calcium carbonate in the form of calcite or aragonite. While the spicules in most species have three points, in some species they have either two or four points.

Biology

Clathrina clathrus, an asconoid calcareous sponge

All sponges in this class are strictly marine, and, while they are distributed worldwide, most are found in shallow tropical waters. Like all other sponges, they are sedentary filter feeders.

All three sponge body plans are represented within class Calcarea : asconoid, syconoid, and leuconoid. Typically, calcareous sponges are small, measuring less than 10 centimetres (3.9 in) in height, and drab in colour. However, a few brightly coloured species are also known.

Calcareous sponges vary from radially symmetrical vase-shaped body types to colonies made up of a meshwork of thin tubes, or irregular massive forms. The skeleton has either a mesh or honeycomb structure.

Classification

Of the 15,000 or so species of Porifera that exist, only 400 of those are Calcareans.

Calcarean sponges first appeared during the Cambrian and their diversity was greatest during the Cretaceous period. Recent molecular analysis suggests that the class Calcarea should be designated as a phylum, in particular the first to have diverged in the Kingdom Animalia; the other sponges belong to the phylum Silicarea.

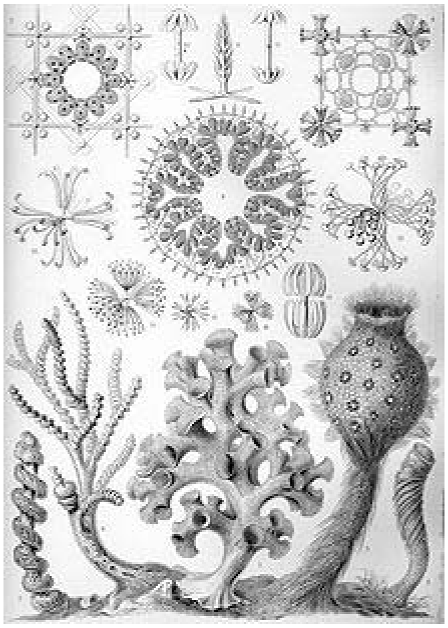
The calcareous sponges are divided into two subclasses and seven orders:

Class **Calcarea**

- Subclass Calcinea
    - Order Clathrinida
    - Order Leucettida
    - Order Murrayonida
- Subclass Calcaronea
    - Order Baerida
    - Order Leucosolenida
    - Order Lithonida
    - Order Sycettida

Hexactinellid

Hexactinellid sponges
Temporal range: Cambrian–Recent



"Hexactinellae" from Ernst Haeckel's *Kunstformen der Natur*, 1904

Scientific classification [e]

Kingdom:	Animalia
Phylum*:	"Porifera"
Class:	**Hexactinellida** Schmidt, 1870

Subclasses

Amphidiscophora
Hexasterophora
†Reticulosa

Hexactinellid sponges are sponges with a skeleton made of four- and/or six-pointed silaceous spicules, often referred to as **glass sponges**. They are usually classified along with other sponges in the phylum Porifera, but some researchers consider them sufficiently distinct to deserve their own phylum, **Symplasma**.

Biology

Staurocalyptus sp.

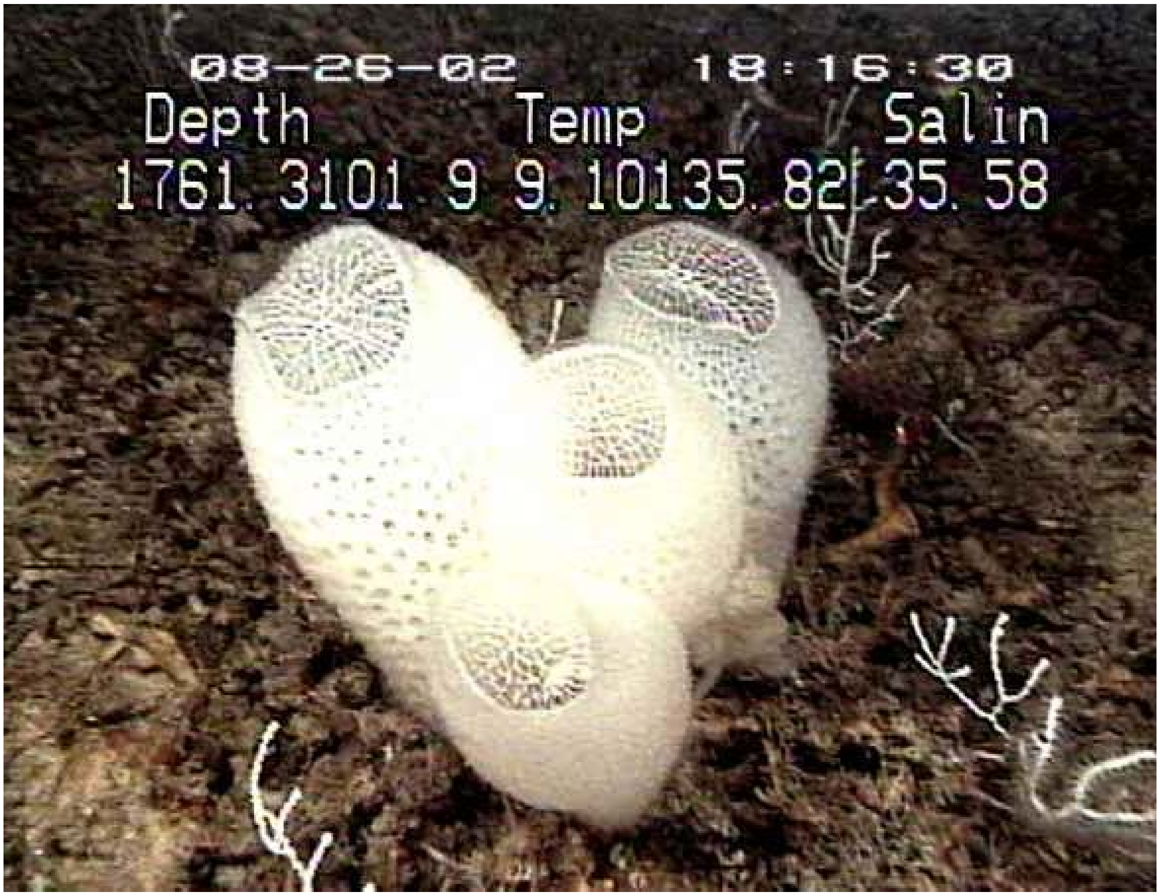
Glass sponges are relatively uncommon and are mostly found at depths from 450 to 900 metres (1,480 to 3,000 ft) although the species *Oopsacas minuta* has been found in shallow water, while others have been found much deeper. They are found in all oceans of the world, although they are particularly common in Antarctic waters.

They are more-or-less cup-shaped animals, ranging from 10 to 30 centimetres (3.9 to 12 in) in height, with sturdy lattice-like internal skeletons made up of fused spicules of silica. The body is relatively symmetrical, with a large central cavity that, in many species, opens to the outside through a sieve formed from the skeleton. Unlike other sponges, they tend to be present as individuals, rather than forming large fused colonies. They are generally pale in colour.

Much of the body is composed of syncitia, extensive regions of multinucleate cytoplasm. In particular, the epidermal cells of other sponges are absent, being replaced by a syncitial net of amoebocytes, through which the spicules penetrate. Unlike other sponges, they do not possess the ability to contract.

One ability they possess is a unique system for rapidly conducting electrical impulses across their bodies, making it possible for them to respond quickly to external stimuli. Glass sponges like "Venus' Flower Basket" have a tuft of fibers that extends outward like an inverted crown at the base of their skeleton. These fibers are 50 to 175 millimetres (2.0 to 6.9 in) long and about the thickness of a human hair. They work as optical fibers somewhat similar to those used in modern telecommunication networks.

Glass sponges are different from other sponges in a variety of other ways. For example, most of the cytoplasm is not divided into separate cells by walls but forms a syncytium or continuous mass of cytoplasm with many nuclei (e.g., Reiswig and Mackie, 1983).



Venus' Flower Basket, *Euplectella aspergillum*

These creatures live for a very long time, but the exact age is hard to measure; one study based on modelling gave an estimated age of a specimen of *Scolymastra joubini* as 23,000 years, which is thought impossible, but is the basis for a listing of ~15,000 years in the AnAge Database. The shallow water occurrence of hexactinellids is rare world wide. In the Antarctic two species occur as shallow as 33 meters under the ice. In the Mediterranean one species occurs as shallow as 18 meters in a cave with deep water upwelling (Boury-Esnault & Vacelet (1994)

Reefs

The sponges form reefs off the coast of British Columbia and Washington State, which are studied in the Sponge Reef Project.

Classification

The earliest known hexactinellids are from the earliest Cambrian or late Neoproterozoic. They are fairly common relative to demosponges as fossils, but this is thought to be, at least in part, because their spicules are sturdier than spongin and fossilize better. Like almost all sponges, the hexactinellids draw water in through a series of small pores by the whip like beating of a series of hairs or flagella in chambers which in this group line the sponge wall. (Sponge Gardens)

The class is divided into six orders, in two subclasses:

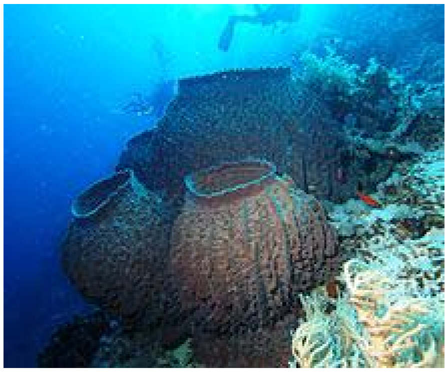
Class **Hexactinellida**

- Subclass Amphidiscophora
    - Order Amphidiscosida
- Subclass Hexasterophora
    - Order Aulocalycoida
    - Order Hexactinosa
    - Order Lychniscosa
    - Order Lyssacinosa

Chapter 3

Demosponge

Demosponge



Barrel sponge (*Xestospongia testudinaria*)

Scientific classification [e]

Kingdom:	Animalia
Phylum*:	"Porifera"
Class:	**Demospongiae** Sollas, 1885

Subclasses

Homoscleromorpha
Tetractinomorpha

The **Demospongiae** are the largest class in the phylum Porifera. Their "skeletons" are made of spicules consisting of fibers of the protein spongin, the mineral silica, or both. Where spicules of silica are present, they have a different shape from those in the otherwise similar glass sponges. The demosponges include 90% of all species of sponges and are predominantly leuconoid in structure.

There are many diverse orders in this class, including all of the large sponges. Most are marine dwellers, but several live in freshwater environments. Some species are brightly colored, and there is great variety in body shape; the largest species are over 1 metre (3.3 ft) across. They reproduce both sexually and asexually.

Classification

The Demospongia have an ancient history with the first demosponge fossils appearing in Precambrian deposits at the end of the Cryogenian "Snowball Earth" period, where their presence has been detected by fossilized steroids, called steranes, hydrocarbon markers that are characteristic of the cell membranes of the sponges, rather than from direct fossils of the sponges themselves. They represent a continuous 100-Myr-long chemical fossil record of demosponges through the end of the Neoproterozoic. The earliest sponge-bearing reefs date to the Early Cambrian, exemplified by a small bioherm constructed by archaeocyathids and calcified microbes at the start of the Tommotian stage (about 540–535 Ma), found in southeast Siberia. A major radiation occurred in the Lower Cambrian and further major radiations in the Ordovician possibly from the middle Cambrian. (Finks, 1970

The extant Demospongiae have been organised into 14 orders that encompass 88 families, 500 genera and more than 8000 described species.

Hooper and van Soest give the following classification of demosponges into orders:

Monanchora barbadensis (red encrusting sponge)

- Subclass **Homoscleromorpha** Bergquist 1978
    - Homosclerophorida Dendy 1905
- Subclass **Tetractinomorpha**
    - Astrophorida Sollas 1888
    - Chondrosida Boury-Esnault & Lopès 1985
    - Hadromerida Topsent 1894
    - Lithistida Sollas 1888
    - Spirophorida Bergquist & Hogg 1969
- Subclass **Ceractinomorpha** Levi 1953
    - Agelasida Verrill 1907
    - Dendroceratida Minchin 1900
    - Dictyoceratida Minchin 1900
    - Halichondrida Gray 1867
    - Halisarcida Bergquist 1996
    - Haplosclerida Topsent 1928
    - Poecilosclerida Topsent 1928
    - Verongida Bergquist 1978
    - Verticillitida Termier & Termier 1977

However, molecular evidence suggests that the *Homoscleromorpha* may not belong in this class and that other classifications may need to be revised.

Systematics

Demosponge systematics is an active area of research, and much is still to be learned. However, some rudimentary outlines can be made. The basal clade of the Demospongia is the Homoscleromorpha, characterized by the possession of a larva more reminiscent of that of the Calcarea than that of the rest of the Demospongia. Demosponges other than the Homoscleromorpha are split into two major groups, the Tetractinomorpha and the Ceractinomorpha. These two groups share characters that indicate common descent such as a distinctive larval type and the presence of spongin. Currently, the two groups are each characterized by distinctive types of microscleres, though some doubt still remains as to whether the distinctive microsclere types evolved only once in each group. Fossils of each of these groups is known from the Cambrian suggesting an early radiation of the major clades of demosponges. The Lithistida, a taxonomic grouping into which many of the fossil demosponges fall, is most certainly polyphyletic with members in both the Tetractinomorpha and the Ceractinomorpha.

A molecular study of the mitochondrial genome suggests that five major clades exist in the Demospongiae. These clades are

- Homoscleromorpha: order Homosclerophorida
- Keratosa: orders Dendroceratida, Dictyoceratida and Verticillitida
- Myxospongiae: orders Chondrosida, Halisarcida and Verongida
- Haplosclerida (marine species)
- Remainder of the demosponges: orders Agelasida, Astrophorida, Hadromerida, Halichondrida, Poecilosclerida, Spirophorida and Haploscerida (freshwater species)

The branching order appears to be (Homoscleromorpha, (Keratosa, Myxospongiae)(Haplosclerida [marine species], Remainder of the demosponges))

Reproduction

Red volcano sponge (*Acarnus erithacus*).

Spermatocytes develop from the transformation of choanocytes and oocytes arise from archeocytes. Repeated cleavage of the zygote egg takes place in the mesohyl and forms a parenchymula larva with a mass of larger internal cells surrounded by small, externally flagellated cells. The resulting swimming larva enters a canal of the central cavity and is expelled with the exhalant current.

Methods of asexual reproduction include both budding and the formation of gemmules. In budding, aggregates of cells differentiate into small sponges that are released superficially or expelled through the oscula. Gemmules are found in the freshwater family Spongellidae. They are produced in the mesohyl as clumps of archeocytes, are surrounded with a hard layer secreted by other amoebocytes. Gemmules are released when the parent body breaks down, and are capable of surviving harsh conditions. In a favorable situation, an opening called the micropyle appears and releases amoebocytes, which differentiate into cells of all the other types.

Economic Importance

The most economically important group of demospongians to human are the bath sponges. These are harvested by divers and can also be grown commercially. They are bleached and marketed; the spongin gives the sponge its softness and absorbency.

Chapter 4

Archaeocyatha and Cliona celata

Archaeocyatha

Archaeocyatha
Temporal range: Early — Late Cambrian

Scientific classification

Domain:	Eukaryota
(unranked):	Opisthokonta
Kingdom:	Animalia
Subkingdom:	Parazoa
Phylum:	Porifera(sponges)
(unranked):	**Archaeocyatha** Vologdin, 1937

Synonyms

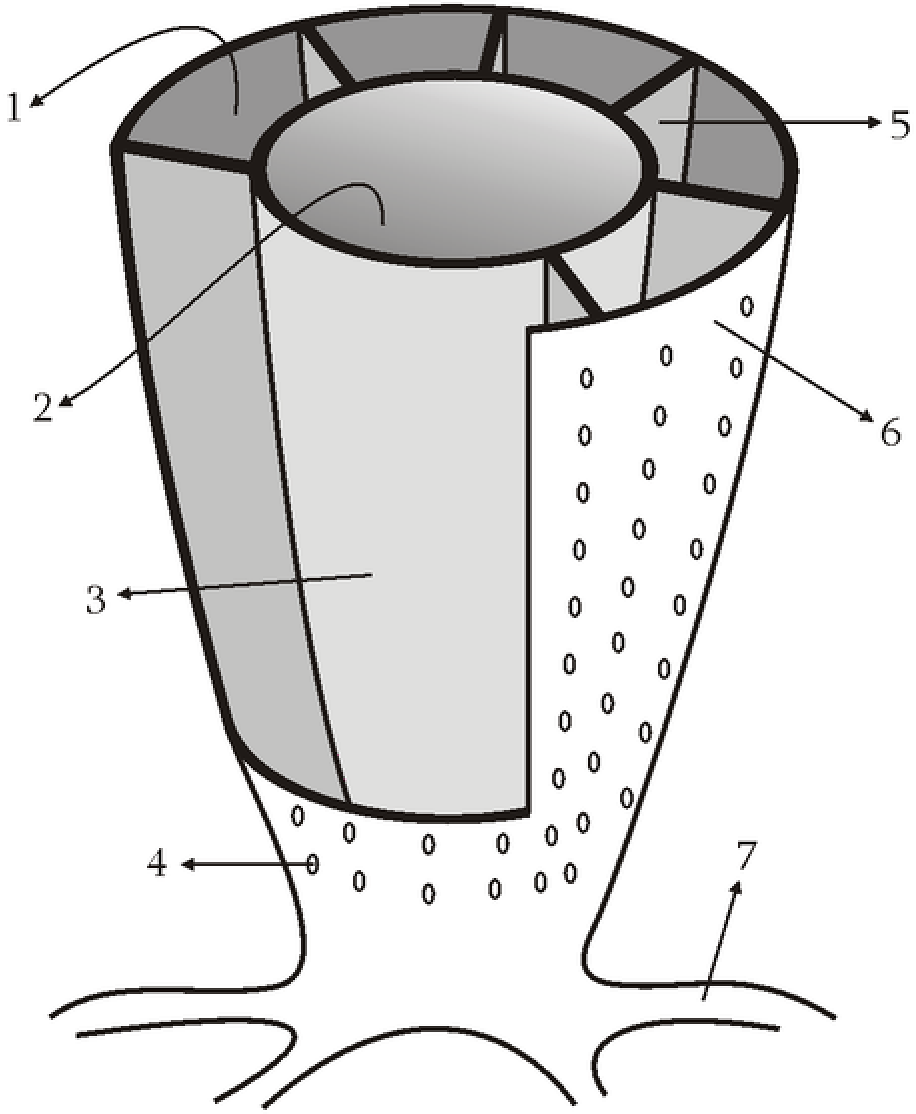
- Cyathospongia Okulitch, 1935
- Pleospongia Okulitch, 1935

The **Archaeocyatha** or **archaeocyathids** ("ancient cups") were sessile, reef-building marine organisms of warm tropical and subtropical waters that lived during the early (lower) Cambrian period. It is believed that the centre of the Archaeocyatha origin is in East Siberia, where they are first known from the beginning of the Tommotian Age of the Cambrian, 525 million years ago (mya). In other regions of the world, they appeared much later, during the Atdabanan, and quickly diversified into over a hundred families. They became the planet's very first reef-building animals and are an index fossil for the Lower Cambrian worldwide.

Geological history

Today, the archaeocyathan families are recognizable by small but consistent differences in their fossilized structures: Some archaeocyathans were built like nested bowls, while others were as long as 30 cm. Some archaeocyaths were solitary organisms, while others formed colonies. Then, in the beginning of the Toyonian Age around 516 mya, the archaeocyaths went into a sharp decline. Almost all species became extinct by the Middle Cambrian, with the final-known species disappearing just prior to the end of the Cambrian period, *Antarcticocyathus webberi*. Their rapid decline and disappearance coincided with a rapid diversification of the Demosponges.

The group were important reef-builders in the early to middle Cambrian, with reefs (and indeed any accumulation of carbonates) becoming very rare after their extinction until the diversification of coral reef-builders in the Ordovician.



*1 – Gap (*intervallum*) *2 – Central cavity *3 – Internal wall *4 – Pore (all the walls and septa have pores, not all are represented) *5 – Septum *6 – External wall *7 – Rizoid

Morphology

The typical archaeocyathid resembled a hollow horn coral. Each had a conical or vase-shaped porous skeleton of calcite similar to that of a sponge. The structure appeared like a pair of perforated, nested ice cream cones. Their skeletons consisted of either a single porous wall (Monocyathida), or more commonly as two concentric porous walls, an inner and outer wall separated by a space. Inside the inner wall was a cavity (like the inside of an empty ice cream cone). At the base, these pleosponges were held to the substrate by a holdfast. The body presumably occupied the space between the inner and outer shells (the intervallum).

Ecology

Flow tank experiments suggest that archaeocyathan morphology allowed them to exploit flow gradients, either by passively pumping water through the skeleton, or, as in present-day, extant sponges, by drawing water through the pores, removing nutrients, and expelling spent water and wastes through the pores into the central space.

Distribution

The archaeocyathans inhabited coastal areas of shallow seas. Their widespread distribution over almost the entire Cambrian world, as well as the taxonomic diversity of the species, might be explained by surmising that that they were planktonic during their larval stage.

Archeocyathids from the Poleta formation, eastern California

Their phylogenetic affiliation has been subject to changing interpretations, yet the consensus is growing that the archaeocyath was indeed a kind of sponge, thus sometimes called a pleosponge. But some invertebrate paleontologists have placed them in an extinct, separate phylum, known appropriately as the Archaeocyatha. However, one cladistic analysis suggests that Archaeocyatha is a clade nested within the phylum Porifera (better known as the true sponges).

Taxonomy

The clade Archaeocyatha have traditionally been divided into Regulares and Irregulares (Rowland, 2001):

- Hetairacyathida (incertae sedis)
- Regulares
    - Monocyathida
    - Capsulocyathida
    - Ajacicyathida
- Irregulares
    - Thalassocyathida
    - Archaeocyathida
    - Kazakhstanicyathida

However, Okulitch (1955), divided the phylum in three classis:

- Phylum Archaeocyatha Vologdin, 1937
    - Class Monocyathea Okulitch, 1943
    - Class Archaeocyathea Okulitch, 1943
    - Class Anthocyathea Okulitch, 1943

Cliona celata

Cliona celata

Scientific classification

Kingdom:	Animalia
Phylum:	Porifera
Class:	Demospongiae

Subclass:	Tetractinomorpha
Order:	Hadromerida
Family:	Clionaidae
Genus:	*Cliona*
Species:	***C. celata***

Binomial name

Cliona celata
Grant, 1826

Cliona celata, occasionally called the **Red Boring Sponge**, is a species of demosponge belonging the family Clionaidae. It is found worldwide. This sponge creates round holes up to 5 cm in diameter in limestone or the shells of molluscs, especially oysters. The sponge itself is often visible as a rather featureless yellow or orange lump at the bottom of the hole.

Habitat

These sponges are common in Southern New England and in Narragansett Bay. They also live in the Bahamas, and the western Atlantic Ocean. They usually live in lagoons or on reefs. They will sometimes make their home on dead mollusks or other shelled creatures.

Reproduction

Red Boring Sponges can reproduce asexually and sexually. They can simply separate by mitosis, as single cells do, or they can release sperm into the water in hopes of them finding a female's eggs. They may also attach their larvae onto mollusks like clams and mussels. This usually results in the death of the host. They then will begin to grow and colonize.

Chapter 5

Halichondria Panicea and Hexasterophora

Halichondria panicea

Halichondria panicea

Scientific classification

Kingdom:	Animalia
Phylum:	Porifera
Class:	Demospongiae
Order:	Halichondrida
Family:	Halichondriidae
Genus:	*Halichondria*
Species:	***H. panicea***

Binomial name

Halichondria panicea
Pallas, 1766

Halichondria panicea, commonly known as the **breadcrumb sponge**, is a species of marine demosponge belonging to the family Halichondriidae. This is an abundant sponge of coastal areas of the North Atlantic and the Mediterranean Sea ranging from the intertidal zone to a recorded depth of over 550 m. It is very tolerant of a wide range of coastal habitats, including strong currents, high salinity and exposure to powerful wave action. Its only requirement is a rocky substrate which can include small cobbles.

Morphology

Halichondria panicea occurs in a very wide range of forms and can be difficult to identify. Some forms have a granular surface which gives rise to the common name but sometimes the surface is smooth, even glassy. The surface is often marked with pores (osculae) which can extend into tubular "chimneys" in wave-sheltered habitats. The overall form is determined largely by the habitat: wave-exposed forms usually form thin widespread sheets but wave-sheltered forms often form massive encrustations up to 20 cm thick. This diversity has led to its being described as a new species 56 times.

The colour is also variable. The "natural" colour is cream or grey: this is usually found in specimens from relatively deep water. However at shallower depths, the sponge is usually green due to symbiotic algae which live close to the surface of the sponge. At intermediate depths the sponge tends to be green in summer, cream or grey in winter. It smells like "exploded gunpowder".

Biology

Halichondria panicea is a suspension feeder feeding mainly on phytoplankton. For such a common species, relatively little is known about its reproduction: It appears to be a hermaphrodite and oogenesis has been reported as occurring in a very narrow timeband within a single population although exceptions have been observed.

Other names

1. *Halichondria panicea* Pallas, 1766
2. *Halina panicea* Pallas, 1766
3. *Spongia panicea* Pallas, 1766
4. *Spongia tomentosa* Linnaeus, 1767
5. *Spongia cristata* Ellis & Solander, 1786
6. *Spongia tubulosa* Ellis & Solander, 1786
7. *Spongia urens* Ellis & Solander, 1786
8. *Halichondria papillaris* Linnaeus, 1791
9. *Alcyonium manusdiaboli sensu* Esper, 1794
10. *Spongia compacta* Sowerby, 1806
11. *Alcyonium medullare* Lamarck, 1815
12. *Halichondria albescens* Rafinesque, 1818
13. *Seriatula seriata* Grant, 1826
14. *Spongia seriata* Grant, 1826

15. *Halichondria sevosa* Johnston, 1842
16. *Halichondria reticulata* Lieberkühn, 1859
17. *Halichondria coccinea* Bowerbank, 1861
18. *Hymeniacidon coccinea* Bowerbank, 1861
19. *Halichondria brettii* Bowerbank, 1866
20. *Hymeniacidon brettii* Bowerbank, 1866
21. *Hymeniacidon fallaciosus* Bowerbank, 1866
22. *Halichondria caduca* Bowerbank, 1866
23. *Halichondria glabra* Bowerbank, 1866
24. *Halichondria incerta* Bowerbank, 1866
25. *Halichondria lactea* Bowerbank, 1866
26. *Halichondria membrana* Bowerbank, 1866
27. *Hymeniacidon fragilis* Bowerbank, 1866
28. *Hymeniacidon lactea* Bowerbank, 1866
29. *Hymeniacidon membrana* Bowerbank, 1866
30. *Hymeniacidon thomasii* Bowerbank, 1866
31. *Hymeniacidon parfitti* Parfitt, 1868
32. *Hymeniacidon reticulatus* Bowerbank, 1866
33. *Pellina bibula* Schmidt, 1870
34. *Spuma borealis* var. *convoluta* Miklucho-Maclay, 1870
35. *Spuma borealis* var. *tuberosa* Miklucho-Maclay, 1870
36. *Spuma borealis* var. *velamentosa* Miklucho-Maclay, 1870
37. *Halichondria ambigua* Bowerbank, 1874
38. *Halichondria edusa* Bowerbank, 1874
39. *Halichondria firmus* Bowerbank, 1874
40. *Halichondria pannosus* Verrill, 1874
41. *Hymeniacidon firmus* Bowerbank, 1874
42. *Hymeniacidon solida* Bowerbank, 1874
43. *Hymeniacidon tegeticula* Bowerbank, 1874
44. *Amorphina appendiculata* Schmidt, 1875
45. *Halichondria paciscens* Schmidt, 1875
46. *Amorphina paciscens* Schmidt, 1875
47. *Halichondria coralloides* Bowerbank, 1882
48. *Isodictya crassa* Bowerbank, 1882
49. *Isodictya perplexa* Bowerbank, 1882
50. *Microciona tumulosa* Bowerbank, 1882
51. *Amorphina grisea* Fristedt, 1887
52. *Halichondria grisea* Fristedt, 1887
53. *Menanetia minchini* Topsent, 1896
54. *Halichondriella corticata* Burton, 1931
55. *Trachyopsilla glaberrima* Burton, 1931
56. *Halichondria topsenti* de Laubenfels, 1936

Hexasterophora

Hexasterophora	
Scientific classification	
Kingdom:	Animalia
Phylum:	Porifera
Class:	Hexactinellida
Subclass:	**Hexasterophora** Schulze, 1886
Orders	
Lyssacinosa Hexactinosa Lychniscosa	

Hexasterophora are sponges, a subclass in the class Hexactinellida. The Hexasterophora first appeared in the Ordovician and is separated into five recent orders, including the Lyssacinosa, the Hexactinosa, and the Lychniscosa, all of which have living representatives in the seas today.

Hexasterophorans have skeletons composed of overlapping six-rayed spicules. The sponge is commonly firmly attached by its base to a hard substratum; less often rooted by the anchoring spicules and rarely inserted directly into the loose bottom sediments. The three groups are differentiated by the extent of fusion of adjacent spicules.

The Lyssacinosa, Hexactinosa, and Lychniscosa appear sequentially in the fossil record. The least fused group, the Lyssacinosa, appears in the Ordovician, while the intermediate group, the Hexactinosa is known from the Devonian. Finally, the Lychniscosa, with the most tightly interlocking spicules is first found in rocks of Triassic age.

Chapter 6

Spongilla and Spongilla Argyrosperma

Spongilla

Spongilla

Scientific classification	
Kingdom:	Animalia
Phylum:	Porifera
Class:	Demospongiae Sollas, 1885
Order:	Haplosclerida
Family:	Spongillidae
Genus:	***Spongilla***

Species

Spongilla alba
Spongilla arctica
Spongilla argyrosperma
Spongilla aspinosa
Spongilla cenota
Spongilla helvetica
Spongilla inarmata
Spongilla lacustris
Spongilla wagneri

Spongilla dwells in lakes and slow streams. There are around twenty species of freshwater sponges, all occurring in this genus. Sponges of the genus *Spongilla* attach themselves to rocks and logs and filter the water for various small aquatic organisms such as protozoa, bacteria, and other free-floating pond life. Unlike marine sponges, freshwater sponges are exposed to far more adverse and variable environmental conditions, and therefore they have developed gemmules as a means of dormancy. When exposed to excessively cold or otherwise harsh situations, the sponges form these gemmules, which are highly resistant "buds" that can live dormantly after the mother sponge has died. When conditions improve, the gemmules will "germinate" and a new sponge is born.

Spongilla was used by John Hogg (biologist) in the nineteenth century to attempt to justify a fourth kingdom of Life.

Spongilla argyrosperma

Freshwater sponge (North America)	
Scientific classification	
Kingdom:	Animalia
Phylum:	Porifera
Class:	Demospongiae
Order:	Haplosclerida
Suborder:	Spongillina
Family:	Spongillidae
Genus:	*Spongilla*
Species:	*S. argyrosperma*
Binomial name	
Spongilla argyrosperma (Potts, 1880)	
Synonyms	
- *Heteromeyenia (Anheteromeyenia) argyrosperma*	

Spongilla argyrosperma (Potts, 1880) is a freshwater sponge found across North America.

Geographical Range

Nearctic region from Canada (Quebec, New Brunswick) to Florida and northern Alaska to southern California.

Habitat

Spongilla argyrosperma is found in both lotic (flowing water) and lentic (still) habitats. Typically in waters of about neutral pH with low to moderate alkalinity and high conductivity; in temperatures of 9 to 23 °C. They are sessile suspension feeders that attach to submerged surfaces such as rocks and logs in most inland habitats.

Diet

Sponges filter the water through them to collect numerous species of smaller organisms such as bacteria and protozoa. *Spongilla argyrosperma* are especially important in nutrient cycling and primary production.

Physical Characteristics (Morphology)

Spongilla argyrosperma have a thin, encrusting form with a hispid surface due to emerging spicules. Their color is grey unless green from being in symbiosis with zoocholrellae (algae). Their bodies are permeated with pores, chambers, and canals for the flow of water through them. The smaller, more prevalent incurrent pores are the ostia and the larger excurrent pores are the oscula. Within *S. argyrosperma* the oscules are inconspicuous.

Cell Structure/Internal Characteristics

Sponges have no true tissues or germ layers. While the cells are loosely organized, different cells are responsible for different functions within the animal but have the ability to transform into different cell types. *Spongilla* are the Leuconoid stage of progression which means their form is of many collected channels and chambers clustered together so water moves throughout the specimen. The tissue is called the mesohyl and the water movement occurs through flagellated cells called choanocytes. *S. argyrosperma* have siliceous spicules and collagen fibers to give it its form. Spicules are needle like structures which form the mineral skeleton. Megascleres are large spicules that form the main skeleton. Within *S. argyrosperma* the megascleres are slender, slightly curved acanthoxeas that range in length from 250- 329 μm and in width from 10-15 μm. Microscleres are absent.

Reproduction

Spongilla can reproduce sexually or asexually. They can produce live larvae sexually or asexually they may bud or if a section breaks off the cells can reaggragate and grow into new specimens. In times of environmental stress, which is much more often in freshwater sponges, they can reduce their bodies or produce gemmules or “cysts” which form a hard, protective coating over the asexual larvae so they can be moved about and grow when the conditions permit or are more favorable. In *S. argyrosperma* the gemmules are yellow and spherical with a diameter ranging from 400-700 µm. The gemmuloscleres have birotulates of two notably different lengths. These details of long recurved rays with shaft spines and the shorter more abundant variation along with the length range of gemmuloscleres are some of the most reliable details to observe in identification. The specimen pictured is lacking gemmules, probably because of being collected in early summer.

Misidentification

May be mistaken for common algae growth on rocks in habitat because of similar green color and flat, encrusting form. May also be living within algae growths or other *Spongilla* colonies symbiotically. There are abundant misidentifications of these and other species because of incomplete, fragmentary keys for freshwater sponges that have incomplete taxonomic and ecological information. Especially important to this range of varieties and synonyms is a lack of information concerning environmental variation, in morphological types within a given species.

Additional Importance

Spongilla argyrosperma live very much within a symbiosis state with many forms of algae. This zoochlorellae may augment or supplement their sponge host's nutrition. Also, because of being a susceptible and responsive freshwater animal, *Spongilla* species are potentially very valuable indicators of water quality.

Chapter 7

Ctenophora

Comb jellies
Temporal range: Cambrian - Recent.

"Ctenophorae" from Ernst Haeckel's *Kunstformen der Natur*, 1904

Scientific classification

Domain:	Eukaryota
Kingdom:	Animalia
Subkingdom:	Eumetazoa
Phylum:	**Ctenophora** Eschscholtz, 1829

Classes

Tentaculata
Nuda

The **Ctenophora** commonly known as **comb jellies**, are a phylum of animals that live in marine waters worldwide. Their most distinctive feature is the "combs", groups of cilia that they use for swimming, and they are the largest animals that swim by means of cilia — adults of various species range from a few millimeters to 1.5 meters (59 in) in size. Like cnidarians, their bodies consist of a mass of jelly with one layer of cells on the outside and another lining the internal cavity. In ctenophores these layers are two cells deep while those in cnidarians are only one cell deep. Ctenophores also resemble cnidarians in having a decentralized nerve net rather than a brain. Some authors combined ctenophores and cnidarians in one phylum, Coelenterata, as both groups rely on water flow through the body cavity for both digestion and respiration. Increasing awareness of the differences persuaded more recent authors to classify them in separate phyla.

Almost all ctenophores are predators, taking prey ranging from microscopic larvae and rotifers to the adults of small crustaceans; the exceptions are juveniles of two species, which live as parasites on the salps on which adults of their species feed. In favorable circumstances ctenophores can eat ten times their own weight in a day. There are only 100–150 valid species and possibly another 25 that have not been fully described and named. The textbook examples are cydippids with egg-shaped bodies and a pair of retractable tentacles fringed with tentilla ("little tentacles") that are covered with colloblasts, sticky cells that capture prey. The phylum has a wide range of body forms, including the flattened deep-sea platyctenids, in which the adults of most species lack combs, and the coastal beroids, which lack tentacles and prey on other ctenophores by using huge mouths armed with groups of large, stiffened cilia that act as teeth. These variations enable different species to build huge populations in the same area, because they specialize in different types of prey, which they capture by as wide a range of methods as spiders use.

Most species are hermaphrodites, in other words a single animal can produce both eggs and sperm; if they are both produced at the same time, the animal is a simultaneous hermaphrodite, and if the eggs and sperm mature at different times, the animal is a sequential hermaphrodite. Fertilization is generally external, although platyctenids' eggs are fertilized inside their parents' bodies and kept there until they hatch. The young are generally planktonic and in most species look like miniature cydippids, gradually changing into the adult shape as they grow. The exceptions are the beroids, whose young are miniature beroids with large mouths and no tentacles, and the platyctenids, whose young live as cydippid-like plankton until they reach near-adult size, but then sink to the bottom and rapidly metamorphose into the adult form. In at least some species, juveniles are capable of reproduction before reaching the adult size and shape. The combination of hermaphroditism and early reproduction enables small populations to grow at an explosive rate.

Ctenophores may be abundant during the summer months in some coastal locations, but in other places they are uncommon and difficult to find. In bays where they occur in very high numbers, predation by ctenophores may control the populations of small zooplanktonic organisms such as copepods, which might otherwise wipe out the phytoplankton (planktonic plants), which are a vital part of marine food chains. One ctenophore, *Mnemiopsis*, has accidentally been introduced into the Black Sea, where it is blamed for causing fish stocks to collapse by eating both fish larvae and organisms that would otherwise have fed the fish. The situation was aggravated by other factors, such as over-fishing and long-term environmental changes that promoted the growth of the *Mnemiopsis* population. The later accidental introduction of *Beroe* helped to mitigate the problem, as *Beroe* preys on other ctenophores.

Despite their soft, gelatinous bodies, fossils thought to represent ctenophores, apparently with no tentacles but many more comb-rows than modern forms, have been found in lagerstätten as far back as the early Cambrian, about 525 million years ago. The position of the ctenophores in the evolutionary family tree of animals has long been debated, and the majority view at present, based on molecular phylogenetics, is that cnidarians and bilaterians are more closely related to each other than either is to ctenophores. A recent molecular phylogenetics analysis concluded that the common ancestor of all modern ctenophores was cydippid-like, and that all the modern groups appeared relatively recently, probably after the Cretaceous-Tertiary extinction 65.5 million years ago. Evidence accumulating since the 1980s indicates that the "cydippids" are not monophyletic, in other words do not include all and only the descendants of a single common ancestor, because all the other traditional ctenophore groups are descendants of various cydippids.

Distinguishing features

Ctenophores form an animal phylum that is more complex than sponges, about as complex as cnidarians (jellyfish, sea anemones, etc.), and less complex than bilaterians, which include almost all other animals. Unlike sponges, both ctenophores and cnidarians have: cells bound by inter-cell connections and carpet-like basement membranes; muscles; nervous systems; and some have sensory organs. Ctenophores are distinguished from all other animals by having colloblasts that capture prey by squirting glue on them, although a few ctenophore species lack them.

Like sponges and cnidarians, ctenophores have two main layers of cells that sandwich a middle layer of jelly-like material, which is called the mesoglea in cnidarians and ctenophores; more complex animals have three main cell layers and no intermediate jelly-like layer. Hence ctenophores and cnidarians have traditionally been labelled diploblastic, along with sponges. Both ctenophores and cnidarians have a type of muscle that, in more complex animals, arises from the middle cell layer, and as a result some recent text books classify ctenophores as triploblastic, while others still regard them as diploblastic.

Ranging from about 1 millimeter (0.039 in) to 1.5 meters (4.9 ft) in size, ctenophores are the largest non-colonial animals that use cilia ("hairs") as their main method of locomotion. Most species have eight strips, called comb rows, that run the length of their bodies and bear comb-like bands of cilia, called "ctenes," stacked along the comb rows so that when the cilia beat, those of each comb touch the comb below. The name "ctenophora" means "comb-bearing", from the Greek *κτείς* (stem-form κτεν-) meaning "comb" and the Greek suffix *-φορος* meaning "carrying".

Comparison with other major animal groups

	Sponges	**Cnidarians**	**Ctenophores**	**Bilateria**
Cnidocytes	No	Yes	No	
Colloblasts	No		In most species	No
Digestive and circulatory organs	No			Yes
Number of main cell layers	Two, with jelly-like layer between them		Debate about whether two or three	Three
Cells in each layer bound together	No, except that Homoscleromorpha have basement membranes.	Yes: Inter-cell connections; basement membranes		
Sensory organs	No	Yes		
Number of cells in middle "jelly" layer	Many	Few		(Not applicable)
Cells in outer layers can move inwards and change functions	Yes	No		(Not applicable)
Nervous system	No	Yes, simple		Simple to complex
Muscles	None	Mostly epitheliomuscular	Mostly myoepithelial	Mostly myocytes

Description

For a phylum with relatively few species, ctenophores have a wide range of body plans. Coastal species need to be tough enough to withstand waves and swirling sediment particles, while some oceanic species are so fragile that it is very difficult to capture them intact for study. In addition oceanic species do not preserve well, and are known mainly from photographs and from observers' notes. Hence most attention has until recently concentrated on three coastal genera — *Pleurobrachia*, *Beroe* and *Mnemiopsis*. At least two textbooks base their descriptions of ctenophores on the cydippid *Pleurobrachia*.

Since the body of many species is *almost* radially symmetrical, the main axis is oral to aboral (from the mouth to the opposite end). However since only two of the canals near the statocyst terminate in anal pores, ctenophores have no mirror-symmetery, although many have rotational symmetry, in other words if the animal rotates in a half-circle it looks the same as when it started.

Common features

Body layers

Like those of cnidarians, (jellyfish, sea anemones, etc.), ctenophores' bodies consist of a relatively thick, jelly-like mesoglea sandwiched between two epithelia, layers of cells bound by inter-cell connections and by a fibrous basement membrane that they secrete. The epithelia of ctenophores have two layers of cells rather than one, and some of the cells in the upper layer have several cilia per cell.

The outer layer of the epidermis (outer skin) consists of: sensory cells; cells that secrete mucus, which protects the body; and interstitial cells, which can transform into other types of cell. In specialized parts of the body the outer layer also contains colloblasts, found along the surface of tentacles and used in capturing prey, or cells bearing multiple large cilia, for locomotion. The inner layer of the epidermis contains a nerve net, and myoepithelial cells that act as muscles.

The internal cavity forms: a mouth that can usually be closed by muscles; a pharynx ("throat"); a wider area in the center that acts as a stomach; and a system of internal canals. These branch through the mesoglea to the most active parts of the animal: the mouth and pharynx; the roots of the tentacles, if present; all along the underside of each comb row; and four branches round the sensory complex at the far end from the mouth — two of these four branches terminate in anal pores. The inner surface of the cavity is lined with an epithelium, the gastrodermis. The mouth and pharynx have both cilia and well-developed muscles. In other parts of the canal system, the gastrodermis is different on the sides nearest to and furthest from the organ that it supplies. The nearer side is composed of tall nutritive cells that store nutrients in vacuoles (internal compartments), germ cells that produce eggs or sperm, and photocytes that produce bioluminescence. The side furthest from the organ is covered with ciliated cells that circulate water through the canals, punctuated by ciliary rosettes, pores that are surrounded by double whorls of cilia and connect to the mesoglea.

Feeding, excretion and respiration

When prey is swallowed, it is liquefied in the pharynx by enzymes and by muscular contractions of the pharynx. The resulting slurry is wafted through the canal system by the beating of the cilia, and digested by the nutritive cells. The ciliary rosettes in the canals may help to transport nutrients to muscles in the mesoglea. The anal pores may eject unwanted small particles, but most unwanted matter is regurgitated via the mouth.

Little is known about how ctenophores get rid of waste products produced by the cells. The ciliary rosettes in the gastrodermis may help to remove wastes from the mesoglea, and may also help to adjust the animal's buoyancy by pumping water into or out of the mesoglea.

Locomotion

The outer surface bears usually eight comb rows, which are used for swimming. The rows are oriented to run from near the mouth (the "oral pole") to the opposite end (the "aboral pole"), and are spaced more or less evenly around the body, although spacing patterns vary by species and in most species the comb rows extend only part of the distance from the aboral pole towards the mouth. The "combs" (also called "ctenes" or "comb plates") run across each row, and each consists of thousands of unusually long cilia, up to 2 millimeters (0.079 in). These normally beat so that the propulsion stroke is away from the mouth, although they can also reverse direction. Hence ctenophores usually swim in the direction in which the mouth is pointing, unlike jellyfish. When trying to escape predators, one species can accelerate to six times its normal speed; some other species reverse direction as part of their escape behavior, by reversing the power stroke of the comb plate cilia.

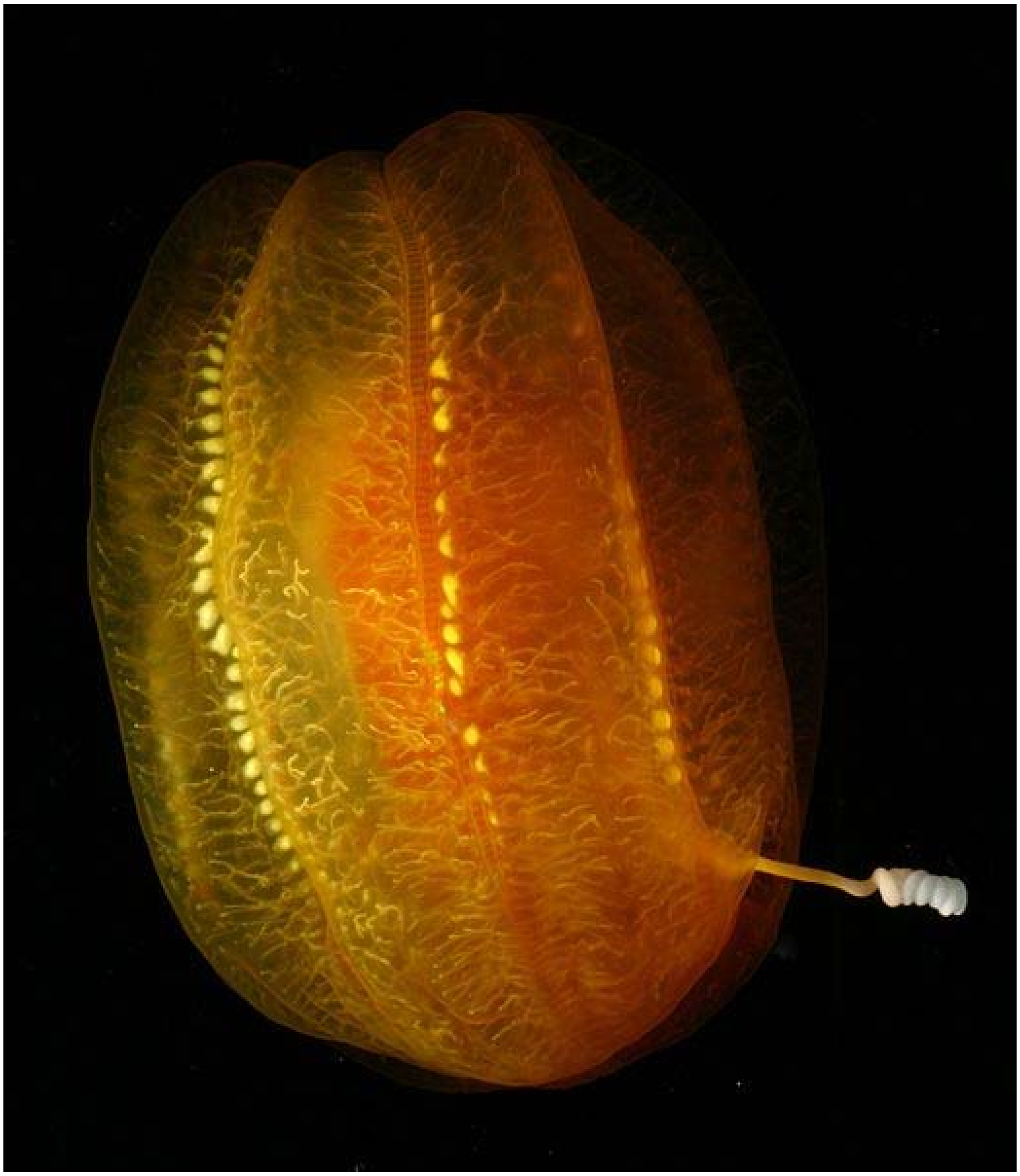
It is uncertain how ctenophores control their buoyancy, but experiments have shown that some species rely on osmotic pressure to adapt to water of different densities. Their body fluids are normally as concentrated as seawater. If they enter less dense brackish water, the ciliary rosettes in the body cavity may pump this into the mesoglea to increase its bulk and decrease its density, to avoid sinking. Conversely if they move from brackish to full-strength seawater, the rosettes may pump water out of the mesoglea to reduce its volume and increase its density.

Nervous system and senses

Ctenophores have no brain or central nervous system, but instead have a nerve net (rather like a cobweb) that forms a ring round the mouth and is densest near structures such as the comb rows, pharynx, tentacles (if present) and the sensory complex furthest from the mouth.

The largest single sensory feature is the aboral organ (at the opposite end from the mouth). Its main component is a statocyst, a balance sensor consisting of a statolith, a solid particle supported on four bundles of cilia, called "balancers", that sense its orientation. The statocyst is protected by a transparent dome made of long, immobile cilia. A ctenophore does not automatically try to keep the statolith resting equally on all the balancers. Instead its response is determined by the animal's "mood", in other words the overall state of the nervous system. For example if a ctenophore with trailing tentacles captures prey, it will often put some comb rows into reverse, spinning the mouth towards the prey.

Cydippids



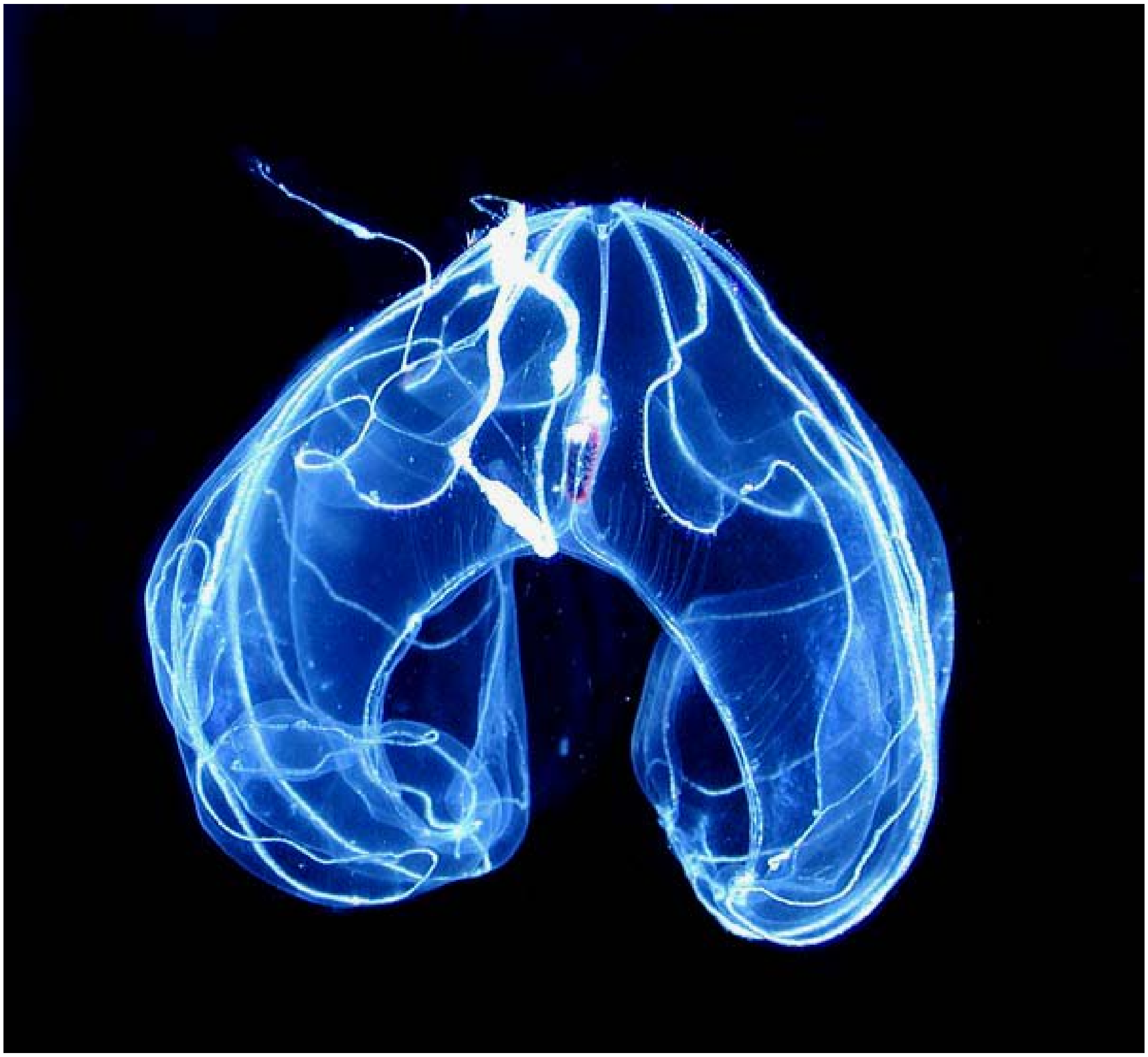
Aulacoctena sp., a cydippid ctenophore

Cydippid ctenophores have bodies that are more or less rounded, sometimes nearly spherical and other times more cylindrical or egg-shaped; the common coastal "sea gooseberry," *Pleurobrachia*, sometimes has an egg-shaped body with the mouth at the narrow end, although some individuals are more uniformly round. From opposite sides of the body extends a pair of long, slender tentacles, each housed in a sheath into which it can be withdrawn. Some species of cydippids have bodies that are flattened to various extents, so that they are wider in the plane of the tentacles.

The tentacles of cydippid ctenophores are typically fringed with tentilla ("little tentacles"), although a few genera have simple tentacles without these sidebranches. The tentacles and tentilla are densely covered with microscopic colloblasts that capture prey by sticking to it. Colloblasts are specialized mushroom-shaped cells in the outer layer of the epidermis, and have three main components: a domed head with vesicles (chambers) that contain adhesive; a stalk that anchors the cell in the lower layer of the epidermis or in the mesoglea; and a spiral thread that coils round the stalk and is attached to the head and to the root of the stalk. The function of the spiral thread is uncertain, but it may absorb stress when prey tries to escape, and thus prevent the collobast from being torn apart. In addition to colloblasts, members of the genus *Haeckelia*, which feed mainly on jellyfish, incorporate their victims' stinging nematocytes into their own tentacles — some cnidaria-eating nudibranchs similarly incorporate nematocytes into their bodies for defense. The tentilla of *Euplokamis* differ significantly from those of other cydippids: they contain striated muscle, a cell type otherwise unknown in the phylum Ctenophora; and they are coiled when relaxed, while the tentilla of all other known ctenophores elongate when relaxed. *Euplokamis'* tentilla have three types of movement that are used in capturing prey: they may flick out very quickly (in 40 to 60 milliseconds); they can wriggle, which may lure prey by behaving like small planktonic worms; and they coil round prey. The unique flicking is an uncoiling movement powered by contraction of the striated muscle. The wriggling motion is produced by smooth muscles, but of a highly specialized type. Coiling around prey is accomplished largely by the return of the tentilla to their inactive state, but the coils may be tightened by smooth muscle.

There are eight rows of combs that run from near the mouth to the opposite end, and are spaced evenly round the body. The "combs" beat in a metachronal rhythm rather like that of a Mexican wave. From each balancer in the statocyst a ciliary groove runs out under the dome and then splits to connect with two adjacent comb rows, and in some species runs all the way along the comb rows. This forms a *mechanical* system for transmitting the beat rhythm from the combs to the balancers, via water disturbances created by the cilia.

Lobates



Bathocyroe fosteri a common but fragile deep-sea lobate, oriented mouth down

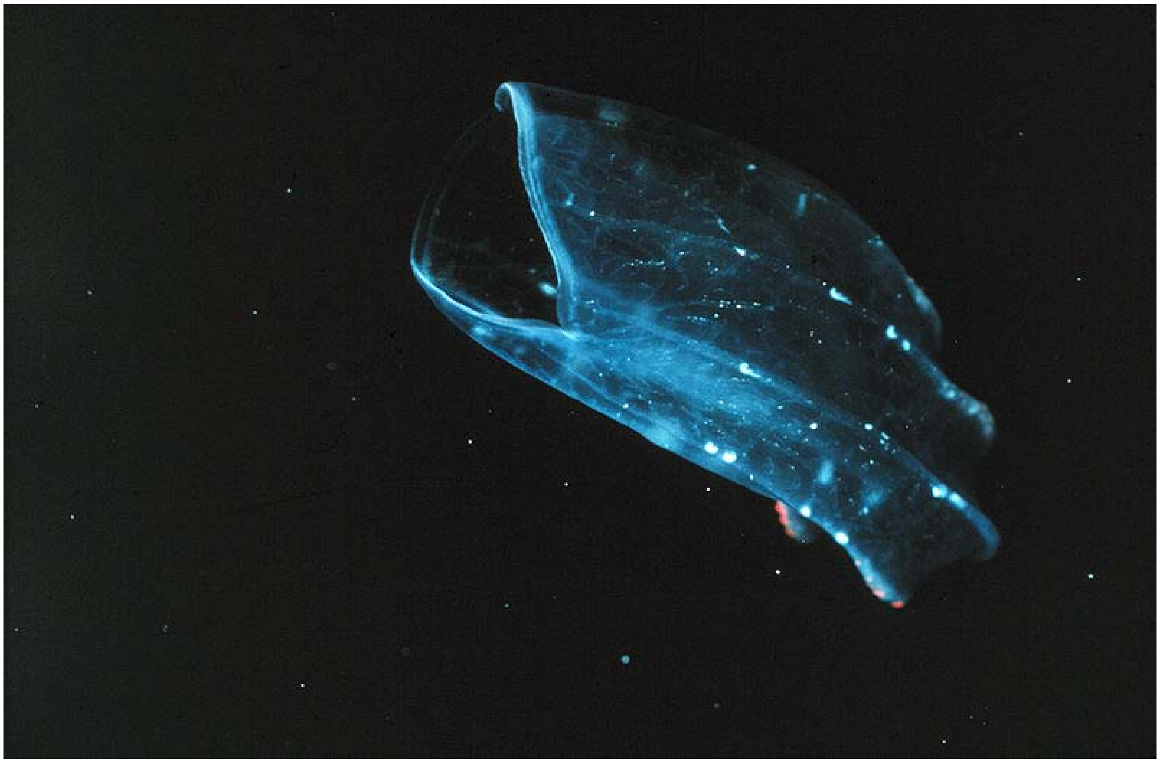
The Lobata have a pair of lobes, which are muscular, cuplike extensions of the body that project beyond the mouth. Their inconspicuous tentacles originate from the corners of the mouth, running in convoluted grooves and spreading out over the inner surface of the lobes (rather than trailing far behind, as in the Cydippida). Between the lobes on either side of the mouth, many species of lobates have four auricles, gelatinous projections edged with cilia that produce water currents that help direct microscopic prey toward the mouth. This combination of structures enables lobates to feed continuously on suspended planktonic prey.

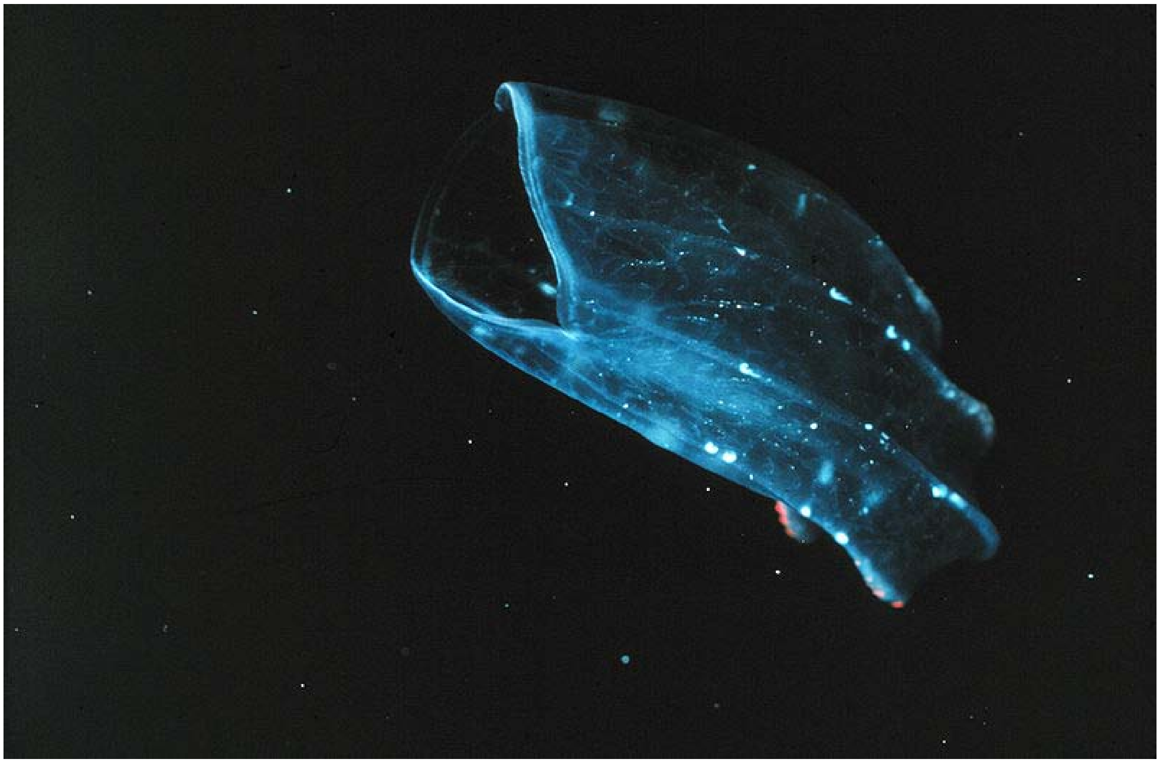
Lobates have eight comb-rows, originating at the aboral pole and usually not extending beyond the body to the lobes; in species with (four) auricles, the cilia edging the auricles are extensions of cilia in four of the comb rows. Most lobates are quite passive when moving through the water, using the cilia on their comb rows for propulsion, although

Leucothea has long and active auricles whose movements also contribute to propulsion. Members of the lobate genera *Bathocyroe* and *Ocyropsis* can escape from danger by clapping their lobes, so that the jet of expelled water drives them backwards very quickly. Unlike cydippids, the movements of lobates' combs are coordinated by nerves rather than by via water disturbances created by the cilia, yet combs on the same row beat beat in the same Mexican wave style as the mechanically-coordinated comb rows of cydippids and beroids. This may have enabled lobates to grow larger than cydippids and to have shapes that are less egg-like.

An unusual species first described in 2000, *Lobatolampea tetragona*, has been classified as a lobate, although the lobes are "primitive" and the body is medusa-like when floating and disk-like when resting on the sea-bed.

Beroids





Beroe sp. swimming with open mouth, at left. This animal is 3–6 cm long.

The Beroida, also known as Nuda, have no feeding appendages, but their large pharynx, just inside the large mouth and filling most of the saclike body, bears "macrocilia" at the oral end. These fused bundles of several thousand large cilia are able to "bite" off pieces of prey that is too large to swallow whole — almost always other ctenophores. In front of the field of macrocilia, on the mouth "lips" in some species of *Beroe*, is a pair of narrow strips of adhesive epithelial cells on the stomach wall that "zip" the mouth shut when the animal is not feeding, by forming intercellular connections with the opposite adhesive strip. This tight closure streamlines the front of the animal when it is pursuing prey.

Other body forms

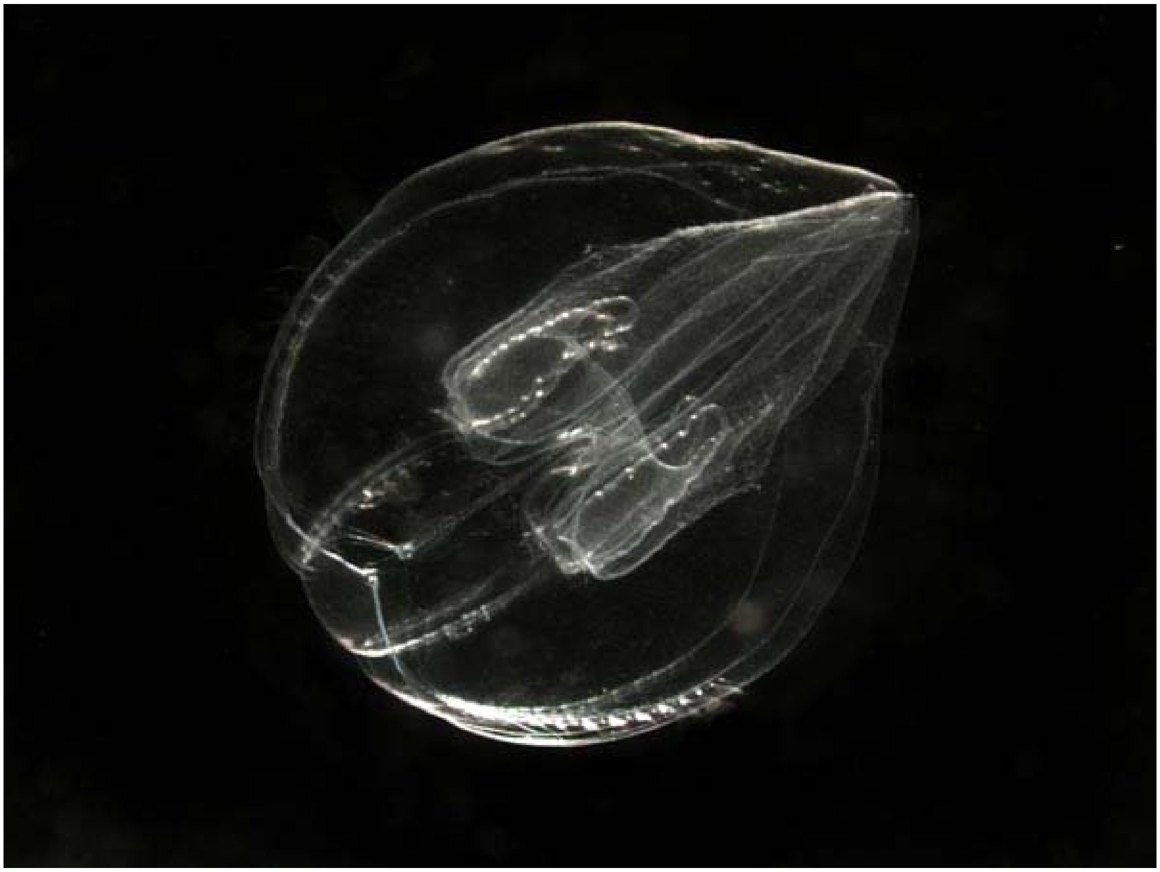
The Ganeshida have a pair of small oral lobes and a pair of tentacles. The body is circular rather than oval in cross-section, and the pharynx extends over the inner surfaces of the lobes.

The Thalassocalycida, only discovered in 1978 and known from only one species, are medusa-like, with bodies that are shortened in the oral-aboral direction, and short comb-rows on the surface furthest from the mouth, originating from near the aboral pole. They capture prey by movements of the bell and possibly by using two short tentacles.

The Cestida ("belt animals") are ribbon-shaped planktonic animals, with the mouth and aboral organ aligned in the middle of opposite edges of the ribbon. There is a pair of comb-rows along each aboral edge, and tentilla emerging from a groove all along the oral edge, which stream back across most of the wing-like body surface. Cestids can swim by undulating their bodies as well as by the beating of their comb-rows. There are two known species, with worldwide distribution in warm, and warm-temperate waters: *Cestum veneris* ("Venus' girdle") is among the largest ctenophores — up to 1.5 meters (4.9 ft) long, and can undulate slowly or quite rapidly. *Velamen parallelum*, which is typically less than 20 centimeters (0.66 ft) long, can move much faster in what has been described as a "darting motion".

Most Platyctenida have oval bodies that are flattened in the oral-aboral direction, with a pair of tentilla-bearing tentacles on the aboral surface. They cling to and creep on surfaces by everting the pharynx and using it as a muscular "foot". All but one of the known platyctenid species lack comb-rows. Platyctenids are usually cryptically-colored, live on rocks, algae, or the body surfaces of other invertebrates, and are often revealed by their long tentacles with many sidebranches, seen streaming off the back of the ctenophore into the current.

Reproduction and development



Cydippid larva of *Bolinopsis* sp., a few mm long.

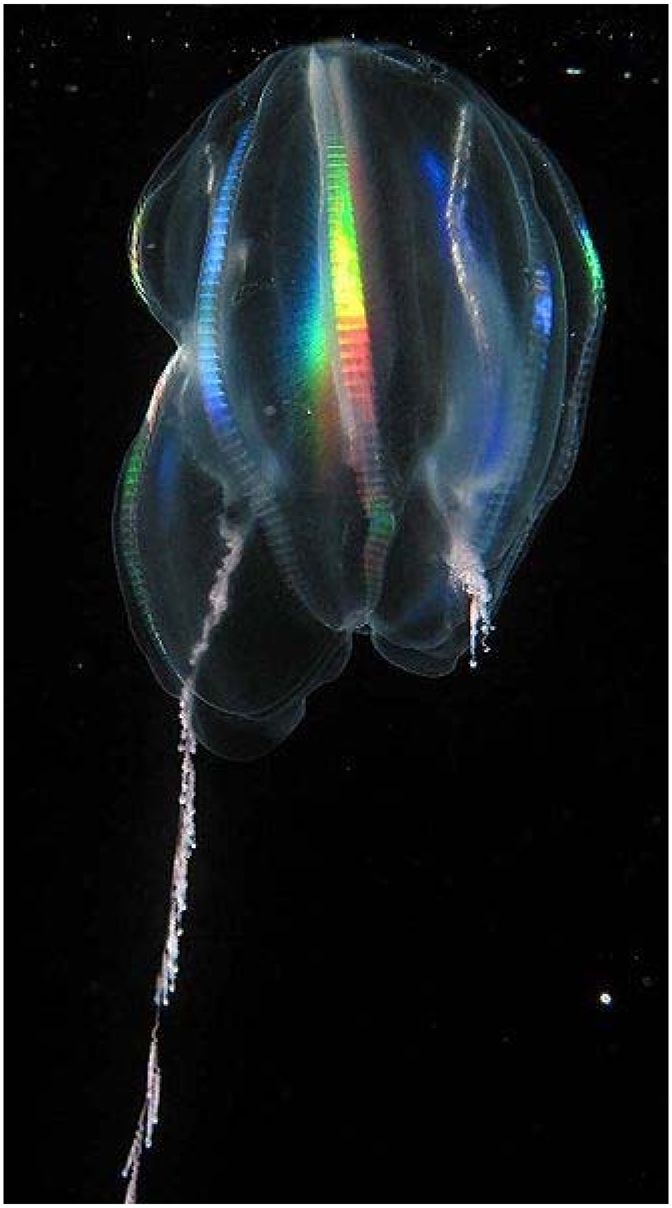
Adults of most species can regenerate tissues that are damaged or removed, although only platyctenids reproduce by cloning, splitting off from the edges of their flat bodies fragments that develop into new individuals.

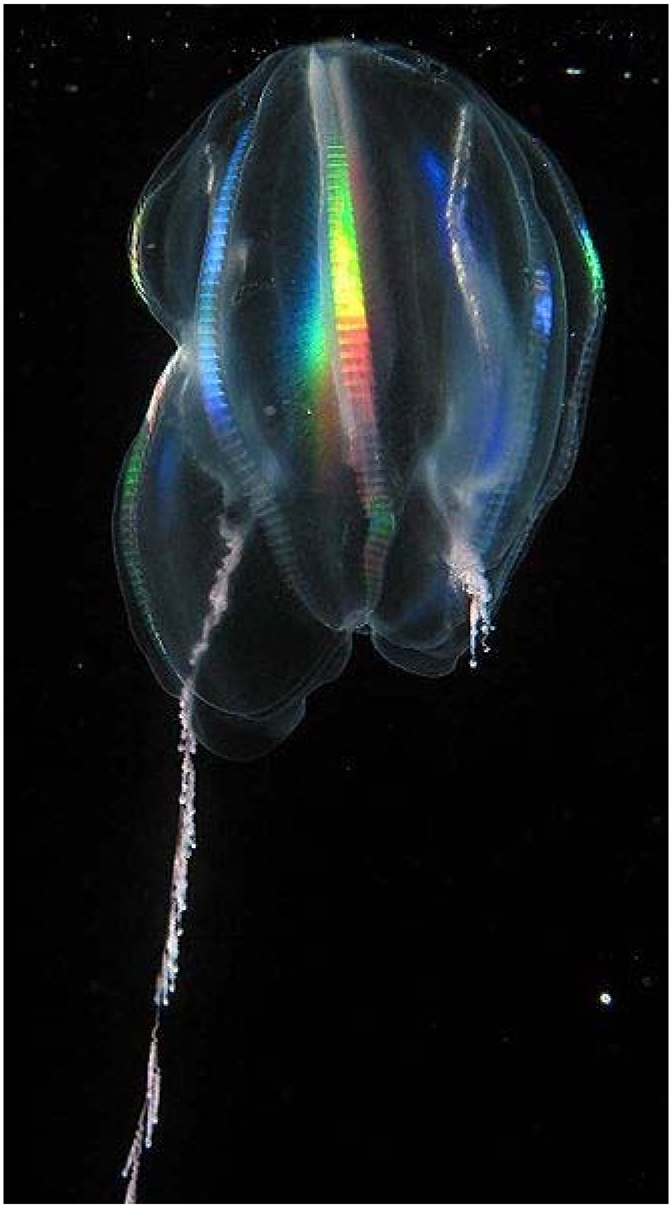
Almost all species are hermaphrodites, in other words they function as both males and females at the same time — except that in two species of the genus *Ocryopsis* individuals remain of the same single sex all their lives. The gonads are located in the parts of the internal canal network under the comb rows, and eggs and sperm are released via pores in the epidermis. Fertilization is external in most species, but platyctenids use internal fertilization and keep the eggs in brood chambers until they hatch. Self-fertilization has occasionally been seen in species of the genus *Mnemiopsis*, and it is thought that most of the hermaphroditic species are self-fertile.

Development of the fertized eggs is direct, in other words there is no distinctive larval form, and juveniles of all groups generally resemble miniature cydippid adults. In the genus *Beroe* the juveniles, like the adults, lack tentacles and tentacle sheaths. In most species the juveniles gradually develop the body forms of their parents. In some groups, such as the flat, bottom-dwelling platyctenids, the juveniles behave more like true larvae, as they live among the plankton and thus occupy a different ecological niche from their parents and attain the adult form by a more radical metamorphosis, after dropping to the sea-floor.

At least in some species, juvenile ctenophores appear capable of producing small quantities of eggs and sperm while they are well below adult size, and adults produce eggs and sperm for long as they have sufficient food. If they run short of food, they first stop producing eggs and sperm, and then shrink in size. When the food supply improves, they grow back to normal size and then resume reproduction. These features make ctenophores capable of increasing their populations very quickly.

Colors and bioluminescence





Light diffracting along the comb rows of a *Mertensia ovum*. The right lower portion of the body is regenerating from previous damage.

Undescribed deep-sea species known as "Tortugas red", with trailing tentacles and clearly visible tentilla

Most ctenophores that live near the surface are mostly colorless and almost transparent. However some deeper-living species are strongly pigmented, for example the species known as "Tortugas red", which has not yet been formally described. Platyctenids generally live attached to other sea-bottom organisms, and often have similar colors to these host organisms. The gut of the deep-sea genus *Bathocyroe* is red, which hides the bioluminescence of copepods it has swallowed.

The comb rows of most planktonic ctenophores produce a rainbow effect, which is not caused by bioluminescence but by the scattering of light as the combs move. Most species are also bioluminescent, but the light is usually blue or green and can only been seen in darkness. However some significant groups, including all known platyctenids and the cydippid genus *Pleurobrachia*, are incapable of bioluminescence.

When some species, including *Bathyctena chuni*, *Euplokamis stationis* and *Eurhamphaea vexilligera*, are disturbed, they produce secretions (ink) that luminesce at much the same wavelengths as their bodies. Juveniles will luminesce more brightly in relation to their body size than adults, whose luminescence is diffused over their bodies. Detailed statistical investigation has not suggested the function of ctenophores' bioluminescence nor produced any correlation between its exact color and any aspect of the animals' environments, such as depth or whether they live in coastal or mid-ocean waters.

Ecology

Distribution

Ctenophores are found in most marine environments: from polar waters to the tropics; near coasts and in mid-ocean; from the surface waters to the ocean depths. The best-understood are the genera *Pleurobrachia*, *Beroe* and *Mnemiopsis*, as these planktonic coastal forms are among the most likely to be collected near shore. No ctenophores have been found in fresh water.

Prey and predators

Almost all ctenophores are predators — there are no vegetarians and only one genus that is partly parasitic. If food is plentiful, they can eat 10 times their own weight per day. While *Beroe* preys mainly on other ctenophores, other surface-water species prey on zooplankton (planktonic animals) ranging in size from the microscopic, including mollusc and fish larvae, to small adult crustaceans such as copepods, amphipods, and even krill. Members of the genus *Haeckelia* prey on jellyfish and incorporate their prey's nematocysts (stinging cells) into their own tentacles instead of colloblasts. Ctenophores have been compared to spiders in their wide range of techniques from capturing prey — some hang motionless in the water using their tentacles as "webs", some are ambush predators like Salticid jumping spiders, and some dangle a sticky droplet at the end of a fine thread, as Bola spiders do. This variety explains the wide range of body forms in a phylum with rather few species. The two-tentacled "cydippid" *Lampea* feeds exclusively on salps, close relatives of sea-squirts that form large chain-like foating colonies, and juveniles of *Lampea* attach themselves like parasites to salps that are too large for them to swallow. Members of the cydippid genus *Pleurobrachia* and the lobate *Bolinopsis* often reach high population densities at the same place and time because they specialize in different types of prey: *Pleurobrachia'*s long tentacles mainly capture relatively strong swimmers such as adult copepods, while *Bolinopsis* generally feeds on smaller, weaker swimmers such as rotifers and mollusc and crustacean larvae.

Ctenophores used to be regarded as "dead ends" in marine food chains because it was thought their low ratio of organic matter to salt and water made them a poor diet for other animals. It is also often difficult to identify the remains of ctenophores in the guts of possible predators, although the combs sometimes remain intact long enough to provide a clue. Detailed investigation of chum salmon, *Oncorhynchus keta*, showed that these fish digest ctenophores 20 times as fast as an equal weight of shrimps, and that ctenophores can provide a good diet if there are enough of them around. Beroids prey mainly on other ctenophores. Some jellyfish and turtles eat large quantities of ctenophores, and jellyfish may temporarily wipe out ctenophore populations. Since ctenophores and jellyfish often have large seasonal variations in population, most fish that prey on them are generalists, and may have a greater effect on populations than the specialist jelly-eaters. The larvae of some sea anemones are parasites on ctenophores, as are the larvae of some flatworms that parasitize fish when they reach adulthood.

Ecological impacts

Beroe ovata at the surface on the Black Sea coast

Ctenophores may balance marine ecosystems by preventing an over-abundance of copepods from eating all the phytoplankton (planktonic plants), which are the dominant marine producers of organic matter from non-organic ingredients.

On the other hand in the late 1980s the North Atlantic ctenophore *Mnemiopsis leidyi* was accidentally introduced into the Black Sea and Sea of Azov via the ballast tanks of ships, and has been blamed for causing sharp drops in fish catches by eating both fish larvae and small crustaceans that would otherwise feed the adult fish. *Mnemiopsis* is well-equipped to invade new territories, as it can breed very rapidly and tolerate a wide range of water temperatures and salinities. The impact was increased by chronic overfishing, and by eutrophication that gave the entire ecosystem a short-term boost, causing the

Mnemiopsis population to increase even faster than normal — and above all by the absence of efficient predators on ctenophores. *Mnemiopsis* populations in those areas were eventually brought under control by the accidental introduction of the ctenophore-eating ctenophore *Beroe*, and by a cooling of the local climate from 1991 to 1993, which significantly slowed the animal's metabolism. However the abundance of plankton in the area seems unlikely to reach pre-*Mnemiopsis* levels.

In the late 1990s *Mnemiopsis* appeared in the Caspian Sea. *Beroe* arrived shortly after, and is expected to reduce but not eliminate the impact of *Mnemiopsis*. *Mnemiopsis* also reached the eastern Mediterranean in the late 1990s and now appears to be thriving in the North Sea and Baltic Sea.

Classification

The number of known living ctenophore species is uncertain, since many of those named and formally described have turned out to be identical to species known under other scientific names. Claudia Mills estimates that there about 100 to 150 valid species that are not duplicates, and that at least another 25, mostly deep-sea forms, have been recognized as distinct but not yet analyzed in enough detail to support a formal description and naming.

The traditional classification divides ctenophores into two classes, those with tentacles (Tentaculata) and those without (Nuda). The Nuda contains only one order (Beroida) and family (Beroidae), and two genera, *Beroe* (several species) and *Neis* (one species).

The Tentaculata are divided into the following eight orders:

- Cydippida, egg-shaped animals with long tentacles
- Lobata, with paired thick lobes
- Platyctenida, flattened animals that live on or near the sea-bed; most lack combs as adults, and use their pharynges as suckers to attach themselves to surfaces
- Ganeshida, with a pair of small lobes round the mouth, but an extended pharynx like that of platyctenids
- Cambojiida
- Cryptolobiferida
- Thalassocalycida, with short tentacles and a jellyfish-like "umbrella"
- Cestida, ribbon-shaped and the largest ctenophores

Evolutionary history

Fossil record

Because of their soft, gelatinous bodies, ctenophores are extremely rare as fossils, and fossils that have been interpreted as ctenophores have been found only in lagerstätten, places where the environment was exceptionally suited to preservation of soft tissue. Until the mid-1990s only two specimens good enough for analysis were known, both from the early Devonian period. Three additional putative species were then found in the Burgess Shale and other Canadian rocks of similar age, about 505 million years ago in the mid-Cambrian period. All three apparently lacked tentacles but had between 24 and 80 comb rows, far more than the 8 typical of living species. They also appear to have had internal organ-like structures unlike anything found in living ctenophores. One of the fossil species first reported in 1996 had a large mouth, apparently surrounded by a folded edge that may have been muscular. Evidence from China a year later suggests that such ctenophores were widespread in the Cambrian, but perhaps very different from modern species — for example one fossil's comb-rows were mounted on prominent vanes.

The early Cambrian sessile frond-like fossil *Stromatoveris*, from China's Chengjiang lagerstätte and dated to about 525 million years ago, is very similar to Vendobionta of the preceding Ediacaran period. De-Gan Shu, Simon Conway Morris *et al.* found on its branches what they considered rows of cilia, used for filter feeding. They suggested that *Stromatoveris* was an evolutionary "aunt" of ctenophores, and that ctenophores originated from sessile animals whose descendants became swimmers and changed the cilia from a feeding mechanism to a propulsion system.

Family tree

It is difficult to reconstruct the early stages in the evolutionary "family tree" of animals using only morphology (their shapes and structures), because the large differences between Porifera (sponges), Cnidaria (jellyfish, sea anemones, etc.), Ctenophora, Placozoa and Bilateria (all the more complex animals) make comparisons difficult. Hence reconstructions now rely largely or entirely on molecular phylogenetics, which groups organisms according to similarities and differences in their biochemistry, usually in their DNA or RNA.

It is now generally thought that the Calcarea (sponges with calcium carbonate spicules) are more closely related to Cnidaria, Ctenophora (comb jellies) and Bilateria (all the more complex animals) than they are to the other groups of sponges. In 1866 it was proposed that Cnidaria and Ctenophora were more closely related to each other than to Bilateria and formed a group called Coelenterata ("hollow guts"), because Cnidaria and Ctenophora both rely on the flow of water in and out of a single cavity for feeding, excretion and respiration. In 1881 it was proposed that Ctenophora and Bilateria were more closely related to each other, since they shared features that Cnidaria lack, for example muscles in the middle layer (mesoglea in Ctenophora, mesoderm in Bilateria). More recent analyses indicate that these similarities are rather vague, and the current view, based on molecular phylogenetics, is that Cnidaria and Bilateria are more closely related to each other than either is to Ctenophora. This grouping of Cnidaria and Bilateria has been labelled "Planulozoa" because it suggests that the earliest Bilateria were similar to the planula larvae of Cnidaria.

In 2005 Katja Seipel and Volker Schmid suggested that cnidarians and ctenophores are simplified descendants of triploblastic animals, since ctenophores and the medusa stage of some cnidarians have striated muscle, which in bilaterians arises from the mesoderm.

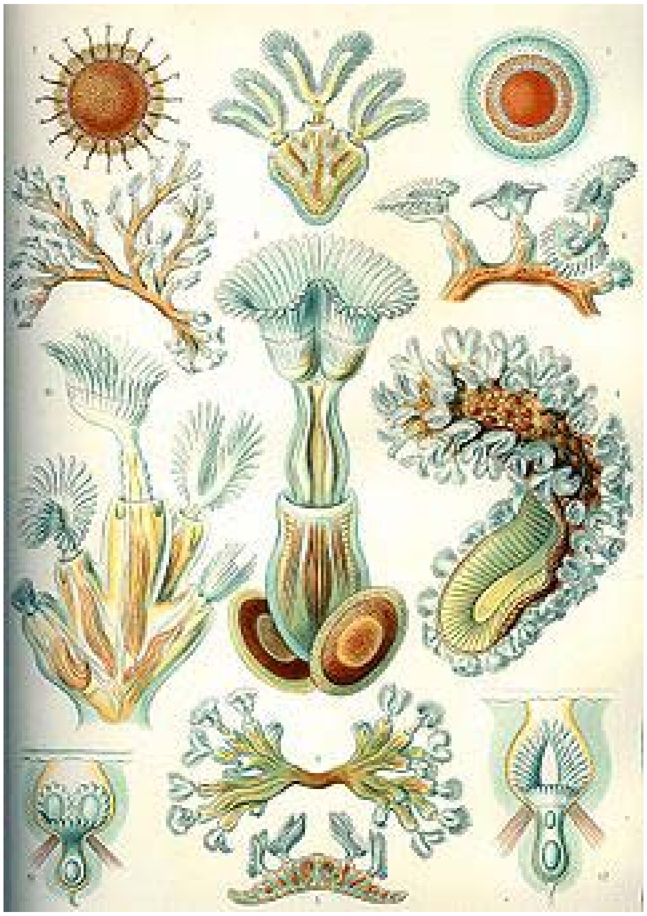
They did not commit themselves on whether bilaterians evolved from early cnidarians or from the hypothesized triploblastic ancestors of cnidarians. A study in 2008 of 150 genes in 21 genera proposed a third hypothesis, that sponges and cnidarians are more closely related to each other than either is to ctenophores.

Since all modern ctenophores except the beroids have cydippid-like larvae, it has widely been assumed that their last common ancestor also resembled cydippids, having an egg-shaped body and a pair of retractable tentacles. Richard Harbison's purely morphological analysis in 1985 concluded that the cydippids are not monophyletic, in other words do not contain all and only the descendants of a single common ancestor that was itself a cydippid. Instead he found that various cydippid families were more similar to members of other ctenophore orders than to other cydippids. He also suggested that the last common ancestor of modern ctenophores was either cydippid-like or beroid-like. A molecular phylogeny analysis in 2001, using 26 species including 4 recently-discovered ones, concluded that the cydippids are not monophyletic and that the last common ancestor of modern ctenophores was cydippid-like. It also found that the genetic differences between these species were very small — so small that the relationships between the Lobata, Cestida and Thalassocalycida remained uncertain. This suggests that the last common ancestor of modern ctenophores was relatively recent, and perhaps was lucky enough to survive the Cretaceous-Tertiary extinction 65.5 million years ago while other lineages perished. When the analysis was broadened to include representatives of other phlya, it concluded that cnidarians are probably more closely related to bilaterians than either group is to ctenophores but that this diagnosis is uncertain.

Chapter 8

Bryozoa

Bryozoa
Temporal range: Upper Cambrian–Recent



"Bryozoa", from Ernst Haeckel's *Kunstformen der Natur*, 1904

Scientific classification [e]

Kingdom:	Animalia

Superphylum:	Lophotrochozoa
Phylum:	**Bryozoa** Ehrenberg, 1831

Synonyms

Ectoprocta (Nitsche, 1869)

The **Bryozoa**, also known as **Ectoprocta** or commonly as **moss animals**, are a phylum of aquatic invertebrate animals. Typically about 0.5 millimetres (0.020 in) long, they are filter feeders that sieve food particles out of the water using a retractable lophophore, a "crown" of tentacles lined with cilia. Most marine species live in tropical waters, but a few occur in oceanic trenches, and others are found in polar waters. One class lives only in a variety of freshwater environments, and a few members of a mostly marine class prefer brackish water. Over 4,000 living species are known. One genus is solitary and the rest colonial.

The phylum was originally called "Polyzoa", but this term was superseded by "Bryozoa" in 1831. Another group of animals discovered subsequently, whose filtering mechanism looked similar, was also included in "Bryozoa" until 1869, when the two groups were noted to be very different internally. The more recently discovered group were given the name Entoprocta, while the original "Bryozoa" were called "Ectoprocta". However, "Bryozoa" has remained the more widely used term for the latter group.

Individuals in bryozoan (ectoproct) colonies are called ***zooids***, since they are not fully-independent animals. All colonies contain autozooids, which are responsible for feeding and excretion. Colonies of some classes have various types of non-feeding specialist zooids, some of which are hatcheries for fertilized eggs, and some classes also have special zooids for defense of the colony. The class Cheilostomata have the largest number of species, possibly because they have the widest range of specialist zooids. A few species can creep very slowly by using spiny defensive zooids as legs. Autozooids supply nutrients to non-feeding zooids by channels that vary between classes. All zooids, including those of the solitary species, consist of a *cystid* that provides the body wall and produces the exoskeleton and a *polypide* that contains the internal organs and the lophophore or other specialist extensions. Zooids have no special excretory organs, and the polypides of autozooids are scrapped when the polypides become overloaded by waste products; usually the body wall then grows a replacement polypide. In autozooids the gut is U-shaped, with the mouth inside the "crown" of tentacles and the anus outside it. Colonies take a variety of forms, including fans, bushes and sheets. The Cheilostomata produce mineralized exoskeletons and form single-layered sheets that encrust over surfaces.

Zooids of all the freshwater species are simultaneous hermaphrodites. Although those of many marine species function first as males and then as females, their colonies always contain a combination of zooids that are in their male and female stages. All species emit sperm into the water. Some also release ova into the water, while others capture sperm via their tentacles to fertilize their ova internally. In some species the larvae have large yolks, go to feed, and quickly settle on a surface. Others produce larvae that have little yolk but swim and feed for a few days before settling. After settling, all larvae undergo a radical metamorphosis that destroys and rebuilds almost all the internal tissues. Freshwater species also produce statoblasts that lie dormant until conditions are favorable, which enables a colony's lineage to survive even if severe conditions kill the mother colony.

Predators of marine bryozoans include nudibranchs (sea slugs), fish, sea urchins, pycnogonids, crustaceans, mites and starfish. Freshwater bryozoans are preyed on by snails, insects, and fish. In Thailand, many populations of one freshwater species have been wiped out by an introduced species of snail. A fast-growing invasive bryozoan off the northeast and northwest coasts of the USA has reduced kelp forests so much that it has affected local fish and invertebrate populations. Bryozoans have spread diseases to fish farms and fishermen. Chemicals extracted from a marine bryozoan species have been investigated for treatment of cancer and Alzheimer's Disease, but analyses have not been encouraging.

Mineralized skeletons of bryozoans appear in rocks from Early Ordovician period, about 480 million years ago, while all other fossilized phyla appear in earlier periods. This has led researchers to suspect that bryozoans had arisen earlier but were initially unmineralized, and may have differed significantly from fossilized and modern forms. Early fossils are mainly of erect forms, but encrusting forms gradually became dominant. It is uncertain whether the phylum is monophyletic. Bryozoans' evolutionary relationships to other phyla are also unclear, partly because scientists' view of the family tree of animals is mainly influenced by better-known phyla. Both morphological and molecular phylogeny analyses disagree over bryozoans' relationships with entoprocts, about whether bryozoans should be grouped with brachiopods and phoronids in Lophophorata, and whether bryozoans should be considered protostomes or deuterostomes.

Description

Distinguishing features

Freshwater bryozoan with lophophore extended

Bryozoans, phoronids and brachiopods strain food out of the water by means of a lophophore, a "crown" of hollow tentacles. Bryozoans form colonies consisting of clones called zooids that are typically about 0.5 millimetres (0.020 in) long. Phoronids resemble bryozoan zooids but are 2 to 20 centimetres (0.79 to 7.9 in) long and, although they often grow in clumps, do not form colonies consisting of clones. Brachiopods, generally thought to be closely related to bryozoans and phoronids, are distinguished by having shells rather like those of bivalves. All three of these phyla have a coelom, an internal cavity lined by mesothelium. Some encrusting bryozoan colonies with mineralized exoskeletons look very like small corals. However, bryozoan colonies are founded by an ancestrula, which is round rather than shaped like a normal zooid of that species. On the other hand the founding polyp of a coral has a shape like that of its daughter polyps, and coral zooids have no coelom or lophophore.

Entoprocts, another phylum of filter-feeders, look rather like bryozoans but their lophophore-like feeding structure has solid tentacles, their anus lies inside rather than outside the base of the "crown" and they have no coelom.

Summary of distinguishing features

		Other lophophorates		Other Lophotrochozoa	Similar-looking phyla	
	Bryozoa (Ectoprocta)	Phoronida	Brachiopoda	Annelida, Mollusca	Entoprocta	Corals (class in phylum Cnidaria)
Coelom	Three-part, if the cavity of the epistome is included	Three-part		One per segment in basic form; merged in some taxa	none	
Formation of coelom	Uncertain because metamorphosis of larvae into adults makes this impossible to trace	Enterocoely		Schizocoely	not applicable	
Lophophore	With hollow tentacles			none	Similar-looking feeding structure, but with solid tentacles	none
Feeding current	From tips to bases of tentacles			not applicable	From bases to tips of tentacles	not applicable
Multiciliated cells in epithelium	Yes	no		Yes		not applicable
Position of anus	Outside base of lophophore		Varies, none in some species	Rear end, but none in Siboglinidae	Inside base of lophophore-like organ	none
Colonial	Colonies of clones in most; one solitary genus	Sessile species often form clumps, but with no active co-operation			Colonies of clones in some species; some solitary species	Colonies of clones
Shape of founder zooid	Round, unlike normal zooids	not applicable			Same as other zooids	
Mineralized exoskeletons	Some taxa	no	Bivalve-like shells	Some sessile annelids build	no	Some taxa

mineralized tubes;
most molluscs have
shells, but most
modern cephalopods
have internal shells
or none.

Types of zooid

All bryozoans are colonial except for one genus, *Monobryozoon*. Individual members of a bryozoan colony are about 0.5 millimetres (0.020 in) long and are known as *zooids*, since they are not fully-independent animals. All colonies contain feeding zooids, known as autozooids, and those of some groups also contain non-feeding specialist heterozooids; colony members are genetically identical and co-operate, rather like the organs of larger animals. What type of zooid grows where in a colony is determined by chemical signals from the colony as a whole or sometimes in response to the scent of predators or rival colonies.

The bodies of all types have two main parts. The *cystid* consists of the body wall and whatever type of exoskeleton is secreted by the epidermis. The exoskeleton may be organic (chitin, polysaccharide or protein) or made of the mineral calcium carbonate. The body wall consists of the epidermis, basal lamina (a mat of non-cellular material), connective tissue, muscles, and the mesothelium which lines the coelom (main body cavity) – except that in one class, the mesothelium is split into two separate layers, the inner one forming a membranous sac that floats freely and contains the coelom, and the outer one attached to the body wall and enclosing the membranous sac in a pseudocoelom. The other main part of the bryozoan body, known as the *polypide* and situated almost entirely within the cystid, contains the nervous system, digestive system, some specialized muscles and the feeding apparatus or other specialized organs that take the place of the feeding apparatus.

Feeding zooids

The most common type of zooid is the feeding autozooid, in which the polypide bears a "crown" of hollow tentacles called a lophophore, which captures food particles from the water. In all colonies a large percentage of zooids are autozooids, and some consist entirely of autozooids, some of which also engage in reproduction.

The basic shape of the "crown" is a full circle. In the class Phylactolaemata the crown appears U-shaped, but this impression is created by a deep dent in the rim of the crown, which has no gap in the fringe of tentacles. The sides of the tentacles bear fine hairs called cilia, whose beating drives a water current from the tips of the tentacles to their bases, where it exits. Food particles that collide with the tentacles are trapped by mucus, and further cilia on the inner surfaces of the tentacles convey the particles towards the mouth, which lies in the center of the base of the "crown". The method used by ectoprocts is known as "upstream collecting", as food particles are captured before they pass through the field of cilia that creates the feeding current. This method is also used by phoronids, brachiopods and pterobranchs.

The lophophore and mouth are mounted on a flexible tube, called the "invert" because it can be turned inside-out and withdrawn into the polypide, rather like the finger of a rubber glove; in this position the lophophore lies inside the invert and is folded like the spokes of an umbrella. The invert is withdrawn, sometimes within 60 milliseconds, by a pair of retractor muscles that are anchored at the far end of the cystid. Sensors at the tips of the tentacles may check for signs of danger before the invert and lophophore are fully extended. Extension is driven by an increase in internal fluid pressure, which species with flexible exoskeletons produce by contracting circular muscles that lie just inside the body wall, while species with a membranous sac use circular muscles to squeeze this. Some species with rigid exoskeletons have a flexible membrane that replaces part of the exoskeleton, and transverse muscles anchored on the far side of the exoskeleton increase the fluid pressure by pulling the membrane inwards. In others there is no gap in the protective skeleton, and the transverse muscles pull on a flexible sac which is connected to the water outside by a small pore; the expansion of the sac increases the pressure inside the body and pushes the invert and lophophore out. In some species the retracted invert and lophophore are protected by an operculum ("lid"), which is closed by muscles and opened by fluid pressure. In one class, a hollow lobe called the "epistome" overhands the mouth.

The gut is U-shaped, running from the mouth, in the center of the lophophore, down into the animal's interior and then back to the anus, which is located on the invert, outside and usually below the lophophore. A network of strands of mesothelium called "funiculi" ("little ropes") connects the mesothelium covering the gut with that lining the body wall. The wall of each strand is made of mesothelium, and surrounds a space filled with fluid, thought to be blood. A colony's zooids are connected, enabling autozooids to share food with each other and with any non-feeding heterozooids. The method of connection varies between the different classes of bryozoans, ranging from quite large gaps in the body walls to small pores through which nutrients are passed by funiculi.

There is a nerve ring round the pharynx (throat) and a ganglion that serves as a brain to one side of this. Nerves run from the ring and ganglion to the tentacles and to the rest of the body. Bryozoans have no specialized sense organs, but cilia on the tentacles act as sensors. Members of the genus *Bugula* grow towards the sun, and therefore must be able to detect light. In colonies of some species, signals are transmitted between zooids through nerves that pass through pores in the body walls, and coordinate activities such as feeding and the retraction of lophophores.

The solitary individuals of *Monobryozoon* are autozooids with pear-shaped bodies. The wider ends have up to 15 short, muscular projections by which the animals anchor themselves to sand or gravel and pull themselves through the sediments.

Avicularia and vibracula

Some authorities use the term *avicularia* to refer to any type of zooid in which the lophophore is replaced by an extension that serves some protective function, while others restrict the term to those that defend the colony by snapping at invaders and small predators, killing some and biting the appendages of others. In some species the snapping zooids are mounted on a peduncle (stalk), their bird-like appearance responsible for the term – Charles Darwin described these as like "the head and beak of a vulture in miniature, seated on a neck and capable of movement". Stalked avicularia are placed upside-down on their stalks. The "lower jaws" are modified versions of the opercula that protect the retracted lophophores in autozooids of some species, and are snapped shut "like a mousetrap" by similar muscles, while the beak-shaped upper jaw is the inverted body wall. In other species the avicularia are stationary box-like zooids laid the normal way up, so that the modified operculum snaps down against the body wall. In both types the modified operculum is opened by other muscles that attach to it, or by internal muscles that raise the fluid pressure by pulling on a flexible membrane. The actions of these snapping zooids are controlled by small, highly modified polypides that are located inside the "mouth" and bear tufts of short sensory cilia. These zooids appear in various positions: some take the place of autozooids, some fit into small gaps between autozooids, and small avicularia may occur on the surfaces of other zooids.

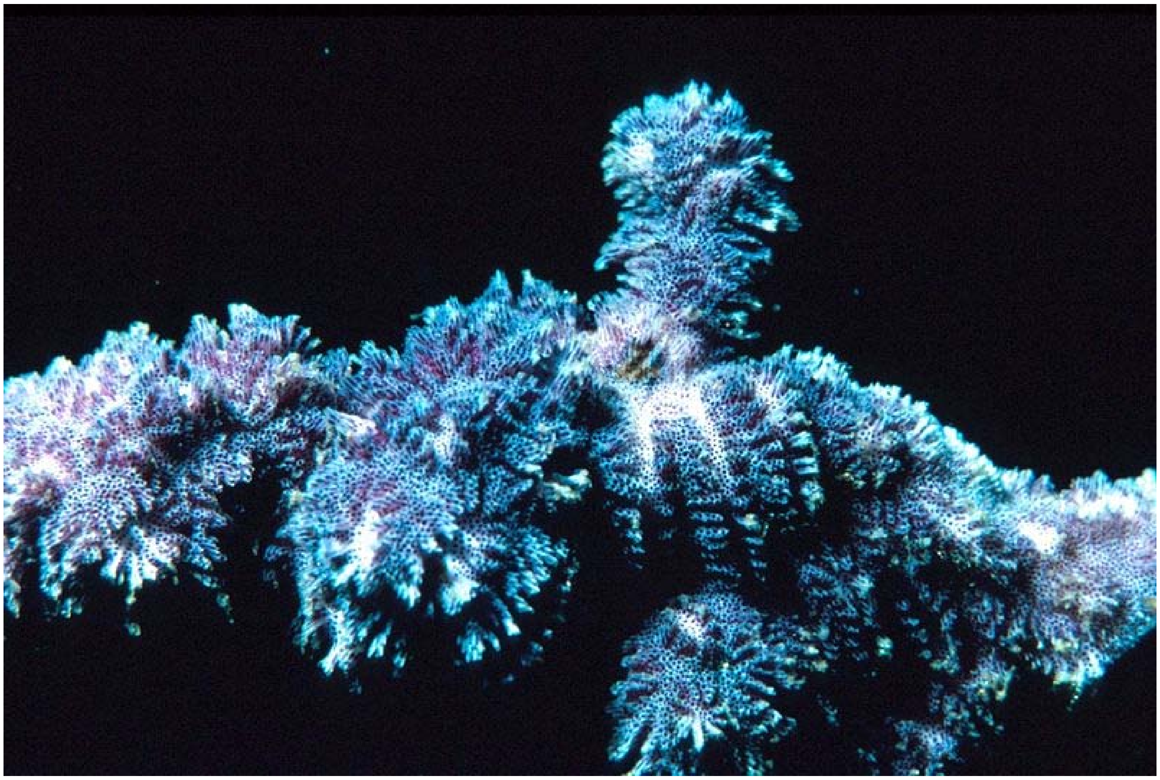
In vibracula, regarded by some as a type of avicularia, the operculum is modified to form a long bristle that has a wide range of motion. They may function as defenses against predators and invaders, or as cleaners. In some species that form mobile colonies, vibracula around the edges are used as legs for burrowing and walking.

Other types of colonial zooid

Kenozooids (from Greek κενος meaning "empty") consist only of the body wall and funicular strands crossing the interior, and no polypide. In some species they form the stems of branching structures, while in others they act as spacers that enable colonies to grow quickly in a new direction.

Spinozooids form defensive spines, and sometimes appear on top of autozooids. Gonozooids act as brood chambers for fertilized eggs. Some species have miniature nanozooids with small single-tentacled polypides, and these may grow on other zooids or within the body walls of autozooids that have degenerated.

Colony forms and composition



A marine colony

Although zooids are microscopic, colonies range in size from 1 centimeter (0.39 in) to over 1 meter (3.3 ft). However, the majority are under 10 centimeters (3.9 in) across. The shapes of colonies vary widely, depend on the pattern of budding by which they grow, the variety of zooids present and the type and amount of skeletal material they secrete.

Some marine species are bush-like or fan-like, supported by "trunks" and "branches" formed by kenozooids, with feeding autozooids growing from these. Colonies of these types are generally unmineralized but may have exoskeletons made of chitin. Others look like small corals, producing heavy lime skeletons. Many species form colonies which consist of sheets of autozooids. These sheets may form leaves, tufts or, in the genus *Thalmoporella*, structures that resemble an open head of lettuce.

The most common marine form, however, is encrusting, in which a one-layer sheet of zooids spreads over a hard surface or over seaweed. Some encrusting colonies may grow to over 50 centimeters (1.6 ft) and contain about 2,000,000 zooids. These species generally have exoskeletons reinforced with calcium carbonate, and the openings through which the lophophores protrude are on the top or outer surface. The moss-like appearance of encrusting colonies is responsible for the phylum's alternative name Bryozoa (Ancient Greek words βρυος *bryos* meaning "moss" and ζωον *zoon* meaning "animal"). Large colonies of encrusting species often have "chimneys", gaps in the canopy of lophophores, through which they swiftly expel water that has been sieved, and thus avoid re-filtering water that is already exhausted. They are formed by patches of non-feeding heterozooids. New chimneys appear near the edges of expanding colonies, at points where the speed of the outflow is already high, and do not change position if the water flow changes.

Some freshwater species secrete a mass of gelatinous material, up to 1 meter (3.3 ft) in diameter, to which the zooids stick. Other freshwater species have plant-like shapes with "trunks" and "branches", which may stand erect or spread over the surface. A few species can creep at about 2 centimeters (0.79 in) per day.

Each colony grows by asexual budding from a single zooid known as the ancestrula, which is round rather than shaped like a normal zooid. This occurs at the tips of "trunks" or "branches" in forms that have this structure. Encrusting colonies grow round their edges. In species with calcareous exoskeletons, these do not mineralize until the zooids are fully grown. Colony lifespans range from one to about 12 years, and the short-lived species pass though several generations in one season.

Species that produce defensive zooids do so only when threats have already appeared, and may do so within 48 hours. The theory of "induced defenses" suggests that production of defenses is expensive and that colonies which defend themselves too early or too heavily will have reduced growth rates and lifespans. This "last minute" approach to defense is feasible because the loss of zooids to a single attack is unlikely to be significant. Colonies of some encrusting species also produce special heterozooids to limit the expansion of other encrusting organisms, especially other bryozoans. In some cases this response is more belligerent if the opposition is smaller, which suggests that zooids on the edge of a colony can somehow sense the size of the opponent. Some species consistently prevail against certain others, but most turf wars are indecisive and the combatants soon turn to growing in uncontested areas. Bryozoans competing for territory do not use the sophisticated techniques employed by sponges or corals, possibly because the shortness of bryozoan lifespans makes heavy investment in turf wars unprofitable.

Taxonomy and Evolution

The phylum was originally called "Polyzoa", but this name was soon replaced by Ehrenberg's term "Bryozoa". The name "Bryozoa" was originally applied only to the animals also known as "Ectoprocta", in which the anus lies outside the "crown" of tentacles (based on the Ancient Greek prefix ἐκτο meaning "outside" and word πρωκτος meaning "anus"). After the discovery of the Entoprocta, in which the anus lies within a "crown" of tentacles (based on the Ancient Greek prefix ἐντο meaning "inside" and word πρωκτος meaning "anus"), the name "Bryozoa" was used at phylum level to include the two classes Ectoprocta and Entoprocta. However, in 1869 Hinrich Nitsche regarded the two groups as quite distinct for a variety of reasons, and coined the name "Ectoprocta" for Ehrenberg's "Bryozoa". Despite their apparently similar methods of feeding, they differed markedly anatomically; in addition to the different positions of the anus, ectoprocts have hollow tentacles and a coelom, while entoprocts have solid tentacles and no coelom. Hence the two groups are now widely regarded as separate phyla, and the name "Bryozoa" is now synonymous with "Ectoprocta". This has remained the majority view ever since, although most publications have preferred the name "Bryozoa" rather than "Ectoprocta". Nevertheless some notable scientists have continued to regard the "Ectoprocta" and Entoprocta as close relatives and group them under "Bryozoa".

The ambiguity about the scope of the name "Bryozoa" led to proposals in the 1960s and 1970s that it should be avoided and the unambiguous term "Ectoprocta" should be used. However, the change would have made it harder to find older works about in which the phylum was called "Bryozoa", and the desire to avoid ambiguity, if applied consistently to all classifications, would have necessitated renaming of several other phyla and many lower-level groups. In practice, zoological naming of split or merged groups of animals is complex and not completely consistent. Works since 2000 have used various names to resolve the ambiguity, including: "Bryozoa", "Ectoprocta", "Bryozoa (Ectoprocta)", and "Ectoprocta (Bryozoa)". Some have used more than one approach in the same work.

The common name "moss animals" is based on the Greek βρυόν (moss) and ζῷα (animals), and refers to the mossy appearance of encrusting species.

Classification and diversity

Counts of formally described species range between 4,000 and 4,500. The Gymnolaemata and especially Cheilostomata have the greatest numbers of species, possibly because of their wide range of specialist zooids. Under the Linnaean system of classification, which is still used as a convenient way to label groups of organisms, living members of the phylum Bryozoa are divided into:

Class	**Phylactolaemata**	**Stenolaemata**	**Gymnolaemata**	
Order	**Plumatellida**	**Cyclostomata**	**Ctenostomata**	**Cheilostomata**
Environments	Freshwater	Marine	Mostly marine	
Lip-like epistome overhanging mouth	Yes	none		
Colony shapes	Gelatinous masses or tubular branching structures	Erect or encrusting		Erect, encrusting or free-living
Exoskeleton material	Gelatinous or membranous; unmineralized	Mineralized	Chitin, gelatinous or membranous; unmineralized	Mineralized
Operculum ("lid")	none	none (except in family Eleidae)	None in most species	Yes (except in genus *Bugula*)
Shape of	U-shaped	Circular		

lophophore	appearance (except in genus *Fredericella*, whose lophophore is circular)			
How lophophore extended	Compressing the whole body wall	Compressing the membranous sac (separate inner layer of epithelium that lines the coelom)	Compressing the whole body wall	Pulling inwards of a flexible section of body wall, or making an internal sac expand.
Types of zooid	Autozooids only	Limited heterozooids, mainly gonozooids	Stolons and spines as well as autozooids	Full range of types

Fossil record

Bryozoan fossils in an Upper Ordovician oil shale (kukersite), northern Estonia.

Fossils of about 15,000 bryozoan species have been found. Marine taxa with mineralized skeletons appear in rocks dating from the Arenigian stage of the Early Ordovician period, about 480 million years ago. At this point all the modern orders of stenolaemates were present, and the ctenostome order of gymnolaemates had appeared by the Middle Ordovician, about 465 million years ago. Other types of filter feeders appeared around the same time, which suggests that some change made the environment more favorable for this lifestyle. Fossils of cheilostomates, another order of gymnolaemates, first appear in the Mid Jurassic, about 172 million years ago, and these have been the most abundant and diverse bryozoans from the Cretaceous to the present. Evidence compiled from the last 100 million years show that cheilostomates consistently grew over cyclostomates in territorial struggles, which may help to explain how cheilostomates replaced cyclostomates as the dominant marine bryozoans. Marine fossils from the Paleozoic era, which ended 251 million years ago, are mainly of erect forms, those from the Mesozoic are fairly equally divided by erect and encrusting forms, and more recent ones are predominantly encrusting. Fossils of the soft, freshwater phylactolaemates are very rare, appear in and after the Late Permian (which began about 260 million years ago) and consist entirely of their durable statoblasts. There are no known fossils of freshwater members of other classes.

Since all the other phyla that have left fossils are found in Cambrian rocks, it is surprising that the earliest bryozoan fossil dates from the Ordovician, which immediately followed the Cambrian. This suggests that the first bryozoans appeared much earlier and were entirely soft-bodied, and the Ordovician fossils record the appearance of mineralized skeletons in this phylum. The Early Ordovician fossils may also represent forms that had already become significantly different from the original members of the phylum.

Evolutionary family tree

Scientists are divided about whether the Bryozoa (Ectoprocta) are a monophyletic group (whether they include all and only a single ancestor species and all its descendants), about what are the phylum's closest relatives in the family tree of animals, and even about whether they should be regarded as members of the protostomes or deuterostomes, the two major groups that account for all moderately complex animals.

An Upper Ordovician cobble with the edrioasteroid *Cystaster stellatus* and the thin branching cyclostome bryozoan *Corynotrypa*. Kope Formation, northern Kentucky.

The traditional view is that the Bryozoa are a monophyletic group, in which the class Phylactolaemata is most closely related to Stenolaemata and Ctenostomata, the classes that appear earliest in the fossil record. However, in 2005 a molecular phylogeny study that focused on phylactolaemates concluded that these are more closely related to the phylum Phoronida, and especially to the only phoronid species that is colonial, than they are to the other ectoproct classes. That implies that the Entoprocta are not monophyletic, as the Phoronida are a sub-group of ectoprocts but the standard definition of Entoprocta excludes the Phoronida. In 2009 another molecular phylogeny study, using a combination of genes from mitochondria and the cell nucleus, concluded that Bryozoa is a monophyletic phylum, in other words includes all the descendants of a common ancestor that is itself a bryozoan. The analysis also concluded that the classes Phylactolaemata, Stenolaemata and Gymnolaemata are also monophyletic, but could not determine whether Stenolaemata are more closely related to Phylactolaemata or Gymnolaemata. The Gymnolaemata are traditionally divided into the soft-bodied Ctenostomata and mineralized Cheilostomata, but the 2009 analysis considered it more likely that neither of these orders is monophyletic and that mineralized skeletons probably evolved more than once within the early Gymnolaemata.

Bryozoans' relationships with other phyla are uncertain and controversial. Traditional phylogeny, based on anatomy and on the development of the adult forms from embryos, has produced no enduring consensus about the position of ectoprocts. Attempts to reconstruct the family tree of animals have largely ignored ectoprocts and other "minor phyla", which have received little scientific study because they are generally tiny, have relatively simple body plans, and have little impact on human economies – despite the fact that the "minor phyla" include most of the variety in the evolutionary history of animals. In the opinion of Ruth Dewel, Judith Winston and Frank McKinney, "Our standard interpretation of bryozoan morphology and embryology is a construct resulting from over 100 years of attempts to synthesize a single framework for all invertebrates," and takes little account of some peculiar features of ectoprocts. In ectoprocts, all of the larva's internal organs are destroyed during the metamorphosis to the adult form and the adult's organs are built from the larva's epidermis and mesoderm, while in other bilaterians some organs including the gut are built from endoderm. In most bilaterian embryos the blastopore, a dent in the outer wall, deepens to become the larva's gut, but in ectoprocts the blastopore disappears and a new dent becomes the point from which the gut grows. The ectoproct coelom is formed by neither of the processes used by other bilaterians, enterocoely, in which pouches that form on the wall of the gut become separate cavities, nor schizocoely, in which the tissue between the gut and the body wall splits, forming paired cavities.

Molecular phylogeny, which attempts to work out the evolutionary family tree of organisms by comparing their biochemistry and especially their genes, has done much to clarify the relationships between the better-known invertebrate phyla. However, the shortage of genetic data about "minor phyla" such as bryozoans and entoprocts has left their relationships to other groups unclear.

When entoprocts were discovered in the nineteenth century, they and bryozoans (ectoprocts) were regarded as classes within the phylum Bryozoa, because both groups were sessile animals that filter-fed by means of a crown of tentacles that bore cilia. However, from 1869 onwards increasing awareness of differences, including the position of the entoproct anus inside the feeding structure and the difference in the early pattern of division of cells in their embryos, caused scientists to regard the two groups as separate phyla, and "Bryozoa" became just an alternative name for ectoprocts, in which the anus is outside the feeding organ. A series of molecular phylogeny studies from 1996 to 2006 have also concluded that bryozoans (ectoprocts) and entoprocts are not sister groups. However, two well-known zoologists, Claus Nielsen and Thomas Cavalier-Smith, maintain on anatomical and developmental grounds that bryozoans and entoprocts are member of the same phylum, Bryozoa. A molecular phylogeny study in 2007 also supported this old idea, while its conclusions about other phyla agreed with those of several other analyses.

By 1891 bryozoans (ectoprocts) were grouped with phoronids in a super-phylum called "Tentaculata". In the 1970s comparisons between phoronid larvae and the cyphonautes larva of some gymnolaete bryozoans produced suggestions that the bryozoans, most of which are colonial, evolved from a semi-colonial species of phoronid. Brachiopods were also assigned to the "Tentaculata", which were renamed Lophophorata as they all use a lophophore for filter feeding. Although the majority of scientists accept this, Claus Nielsen thinks these similarities are superficial. The Lophophorata are usually defined as animals with a lophophore, a three-part coelom and a U-shaped gut. In Nielsen's opinion, phoronids' and brachiopods' lophophores are more like those of pterobranchs, which are members of the phylum Hemichordata. Bryozoan's tentacles bear cells with multiple cilia, while the corresponding cells of phoronids', brachiopods' and pterobranchs' lophophores have one cilium per cell; and bryozoan tentacles have no hemal canal ("blood vessel"), which those of the other three phyla have.

If the grouping of bryozoans with phoronids and brachiopods into Lophophorata is correct, the next issue is whether the Lophophorata are protostomes, along with most invertebrate phyla, or deuterostomes, along with chordates, hemichordates and echinoderms. The traditional view was that lophophorates were a mix of protostome and deuterostome features. Research from the 1970s onwards suggested they were deuterostomes, because of some features that were thought characteristic of deuterostomes: a three-part coelom; radial rather than spiral cleavage in the development of the embryo; and formation of the coelom by enterocoely. However the coelom of ectoproct larvae shows no sign of division into three sections, and that of adult ectoprocts is different from that of other coelomate phyla as it is built anew from epidermis and mesoderm after metamorphosis has destroyed the larval coelom.

Molecular phylogeny analyses from 1995 onwards, using a variety of biochemical evidence and analytical techniques, placed the lophophorates as protostomes and closely related to annelids and molluscs in a super-phylum called Lophotrochozoa. "Total evidence" analyses, which used both morphological features and a relatively small set of genes, came to various conclusions, mostly favoring a close relationship between lophophorates and Lophotrochozoa. A study in 2008, using a larger set of genes, concluded that the lophophorates were closer to the Lophotrochozoa than to deuterostomes, but also that the lophophorates were not monophyletic. Instead, it concluded that brachiopods and phoronids formed a monophyletic group, but bryozoans (ectoprocts) were closest to entoprocts, supporting the original definition of "Bryozoa".

Physiology

Feeding and excretion

Most species are filter feeders that sieve small particles, mainly phytoplankton (microscopic floating plants), out of the water. The freshwater species *Plumatella emarginata* feeds on diatoms, green algae, cyanobacteria, non-photosynthetic bacteria, dinoflagellates, rotifers, protozoa, small nematodes, and microscopic crustaceans. While the currents that bryozoans generate to draw food towards the mouth are well understood, the exact method of capture is still debated. All species also flick larger particles towards the mouth with a tentacle, and a few capture zooplankton (planktonic animals) by using their tentacles as cages. In addition the tentacles, whose surface area is increased by microvilli (small hairs and pleats), absorb organic compounds dissolved in the water.

Unwanted particles may be flicked away by tentacles or shut out by closing the mouth. A study in 2008 showed that both encrusting and erect colonies fed more quickly and grew faster in gentle than in strong currents.

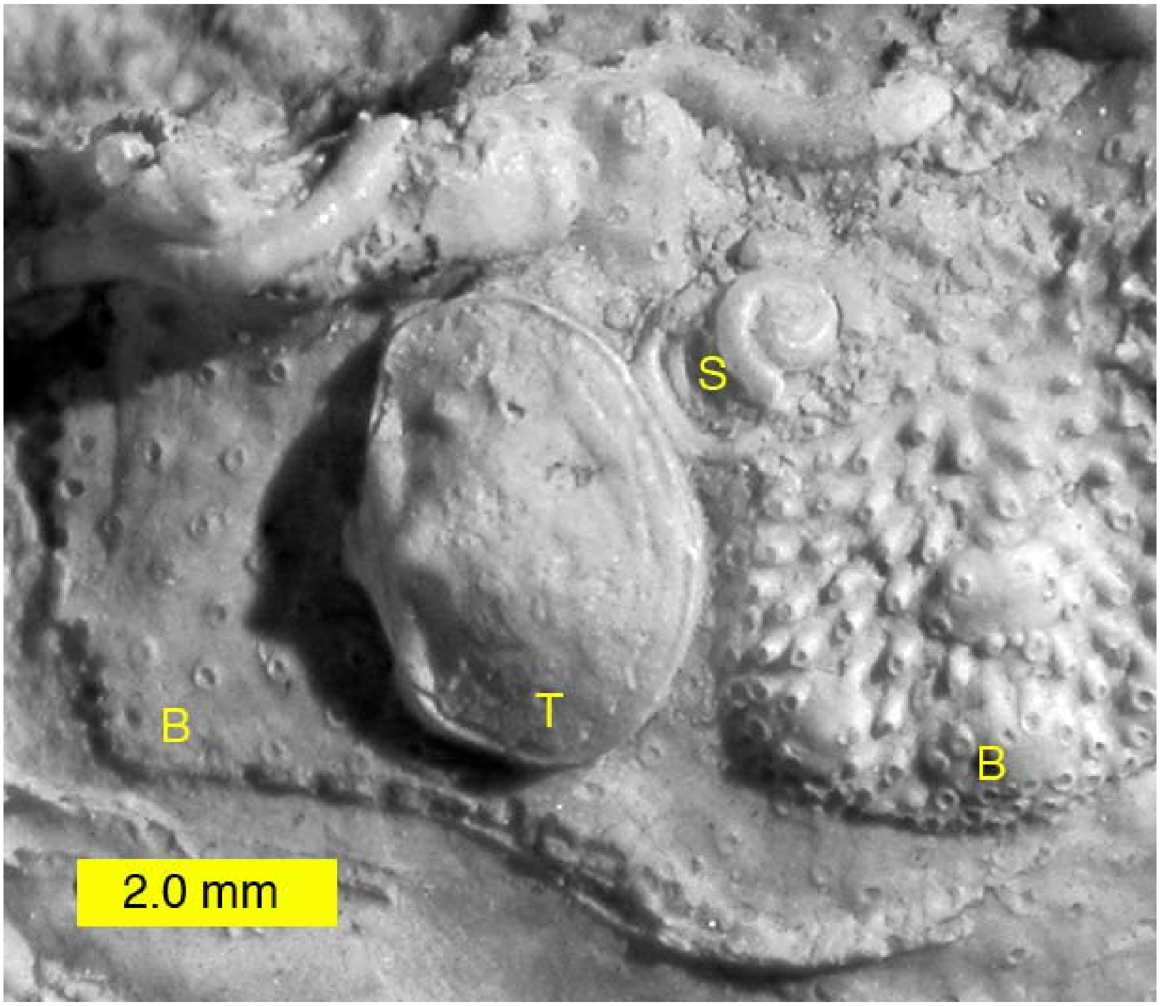
In some species the first part of the stomach forms a muscular gizzard lined with chitinous teeth that crush armored prey such as diatoms. Wave-like peristaltic contractions move the food through the stomach for digestion. The final section of the stomach is lined with cilia (minute hairs) that compress undigested solids, which then pass through the intestine and out through the anus.

There are no nephridia ("little kidneys") or other excretory organs in bryzoa, and it is thought that ammonia diffuses out through the body wall and lophophore. More complex waste products are not excreted but accumulate in the polypide, which degenerates after a few weeks. Some of the old polypide is recycled, but much of it remains as a large mass of dying cells containing accumulated wastes, and this is compressed into a "brown body". When the degeneration is complete, the cystid (outer part of the animal) produces a new polypide, and the brown body remains in the coelom, or in the stomach of the new polypide and is expelled next time the animal defecates.

Respiration and circulation

There are no respiratory organs, heart or blood vessels. Instead zooids absorb oxygen and eliminate carbon dioxide through the body wall and especially the lophophore. The fluid in the coelom transports gases and nutrients and its circulation is passive, except that some relatively large species use cilia to boost its speed. The different bryozoan groups use various methods to share nutrients and oxygen between zooids: some have quite large gaps in the body walls, allowing the coelomic fluid to circulate freely; in others the funiculi (internal "little ropes") of adjacent zooids connect via small pores in the body wall.

Reproduction and life cycles



Encrusting cyclostome bryozoans (B), the one on the right showing swollen gonozooids; T = thecideide brachiopod and S = sabellid worm tube; Jurassic of Poland.

Zooids of all phylactolaemate species are simultaneous hermaphrodites. Although those of many marine species are protandric, in other words function first as males and then as females, their colonies contain a combination of zooids that are in their male and female stages. In all species the ovaries develop on the inside of the body wall, and the testes on the funiculus connecting the stomach to the body wall. Eggs and sperm are released into the coelom, and sperm exit into the water through pores in the tips of some of the tentacles, and then are captured by the feeding currents of zooids that are producing eggs. Some species' eggs are fertilized externally after being released through a pore between two tentacles, which in some cases is at the tip of a small projection called the "intertentacular organ" in the base of a pair of tentacles. Others' are fertilized internally, in the intertentacular organ or in the coelom. In ctenostomes the mother provides a brood chamber for the fertilized eggs, and her polypide disintegrates, providing nourishment to the embryo. Stenolaemates produce specialized zooids to serve as brood chambers, and their eggs divide within this to produce up to 100 identical embryos.

The cleavage of bryozoan eggs is biradial, in other words the early stages are bilaterally symmetrical. It is unknown how the coleom forms, since the metamorphosis from larva to adult destroys all of the larva's internal tissues. In many animals the blastopore, an opening in the surface of the early embryo, tunnels through to form the gut. However, in bryozoans the blastopore closes, and a new opening develops to create the mouth.

Bryozoan larvae vary in form, but all have a band of cilia round the body which enables them to swim, a tuft of cilia at the top, and an adhesive sac that everts and anchors them when they settle on a surface. Some gymnolaemate species produce cyphonautes larvae which have little yolk but a well-developed mouth and gut, and live as plankton for a considerable time before settling. These larvae have triangular shells of chitin, with one corner at the top and the base open, forming a hood round the downward-facing mouth. In 2006 it was reported that the cilia of cyphonautes larvae use the same range of techniques as those of adults to capture food. Species that brood their embryos form larvae that are nourished by large yolks, have no gut and do not feed, and such larvae quickly settle on a surface. In all marine species the larvae produce cocoons in which they metamorphose completely after settling: the larva's epidermis becomes the lining of the coelom, and the internal tissues are converted to a food reserve that nourishes the developing zooid until it is ready to feed. The larvae of phylactolaemates produce multiple polypides, so that each new colony starts with several zooids. In all species the founder zooids then grow the new colonies by budding clones of themselves. In phylactolaemates, zooids die after producing several clones, so that living zooids are found only round the edges of a colony.

Phylactolaemates also reproduce asexually by a method that enables a colony's lineage to survive the variable and uncertain conditions of freshwater environments. Throughout summer and autumn they produce disc-shaped statoblasts, masses of cells that function as "survival pods" rather like the gemmules of sponges. Statoblasts form on the funiculus connected to the parent's gut, which nourishes them. As they grow, statoblasts develop protective bivalve-like shells made of chitin. When they mature, some statoblasts stick to the parent colony, some fall to the bottom ("sessoblasts"), some contain air spaces that enable them to float ("floatoblasts"), and some remain in the parent's cystid to re-build the colony if it dies. Statoblasts can remain dormant for considerable periods, and while dormant can survive harsh conditions such as freezing and desiccation. They can be transported across long distances by animals, floating vegetation, currents and winds, and even in the guts of larger animals. When conditions improve, the valves of the shell separate and the cells inside develop into a zooid that tries to form a new colony. *Plumatella emarginata* produces both "sessoblasts", which enable the lineage to control a good territory even if hard times decimate the parent colonies, and "floatoblasts", which spread to new sites. New colonies of *Plumatella repens* produce mainly "sessoblasts" while mature ones switch to "floatoblasts". A study estimated that one group of colonies in a patch measuring 1 square metre (11 sq ft) produced 800,000 statoblasts.

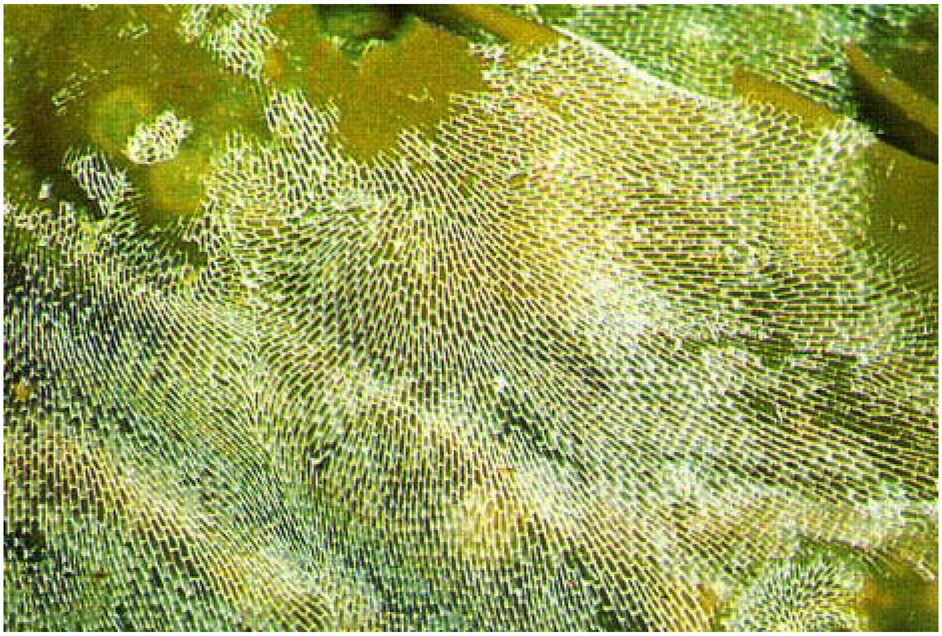
Ecology

Habitats and distribution

Most marine species live in tropical waters at depths less than 100 metres (330 ft). However, a few have been found in deep-sea trenches, especially around cold seeps, and others near the poles. The great majority are sessile. Encrusting forms are much the commonest of these in shallow seas, but erect forms become more common as the depth increases. A few marine species can move, and an Antarctic species forms floating colonies.

The phylactolaemates live in all types of freshwater environment – lakes and ponds, rivers and streams, and estuaries – and are among the most abundant sessile freshwater animals. Some ctenostomes are exclusively freshwater while others prefer brackish water but can survive in freshwater. Scientists' knowledge of freshwater bryozoan populations in many parts of the world is incomplete, even in some parts of Europe. It was long thought that some freshwater species occurred worldwide, but since 2002 all of these have been split into more localized species.

Interactions with non-human organisms



lacelike *Membranipora membranacea*

Marine species are common on coral reefs, but seldom a significant proportion of the total biomass. In temperate waters, the skeletons of dead colonies form a significant component of shell gravels, and live ones are abundant in these areas. The marine lace-like bryozoan *Membranipora membranacea* produces spines in response to predation by several species of nudibranchs ("sea slugs"). Other predators on marine bryozoans include fish, sea urchins, pycnogonids, crustaceans, mites and starfish. In general marine echinoderms and molluscs eat masses of zooids by gouging pieces of colonies, breaking their mineralized "houses", while most arthropod predators on bryozoans eat individual zooids.

In freshwater, bryozoans are among the most important filter feeders, along with sponges and mussels. Freshwater bryozoans are attacked by many predators, including snails, insects, and fish.

In Thailand the introduced species *Pomacea canaliculata* (golden apple snail), which is generally a destructive herbivore, has wiped out phylactolaemate populations wherever it has appeared. *P. canaliculata* also preys on a common freshwater gymnolaemate, but with less devastating effect. Indigenous snails do not feed on bryozoans.

Several species of the hydroid family Zancleidae have symbiotic relationships with bryozoans, some of which are beneficial to the hydroids while others are parasitic. Modifications appear in the shapes of some these hydroids, for example smaller tentacles or encrustation of the roots by bryozoans. The bryozoan *Alcyonidium nodosum* protects the whelk *Burnupena papyracea* against predation by the powerful and voracious rock lobster *Jasus lalandii*. While whelk shells encrusted by the bryozoans are stronger than those without this reinforcement, chemical defenses produced by the bryozoans are probably the more significant deterrent.

Some phylactolaemate species are parasitized by a group of myxozoa that have also been found to cause Proliferative Kidney Disease, which is often fatal in salmonid fish, and has severely reduced wild fish populations in Europe and North America.

Membranipora membranacea, whose colonies feed and grow exceptionally fast in a wide range of current speeds, was first noticed in the Gulf of Maine in 1987 and quickly became the most abundant organism living on kelps. This invasion reduced the kelp population by breaking their fronds, so that its place as the dominant "vegetation" in some areas was taken by another invader, the large alga *Codium fragile tomentosoides*. These changes reduced the area of habitat available for local fish and invertebrates. *M. membranacea* has also invaded the northwest coast of the U.S.A. A few freshwater species have been also found thousands of kilometers from their native ranges. Some may have been transported naturally as statoblasts. Others more probably were spread by humans, for example on imported water plants or as stowaways on ships.

Interaction with humans

Fish farms and hatcheries have lost stock to proliferative kidney disease, which is apparently caused by one or more myxozoans that also parasitize bryozoans.

Fishermen in the North Sea have had to find other work because of a form of eczema (a skin disease) known as "Dogger Bank itch", caused by contact with bryozoans that have stuck to nets and lobster pots.

Marine bryozoans are often responsible for biofouling on ships' hulls, on docks and marinas, and on offshore structures. They are among the first colonizers of new or recently-cleaned structures. Freshwater species are occasional nuisances in water pipes, drinking water purification equipment, sewage treatment facilities, and the cooling pipes of power stations.

A group of chemicals called bryostatins can be extracted from the marine bryozoan *Bugula neritina*. In 2001 pharmaceutical company GPC Biotech licensed Bryostatin 1 from Arizona State University for commercial development as a treatment for cancer. GPC Biotech canceled development in 2003, saying that Bryostatin 1 showed little effectiveness and some toxic side-effects. In January 2008 a clinical trial was submitted to the United States National Institutes of Health to measure the safety and effectiveness of Bryostatin 1 in the treatment of Alzheimer's Disease. However, no participants had been recruited by the end of December 2008, when the study was scheduled for completion. About 1 tonne (160 st) of bryozoans must processed to extract 1 gram (0.035 oz) of bryostatin. As a result, synthetic equivalents have been developed that are simpler to produce and apparently at least as effective.