Animal Kingdom

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Animal

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Temporal range: Ediacaran - Recent

Scientific classification

Domain:	Eukarya
(unranked)	Opisthokonta
(unranked)	Holozoa
(unranked)	Filozoa
Kingdom:	**Animalia** Linnaeus, 1758

Phyla

- **Subkingdom Parazoa**
    - Porifera
    - Placozoa
- **Subkingdom Eumetazoa**
    - **Radiata (unranked)**
        - Ctenophora
        - Cnidaria
    - **Bilateria (unranked)**
        - Orthonectida
        - Rhombozoa
        - Acoelomorpha
        - Chaetognatha
        - **Superphylum Deuterostomia**
            - Chordata
            - Hemichordata
            - Echinodermata
            - Xenoturbellida
            - Vetulicolia †
        - **Protostomia (unranked)**
            - **Superphylum Ecdysozoa**
                - Kinorhyncha
                - Loricifera
                - Priapulida
                - Nematoda
                - Nematomorpha
                - Lobopodia
                - Onychophora
                - Tardigrada
                - Arthropoda
            - **Superphylum Platyzoa**
                - Platyhelminthes
                - Gastrotricha
                - Rotifera
                - Acanthocephala
                - Gnathostomulida
                - Micrognathozoa
                - Cycliophora
            - **Superphylum Lophotrochozoa**
                - Sipuncula
                - Hyolitha †
                - Nemertea
                - Phoronida
                - Bryozoa
                - Entoprocta
                - Brachiopoda
                - Mollusca

        - Annelida
        - Echiura

Animals are a major group of multicellular, eukaryotic organisms of the kingdom **Animalia** or **Metazoa**. Their body plan eventually becomes fixed as they develop, although some undergo a process of metamorphosis later on in their life. Most animals are motile, meaning they can move spontaneously and independently. All animals are also heterotrophs, meaning they must ingest other organisms for sustenance.

Most known animal phyla appeared in the fossil record as marine species during the Cambrian explosion, about 542 million years ago.

Etymology

The word "animal" comes from the Latin word *animalis*, meaning "having breath". In everyday colloquial usage, the word usually refers to non-human animals. Frequently, only closer relatives of humans such as mammals and other vertebrates are meant in colloquial use. The biological definition of the word refers to all members of the kingdom Animalia, encompassing creatures as diverse as sponges, jellyfish, insects and humans.

Characteristics

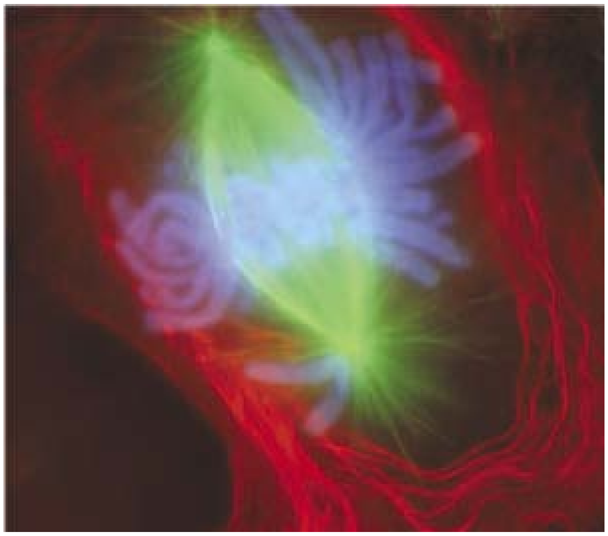
Animals have several characteristics that set them apart from other living things. Animals are eukaryotic and mostly multicellular, which separates them from bacteria and most protists. They are heterotrophic, generally digesting food in an internal chamber, which separates them from plants and algae. They are also distinguished from plants, algae, and fungi by lacking rigid cell walls. All animals are motile, if only at certain life stages. In most animals, embryos pass through a blastula stage, which is a characteristic exclusive to animals.

Structure

With a few exceptions, most notably the sponges (Phylum Porifera) and Placozoa, animals have bodies differentiated into separate tissues. These include muscles, which are able to contract and control locomotion, and nerve tissues, which send and process signals. Typically, there is also an internal digestive chamber, with one or two openings. Animals with this sort of organization are called metazoans, or eumetazoans when the former is used for animals in general.

All animals have eukaryotic cells, surrounded by a characteristic extracellular matrix composed of collagen and elastic glycoproteins. This may be calcified to form structures like shells , bones, and spicules. During development, it forms a relatively flexible framework upon which cells can move about and be reorganized, making complex structures possible. In contrast, other multicellular organisms, like plants and fungi, have cells held in place by cell walls, and so develop by progressive growth. Also, unique to animal cells are the following intercellular junctions: tight junctions, gap junctions, and desmosomes.

Reproduction and development



A newt lung cell stained with fluorescent dyes undergoing mitosis, specifically early anaphase

Nearly all animals undergo some form of sexual reproduction. They have a few specialized reproductive cells, which undergo meiosis to produce smaller, motile spermatozoa or larger, non-motile ova. These fuse to form zygotes, which develop into new individuals.

Many animals are also capable of asexual reproduction. This may take place through parthenogenesis, where fertile eggs are produced without mating, budding, or fragmentation.

A zygote initially develops into a hollow sphere, called a blastula, which undergoes rearrangement and differentiation. In sponges, blastula larvae swim to a new location and develop into a new sponge. In most other groups, the blastula undergoes more complicated rearrangement. It first invaginates to form a gastrula with a digestive chamber, and two separate germ layers — an external ectoderm and an internal endoderm. In most cases, a mesoderm also develops between them. These germ layers then differentiate to form tissues and organs.

Food and energy sourcing

All animals are heterotrophs, meaning that they feed directly or indirectly on other living things. They are often further subdivided into groups such as carnivores, herbivores, omnivores, and parasites.

Predation is a biological interaction where a predator (a heterotroph that is hunting) feeds on its prey (the organism that is attacked). Predators may or may not kill their prey prior to feeding on them, but the act of predation always results in the death of the prey. The other main category of consumption is detritivory, the consumption of dead organic matter. It can at times be difficult to separate the two feeding behaviours, for example, where parasitic species prey on a host organism and then lay their eggs on it for their offspring to feed on its decaying corpse. Selective pressures imposed on one another has led to an evolutionary arms race between prey and predator, resulting in various antipredator adaptations.

Most animals feed indirectly from the energy of sunlight. Plants use this energy to convert sunlight into simple sugars using a process known as photosynthesis. Starting with the molecules carbon dioxide (CO_2) and water (H_2O), photosynthesis converts the energy of sunlight into chemical energy stored in the bonds of glucose ($C_6H_{12}O_6$) and releases oxygen (O_2). These sugars are then used as the building blocks which allow the plant to grow. When animals eat these plants (or eat other animals which have eaten plants), the sugars produced by the plant are used by the animal. They are either used directly to help the animal grow, or broken down, releasing stored solar energy, and giving the animal the energy required for motion. This process is known as glycolysis.

Animals living close to hydrothermal vents and cold seeps on the ocean floor are not dependent on the energy of sunlight. Instead chemosynthetic archaea and bacteria form the base of the food chain.

Origin and fossil record

Dunkleosteus was a gigantic, 10-metre-long (33 ft) prehistoric fish.

Vernanimalcula guizhouena is a fossil believed by some to represent the earliest known member of the *Bilateria*.

Animals are generally considered to have evolved from a flagellated eukaryote. Their closest known living relatives are the choanoflagellates, collared flagellates that have a morphology similar to the choanocytes of certain sponges. Molecular studies place animals in a supergroup called the opisthokonts, which also include the choanoflagellates, fungi and a few small parasitic protists. The name comes from the posterior location of the flagellum in motile cells, such as most animal spermatozoa, whereas other eukaryotes tend to have anterior flagella.

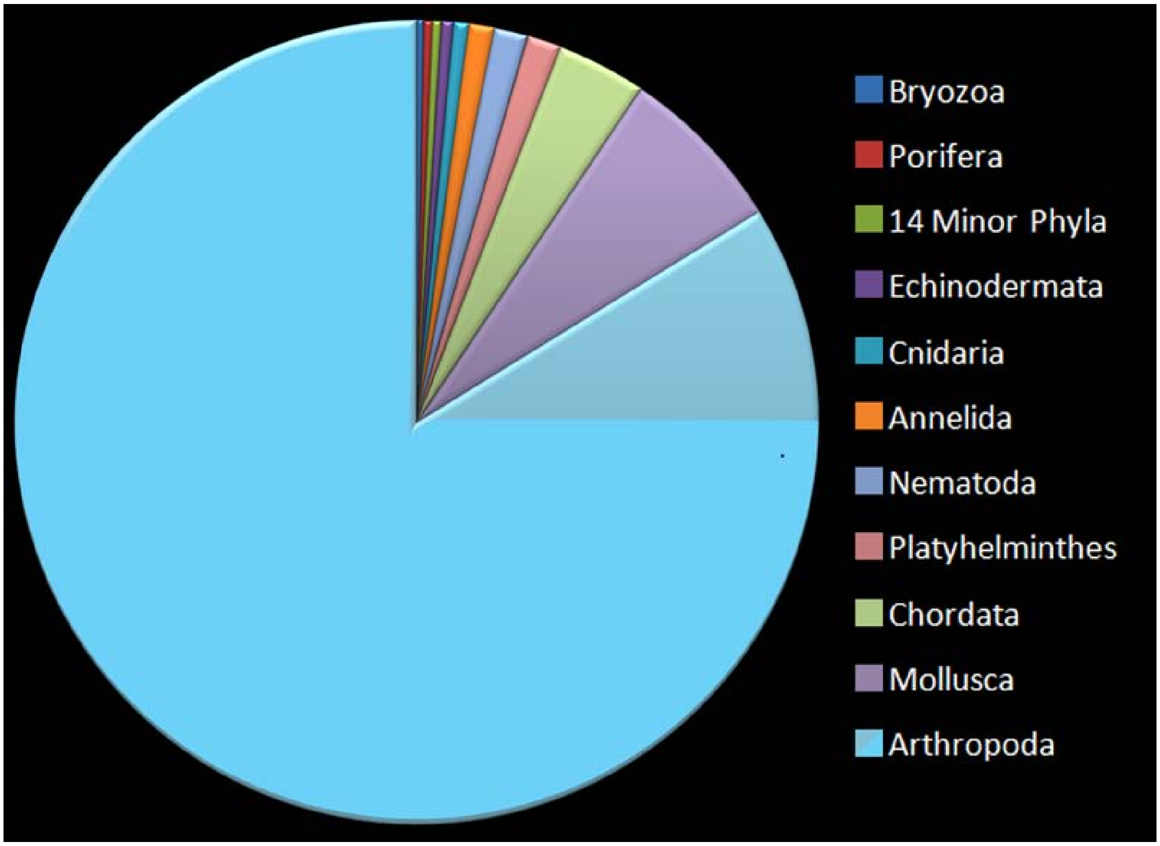
The first fossils that might represent animals appear in the Trezona Formation at Trezona Bore, West Central Flinders, South Australia. These fossils are interpreted as being early sponges. They were found in 665-million-year-old rock.

The next oldest possible animal fossils are found towards the end of the Precambrian, around 610 million years ago, and are known as the Ediacaran or Vendian biota. These are difficult to relate to later fossils, however. Some may represent precursors of modern phyla, but they may be separate groups, and it is possible they are not really animals at all.

Aside from them, most known animal phyla make a more or less simultaneous appearance during the Cambrian period, about 542 million years ago. It is still disputed whether this event, called the Cambrian explosion, represents a rapid divergence between different groups or a change in conditions that made fossilization possible.

Some paleontologists suggest that animals appeared much earlier than the Cambrian explosion, possibly as early as 1 billion years ago. Trace fossils such as tracks and burrows found in the Tonian era indicate the presence of triploblastic worms, like metazoans, roughly as large (about 5 mm wide) and complex as earthworms. During the beginning of the Tonian period around 1 billion years ago, there was a decrease in Stromatolite diversity, which may indicate the appearance of grazing animals, since Stromatolites diversity increased when grazing animals went extinct at the End Permian and End Ordovician extinction events, and decreased shortly after the grazer populations recovered. However the discovery that tracks very similar to these early trace fossils are produced today by the giant single-celled protist *Gromia sphaerica* casts doubt on their interpretation as evidence of early animal evolution.

Groups of animals



The relative number of species contributed to the total by each phylum of animals.

Porifera, Radiata and basal Bilateria

Orange elephant ear sponge, *Agelas clathrodes*, in foreground. Two corals in the background: a sea fan, *Iciligorgia schrammi*, and a sea rod, *Plexaurella nutans*.

The sponges (Porifera) were long thought to have diverged from other animals early. They lack the complex organization found in most other phyla. Their cells are differentiated, but in most cases not organized into distinct tissues. Sponges typically feed by drawing in water through pores. Archaeocyatha, which have fused skeletons, may represent sponges or a separate phylum. However, a phylogenomic study in 2008 of 150 genes in 29 animals across 21 phyla revealed that it is the Ctenophora or comb jellies which are the basal lineage of animals, at least among those 21 phyla. The authors speculate that sponges—or at least those lines of sponges they investigated—are not so primitive, but may instead be secondarily simplified.

Among the other phyla, the Ctenophora and the Cnidaria, which includes sea anemones, corals, and jellyfish, are radially symmetric and have digestive chambers with a single opening, which serves as both the mouth and the anus. Both have distinct tissues, but they are not organized into organs. There are only two main germ layers, the ectoderm and endoderm, with only scattered cells between them. As such, these animals are sometimes called diploblastic. The tiny placozoans are similar, but they do not have a permanent digestive chamber.

The remaining animals form a monophyletic group called the Bilateria. For the most part, they are bilaterally symmetric, and often have a specialized head with feeding and sensory organs. The body is triploblastic, i.e. all three germ layers are well-developed, and tissues form distinct organs. The digestive chamber has two openings, a mouth and an anus, and there is also an internal body cavity called a coelom or pseudocoelom. There are exceptions to each of these characteristics, however — for instance adult echinoderms are radially symmetric, and certain parasitic worms have extremely simplified body structures.

Genetic studies have considerably changed our understanding of the relationships within the Bilateria. Most appear to belong to two major lineages: the deuterostomes and the protostomes, the latter of which includes the Ecdysozoa, Platyzoa, and Lophotrochozoa. In addition, there are a few small groups of bilaterians with relatively similar structure that appear to have diverged before these major groups. These include the Acoelomorpha, Rhombozoa, and Orthonectida. The Myxozoa, single-celled parasites that were originally considered Protozoa, are now believed to have developed from the Medusozoa as well.

Deuterostomes

Superb Fairy-wren, *Malurus cyaneus*

Deuterostomes differ from the other Bilateria, called protostomes, in several ways. In both cases there is a complete digestive tract. However, in protostomes, the initial opening (the archenteron) develops into the mouth, and an anus forms separately. In deuterostomes this is reversed. In most protostomes, cells simply fill in the interior of the gastrula to form the mesoderm, called schizocoelous development, but in deuterostomes, it forms through invagination of the endoderm, called enterocoelic pouching. Deuterostomes also have a dorsal, rather than a ventral, nerve chord and their embryos undergo different cleavage.

All this suggests the deuterostomes and protostomes are separate, monophyletic lineages. The main phyla of deuterostomes are the Echinodermata and Chordata. The former are radially symmetric and exclusively marine, such as starfish, sea urchins, and sea cucumbers. The latter are dominated by the vertebrates, animals with backbones. These include fish, amphibians, reptiles, birds, and mammals.

In addition to these, the deuterostomes also include the Hemichordata, or acorn worms. Although they are not especially prominent today, the important fossil graptolites may belong to this group.

The Chaetognatha or arrow worms may also be deuterostomes, but more recent studies suggest protostome affinities.

Ecdysozoa

Yellow-winged darter, *Sympetrum flaveolum*

The Ecdysozoa are protostomes, named after the common trait of growth by moulting or ecdysis. The largest animal phylum belongs here, the Arthropoda, including insects, spiders, crabs, and their kin. All these organisms have a body divided into repeating segments, typically with paired appendages. Two smaller phyla, the Onychophora and Tardigrada, are close relatives of the arthropods and share these traits.

The ecdysozoans also include the Nematoda or roundworms, perhaps the second largest animal phylum. Roundworms are typically microscopic, and occur in nearly every environment where there is water. A number are important parasites. Smaller phyla related to them are the Nematomorpha or horsehair worms, and the Kinorhyncha, Priapulida, and Loricifera. These groups have a reduced coelom, called a pseudocoelom.

The remaining two groups of protostomes are sometimes grouped together as the Spiralia, since in both embryos develop with spiral cleavage.

Platyzoa

Pseudobiceros bedfordi, (Bedford's flatworm)

The Platyzoa include the phylum Platyhelminthes, the flatworms. These were originally considered some of the most primitive Bilateria, but it now appears they developed from more complex ancestors. A number of parasites are included in this group, such as the flukes and tapeworms. Flatworms are acoelomates, lacking a body cavity, as are their closest relatives, the microscopic Gastrotricha.

The other platyzoan phyla are mostly microscopic and pseudocoelomate. The most prominent are the Rotifera or rotifers, which are common in aqueous environments. They also include the Acanthocephala or spiny-headed worms, the Gnathostomulida, Micrognathozoa, and possibly the Cycliophora. These groups share the presence of complex jaws, from which they are called the Gnathifera.

Lophotrochozoa

Roman snail, *Helix pomatia*

The Lophotrochozoa include two of the most successful animal phyla, the Mollusca and Annelida. The former, which is the second-largest animal phylum by number of described species, includes animals such as snails, clams, and squids, and the latter comprises the segmented worms, such as earthworms and leeches. These two groups have long been considered close relatives because of the common presence of trochophore larvae, but the annelids were considered closer to the arthropods because they are both segmented. Now, this is generally considered convergent evolution, owing to many morphological and genetic differences between the two phyla.

The Lophotrochozoa also include the Nemertea or ribbon worms, the Sipuncula, and several phyla that have a ring of ciliated tentacles around the mouth, called a lophophore. These were traditionally grouped together as the lophophorates. but it now appears that the lophophorate group may be paraphyletic, with some closer to the nemerteans and some to the molluscs and annelids. They include the Brachiopoda or lamp shells, which are prominent in the fossil record, the Entoprocta, the Phoronida, and possibly the Bryozoa or moss animals.

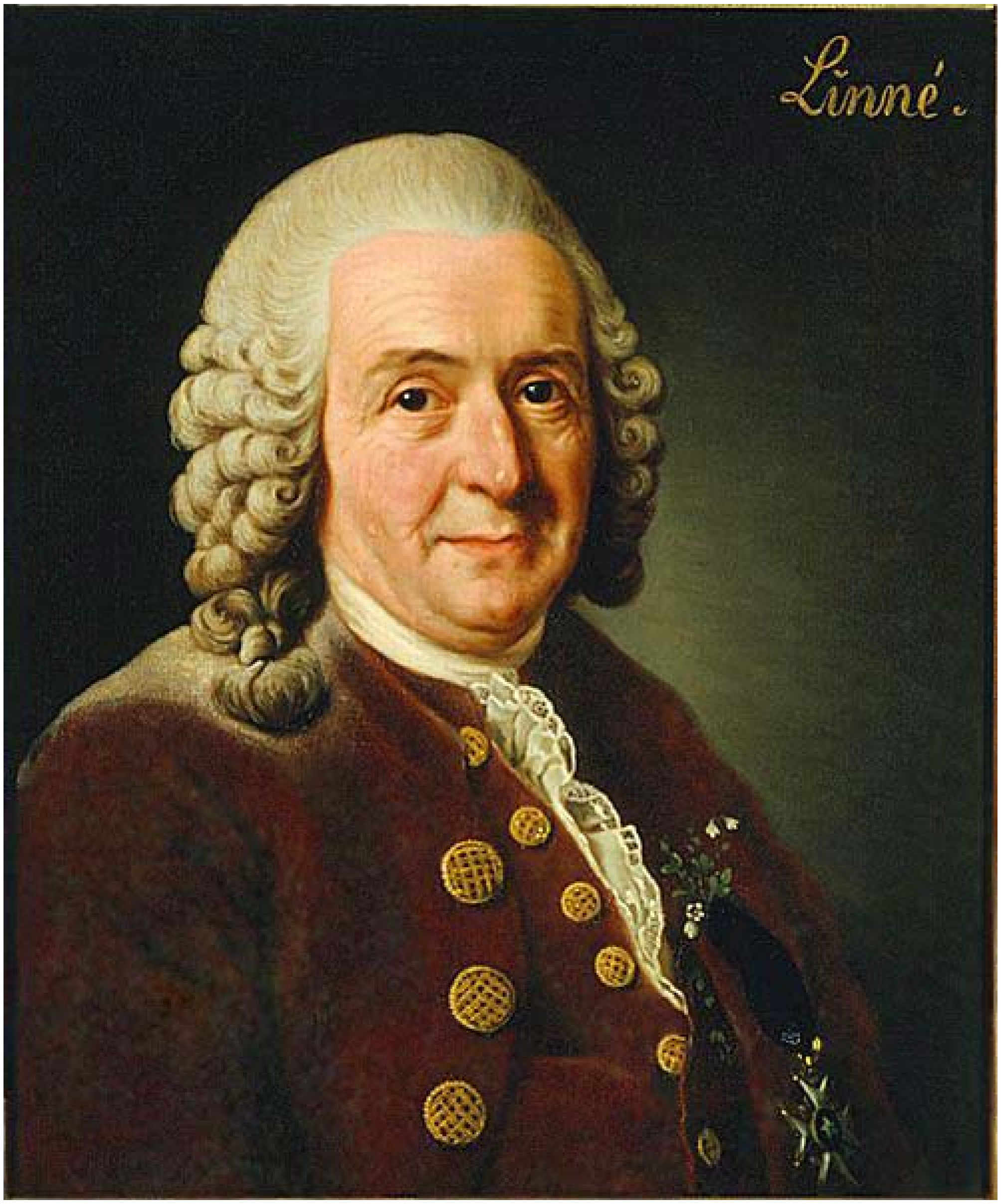
Model organisms

Because of the great diversity found in animals, it is more economical for scientists to study a small number of chosen species so that connections can be drawn from their work and conclusions extrapolated about how animals function in general. Because they are easy to keep and breed, the fruit fly *Drosophila melanogaster* and the nematode

Caenorhabditis elegans have long been the most intensively studied metazoan model organisms, and were among the first life-forms to be genetically sequenced. This was facilitated by the severely reduced state of their genomes, but as many genes, introns, and linkages lost, these ecdysozoans can teach us little about the origins of animals in general. The extent of this type of evolution within the superphylum will be revealed by the crustacean, annelid, and molluscan genome projects currently in progress. Analysis of the starlet sea anemone genome has emphasised the importance of sponges, placozoans, and choanoflagellates, also being sequenced, in explaining the arrival of 1500 ancestral genes unique to the Eumetazoa.

An analysis of the homoscleromorph sponge *Oscarella carmela* also suggests that the last common ancestor of sponges and the eumetazoan animals was more complex than previously assumed.

Other model organisms belonging to the animal kingdom include the mouse (*Mus musculus*) and zebrafish (*Danio rerio*).



Carolus Linnaeus, known as the father of modern taxonomy

History of classification

Aristotle divided the living world between animals and plants, and this was followed by Carolus Linnaeus (Carl von Linné), in the first hierarchical classification. Since then biologists have begun emphasizing evolutionary relationships, and so these groups have been restricted somewhat. For instance, microscopic protozoa were originally considered animals because they move, but are now treated separately.

In Linnaeus's original scheme, the animals were one of three kingdoms, divided into the classes of Vermes, Insecta, Pisces, Amphibia, Reptila, Aves, and Mammalia. Since then the last five have all been subsumed into a single phylum, the Chordata, whereas the various other forms have been separated out. The above lists represent our current understanding of the group, though there is some variation from source to source.

Chapter 2

Parazoa and Eumetazoa

Parazoa

Parazoa
Temporal range: Ediacaran - Recent

A sponge

Scientific classification

Domain:	Eukaryota
Kingdom:	Animalia
Subkingdom:	**Parazoa** Grant & Todd, 1838

Phyla

- Porifera
- Placozoa

The **Parazoa** are an ancestral subkingdom of animals, literally translated as "beside the animals".

Description

Parazoans differ from their choanoflagellate ancestors in that they are not microscopic and have differentiated cells, but unlike "true animals" (Eumetazoa), they do not have tissues. The only surviving parazoans are the sponges, which belong to the phylum Porifera, and one surviving species (*Trichoplax adhaerens*) in the phylum Placozoa.

Parazoa display no body symmetry (are asymmetrical); all other animal groups display some sort of symmetry. There are currently 5000 species, 150 of which are freshwater. Larvae are planktonic and adults are sessile.

Cladistics

The Parazoa-Eumetazoa split has been estimated at 940 million years ago.

The parazoa group is now considered paraphyletic. It is not included in most modern cladistic analyses. When referenced, it is sometimes considered an equivalent to Porifera.

Some authors include Placozoa, a phylum that consists of only one species, *Trichoplax adhaerens*, in the division, but they are also sometimes placed in the subkingdom Agnotozoa.

Eumetazoa

Eumetazoa
Temporal range: Ediacaran–Recent

A lancelet

Scientific classification

Domain:	Eukaryota
(unranked):	Opisthokonta
Kingdom:	Animalia
Subkingdom:	**Eumetazoa** Butschli, 1910

Phyla

Radiata (unranked)

- Ctenophora

- Cnidaria

Bilateria (unranked)

- Orthonectida
- Rhombozoa
- Acoelomorpha
- Chaetognatha
- **Superphylum Deuterostomia**
    - Chordata
    - Hemichordata
    - Echinodermata
    - Xenoturbellida
    - Vetulicolia †
- ***Protostomia (unranked)***
    - **Superphylum Ecdysozoa**
        - Kinorhyncha
        - Loricifera
        - Priapulida
        - Nematoda
        - Nematomorpha
        - Lobopodia†
        - Onychophora
        - Tardigrada
        - Arthropoda
    - **Superphylum Platyzoa**
        - Platyhelminthes
        - Gastrotricha
        - Rotifera
        - Acanthocephala
        - Gnathostomulida
        - Micrognathozoa
        - Cycliophora
    - **Superphylum Lophotrochozoa**
        - Sipuncula
        - Hyolitha†
        - Nemertea
        - Phoronida
        - Bryozoa
        - Entoprocta
        - Brachiopoda
        - Mollusca
        - Annelida
        - Echiura

Eumetazoa is a clade comprising all major animal groups except sponges, placozoa and several other little known animals. Characteristics of eumetazoans include true tissues organized into germ layers, and an embryo that goes through a gastrula stage. The clade is usually held to contain at least Ctenophora, Cnidaria, and Bilateria. Whether mesozoans and placozoans belong is in dispute.

Some phylogenists have speculated the sponges and eumetazoans evolved separately from single-celled organisms, which would mean that the animal kingdom does not form a clade (a complete grouping of organisms descended from a common ancestor). However, genetic studies and some morphological characteristics, like the common presence of choanocytes, support a common origin.

Eumetazoans are a major group of animals in the *Five Kingdoms* classification of Lynn Margulis and K. V. Schwartz, comprising the Radiata and Bilateria — all animals except the sponges, placozoans and mesozoans. When treated as a formal taxon Eumetazoa is typically ranked as a subkingdom. The name **Metazoa** has also been used to refer to this group, but more often refers to the Animalia as a whole. Many classification schemes do not include a subkingdom Eumetazoa.

Taxonomy

Over the last decade, the work of developmental biologists and molecular phylogeneticists spawned new ideas about bilaterian relationships resulting in a paradigm shift.

The current widely accepted hypothesis, based on molecular data (mostly 18S rRNA sequences), divides bilateria into the following four groups: Deuterostomia, Ecdysozoa, Lophotrochozoa, and Platyzoa (sometimes included in Lophotrochozoa). The last three groups are also collectively known as Protostomia.

However, many skeptics emphasize the pitfalls and inconsistencies associated with the new data. Claus Nielsen, a professor of evolutionary invertebrate embryology at the Zoological Museum University of Copenhagen champions one of the most prominent alternative views based on morphological evidence. In his 2001 book *Animal Evolution: Interrelationships of the Living Phyla*, he maintains the traditional divisions of Protostomia and Deuterostomia.

Evolutionary origins

It has been suggested that one type of molecular clock and one approach to interpretation of the fossil record both place the evolutionary origins of eumetazoa in the Ediacaran. However, the earliest eumetazoans may not have left a clear impact on the fossil record and other interpretations of molecular clocks suggest the possibility of an earlier origin. The discoverers of *Vernanimalcula* describe it as the fossil of a bilateral triploblastic animal that appeared at the end of the Marinoan glaciation prior to the Ediacaran Period, implying an even earlier origin for eumetazoans.

Chapter 3

Bilateria, Deuterostome and Ecdysozoa

Bilateria

Bilateria
Temporal range: Ediacaran–Recent

A Bowfin , *Amia calva*

Scientific classification

Domain:	Eukaryota
(unranked):	Opisthokonta
Kingdom:	Animalia
Subkingdom:	Eumetazoa
(unranked):	**Bilateria** Hatschek, 1888

Phyla

- Orthonectida
- Rhombozoa
- Acoelomorpha (disputed)
- Chaetognatha
- **Superphylum Deuterostomia**
  - Chordata
  - Hemichordata
  - Echinodermata
  - Xenoturbellida
  - Vetulicolia †
- *Protostomia (unranked)*
  - **Superphylum Ecdysozoa**
    - Scalidophora (unranked)

            - Kinorhyncha
            - Loricifera
            - Priapulida
        - Nematoda
        - Nematomorpha
        - Panarthropoda (unranked)
            - Lobopodia †
                - Onychophora
                - Tardigrada
            - Arthropoda
    - **Superphylum Platyzoa**
        - Platyhelminthes
        - Gastrotricha
        - Rotifera
        - Acanthocephala
        - Gnathostomulida
        - Micrognathozoa
        - Cycliophora
    - **Superphylum Lophotrochozoa**
        - Sipuncula
        - Hyolitha †
        - Nemertea
        - Phoronida
        - Bryozoa
        - Entoprocta
        - Brachiopoda
        - Mollusca
        - Annelida
        - Echiura

Illustration of the different types of symmetry of Life Forms On Earth. Display at the Field Museum, Chicago. The forms with bilateral symmetry can have heads. Life Forms with other types of symmetry have corresponding organs, if not a head.

The **bilateria** are all animals having a bilateral symmetry, i.e. they have a front and a back end, as well as an upside and downside. Radially symmetrical animals like jellyfish have a topside and downside, but no front and back. The bilateralia are a subregnum (a major group) of animals, including the majority of phyla; the most notable exceptions are the sponges, belonging to Parazoa, and cnidarians belonging to Radiata. For the most part, Bilateria have bodies that develop from three different germ layers, called the endoderm, mesoderm, and ectoderm. From this they are called triploblastic. Nearly all are bilaterally symmetrical, or approximately so. The most notable exception is the echinoderms, which achieve near-radial symmetry as adults, but are bilaterally symmetrical as larvae.

Except for a few highly reduced forms, the Bilateria have complete digestive tracts with separate mouth and anus. Most Bilateria also have a type of internal body cavity, called a coelom. It was previously thought that acoelomates gave rise to the other group, but there is some evidence now that in the main acoelomate phyla (flatworms and gastrotrichs) the absence could be secondary.

Evolution

The hypothetical last common ancestor of all bilateria is termed the "Urbilaterian". There is some debate about its appearance. The first evidence of bilateria in the fossil record comes from trace fossils in Ediacaran sediments, and the first *bona fide* bilaterian fossil is *Kimberella*, dating to 555 million years ago. Earlier fossils are controversial; The fossil *Vernanimalcula* may be the earliest known bilaterian, but may also represent an infilled bubble. Fossil embryos are known from around the time of *Vernanimalcula* (580 million years ago), but none of these have bilaterian affinities.

Phylogeny

There are two or more superphyla (main lineages) of Bilateria. The deuterostomes include the echinoderms, hemichordates, chordates, and possibly a few smaller phyla. The protostomes include most of the rest, such as arthropods, annelids, mollusks, flatworms, and so forth. There are a number of differences, most notably in how the embryo develops. In particular, the first opening of the embryo becomes the mouth in protostomes, and the anus in deuterostomes. Many taxonomists now recognize at least two more superphyla among the protostomes, Ecdysozoa (molting animals) and Lophotrochozoa. Some taxonomists also recognize another protostome superphylum, Platyzoa, while others would include the Platyzoans in Lophotrochozoa or not include them in any superphylum. The arrow worms (Chaetognatha) have proven particularly difficult to classify, with some taxonomists placing them among the deuterostomes and others placing them among the protostomes. The two most recent studies to address the question of chaetognath origins support protostome affinities.

Deuterostome

Deuterostomes
Temporal range: Late Ediacaran – Recent

Sea cucumbers and other echinoderms are deuterostomes.

Scientific classification

Kingdom:	Animalia

Subkingdom:	Eumetazoa
(unranked):	Bilateria
Superphylum:	**Deuterostomia** Grobben, 1908

Phyla

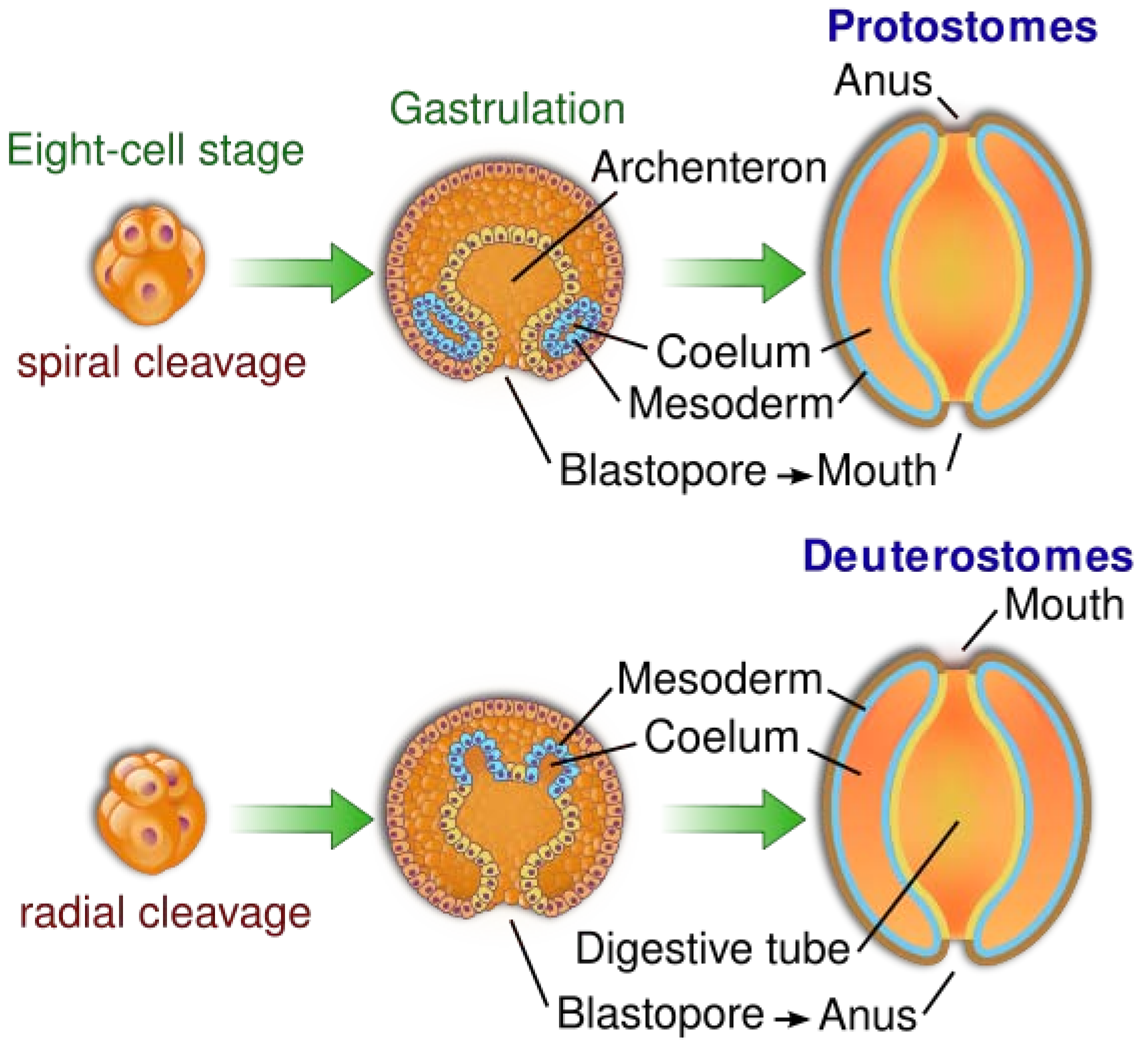
- Chordata
- Hemichordata
- Echinodermata
- Xenoturbellida
- Vetulicolia †

Deuterostomes (taxonomic term: **Deuterostomia**; from the Greek: "second mouth") are a superphylum of animals. They are a subtaxon of the Bilateria branch of the subregnum Eumetazoa, and are opposed to the protostomes. Deuterostomes are distinguished by their embryonic development; in deuterostomes, the first opening (the blastopore) becomes the anus, while in protostomes it becomes the mouth. Deuterostomes are also known as **enterocoelomates** because their coelom develops through enterocoely.

There are four extant phyla of deuterostomes:

- Phylum Chordata (vertebrates and their kin)
- Phylum Echinodermata (sea stars, sea urchins, sea cucumbers, etc.)
- Phylum Hemichordata (acorn worms and possibly graptolites)
- Phylum Xenoturbellida (2 species of worm-like animals)

The phylum Chaetognatha (arrow worms) may also belong here. Extinct groups may include the phylum Vetulicolia. Echinodermata, Hemichordata and Xenoturbellida form the clade Ambulacraria.



In both deuterostomes and protostomes, a zygote first develops into a hollow ball of cells, called a blastula. In deuterostomes, the early divisions occur parallel or perpendicular to the polar axis. This is called radial cleavage, and also occurs in certain protostomes, such as the lophophorates. Most deuterostomes display indeterminate cleavage, in which the developmental fate of the cells in the developing embryo are not determined by the identity of the parent cell. Thus if the first four cells are separated, each cell is capable of forming a complete small larva, and if a cell is removed from the blastula the other cells will compensate.

In deuterostomes the mesoderm forms as evaginations of the developed gut that pinch off, forming the coelom. This is called enterocoely.

Both the Hemichordata and Chordata have gill slits, and primitive fossil echinoderms also show signs of gill slits. A hollow nerve cord is found in all chordates, including tunicates (in the larval stage). Some hemichordates also have a tubular nerve cord. In the early embryonic stage it looks like the hollow nerve cord of chordates. Because of the degenerated nervous system of echinoderms, it is not possible to discern much about their ancestors in this matter, but based on different facts it is quite possible that all the present deuterostomes evolved from a common ancestor that had gill slits, a hollow nerve cord and a segmented body. It could have resembled the small group of Cambrian deuterostomes named Vetulicolia.

Formation of mouth and anus

All chordates, such as birds and mammals, are deuterostomes. Shown here is a Barred Owl.

The defining characteristic of the dueterostome is the fact that the blastopore, the opening at the bottom of the forming blastula, is turned into the anus. Whereas in protosomes the blastopore becomes the mouth. A mouth is then developed at the top and a digestive tract develops in the middle connecting the two for digestive purposes.

Origins

The majority of animals more complex than jellyfish and other Cnidarians are split into two groups, the protostomes and deuterostomes, and chordates are deuterostomes. It seems very likely that 555 million years old *Kimberella* was a member of the protostomes. If so, this means that the protostome and deuterostome lineages must have split some time before *Kimberella* appeared — at least 558 million years ago, and hence well before the start of the Cambrian 542 million years ago. The Ediacaran fossil *Ernietta*, from about 549 to 543 million years ago, may represent a deuterostome animal.

Fossils of one major deuterostome group, the echinoderms (whose modern members include sea stars, sea urchins and crinoids) are quite common from the start of the Cambrian, 542 million years ago. The Mid Cambrian fossil *Rhabdotubus johanssoni* has been interpreted as a pterobranch hemichordate. Opinions differ about whether the Chengjiang fauna fossil *Yunnanozoon*, from the earlier Cambrian, was a hemichordate or chordate. Another Chenjiang fossil, *Haikouella lanceolata*, also from the Chengjiang fauna, is interpreted as a chordate and possibly a craniate, as it shows signs of a heart, arteries, gill filaments, a tail, a neural chord with a brain at the front end, and possibly eyes — although it also had short tentacles round its mouth. *Haikouichthys* and *Myllokunmingia*, also from the Chenjiang fauna, are regarded as fish. *Pikaia*, discovered much earlier but from the Mid Cambrian Burgess Shale, is also regarded as a primitive chordate. On the other hand fossils of early chordates are very rare, since non-vertebrate chordates have no bones or teeth, and none have been reported for the rest of the Cambrian.

Ecdysozoa

Ecdysozoa
Temporal range: Early Cambrian–Recent

Centipede

Scientific classification [e]

Kingdom:	Animalia
(unranked):	Bilateria
(unranked):	Nephrozoa
(unranked):	Protostomia
Superphylum:	**Ecdysozoa** Aguinaldo et al., 1997

Phyla

- Kinorhyncha

- Loricifera
- Priapulida
- Nematoda
- Nematomorpha
- Lobopodia
- Onychophora
- Tardigrada
- Arthropoda

Ecdysozoa is a group of protostome animals, including Arthropoda (insects, chelicerata, crustaceans, and myriapods), Nematoda, and several smaller phyla. They were first defined by Aguinaldo *et al.* in 1997, based mainly on trees constructed using 18S ribosomal RNA genes. A large study in 2008 by Dunn *et al.* strongly supported the Ecdysozoa as a clade, that is, a group consisting of a common ancestor and all its descendants.

The group is also supported by morphological characters, and can be considered as including all animals that shed their exoskeleton. Groups corresponding roughly to the Ecdysozoa had been proposed previously by Perrier in 1897 and Seurat in 1920 based on morphology alone.

The group has been contested by a significant minority of biologists. Some have argued for groupings based on more traditional taxonomic techniques, while others have contested the interpretation of the molecular data.

Group characters

A tardigrade (water bear) and a nematode (roundworm)

notable characteristic shared by ecdysozoans is a three-layered cuticle composed of organic material, which is periodically molted as the animal grows. This process of molting is called ecdysis and gives the group its name. The Ecdysozoans lack locomotory cilia, produce mostly amoeboid sperm, and their embryos do not undergo spiral cleavage as in most other protostomes. Various other features are found in the group, for instance, tardigrades, pycnogonids and roundworms have a triradiate pharynx.

The Ecdysozoa include the following phyla: Arthropoda, Onychophora, Tardigrada, Kinorhyncha, Priapulida, Loricifera, Nematoda and Nematomorpha. A few other groups, such as the gastrotrichs, have been considered possible members but lack the main characters of the group, and are now placed elsewhere. The Arthropoda, Onychophora and Tardigrada have been grouped together as the Panarthropoda because they are distinguished by segmented body plans. Dunn *et al.* in 2008 suggested that the tardigrada could be grouped along with the nematodes, leaving Onychophora as the sister group to the arthropods.

The non-panarthropod members of Ecdysozoa have been grouped as Cycloneuralia but they are more usually considered paraphyletic.

Criticism

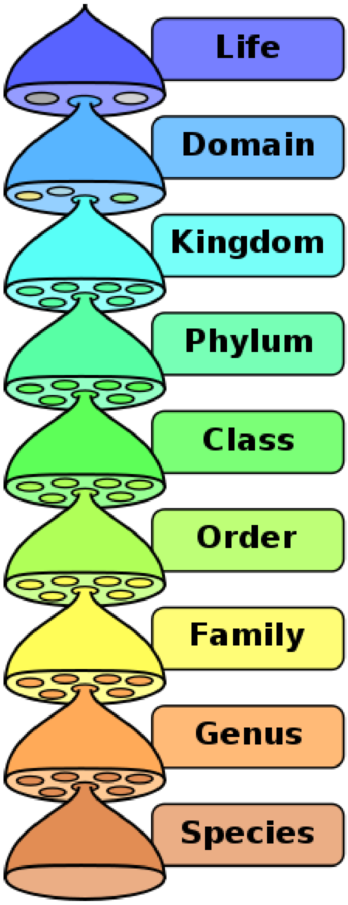
The grouping proposed by Aguinaldo *et al.* is not universally accepted. Some zoologists still hold to the original view that Panarthropoda should be classified with Annelida in a group called the Articulata, and that Ecdysozoa are polyphyletic. The highly derived roundworms, with their many highly derived parasitic taxa and a considerable number of autapomorphies continue to pose problems, and are one of the most contested inclusions of grouping.

1. Cuticular epithelia are widely spread over diverse phyla of invertebrates (including some groups outside Ecdysozoa, such as annelids and molluscs of the superphylum Lophotrochozoa, where it acts as a skin instead of an exoskeleton) and show a considerable degree of variation. They are believed to have evolved independently, at least in some groups. In Nematoda and Panarthropoda, the cuticle is different in both chemical composition and ultrastructure. While the cuticle in arthropods like insects contains chitin, or can be a combination of both chitin and keratin in crustaceans, chitin has never been found in the complex cuticle of Nematoda which is a fibrous and multilayered structure made of collagen and keratin of types unique to the Nematoda.
2. Molecular evidence for the monophyly of Ecdysozoa is also ambiguous.

One of the proposed solutions is to regard Ecdysozoa as a sister-group of Annelida, however the controversy is still far from closure.

Chapter 4

Phylum



The hierarchy of biological classification's eight major taxonomic ranks, which is an example of definition by genus and differentia. A kingdom contains one or more phyla. Intermediate minor rankings are not shown.

In biology, a **phylum** is a taxonomic rank below Kingdom and above Class. "Phylum" is equivalent to the botanical term **division**. The kingdom Animalia contains approximately forty phyla; the kingdom Plantae contains twelve divisions. Current research in phylogenetics is uncovering the relationships between phyla, which are contained in larger clades, like Ecdysozoa and Embryophyta.

General description and familiar examples

Informally, phyla can be thought of as grouping organisms based on general specialization of body plan, as well as developmental or internal organizations. For example, though seemingly divergent, spiders and crabs both belong to Arthropoda, whereas earthworms and tapeworms, similar in shape, are from Annelida and Platyhelminthes, respectively. Although Article 3.1 of the International Code of Botanical Nomenclature allows the use of the term "phylum" in reference to plants, the term "division" is almost always used by botanists.

The best known animal phyla are the Mollusca, Porifera, Cnidaria, Platyhelminthes, Nematoda, Annelida, Arthropoda, Echinodermata, and Chordata, the phylum to which humans belong, along with all other vertebrate species. Although there are 36 animal phyla, these nine include over 96% of animal species. Many phyla are exclusively marine, and only one phylum, the Onychophora (velvet worms) is entirely absent from the world's oceans—although ancestral onycophorans were marine.

Defining a phylum

At the most basic level, a phylum can be defined in two ways: as a group of organisms with a certain degree of morphological or developmental similarity (the phenetic definition), or a group of organisms with a certain degree of evolutionary relatedness (the phylogenetic definition). Attempting to define a level of the Linnean hierarchy without referring to (evolutionary) relatedness is an unsatisfactory approach, but the phenetic definition is more useful when addressing questions of a morphological nature—such as how successful different body plans were.

Definition based on genetic relation

The largest objective measure in the above definitions is the "certain degree"—how unrelated do organisms need to be to be members of different phyla? The minimal requirement is that all organisms in a phylum should be related closely enough for them to be clearly more closely related to one another than to any other group. However, even this is problematic, as the requirement depends on our current knowledge about organisms' relationships: As more data becomes available, particularly from molecular studies, we are better able to judge the relationships between groups. So phyla can be merged or split if it becomes apparent that they are related to one another or not; for example, since the onychophora and the tardigrada have now been accepted as stem groups of the arthropods, these three phyla should be combined.

This changeability of phyla has led some biologists to call for the concept of a phylum to be abandoned in favour of cladistics, a method in which groups are placed on a "family tree" without any formal ranking of group size. So as to provide a handle on the size and significance of groups, a "body-plan" based definition of a phylum has been proposed by paleontologists Graham Budd and Sören Jensen. The definition was posited by paleontologists because it is extinct organisms that are typically hardest to classify, because they can be extinct off-shoots that diverged from a phylum's history before the characters that define the modern phylum were all acquired.

Definition based on body plan

By Budd and Jensen's definition, phyla are defined by a set of characters shared by all their living representatives. This has a couple of small problems—for instance, characters common to most members of a phylum may be secondarily lost by some members. It is also defined based on an arbitrary point of time (the present). However, as it is character based, it is easy to apply to the fossil record. A more major problem is that it relies on an objective decision of which group of organisms should be considered a phylum.

Its utility is that it makes it easy to classify extinct organisms as "stem groups" to the phyla with which they bear the most resemblance, based only on the taxonomically important similarities. However, proving that a fossil belongs to the crown group of a phylum is difficult, as it must display a character unique to a sub-set of the crown group. Further, organisms in the stem group to a phylum can bear all the aspects of the "body plan" of the phylum without all the characters necessary to fall within it. This weakens the idea that each of the phyla represents a distinct body plan.

Based upon this definition, which some say is unreasonably affected by the chance survival of rare groups, which vastly increase the size of phyla, representatives of many modern phyla did not appear until long *after* the Cambrian.

Lists

Animal phyla

Phylum	Meaning	Common Name	Distinguishing characteristic	Species described
Acanthocephala	Thorny headed worms	Thorny-headed worms	Reversible spiny proboscis	about 756
Acoelomorpha	Without gut	Acoels	No mouth or alimentary canal (alimentary canal = digestive tract in digestive system)	
Annelida	Little ring	Segmented worms	Multiple circular segment	about 16,300 modern
Arthropoda	Jointed foot	Arthropods	Chitin exoskeleton	1,134,000+
Brachiopoda	Arm foot	Lamp shells	Lophophore and pedicle	between 300 and 500 extant
Bryozoa	Moss animals	Moss animals, sea mats	Lophophore, no pedicle, ciliated tentacles	about 5,000 living species
Chaetognatha	Longhair jaw	Arrow worms	Chitinous spines either side of head, fins	about 100 modern species
Chordata	Cord	Chordates	Hollow dorsal nerve cord, notochord, pharyngeal slits, endostyle, post-anal tail	about 100,000+
Cnidaria	Stinging nettle	Coelenterates	Nematocysts (stinging cells)	about 11,000
Ctenophora	Comb bearer	Comb jellies	Eight "comb rows" of fused cilia	about 100 modern species
Cycliophora	Wheel carrying	Symbion	Circular mouth	at least 3

			surrounded by small cilia	
Echinodermata	Spiny skin	Echinoderms	Fivefold radial symmetry in living forms, mesodermal calcified spines	about 7,000 extant and 13,000 extinct species
Echiura	Spine tail	Spoon worms	Set of hooks at posterior end	about 140
Entoprocta	Inside anus	Goblet worm	Anus inside ring of cilia	about 150
Gastrotricha	Hair stomach	Meiofauna	Two terminal adhesive tubes	about 690
Gnathostomulida	Jaw orifice	Jaw worms		about 100
Hemichordata	Half cord	Acorn worms, pterobranchs	Stomochord in collar, pharyngeal slits	about 100 living species
Kinorhyncha	Motion snout	Mud dragons	Eleven segments, each with a dorsal plate	about 150
Loricifera	Corset bearer	Brush heads	Umbrella-like scales at each end	about 122
Micrognathozoa	Tiny jaw animals	—	Accordion like extensible thorax	1
Mollusca	Thin shell	Mollusks / molluscs	Muscular foot and mantle round shell	112,000
Nematoda	Thread like	Round worms	Round cross section, keratin cuticle	80,000–1,000,000
Nematomorpha	Thread form	Horsehair worms		about 320
Nemertea	A sea nymph	Ribbon worms		about 1,200
Onychophora	Claw bearer	Velvet worms	Legs tipped by chitinous claws	about 200 modern
Orthonectida	Straight swim		Single layer of ciliated cells surrounding a mass of sex cells	about 20
Phoronida	Zeus's mistress	Horseshoe worms	U-shaped gut	20
Placozoa	Plate animals			1
Platyhelminthes	Flat worms	Flat worms		about 25,000
	Pore bearer	Sponges	Perforated interior wall	over 5,000 modern
Priapulida	Little Priapus			16
Rhombozoa	Lozenge animal	—	Single axial cell surrounded by ciliated cells	75
Rotifera	Wheel bearer	Rotifers	Anterior crown of cilia	about 2,000
Sipuncula	Small tube	Peanut worms	Mouth surrounded by invertible tentacles	144–320
Tardigrada	Slow step	Water bears	Four segmented body and head	1,000+
Xenoturbellida	Strange flatworm	—	Ciliated deuterostome	2
Total: 36				**2,000,000-**

🟥 Protostome
🟨 Deuterostome Bilateria
🟫 Basal/disputed
🟦 Other

[*]Porifera-simplest CLASS of metazoan phyla

- has been restructured into several classes under this phyla

Groups formerly ranked as phyla

Name as phylum	Common name	Current consensus
Aschelminthes	Pseudocoelomates	Divided into several pseudocoelomate phyla.
Craniata	—	Subgroup of phylum Chordata; perhaps synonymous with Vertebrata.
Cephalochordata	Lancelets	Subphylum of phylum Chordata.
Cephalorhyncha	—	Superphylum Scalidophora.
Enterepneusta	Acorn worms	Class of phylum Hemichordata.
Gephyra	Peanut worms and spoon worms	Divided into phyla Sipuncula and Echiura.
Mesozoa	Mesozoans	Divided into phyla Orthonectida and Rhombozoa.
Myxozoa		Severely modified Cnidarians.
Pentastomida	Tongue worms	Subclass of Maxillopoda of phylum Arthropoda.
Pogonophora	Beard worms	Part of family Siboglinidae of phylum Annelida.
Pterobranchia	—	Class of phylum Hemichordata.
Symplasma	Glass sponges	Class Hexactinellida of phylum Porifera.
Urochordata	Tunicates	Subphylum of phylum Chordata.
Vestimentifera	Vent worms	Part of family Siboglinidae of phylum Annelida.

Plant divisions

Division	Meaning	Common name	Distinguishing characteristics
Anthocerotophyta	Flower-horn plants	Hornworts	Horn-shaped sporophytes, no vascular system
Bryophyta	Moss plants	Mosses	Persistent unbranched sporophytes, no vascular system
Marchantiophyta	*Marchantia* plants	Liverworts	Ephemeral unbranched sporophytes, no vascular system
Lycopodiophyta	Wolf foot plants	Clubmosses & Spikemosses	Microphyll leaves, vascular system
Pteridophyta	Fern plants	Ferns & Horsetails	Prothallus gametophytes, vascular system
Pteridospermatophyta	Fern with seeds plant	Seed ferns	Only known from fossils, mostly Devonian, ranking in

			dispute
Coniferophyta	Sap/pitch plants	Conifers	Cones containing seeds and wood composed of tracheids
Cycadophyta	Palm plants	Cycads	Seeds, crown of compound leaves
Ginkgophyta	Ginkgo plants	Ginkgo, Maidenhair	Seeds not protected by fruit (single species)
Gnetophyta		Gnetophytes	Seeds and woody vascular system with vessels
Anthophyta (or Magnoliophyta)	Flower plant	Flowering plants	Flowers and fruit, vascular system with vessels

Fungal divisions

Phylum	**Meaning**	**Common name**	**Distinguishing characteristics**
Chytridiomycota	Little pot mushroom	Chytrids	Cellulose in cell walls, flagellated gametes
Deuteromycota	Second mushroom	Imperfect fungi	Unclassified fungi; only asexual reproduction observed
Zygomycota	Yolk mushroom	Zygomycetes	Blend gametangia to form a zygosporangium
Glomeromycota	Ball mushroom	None	Form arbuscular mycorrhizae with plants
Ascomycota	Bag/Wineskin Mushroom	Sac fungi	Produce spores in an 'ascus'
Basidiomycota	Basidium Mushroom	Club Fungi	Produce spores from a 'basidium'

Bacterial Phyla/Divisions

Currently there are 29 phyla accepted by LPSN

1. Acidobacteria, phenotipically diverse and mostly uncultured
2. Actinobacteria, High-G+C Gram positive species
3. Aquificae, only 14 thermophilic genera, deep branching
4. Bacteroidetes
5. Caldiserica, formerly candidate division OP5, *Caldisericum exile* is the sole representative
6. Chlamydiae, only 6 genera
7. Chlorobi, only 7 genera
8. Chloroflexi,
9. Chrysiogenetes, only 3 genera (*Chrysiogenes arsenatis*, *Desulfurispira natronophila*, *Desulfurispirillum alkaliphilum*)

10. Cyanobacteria, also known as the blue-green algae
11. Deferribacteres
12. Deinococcus-Thermus, *Deinococcus radiodurans* and *Thermus aquaticus* are "commonly known" species of this phyla
13. Dictyoglomi
14. Elusimicrobia, formerly candidate division Thermite Group 1
15. Fibrobacteres
16. Firmicutes, Low-G+C Gram positive species, such as the spore-formers Bacilli (aerobic) and Clostridia (anaerobic)
17. Fusobacteria
18. Gemmatimonadetes
19. Lentisphaerae, formerly clade VadinBE97
20. Nitrospira
21. Planctomycetes
22. Proteobacteria, the most know phyla, containing most of the "commonly known" species, such as *Escherichia coli* or *Pseudomonas aeruginosa*
23. Spirochaetes, species include *Borrelia burgdorferi*, which causes Lyme disease
24. Synergistetes
25. Tenericutes, alternatively class Mollicutes in phylum Firmicutes (notable genus: *Mycoplasma*)
26. Thermodesulfobacteria
27. Thermomicrobia
28. Thermotogae, deep branching
29. Verrucomicrobia

Archaeal Phyla/Division

1. Crenarchaeota, Second most common archaeal phylum
2. Euryarchaeota, most common archaeal phylum
3. Korarchaeota
4. Nanoarchaeota, ultra-small symbiotes
5. Thaumarchaeota

Chapter 5

Protostome, Platyzoa and Lophotrochozoa

Protostome

Protostomes
Temporal range: Ediacaran–Recent

A Caribbean Reef Squid, an example of a protostome.

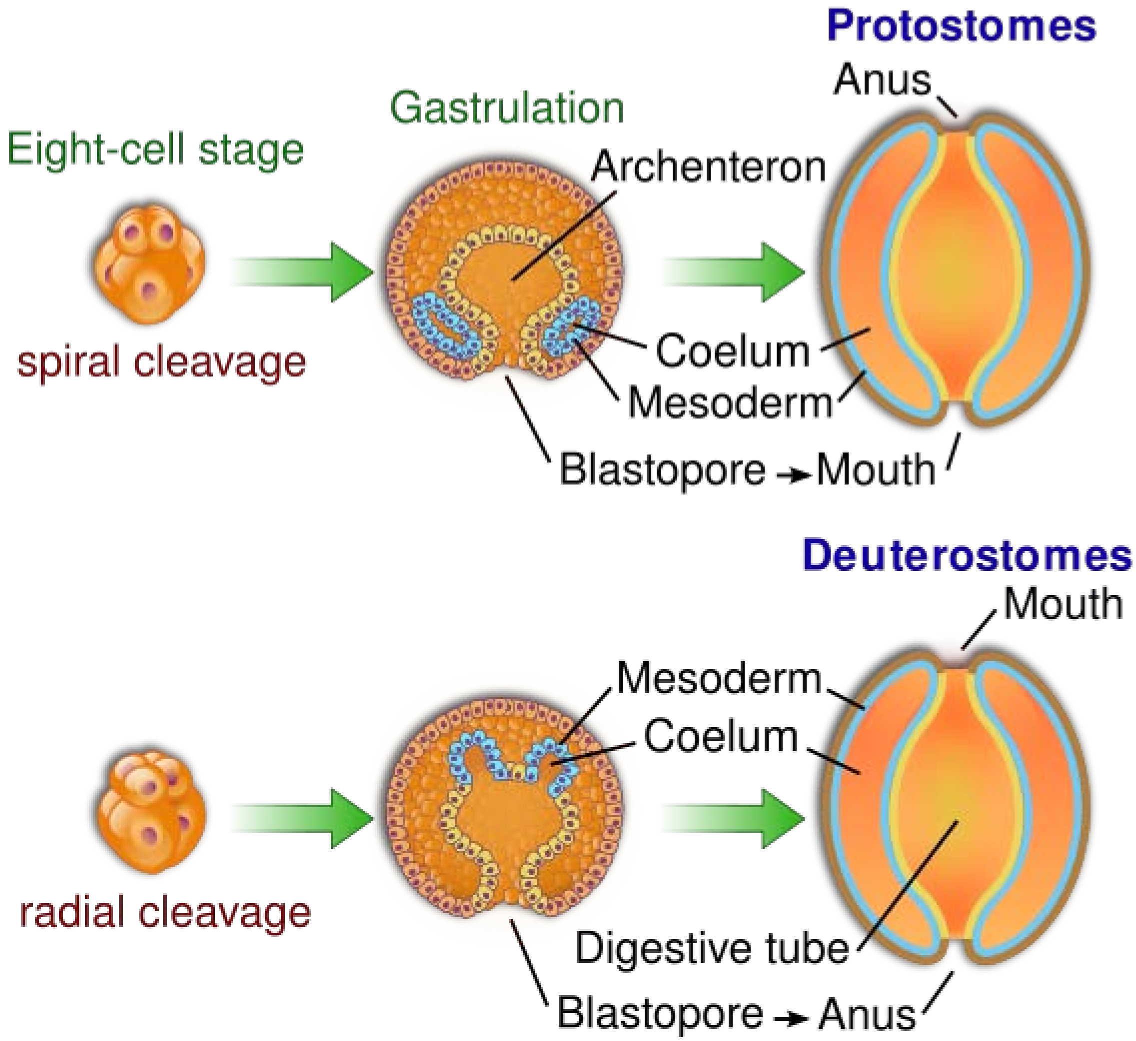
Scientific classification

Kingdom:	Animalia
Subkingdom:	Eumetazoa
(unranked):	**Protostomia** Grobben, 1908

Superphylums

- Ecdysozoa
- Lophotrochozoa
- Platyzoa

Protostomia (from Greek meaning "mouth first") are a clade of animals. Together with the deuterostomes and a few smaller phyla, they make up the Bilateria, mostly comprising animals with bilateral symmetry and three germ layers. The major distinctions between deuterostomes and protostomes are found in embryonic development.



In animals at least as complex as earthworms, the embryo forms a dent on one side, the blastopore, which deepens to become the archenteron, the first phase in the growth of the gut. In deuterostomes, the original dent becomes the anus while the gut eventually tunnels through to make another opening, which forms the mouth. The protostomes were so named because it used to be thought that in their embryos the dent formed the mouth while the anus was formed later, at the opening made by the other end of the gut. More recent research, however, shows that in protostomes the edges of the dent close up in the middle, leaving openings at the ends which become the mouth and anus. However, this idea has been challenged, because the platyhelminthes, a group which forms a sister group to the rest of the bilaterian animals, have a single mouth which leads into a blind gut (with no anus). The genes employed in the embryonic construction of this mouth are the same as those expressed around the protostome mouth,

There are other significant differences between the protostome and deuterostome patterns of development:

- Most protostomes are schizocoelomates, meaning a solid mass of the embryonic mesoderm splits to form a coelom. A few, such as Priapulids, have no coelom, but they may have descended from schizocoelomate ancestors. On the other hand all known deuterostomes are enterocoelous, meaning that the coelom is formed from longitudinal pouches of the archenteron which then become separate cavities.
- Within the Protostomes a number of phyla undergo what is known as spiral cleavage which is determinate, meaning that the fate of the cells is determined as they are formed. This is in contrast to deuterostomes which have radial cleavage that is indeterminate.

Current molecular data suggest that protostome animals can be divided into three major groups:

- Ecdysozoa, e.g. arthropods, nematodes
- Platyzoa, e.g. platyhelminthes, rotifers
- Lophotrochozoa, e.g. molluscs, annelids

as well as a number of minor taxa of basal or ambiguous affinity.

Platyzoa

Platyzoa

Pseudobiceros bedfordi (Bedford's Flatworm)

Scientific classification

Kingdom:	Animalia
Subkingdom:	Eumetazoa
(unranked):	Bilateria
Superphylum:	**Platyzoa** Cavalier-Smith, 1998

Phyla

- Platyhelminthes
- Gastrotricha
- ***Gnathifera (unranked)***
    - Rotifera
    - Acanthocephala
    - Gnathostomulida
    - Micrognathozoa
    - Cycliophora

The **Platyzoa** are a group of protostome animals proposed by Thomas Cavalier-Smith in 1998. Cavalier-Smith included in Platyzoa the Phylum Platyhelminthes or flatworms, and a new phylum, Acanthognatha, into which he gathered several previously described phyla of microscopic animals. Subsequent studies have supported Platyzoa as a clade, a monophyletic group of organisms with a common ancestor, while differing on the phyla included and on relationships within Platyzoa.

Phyla

One current scheme places the following traditional phyla in Platyzoa:

- Platyhelminthes
- Gastrotricha
- Gnathifera
    - Rotifera
    - Acanthocephala
    - Gnathostomulida
    - Micrognathozoa
    - Cycliophora

Characteristics

The Platyhelminthes and Gastrotricha are acoelomate. The other phyla have a pseudocoel, and share characteristics such as the structure of their jaws and pharynx, although these have been secondarily lost in the parasitic Acanthocephala. They form a monophyletic subgroup called the Gnathifera.

The name "Platyzoa" is used because most members are flat, though rotifers are not.

Classification

The Platyzoa are close relatives of the Lophotrochozoa, and are sometimes included in that group. Together the two make up the Spiralia.

Lophotrochozoa

Lophotrochozoa Temporal range: Early Cambrian - Recent	
	
Caribbean Reef Squid or *Sepioteuthis sepioidea* is a complex lophotrochozoan.	
Scientific classification	
Kingdom:	Animalia
Subkingdom:	Eumetazoa
(unranked):	Bilateria
Superphylum:	**Lophotrochozoa**

Phyla

- Sipuncula
- Hyolitha †
- Nemertea
- Phoronida
- Bryozoa
- Entoprocta
- Brachiopoda
- Mollusca
- Annelida
- Echiura

The **Lophotrochozoa** are a major grouping of protostome animals. The taxon was introduced in 1995 in a paper by Kenneth M Halanych *et al.* based on molecular data. Molecular evidence such as a result of studies of the evolution of small-subunit ribosomal RNA (rRNA) supports the monophyly of the phyla listed in the infobox shown at right.

Terminology

The word "lophotrochozoan" is sometimes equated with spiralian. When used in a broader sense (*sensu lato*), it can include rotifers and platyhelminthes. When used *sensu stricto*, it refers to a subgroup of Spiralia.

Groups

The Lophotrochozoa comprise two groups, the trochozoans and the lophophorata. The exact relationships between the different phyla are not entirely certain. However, it appears that neither the lophophorates nor the trochozoa are monophyletic groups by themselves, but are mixed together.

- Trochozoans produce trochophore larvae, which have two bands of cilia around their middle. Previously these were treated together as the Trochozoa, together with the arthropods, which do not produce trochophore larvae but were considered close relatives of the annelids because they are both segmented. However, they show a number of important differences, and the arthropods are now placed separately among the Ecdysozoa. The Trochozoa include the Nemertea, Mollusca, Sipuncula, Echiura, Pogonophora and Annelida.

- The Lophophorata are united by the presence of a lophophore, a fan of ciliated tentacles surrounding the mouth, and so were treated together as the lophophorates. They are unusual in showing radial cleavage, and some authors considered them deuterostomes, before RNA trees placed them together with the trochozoans. The Lophophorata include the Bryozoa, Entoprocta, Phoronida, and Brachiopoda.

Other phyla are included on the basis of molecular data.

Chapter 6

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

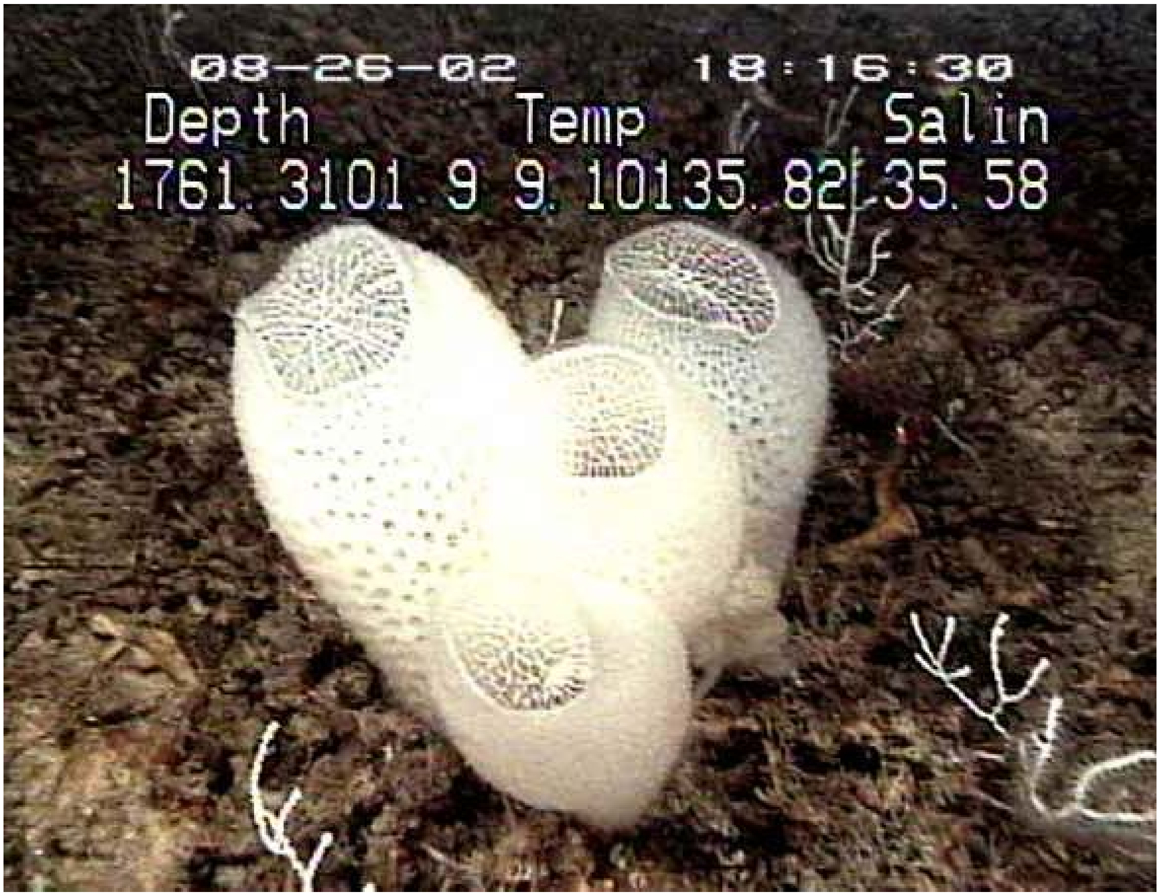
Sponges in temperate regions live for at most a few years, but some tropical species and perhaps some deep-ocean ones may live for 200 years or more. Some calcified demosponges grow by only 0.2 millimetres (0.0079 in) per year and, if that rate is constant, specimens 1 metre (3.3 ft) wide must be about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

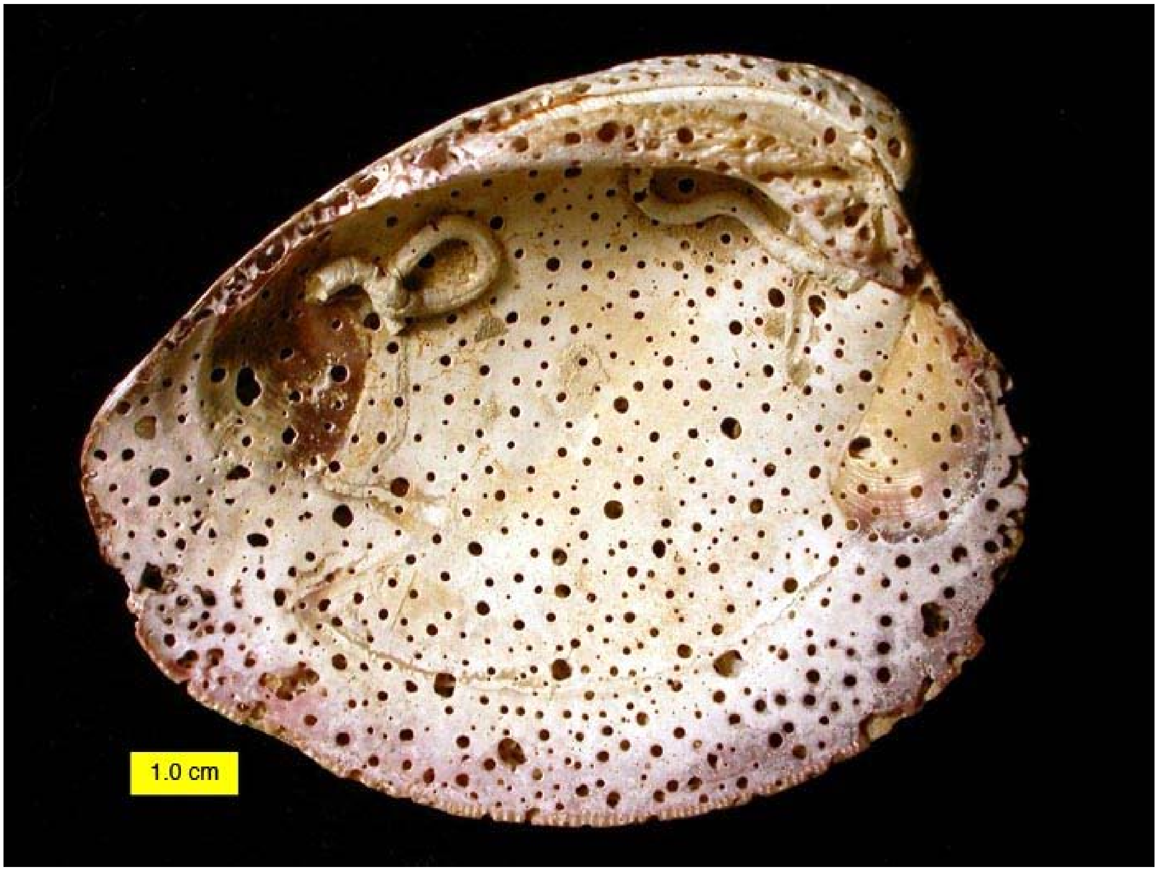
The different classes of sponge live in different ranges of habitat:

	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

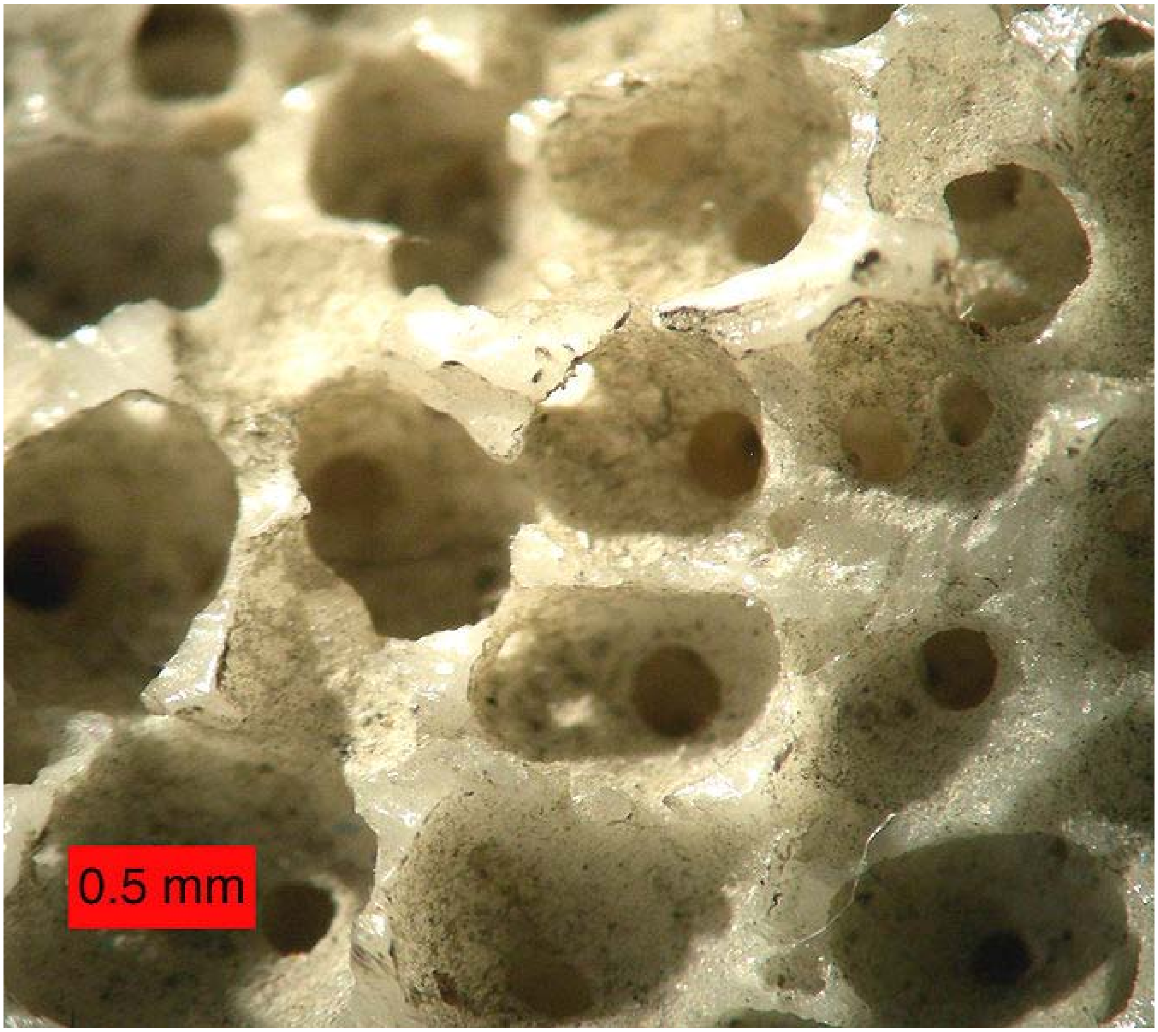
As primary producers

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

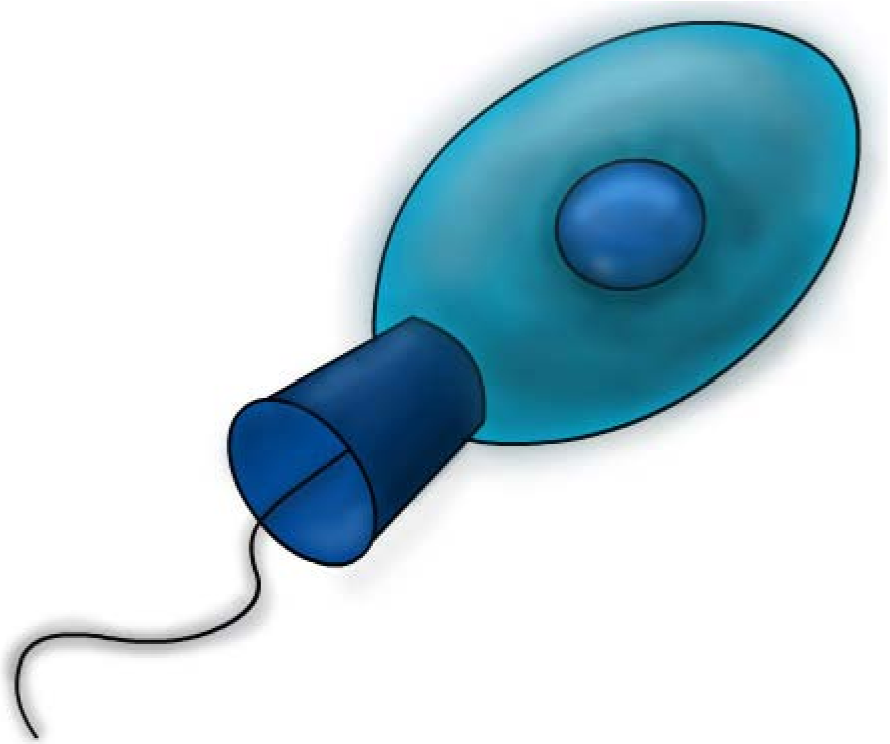
Fossil sponge *Raphidonema faringdonense* from Cretaceous rocks in England

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

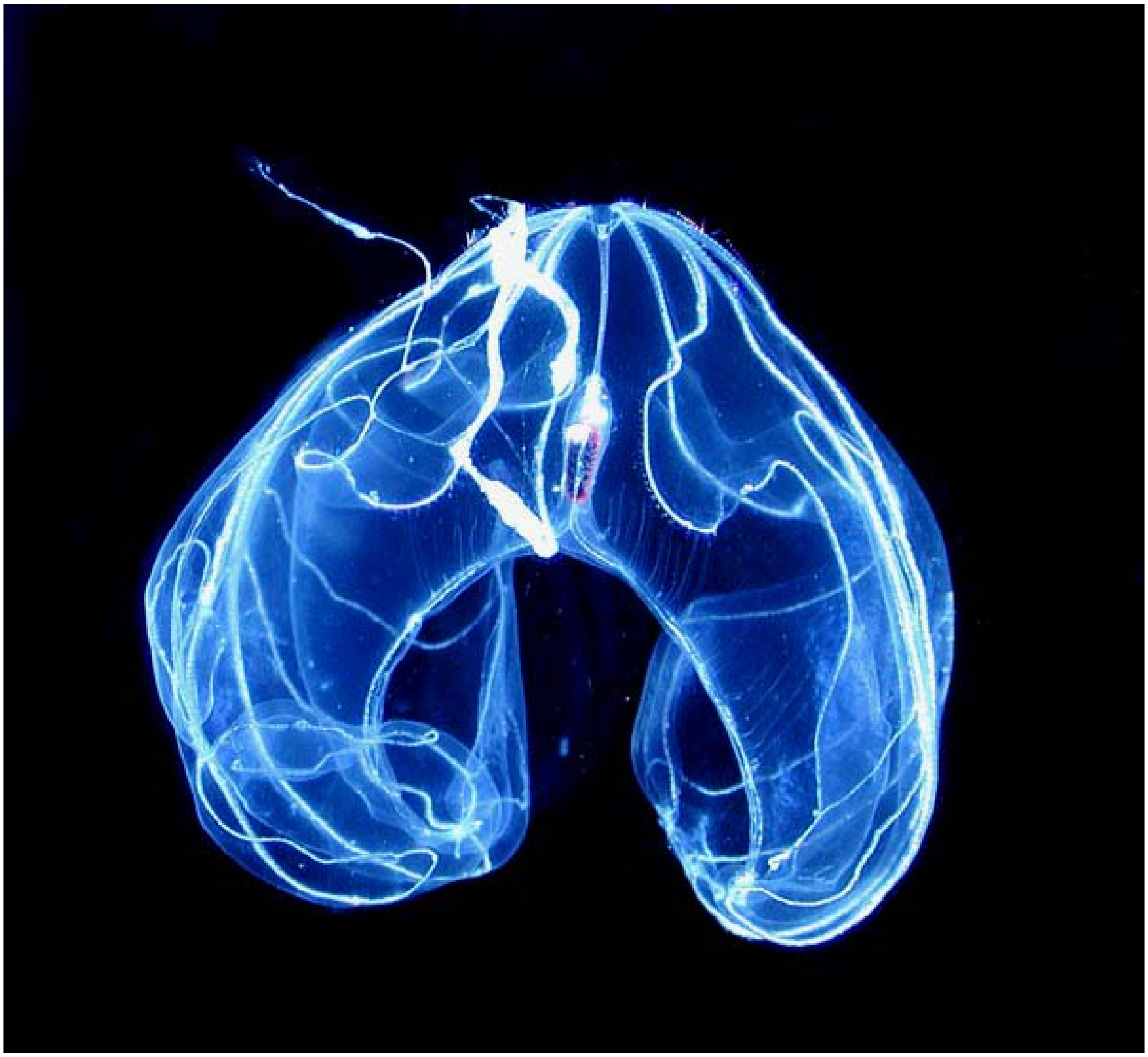


A choanoflagellate

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.



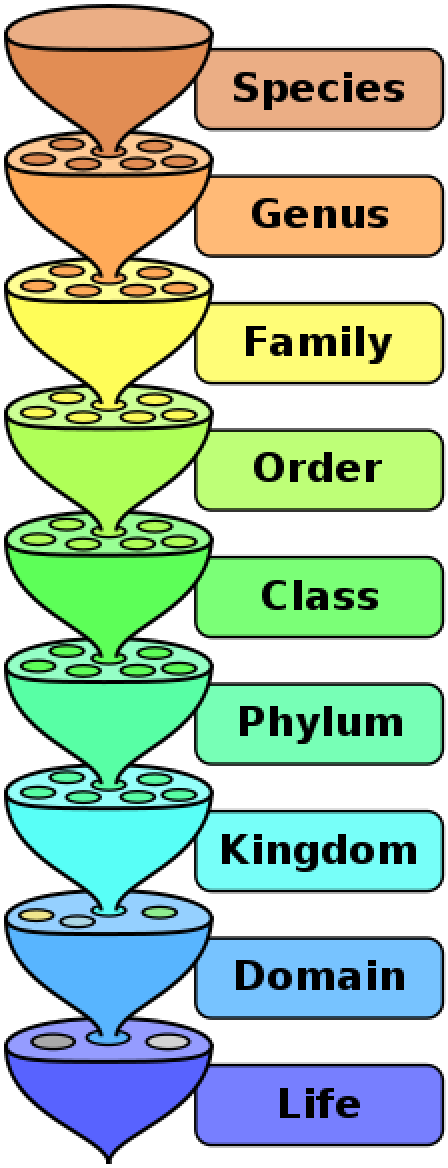
A comb jelly

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.

By humans

Display of natural sponges for sale on Kalymnos in Greece

Skeleton

The calcium carbonate or silica spicules of most sponge genera make them too rough for most uses, but two genera, *Hippospongia* and *Spongia*, have soft, entirely fibrous skeletons. Early Europeans used soft sponges for many purposes, including padding for helmets, portable drinking utensils and municipal water filters. Until the invention of synthetic sponges, they were used as cleaning tools, applicators for paints and ceramic glazes and discreet contraceptives. However by the mid-20th century, over-fishing brought both the animals and the industry close to extinction.

Many objects with sponge-like textures are now made of substances not derived from poriferans. Synthetic sponges include personal and household cleaning tools, breast implants, and contraceptive sponges. Typical materials used are cellulose foam, polyurethane foam, and less frequently, silicone foam.

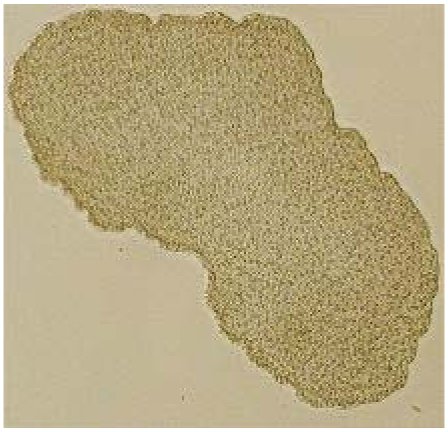
The luffa "sponge", also spelled *loofah*, which is commonly sold for use in the kitchen or the shower, is not derived from an animal but from the fibrous "skeleton" of a gourd (Cucurbitaceae).

Antibiotic compounds

Sponges have medicinal potential due to the presence in sponges themselves or their microbial symbionts of chemicals that may be used to control viruses, bacteria, tumors and fungi.

Chapter 7

Placozoa

Placozoa	
	
Scientific classification [e]	
Kingdom:	Animalia
Phylum:	**Placozoa** Grell, 1971
Classes	
Trichoplacia *Trichoplax*	

The **Placozoa** are a basal form of invertebrate. They are the simplest in structure of all non-parasitic multicellular animals (Metazoa). They are generally classified as a single species, *Trichoplax adhaerens*, although there is enough genetic diversity that it is likely that there are multiple, morphologically similar species. Although they were first discovered in 1883, a common name does not yet exist for the taxon; the scientific name literally means "flat animals".

Biology

Trichoplax is a small, flattened, animal around 1 millimetre across. Like an *Amoeba*, it has no regular outline, although the lower surface is somewhat concave, and the upper surface is always flattened. The body consists of an outer layer of simple epithelium enclosing a loose sheet of stellate cells resembling the mesenchyme of some more advanced animals. The epithelial cells bear flagella, which the animal uses to help it creep along the seafloor.

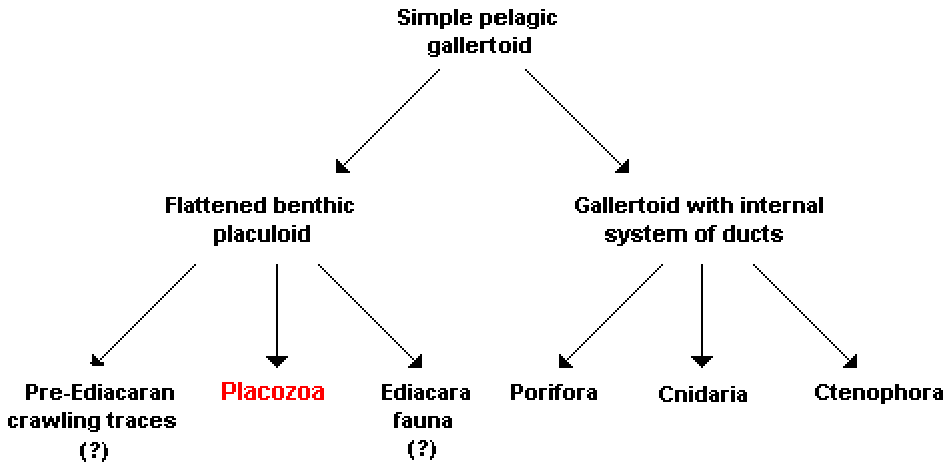
The lower surface engulfs small particles of organic detritus, on which the animal feeds. It reproduces asexually, budding off smaller individuals, and the lower surface may also bud off eggs into the mesenchyme.

Evolutionary relationships

There is no convincing fossil record of the placozoa, although the Ediacaran (Precambrian, 550 million years ago) organism *Dickinsonia* appears to be closely allied with this phylum.

Traditionally, classification has been based on their level of organization: i.e. they possess no tissues or organs. However this may be as a result of secondary loss, so is inadequate to demark a clade. More recent work has attempted to classify them based on the DNA sequences in their genome; this has placed the phylum between the sponges and the eumetazoa. In such a feature-poor phylum, molecular data are considered to provide the most reliable approximation of the placozoans' phylogeny.

Functional-morphology hypothesis



The Placozoa descending side by side with the sponges, cnidarians and ctenophores from a gallertoid by processes of differentiation

On the basis of their simple structure, the Placozoa were frequently viewed as a model organism for the transition from unicellular organisms to the multicellular animals (Metazoa) and are thus considered a sister taxon to all other metazoans:

According to a functional-morphology model, all or most animals are descended from a *gallertoid*, a free-living (pelagic) sphere in seawater, consisting of a single ciliated layer of cells supported by a thin, noncellular separating layer, the basal lamina. The interior of the sphere is filled with contractile fibrous cells and a gelatinous extracellular matrix. Both the modern Placozoa and all other animals then descended from this multicellular beginning stage via two different processes:

- Infolding of the epithelium led to the formation of an internal system of ducts and thus to the development of a modified gallertoid from which the sponges (Porifera), Cnidaria and Ctenophora subsequently developed.
- Other gallertoids, according to this model, made the transition over time to a benthic mode of life; that is, their habitat has shifted from the open ocean to the floor (benthic zone). While the probability of encountering food, potential sexual partners, or predators is the same in all directions for animals floating freely in the water, there is a clear difference on the seafloor between the sides facing toward and away from the substrate, and between their orientation and the vertical direction perpendicular to the substrate. This results naturally in a selective advantage for flattening of the body, as of course can be seen in many benthic species. In the proposed functional-morphology model, the Placozoa, and possibly also several organisms known only from the fossil state, are descended from such a life form, which is now termed *placuloid*. Three different life strategies have accordingly led to three different lines of development:
    - Animals that live interstitially in the sand of the ocean floor were responsible for the fossil crawling traces that are considered the earliest evidence of animals and are detectable even prior to the dawn of the Ediacaran Period in geology. These are usually attributed to bilaterally symmetrical worms, but the hypothesis presented here views animals derived from placuloids, and thus close relatives of *Trichoplax adhaerens*, to be the producers of the traces.
    - Animals that incorporated algae as photosynthetically active endosymbionts, i.e. primarily obtaining their nutrients from their partners in symbiosis, were accordingly responsible for the mysterious creatures of the Ediacara fauna that are not assigned to any modern animal taxon and lived during the Ediacaran Period, before the start of the Paleozoic. Recent work has shown that some of the Ediacaran assemblages (e.g. Mistaken Point) were in deep water, below the photic zone, and that the organisms were not dependent on endosymbiotic photosynthesisers.
    - Animals that grazed on algal mats were ultimately the direct ancestors of the Placozoa. The advantages of an amoeboid multiplicity of shapes thus allowed a previously present basal lamina and a gelatinous extracellular matrix to be lost *secondarily*. Pronounced differentiation between the ventral surface facing the substrate and the dorsal, facing away from it,

> accordingly led to the physiologically distinct cell layers of *Trichoplax adhaerens* that can still be seen today. Consequently, these are analogous, but not homologous, to ectoderm and endoderm, the "external" and "internal" cell layers in eumetazoans; i.e. the structures corresponding functionally to one another have, according to the proposed hypothesis, no common evolutionary origin.

Should the analysis presented above turn out to be correct, *Trichoplax adhaerens* would be the oldest branch of the multicellular animals and a relic of the Ediacara fauna, or even the pre-Ediacara fauna. Due to the absence of extracellular matrix and basal lamina, the development potential of these animals, very successful in their ecological niche, was of course limited, which would explain the low rate of evolution, referred to as *bradytely*, of their phenotype, their outward form as adults.

This hypothesis was supported by a recent analysis of the *Trichoplax adhaerens* mitochondrial genome in comparison to those of other animals, The hypothesis was, however, rejected in a statistical analysis of the *Trichoplax adhaerens* whole genome sequence in comparison to the whole genome sequences of six other animals and two related non-animal species, but only at the $p=0.07$ level, which indicates a marginal level of statistical significance.

Epitheliozoa hypothesis

Functional-morphology hypotheses are not undisputed among scientists and are often rejected because of their highly theoretical character, which is not directly accessible to empirical study. Cladistics, a modern form of systematics research, is based exclusively on demonstrable features of living and fossil animal groups (taxa) for reconstructing the genealogy of a species or group.

The principle support for such a relationship comes from special cell/cell junctions, the belt desmosomes, that occur not just in the Placozoa but in all animals except the sponges; they enable the cells to join together in an unbroken layer like the epitheloid of the Placozoa. *Trichoplax adhaerens* also shares the ventral gland cells with most eumetazoans. Both characteristics can be considered apomorphies, i.e. evolutionarily derived features, and thus form the basis of a common taxon for all animals that possess them.

One possible scenario inspired by the proposed hypothesis starts with the idea that the monociliated cells of the epitheloid in *Trichoplax adhaerens* evolved by reduction of the collars in the collar cells (choanocytes) of sponges as the ancestors of the Placozoa abandoned a filtering mode of life. The epitheloid would then have served as the precursor to the true epithelial tissue of the eumetazoans.

In contrast to the model based on functional morphology described earlier, in the Epitheliozoa concept the ventral and dorsal cell layers of the Placozoa are homologs of endoderm and ectoderm, the two basic embryonic cell layers of the eumetazoans — the digestive *gastrodermis* in the Cnidaria or the gut epithelium in the bilaterally symmetrical Bilateria may have developed from endoderm, whereas ectoderm is, among other things, the precursor to the external skin layer (epidermis). The interior space pervaded by a fiber syncytium in the Placozoa would then correspond to connective tissue in the other animals. It is uncertain whether the calcium ions stored in the syncytium are related to the lime skeletons of many cnidarians.

As noted above, this hypothesis was supported in a statistical analysis of the *Trichoplax adhaerens* whole genome sequence in comparison to the whole genome sequences of six other animals and two related non-animal species.

The most important concept based on purely morphological characteristics pictures the Placozoa as the nearest relative of the animals with true tissues (Eumetazoa). The taxon they share, called the Epitheliozoa, is itself construed to be a sister group to the sponges (Porifera):

Eumetazoa hypothesis

A third hypothesis, based primarily on molecular genetics, views the Placozoa as highly simplified eumetazoans. According to this, *Trichoplax adhaerens* is descended from considerably more complex animals that already had muscles and nerve tissues. Both tissue types, as well as the basal lamina of the epithelium, were accordingly lost more recently by radical secondary simplification.

Various studies in this regard so far yield differing results for identifying the exact sister group: in one case the Placozoa would qualify as the nearest relatives of the Cnidaria, while in another they would be a sister group to the Ctenophora, and occasionally they are placed directly next to the Bilateria:

An argument raised against the proposed scenario is that it leaves morphological features of the animals completely out of consideration. The extreme degree of simplification that would have to be postulated for the Placozoa in this model, moreover, is known only for parasitic organisms but would be difficult to explain functionally in a free-living species like *Trichoplax adhaerens*.

All versions of this hypothesis were rejected with high confidence in a statistical analysis of the *Trichoplax adhaerens* whole genome sequence in comparison to the whole genome sequences of six other animals and two related non-animal species.

Chapter 8

Ctenophora

Comb jellies
Temporal range: Cambrian - Recent.

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

Scientific classification

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

Classes

Tentaculata
Nuda

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

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

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

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

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

Distinguishing features

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

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

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

Comparison with other major animal groups

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

Description

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

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

Common features

Body layers

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

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

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

Feeding, excretion and respiration

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

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

Locomotion

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

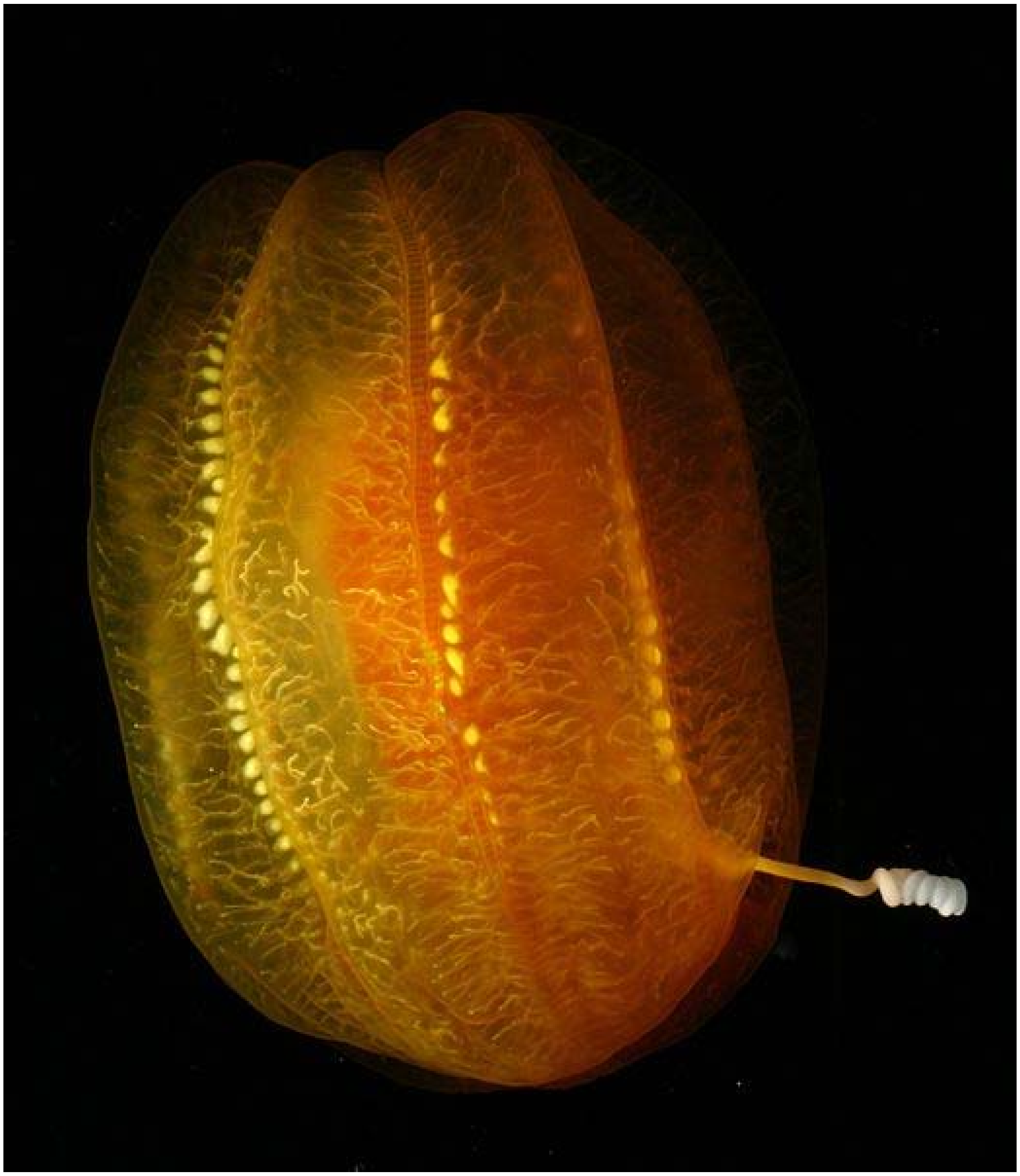
It is uncertain how ctenophores control their buoyancy, but experiments have shown that some species rely on osmotic pressure to adapt to water of different densities. Their body fluids are normally as concentrated as seawater. If they enter less dense brackish water, the ciliary rosettes in the body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

Nervous system and senses

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

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

Cydippids



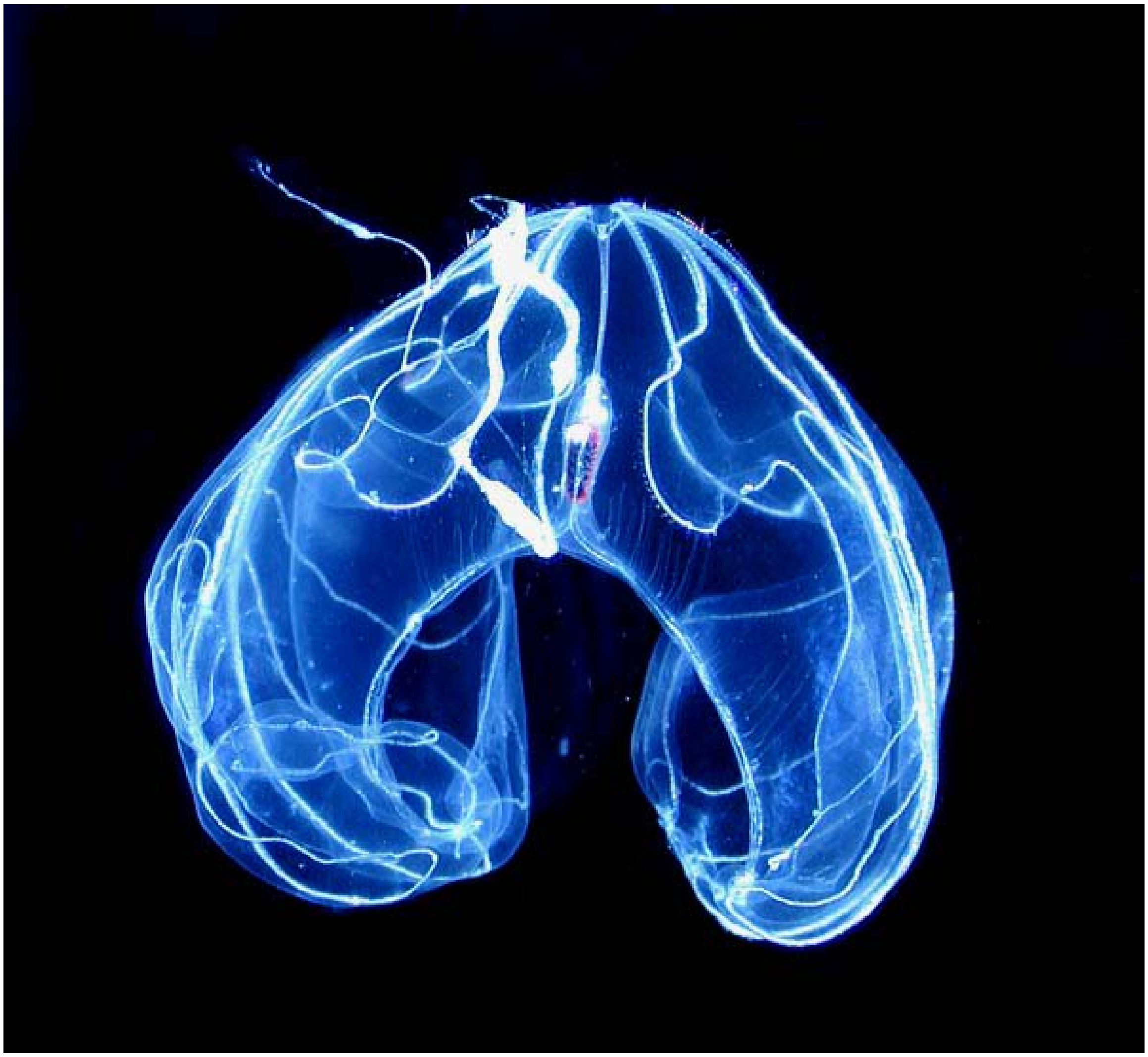
Aulacoctena sp., a cydippid ctenophore

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

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

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

Lobates



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

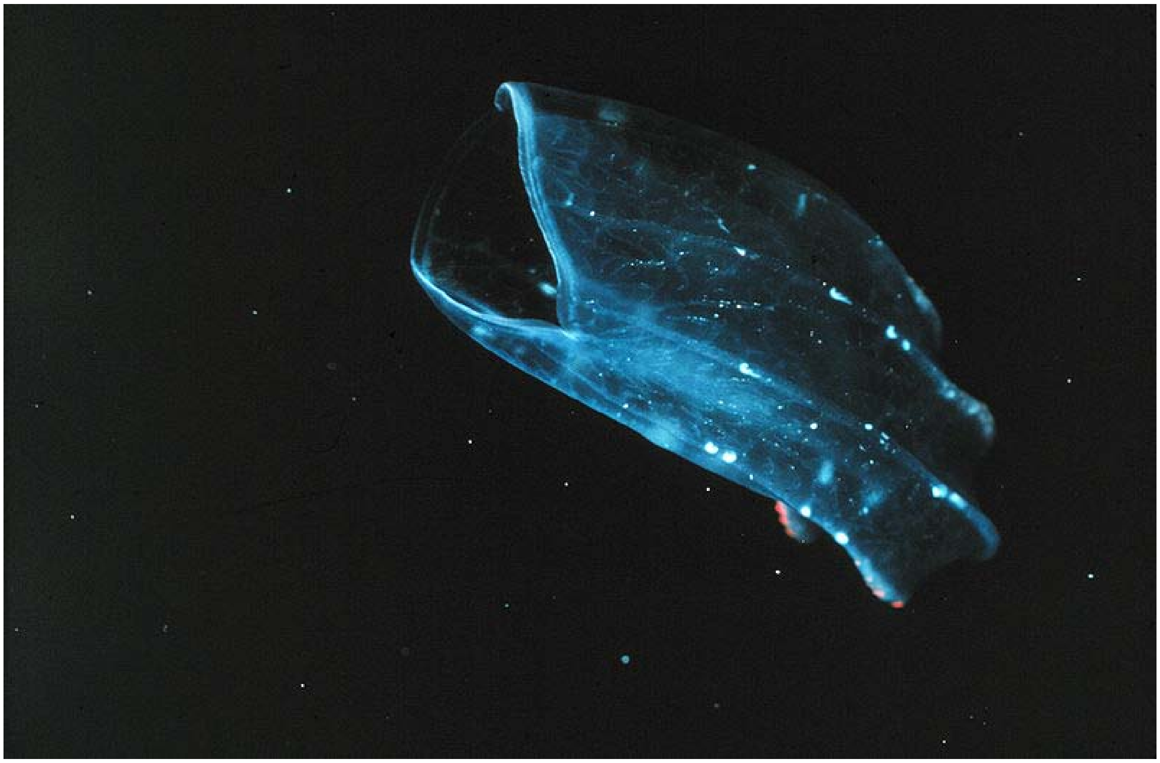
The Lobata have a pair of lobes, which are muscular, cuplike extensions of the body that project beyond the mouth. Their inconspicuous tentacles originate from the corners of the mouth, running in convoluted grooves and spreading out over the inner surface of the lobes (rather than trailing far behind,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

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

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

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

Beroids



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

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

Other body forms

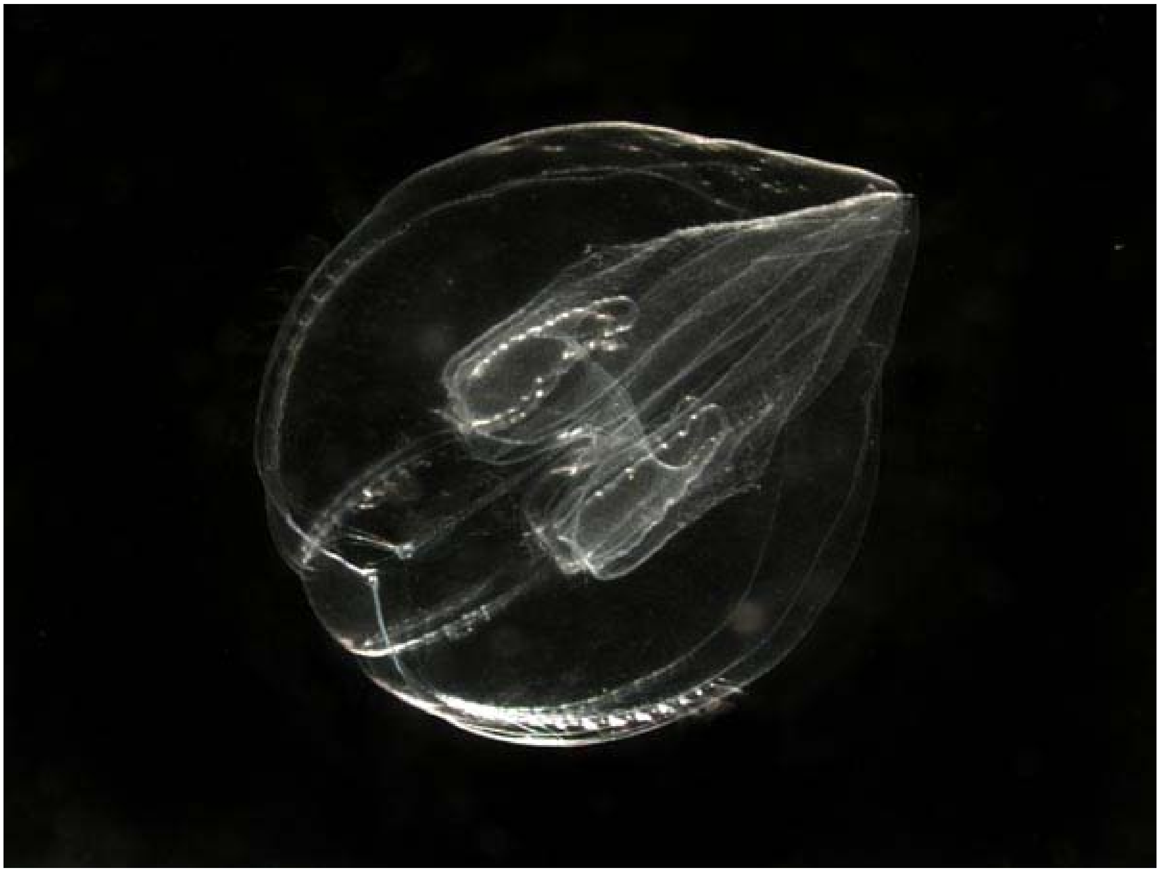
The Ganeshida have a pair of small oral lobes and a pair of tentacles. The body is circular rather than oval in cross-section, and the pharynx extends over the inner surfaces of the lobes.

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

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

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

Reproduction and development



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

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

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

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

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

Colors and bioluminescence

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

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

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

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

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

Ecology

Distribution

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

Prey and predators

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

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

Ecological impacts

Beroe ovata at the surface on the Black Sea coast

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

On the other hand in the late 1980s the North Atlantic ctenophore *Mnemiopsis leidyi* was accidentally introduced into the Black Sea and Sea of Azov via the ballast tanks of ships, and has been blamed for causing sharp drops in fish catches by eating both fish larvae and small crustaceans that would otherwise feed the adult fish. *Mnemiopsis* is well-equipped to invade new territories, as it can breed very rapidly and tolerate a wide range of water temperatures and salinities. The impact was increased by chronic overfishing, and by eutrophication that gave the entire ecosystem a short-term boost, causing the *Mnemiopsis* population to increase even faster than normal — and above all by the absence of efficient predators on ctenophores. *Mnemiopsis* populations in those areas were eventually brought under control by the accidental introduction of the ctenophore-eating ctenophore *Beroe*, and by a cooling of the local climate from 1991 to 1993, which significantly slowed the animal's metabolism. However the abundance of plankton in the area seems unlikely to reach pre-*Mnemiopsis* levels.

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

Classification

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

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

The Tentaculata are divided into the following eight orders:

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

- Thalassocalycida, with short tentacles and a jellyfish-like "umbrella"
- Cestida, ribbon-shaped and the largest ctenophores

Evolutionary history

Fossil record

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

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

Family tree

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

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

In 2005 Katja Seipel and Volker Schmid suggested that cnidarians and ctenophores are simplified descendants of triploblastic animals, since ctenophores and the medusa stage of some cnidarians have striated muscle, which in bilaterians arises from the mesoderm. They did not commit themselves on whether bilaterians evolved from early cnidarians or from the hypothesized triploblastic ancestors of cnidarians. A study in 2008 of 150 genes in 21 genera proposed a third hypothesis, that sponges and cnidarians are more closely related to each other than either is to ctenophores.

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

Chapter 9

Cnidaria

Cnidaria
Temporal range: 580–0 Ma
Ediacaran–Recent

Pacific sea nettles, *Chrysaora fuscescens*

Scientific classification

Domain:	Eukaryota
Kingdom:	Animalia
Phylum:	**Cnidaria** Hatschek, 1888

Subphylum/Classes

Anthozoa—corals and sea anemones
Medusozoa—jellyfish:
Cubozoa—box jellyfish, sea wasps
Hydrozoa—hydroids, hydra-like animals
Scyphozoa—true jellyfish
Staurozoa—stalked jellyfish
Unranked, may not be scyphozoans

Myxozoa—parasites
Polypodiozoa—parasites

Cnidaria is a phylum containing over 9,000 species of animals found exclusively in aquatic and mostly marine environments. Their distinguishing feature is cnidocytes, specialized cells that they use mainly for capturing prey. Their bodies consist of mesoglea, a non-living jelly-like substance, sandwiched between two layers of epithelium that are mostly one cell thick. They have two basic body forms: swimming medusae and sessile polyps, both of which are radially symmetrical with mouths surrounded by tentacles that bear cnidocytes. Both forms have a single orifice and body cavity that are used for digestion and respiration. Many cnidarian species produce colonies that are single organisms composed of medusa-like or polyp-like zooids, or both. Cnidarians' activities are coordinated by a decentralized nerve net and simple receptors. Several free-swimming Cubozoa and Scyphozoa possess balance-sensing statocysts, and some have simple eyes. Not all cnidarians reproduce sexually. Many have complex lifecycles with asexual polyp stages and sexual medusae, but some omit either the polyp or the medusa stage.

Cnidarians were for a long time grouped with Ctenophores in the phylum Coelenterata, but increasing awareness of their differences caused them to be placed in separate phyla. Cnidarians are classified into four main groups: sessile Anthozoa (sea anemones, corals, and sea pens (sea anemones are not sessile but only move 3-4 inches an hour); swimming Scyphozoa (jellyfish); Cubozoa (box jellies); and Hydrozoa, a diverse group that includes all the freshwater cnidarians as well as many marine forms, and has both sessile members such as *Hydra* and colonial swimmers such as the Portuguese Man o' War. Staurozoa have recently been recognised as a class in their own right rather than a sub-group of Scyphozoa, and there is debate about whether Myxozoa and Polypodiozoa are cnidarians or closer to bilaterians (more complex animals).

Most cnidarians prey on organisms ranging in size from plankton to animals several times larger than themselves, but many obtain much of their nutrition from endosymbiotic algae, and a few are parasites. Many are preyed upon by other animals including starfish, sea slugs, fish and turtles. Coral reefs, whose polyps are rich in endosymbiotic algae, support some of the world's most productive ecosystems, and protect vegetation in tidal zones and on shorelines from strong currents and tides. While corals are almost entirely restricted to warm, shallow marine waters, other cnidarians live in the depths, in polar seas and in freshwater.

Fossil cnidarians have been found in rocks formed about 580 million years ago, and other fossils show that corals may have been present shortly before 490 million years ago and diversified a few million years later. Fossils of cnidarians that do not build mineralized structures are very rare. Scientists currently think that cnidarians, ctenophores and bilaterians are more closely related to calcareous sponges than these are to other sponges, and that anthozoans are the evolutionary "aunts" or "sisters" of other cnidarians, and the most closely related to bilaterians. Recent analyses have concluded that cnidarians, although considered more "primitive" than bilaterians, have a wider range of genes.

Jellyfish stings killed several hundred people in the 20th century, and cubozoans are particularly dangerous. On the other hand, some large jellyfish are considered a delicacy in eastern and southern Asia. Coral reefs have long been economically important as providers of fishing grounds, protectors of shore buildings against currents and tides, and more recently as centers of tourism. However, they are vulnerable to over-fishing, mining for construction materials, pollution, and damage caused by tourism.

Classification

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Modern cnidarians are generally classified into four classes:

	Hydrozoa	**Scyphozoa**	**Cubozoa**	**Anthozoa**
Number of species	2,700	200	20	6,000
Examples	*Hydra*, siphonophores	Jellyfish	Box jellies	Sea anemones, corals, sea pens
Cells found in mesoglea	No	Yes	Yes	Yes
Nematocysts in exodermis	No	Yes	Yes	Yes
Medusa phase in life cycle	In some species	Yes, except for Stauromedusae if they are scyphozoans	Yes	No
Number of medusae produced per polyp	Many	Many	One	(not applicable)

Stauromedusae, small sessile cnidarians with stalks and no medusa stage, have traditionally been classified as members of the Scyphozoa, but recent research suggests they should be regarded as a separate class, Staurozoa.

The Myxozoa, microscopic parasites, were first classified as protozoans, but recently as heavily modified cnidarians, and more closely related to Hydrozoa and Scyphozoa than to Anthozoa. However other recent research suggests that *Polypodium hydriforme*, a parasite *within* the egg cells of sturgeon, is closely related to the Myxozoa and that both

Polypodium and the Myxozoa are intermediate between cnidarians and bilaterian animals.

Some researchers classify the extinct conulariids as cnidarians, while others propose that they form a completely separate phylum.

Ecology

Coral reefs support rich ecosystems

Many cnidarians are limited to shallow waters because they depend on endosymbiotic algae for much of their nutrients. The life cycles of most have polyp stages, which are limited to locations that offer stable substrates. Nevertheless major cnidarian groups contain species that have escaped these limitations. Hydrozoans have a worldwide range: some, such as *Hydra*, live in freshwater; *Obelia* appears in the coastal waters of all the oceans; and *Liriope* can form large shoals near the surface in mid-ocean. Among anthozoans, a few scleractinian corals, sea pens and sea fans live in deep, cold waters, and some sea anemones inhabit polar seabeds while others live near hydrothermal vents over 10 kilometres (6.2 mi) below sea-level. Reef-building corals are limited to tropical seas between 30°N and 30°S with a maximum depth of 46 metres (151 ft), temperatures between 20°C and 28°C, high salinity and low carbon dioxide levels. Stauromedusae, although usually classified as jellyfish, are stalked, sessile animals that live in cool to Arctic waters. Cnidarians range in size from *Hydra*, 5–20 millimetres (0.20–0.79 in) long, to the Lion's mane jellyfish, which may exceed 2 metres (6.6 ft) in diameter and 75 metres (246 ft) in length.

Prey of cnidarians ranges from plankton to animals several times larger than themselves. Some cnidarians are parasites, mainly on jellyfish but a few are major pests of fish. Others obtain most of their nourishment from endosymbiotic algae or dissolved nutrients. Predators of cnidarians include: sea slugs, which can incorporate nematocysts into their own bodies for self-defense; starfish, notably the crown of thorns starfish, which can devastate corals; butterfly fish and parrot fish, which eat corals; and marine turtles, which eat jellyfish. Some sea anemones and jellyfish have a symbiotic relationship with some fish; for example clown fish live among the tentacles of sea anemones, and each partner protects the other against predators.

Coral reefs form some of the world's most productive ecosystems. Common coral reef cnidarians include both Anthozoans (hard corals, octocorals, anemones) and Hydrozoans (fire corals, lace corals) The endosymbiotic algae of many cnidarian species are very effective primary producers, in other words converters of inorganic chemicals into organic ones that other organisms can use, and their coral hosts use these organic chemicals very efficiently. In addition reefs provide complex and varied habitats that support a wide range of other organisms. "Fringing" reefs just below low-tide level also have a mutually beneficial relationship with mangrove forests at high-tide level and sea grass meadows in between: the reefs protect the mangroves and seagrass from strong currents and waves that would damage them or erode the sediments in which they are rooted, while the mangroves and seagrass protect the coral from large influxes of silt, fresh water and pollutants. This additional level of variety in the environment is beneficial to many types of coral reef animals, which for example may feed in the sea grass and use the reefs for protection or breeding.

History

Fossil cnidarians have been found in rocks formed about 580 million years ago, and other fossils show that corals may have been present shortly before 490 million years ago and diversified a few million years later. Fossils of cnidarians that do not build mineralized structures are very rare. Scientists currently think that cnidarians, ctenophores and bilaterians are more closely related to calcareous sponges than these are to other sponges, and that anthozoans are the evolutionary "aunts" or "sisters" of other cnidarians, and the most closely related to bilaterians. Recent analyses have concluded that cnidarians, although considered more "primitive" than bilaterians, have a wider range of genes.

Distinguishing features

Cnidarians form an animal phylum that is more complex than sponges, about as complex as ctenophores (comb jellies), and less complex than bilaterians, which include almost all other animals. However, both cnidarians and ctenophores are more complex than sponges as they have: cells bound by inter-cell connections and carpet-like basement membranes; muscles; nervous systems; and **some** have sensory organs. Cnidarians are distinguished from all other animals by having cnidocytes that fire like harpoons and are used mainly to capture prey but also as anchors in some species.

Like sponges and ctenophores, cnidarians have two main layers of cells that sandwich a middle layer of jelly-like material, which is called the mesoglea in cnidarians; more complex animals have three main cell layers and no intermediate jelly-like layer. Hence, cnidarians and ctenophores have traditionally been labelled diploblastic, along with sponges. However, both cnidarians and ctenophores have a type of muscle that, in more complex animals, arises from the middle cell layer. As a result some recent text books classify ctenophores as triploblastic, and it has been suggested that cnidarians evolved from triploblastic ancestors.

	Sponges	**Cnidarians**	**Ctenophores**	**Bilateria**
Cnidocytes	No	Yes	No	
Colloblasts	No		Yes	No
Digestive and circulatory organs	No			Yes
Number of main cell layers	Two, with jelly-like layer between them		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

Main cell layers

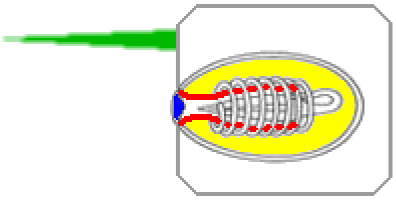
Cnidaria are diploblastic animals, in other words they have two main cell layers, while more complex animals are triploblasts having three main layers. The two main cell layers of cnidarians form epithelia that are mostly one cell thick, and are attached to a fibrous basement membrane, which they secrete. They also secrete the jelly-like mesoglea that separates the layers. The layer that faces outwards, known as the ectoderm ("outside skin"), generally contains the following types of cells:

- Epitheliomuscular cells whose bodies form part of the epithelium but whose bases extend to form muscle fibers in parallel rows. The fibers of the outward-facing cell layer generally run at right angles to the fibers of the inward-facing one. In Anthozoa (anemones, corals, etc.) and Scyphozoa (jellyfish), the mesoglea also contains some muscle cells.
- Cnidocytes, the harpoon-like "nettle cells" that give the phylum Cnidaria its name. These appear between or sometimes on top of the muscle cells.
- Nerve cells. Sensory cells appear between or sometimes on top of the muscle cells, and communicate via synapses (gaps across which chemical signals flow) with motor nerve cells, which lie mostly between the bases of the muscle cells.
- Interstitial cells, which are unspecialized and can replace lost or damaged cells by transforming into the appropriate types. These are found between the bases of muscle cells.

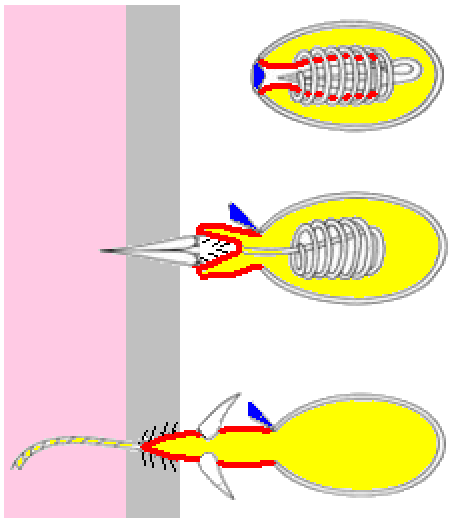
In addition to epitheliomuscular, nerve and interstitial cells, the inward-facing gastroderm ("stomach skin") contains gland cells that secrete digestive enzymes. In some species it also contains low concentrations of cnidocytes, which are used to subdue prey that is still struggling.

The mesoglea contains small numbers of amoeba-like cells, and muscle cells in some species. However the number of middle-layer cells and types are much lower than in sponges.

Cnidocytes



A hydra's nematocyst, before firing.
🟩 "trigger" cilium



Firing sequence of the cnida in a hydra's nematocyst
🟦 Operculum (lid)
🟥 "Finger" that turns inside out
/ / / Barbs
🟨 Venom
▨ Victim's skin
⬜ Victim's tissues

These "nettle cells" function as harpoons, since their payloads remain connected to the bodies of the cells by threads. Three types of cnidocytes are known:

- Nematocysts inject venom into prey, and usually have barbs to keep them embedded in the victims. Most species have nematocysts.
- Spirocysts do not penetrate the victim or inject venom, but entangle it by means of small sticky hairs on the thread. Only members of the class Anthozoa (sea anemones and corals) have spirocysts.
- Ptychocysts are not used for prey capture — instead the threads of discharged ptychocysts are used for building protective tubes in which their owners live. Ptychocysts are found only in the order Ceriantharia, tube anemones.

The main components of a cnidocyte are:

- A cilium (fine hair) which projects above the surface and acts as a trigger. Spirocysts do not have cilia.
- A tough capsule, the cnida, which houses the thread, its payload and a mixture of chemicals which may include venom or adhesives or both. ("cnida" is derived from the Greek word κνίδη, which means "nettle")
- A tube-like extension of the wall of the cnida that points into the cnida, like the finger of a rubber glove pushed inwards. When a cnidocyte fires, the finger pops out. If the cell is a venomous nematocyte, the "finger"'s tip reveals a set of barbs that anchor it in the prey.

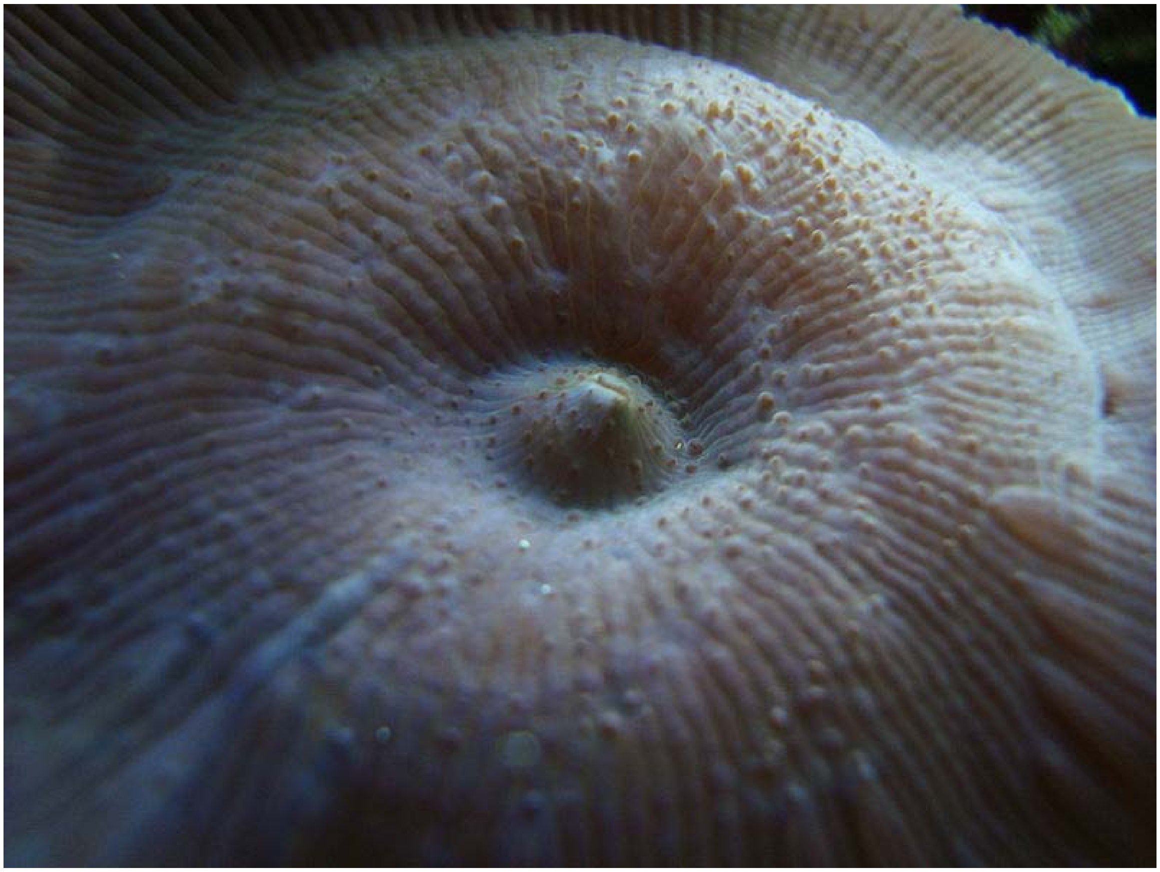
- The thread, which is an extension of the "finger" and coils round it until the cnidocyte fires. The thread is usually hollow and delivers chemicals from the cnida to the target.
- An operculum (lid) over the end of the cnida. The lid may be a single hinged flap or three flaps arranged like slices of pie.
- The cell body which produces all the other parts.

It is difficult to study the firing mechanisms of cnidocytes as these structures are small but very complex. At least four hypotheses have been proposed:

- Rapid contraction of fibers round the cnida may increase its internal pressure.
- The thread may be like a coiled spring that extends rapidly when released.
- In the case of *Chironex* (the "sea wasp"), chemical changes in the cnida's contents may cause them to expand rapidly by polymerization.
- Chemical changes in the liquid in the cnida make it a much more concentrated solution, so that osmotic pressure forces water in very rapidly to dilute it. This mechanism has been observed in nematocysts of the class Hydrozoa, sometimes producing pressures as high as 140 atmospheres, similar to that of scuba air tanks, and fully extending the thread in as little as 2 milliseconds (0.002 second).

Cnidocytes can only fire once, and about 25% of a hydra's nematocysts are lost from its tentacles when capturing a brine shrimp. Used cnidocytes have to be replaced, which takes about 48 hours. To minimise wasteful firing, two types of stimulus are generally required to trigger cnidocytes: their cilia detect contact, and nearby sensory cells "smell" chemicals in the water. This combination prevents them from firing at distant or non-living objects. Groups of cnidocytes are usually connected by nerves and, if one fires, the rest of the group requires a weaker minimum stimulus than the cells that fire first.

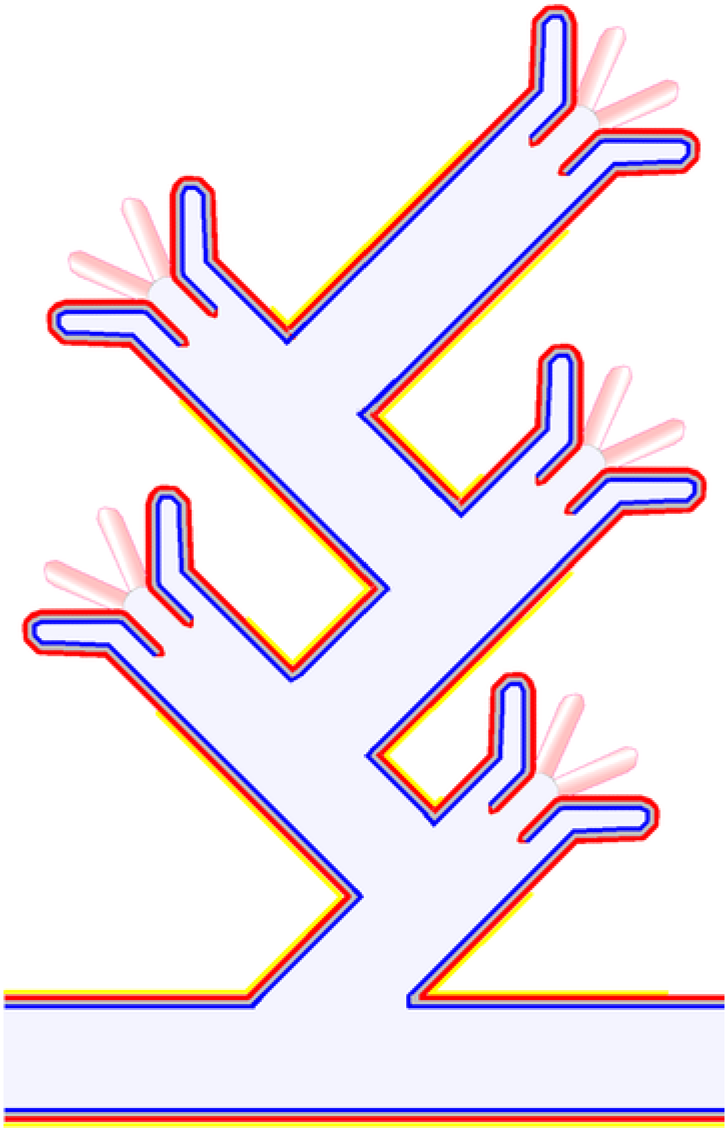
Basic body forms



Oral end of actinodiscus polyp, with close-up of the mouth

Adult cnidarians appear as either swimming medusae or sessile polyps. Both are radially symmetrical, like a wheel and a tube respectively. Since these animals have no heads, their ends are described as "oral" (nearest the mouth) and "aboral" (furthest from the mouth). Most have fringes of tentacles equipped with cnidocytes around their edges, and medusae generally have an inner ring of tentacles around the mouth. The mesoglea of polyps is usually thin and often soft, but that of medusae is usually thick and springy, so that it returns to its original shape after muscles around the edge have contracted to squeeze water out, enabling medusae to swim by a sort of jet propulsion.

Colonial forms



Tree-like polyp colony

Cnidaria produce a variety of colonial forms, each of which is one organism but consists of polyp-like zooids. The simplest is a connecting tunnel that runs over the substrate (rock or seabed) and from which single zooids sprout. In some cases the tunnels form visible webs, and in others they are enclosed in a fleshy mat. More complex forms are also based on connecting tunnels but produce "tree-like" groups of zooids. The "trees" may be formed either by a central zooid that functions as a "trunk" with later zooids growing to the sides as "branches", or in a zig-zag shape as a succession of zooids, each of which grows to full size and then produces a single bud at an angle to itself. In many cases the connecting tunnels and the "stems" are covered in periderm, a protective layer of chitin. Some colonial forms have other specialized types of zooid, for example, to pump water through their tunnels.

Siphonophores form complex colonies that consist of: an upside-down polyp that forms a central stem with a gas-filled float at the top; one or more sets of medusa-like zooids that provide propulsion; leaf-like bracts that give some protection to other parts; sets of tentacles that bear nematocytes that capture prey; other tentacles that act as sensors; near the base of each set of tentacles, a polyp-like zooid that acts as a stomach for the colony; medusa-like zooids that serve as gonads. Although some of these zooids resemble polyps or medusae in shape, they lack features that are not relevant to their specific functions, for example the swimming "medusae" have no digestive, sensory or reproductive cells. The best-known siphonophore is the Portuguese Man o' War (*Physalia physalis*).

Skeletons

In medusae the only supporting structure is the mesoglea. *Hydra* and most sea anemones close their mouths when they are not feeding, and the water in the digestive cavity then acts as a hydrostatic skeleton, rather like a water-filled balloon. Other polyps such as *Tubularia* use columns of water-filled cells for support. Sea pens stiffen the mesoglea with calcium carbonate spicules and tough fibrous proteins, rather like sponges.

In some colonial polyps a chitinous periderm gives support and some protection to the connecting sections and to the lower parts of individual polyps. Stony corals secrete massive calcium carbonate exoskeletons. A few polyps collect materials such as sand grains and shell fragments, which they attach to their outsides. Some colonial sea anemones stiffen the mesoglea with sediment particles.

Locomotion

Chrysaora quinquecirrha ("sea nettle") swimming

Medusae swim by a form of jet propulsion: muscles, especially inside the rim of the bell, squeeze water out of the cavity inside the bell, and the springiness of the mesoglea powers the recovery stroke. Since the tissue layers are very thin, they provide too little power to swim against currents and just enough to control movement within currents.

Hydras and some sea anemones can move slowly over rocks and sea or stream beds by various means: creeping like snails, crawling like inchworms, or by somersaulting. A few can swim clumsily by waggling their bases.

Nervous system and senses

Cnidaria have no brains or even central nervous systems. Instead they have decentralized nerve nets consisting of : sensory neurons that generate signals in response to various types of stimulus, such as odors; motor neurons that tell muscles to contract; all connected by "cobwebs" of intermediate neurons. As well as forming the "signal cables", intermediate neurons also form ganglia that act as local coordination centers. The cilia of the cnidocytes detect physical contact. Nerves inform cnidocytes when odors from prey or attackers are detected and when neighbouring cnidocytes fire. Most of the communications between nerve cells are via chemical synapses, small gaps across which chemicals flow. As this process is too slow to ensure that the muscles round the rim of a medusa's bell contract simultaneously in swimming the neurons which control this communicate by much faster electrical signals across gap junctions.

Medusae and complex swimming colonies such as siphonophores and chondrophores sense tilt and acceleration by means of statocysts, chambers lined with hairs which detect the movements of internal mineral grains called statoliths. If the body tilts in the wrong direction, the animal rights itself by increasing the strength of the swimming movements on the side that is too low. They also have ocelli ("little eyes"), which can detect the direction from which light is coming. Box jellies have camera eyes, although these probably do not form images, and their lenses simply produce a clearer indication of the direction from which light is coming.

Feeding and excretion

Cnidarians feed in several ways: predation, absorbing dissolved organic chemicals, filtering food particles out of the water, and obtaining nutrients from symbiotic algae within their cells. Most obtain the majority of their food from predation but some, including the corals *Hetroxenia* and *Leptogorgia*, depend almost completely on their endosymbionts and on absorbing dissolved nutrients. Cnidaria give their symbiotic algae carbon dioxide, some nutrients and a place in the sun.

Predatory species use their cnidocytes to poison or entangle prey, and those with venomous nematocysts may start digestion by injecting digestive enzymes. The "smell" of fluids from wounded prey makes the tentacles fold inwards and wipe the prey off into the mouth. In medusae the tentacles round the edge of the bell are often short and most of the prey capture is done by "oral arms", which are extensions of the edge of the mouth and are often frilled and sometimes branched to increase their surface area. Medusae often trap prey or suspended food particles by swimming upwards, spreading their tentacles and oral arms and then sinking. In species for which suspended food particles are important, the tentacles and oral arms often have rows of cilia whose beating creates currents that flow towards the mouth, and some produce nets of mucus to trap particles.

Once the food is in the digestive cavity, gland cells in the gastroderm release enzymes that reduce the prey to slurry, usually within a few hours. This circulates through the digestive cavity and, in colonial cnidarians, through the connecting tunnels, so that gastroderm cells can absorb the nutrients. Absorption may take a few hours, and digestion within the cells may take a few days. The circulation of nutrients is driven by water currents produced by cilia in the gastroderm or by muscular movements or both, so that nutrients reach all parts of the digestive cavity. Nutrients reach the outer cell layer by diffusion or, for animals or zooids such as medusae which have thick mesogleas, are transported by mobile cells in the mesoglea.

Indigestible remains of prey are expelled through the mouth. The main waste product of cells' internal processes is ammonia, which is removed by the external and internal water currents.

Respiration

There are no respiratory organs, and both cell layers absorb oxygen from and expel carbon dioxide into the surrounding water. When the water in the digestive cavity becomes stale it must be replaced, and nutrients that have not been absorbed will be expelled with it. Some Anthozoa have ciliated grooves on their tentacles, allowing them to pump water out of and into the digestive cavity without opening the mouth. This improves respiration after feeding and allows these animals, which use the cavity as a hydrostatic skeleton, to control the water pressure in the cavity without expelling undigested food.

Cnidaria that carry photosynthetic symbionts may have the opposite problem, an excess of oxygen, which may prove toxic. The animals produce large quantities of antioxidants to neutralize the excess oxygen.

Regeneration

All cnidarians can regenerate, allowing them to recover from injury and to reproduce asexually. Medusae have limited ability to regenerate, but polyps can do so from small pieces or even collections of separated cells. This enables corals to recover even after apparently being destroyed by predators.

Reproduction

Sexual

In the Cnidaria sexual reproduction often involves a complex life cycle with both polyp and medusa stages. For example in Scyphozoa (jellyfish) and Cubozoa (box jellies) a larva swims until it finds a good site, and then becomes a polyp. This grows normally but then absorbs its tentacles and splits horizontally into a series of disks that become juvenile medusae, a process called strobilation. The juveniles swim off and slowly grow to maturity, while the polyp re-grows and may continue strobilating periodically. The adults have gonads in the gastroderm, and these release ova and sperm into the water in the breeding season.

Shortened forms of this life cycle are common, for example some oceanic scyphozoans omit the polyp stage completely, and cubozoan polyps produce only one medusa. Hydrozoa have a variety of life cycles. Some have no polyp stages and some (e.g. *hydra*) have no medusae. In some species the medusae remain attached to the polyp and are responsible for sexual reproduction; in extreme cases these reproductive zooids may not look much like medusae. Anthozoa have no medusa stage at all and the polyps are responsible for sexual reproduction.

Spawning is generally driven by environmental factors such as changes in the water temperature, and their release is triggered by lighting conditions such as sunrise, sunset or the phase of the moon. Many species of Cnidaria may spawn simultaneously in the same location, so that there are too many ova and sperm for predators to eat more than a tiny percentage — one famous example is the Great Barrier Reef, where at least 110 corals and a few non-cnidarian invertebrates produce enough to turn the water cloudy. These mass spawnings may produce hybrids, some of which can settle and form polyps, but it is not known how long these can survive. In some species the ova release chemicals that attract sperm of the same species.

The fertilized eggs develop into larvae by dividing until there are enough cells to form a hollow sphere (blastula) and then a depression forms at one end (gastrulation) and eventually become the digestive cavity. However in cnidarians the depression forms at the end further from the yolk (at the animal pole), while in bilaterians it forms at the other end (vegetal pole). The larvae, called planulae, swim or crawl by means of cilia. They are cigar-shaped but slightly broader at the "front" end, which is the aboral, vegetal-pole end and eventually attaches to a substrate if the species has a polyp stage.

Anthozoan larvae either have large yolks or are capable of feeding on plankton, and some already have endosymbiotic algae that help to feed them. Since the parents are immobile, these feeding capabilities extend the larvae's range and avoid overcrowding of sites. Scyphozoan and hydrozoan larvae have little yolk and most lack endosymbiotic algae, and therefore have to settle quickly and metamorphose into polyps. Instead these species rely on their medusae to extend their ranges.

Asexual

All known cnidaria can reproduce asexually by various means, in addition to regenerating after being fragmented. Hydrozoan polyps only bud, while the medusae of some hydrozoans can divide down the middle. Scyphozoan polyps can both bud and split down the middle. In addition to both of these methods, Anthozoa can split horizontally just above the base.

Evolutionary history

Fossil record

The fossil coral *Cladocora* from Pliocene rocks in Cyprus

The earliest widely accepted animal fossils are rather modern-looking cnidarians, possibly from around 580 million years ago, although fossils from the Doushantuo Formation can only be dated approximately. The identification of some of these as embryos of animals has been contested, but other fossils from these rocks strongly resemble tubes and other mineralized structures made by corals. Their presence implies that the cnidarian and bilaterian lineages had already diverged. Although the Ediacaran fossil *Charnia* used to be classified as a jellyfish or sea pen, more recent study of growth patterns in *Charnia* and modern cnidarians has cast doubt on this hypothesis, and there are now no bona-fide cnidarian body fossils in the Ediacaran. Few fossils of cnidarians without mineralized skeletons are known from more recent rocks, except in lagerstätten that preserved soft-bodied animals.

A few mineralized fossils that resemble corals have been found in rocks from the Cambrian period, and corals diversified in the Early Ordovician. These corals, which were wiped out in the Permian-Triassic extinction about 251 million years ago, did not dominate reef construction since sponges and algae also played a major part. During the Mesozoic era rudist bivalves were the main reef-builders, but they were wiped out in the

Cretaceous-Tertiary extinction 65 million years ago, and since then the main reef-builders have been scleractinian corals.

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 plus Ctenophora (comb jellies), 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). However 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.

Within the Cnidaria, the Anthozoa (sea anemones and corals) are regarded as the sister-group of the rest, which suggests that the earliest cnidarians were sessile polyps with no medusa stage. However it is unclear how the other groups acquired the medusa stage, since Hydrozoa form medusae by budding from the side of the polyp while the other Medusozoa do so by splitting them off from the tip of the polyp. The traditional grouping of Scyphozoa included the Staurozoa, but morphology and molecular phylogenetics indicate that Staurozoa are more closely related to Cubozoa (box jellies) than to other "Scyphozoa". Similarities in the double body walls of Staurozoa and the extinct Conulariida suggest that they are closely related. The position of Anthozoa nearest the beginning of the cnidarian family tree also implies that Anthozoa are the cnidarians most closely related to Bilateria, and this is supported by the fact that Anthozoa and Bilateria share some genes that determine the main axes of the body.

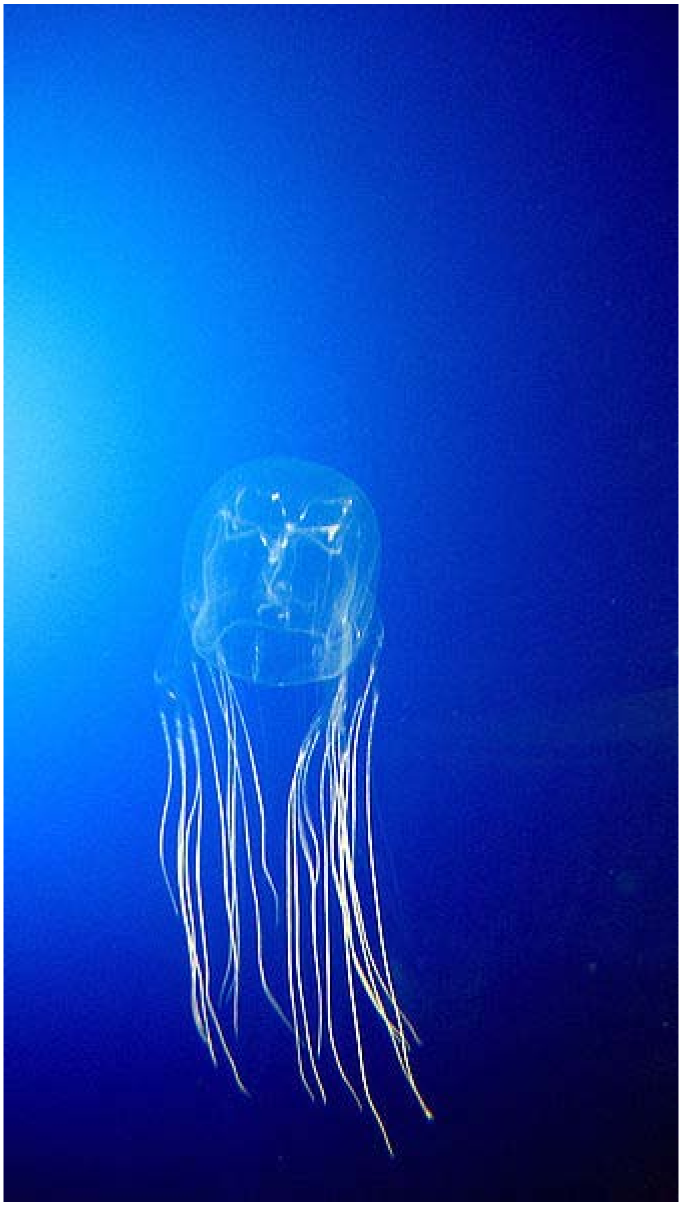
However in 2005 Katja Seipel and Volker Schmid suggested that cnidarians and ctenophores are simplified descendants of triploblastic animals, since ctenophores and the medusa stage of some cnidarians have striated muscle, which in bilaterians arises from the mesoderm. They did not commit themselves on whether bilaterians evolved from early cnidarians or from the hypothesized triploblastic ancestors of cnidarians.

In molecular phylogenetics analyses from 2005 onwards, important groups of developmental genes show the same variety in cnidarians as in chordates. In fact cnidarians, and especially anthozoans (sea anemones and corals), retain some genes that are present in bacteria, protists, plants and fungi but not in bilaterians.

Interaction with humans

Jellyfish stings killed about 1,500 people in the 20th century, and cubozoans are particularly dangerous. On the other hand, some large jellyfish are considered a delicacy in eastern and southern Asia. Coral reefs have long been economically important as providers of fishing grounds, protectors of shore buildings against currents and tides, and more recently as centers of tourism. However, they are vulnerable to over-fishing, mining for construction materials, pollution, and damage caused by tourism.

Beaches protected from tides and storms by coral reefs are often the best places for housing in tropical countries. Reefs are an important food source for low-technology fishing, both on the reefs themselves and in the adjacent seas. However despite their great productivity reefs are vulnerable to over-fishing, because much of the organic carbon they produce is exhaled as carbon dioxide by organisms at the middle levels of the food chain and never reaches the larger species that are of interest to fishermen. Tourism centered on reefs provides much of the income of some tropical islands, attracting photographers, divers and sports fishermen. However human activities damage reefs in several ways: mining for construction materials; pollution, including large influxes of fresh water from storm drains; commercial fishing, including the use of dynamite to stun fish and the capture of young fish for aquariums; and tourist damage caused by boat anchors and the cumulative effect of walking on the reefs. Coral, mainly from the Pacific Ocean has long been used in jewellery, and demand rose sharply in the 1980s.



The dangerous "sea wasp" *Chironex fleckeri*

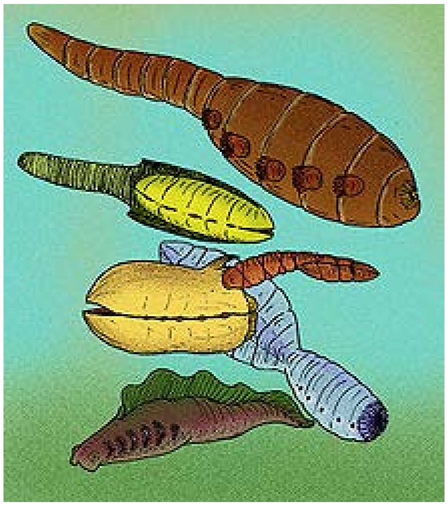
Some large jellyfish species have been used in Chinese cuisine at least since 200 AD, and are now fished in the seas around most of South East Asia. Japan is the largest single consumer of edible jellyfish, importing at first only from China but now from all of South East Asia as prices rose in the 1970s. This fishing industry is restricted to daylight hours and calm conditions in two short seasons, from March to May and August to November. The commercial value of jellyfish food products depends on the skill with which they are prepared, and "Jellyfish Masters" guard their trade secrets carefully. Jellyfish is very low in cholesterol and sugars, but cheap preparation can introduce undesirable amounts of heavy metals.

The "sea wasp" *Chironex fleckeri* has been described as the world's most venomous animal and is held responsible for 67 deaths, although it is difficult to identify the animal as it is almost transparent. Most stingings by *C. fleckeri* cause only mild symptoms. Seven other box jellies can cause a set of symptoms called Irukandji syndrome, which takes about 30 minutes to develop, and from a few hours to two weeks to disappear. Hospital treatment is usually required, and there have been a few deaths.

Chapter 10

Vetulicolia

Vetulicolia
Temporal range: Cambrian



Scientific classification

Kingdom:	Animalia
Superphylum:	?Deuterostomia
Phylum:	**Vetulicolia** Shu, et al. 2001

Classes

- Vetulicolida
- Banffozoa
- Heteromorphida
- ? Yunnanozoa
- ? *Yuyuanozoon*

Vetulicolia is an extinct phylum encompassing several Cambrian organisms. Their bodies comprise two parts; their front is voluminous and is tipped with a large "mouth" and a row of five round to oval-shaped features on each side which have been interpreted as gills - or at least openings in the vicinity of the pharynx. Their posterior section comprises seven segments. They lack preserved appendages of any kind. The area where the anterior and posterior parts join is constricted. Their affinity is very uncertain; they have been considered to represent stem- and crown-group arthropods, stem-group vertebrates, and early deuterostomes.

Taxonomy and evolution

Restoration of a generalized didazoonid

As originally proposed, the phylum included the Didazoonidae (*Didazoon*, *Pomatrum*, and *Xidazoon*) and the Vetulicolidae (*Vetulicola*, and *Banffia*). Other groups which may be related include the yunnanozoans.

The taxonomic placement of the Vetulicolians remains controversial. Shu (2003) has argued that the vetulicolians probably represent an early side-branch of deuterostomes, and that this implies that segmentation in cephalochordates and vertebrates may be derived from the common ancestor of protostomes and deuterostomes. Briggs *et al.* (2005) described *Skeemella* from the Middle Cambrian of Utah as having affinity to Vetulicolia, but also as having arthropod features, thus confounding assignment of Vetulicolia to Deuterostomia. Dominguez and Jefferies have argued, based on morphological analysis, that *Vetulicola* (and by implication, other Vetulicolians) is a urochordate, and probably a stem-group larvacean. However, some question the relation to tunicates and larvaceans, as there is no evidence of segmentation in tunicates, larval or adult, that is comparable to segmentation in vetulicolians, that the anus of urochordates is within the atrium, while that of vetulicolians is positioned at the terminal end of the tail, and, perhaps most importantly, there is no exhalant siphon, or analogous structure, seen in vetulicolians.

Ecology and Lifestyle

From their superficially tadpole-like forms, leaf or paddle-shaped tails, and various degrees of streamlining, it is assumed that all vetulicolians discovered thus far were swimming animals that spent much, if not all, of their time living in the water column. Some groups, like the genus *Vetulicola*, were more streamlined (complete with ventral keels) than other groups, such as the tadpole-like Didazoonidae. Because all vetulicolians had mouths which had no features for chewing or grasping, it is automatically assumed that they were not predators. Because of their gill slits, many researchers regard the vetulicolians as being planktivores. The sediment infills in the guts of their fossils have led some to suggest that they were deposit feeders. This idea has been contested, as deposit feeders tend to have straight guts, whereas the hindguts of vetulicolians were spiral-shaped. Some researchers propose that the vetulicolians were "selective deposit-feeders" which actively swam from one region of the seafloor to another, while supplementing their nutrition with filter-feeding.

Classification

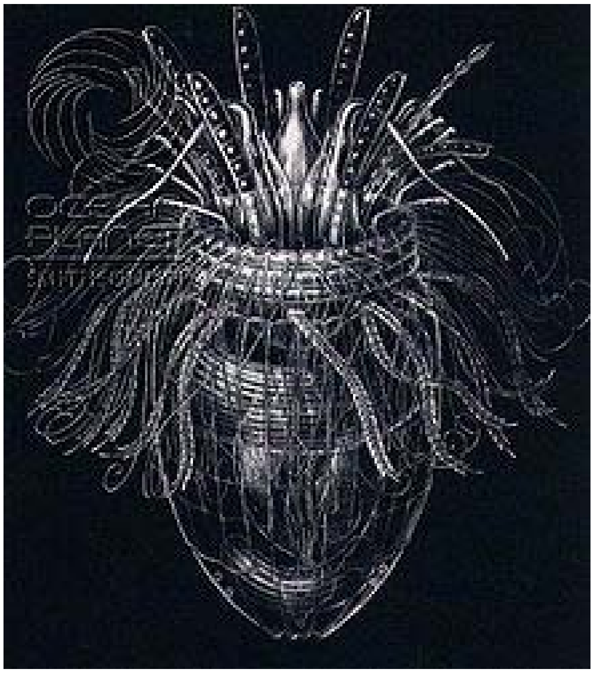
- Phylum **Vetulicolia**
    - Class Vetulicolida
        - Order Vetulicolata
            - Family Vetulicolidae
                - Genus *Vetulicola*
                    - *Vetulicola rectangulata*
                    - *Vetulicola cuneata*
                    - *Vetulicola gangtoucunensis*
                    - *Vetulicola monile*
            - Family **Beidazooidae**
                - Genus *Beidazoon*
                    - *Beidazoon venustum* (synonym = *Bullivetula variola*)
            - Family Didazoonidae
                - Genus *Didazoon*
                    - *Didazoon haoae*
                - Genus *Xidazoon*
                    - *Xidazoon stephanus*
                - Genus *Pomatrum*
                    - *Pomatrum ventralis*
        - ?Order Yunnanozoa
            - Family Yunnanozoonidae
                - Genus *Yunnanozoon*
                    - *Yunnanozoon lividum*
                - Genus *Haikouella*

      - *Haikouella lanceolata*
  - Class Banffozoa
    -
      -
        -
        - *Skeemella clavula*
    - Family **Banffiidae**
      - Genus *Banffia*
        - *Banffia constricta*
  - Class Heteromorphida
    -
    - Family **Heteromorphidae**
      - Genus *Heteromorphus*
        - *Heteromorphus longicaudatus* (synonym=*Banffia confusa*)
        - "Form A" (unnamed species)
- *incertae sedis Yuyuanozoon magnificissimi*

Chapter 11

Loricifera

Loricifera



Pliciloricus enigmatus

Scientific classification [e]

Kingdom:	Animalia
clade:	Cycloneuralia
(unranked):	Scalidophora
(unranked):	Vinctiplicata
Phylum:	**Loricifera** Kristensen, 1983

Genera

Armorloricus
Australoricus

Nanaloricus
Phoeniciloricus
Pliciloricus
Rugiloricus
Spinoloricus
Titaniloricus
Urnaloricus

Loricifera (from Latin, *lorica*, corselet + *ferre*, to bear) is a phylum of very small to microscopic marine sediment-dwelling animals with twenty-two described species, in eight genera. Aside from these described species, there are approximately 100 more that have been collected and not yet described. Their size ranges from 100 µm to ca. 1 mm. They are characterised by a protective outer case called a lorica and their habitat, which is in the spaces between marine gravel to which they attach themselves. The phylum was discovered in 1983 by Reinhardt Kristensen, in Roscoff, France. They are among the most recently discovered groups of Metazoans. They attach themselves quite firmly to the substratum, and hence remained undiscovered for so long. The first specimen was collected in the 1970s, and later described in 1983. They are found at all depths, in different sediment types, and in all latitudes.

Morphology

The animals have a head, mouth and digestive system as well as a lorica. The armor-like lorica consists of a protective external shell or case of encircling plicae. There is no circulatory system and no endocrine system. Many of the larvae are acoelomate, with some adults being pseudocoelomate, and some remaining acoelomate. Development is generally direct, though there are so called Higgins-larvae, which differ from adults in several respects. The animals have two sexes as adults. Very complex and plastic life cycles of pliciloricids include also paedogenetic stages with different forms of parthenogenetic reproduction. They are not known to be present in the fossil record.

Taxonomic affinity

Morphological studies have traditionlally placed the phylum in the vinctiplicata with the Priapulida; this plus the Kinorhyncha constitutes the taxon Scalidophora. The three phyla share four characters in common — chitinous cuticle, rings of scalids on the introvert, flosculi, and two rings of introvert retracts. However, mounting molecular evidence indicates a closer relationship with the nematomorpha.

Light microscopy image of the undescribed species of *Spinoloricus* that is living in an anoxic environment (Stained with Rose Bengal). Scale bar is 50 µm.

Evolutionary history

The loricates are believed to be miniaturized descendants of a larger organism perhaps resembling the Cambrian fossil *Sirilorica*. However, the fossil record of the microscopic non-mineralized group is (perhaps unsurprisingly) scarce, so it is difficult to trace out the phylum's evolutionary history in any detail.

In anoxic environment

Three species of Loricifera have been found in the sediments at the bottom of the L'Atalante basin in Mediterranean Sea, more than 3,000 meters down, the first multicellular organisms known to spend their entire lives in an oxygen-free environment. They are able to do this because they rely on hydrogenosomes (or similar organelles) instead of on mitochondria for energy.

The newly reported animals complete their life cycle in the total absence of light and oxygen, and they are less than a millimetre in size. They were collected from a deep basin at the bottom of the Mediterranean Sea, where they inhabit a nearly salt-saturated brine that, because of its density (> 1.2 g/cm³), does not mix with the waters above. As a consequence, this environment is completely anoxic and, due to the activity of sulphate reducers, contains sulphide at a concentration of 2.9 mM. Despite such harsh conditions, this anoxic and sulphidic environment is teeming with microbial life, both chemosynthetic prokaryotes that are primary producers, and a broad diversity of eukaryotic heterotrophs at the next trophic level.

Species

Armorloricus

- *Armorloricus davidi* Kristensen & Gad, 2004
- *Armorloricus elegans* Kristensen & Gad, 2004
- *Armorloricus kristenseni* Heiner, 2004

Australoricus

- *Australoricus oculatus*

Nanaloricus

- *Nanaloricus khaitatus* Todaro & Kristensen, 1998
- *Nanaloricus mysticus* Kristensen, 1983

Phoeniciloricus

- *Phoeniciloricus implidigitatus* Gad, 2004

Pliciloricus

- *Pliciloricus cavernicola*
- *Pliciloricus corvus* Gad, 2005
- *Pliciloricus dubius* Higgins & Kristensen, 1986
- *Pliciloricus enigmaticus* Higgins & Kristensen, 1986
- *Pliciloricus gracilis* Higgins & Kristensen, 1986

- *Pliciloricus hadalis* Kristensen & Shirayama 1988
- *Pliciloricus leocaudatus* Heiner & Kristensen, 2005
- *Pliciloricus orphanus* Higgins & Kristensen, 1986
- *Pliciloricus pedicularis* Gad 2005
- *Pliciloricus profundus* Higgins & Kristensen, 1986
- *Pliciloricus senicirrus* Gad, 2005
- *Pliciloricus shukeri* Heiner & Kristensen, 2005

Rugiloricus

- *Rugiloricus carolinensis* Higgins & Kristensen, 1986
- *Rugiloricus cauliculus* Higgins & Kristensen, 1986
- *Rugiloricus ornatus* Higgins & Kristensen, 1986
- *Rugiloricus polaris* Gad and Arbizu, 2005

Titaniloricus

- *Titaniloricus inexpectatovus* Gad, 2005

Chapter 12

Nematode

Nematodes

Unidentified roundworm from wet soil.
The mouth is at the top left corner.

Scientific classification [e]

Kingdom:	Animalia
clade:	Nematoida
Phylum:	**Nematoda** Diesing, 1861

Classes

Chromadorea (disputed)
Enoplea (disputed)
Secernentea

Synonyms

Adenophorea
Aphasmidia
Nematoidea Rudolphi, 1808
Nematodes Burmeister, 1837
Nemates Cobb, 1919
Nemata Cobb, 1919

The **nematodes** are the most diverse phylum of pseudocoelomates, and one of the most diverse of all animals. Nematode species are very difficult to distinguish; over 28,000 have been described, of which over 16,000 are parasitic. It has been estimated that the total number of nematode species might be approximately 1,000,000. Unlike cnidarians or flatworms, roundworms have a digestive system that is like a tube with openings at both ends.

Habitats

Nematodes have successfully adapted to nearly every ecosystem from marine to fresh water, from the polar regions to the tropics, as well as the highest to the lowest of elevations. They are ubiquitous in freshwater, marine, and terrestrial environments, where they often outnumber other animals in both individual and species counts, and are found in locations as diverse as mountains, deserts and oceanic trenches. They represent, for example, 90% of all life on the seafloor of the Earth. Their many parasitic forms include pathogens in most plants and animals (including humans). Some nematodes can undergo cryptobiosis.

One group of carnivorous fungi, the nematophagous fungi, are predators of soil nematodes. They set enticements for the nematodes in the form of lassos or adhesive structures.

Taxonomy and systematics

Eophasma jurasicum, a fossilized nematode

The group was originally defined by Karl Rudolphi in 1808 under the name **Nematoidea**, from Ancient Greek νῆμα (*nêma, nêmatos*, 'thread') and -ειδής (*-eidēs*, 'species'). The vernacular word "nematode" is a corruption of this taxon, reclassified as family **Nematodes** by Burmeister in 1837 and order **Nematoda** by K. M. Diesing in 1861.

At the origin, the "Nematoidea" included both roundworms and horsehair worms. Along with Acanthocephala, Trematoda and Cestoidea, it formed the group Entozoa. The first differentiation of roundworms from horsehair worms, though erroneous, is due to von Siebold (1843) with orders Nematoidea and Gordiacei (Gordiacea). They were classed along with Acanthocephala in the new phylum Nemathelminthes (today obsolete) by Gegenbaur (1859). Then the taxon Nematoidea has been promoted to the rank of phylum by Ray Lankester (1877) including the family Gordiidae (horsehair worms). In 1919, Nathan Cobb proposed that roundworms should be recognized alone as a phylum. He argued that they should be called **nema**(s) in English rather than "nematodes" and defined the taxon **Nemates** (Latin plural of *nema*). For ITIS, the taxon Nematoda is invalid. Since Cobb was the first to exclude all but nematodes from the group, the valid taxon should be ***Nemates*** Cobb 1919 or ***Nemata*** Cobb 1919.

Phylogeny

The mysterious Gastrotricha seem to hold the key to the "Ecdysozoa debate", but they have been little studied. Whether they are relatives of the nematodes is still unknown.

The relationships of the nematodes and their close relatives among the protostomian Metazoa are unresolved. Traditionally, they were held to be a lineage of their own, but in the 1990s it was proposed that they form a clade together with moulting animals such as arthropods. This group has been named Ecdysozoa. However, the monophyly of the Ecdysozoa was never unequivocally accepted: while most researchers consider at least the placement of arthropods as more distant relatives of annelids — with which they were formerly united — to be warranted, the presumed close relationships of the nematodes and relatives with the arthropods has been a major point of contention.

Even though the amount of data since accumulated in regard to this problem is staggering, the situation seems if anything less clear these days. DNA sequence data, initially strongly supporting the Ecdysozoa hypothesis, has become rather equivocal on ecdysozoan monophyly, and is simply unable to refute either a close or a more distant relationship between the arthropod and nematode lineages. That the roundworms have a large number of peculiar apomorphies and in many cases a parasitic lifestyle confounds morphological analyses. Genetic analyses of roundworms suggest that — as is also indicated by their unique morphological features — the group has been under intense selective pressure during its early radiation, resulting apparently in accelerated rates of both morphological and molecular evolution. Furthermore, no distinctive apomorphies of Ecdysozoa are known; even moulting has recently been confirmed to occur outside the presumed clade.

Conversely, the identity of the closest living relatives of the Nematoda has always been considered to be well resolved. Morphological characters and molecular phylogenies agree with placement of the roundworms as sister taxon to the parasitic horsehair worms (Nematomorpha); together they make up the Nematoida. Together with the Scalidophora (formerly Cephalorhyncha), the Nematoida form the Introverta. It is entirely unclear whether the Introverta are, in turn, the closest living relatives of the enigmatic Gastrotricha; if so, they are considered a clade Cycloneuralia, but there is much disagreement both between and among the available morphological and molecular data. The Cycloneuralia or the Introverta — depending on the validity of the former — are often ranked as a superphylum.

Nematode systematics

Due to the lack of knowledge regarding many nematodes, their systematics is contentious. Traditionally, they are divided into two classes, the Adenophorea and the Secernentea, and initial DNA sequence studies suggested the existence of five clades:

- Dorylaimia
- Enoplia
- Spirurina
- Tylenchina
- Rhabditina

As it seems, the Secernentea are indeed a natural group of closest relatives. But the "Adenophorea" appear to be a paraphyletic assemblage of roundworms simply retaining a good number of ancestral traits. The old Enoplia do not seem to be monophyletic either but to contain two distinct lineages. The old group "Chromadoria" seem to be another paraphyletic assemblage, with the Monhysterida representing a very ancient minor group of nematodes. Among the Secernentea, the Diplogasteria may need to be united with the Rhabditia. while the Tylenchia might be paraphyletic with the Rhabditia.

The understanding of roundworm systematics and phylogeny as of 2002 is summarised below:

Phylum Nematoda

- Basal order Monhysterida
- Class Dorylaimea
- Class Enoplea
- Class Secernentea
    - Subclass Diplogasteria (disputed)
    - Subclass Rhabditia (paraphyletic?)
    - Subclass Spiruria
    - Subclass Tylenchia (disputed)
- "Chromadorea" assemblage

Anatomy

Nematodes are slender, worm-like animals, typically less than 2.5 millimetres (0.10 in) long. The smallest nematodes are microscopic, while free-living species can reach as much as 5 centimetres (2.0 in) and some parasitic species are larger still. The body is often ornamented with ridges, rings, warts, bristles or other distinctive structures.

The head of a nematode is relatively distinctive. Whereas the rest of the body is bilaterally symmetrical, the head is radially symmetrical, with sensory bristles and, in many cases, solid *head-shields* radiating outwards around the mouth. The mouth has either three or six lips, which often bear a series of teeth on their inner edge. An adhesive *caudal gland* is often found at the tip of the tail.

The epidermis is either a syncytium or a single layer of cells, and is covered by a thick collagenous cuticle. The cuticle is often of complex structure, and may have two or three distinct layers. Underneath the epidermis lies a layer of muscle cells. Projections run from the inner surface of these cells towards the nerve cords; this is a unique arrangement in the animal kingdom, in which nerve cells normally extend fibres into the muscles rather than *vice versa*.

The muscle layer surrounds the body cavity, which is filled with a fluid that lacks any form of blood cells. The gut runs down the centre of the cavity.

Digestive system

The oral cavity is lined with cuticle, which is often strengthened with ridges or other structures, and, especially in carnivorous species, may bear a number of teeth. The mouth often includes a sharp stylet which the animal can thrust into its prey. In some species, the stylet is hollow, and can be used to suck liquids from plants or animals.

The oral cavity opens into a muscular sucking pharynx, also lined with cuticle. Digestive glands are found in this region of the gut, producing enzymes that start to break down the food. In stylet-bearing species, these may even be injected into the prey.

There is no stomach, with the pharynx connecting directly to the intestine that forms the main length of the gut. This produces further enzymes, and also absorbs nutrients through its lining. The last portion of the intestine is lined by cuticle, forming a rectum which expels waste through the anus just below and in front of the tip of the tail. The intestine also has valves or sphincters at either end to help control the movement of food through the body.

Excretory system

Nitrogenous waste is excreted in the form of ammonia through the body wall, and is not associated with any specific organs. However, the structures for excreting salt to maintain osmoregulation are typically more complex.

In many marine nematodes, there are one or two unicellular *renette glands* that excrete salt through a pore on the underside of the animal, close to the pharynx. In most other nematodes, these specialised cells have been replaced by an organ consisting of two parallel ducts connected by a single transverse duct. This transverse duct opens into a common canal that runs to the excretory pore.

Nervous system

Four nerves run the length of the body on the dorsal, ventral, and lateral surfaces. Each nerve lies within a cord of connective tissue lying beneath the cuticle and between the muscle cells. The ventral nerve is the largest, and has a double structure forward of the excretory pore. The dorsal nerve is responsible for motor control, while the lateral nerves are sensory, and the ventral combines both functions.

At the anterior end of the animal, the nerves branch from a dense circular nerve ring surrounding the pharynx, and serving as the brain. Smaller nerves run forward from the ring to supply the sensory organs of the head.

The body of nematodes is covered in numerous sensory bristles and papillae that together provide a sense of touch. Behind the sensory bristles on the head lie two small pits, or *amphids*. These are well supplied with nerve cells, and are probably chemoreception organs. A few aquatic nematodes possess what appear to be pigmented eye-spots, but is unclear whether or not these are actually sensory in nature.

Reproduction

Most nematode species are dioecious, with separate male and female individuals. Both sexes possess one or two tubular gonads. In males, the sperm are produced at the end of the gonad, and migrate along its length as they mature. The testes each open into a relatively wide sperm duct and then into a glandular and muscular ejaculatory duct associated with the cloaca. In females, the ovaries each open into an oviduct and then a glandular uterus. The uteri both open into a common vagina, usually located in the middle of the ventral surface.

Reproduction is usually sexual. Males are usually smaller than females (often much smaller) and often have a characteristically bent tail for holding the female for copulation. During copulation, one or more chitinized spicules move out of the cloaca and are inserted into genital pore of the female. Amoeboid sperm crawl along the spicule into the female worm. Nematode sperm is thought to be the only eukaryotic cell without the globular protein G-actin.

Eggs may be embryonated or unembryonated when passed by the female, meaning that their fertilized eggs may not yet be developed. A few species are known to be ovoviviparous. The eggs are protected by an outer shell, secreted by the uterus. In free-living roundworms, the eggs hatch into larvae, which appear essentially identical to the adults, except for an under-developed reproductive system; in parasitic roundworms, the life cycle is often much more complicated.

Nematodes as a whole possess a wide range of modes of reproduction. Some nematodes, such as *Heterorhabditis* spp., undergo a process called *endotokia matricida*: intrauterine birth causing maternal death. Some nematodes are hermaphroditic, and keep their self-fertilized eggs inside the uterus until they hatch. The juvenile nematodes will then ingest the parent nematode. This process is significantly promoted in environments with a low or reducing food supply.

The nematode model species *Caenorhabditis elegans* and *C. briggsae* exhibit androdioecy, which is very rare among animals. The single genus *Meloidogyne* (root-knot nematodes) exhibit a range of reproductive modes including sexual reproduction, facultative sexuality (in which most, but not all, generations reproduce asexually), and both meiotic and mitotic parthenogenesis.

The genus *Mesorhabditis* exhibits an unusual form of parthenogenesis, in which sperm-producing males copulate with females, but the sperm do not fuse with the ovum. Contact with the sperm is essential for the ovum to begin dividing, but because there is no fusion of the cells, the male contributes no genetic material to the offspring, which are essentially clones of the female.

Free-living species

In free-living species, development usually consists of four molts of the cuticle during growth. Different species feed on materials as varied as algae, fungi, small animals, fecal matter, dead organisms and living tissues. Free-living marine nematodes are important and abundant members of the meiobenthos. They play an important role in the decomposition process, aid in recycling of nutrients in marine environments and are sensitive to changes in the environment caused by pollution. One roundworm of note is *Caenorhabditis elegans*, which lives in the soil and has found much use as a model organism. *C. elegans* has had its entire genome sequenced, as well as the developmental fate of every cell determined, and every neuron mapped.

Parasitic species

Nematodes commonly parasitic on humans include ascarids (*Ascaris*), filarias, hookworms, pinworms (*Enterobius*) and whipworms (*Trichuris trichiura*). The species *Trichinella spiralis*, commonly known as the *trichina worm*, occurs in rats, pigs, and humans, and is responsible for the disease trichinosis. *Baylisascaris* usually infests wild animals but can be deadly to humans as well. *Dirofilaria immitis* are Heartworms known for causing Heartworm disease by inhabiting the hearts, arteries, and lungs of dogs and some cats. *Haemonchus contortus* is one of the most abundant infectious agents in sheep around the world, causing great economic damage to sheep farms. In contrast, entomopathogenic nematodes parasitize insects and are considered by humans to be beneficial.

One form of nematode is entirely dependent upon fig wasps, which are the sole source of fig fertilization. They prey upon the wasps, riding them from the ripe fig of the wasp's birth to the fig flower of its death, where they kill the wasp, and their offspring await the birth of the next generation of wasps as the fig ripens.

A newly discovered parasitic tetradonematid nematode, *Myrmeconema neotropicum*, apparently induces fruit mimicry in the tropical ant*Cephalotes atratus*. Infected ants develop bright red gasters, tend to be more sluggish, and walk with their gasters in a conspicuous elevated position. These changes likely cause frugivorous birds to confuse the infected ants for berries and eat them. Parasite eggs passed in the bird's feces are subsequently collected by foraging *Cephalotes atratus* and are fed to their larvae, thus completing the life cycle of *Myrmeconema neotropicum*.

Colorized electron micrograph of soybean cyst nematode (*Heterodera* sp.) and egg

Plant parasitic nematodes include several groups causing severe crop losses. The most common genera are *Aphelenchoides* (foliar nematodes), *Ditylenchus*, *Globodera* (potato cyst nematodes), *Heterodera* (soybean cyst nematodes), *Longidorus*, *Meloidogyne* (root-knot nematodes), *Nacobbus*, *Pratylenchus* (lesion nematodes), *Trichodorus* and *Xiphinema* (dagger nematodes). Several phytoparasitic nematode species cause histological damages to roots, including the formation of visible galls (e.g. by root-knot nematodes), which are useful characters for their diagnostic in the field. Some nematode species transmit plant viruses through their feeding activity on roots. One of them is *Xiphinema index*, vector of GFLV (Grapevine Fanleaf Virus), an important disease of grapes.

Other nematodes attack bark and forest trees. The most important representative of this group is *Bursaphelenchus xylophilus*, the pine wood nematode, present in Asia and America and recently discovered in Europe.

Agriculture and horticulture

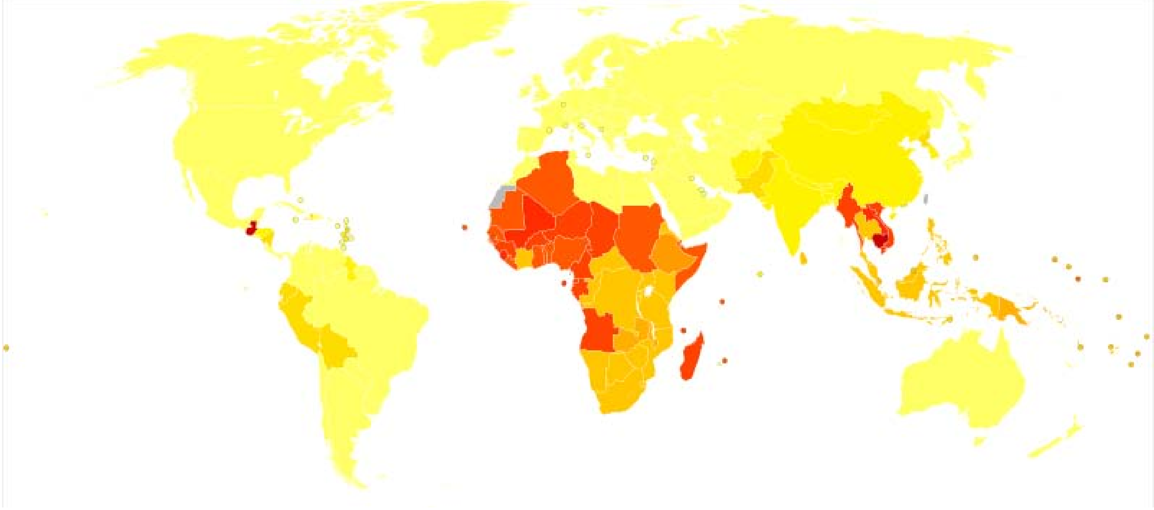
Depending on the species, a nematode may be beneficial or detrimental to plant health. From agricultural and horticulture perspectives, there are two categories of nematode: predatory ones, which will kill garden pests like cutworms, and pest nematodes, like the root-knot nematode, which attack plants and those that act as vectors spreading plant viruses between crop plants. Predatory nematodes can be bred by soaking a specific recipe of leaves and other detritus in water, in a dark, cool place, and can even be purchased as an organic form of pest control.

Rotations of plants with nematode resistant species or varieties is one means of managing parasitic nematode infestations. For example, marigolds, grown over one or more seasons (the effect is cumulative), can be used to control nematodes. Another is treatment with natural antagonists such as the fungus *Gliocladium roseum*. Chitosan is a natural biocontrol that elicits plant defense responses to destroy parasitic cyst nematodes on roots of soybean, corn, sugar beets, potatoes and tomatoes without harming beneficial nematodes in the soil. Furthermore soil steaming is an efficient method to kill nematodes before planting crop.

CSIRO has found that there was 13- to 14-fold reduction of nematode population densities in plots having Indian mustard (*Brassica juncea*) green manure or seed meal in the soil.

Hundreds of *Caenorhabditis elegans* were featured in a research project on NASA's STS-107 space mission (which ended in the Space Shuttle Columbia Disaster).

Epidemiology



Disability-adjusted life year for intestinal nematode infections per 100,000 inhabitants in 2002.

▨ no data

🟨 less than 25

🟨 25-50
🟨 50-75
🟨 75-100
🟧 100-120
🟧 120-140
🟧 140-160
🟧 160-180
🟧 180-200
🟥 200-220
🟥 220-240
🟥 more than 240

A number of intestinal nematodes affect human beings. These include ascariasis, trichuriasis and hookworm disease.

Chapter 13

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 vagaries 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 14

Rotifer

Rotifera
Temporal range: Eocene–Recent

Rotaria

Scientific classification [e]

Kingdom:	Animalia
(unranked):	Protostomia
(unranked):	Spiralia
(unranked):	Platyzoa
Phylum:	**Rotifera** Cuvier, 1798

Classes and orders

Digononta
Bdelloidea
Seisonidea
Monogononta
Collothecida
Flosculariida
Ploimida

The **rotifers** (commonly called **wheel animals**) make up a phylum of microscopic and near-microscopic pseudocoelomate animals. They were first described by Rev. John

Harris in 1696, and other forms were described by Anton van Leeuwenhoek in 1703. Most rotifers are around 0.1–0.5 mm long (although their size can range from 50 μm to over 2 millimeters), and are common in freshwater environments throughout the world with a few saltwater species; for example, those of genus *Synchaeta*. Some rotifers are free swimming and truly planktonic, others move by inchworming along a substrate, and some are sessile, living inside tubes or gelatinous holdfasts that are attached to a substrate. About 25 species are colonial (e.g., *Sinantherina semibullata*), either sessile or planktonic. Rotifers are an important part of the freshwater zooplankton, being a major foodsource and with many species also contributing to the decomposition of soil organic matter. Most species of the rotifers are cosmopolitan, but there are also some endemic species, like *Cephalodella vittata* to the Lake Baikal

Taxonomy and naming

Rev. John Harris first described the rotifers (in particular the Bdelloid Rotifer) in 1696 as "an animal like a large maggot which could contract itself into a spherical figure and then stretch itself out again; the end of its tail appeared with a forceps like that of an earwig". In 1702, Anton van Leeuwenhoek gave a detailed description of *Rotifer vulgaris* and subsequently described *Melicerta ringens* and other species. He was also the first to publish observations of the revivification of certain species after drying. Other forms were described by other observers, but it wasn't until the publication of Christian Gottfried Ehrenberg's *Die Infusionsthierchen als vollkommene Organismen* in 1838 that the rotifers were recognized as being multicellular animals.

About 2200 species of rotifers have been described. Taxonomically, they are placed in the phylum Rotifera. This phylum is subdivided into four classes: Monogononta, Digononta, Bdelloidea, and Seisonidea. The largest group is the Monogononta, with about 1500 species, followed by the Bdelloidea, with about 350 species. There are only two known species of Seisonidea. The Acanthocephala, previously considered to be a separate phylum, have been unequivocally demonstrated to be modified rotifers. However, the exact relationship to other members of the phylum has not yet been resolved.

Etymology

The word "rotifer" is derived from a Latin word meaning "wheel-bearer, due to the corona around the mouth that in motion resemble a wheel (though the organ does not actually rotate).

Anatomy

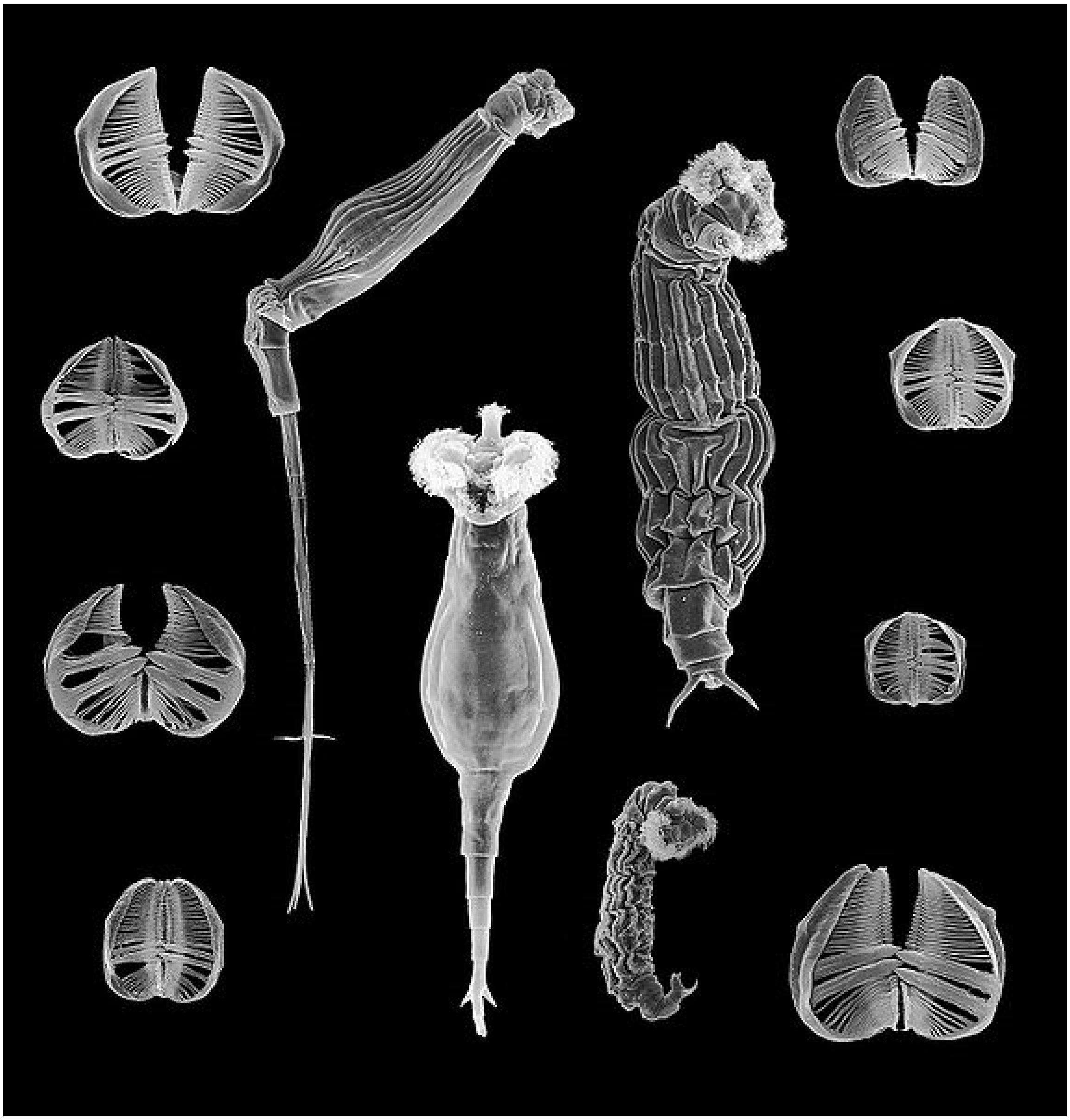
Rotifers have bilateral symmetry and a variety of different shapes. The body of a rotifer is divided into a head, trunk, and foot, and is typically somewhat cylindrical. There is a well-developed cuticle, which may be thick and rigid, giving the animal a box-like shape, or flexible, giving the animal a worm-like shape; such rotifers are respectively called *loricate* and *illoricate*. Rigid cuticles are often composed of multiple plates, and may bear spines, ridges, or other ornamentation.

The most distinctive feature of rotifers is the presence of a ciliated structure, called the *corona*, on the head. In the more primitive species, this forms a simple ring of cilia around the mouth from which an additional band of cilia stretches over the back of the head. In the great majority of rotifers, however, this has evolved into a more complex structure.

Modifications to the basic plan of the corona include alteration of the cilia into bristles or large tufts, and either expansion or loss of the ciliated band around the head. In genera such as *Collotheca*, the corona is modified to form a funnel surrounding the mouth. In many species, such as *Testudinella*, the cilia around the mouth have disappeared, leaving just two small circular bands on the head. In the bdelloids, this plan is further modified, with the upper band splitting into two rotating wheels, raised up on a pedestal projecting from the upper surface of the head.

The trunk forms the major part of the body, and encloses most of the internal organs. The foot projects from the rear of the trunk, and is usually much narrower, giving the appearance of a tail. The cuticle over the foot often forms rings, making it appear segmented, although the internal structure is uniform. Many rotifers can retract the foot partially or wholly into the trunk. The foot ends in from one to four toes, which, in sessile and crawling species, contain adhesive glands to attach the animal to the substratum. In many free-swimming species, the foot as a whole is reduced in size, and may even be absent.

Digestive system



Scanning electron micrographs showing morphological variation of bdelloid rotifers and their jaws.

The coronal cilia create a current that sweeps food into the mouth. The mouth opens into a characteristic chewing pharynx (called the *mastax*), sometimes via a ciliated tube, and sometimes directly. The pharynx has a powerful muscular wall and contains tiny, calcified, jaw-like structures called *trophi*. The shape of the trophi varies between different species, depending partly on the nature of their diet. In suspension feeders, the trophi are covered in grinding ridges, while in more actively carnivorous species, they may be shaped like forceps to help bite into prey. In some ectoparasitic rotifers, the mastax is adapted to grip onto the host, although, in others, the foot performs this function instead.

Behind the mastax lies an oesophagus, which opens into a stomach where most of the digestion and absorption occurs. The stomach opens into a short intestine that terminates in a cloaca on the posterior dorsal surface of the animal. Up to seven salivary glands are present in some species, emptying to the mouth in front of the oesophagus, while the stomach is associated with two gastric glands that produce digestive enzymes.

A pair of protonephridia open into a bladder that drains into the cloaca. These organs expel water from the body, helping to maintain osmotic balance.

Nervous system

Rotifers have a small brain, located just above the mastax, from which a number of nerves extend throughout the body. The number of nerves varies between species, although the nervous system usually has a simple layout. Close to the brain lies a *retrocerebral organ*, consisting of two glands either side of a medial sac. The sac drains into a duct that divides into two before opening through pores on the uppermost part of the head. Its function is unclear.

Rotifers typically possess one or two pairs of short antennae and up to five eyes. The eyes are simple in structure, sometimes with just a single photoreceptor cell. In addition, the bristles of the corona are sensitive to touch, and there are also a pair of tiny sensory pits lined by cilia in the head region.

Biology

The coronal cilia pull the animal, when unattached, through the water.

Like many other microscopic animals, adult rotifers frequently exhibit eutely — they have a fixed number of cells within a species, usually on the order of 1,000.

Bdelloid rotifer genomes contain two or more divergent copies of each gene, suggesting a long-term asexual evolutionary history. For example, four copies of hsp82 are found. Each is different and found on a different chromosome excluding the possibility of homozygous sexual reproduction.

Like nemertine worms, the rotifers have not been proven to be derived from cilia. Its thin lamellae resemble cabbage leaves, and are composed from their creases of the receptor membrane.

Reproduction and life cycle

Rotifers are dioecious and reproduce sexually or parthenogenetically. They are sexually dimorphic, with the females always being larger than the males. In some species, this is relatively mild, but in others the female may be up to ten times the size of the male. In parthenogenetic species, males may be present only at certain times of the year, or absent altogether.

The female reproductive system consists of one or two ovaries, each with a *vitellarium* gland that supplies the eggs with yolk. Together, each ovary and vitellarium form a single syncitial structure in the anterior part of the animal, opening through an oviduct into the cloaca.

Males do not usually possess a functional digestive system, and are therefore short-lived, often already being sexually fertile at birth. They have a single testis and sperm duct, associated with a pair of glandular structures referred to as "prostates" (although they are unrelated to the vertebrate organ of the same name). The sperm duct opens into a gonopore at the posterior end of the animal, which is usually modified to form a penis. The gonopore is homologous to the cloaca of females, but in most species has no connection to the vestigial digestive system, which lacks an anus.

Fertilisation is internal. The male either inserts his penis into the female's cloaca or uses it to penetrate her skin, injecting the sperm into the body cavity. The egg secretes a shell, and is attached either to the substratum, nearby plants, or the female's own body. A few species, such as *Rotaria*, are ovoviviparous, retaining the eggs inside their body until they hatch.

Most species hatch as miniature versions of the adult. Sessile species, however, are born as free-swimming larvae, which closely resemble the adults of related free-swimming species. Females grow rapidly, reaching their adult size within a few days, while males typically do not grow in size at all.

The life span of monogonont females varies from a couple of days to about three weeks.

Resting eggs and anhydrobiosis

Males in the class Monogononta may be either present or absent depending on the species and environmental conditions. In the absence of males, reproduction is by parthenogenesis and results in offspring that are genetically identical to the parent. Individuals of some species form two distinct types of parthenogenetic eggs; one type develops into a normal parthenogenetic female, while the other occurs in response to a changed environment and develops into a degenerate male that lacks a digestive system, but does have a complete male reproductive system that is used to inseminate females thereby producing fertilized 'resting eggs'. Resting eggs develop into zygotes that are able to survive extreme environmental conditions such as may occur during winter or when the pond dries up. These eggs resume development and produce a new female generation when conditions improve again.

Bdelloid rotifers are unable to produce resting eggs, but many can survive prolonged periods of adverse conditions after desiccation. This facility is termed anhydrobiosis, and organisms with these capabilities are termed anhydrobionts. Under drought conditions, bdelloid rotifers contract into an inert form and lose almost all body water; when rehydrated, however, they resume activity within a few hours. Bdelloids can survive the dry state for prolonged periods, with the longest well-documented dormancy being nine years. While in other anhydrobionts, such as the brine shrimp, this desiccation tolerance is thought to be linked to the production of trehalose, a non-reducing disaccharide (sugar), bdelloids apparently lack the ability to synthesise trehalose.

Feeding

A rotifer feeding

Rotifers eat partuculate organis detritus, dead bacteria, algae, and protozoans. They eat particles up to 10 micrometres in size. Like crustaceans, rotifers contribute to nutrient recycling. For this reason, they are used in fish tanks to help clean the water, to prevent clouds of waste matter. Rotifers affect the species composition of algae in ecosystems through their choice in grazing. Rotifers may be in competition with cladocera and copepods for phytoplanktonic food sources.

Predators

Rotifers fall prey to many animals, such as copepods, fish (e.g. herring, salmon), moss animals, comb jellies, jellyfish, and starfish

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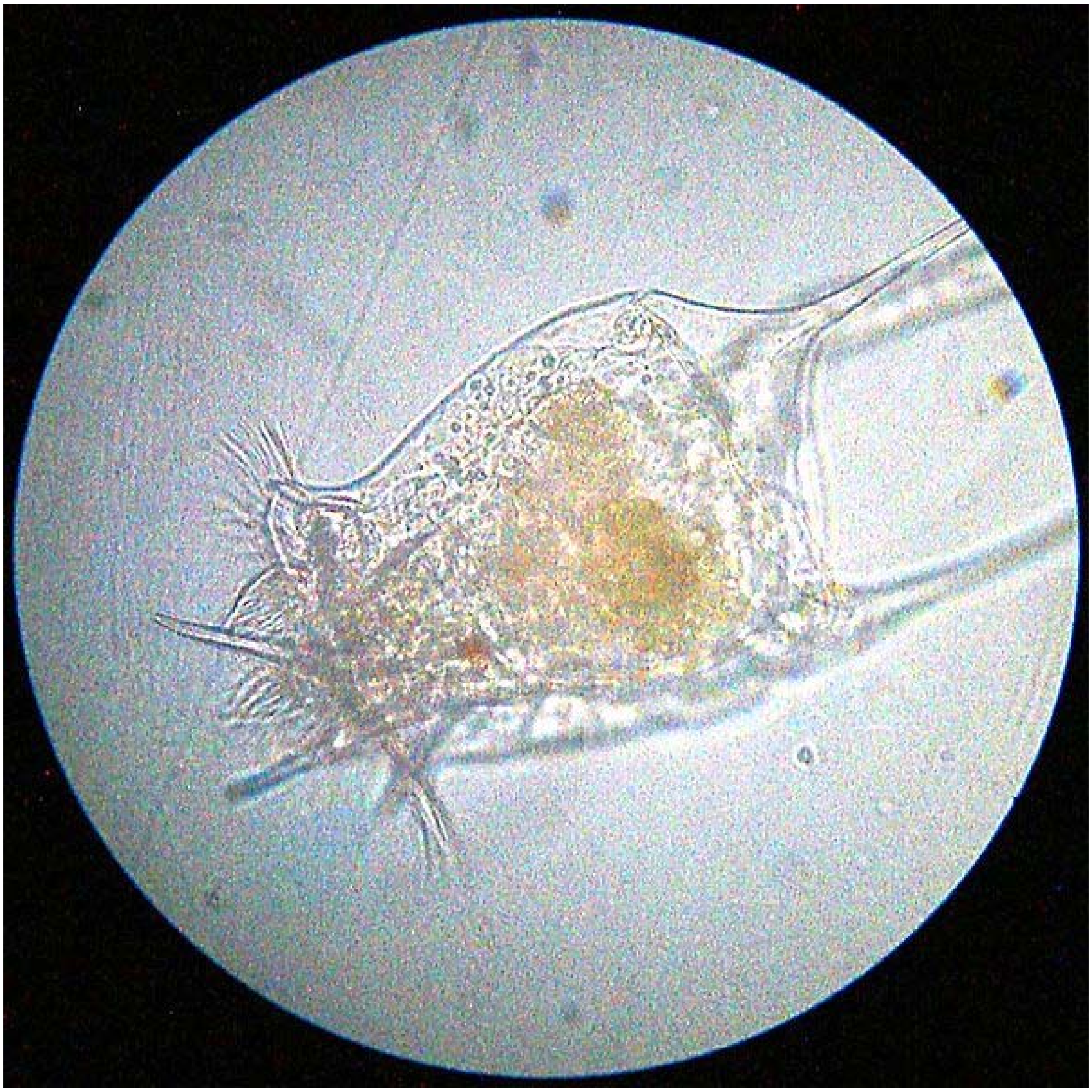


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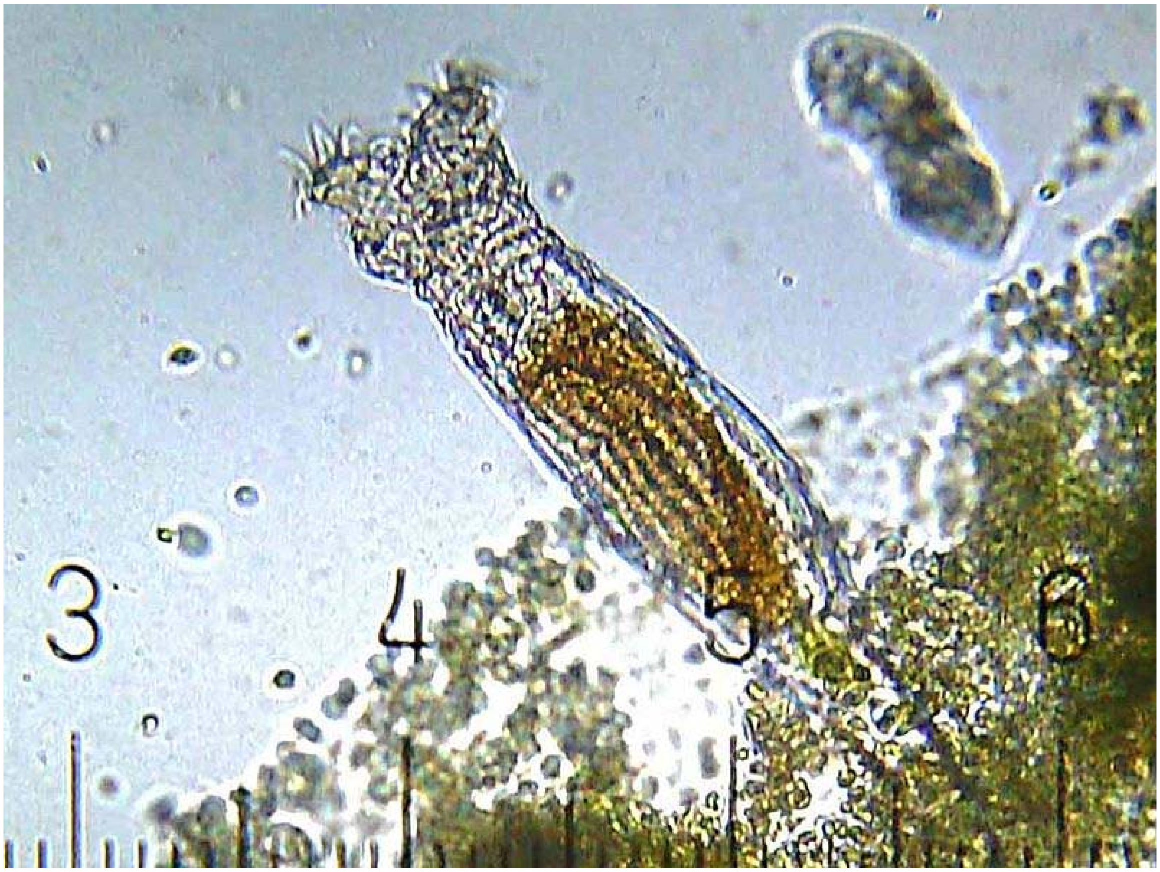
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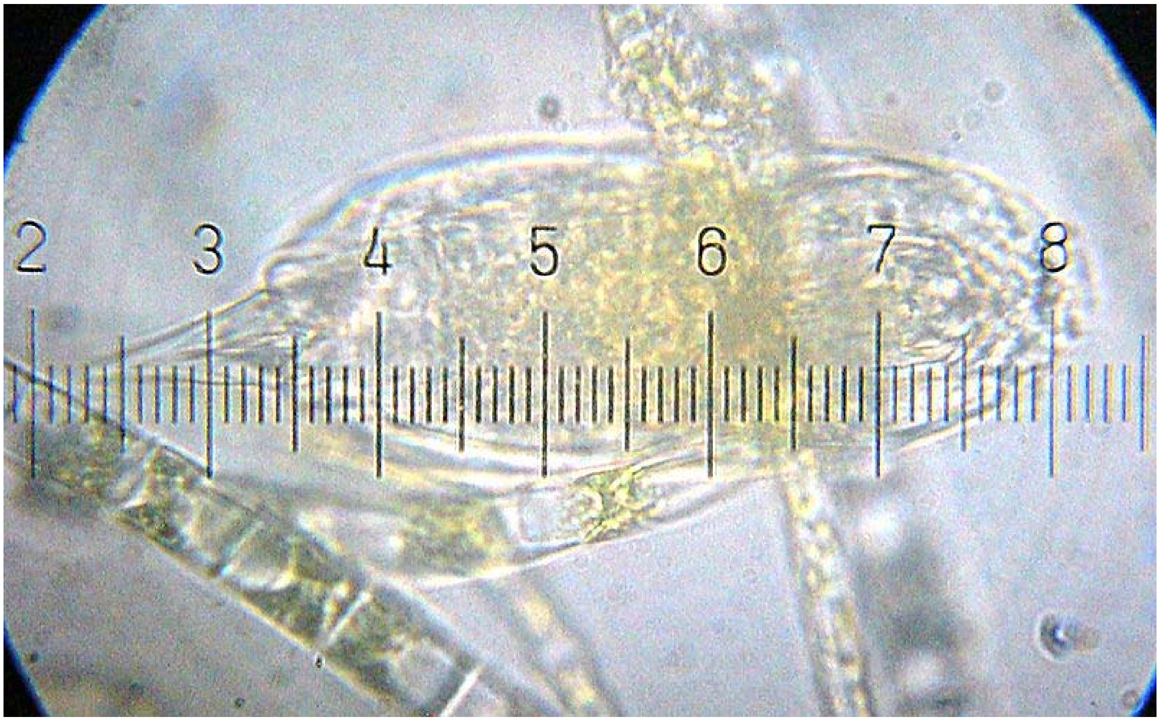
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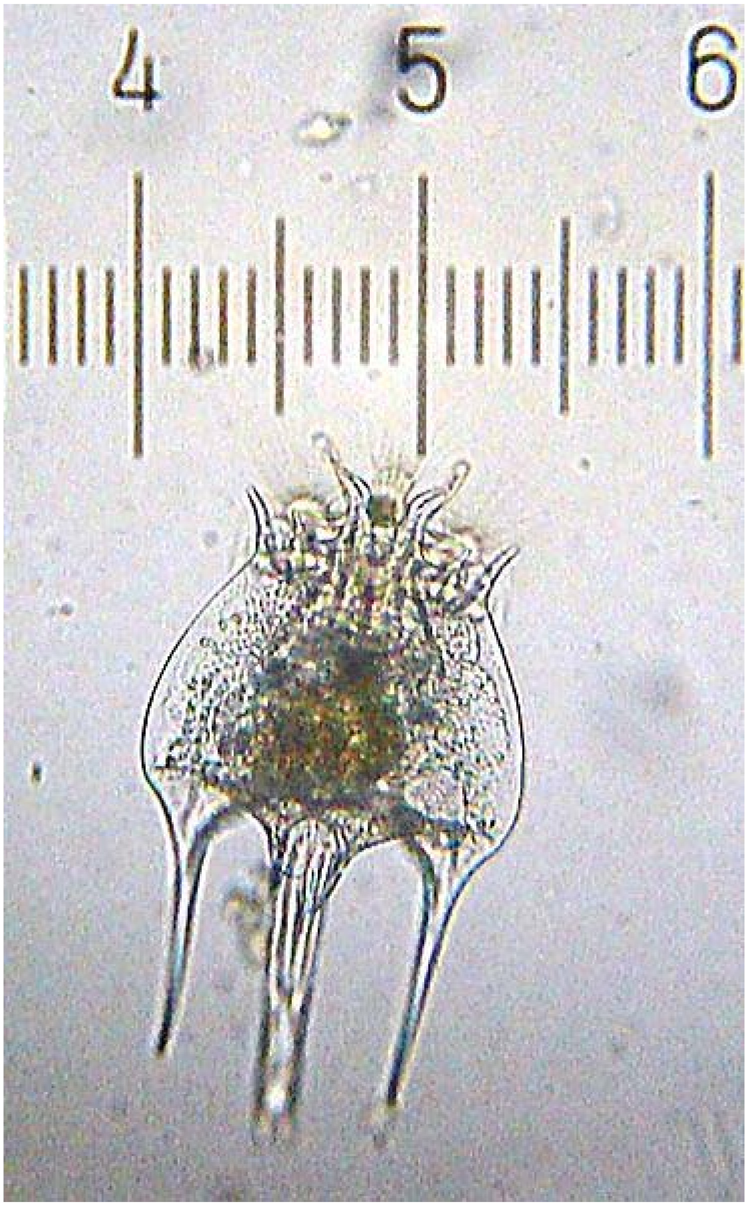
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