Encyclopedia of
Onychophora, Brachiopoda, Acoelomorpha, Porifera and Ctenophora
(Animal Phylum)

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Chapter 1

Onychophora

Onychophora
Temporal range: 40–0 Ma

Scientific classification [e]

Kingdom:	Animalia
Superphylum:	Ecdysozoa
(unranked):	Panarthropoda
Phylum:	**Onychophora** Grube, 1853

Extant families

Peripatidae
Peripatopsidae

Global range of Onychophora: Peripatidae in green, Peripatopsidae in blue

The **velvet worms** (**Onychophora** — literally "claw bearers", also known as **Protracheata**) are a minor ecdysozoan phylum. These obscurely segmented organisms have tiny eyes, antennae, multiple pairs of legs and slime glands. They have variously been compared to worms with legs, caterpillars and slugs. Most common in tropical regions of the Southern Hemisphere, they prey on smaller animals such as insects, which they catch by squirting an adhesive slime. In modern zoology, they are particularly renowned for their curious mating behaviour and for bearing live young. They are becoming increasingly popular as pets due to their bizarre appearance and eating habits.

The two extant families of velvet worms are Peripatidae and Peripatopsidae. They show a peculiar distribution, with the peripatids being predominantly equatorial and tropical, while the peripatopsids are all found in what used to be Gondwanaland.

Formerly considered part of Tracheata, velvet worms are now considered close relatives of the Arthropoda and Tardigrada, with which they form the taxon Panarthropoda. This makes them of palaeontological interest, as they can help to reconstruct the ancestral arthropod.

Anatomy

A dissection of *Euperipatoides kanangrensis*. The width of the dish is approx. 4 cm. The two ovaries, full of stage II embryos, are floating to the bottom of the image. The brown mass of the viscera is partially protruding from the body cavity.

Velvet worms are segmented creatures with a flattened cylindrical body cross-section and rows of unstructured body appendages known as lobopods (informally: stub feet). The animals grow to between 0.5 and 20 cm, with the average being about 5 cm, and have between 13 and 43 pairs of legs. Their skin consists of numerous, fine transverse rings and is often inconspicuously coloured orange, red or brown, but sometimes also bright green, blue, gold or white, and occasionally patterned with other colours.

Segmenting—outwardly inconspicuous and identifiable only in the regular spacing of the pairs of legs—is visible in the regular arrangement of skin pores, excretion organs and concentrations of nerve cells. The individual body sections are largely unspecialised; even the head develops only a little differently from any abdominal segment. Segmentation is apparently specified by the same gene as traceable in other groups of animals and is activated in each case, during embryonic development, at the rear border of each segment and in the growth zone of the stub feet.

Body appendages

The stub feet that characterise the velvet worms are conical, baggy appendages of the body, which are internally hollow and exhibit no joints. Although the number of feet can vary considerably between species, their structure is basically very similar. Rigidity is provided by the hydrostatic pressure of their fluid contents, and movement is usually obtained passively by stretching and contraction of the animal's entire body. However, each leg can also be shortened and bent by internal muscles; due to the lack of joints, this bending can take place at any point along the sides of the leg.

In some species, two different organs are found within the feet:

- Crural glands are situated at the shoulder of the legs, extending into the body cavity. They open outwards at the crural papillae—small wart-like bumps on the belly side of the leg—and secrete chemical messenger materials called pheromones. Their name comes from the Latin *cruralis* meaning "of the legs".

- Coxal vesicles are pouches located on the belly side of the leg, which can be everted and probably serve in water absorption. They are only found within the family Peripatidae and are named from *coxa*, the Latin word for "hip".

On each foot is a pair of retractable, hardened (sclerotised) chitin claws, which give the taxon its scientific name: Onychophora is derived from the Greek *onyches*, "claws"; and *pherein*, "to carry". At the base of the claws are three to six spiny "cushions" on which the leg sits in its resting position and on which the animal walks over smooth substrates; the claws are used mainly to gain a firm foothold on uneven terrain.

Apart from the pairs of legs, there are three further body appendages, which are at the head and comprise three segments:

- On the first head segment is a pair of slender antennae, which serve in sensory perception. They probably do not correspond directly to the antennae of the Arthropoda, but perhaps rather with their "lips" or labrum. At their base is found a pair of simple eyes, except in a few blind species. In front of these, in many Australian species, are various dimples, the function of which is not yet clear. It appears that in at least some species, these serve in the transfer of sperm-cell packages (spermatophores).

- On the belly side of the second head segment is the labrum, a mouth opening surrounded by sensitive "lips". In the velvet worms, this structure is a muscular outgrowth of the throat, so, despite its name, it is probably not homologous to the labrum of the Arthropoda. Deep within the oral cavity lie the sharp, crescent-shaped "jaws", or mandibles, which are strongly hardened and resemble the claws of the feet, with which they are probably homologous. The jaws are divided into internal and external mandibles and are covered with fine toothlets. They move backward and forward in a longitudinal direction, tearing apart the prey.
- On the third head segment, to the left and right of the mouth, are two openings designated "oral papillae". Within these are a pair of large, heavily internally branched slime glands. These lie roughly in the centre of the body and secrete a sort of milky-white slime, which is used to ensnare prey and for defensive purposes. Sometimes the connecting "slime conductor" is broadened into a reservoir, which can buffer pre-produced slime. The slime glands themselves are probably modified crural glands.

All three structures correspond to an evolutionary origin in the leg pairs of the other segments.

Skin and musculature

Unlike the arthropods, velvet worms do not possess a rigid exoskeleton. Instead, their fluid-filled body cavity acts as a hydrostatic skeleton, similarly to many unrelated soft-bodied animals that are cylindrically shaped, for example sea anemones and various worms. Pressure of their incompressible internal bodily fluid on the body wall provides rigidity, and muscles are able to act against it.

The body wall consists of a non-cellular outer skin, the cuticula; a single layer of epidermis cells forming an internal skin; and beneath this, usually three layers of muscle, which are embedded in connective tissues.

The cuticula is about a micrometer thick and covered with fine villi. In composition and structure, it resembles the cuticula of the arthropods, consisting of α-chitin and various proteins, although not containing collagen. It can be divided into an external epicuticula and an internal procuticula, which themselves consist of exo- and endo-cuticula. This multi-level structure is responsible for the high flexibility of the outer skin, which enables the velvet worm to squeeze itself into the narrowest crevices. Although outwardly water-repellant, the cuticula is not able to prevent water loss by respiration, and, as a result, velvet worms can only live in microclimates with high humidity to avoid desiccation.

The surface of the cuticula is scattered with numerous fine papillae, the larger of which carry visible villi-like sensitive bristles. The papillae themselves are covered with tiny scales, lending the skin a velvety appearance (from which the common name is likely derived). It also feels like dry velvet to the touch, for which its water-repellant nature is responsible. Moulting of the skin (ecdysis) takes place regularly, sometimes every 14 days, induced by the hormone ecdysone.

At each moult, the shed skin is replaced by the epidermis, which lies immediately beneath it; unlike the cuticula, this consists of living cells. Beneath this lies a thick layer of connective tissue, which is composed primarily of collagen fibres aligned either parallel or perpendicular to the body's longitudinal axis. Within the connective tissue lie three continuous layers of unspecialised smooth muscular tissue. The relatively thick outer layer is composed of annular (sphincter) muscles, and the similarly voluminous inner layer of longitudinal muscles. Between them lie thin diagonal muscles that wind backward and forward along the body axis in a spiral. Between the annular and diagonal muscles exist fine blood vessels, which lie below the superficially recognisable transverse rings of the skin and are responsible for the pseudo-segmented markings.

Beneath the internal muscle layer lies the body cavity. In cross-section, this is divided into three regions by so-called dorso-ventral muscles, which run from the middle of the underbelly through to the edges of the upper side: a central mid-section and on the left and right, two side regions that also include the legs.

The colouration of Onychophora is generated by a range of pigments. The solubility of these pigments is a key utensil in classification: in all arthropods and tardigrades, the body pigment is soluble in ethanol. This is also true for the Peripatidae, but in the case of the Peripatopsidae, the body pigment is insoluble in ethanol.

Haemocoel and circulation

The body cavity is known as a "pseudocoel", or haemocoel. Unlike a true coelom, a pseudocoel is not fully enclosed by a cell layer derived from the embryonic mesoderm. A coelom is, however, formed around the gonads and the waste-eliminating nephridia.

As the name *haemocoel* suggests, the body cavity is filled with a blood-like liquid, in which all the organs are embedded; in this way, they can be easily supplied with nutrients circulating in the blood. This liquid is colourless as it does not contain pigments; for this reason, it only serves a limited role in oxygen transport. Two different types of blood cells (or haemocytes) circulate in the fluid: amoebocytes and nephrocytes. The amoebocytes probably function in protection from bacteria and other foreign bodies; in some species, they also play a role in reproduction. Nephrocytes absorb toxins or convert them into a form suitable for elimination by the nephridia.

The haemocoel is divided by a horizontal partition, the diaphragm, into two parts: the pericardial sinus along the back and the perivisceral sinus along the belly. The former encloses the tube-like heart, and the latter, the other organs. The diaphragm is perforated in many places, enabling the exchange of fluids between the two cavities.

The heart itself is a tube of annular muscles consisting of epithelial tissues, with two lateral openings (ostia) per segment. While it is not known whether the rear end is open or closed, from the front, it opens directly into the body cavity. Since there are no blood vessels, apart from the fine vessels running between the muscle layers of the body wall and a pair of arteries that supply the antennae, this is referred to as an open circulation.

The timing of the pumping procedure can be divided into two parts: diastole and systole. During diastole, blood flows through the ostia from the pericardial sinus (the cavity containing the heart) into the heart. When the systole begins, the ostia close and the heart muscles contract inwards, reducing the volume of the heart. This pumps the blood from the front end of the heart into the perivisceral sinus containing the organs. In this way, the various organs are supplied with nutrients before the blood finally returns to the pericardial sinus via the perforations in the diaphragm. In addition to the pumping action of the heart, body movements also have an influence on circulation.

Respiration

Oxygen uptake occurs to an extent via simple diffusion through the entire body surface, with the coxal vesicles on the legs possibly being involved in some species. However, of most importance is gas exchange via fine unbranched tubes, the tracheae, which draw oxygen from the surface deep into the various organs, particularly the heart. The walls of these structures, which are less than three micrometers thick in their entirety, consist only of an extremely thin membrane through which oxygen can easily diffuse. The tracheae originate at tiny openings, the spiracles, which themselves are clustered together in dent-like recesses of the outer skin, the atria. The number of "tracheae bundles" thus formed is on average around 75 per body segment; they accumulate most densely on the back of the animal.

Unlike the arthropods, the velvet worms are unable to control the openings of their tracheae; the tracheae are always open, entailing considerable water loss in arid conditions. For this reason, velvet worms are dependent upon habitats with high air humidity.

Digestive system

The digestive tract begins slightly behind the head, the mouth lying on the underside a little way from the frontmost point of the body. Here, prey can be mechanically dismembered by the mandibles with their covering of fine toothlets. Two salivary glands discharge via a common conductor into the subsequent "throat", which makes up the first part of the front intestine. The saliva that they produce contains mucus and hydrolytic enzymes, which initiate digestion both within and outside the mouth. Historically, the salivary glands probably evolved from the waste-elimination organs known as nephridia, which are found homologously in the other body segments.

The throat itself is very muscular, serving to absorb the partially liquified food and to pump it, via the oesophagus, which forms the rear part of the front intestine, into the central intestine. Unlike the front intestine, this is not lined with a cuticula but instead consists only of a single layer of epithelial tissue, which does not exhibit conspicuous indentation as is found in other animals. On entering the central intestine, food particles are coated with a mucus-based peritrophic membrane, which serves to protect the lining of the intestine from damage by sharp-edged particles. The intestinal epithelium secretes further digestive enzymes and absorbs the released nutrients, although the majority of digestion has already taken place externally or in the mouth. Indigestible remnants arrive in the rear intestine, or rectum, which is once again lined with a cuticula and which opens at the anus, located on the underside near to the rear end.

Excretory organs

In almost every segment is a pair of excretory organs called nephridia, which are derived from coelom tissue. Each consists of a small pouch that is connected, via a flagellated conductor called a nephridioduct, to an opening at the base of the nearest leg known as a nephridiopore. The pouch is occupied by special cells called podocytes, which facilitate ultrafiltration of the blood through the partition between haemocoelom and nephridium. The composition of the urinary solution is modified in the nephridioduct by selective recovery of nutrients and water and by isolation of poison and waste materials, before it is excreted to the outside world via the nephridiopore. The most important nitrogenous excretion product is the water-insoluble uric acid; this can be excreted in solid state, with very little water. This so-called uricotelic excretory mode represents an adjustment to life on land and the associated necessity of dealing economically with water.

A pair of former nephridia in the head were converted secondarily into the salivary glands, while another pair in the final segment of male specimens now serve as glands that apparently play a role in reproduction.

Sensory organs

The entire body—including the stub feet—is littered with numerous papillae: warty protrusions that carry a mechanoreceptive bristle (responsive to mechanical stimuli) at the tip, each of which is also connected to further sensory nerve cells lying beneath. The mouth papillae, the exits of the slime glands, probably also have a function in sensory perception. Sensory cells known as "sensills" on the "lips" or labrum respond to chemical stimuli and are known as chemoreceptors. These are also found on the two antennae, which can be regarded as the velvet worm's most important sensory organs. Except in a few (typically subterranean) species, one simply constructed eye (ocellus) lies laterally, just underneath the head, behind each antenna. This consists of a chitinous ball lens, a cornea and a retina and is connected to the centre of the brain via an optic nerve. The retina comprises numerous pigment cells and photoreceptors; the latter are easily modified flagellated cells, whose flagellum membranes carry a photosensitive pigment on their surface.

The rhabdomeric eyes of the Onychophora are thought to be homologous with the median ocelli of arthropods; this would imply that the last common ancestor of arthropods bore only median ocelli. However, the innervation shows that the homology is limited: the eyes of Onychophora form behind the antenna, whereas the opposite is true in arthropods.

Reproductive organs

Both sexes possess pairs of gonads, opening via a channel called a gonoduct into a common genital opening, the gonopore, which is located on the rear ventral side. Both the gonads and the gonoduct are derived from true coelom tissue.

In females, the two ovaries are joined in the middle and to the horizontal diaphragm. The gonoduct appears differently depending on whether the species is live-bearing or egg-laying. In the former, each exit channel divides into a slender oviduct and a roomy "womb", the uterus, in which the embryos develop. The single vagina, to which both uteri are connected, runs outward to the gonopore. In egg-laying species, whose gonoduct is uniformly constructed, the genital opening lies at the tip of a long egg-laying apparatus, the ovipositor. The females of many species also possess a sperm repository called the receptacle seminis, in which sperm cells from males can be stored temporarily or for longer periods.

Males possess two separate testes, along with the corresponding sperm vesicle (the vesicula seminalis) and exit channel (the vasa efferentia). The two vasa efferentia unite to a common sperm duct, the vas deferens, which in turn widens through the ejaculatory channel to open at the gonopore. Directly beside or behind this lie two pairs of special glands, which probably serve an auxiliary reproductive function; the rearmost glands are also known as anal glands.

A penis-like structure has so far only been found in males of the genus *Paraperipatus* but has not yet been observed in action. As previously mentioned, males of many Australian species exhibit special structures on the head, which apparently take over certain tasks in transferring sperm to the females. In the species *Euperipatoides rowelli*, sperm is collected by these structures, and, when a female is encountered, the worm inserts its head in the vagina.

Distribution and habitat

Velvet worms live in all tropical habitats and in the temperate zone of the Southern Hemisphere, showing a circumtropical and circumaustral distribution. Individual species are found in Central and South America; the Caribbean islands; equatorial West Africa and South Africa; northeastern India; Indonesia and parts of Malaysia; New Guinea; Australia; and New Zealand. Fossils have been found in Baltic amber, indicating that they were formerly more widespread in the Northern Hemisphere when conditions were more suitable.

All extant velvet worms are terrestrial (land-living) and prefer dark environments with high air humidity. They are found particularly in the rainforests of the tropics and temperate zones, where they live among moss cushions and leaf litter, under tree trunks and stones, in rotting wood or in termite tunnels. They also occur in unforested grassland, if there exist sufficient crevices in the soil into which they can withdraw during the day.

Two species live in caves, a habitat to which their ability to squeeze themselves into the smallest cracks makes them exceptionally well-adapted and in which constant living conditions are guaranteed. Since the essential requirements for cave life were probably already present prior to the settlement of these habitats, this may be described as exaptation. Agriculture has apparently made available new habitats for velvet worms; in any case, they are found in man-made cocoa and banana plantations in South America and the Caribbean.

Because the danger of desiccation is greatest during the day and in dry weather, it is not surprising that velvet worms are usually most active at night and during rainy weather. Under cold or dry conditions, they actively seek out crevices in which they shift their body into a resting state. Velvet worms are negatively phototactical: they are repelled by bright light sources.

The largest measured population density is very low, at approximately ten individuals per square meter; velvet worms are often difficult to find in their natural habitat.

Slime

The slime of the Onychophora is forcefully squirted from a pair of slime glands in defence against predators and to capture prey. The slime glands, positioned on the sides of the head below the antennae, are a pair of highly modified limbs and typically propel the slime around a centimetre. The slime can be propelled up to four centimetres, although accuracy drops with range, which is usually much shorter than this. One squirt usually suffices to snare a prey item, although larger prey may be further immobilised by smaller squirts targeted at the limbs; additionally, the fangs of spiders are sometimes targeted.

The slime, which can account for up to 11% of the organism's dry weight, is 90% water; its dry residue consists mainly of proteins—primarily a collagen-type protein. 1.3% of the slime's dry weight consists of sugars, mainly glactosamine. The slime also contains lipids and the surfactant nonylphenol. Onychophora are the only organisms known to produce this latter substance.

The proteinaceous composition accounts for the slime's high tensile strength and stretchiness. Upon ejection, it forms a net of threads about 20 µm in diameter, with evenly spaced droplets of viscous adhesive fluid along their length. It subsequently dries, shrinking, losing its stickiness, and becoming brittle. Onychophora will eat and "reuse" any dried slime.

The lipid and nonylphenol constituents may serve one of two purposes. They may line the ejection channel, stopping the slime from sticking to the organism when it is secreted; or they may slow the drying process long enough for the slime to reach its target.

It takes an onychophoran around 24 days to replenish an exhausted slime repository.

Behaviour

Locomotion

Peripatoides sp., clearly showing the stub feet

Velvet worms move in a slow and gradual motion that makes them difficult for prey to notice. Their trunk is raised relatively high above the ground, and they walk with non-overlapping steps. To move from place to place, the velvet worm crawls forward using its legs; unlike in arthropods, both legs of a pair are moved simultaneously. The claws of the feet are only used on hard, rough terrain where a firm grip is needed; on soft substrates such as moss, the velvet worm walks on the foot cushions at the base of the claws.

The actual locomotion is achieved less by the exertion of the leg muscles than by local changes of body length. This can be controlled using the annular and longitudinal muscles. If the annular muscles are contracted, the body cross-section is reduced, and the corresponding segment stretches, since its volume must remain constant due to the incompressible behaviour of the coelom's liquid contents; this is the usual mode of operation of the hydrostatic skeleton as also employed by other worms. Due to the stretching, the legs of the segment concerned are lifted and swung forward. Local contraction of the longitudinal muscles then shortens the appropriate segment, and the legs, which are now in contact with the ground, are moved to the rear. This part of the locomotive cycle is the actual leg stroke that is responsible for forward movement. The individual stretches and contractions of the segments are coordinated by the nervous system such that contraction waves run the length of the body, each pair of legs swinging forward and then down and rearward in succession. The organisms can reach speeds of up to four centimetres per second.

Social interaction

The brains of Onychophora, whilst small, are very complex; consequently, the organisms are capable of rather sophisticated social interactions. Behaviour may vary from genus to genus, so here we reflects the most studied genus, *Euperipatoides*.

They form social groups of up to fifteen individuals, usually closely related, which will typically live and hunt together. Groups usually live together; an example in drier regions would be in a region of the moist interior of a rotting log. Group members are extremely aggressive towards individuals from other logs. Dominance is achieved through aggression and maintained through submissive behaviour. After a kill, the dominant female always feeds first, followed in turn by the other females, then males, then the young. Social hierarchy is established by a number of interactions: higher-ranking individuals will chase, bite and crawl on top of their subordinates. Juveniles never engage in aggressive behaviour, but climb on top of adults, which tolerate their presence on their backs. Size is probably important in establishing the hierarchy, which may account for the dominance of females. When assessing other individuals, individuals often measure one another up by running their antennae down the length of the other individual. Once hierarchy has been established, paired individuals will often cluster together to form an aggregate; this is fastest in male-female pairings, followed by pairs of females, then pairs of males. Whilst hierarchy is quickly established between individuals from a single group, this is not the case with organisms from different groups; these are substantially more aggressive and very rarely climb one another or form aggregates.

Distribution

Individuals within an individual log are usually closely related; especially so with males. This may be related to the intense aggression between unrelated females.

Feeding

Velvet worms are ambush predators, hunting only by night, and are able to capture animals at least their own size, although it may take almost all of their slime-secreting capacity to capture a large prey item. They feed on almost any small invertebrates, including woodlice (Isopoda), termites (Isoptera), crickets (Gryllidae), book/bark lice (Psocoptera), cockroaches (Blattidae), millipedes and centipedes (Myriapoda), spiders (Araneae), various worms and even large snails (Gastropoda). Depending on their size, they eat on average every one to four weeks. They are considered to be ecologically equivalent to centipedes (Chilopoda).

Potential victims can be detected from up to four centimetres away and are investigated by the gentle application of the antennae. If they are judged to be a suitable size, slime is ejected to immobilise the prey item. The most energetically favourable prey are two-fifths the size of the hunting onychophoran. The onychophoran bites into the prey and injects saliva, which further reduces motion and may initiate digestion of the prey item's innards. Ninety percent of the time involved in eating a specimen is spent ingesting it; reingestion of the slime used to trap the insect is performed whilst the onychophoran locates a suitable place to puncture the prey, and this phase accounts for around 8% of the feeding time, with the remaining time evenly split between examining, squirting and injecting the prey.

Onychophora probably do not primarily use vision to detect their prey; although their tiny eyes do have a good image-forming capacity, their forward vision is obscured by their antennae; their nocturnal habit also limits the utility of eyesight. Air currents, formed by prey motion, are thought to be the primary mode of locating prey; the role of scent, if any, is unclear. The animals literally creep up on their prey, with their smooth, gradual and fluid movement escaping detection by predators. Once they reach their prey, they touch it very softly with their antennae to assess its size and nutritional value. After each poke, the antenna is hastily retracted to avoid detection by the prey individual. This investigation may last anywhere upwards of ten seconds, until the velvet worm makes a decision on whether to attack it—or until it disturbs the prey and flees. Hungry Onychophora spend less time investigating their prey and are quicker to apply their slime. Once slime has been squirted, Onychophora will stop at nothing to hound down and devour their prey, in order to recoup the energetic investment. They have been observed to spend up to ten minutes searching for removed prey, after which they return to their slime to eat it. In the case of smaller prey, they may opt not to slime it at all.

Subsequently, a soft part of the prey item (usually a joint membrane in arthropod prey) is identified, punctured with a bite from the jaws, and injected with saliva. This kills the prey very quickly and begins a slower process of digestion. Whilst the onychophoran waits for the prey to digest, it salivates on its slime and begins to eat it (and anything attached to it). It subsequently tugs and slices at the earlier perforation to allow access to the now-liquidised innards of its prey.

In social groups, the dominant female is the first to feed, not permitting competitors access to the prey item for the first hour of feeding. Subsequently, subordinate individuals begin to feed. The number of males reaches a peak after females start to leave the prey item. After feeding, individuals clean their antennae and mouth parts before re-joining the rest of their group. Because it takes so long to ingest a prey item, hunting mainly happens around dusk; the onychophorans will abandon their prey at sunrise.

This predatory way of life is probably a consequence of the velvet worm's need to remain moist. Due to the continual risk of desiccation, often only a few hours per day are available for finding food. This leads to a strong selection for a low cost-benefit ratio, which can barely be achieved with a herbivorous diet.

Reproduction and life-cycle

Almost all species of velvet worm reproduce sexually. The sole exception is *Epiperipatus imthurni*, of which no males have been observed; reproduction instead occurs by parthenogenesis.

All species are in principle sexually distinct and bear, in many cases, a marked sexual dimorphism: the females are usually larger than the males and have, in species where the number of legs is variable, more legs. The females of many species are fertilized only once during their lives, which leads to copulation sometimes taking place before the reproductive organ of the females are fully developed. In such cases, for example at the age of three months in *Macroperipatus torquatus*, the transferred sperm cells are kept in a special reservoir, where they can remain viable for longer periods.

Fertilization takes place internally, although the mode of sperm transmission varies widely. In most species, for example in the genus *Peripatus*, a package of sperm cells called the spermatophore is placed into the genital opening of the female. The detailed process by which this is achieved is in most cases still unknown, a true penis having only been observed in species of the genus *Paraperipatus*. In many Australian species, there exist dimples or special dagger- or axe-shaped structures on the head; the male of *Florelliceps stutchburyae* presses a long spine against the female's genital opening and probably positions its spermatophore there in this way. During the process, the female supports the male by keeping him clasped with the claws of her last pair of legs. The mating behavior of two species of the genus *Peripatopsis* is particularly curious. Here, the male places two-millimetre spermatophores on the back or flanks of the female. Amoebocytes from the female's blood collect on the inside of the deposition site, and both the spermatophore's casing and the body wall on which it rests are decomposed via the secretion of enzymes. This releases the sperm cells, which then move freely through the haemocoel, penetrate the external wall of the ovaries and finally fertilize the ova. Why this self-inflicted skin injury does not lead to bacterial infections is not yet understood (though likely related to the enzymes used to deteriorate the skin or facilitate the transfer of viable genetic material from male to female).

Velvet worms are found in egg-laying (oviparous), egg-live-bearing (ovoviviparous) and live-bearing (viviparous) forms.

- Ovipary occur solely in the Peripatopsidae, often in regions with erratic food supply or unsettled climate. In these cases, the yolk-rich eggs measure 1.3 to 2.0 mm and are coated in a protective chitinous shell. Maternal care is unknown.

- The majority of species are ovoviviparous: the medium-sized eggs, encased only by a double membrane, remain in the uterus. The embryos do not receive food directly from the mother, but are supplied instead by the moderate quantity of yolk contained in the eggs—they are therefore described as lecithotrophic. The young emerge from the eggs only a short time before birth. This probably represents the velvet worm's original mode of reproduction, i.e., both oviviparous and viviparous species developed from ovoviviparous species.

- True live-bearing species are found in both families, particularly in tropical regions with a stable climate and regular food supply throughout the year. The embryos develop from eggs only micrometres in size and are nourished in the uterus by their mother, hence the description "matrotrophic". The supply of food

> takes place either via a secretion from the mother directly into the uterus or via a genuine tissue connection between the epithelium of the uterus and the developing embryo, known as a placenta. The former is found only outside the American continent, while the latter occurs primarily in America and the Caribbean and more rarely in the Old World. The gestation period can amount to up to 15 months, at the end of which the offspring emerge in an advanced stage of development. The embryos found in the uterus of a single female do not necessarily have to be of the same age; it is quite possible for there to be offspring at different stages of development and descended from different males. In some species, young tend to be only released at certain points in the year.

A female can have between 1 and 23 offspring per year; development from fertilized ovum to adult takes between 6 and 17 months and does not have a larval stage. This is probably also the original mode of development. Velvet worms have been known to live for up to six years.

Ecology

Predators and parasites

The velvet worm's important predators are primarily various spiders and centipedes, along with rodents and birds, such as, in Central America, the Clay-coloured Thrush (*Turdus grayi*). Hemprichi's Coral Snake (*Micrurus hemprichii*) feeds almost exclusively on velvet worms. For defence, some species roll themselves reflexively into a spiral, while they can also fight off smaller opponents by ejecting slime.

Various mites (Acari) are known as ectoparasites, which infest the skin of the velvet worm. Skin injuries are usually accompanied by bacterial infections, which are almost always fatal.

Conservation status

The global conservation status of velvet worm species is difficult to estimate; many species are only known to exist at their type locality (the location at which they were first observed and described). The collection of reliable data is also hindered by low population densities, their typically nocturnal behaviour and possibly also as-yet undocumented seasonal influences and sexual dimorphism.

To date, only eleven species have been studied in sufficient detail to enable population estimates, of which three—*Opistopatus roseus*, *Speleoperipatus spelaeus* and *Peripatopsis leonina*—are considered critically endangered, the last being probably already extinct. Two species—*Macroperipatus insularis* and *Tasmanipatus anophthalmus*—are assessed by the IUCN as endangered, while four further species are listed as threatened.

The primary threat comes from destruction and fragmentation of velvet worm habitat due to industrialisation, draining of wetlands and "slash and burn" for agriculture. Many species also have naturally low population densities and closely restricted geographic ranges; as a result, relatively small localised disturbances of important ecosystems can lead to the extinction of entire populations or species. Collection of specimens for universities or research institutes also plays a role on a local scale.

There is a very pronounced difference in the protection afforded to velvet worms between regions: in some countries, such as South Africa, there are restrictions on both collecting and exporting, while in others, such as Australia, only export restrictions exist. Many countries offer no specific safeguards at all. Tasmania has a protection programme that is unique worldwide: one region of forest has its own velvet worm conservation plan, which is tailored to a particular velvet worm species.

Phylogeny

In their present forms, the velvet worms are probably very closely related to the arthropods, a very extensive taxon that incorporates, for instance, the crustaceans, insects and arachnids. They share, among other things, an exoskeleton consisting of α-chitin and non-collagenous proteins; gonads and waste-elimination organs enclosed in true coelom tissue; an open blood system with a tubular heart situated at the rear; an abdominal cavity divided into pericardial and perivisceral cavities; respiration via tracheae; and similar embryonic development. Segmentation, with two body appendages per segment, is also shared. However, antennae, mandibles and oral papillae are probably not homologous to the corresponding features in arthropods, i.e., they probably developed independently.

Another closely related group are the comparatively obscure water bears (Tardigrada); however, due to their very small size, these lack some characteristics of the velvet worms and arthropods, such as blood circulation and separate respiratory structures. Together, the velvet worms, arthropods and water bears form a monophyletic taxon, the Panarthropoda, i.e., the three groups collectively cover all descendants of their last common ancestor.

Due to certain similarities of form, the velvet worms were usually grouped with the water bears to form the taxon Protoarthropoda. This designation would imply that both velvet worms and water bears are not yet as highly developed as the arthropods. Modern systematic theories reject such conceptions of "primitive" and "highly developed" organisms and instead consider exclusively the historical relationships between the taxa. These relationships are not as yet fully understood, but it is considered probable that the velvet worms' sister groups form a taxon designated Tactopoda, thus:

For a long time, velvet worms were also considered related to the annelids. They share, among other things, a worm-like body; a thin and flexible outer skin; a layered musculature; paired waste-elimination organs; as well as a simply constructed brain and simple eyes. Decisive, however, was the existence of segmentation in both groups, with the segments showing only minor specialisation. The parapodia appendages found in annelids therefore correspond to the stump feet of the velvet worms.

Within the Articulata concept developed by Georges Cuvier, the velvet worms therefore formed an evolutionary link between the annelids and the arthropods: worm-like precursors first developed parapodia, which then developed further into stub feet as an intermediate link in the ultimate development of the arthropods' appendages. Due to their structural conservatism, the velvet worms were thus considered "living fossils". This perspective was expressed paradigmatically in the statement by the French zoologist A. Vandel:

Onychophorans can be considered highly evolved annelids, adapted to terrestrial life, which announced prophetically the Arthropoda. They are a lateral branch which has endured from ancient times until today, without important modifications.

Modern taxonomy strives to avoid criteria such as "higher" and "lower" states of development or distinctions between "main" and "side" branches—only family relationships indicated by cladistic methods are considered relevant. From this point of view, several common characteristics still support the Articulata concept—segmented body; paired appendages on each segment; pairwise arrangement of waste-elimination organs in each segment; and above all, a rope-ladder-like nervous system based on a double nerve strand lying along the belly.

An alternative concept, most widely accepted today, is the so-called Ecdysozoa hypothesis. This places the annelids and Panarthropoda in two very different groups: the former in the Lophotrochozoa and the latter in the Ecdysozoa. Mitochondrial gene sequences also provide support for this hypothesis.

Proponents of this hypothesis assume that the aforementioned similarities between annelids and velvet worms either developed convergently or were primitive characteristics passed unchanged from a common ancestor to both the Lophotrochozoa and Ecdysozoa. For example, in the first case, the rope-ladder nervous system would have developed in the two groups independently, while in the second case, it is a very old characteristic, which does not imply a particularly close relationship between the annelids and Panarthropoda.

The Ecdysozoa concept divides the taxon into two, the Panarthropoda into which the velvet worms are placed, and the sister group Cycloneuralia, containing the threadworms (Nematoda), horsehair worms (Nematomorpha) and three rather obscure groups: the mud dragons (Kinorhyncha); penis worms (Priapulida); and brush-heads (Loricifera).

Particularly characteristic of the Cycloneuralia is a ring of "circumoral" nerves around the mouth opening, which the proponents of the Ecdysozoa hypothesis also recognise in modified form in the details of the nerve patterns of the Panarthropoda. Both groups also share a common skin-shedding mechanism (ecdysis) and molecular biological similarities. One problem of the Ecdysozoa hypothesis is the velvet worms' subterminal mouth position: unlike in the Cycloneuralia, the mouth is not at the front end of the body, but lies further back under the belly. However, investigations into their developmental biology, particularly regarding the development of the head nerves, suggest that this was not always the case and that the mouth was originally terminal (situated at the tip of the body). This is supported by the fossil record.

The "stem-group arthropod" hypothesis is very widely accepted, but some trees suggest that the onychophorans may occupy a different position; their brain anatomy is more closely related to that of the chelicerates than to any other arthropod.

Evolutionary history

Fossils from the early Cambrian bear a striking resemblance to the velvet worms. These fossils, known collectively as the lobopods, were marine and probably represent a stem group to the oncyophorans. They are found in the Cambrian, Ordovician, Silurian and Pennsylvanian periods.

Historically, all fossil Onychophora and lobopods were lumped into the taxon Xenusia, further subdivided by some authors to the Paleozoic Udeonychophora and the Mesozoic/Tertiary Ontonychophora; living Onychophora were termed Euonychophora.

It is not clear when the transition to a terrestrial existence was made, but it is considered plausible that it took place between the Ordovician and late Silurian—approximately 490 to 420 million years ago—via the intertidal zone.

The low preservation potential of the non-mineralised Onychophora means that they have a sparse fossil record, and crown group representatives are known only from amber—there is a single, partial specimen from the Cretaceous, and a more comprehensive record in Eocene deposits from 40 million years ago.

Taphonomy

The vagarities of the preservation process can make fossils difficult to interpret. Experiments on the decay and compaction of onychophora demonstrate difficulties in interpreting fossils; certain parts of living onychophora are only visible in certain conditions. The mouth may or may not be preserved; claws may be re-oriented or lost; leg width may increase or decrease; and mud may be mistaken for organs. More significantly, features seen in fossils may be artefacts of the preservation process: for instance, "shoulder pads" may simply be the second row of legs compressed coaxially onto the body; branching "antennae" may in fact be produced through decay.

Taxonomy

The modern velvet worms form a monophyletic group, incorporating all the descendants of their common ancestor. Important common derivative characteristics (synapomorphies) include, for example, the mandibles of the second body segment and the oral papillae and associated slime glands of the third; nerve strands extending along the underside with numerous cross-linkages per segment; and the special form of the tracheae.

By 2004, some 155 modern species, comprising 47 genera, had been described; the actual number of species is probably about twice this. The best-known is the type genus *Peripatus*, which was described as early as 1825 and which, in English-speaking countries, stands representative for all velvet worms.

All genera are assigned to one of two families, the distribution ranges of which do not overlap but are separated by arid areas or oceans:

- The Peripatopsidae exhibit relatively many characteristics that are perceived as original or "primitive". They have between 13 and 25 pairs of legs, behind or between the last of which is the genital opening (gonopore). Both oviparous and ovoviviparous, as well as genuinely viviparous, species exist, although the Peripatopsidae essentially lack a placenta. Their distribution is circumaustral, encompassing Australia, Tasmania, New Zealand, New Guinea, South Africa and Chile.

- The Peripatidae exhibit a range of derivative features. They are longer, on average, than the Peripatopsidae and also have more leg pairs, numbering between 22 and 43—the gonopore is always between the penultimate pair. There are no oviparous species—the overwhelming majority are viviparous. The females of many viviparous species develop a placenta with which to provide the growing embryo with nutrients. Distribution of the Peripatidae is restricted to the tropical and subtropical zones; in particular, they inhabit Central and northern South America, several Caribbean islands, West Africa, northern India, Malaysia and various Indonesian islands.

Classification

- Phylum Onychophora
  - Class Onychophorida
    - Order † Paronychophora (extinct)
      - Family † Onychodictyidae
        - Genus † *Onychodictyon*
    - Order Euonychophora
      - Family Peripatidae
        - Genera: † *Cretoperipatus*, *Eoperipatus*, *Epiperipatus*, *Heteroperipatus*, *Macroperipatus*, *Mesoperipatus*, *Oroperipatus*, *Peripatus*, *Plicatoperipatus*, *Speleoperipatus*, *Typhloperipatus*
      - Family Peripatopsidae
        - Genera: *Acanthokara*, *Aethrikos*, *Akthinothele*, *Anoplokaros*, *Austroperipatus*, *Baeothele*,

        Centrorumis, *Cephalofovea*, *Critolaus*, *Dactylothele*, *Dystactotylos*, *Euperipatoides*, *Florelliceps*, *Hylonomoipos*, *Konothele*, *Lathropatus*, *Leuropezos*, *Mantonipatus*, *Metaperipatus*, *Minyplanetes*, *Nodocapitus*, *Occiperipatoides*, *Ooperipatellus*, *Ooperipatus*, *Opisthopatus*, *Paraperipatus*, *Paropisthopatus*, *Peripatoides*, *Peripatopsis*, *Phallocephale*, *Planipallipus*, *Regimitra*, *Ruhbergia*, *Sphenoparme*, *Symperipatus*, *Tasmania*, *Tasmanipatus*, *Tetrameraden*, *Vescerro*, *Wambalana*
    - Family † incertae sedis
        - Genus † *Helenodora*

Chapter 2

Peripatus and Typhloperipatus

Peripatus

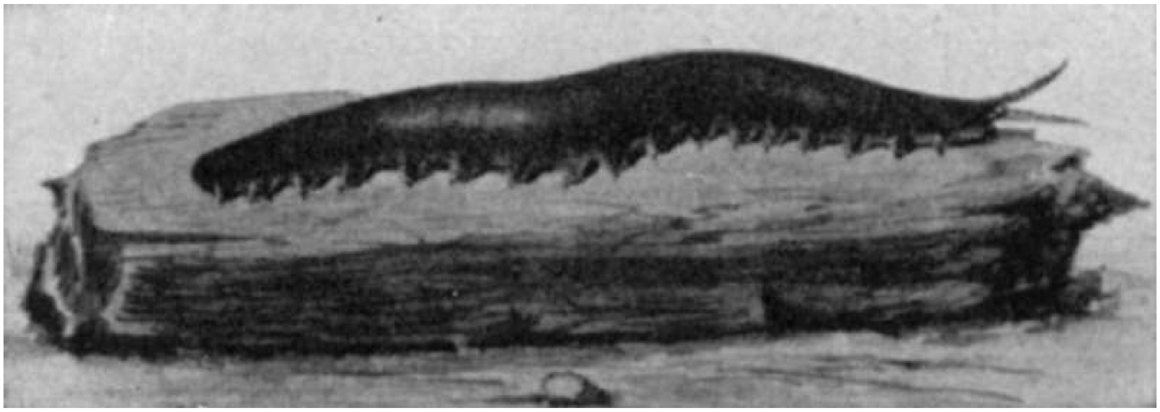
Peripatus

Scientific classification [e]

Kingdom:	Animalia
Phylum:	Onychophora
Class:	Onychophorida
Order:	Euonychophora
Family:	Peripatidae
Genus:	***Peripatus*** Guilding, 1826

Peripatus is a genus of Onychophora (velvet worms). It is a invertebrate which gives birth to live young rather than laying eggs. It is said to be a living fossil because it has been unchanged for approximately 570 million years. *Peripatus* are native to scattered places around the world including Australia, Africa, Asia, New Zealand, Costa Rica, Brazil and other countries, but not in Europe or Antarctica. *Peripatus* is a nocturnal carnivore. This unique animal has the appearance of a caterpillar with its many pairs of legs, while its structure has many similarities to arthropods, but it also has many similarities to annelids, with some special features all of its own.

Anatomy



A defenceless, weaponless animal, it comes out at night, and is said to capture small insects by squirting jets of slime from its mouth

Peripatus shows no external segmentation; the legs are not jointed like arthropod legs although they possess arthropod-like claws. The outer covering is a cuticle, which is covered in unique microscopic projections known as papillae. These papillae give *Peripatus* their velvet texture. The body is composed of segments like annelids with segmentally arranged nephridia. Peripatus respires through tracheae as arthropods do. Antennae are present on the head. Excretion is through nephridia, which are found in each of the legs.

Feeding

Peripatus feeds by trapping its prey (mostly small insects) in a white, sticky fluid it ejects from two antennae near its head. The fluid hardens on contact with the air immoblizing the prey. *Peripatus* then chews a hole in its prey's exoskeleton with its mandibles (which move independently of each other), injects digestive enzymes, and begins sucking out its prey's pre-digested innards.

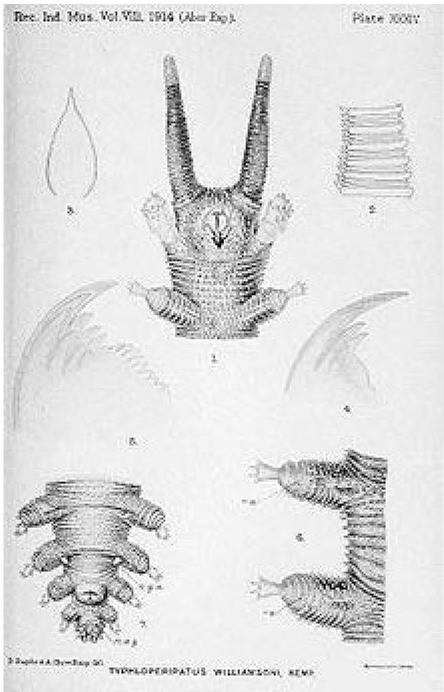
Species

- *Peripatus antiguensis* Bouvier, 1899
- *Peripatus bavaysi* Bouvier, 1899
- *Peripatus bouvieri* Fuhrmann, 1913
- *Peripatus brolemanni* Bouvier, 1899
- *Peripatus dominicae* Pollard, 1894
- *Peripatus evelinae* (Marcus, 1937)
- *Peripatus heloisae* Carvalho, 1941
- *Peripatus juanensis* Bouvier, 1900
- *Peripatus juliformis* Guilding, 1826
- *Peripatus manni* Brues, 1913
- *Peripatus ruber* Fuhrmann, 1913
- *Peripatus sedgwicki* Bouvier, 1899

- *Peripatus swainsonae* Cockerell, 1893

Typhloperipatus

Typhloperipatus



Scientific classification [e]

Kingdom:	Animalia
Phylum:	Onychophora
Class:	Onychophorida
Order:	Euonychophora
Family:	Peripatidae
Genus:	***Typhloperipatus***

Binomial name

Typhloperipatus williamsoni
Kemp, 1913

Typhloperipatus williamsoni is a species of onychophoran (or velvet worm) known from northeastern India. It is the only member of its genus and is the only South Asian species in the phylum. It is said to be evolutionarily close to the Sumatran *Eoperipatus*. It was discovered and described by Stanley Wells Kemp in 1913.

Discovery

The species name was after Noel Williamson, a political officer at Sadiya who was murdered in 1911. The murder led to an expedition being led to the Abor region by the British government in India. Stanley Kemp, then an assistant superintendent at the Indian Museum at Calcutta was a zoologist attached to this expedition. The first specimen was found near the gorge of the Dihang River near Rotung. Although the nearest other species from Malaya was typically found in dead wood, these were found mainly under large stones near the roots of trees. Like other velvet worms they discharges a spray of viscous fluid that hardens to trap and arrest small predators and prey.

Description

These velvet worms have no eyes. The colour of the upperside is a deep umber brown with the tips of the antennae slightly paler brown. The papillae on the skin have pale tips and the underside is pale brown. Some individuals have a dark dorsal stripe. It has 19 to 20 pairs of legs, the inner jaw has a serrate edge. The legs have coxal glands, four complete and spiny pads and the feet have two papillae.

Although Kemp believed that the species was closer to neotropical forms than to Southeast Asian forms, modern studies place them close to *Eoperipatus* of Southeast Asia.

Chapter 3

Acoelomorpha and Convolutidae

Acoelomorpha

Acoelomorphs

Waminoa sp. on *Plerogyra* sp..

Scientific classification [e]

Kingdom:	Animalia
Superphylum:	Deuterostomia (?)
Clade (?):	Xenacoelomorpha
Phylum:	**Acoelomorpha** Ehlers 1985

Classes

Acoela
Nemertodermatida

The **Acoelomorpha** are a disputed phylum of animals with planula-like features that have historically been considered to belong to the phylum Platyhelminthes. More recent molecular studies have demonstrated that they are a separate phylum, although their position in the tree of life is contentious; most researchers believe them to be basal among the Bilateria, slightly more derived than the cnidaria. Recent (2011) results suggest that they (along with *Xenoturbella*) may lie near the base of the deuterostomes.

Earlier (2007) work dismissed the phylum as paraphyletic, with Acoela and Nemertodermatida as separate clades.

An ongoing (Feb. 2011) collaborative research project has "the researchers ... confident that they can reach an agreement about where acoels fit in evolutionary history.

Acoels are almost entirely marine, living between grains of sediment, swimming as plankton, or crawling on algae. Acoels have a statocyst, which presumably helps them orient to gravity. Their soft bodies make them difficult to classify.

Anatomy

The Acoela are very small flattened worms, usually under 2 millimetres (0.079 in) in length (Symsagittifera roscoffensis about 15 mm), that do not have a gut. Digestion is accomplished by means of a syncytium that forms a vacuole around ingested food. There are no epithelial cells lining the digestive vacuole, although there is sometimes a short pharynx leading from the mouth to the vacuole. All other bilateral animals (apart from tapeworms) have a gut lined with epithelial cells. As a result, the acoels appear to be solid-bodied (*a-coel*, or *no body cavity*).

Acoelomorphs resemble flatworms in many respects, but have a simpler anatomy, even beyond the absence of a gut. Like flatworms, they have no circulatory or respiratory systems, but they also lack an excretory system. They have no true brain or ganglia, simply a network of nerves beneath the epidermis, although the nerves are slightly more concentrated towards the forward end of the animal. The sensory organs include a statocyst and, in some cases, very primitive pigment-spot ocelli capable of detecting light.

They are simultaneous hermaphrodites, but have no gonads, and no ducts associated with the female reproductive system. Instead, gametes are produced from the mesenchymal cells that fill the body between the epidermis and the digestive vacuole.

Convolutidae

Convolutidae

Scientific classification

Kingdom:	Animalia
Subkingdom:	Eumetazoa
Phylum:	Acoelomorpha
Class:	Acoela
Order:	not assigned
Family:	**Convolutidae**

Genera

Amphiscolops
Brachypea
Conaperta
Convoluta
Haplodiscus
Heterochaerus
Neochildia
Oligochoerus
Oxyposthia
Picola
Polychoerus
Stomatricha
Wulguru
Pseudoconvoluta?
Waminoa?

Convolutidae are a family of free-living flatworms.

Systematics

Currently the family contains 13 genera, the type genus being *Convoluta* (Turbellarian taxonomic database,2006).

The genus *Waminoa* appears, according to recent studies also belong to the family, or is at least closely related (Ogunlana et al., 2005).

Characteristics

Acoels with a ventral mouth opening. Body-wall musculature with circular, longitudinal, and longitudinal crossover muscle fibers in both the dorsal and ventral body wall, and U-shaped fibers in the ventral body wall.

Male copulatory organ with muscular, often glandular, tubular penis. Penis musculature with inner circular fibers and outer longitudinal fibers that anastomose or cross over each other. When present, a muscular seminal vesicle surrounds all of, or a portion of the penis. Male gonopore ventral, subterminal, or terminal at posterior end; usually positioned behind opening to female seminal bursa. Spermatozoa with 9+0 axonemes and axial microtubules.

Algal symbionts often present. Ocelli, when present, contain reflective platelets in the pigment cell and lack cilia or microvilli as receptor organelles (Hooge & Tyler, 2005).

Species

Amphiscolops

Contains the following species:

- *Amphiscolops bermudensis* Hyman 1939
- *Amphiscolops blumi* Achatz, Hooge & Tyler, 2007
- *Amphiscolops carvalhoi* Marcus 1952
- *Amphiscolops cinereus* (Graff, 1874)
- *Amphiscolops evelinae* Marcus 1947
- *Amphiscolops fuligineus* Peebles 1913
- *Amphiscolops gemelliporus* Marcus 1954
- *Amphiscolops japonicus* Kato 1947
- *Amphiscolops langerhansi* (Graff, 1882)
- *Amphiscolops marinelliensis* Beltagi & Khafagi, 1984
- *Amphiscolops mosaicus* Kozloff 1998
- *Amphiscolops potocani* Achatz, 2008
- *Amphiscolops trifurcatus* (Beltagi 1983)
- *Amphiscolops zeii* Riedl 1956

Brachypea

Contains the following species:

- *Brachypea kenoma* Antonius 1968

Conaperta

Contains the following species:

- *Conaperta antonii* Achatz, Hooge & Tyler, 2007
- *Conaperta cirrata* Achatz, Hooge & Tyler, 2007

Haplodiscus

Contains the following species:

- *Haplodiscus acuminatus* Böhmig, 1895
- *Haplodiscus bocki* Dörjes 1970
- *Haplodiscus obtusus* Böhmig, 1895
- *Haplodiscus ovatus* Böhmig, 1895
- *Haplodiscus piger* Weldon 1888
- *Haplodiscus weldoni* Böhmig, 1895

Heterochaerus

Contains the following species:

- *Heterochaerus australis* Haswell 1905
- *Heterochaerus sargassi* (Hyman 1939)

Neochildia

Contains the following species:

- *Neochildia fusca* Bush, 1975

Oligochoerus

Contains the following species:

- *Oligochoerus bakuensis* Beklemischev 1963
- *Oligochoerus chlorella* Beklemischev 1963
- *Oligochoerus conops* Beklemischev, 1963
- *Oligochoerus erythrophthalmus* Beklemischev 1963
- *Oligochoerus limnophilus* Ax & Doerjes 1966

- *Conaperta flavibacillum* (Jensen, 1878)
- *Conaperta krana* Antonius 1968
- *Conaperta lineata* (Peebles, 1915)
- *Conaperta thela* Antonius 1968

Convoluta

Contains the following species:

- *Convoluta aegyptica* Antonius 1968
- *Convoluta albomaculata* (Pereyaslawzewa, 1892)
- *Convoluta bohmigi* (Brauner, 1920)
- *Convoluta borealis* Sabussow 1900
- *Convoluta boyeri* Bush 1984
- *Convoluta confusa* Graff 1904
- *Convoluta convoluta* (Abildgaard, 1806)
- *Convoluta elegans* Pereyaslawzewa 1892
- *Convoluta enelitta* Antonius 1968
- *Convoluta furugelmi* Mamkaev, 1971
- *Convoluta henseni* Böhmig, 1895
- *Convoluta hipparchia* Pereyaslawzewa 1892
- *Convoluta kikaiensis* Yamasu 1982
- *Convoluta lacazii* Graff 1891
- *Convoluta lacrimosa* Achatz, Hooge & Tyler, 2007
- *Convoluta marginalis* Ivanov 1952
- *Convoluta naviculae* Yamasu 1982
- *Convoluta niphoni* Achatz, 2008
- *Convoluta pelagica* Lohner & Micoletzky 1911
- *Convoluta philippinensis* Bush 1984
- *Convoluta pygopora* Antonius
- *Oligochoerus melanops* Beklemischev 1963
- *Oligochoerus xanthella* Beklemischev 1963

Oxyposthia

Contains the following species:

- *Oxyposthia praedator* Ivanov 1952

Picola

Contains the following species:

- *Picola renei* Achatz & Hooge, 2006

Polychoerus

Contains the following species:

- *Polychoerus carmelensis* Costello and Costello, 1938
- *Polychoerus caudatus* Mark 1892
- *Polychoerus ebenhochi* Achatz, Hooge & Tyler, 2007
- *Polychoerus parvus* Achatz, Hooge & Tyler, 2007

Praesagittifera

Contains the following species:

- *Praesagittifera gracilis* (Yamasu, 1982)
- *Praesagittifera naikaiensis* (Yamasu, 1982)
- *Praesagittifera shikoki* Kostenko & Mamkaev 1990

Stomatricha

Contains the following species:

- *Stomatricha hochbergi* Hooge,

1968

- *Convoluta schmidti* Czerniavsky, 1881
- *Convoluta schuelii* Achatz, 2008
- *Convoluta sordida* Graff 1882
- *Convoluta sutcliffei* Hanson, 1961
- *Convoluta variabilis* (Pereyaslawzewa, 1892)

2003

Waminoa

Contains the following species:

- *Waminoa brickneri* Ogunlana, Hooge, Tekle, Benayahu, Barneah & Tyler, 2005
- *Waminoa litus* Winsor 1990

Wulguru

Contains the following species:

- *Wulguru cuspidata* Winsor 1988

Chapter 4

Brachiopod

Brachiopod
Temporal range: Lower Cambrian–Recent

Platystrophia ponderosa (Ordovician). Scale bar is 5.0 mm.

Scientific classification [e]

Kingdom:	Animalia
(unranked):	Protostomia
(unranked):	Spiralia
Superphylum:	Lophotrochozoa
Phylum:	**Brachiopoda** Duméril, 1806

Diversity

About 100 living genera.
About 5,000 fossil genera.

Brachiopods are a phylum of marine animals that have hard "valves" (shells) on the upper and lower surfaces. Most species of brachiopod went extinct during the P–T extinction over 250 million years ago, but many survive today.

Brachiopod valves are hinged at the rear end, while the front can be opened for feeding or closed for protection. Articulate brachiopods have toothed hinges and simple opening and closing muscles, while inarticulate brachiopods have untoothed hinges and more complex muscles. In a typical brachiopod a stalk-like pedicle projects from an opening in the hinge or from a hole in the larger valve, attaching the animal to the sea bed but clear of silt that would obstruct the opening.

Brachiopods have a mantle that secretes and lines the shell, and encloses the internal organs. The body occupies typically about one-third of the internal space inside the shell, nearest the hinge. The rest of the mantle encloses a water-filled space containing the lophophore, a crown of tentacles that filters food particles out of the water. In all species the lophophore is supported by cartilage and by a hydrostatic skeleton.

The lophophore filters food, mostly phytoplankton, out of the water. From there the food is transported in succession to: the grooves along the bases of the lophophore's tentacles; the mouth; pharynx; oesophagus; and finally the stomach, where the food is digested. Nutrients are transported from the stomach throughout the coelom (main body cavity), including the mantle lobes, by cilia. The wastes produced by metabolism are broken into ammonia, which is eliminated by diffusion through the mantle and lophophore.

The lophophore and mantle are the only surfaces that absorb oxygen and eliminate carbon dioxide. Oxygen seems to be distributed by the fluid of the coelom. The heart is above the stomach, and the blood vessels connect it to the major organs. However, the main function of the blood may be to deliver nutrients. The maximum oxygen consumption of brachiopods is low, and their minimum requirement is not measurable.

The "brain" of adult articulates consists of two ganglia, one above and the other below the oesophagus. Adult inarticulates have only the lower ganglion. Nerves run to the lophophore, the mantle lobes and the muscles that operate the valves. Many brachiopods close their valves if shadows appear above them, but the cells responsible for this are unknown. Some brachiopods have statocysts which detect changes in the animals' balance.

Lifespans range from 3 to over 30 years. Ripe gametes (ova or sperm) float from the gonads into the main coelom and then exit into the mantle cavity. The larvae of inarticulate brachiopods are miniature adults, with lophophores that enable the larvae to feed and swim for months, until the animals become heavy enough to settle to the seabed. Larvae of articulate species are different from the adult forms, live only on yolk, and remain among the plankton for only a few days before metamorphosing.

The traditional classification into inarticulate and articulate brachiopods has been supplemented by two refinements that appeared in the 1990s. One refinement groups the inarticulate Craniida with articulate brachiopods, as both used the same material in the mineral layers of the shell. The other segregates the Craniida into a third group, as their outer organic layer is different from that of either the others. However, some taxonomists believe it is premature to define the higher levels of classification such as order, and recommend instead a bottom-up approach that identifies genera and then groups these into intermediate groups. Traditionally brachiopods have been regarded as members of or as a sister group to the deuterostomes, a super-phylum which includes chordates and echinoderms. One type of analysis of brachiopods' evolutionary relationships has always placed brachiopods as protostomes, while another type has split between placing brachiopods among the protostomes or the deuterostomes.

In 2003 it was suggested that brachiopods evolved from an ancestor similar to *Halkieria*, a slug-like animal with "chain mail" on its back and a shell at the front and rear end, and that the ancestral brachiopod converted its shells into a pair of valves by folding the rear part of its body under its front. However, new fossils found in 2007 to 2008 suggest that brachiopods evolved from tommotiids: the tommotiids' "chain mail" formed the tube of a sessile animal resembling brachiopods. Lineages that have both fossil and extant brachiopods appeared in the early Cambrian, Ordovician and Carboniferous periods. Other lineages have arisen and then become extinct, sometimes during severe mass extinctions. At their peak in the Paleozoic era the brachiopods were among the most abundant filter-feeders and reef-builders, and occupied other ecological niches, including swimming in the jet-propulsion style of scallops. Brachiopod fossils have been useful indicators of climate changes during the Paleozoic era. However, after the Permian–Triassic extinction event, brachiopods recovered only a third of their former diversity. A study in 2007 concluded that brachiopods were especially vulnerable to the Permian–Triassic extinction, as they built calcareous hard parts (made of calcium carbonate) and had low metabolic rates and weak respiratory systems. It was often thought that brachiopods were in decline after the Permian–Triassic extinction, and were out-competed by bivalves. However, a study in 1980 concluded that both brachiopods and bivalves increased all the way from the Paleozoic to modern times, but bivalves increased faster; after the Permian–Triassic extinction, brachiopods for the first time were less diverse than bivalves.

Brachiopods live only in the sea, and most species avoid locations with strong currents or waves. Articulate species have larvae that settle quickly and form dense populations in well-defined areas, while inarticulate larvae swim for up to a month and have wide ranges. Brachiopods now live mainly in cold and low-light conditions. Fish and crustaceans seem to find brachiopod flesh distasteful and seldom attack them. Among brachiopods only the lingulids have been fished commercially, on a very small scale. One brachiopod species may be a measure of environmental conditions around an oil terminal being built in Russia on the shore of the Sea of Japan.

Description

Name

Some brachiopod species are shaped like this oil lamp

The scientific name "Brachiopod" is formed from the Ancient Greek words βραχίων ("arm") and πούς ("foot"). They are often known as "lamp shells", since the curved shells of the class Terebratulida look rather like pottery oil-lamps.

Shells and their mechanisms

An articulate brachiopod:
▆ Pedicle valve

⬜ Brachial valve
🟪 Pedicle
🟫 Surface

Modern brachiopods range from 1 to 100 millimetres (0.039 to 3.9 in) long, and most species are about 10 to 30 millimetres (0.39 to 1.2 in). Each has two valves (shell sections) which are biomineralized. The valves cover the dorsal and ventral surface of the animal, unlike bivalve molluscs whose shells cover the lateral surfaces. The brachial valve bears on its inner surface the brachia ("arms") from which the phylum gets its name, and which supports the lophophore, used for filtering and respiration. The other is known as the pedicle valve, as its inner surface bears the stalk-like pedicle by which most brachiopods attach themselves to surfaces. The brachial and pedicle valves are often called the dorsal ("upper") and ventral ("lower"), but some paleontologists regard "dorsal" and "ventral" as incorrect terms, since they believe that the "ventral" valve was formed by folding of the upper surface under the body. Irrespective of this debate, the valves of brachiopods are differently arranged of those of bivalve molluscs, which lie on the left and right sides of the body. In most brachiopod species both valves are convex, the surfaces often bear growth lines or other ornaments, and the pedicle valve is larger than the brachial. However, the lingulids, which burrow into the seabed, have valves that are smoother, flatter and of similar size and shape.

Brachiopod valves have a hinge, in which the rearmost end of the brachial valve rocks on an internal projection of the pedicle valve. The internal projections of articulate ("jointed") brachiopods have teeth which fit into sockets on the brachial valve, an arrangement that locks the valves together. Inarticulate brachiopods have no matching teeth and sockets, and their valves are held together only by muscles.

All brachiopods have adductor muscles, that are set on the inside of the pedicle valve and close the valves by pulling on the part of the brachial valve ahead of the hinge. These muscles have both "quick" fibers that close the valves in emergencies and "catch" fibers that are slower but can keep the valves closed for long periods. Articulate brachiopods open the valves by means of abductor muscles, also known as diductors, which lie further to the rear and pull on the part of the brachial valve behind the hinge. Inarticulate brachiopods use a different opening mechanism, in which muscles reduce the length of the coelom (main body cavity) and make it bulge outwards, pushing the valves apart. Both classes open the valves to an angle of about 10°. The more complex set of muscles employed by inarticulate brachiopods can also operate the valves as scissors, a mechanism that lingulids use to burrow.

The inarticulate species *Lingula anatina*, showing the long pedicle, flattened shells and prominent chetae around the front edge of the shells

Each valve consists of three layers, an outer periostracum made of organic compounds and two biomineralized layers. Articulated brachiopods have a periostracum made of proteins, a "primary layer" of calcite (a form of calcium carbonate) under that, and finally a mixture of proteins and calcite. Inarticulate brachiopod shells have a similar sequence of layers, but their composition is different from that articulated brachiopods and also varies between the classes of inarticulate brachiopods. Linguids and discinids, which have pedicles, have a matrix of glycosaminoglycans (long, unbranched polysaccharides), in which other material are embedded: chitin in the periostracum; apatite containing calcium phosphate in the primary biomineralized layer; and a complex mixture in the innermost layer, containing collagen and other proteins, chitinophosphate and apatite.

Craniids, which have no pedicle and cement themselves directly to hard surfaces, have a periostracum of chitin and mineralized layers of calcite.

Mantle

Like molluscs, brachiopods have a mantle, an epithelium that lines the shell and encloses the internal organs. The brachiopod body occupies only about one-third of the internal space inside the shell, nearest the hinge. The rest of the space is lined with the mantle lobes, extensions that enclose a water-filled space in which sits the lophophore. The coelom extends into each lobe as a network of canals, which carry nutrients to the edges of the mantle.

Relatively new cells in a groove on the edges of the mantle secrete material that extends the periostracum. These cells are gradually displaced to the underside of the mantle by more recent cells in the groove, and switch to secreting the mineralized material of the shell valves. In other words, on the edge of the valve the periostracum is extended first, and then reinforced by extension of the mineralized layers under the periostracum. In most species the edge of the mantle also bears movable bristles, often called chaetae or setae, that may help defend the animals and may act as sensors. In some brachiopods groups of chaetae help to channel the flow of water into and out of the mantle cavity.

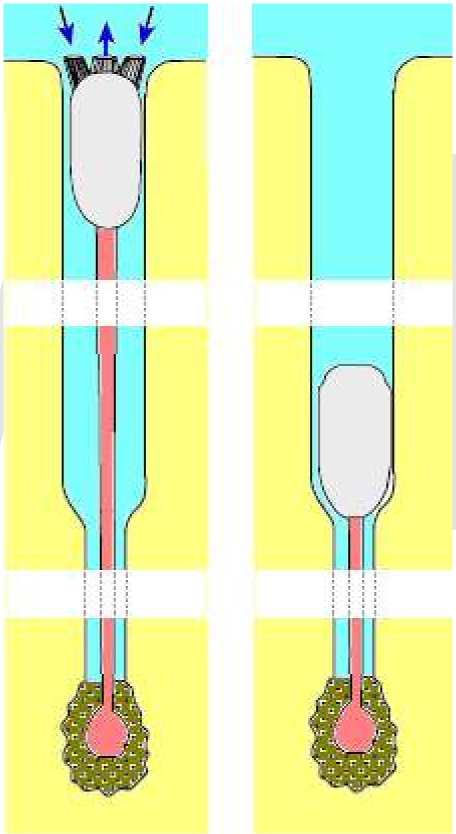
In most brachiopods, diverticula (hollow extensions) of the mantle penetrate through the mineralized layers of the valves into the periostraca. The function of these diverticula is uncertain and it is suggested that they may be storage chambers for chemicals such as glycogen, may secrete repellents to deter organisms that stick to the shell or may help in respiration. Experiments show that a brachiopod's oxygen consumption drops if petroleum jelly is smeared on the shell, clogging the diverticula.

Lophophore

Like bryozoans and phoronids, brachiopods have a lophophore, a crown of tentacles whose cilia (fine hairs) create a water current that enables them to filter food particles out of the water. However a bryozoan or phoronid lophophore is a ring of tentacles mounted on a single, retracted stalk, while the basic form of the brachiopod lophophore is U-shaped, forming the brachia ("arms") from which the phylum gets its name. Brachiopod lophophores are non-retractable and occupy up to two-thirds of the internal space, in the frontmost area where the valves gape when opened. To provide enough filtering capacity in this restricted space, lophophores of larger brachiopods are folded in moderately to very complex shapes – loops and coils are common, and some species' lophophores resemble a hand with the fingers splayed. In all species the lophophore is supported by cartilage and by a hydrostatic skeleton (in other words by the pressure of its internal fluid), and the fluid extends into the tentacles. Some articulate brachiopods also have a brachidium, a calcareous support for the lophophore attached to the inside of the brachial valve.

The tentacles bear cilia (fine mobile hairs) on their edges and along the center. The beating of the outer cilia 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 the cillia down the middle drive this mixture to the base of the tentacles. A brachial groove runs round the bases of the tentacles, and its own cilia pass food along the groove towards the mouth. The method used by brachiopods is known as "upstream collecting", as food particles are captured as they enter the field of cilia that creates the feeding current. This method is used by the related phoronids and bryozoans, and also by pterobranchs. Entoprocts use a similar-looking crown of tentacles, but it is solid and the flow runs from bases to tips, forming a "downstream collecting" system that catches food particles as they are about to exit.

Attachment to substrate



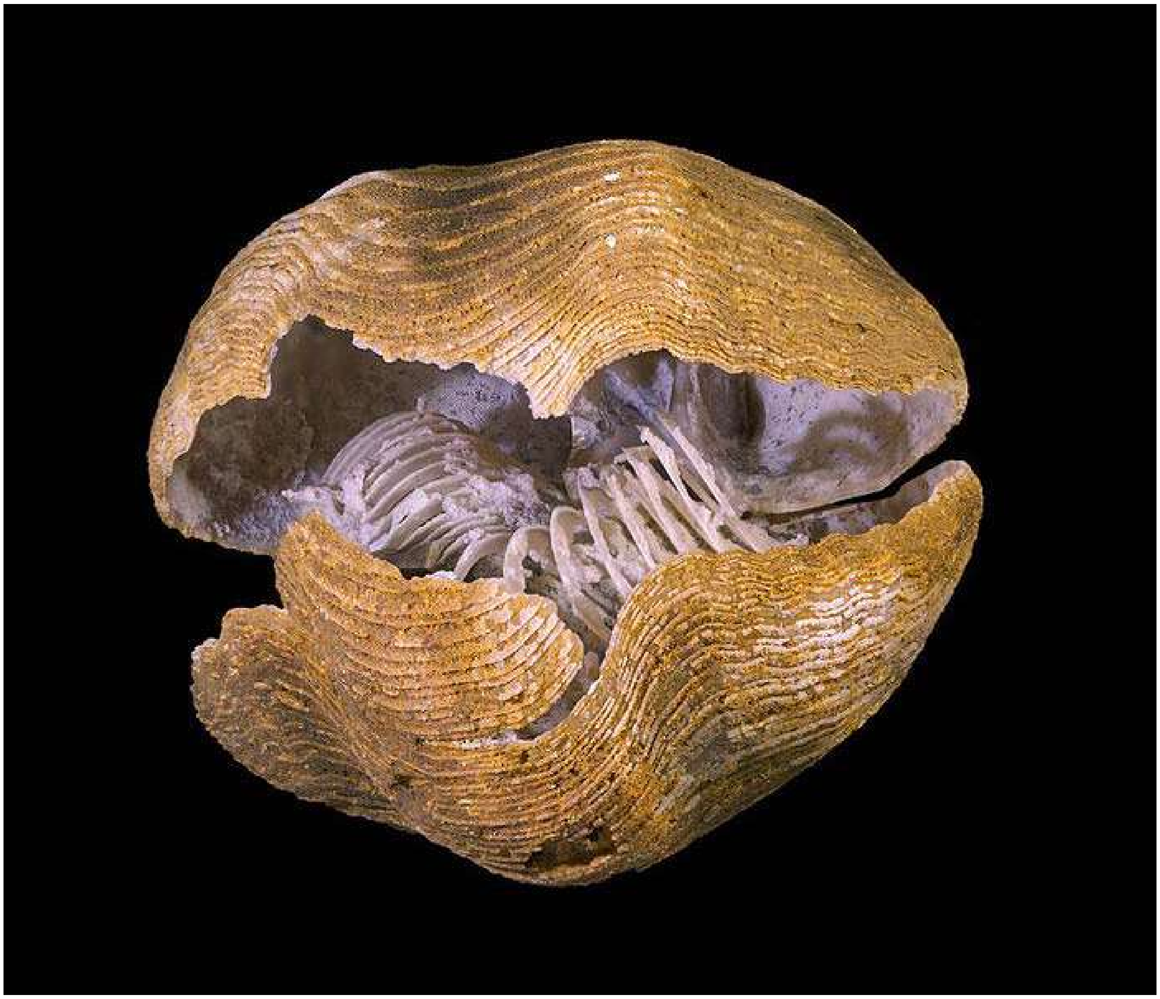
A lingulid in in its burrow, in "up" and retracted positions

Most modern species attach to hard surfaces by means of a cylindrical pedicle ("stalk"), an extension of the body wall. This has a chitinous cuticle (non-cellular "skin") and protrudes through a opening in the hinge. However, some genera such as the inarticulate *Crania* and the articulate *Lacazella* have no pedicle, and cement the rear of the "pedicle" valve to a surface so that the front is slightly inclined up away from the surface. In a few articulate genera such as *Neothyris* and *Anakinetica*, the pedicles wither as the adults grow and finally lie loosely on the surface. In these genera the shells are thickened and shaped so that the opening of the gaping valves is kept free of the sediment.

Pedicles of inarticulate species are extensions of the main coelom, which houses the internal organs. A layer of longitudinal muscles lines the epidermis of the pedicle. Members of the order Lingulida have long pedicles, which they use to burrow into soft substrates, to raise the shell to the opening of the burrow to feed, and to retract the shell when disturbed. A lingulid moves its body up and down the top two-thirds of the burrow, while the remaining third is occupied only by the pedicle, with a bulb on the end that builds a "concrete" anchor. However, the pedicles of the order Discinida are short and attach to hard surfaces.

An articulate pedicle has no coelom, is constructed from a different part of the larval body, and has a core composed of connective tissue. Muscles at the rear of the body can straighten, bend or even rotate the pedicle. The far end of the pedicle generally has rootlike extensions or short papillae ("bumps") which attach to hard surfaces. However, articulate brachiopods of genus *Chlidonophora* use a branched pedicle to anchor in sediment. The pedicle emerges from the pedicle valve, either through a notch in the hinge or, in species where the pedicle valve is longer than the brachial, from a hole where the pedicle valve doubles back to touch the brachial valve. Some species stand with the front end upwards, while others lie horizontal with the pedicle valve uppermost.

Feeding and excretion



Spiriferina rostrata with visible skeleton of the lophophore

The water flow enters the lophophore from the sides of the open valves and exits at the front of the animal. In lingulids the entrance and exit channels are formed by groups of chaetae that function as funnels. In other brachiopods the entry and exit channels are organized by the shape of the lophophore. The lophophore captures food particles, especially phytoplankton (tiny photosynthetic organisms), and deliver them to the mouth via the brachial grooves along the bases of the tentacles. The mouth is at the base of the lophophore. Food passes through the mouth, muscular pharynx ("throat") and oesophagus ("gullet"), all of which are lined with cilia and cells that secrete mucus and digestive enzymes. The stomach wall has branched ceca ("pouches") where food is digested, mainly within the cells.

Nutrients are transported throughout the coelom, including the mantle lobes, by cilia. The wastes produced by metabolism are broken into ammonia, which is eliminated by diffusion through the mantle and lophophore. Brachiopods have metanephridia, used by many phyla to excrete ammonia and other dissolved wastes. However, brachiopods have no sign of the podocytes which perform the first phase of excretion in this process, and brachiopod metanephridia appear to be used only to emit sperm and ova.

The majority of food consumed by brachiopods is digestible, with very little solid waste produced. The cilia of the lophophore can change direction to eject isolated particles of indigestible matter. If the animal encounters larger lumps of undesired matter, the cilia lining the entry channels pause and the tentacles in contact with the lumps move apart to form large gaps and then slowly use their cilia to dump the lumps onto the lining of the mantle. This has its own cilia, which wash the lumps out through the opening between the valves. If the lophophore is clogged, the adductors snap the valves sharply, which creates a "sneeze" that clears the obstructions. In some inarticulate brachiopods the digestive tract is U-shaped and ends with an anus that eliminates solids from the front of the body wall. Other inarticulate brachiopods and all articulate brachiopods have a curved gut that ends blindly, with no anus. These animals bundle solid waste with mucus and periodically "sneeze" it out, using sharp contractions of the gut muscles.

Circulation and respiration

The lophophore and mantle are the only surfaces that absorb oxygen and eliminate carbon dioxide. Oxygen seems to be distributed by the fluid of the coelom, which is circulated through the mantle and driven either by contractions of the lining of the coelom or by beating of its cilia. In some species oxygen is partly carried by the respiratory pigment hemerythrin, which is transported in coelomocyte cells.

Brachiopods also have colorless blood, circulated by a muscular heart which lies in the dorsal part of the body above the stomach. The blood passes through vessels that extend to the front and back of the body, and branch to organs including the lophophore at the front and the gut, muscles, gonads and nephridia at the rear. The blood circulation seems not to be completely closed, and the coelomic and blood fluids must mix to a degree. The main function of the blood may be to deliver nutrients.

Nervous system and senses

The "brain" of adult articulates consists of two ganglia, one above and the other below the oesophagus. Adult inarticulates have only the lower ganglion. From the ganglia and the commissures where they join, nerves run to the lophophore, the mantle lobes and the muscles that operate the valves. The edge of the mantle has probably the greatest concentration of sensors. Although not directly connected to sensory neurons, the mantle's chaetae probably send tactile signals to receptors in the epidermis of the mantle. Many brachiopods close their valves if shadows appear above them, but the cells responsible for this are unknown. Some brachiopods have statocysts which detect changes in the animals' position.

Reproduction and lifecycle

Lifespans range from 3 to over 30 years. Adults of most species are of one sex throughout their lives. The gonads are masses of developing gametes (ova or sperm), and most species have four gonads, two in each valve. Those of articulates lie in the channels of the mantle lobes, while those of inarticulates lie near the gut. Ripe gametes float into the main coelom and then exit into the mantle cavity via the metanephridia, which open on either side of the mouth. Most species release both ova and sperm into the water, but females of some species keep the embryos in brood chambers until the larvae hatch.

The cell division in the embryo is radial (cells form in stacks of rings directly above each other), holoblastic (cells are separate, although adjoining) and regulative (the type of tissue into which a cell develops is controlled by interactions between adjacent cells, rather than rigidly within in each cell). While some animals develop the mouth and anus by deepening the blastopore, a "dent" in the surface of the early embryo, the blastopore of brachiopods closes up, and their mouth and anus develop from new openings.

The larvae of inarticulates swim as plankton for months and are like miniature adults, with valves, mantle lobes, a pedicle that coils in the mantle cavity, and a small lophophore, which is used for both feeding and swimming – except that Craniids have no pedicle. As the shell becomes heavier, the juvenile sinks to the bottom and becomes a sessile adult. The larvae of articulate species live only on yolk, and remain among the plankton for only a few days. This type of larva has a ciliated frontmost lobe that becomes the body and lophophore, a rear lobe that becomes the pedicle, and a mantle like a skirt, with the hem towards the rear. On metamorphosing into an adult, the pedicle attaches to a surface, the front lobe develops the lophophore and other organs, and the mantle rolls up over the front lobe and starts to secrete the shell. The maximum oxygen consumption of brachiopods is low, and their minimal requirement is not measurable. In cold seas, brachiopod growth is seasonal and the animals often lose weight in winter. These variations in growth often form growth lines in the shells. Members of some genera have survived for a year in aquaria without food.

Taxonomy

The fossil brachiopod genera have great diversity but only a few skeletal characteristics, while the modern genera have much lower diversity but provide soft-bodied characteristics as well as skeletal ones – and both sets of specimens have limitations that make it difficult to produce a comprehensive classification of brachiopods. The phylum also has experienced significant convergent evolution and reversals (in which a more recent group seems to have lost a characteristic that is seen in an intermediate group, reverting to a characteristic last seen in an older group). Hence some brachiopod taxonomists believe it is premature to define higher levels of classification such as order, and recommend instead a bottom-up approach that identifies genera and then groups these into intermediate groups.

However, other taxonomists believe that some patterns of characteristics are sufficiently stable to make higher-level classifications worthwhile, although there are different views about what the higher-level classifications should be. The "traditional" classification was defined in 1869; two further approaches were established in the 1990s:

- In the "traditional" classification, the Articulata have toothed hinges between the valves, while the hinges of the Inarticulata are held together only by muscles.
- A classification devised in the 1990s, based on the materials of which the shells are based, united the Craniida and the "articulate" brachiopods in the Calciata, which have calcite shells. The Lingulida and Discinida, combined in the Lingulata, have shells made of chitin and calcium phosphate.
- A three-part scheme, also from the 1990s, places the Craniida in a separate group of its own, the Craniformea. The Lingulida and Discinida are grouped as Linguliformea, and the Rhynchonellida and Terebratulida as Rhynchonelliformea.

Three high-level classifications of brachiopods					
"Traditional" classification	**Inarticulata**			**Articulata**	
"Calciata" approach	**Lingulata**		**Calciata**		
Three-part approach	**Linguliformea**		**Craniformea**	**Rhynchonelliformea**	
Orders	**Lingulida**	**Discinida**	**Craniida**	**Terebratulida**	**Rhynchonellida**
Hinge	No teeth			Teeth and sockets	
Anus	On front of body, at end of U-shaped gut			None	
Pedicle	Contains coelom with muscles running through		No pedicle	No coelom, muscles where joins body	
	Long, burrows	Short, attached to hard surfaces	None, cemented to surface	Short, attached to hard surfaces	
Periostracum	Glycosaminoglycans and chitin		Chitin	Proteins	
Primary (middle) mineralized layer of shell	Glycosaminoglycans and apatite (calcium phosphate)		Calcite (a form of calcium carbonate)		
Inner mineralized layer of shell	Collagen and other proteins, chitinophosphate and apatite (calcium phosphate)		Calcite	Proteins and calcite	

Chetae around opening of shells	Yes	No	Yes
Coelom fully divided	Yes	No	Yes

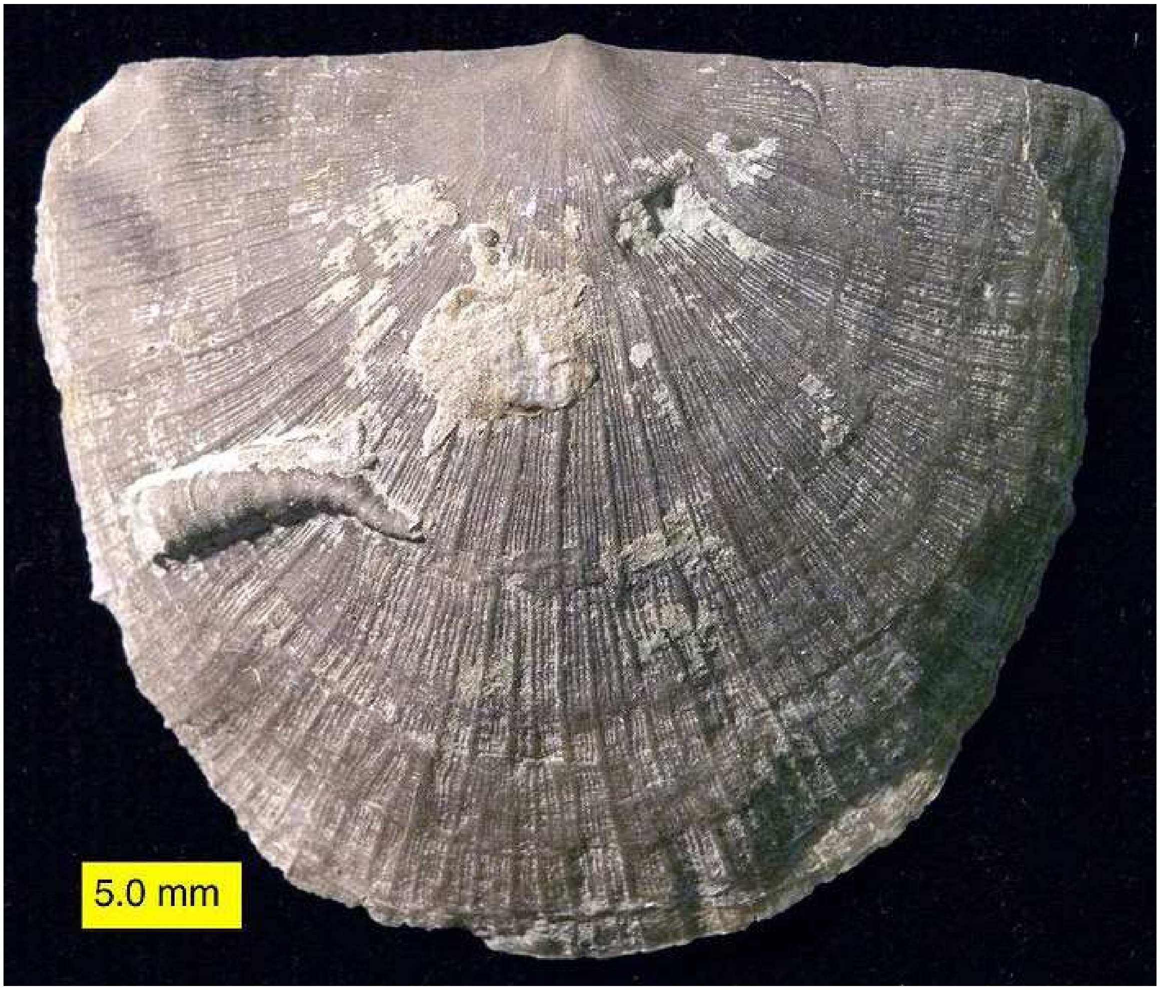
About 330 living species are recognized, grouped into over 100 genera. The great majority of modern brachiopods are rhynchonelliforms (Articulata, but excluding Craniida).

Ecology

Distribution and habitat

Brachiopods live only in the sea. Most species avoid locations with strong currents or waves, and typical sites include rocky overhangs, crevices and caves, steep slopes of continental shelves, and in the bottoms of deep oceans. However, some articulate species attach to kelp or in exceptionally sheltered sites in intertidal zones. The smallest living brachiopod, *Gwynia*, is only about 1 millimetre (0.039 in) long, and lives in gravel. Rhynchonelliforms (Articulata excluding Craniida), whose larvae consume only their yolks and settle and develop quickly, specialize in specific areas and form dense populations that can reach thousands per meter. Young adults often attach to the shells of more mature ones. On the other hand, inarticulate brachipods, whose larva swim for up to a month before settling, have wide ranges. Members of the discinoid genus *Pelagodiscus* have a cosmopolitan distribution.

Interactions with other organisms



Strophomenid brachiopod with attached cornulitid worm tube (Upper Ordovician, SE Indiana, USA). Brachiopod valves often serve as substrates for encrusting organisms.

Brachiopod metabolisms is 3 to 10 times slower than that of bivalves. While brachiopods were abundant in warm, shallow seas during the Cretaceous period, they have been out-bred by bivalves, and now live mainly in cold and low-light conditions.

Brachiopod shells occasionally show evidence of damage by predators, and sometimes of subsequent repair. Fish and crustaceans seem to find brachiopod flesh distasteful. The fossil record shows that drilling predators like gastropods attacked molluscs and echinoids 10 to 20 times more often than they did brachiopods, suggesting that such predators attacked brachiopods by mistake or when other prey was scarce. In waters where food is scarce, the snail *Capulus ungaricus* steals food from bivalves, snails, tube worms, and brachiopods.

Among brachiopods only the lingulids have been fished commercially, and only on a very small scale. Brachiopods seldom settle on artificial surfaces, probably because they are vulnerable to pollution. This may make the population of *Coptothyrus adamsi* useful as a measure of environmental conditions around an oil terminal being built in Russia on the shore of the Sea of Japan.

Evolutionary history

Over 12,000 fossil species are recognized,grouped into over 5,000 genera. While the largest modern brachiopods are 100 millimetres (3.9 in) long, a few fossils measure up to 200 millimetres (7.9 in) wide. The earliest confirmed brachiopods have been found in the early Cambrian, inarticulate forms appearing first, followed soon after by articulate forms. Three unmineralized species have also been found in the Cambrian, and apparently represent two distinct groups that evolved from mineralized ancestors. The inarticulate *Lingula* is often called a "living fossil", as very similar genera have been all the way back to the Ordovician. On the other hand, articulate brachiopods have produced major diversifications, and severe mass extinctions – but the articulate Rhynchonellida and Terebratulida, the most diverse present-day groups, appeared at the start of the Ordovician and Carboniferous respectively.

Since 1991 Nielsen has proposed a hypothesis about the development of brachiopods, adapted in 2003 by Cohen and colleagues as a hypothesis about the earliest evolution of brachiopods. This "brachiopod fold" hypothesis suggests that brachiopods evolved from an ancestor similar to *Halkieria*, a slug-like animal with "chain mail" on its back and a shell at the front and rear end. The hypothesis proposes that the first brachiopod converted its shells into a pair of valves by folding the rear part of its body under its front.

However, fossils from 2007 onwards have supported a new interpretation of the Early-Cambrian tommotiids and a new hypothesis that brachiopods evolved from tommotiids. The "armor mail" of tommotiids was well-known but not in a assembled form, and it was generally assumed that tommotiids were slug-like animals similar to *Halkieria*, except that tommotiids' armor was made of organophosphatic compounds while that of *Halkieria* was made of calcite. However fossils of a new tommotiid, *Eccentrotheca*, showed an assembled mail coat that formed a tube, which would indicate a sessile animal rather than a creeping slug-like one. *Eccentrotheca*'s organophosphatic tube resembled that of phoronids, sessile animals that feed by lophophores and are regarded either very close relatives or a sub-group of brachiopods. *Paterimitra*, another mostly assembled fossil found in 2008 and described in 2009, had two symmetrical plates at the bottom, like brachiopod valves but not fully enclosing the animal's body.

A dense assemblage of the Ordovician species *Dalmanella meeki*

At their peak in the Paleozoic the brachiopods were among the most abundant filter-feeders and reef-builders, and occupied other ecological niches, including swimming in the jet-propulsion style of scallops. However, after the Permian–Triassic extinction event, informally known as the "Great Dying", brachiopods recovered only a third of their former diversity. It was often thought that brachiopods were actually decline in diversity, and that in some way bivalves out-competed them. However, in 1980 Gould and Calloway produced a statistical analysis that concluded that: both brachiopods and bivalves increased all the way from the Paleozoic to modern times, but bivalves increased faster; the Permian–Triassic extinction was moderately severe for bivalves but devastating for brachiopods, so that brachiopods for the first time were less diverse than bivalves and their diversity after the Permian increased from a very low base; there is no evidence that bivalves out-competed brachiopods, and short-term increases or decreases for both groups appeared at the same times. In 2007 Knoll and Bambach concluded that brachiopods were one of several groups that were most vulnerable to the Permian–Triassic extinction, as all had calcareous hard parts (made of calcium carbonate) and had low metabolic rates and weak respiratory systems.

Brachiopod fossils have been useful indicators of climate changes during the Paleozoic era. When global temperatures were low, as in much of the Ordovician, the large difference in temperatures between equator and poles created different collections of fossils at different latitudes. On the other hand, warmer periods, such much of the Silurian, created smaller difference in temperatures, and all seas at the low to middle latitudes were colonized by the same few brachiopod species.

Evolutionary family tree

Deuterostomes or protostomes

From about the 1940s to the 1990s, family trees based on embryological and morphological features placed brachiopods among or as a sister group to the deuterostomes. a super-phylum which includes chordates and echinoderms. Closer examination has found difficulties in the grounds on which brachiopods were affiliated with deuterostomes:

- Radial cleavage in the earliest divisions of the egg appears to be the original condition for the ancestral bilaterians, in the earliest Ecdysozoa and possibly in the earliest Eutrochozoa, a major sub-group of the Lophotrochozoa. Hence radial cleavage does not imply that brachiopods are affiliated with deuterostomes.
- The traditional view is that the coelom(s) in deuterostomes and protostomes form by different process, called enterocoely and schizocoely respectively. However, research since the early 1990s has found significant exceptions. Both types of coelom construction appear among brachiopods, and therefore do not imply that brachiopods are deuterostomes.
- The terms "deuterostomes" and "protostomes" originally defined distinct ways of forming the mouth from the blastopore, a depression that appears in an early stage of the embryo. However, some "protostomes" forming the mouth using a process more like that typical of deuterostomes. Hence forming the mouth via a deuterostome-like process does not imply that brachiopods are affiliated with deuterostomes.

Nielsen views the brachiopods and closely-related phoronids as affiliated with the deuterostome pterobranchs because their lophophores are driven by one cilium per cell, while those of bryozoans, which he regards as protosomes, have multiple cilia per cell. However, pterobranchs are hemichordates and probably closely related to echinoderms, and there is no evidence that the latest common ancestor of pterobranchs and other hemichordates or the latest common ancestor of hemichordates and echinoderms was sessile and fed by means of tentacles.

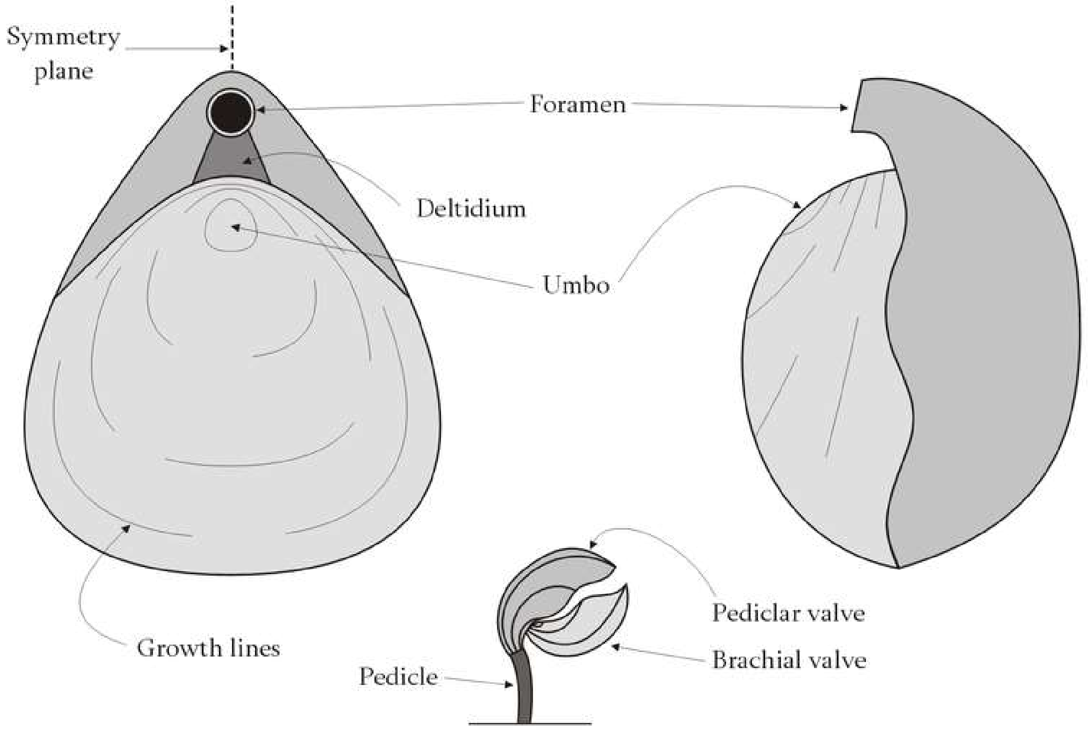
From 1988 onwards analyses based on molecular phylogeny, which compares biochemical features such as similarities in DNA, have placed brachiopods among the Lophotrochozoa, a protostome super-phylum that includes molluscs, annelids and flatworms but excludes the other protostome super-phylum Ecdysozoa, whose members include arthropods. This conclusion is unanimous among molecular phylogeny studies, which use a wide selection of genes: rDNA, Hox genes, mitochondrial protein genes, single nuclear protein genes and sets of nuclear protein genes.

Some combined studies in 2000 and 2001, using both molecular and morphological data, support brachiopods as Lophotrochozoa, while others in 1998 and 2004 concluded that brachiopods were deuterostomes.

Relationship with other lophotrochozoans

The phoronids feed with a lophophore, burrow or encrust on surfaces, and build three-layered tubes made of polysaccharide, possibly chitin, mixed with particles with seabed material. Traditionally they have been regarded as a separate phylum, but increasingly detailed molecular phylogeny studies between 1997 and 2000 have concluded that phoronids are a sub-group of brachiopods. However, an analysis in 2005 concluded that phoronids are a sub-group of bryozoans.

While all molecular phylogeny studies and half the combined studies until 2008 conclude that brachiopods are lophotrochozoans, they could not identify which lophotrochozoan phylum were the closest relatives of brachiopods - except phoronids, which are a sub-group of brachiopods. However in 2008 two analyses found that brachiopods' closest lophotrochozoan relatives were nemertines. The authors found this surprising, since nemertines have spiral cleavage in the early stages of cell division and form a trochophore larva, while brachiopods have radial cleavage and a larva that shows no sign of having evolved from a trochophore. Another study in 2008 also concluded that brachiopods are closely related to nemertines, casting doubt on the idea that brachiopods are part of a clade Lophophorata of lophophore-feeding animals within the lophotrochozoans.

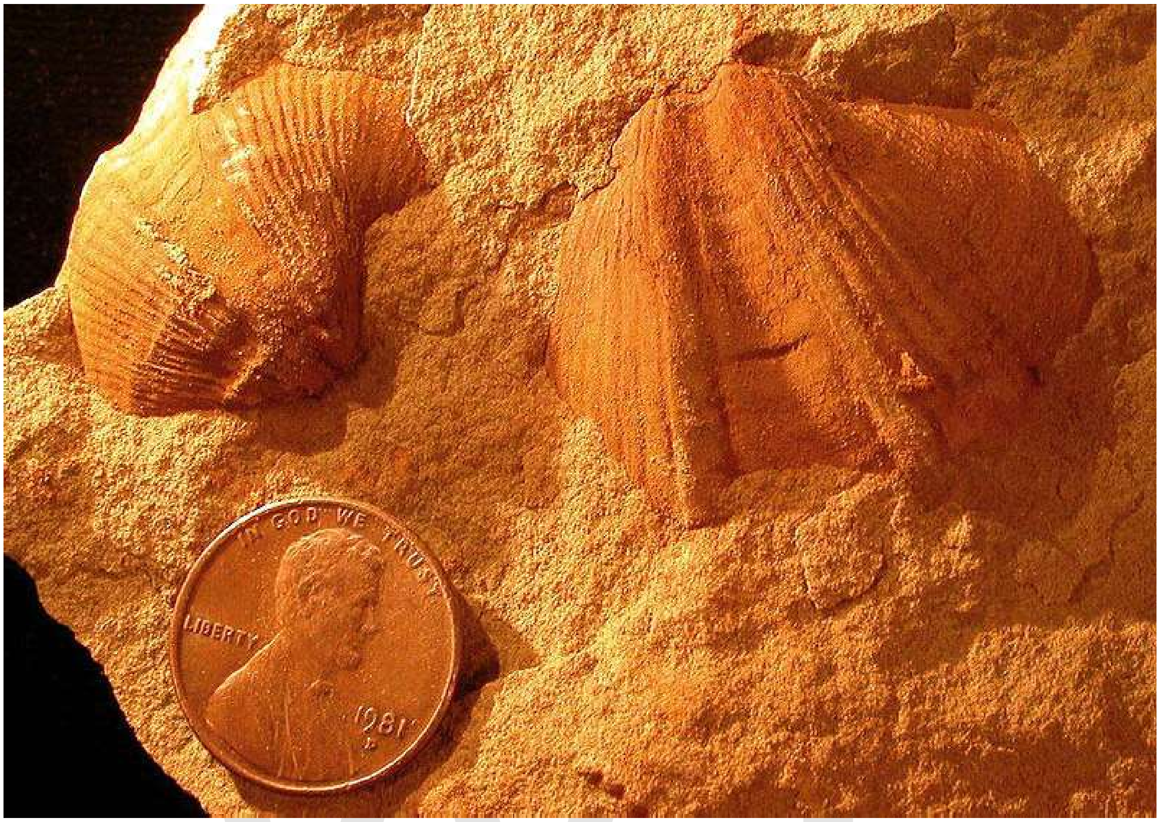


Brachiopod morphology

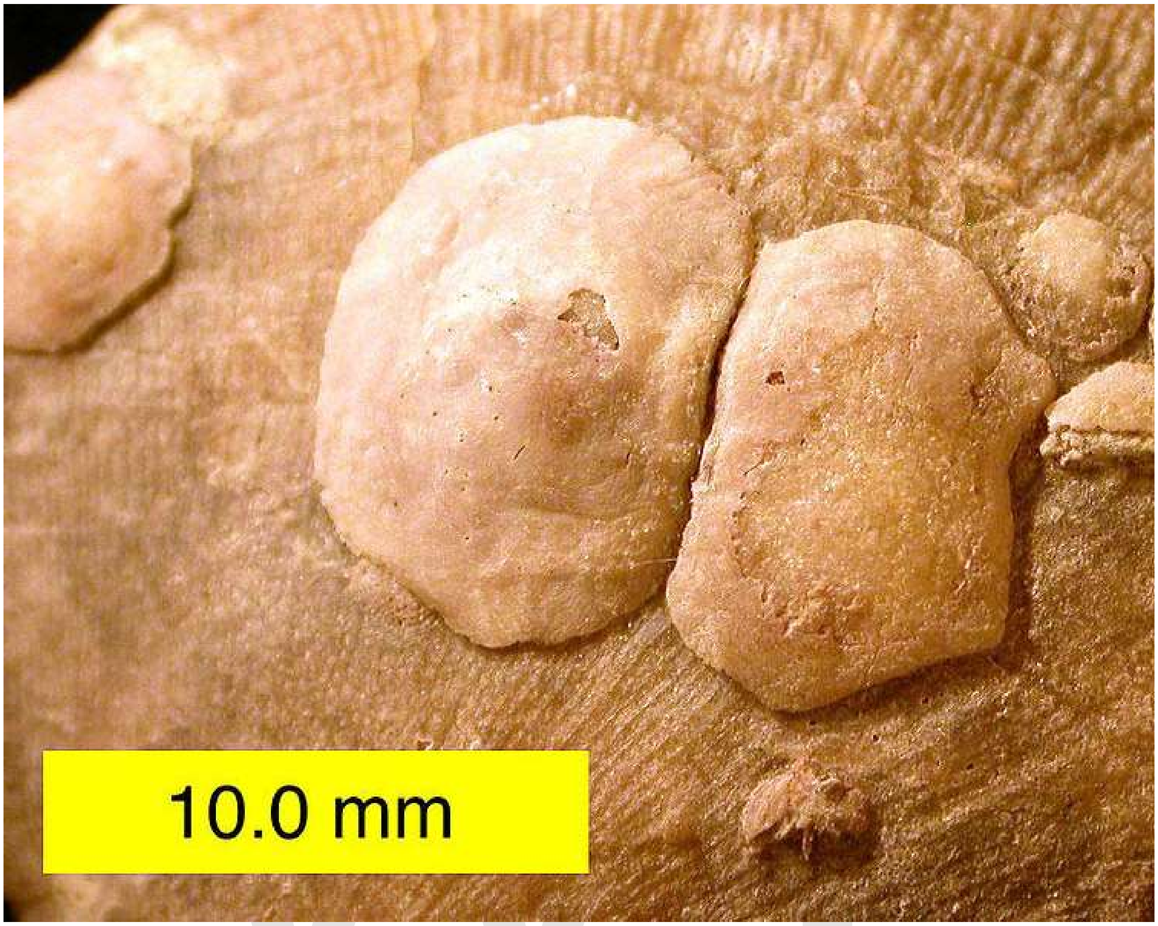
A Carboniferous brachiopod *Neospirifer condor*, from Bolivia. The specimen is 7 cm across.

Rhynchotrema dentatum, a rhynchonellid brachiopod from the Cincinnatian (Upper Ordovician) of southeastern Indiana.

A Devonian spiriferid brachiopod from Ohio that served as a host substrate for a colony of hederellids. The specimen is 5 cm wide.



Syringothyris sp.; a spiriferid brachiopod from the Logan Formation (Lower Carboniferous) of Wooster, Ohio (internal molds).



Petrocrania brachiopods attached to a strophomenid brachiopod; Upper Ordovician of southeastern Indiana.

Lingula anatina from Stradbroke Island, Australia.

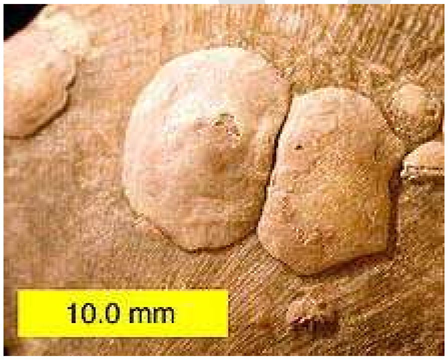
Brachiopod casts in the Lock Haven Formation

Chapter 5

Craniidae, Lingula (Genus) and Lingula Reevii

Craniidae

Craniidae
Temporal range: Ordovician–Recent



Petrocrania brachiopods attached to a strophomenid brachiopod; Upper Ordovician of southeastern Indiana.

Scientific classification [e]

Kingdom:	Animalia
Phylum:	Brachiopoda
Class:	Craniata
Order:	**Craniida** Waagen, 1885
Suborder:	**Craniidina** Waagen, 1885
Superfamily:	**Cranioidea** Menke, 1828
Family:	**Craniidae**

Menke, 1828

Genera

4 living and numerous fossil, including:
†*Ancistrocrania*
†*Crania*
Craniscus
†*Danocrania*
†*Isocrania*
Neoancistrocrania
Novocrania
Valdiviathyris

Synonyms

Craniacea (superfamily)

Valdiviathyrididae (family)

The **Craniidae** are a family of brachiopods (lamp shells). They are the only members of the order **Craniida** and the monotypic suborder **Craniidina** and superfamily **Cranioidea**; consequently, the latter two taxa are presently redundant and not used very often. *Valdiviathyris* and *Neoancistrocrania* were sometimes separated in a family **Valdiviathyrididae** but this has turned out to be unjustified.

Most Craniidae are long-extinct forms known only from fossils like all other Craniforma. However, some 20 species of this 470-million-year-old lineage are extant today. They include *Valdiviathyris quenstedti* which has remained essentially unchanged for the last 35 million years or so. Although some minimal evolution would obviously have taken place in the meantime, this was essentially silent mutations and marginal adaptations to cooler habitat. Present-day *Valdiviathyris* are all but inseparable from those of the Late Eocene and the genus cannot even be divided into chronospecies. Thus, *V. quenstedti* is a true living fossil and one of the oldest and most long-lived species known to science.

Lingula (genus)

Lingula	
	
Lingula anatina from Stradbroke Island, Australia.	
Scientific classification	
Kingdom:	Animalia
Phylum:	Brachiopoda
Class:	Lingulata
Order:	Lingulida
Family:	Lingulidae
Genus:	***Lingula*** Bruguière, 1791
Type species	
Lingula anatina Lamarck, 1801	

Lingula is a genus of brachiopods within the class Lingulata. *Lingula* is among the few brachiopods surviving today but also known from fossils over 500 million years old.

Species

The following species are recognised:

- *Lingula adamsi* Dall, 1873
- *Lingula anatina* Lamarck, 1801
- *Lingula dregeri* Andreae, 1893
- *Lingula eocenica* Moroz & Ermokhyna, 1990
- *Lingula parva* Smith, 1871
- *Lingula reevii* Davidson, 1880
- *Lingula rostrum* (Shaw, 1798)
- *Lingula tenuis* Sowerby
- *Lingula translucida* Dall, 1921
- *Lingula tumidula* Reeve, 1841
- *Lingula waikatoensis* Pen, 1930

Lingula reevii

Lingula reevii	
Scientific classification	
Kingdom:	Animalia
Phylum:	Brachiopoda
Class:	Lingulata
Order:	Lingulida
Family:	Lingulidae
Genus:	*Lingula*
Species:	***L. reevii***
Binomial name	
Lingula reevii Davidson, 1880	

Lingula reevii is a brachiopod species known as the **inarticulated brachiopod** and is in the family Lingulidae. Inarticulated brachiopods have bilaterally symmetrical shells held together only by muscles and not teeth. The species is rare and is only known to occur in shallow, sandy reef flats in Kaneohe Bay, Oahu, Hawaii.

Description

The shell is oblong oval, broadest in the middle, and rather narrow. The sides are very gently curved outwardly, the posterior edge tapers to a sharp point. The shell valves are moderately convex with a smooth surface. Color is blue-green or emerald and verdigris-green, especially along the middle. The lophophore consists of a fold of the body wall that possesses a crown of ciliated tentacles surrounding the mouth. The lateral cilia create a water current and fine plankton are transported down the tentacles to the brachial groove and into the mouth.

Ecology

They burrow vertically in sand, leaving a three-hole siphonal opening at the surface. When disturbed, a rapid contraction of the pedicle pulls the animal below the surface and the siphonal openings are reduced to a slit. This species is capable of upward burrowing through a sediment layer, even if the animal has to autotomize (detach) the pedicle.

Reproduction

Lingula has separate sexes, and gametes are shed into the water column for external fertilization. Embryos develop into a free swimming larva that looks like a tiny adult; they develop a shell while planktonic. As additional shell material is laid down, the animal becomes heavy, sinks to the bottom, and takes up its adult existence. There is no metamorphosis in *Lingula*. The lifespan of *Lingula spp.* is estimated to be 5 to 8 years.

Threats and conservation

The species has declined in density from 500 per square meter in the 1960s to a maximum of 4 per square meter (Cindy Hunter, University of Hawaii, personal communication). The main threats are: 1) habitat degradation and alteration; 2) overexploitation; 3) marine pollution and sedimentation; 4) a vulnerable life history; and 5) a limited distribution.

The inarticulated brachiopod is a U.S. National Marine Fisheries Service Species of Concern,. Species of Concern are those species about which the U.S. Government’s National Oceanic and Atmospheric Administration, National Marine Fisheries Service, has some concerns regarding status and threats, but for which insufficient information is available to indicate a need to list the species under the U.S. Endangered Species Act.

Chapter 6

Lingulata, Mucrospirifer, Obolellida and Rhynchonellata

Lingulata

Lingulata

Lingula anatina from Stradbroke Island, Australia.

Scientific classification [e]

Kingdom:	Animalia
Phylum:	Brachiopoda
Subphylum:	Linguliformea
Class:	**Lingulata**

Orders

†Acrotretida
Lingulida
†Siphonotretida

Lingulata is a class of brachiopod, among the oldest of all brachiopods having existed since the Cambrian period (550 mya). They are also among the most morphologically conservative of the brachiopods, having lasted from their earliest appearance to the present with very little change in shape. Shells of living specimens found today in the waters around Japan are almost identical to ancient Cambrian fossils.

The Lingulata have tongue-shaped shells (hence the name Lingulata, from the Latin word for "tongue") with a long fleshy stalk, or pedicle, with which the animal burrows into sandy or muddy sediments. They inhabit vertical burrows in these soft sediments with the anterior end facing up and slightly exposed at the sediment surface. The cilia of the lophophore generate a feeding and respiratory current through the lophophore and mantle cavity. The gut is complete and J-shaped.

Lingulata shells are composed of a combination of calcium phosphate, protein and chitin. This is unlike most other shelled marine animals, whose shells are made of calcium carbonate. The Lingulata are inarticulate brachiopods, so named for the simplicity of their hinge mechanism. This mechanism lacks teeth and is held together only by a complex musculature. Both valves are roughly symmetrical.

The genus *Lingula* (Bruguiere, 1797) is the oldest known animal genus that still containins extant species. It is primarily an Indo-Pacific genus that is harvested for human consumption in Japan and Australia.

Mucrospirifer

Mucrospirifer
Temporal range: Devonian

Scientific classification

Kingdom:	Animalia
Phylum:	Brachiopoda
Class:	Rhynchonellata
Order:	Spiriferida
Family:	Mucrospiriferidae
Genus:	***Mucrospirifer*** Grabau, 1931

Mucrospirifer is a genus of extinct brachiopod in the class Rhynchonellata (Articulata) and the order Spiriferida. They are sometimes known as "butterfly shells". Like other brachiopods, they were filter feeders. Fossils occur mainly in middle Devonian strata.

The biconvex shell was typically 2.5 cm, but they could grow to 4 cm long. It has a fold, sulcus and costae. It was greatly elongated along the hinge line, which extends outward to form sharp points. This gave them a fin- or wing-like appearance. The apex area (umbo) of the pedicle valve contains a small fold for the pedicle. They lived in muddy marine sediments, and were attached to the sea floor via the pedicle.They sometimes look like two seashells stuck together.

Select species

- *Mucrospirifer albanensis*
- *Mucrospirifer arkonensis*
- *Mucrospirifer bouchardi*
- *Mucrospirifer grabaui*
- *Mucrospirifer medfordsis*
- *Mucrospirifer mucronatus*
- *Mucrospirifer paradoxiformis*
- *Mucrospirifer profundus*
- *Mucrospirifer prolificus*
- *Mucrospirifer refugiensis*
- *Mucrospirifer thedfordensis*
- *Mucrospirifer williamsi*

Obolellida

Obolellida	
Scientific classification	
Kingdom:	Animalia
Phylum:	Brachiopoda
Subphylum:	Rhychonelliformea
Class:	Obolellata
Order:	**Obolellida** Rowell, 1965

Obolellida is a small, extinct order of inarticulate brachiopods that existed from the early to middle Cambrian period. The relationship of the Obolellida with other inarticulates is unclear, and were previously grouped together with the Siphonotretacea, before being given their own order.

Anatomy

The shell is typically impunctate, biconvex, and oval or subcircular in shape. They are like other inarticuates in that, as with the lingulids, the shell has no hinge, at least in the earliest examples. It is thought they may have used a hydraulic mechanism. However they later seem to develop a primitive articulation, in which some used a levator mechanism for opening the shell. At the posterior is a ventral valve with a defined flat-shelf. The pedicle opening can be positioned at various positions.

Rhynchonellata

Rhynchonellata
Temporal range: Lower Cambrian–Recent

Scientific classification [e]

Kingdom:	Animalia
Phylum:	Brachiopoda
Subphylum:	Rhynchonelliformea
Class:	**Rhynchonellata**

Orders

†Athyridida
†Orthida
†Pentamerida
†Protorthida
Rhynchonellida
†Spiriferida
†Spiriferinida
Terebratulida
Thecideida

The **Rhynchonellata** is a class of articulate brachiopods that combines certain orders from within the Rhynchonelliformea (Articulata revised). The class ranges from the Lower Cambrian to Recent.

Orders included in the Rhynchonellata are the Rhynchonellida, Orthida, Pentamerida, Atrypida, Athyridida, Spiriferida, Spiriferinida and Terebratulida. The Atrypida, Athyridida, and Spiriferinida were originally included in the Spiriferida as suborders. The Atrypida is the Atrypacea, the Athyridida, the Rostropiracea and the Spiriferinida the Punctospiracea of Moore, Lalicker, and Fischer.

The Orthida and Spiriferida have wide hinge lines. The Pentamerida, Terebratulida, Atripida and Athyridida have narrow hinge lines. The Orthida, Pentamerida, Rhynchonellida, and Terebratulida have looped brachidia. The Spiriferida, Atrypida, Athyridida, and Spiriferinida have spiral brachidia. Some, like the Rhynchonellida and Spiriferida, may be strongly plicate, with a median fold and sulcus. Others, like the Spiriferinida and Terebratulida are basically smooth. All a primarily or exclusively impunctate but some e.g. Orthida and Rhynchonellida have puctate off shoots.

Chapter 7

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

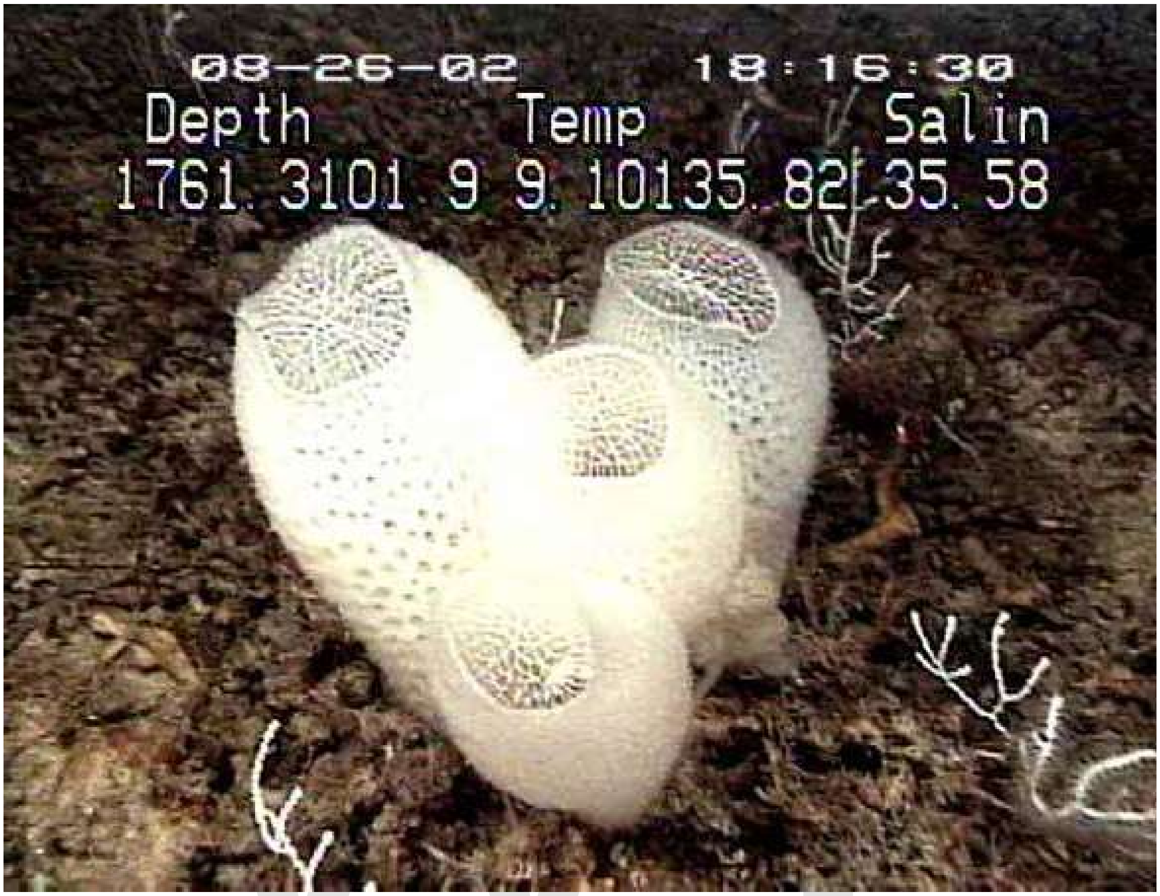
Sponges in temperate regions live for at most a few years, but some tropical species and perhaps some deep-ocean ones may live for 200 years or more. Some calcified demosponges grow by only 0.2 millimetres (0.0079 in) per year and, if that rate is constant, specimens 1 metre (3.3 ft) wide must be about 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.

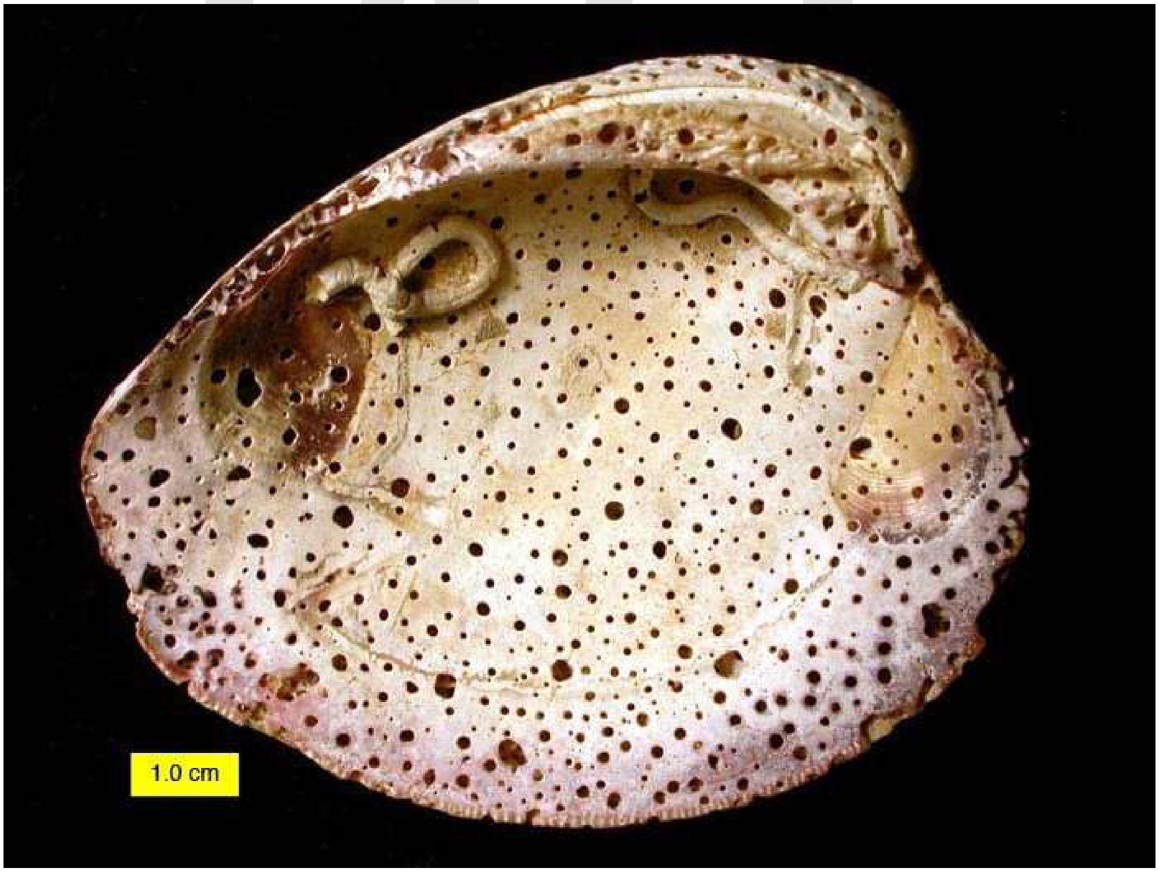
The different classes of sponge live in different ranges of habitat:

	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

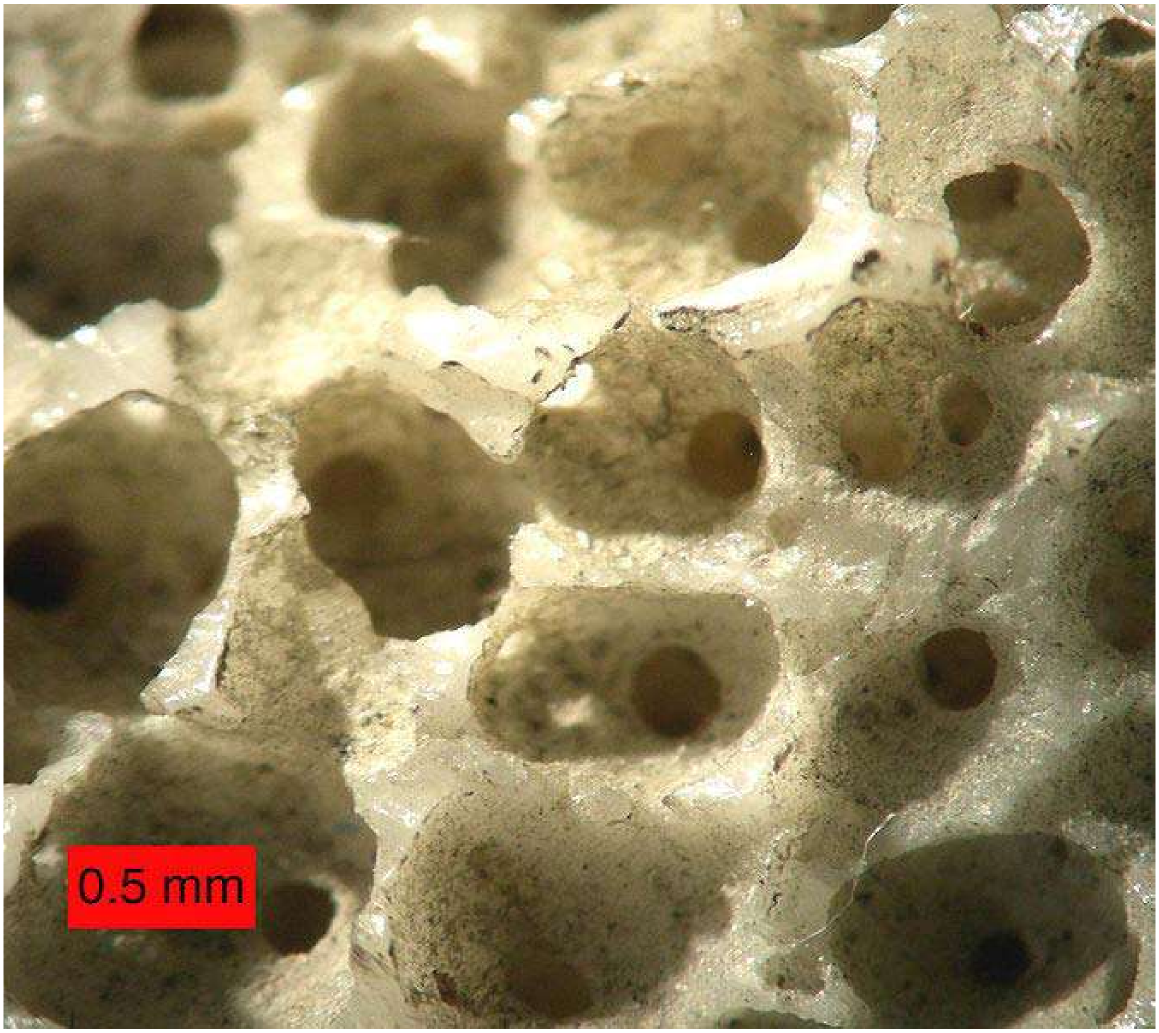
As primary producers

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

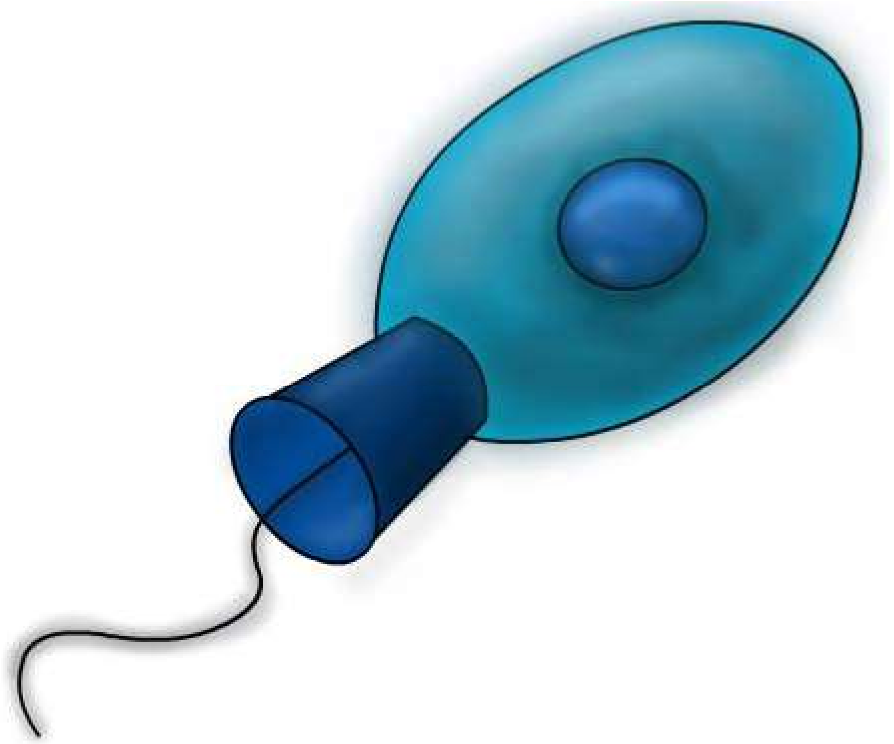
Traces of the chemical 24-isopropylcholestane have been found in rocks formed 1,800 million years ago. This is a stable derivative of 24-isopropylcholesterol, which is thought to be produced by demosponges but not by eumetazoans ("true animals", i.e. cnidarians and bilaterians). Since choanoflagellates 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

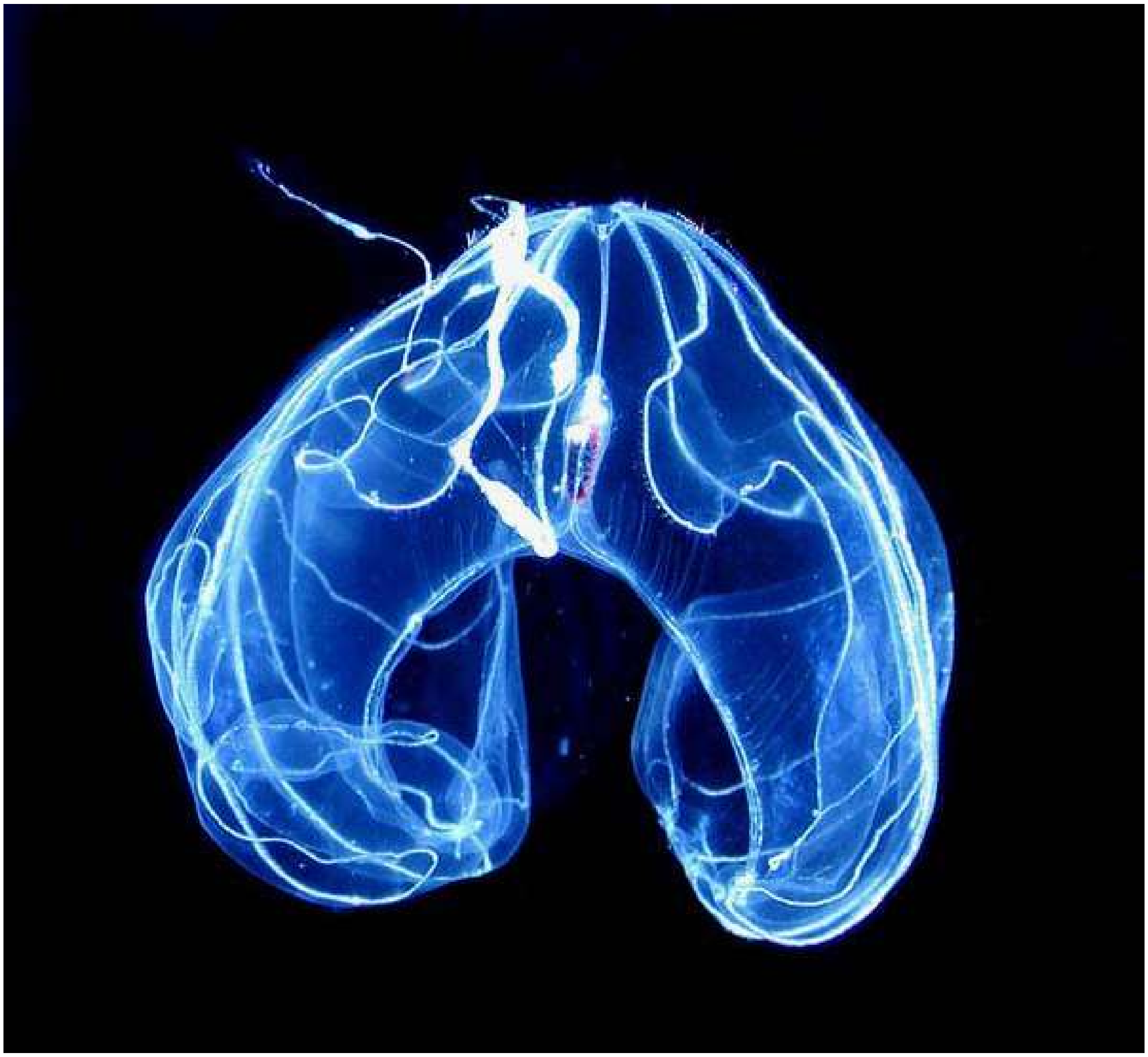


A choanoflagellate

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.



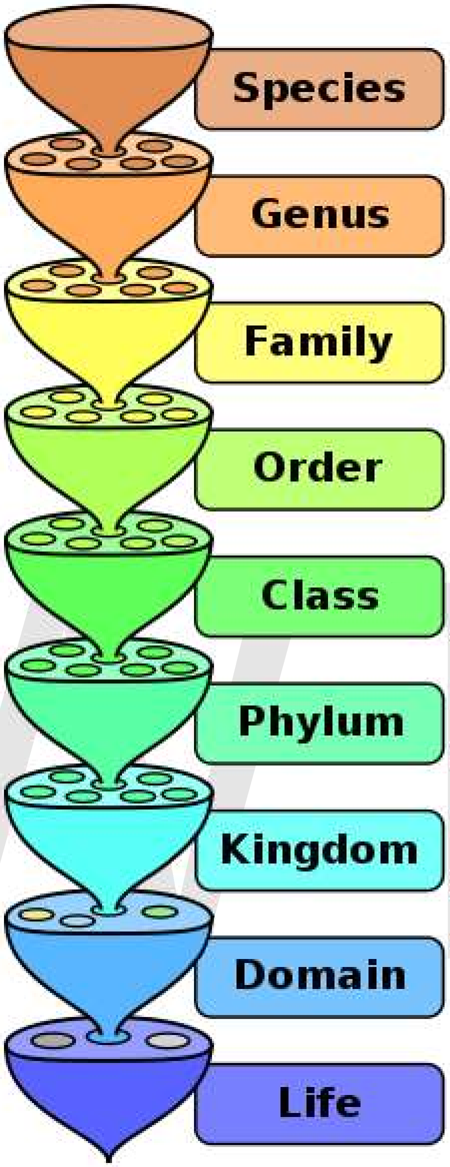
A comb jelly

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 8

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.

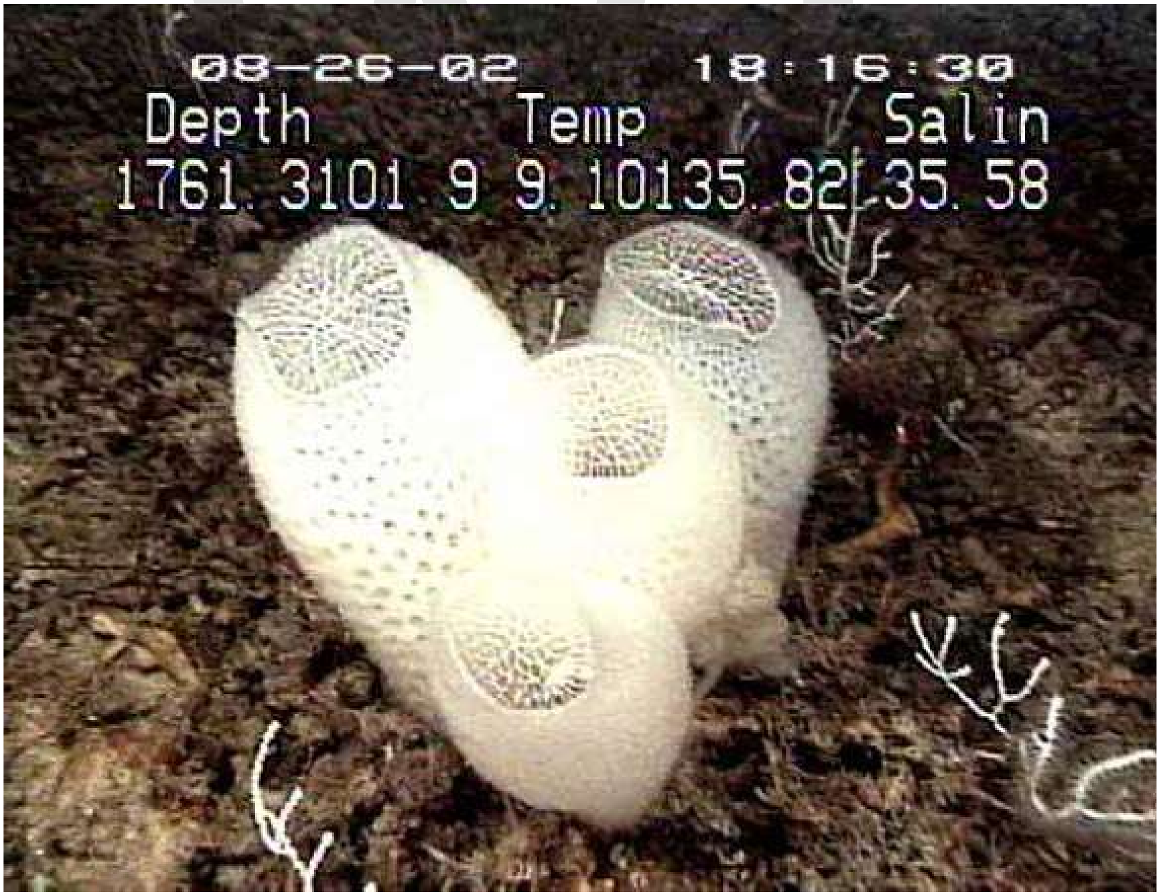
Glass sponges are relatively uncommon and are mostly found at depths from 450 to 900 metres (1,480 to 3,000 ft) although the species *Oopsacas minuta* has been found in shallow water, while others have been found much deeper. They are found in all oceans of the world, although they are particularly common 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 9

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 10

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

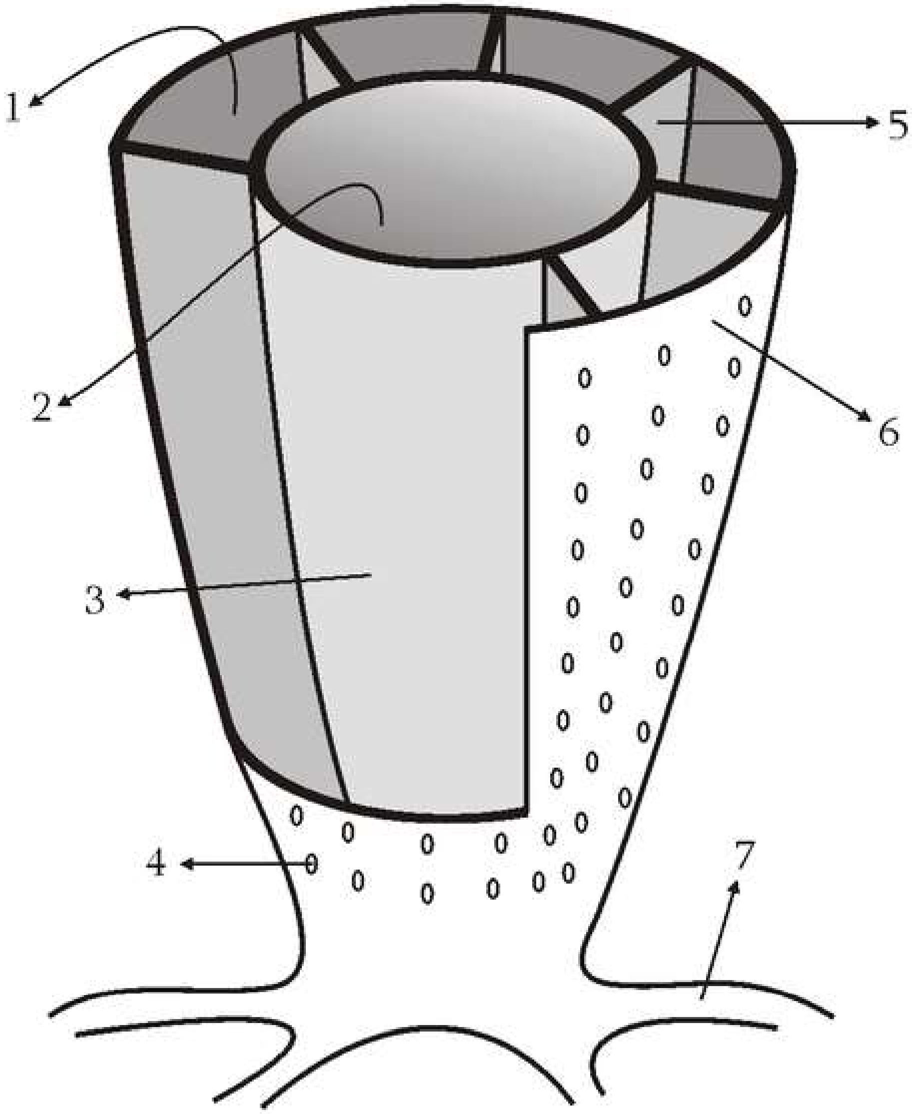
- Cyathospongia Okulitch, 1935
- Pleospongia Okulitch, 1935

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 11

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 12

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 13

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.

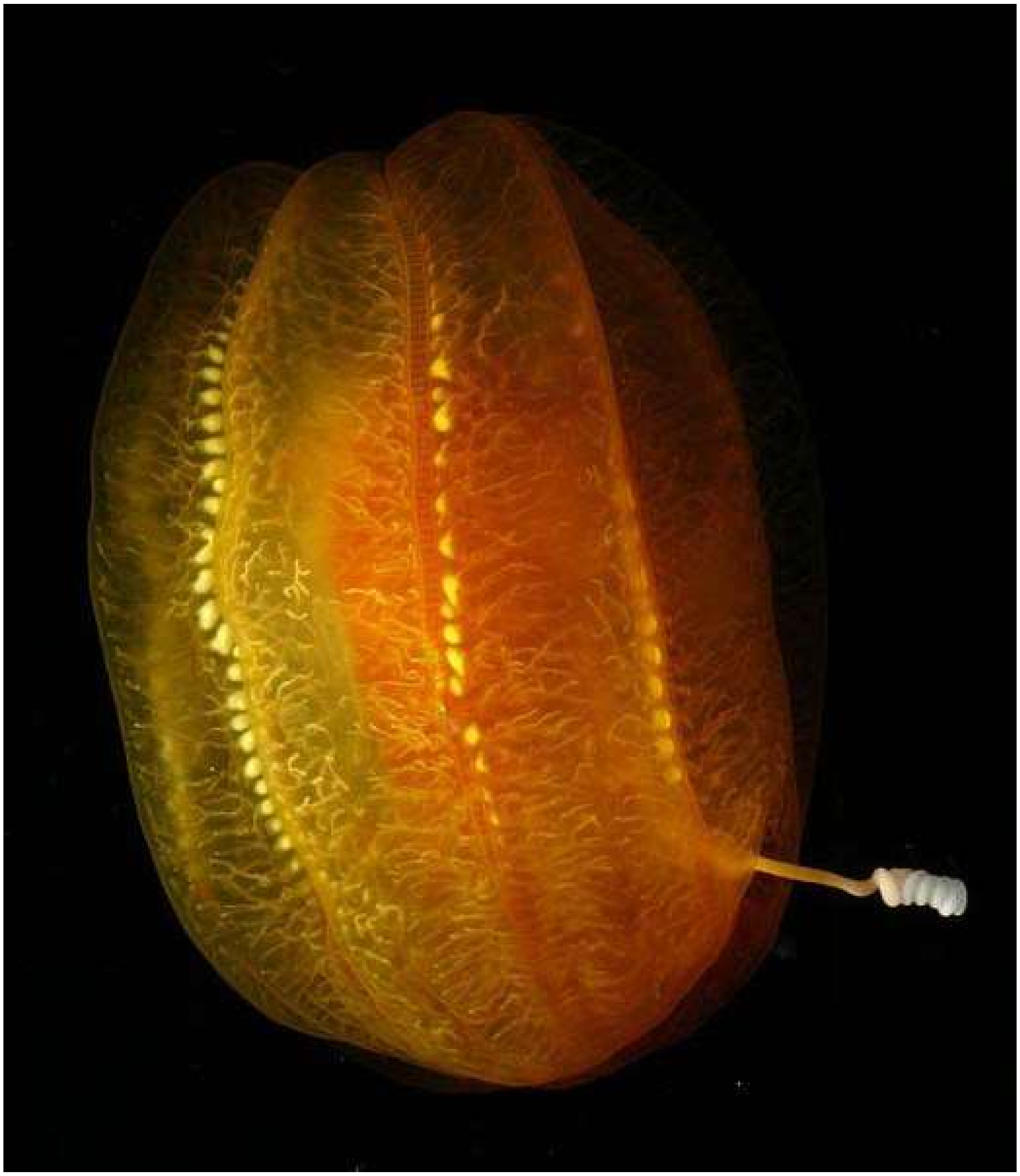
It is uncertain how ctenophores control their buoyancy, but experiments have shown that some species rely on osmotic pressure to adapt to water of different densities. Their body fluids are normally as concentrated as seawater. If they enter less dense brackish water, the ciliary rosettes in the body 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



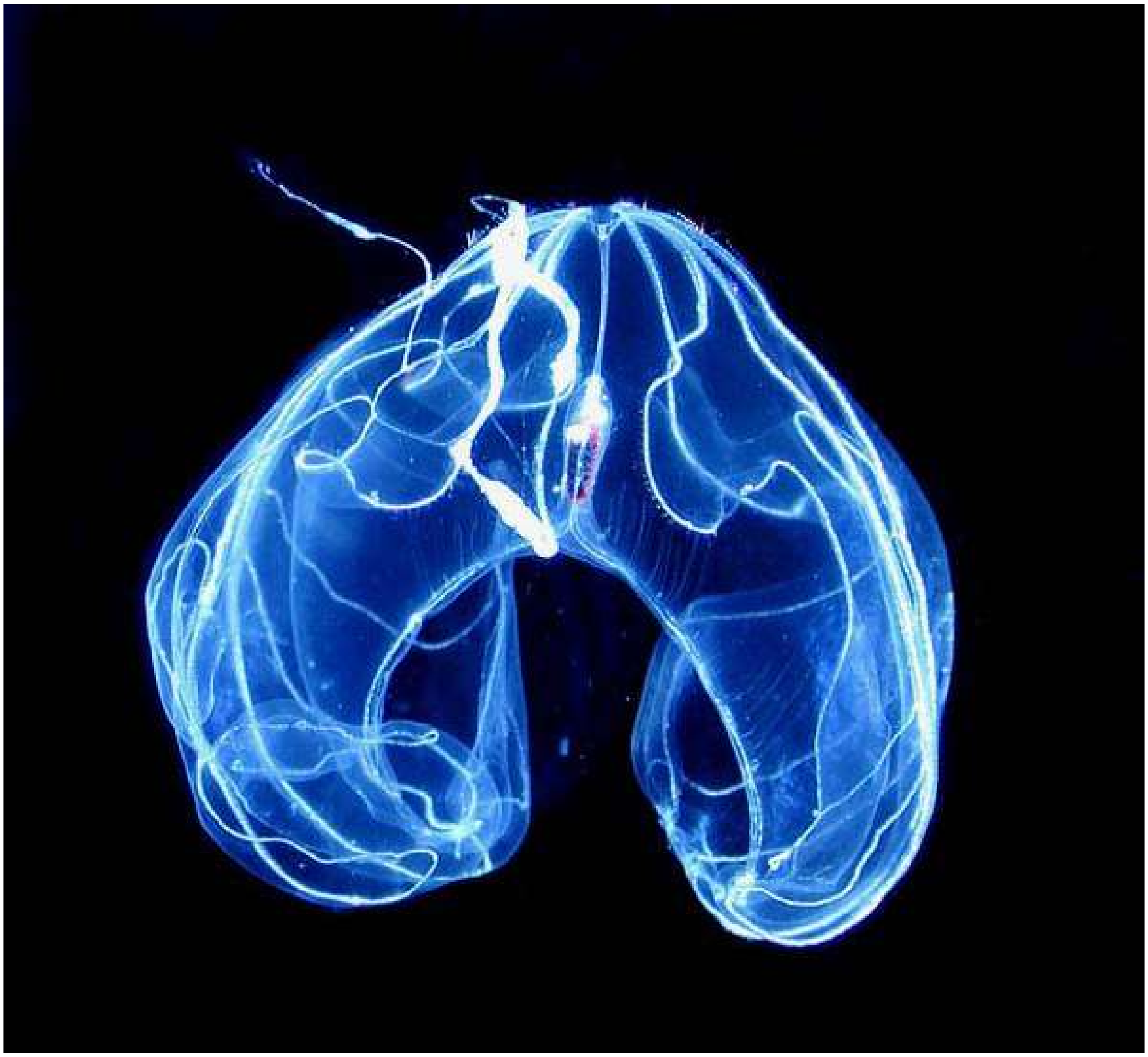
Aulacoctena sp., a cydippid ctenophore

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

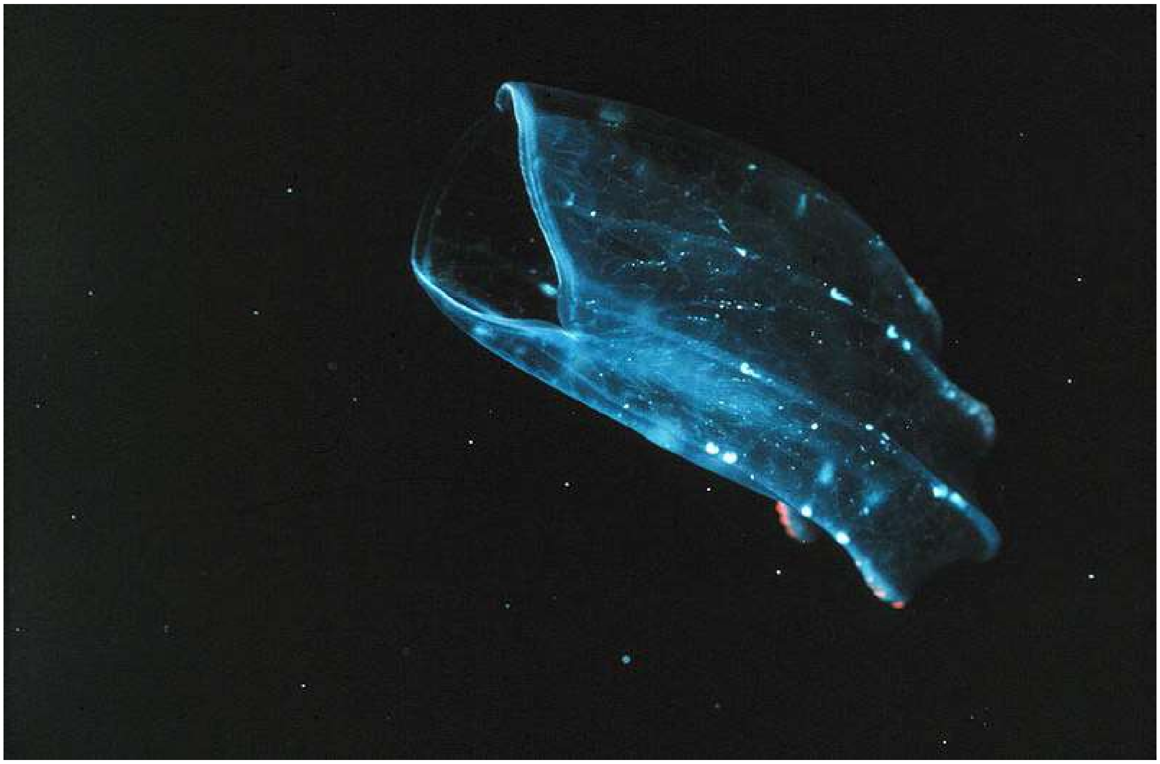
The Lobata have a pair of lobes, which are muscular, cuplike extensions of the body that project beyond the mouth. Their inconspicuous tentacles originate from the corners of the mouth, running in convoluted grooves and spreading out over the inner surface of the lobes (rather than trailing far behind, 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

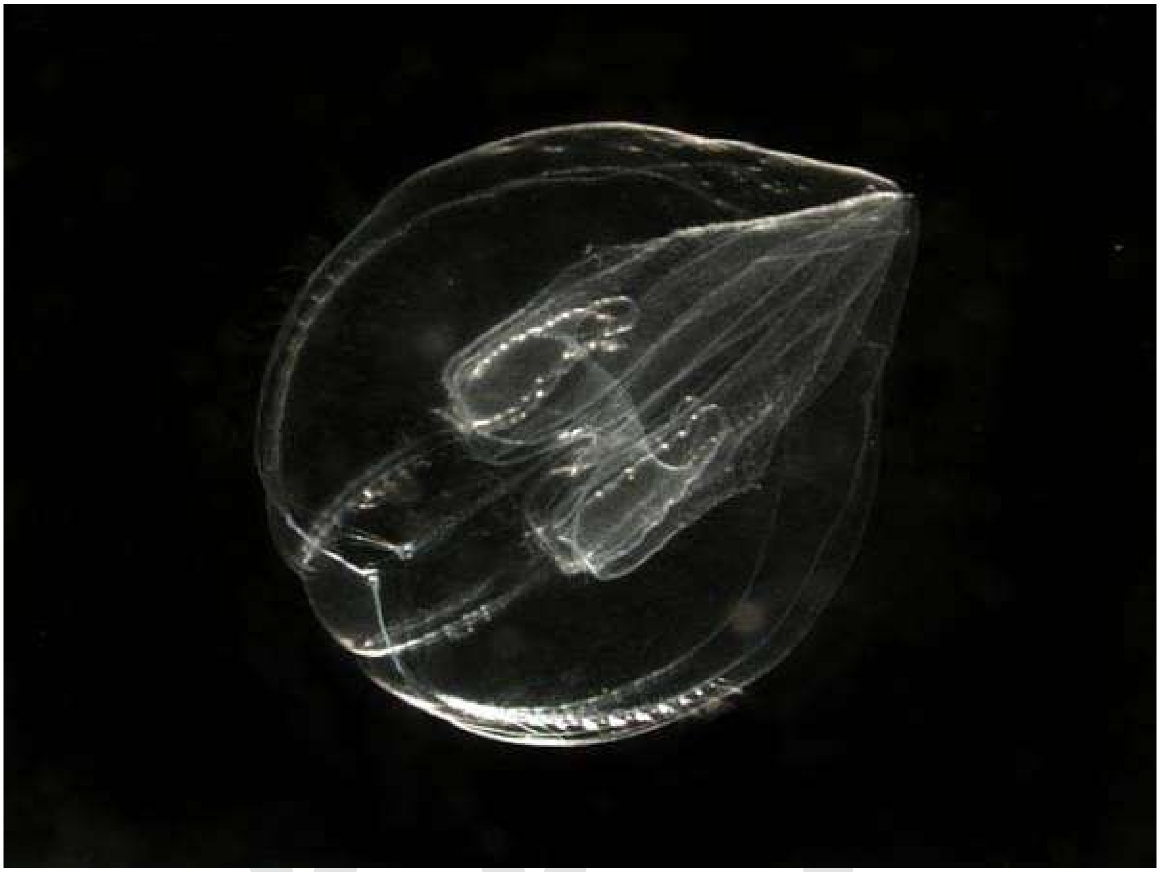
The Ganeshida have a pair of small oral lobes and a pair of tentacles. The body is circular rather than oval in cross-section, and the pharynx extends over the inner surfaces of the lobes.

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.

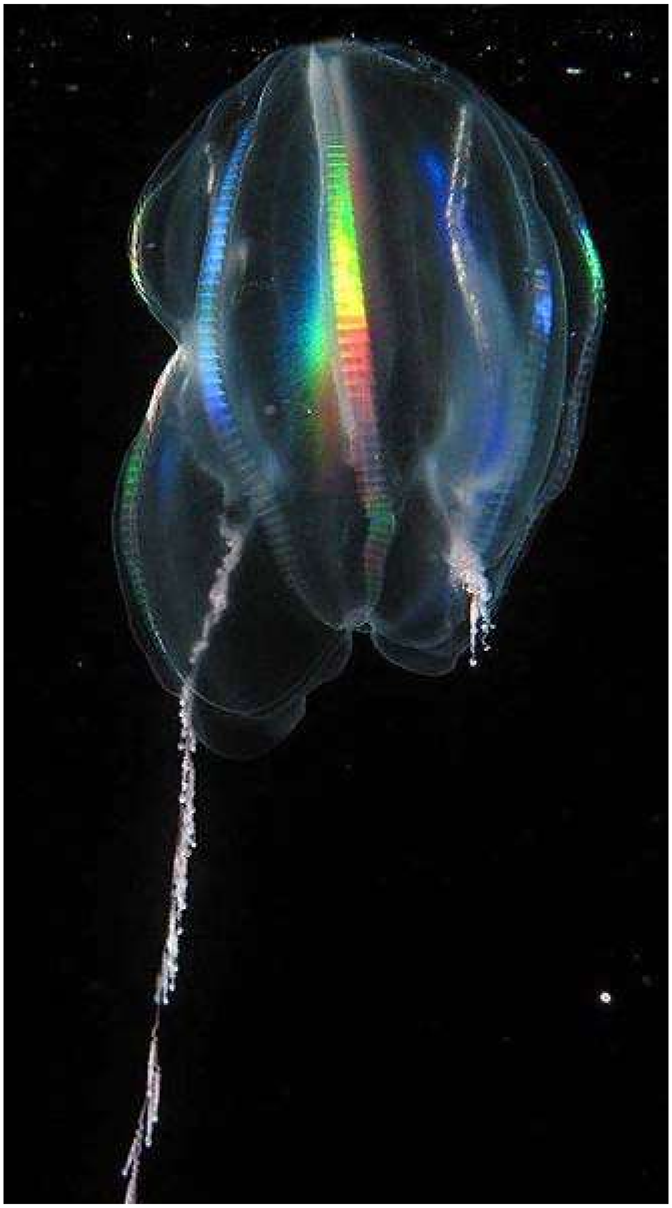
Adults of most species can regenerate tissues that are damaged or removed, although only platyctenids reproduce by cloning, splitting off from the edges of their flat bodies fragments that develop into new individuals.

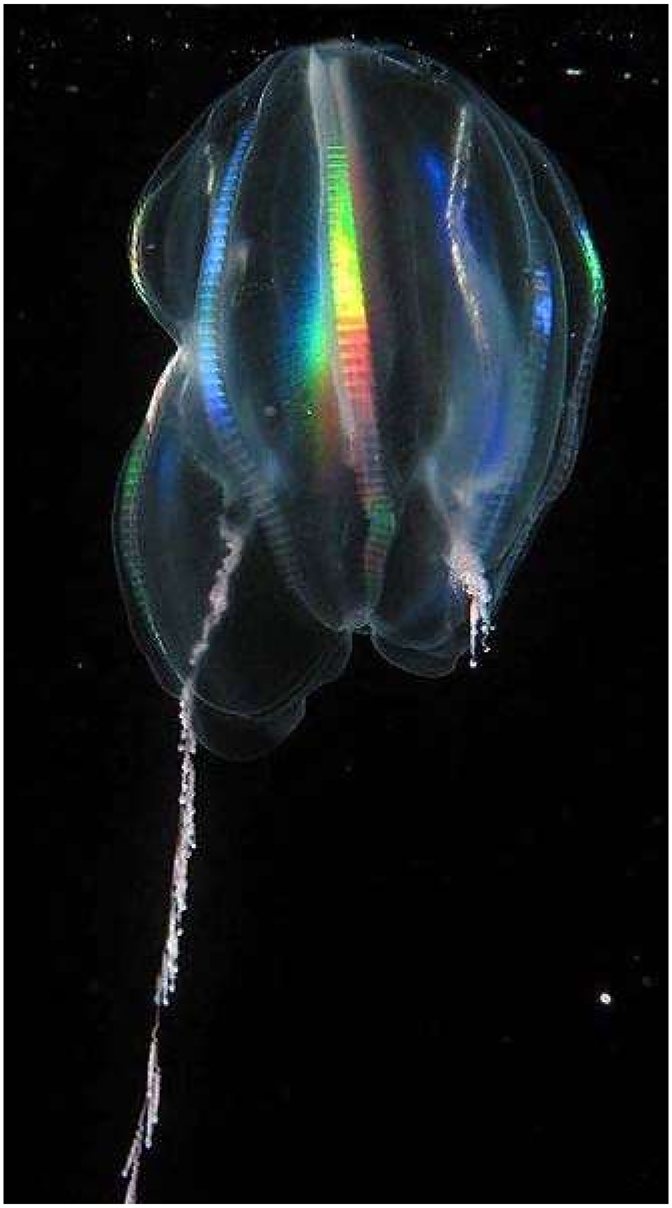
Almost all species are hermaphrodites, in other words they function as both males and females at the same time — except that in two species of the genus *Ocryopsis* individuals remain of the same single sex all their lives. The gonads are located in the parts of the internal canal network under the comb 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.