



Invertebrate Animals

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Chapter- 1

Invertebrate



This invertebrate, *Drosophila melanogaster*, has been the subject of much research.

An **invertebrate** is an animal without a backbone. The group includes 95% of all animal species – all animals except those in the chordate subphylum Vertebrata (fish, amphibians, reptiles, birds, and mammals).

Invertebrates form a paraphyletic group. All the listed phyla are invertebrates along with two of the three subphyla in Phylum Chordata: Urochordata and Cephalochordata. These

two, plus all the other known invertebrates, have only one cluster of Hox genes, while the vertebrates have duplicated their original cluster more than once.

Within palaeozoology and palaeobiology, invertebrates are often studied within the fossil discipline called invertebrate palaeontology.

History

Carl Linnaeus divided these animals into only two groups, the Insecta and the now-obsolete vermes (worms). Jean-Baptiste Lamarck, who was appointed to the position of "Curator of Insecta and Vermes" at the Muséum National d'Histoire Naturelle in 1793, both coined the term "invertebrate" to describe such and divided the original two groups into ten, by splitting off Arachnida and Crustacea from the Linnean Insecta, and Mollusca, Annelida, Cirripedia, Radiata, Coelenterata and Infusoria from the Linnean Vermes. They are now classified into over 30 phyla, from simple organisms such as sea sponges and flatworms to complex animals such as arthropods and molluscs.

Phyla and common examples



The fossil coral *Cladocora* from the Pliocene of Cyprus

- Acanthocephala
- Acoelomorpha
- Annelida – segmented worms (earthworms, leeches, polychaetes)

- Arthropoda – insects, arachnids, crustaceans
- Brachiopoda
- Bryozoa
- Chaetognatha
- Cnidaria – jellyfishes, corals, sea anemones, hydras
- Ctenophora – comb jellies
- Cycliophora
- Echinodermata – starfishes, sea urchins
- Entoprocta
- Gastrotricha
- Gnathostomulida
- Hemichordata
- Kinorhyncha
- Loricifera
- Micrognathozoa
- Mollusca – squid, snails, bivalves
- Nematoda – roundworms
- Nemertea – ribbon worms
- Onychophora
- Phoronida
- Platyhelminthes – flatworms
- Porifera – sponges
- Priapulida
- Rotifera
- Sipuncula
- Tardigrada
- Xenoturbellida

Chapter- 2

Sponge (Porifera)

Sponge

Fossil range: Ediacaran–Recent



Scientific classification

Domain: Eukaryota
Kingdom: Animalia
Phylum: **Porifera***
Grant in Todd, 1836

Included groups

Calcarea
Hexactinellida
Demospongiae

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 and meeting ova that in species are released and others are retained 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 recolonize 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 Dan Rouse'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 <i>Homoscleromorpha</i> 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	Leuconoid

aragonite if present.

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 photosynthesizing 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 spermatocysts 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 syncytium draped around and between them and choanosyncytia with multiple collar bodies in the center. The larvae then leave their parents' bodies.

Life cycle

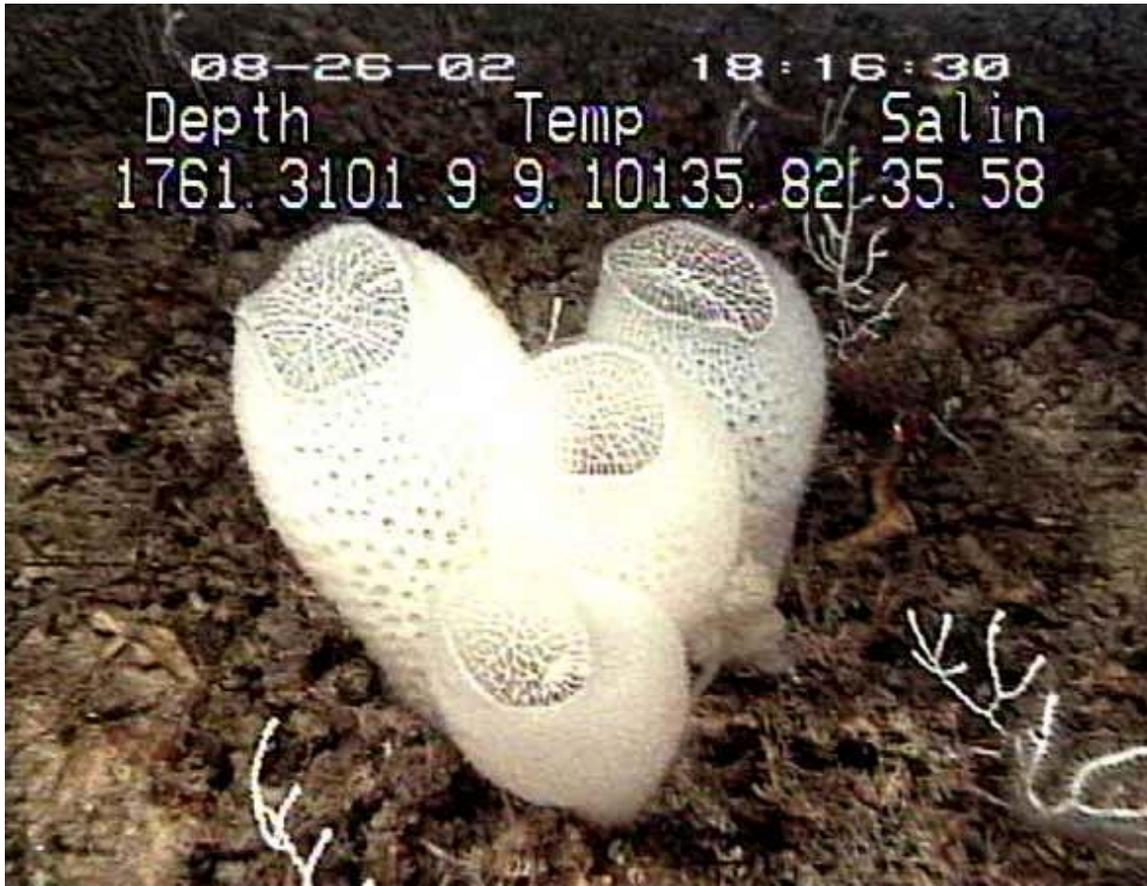
Sponges in temperate regions live for at most a few years, but some tropical species and perhaps some deep-ocean ones may live for 200 years or more. Some calcified demosponges grow by only 0.2 millimetres (0.0079 in) per year and, if that rate is constant, specimens 1 metre (3.3 ft) wide must be about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

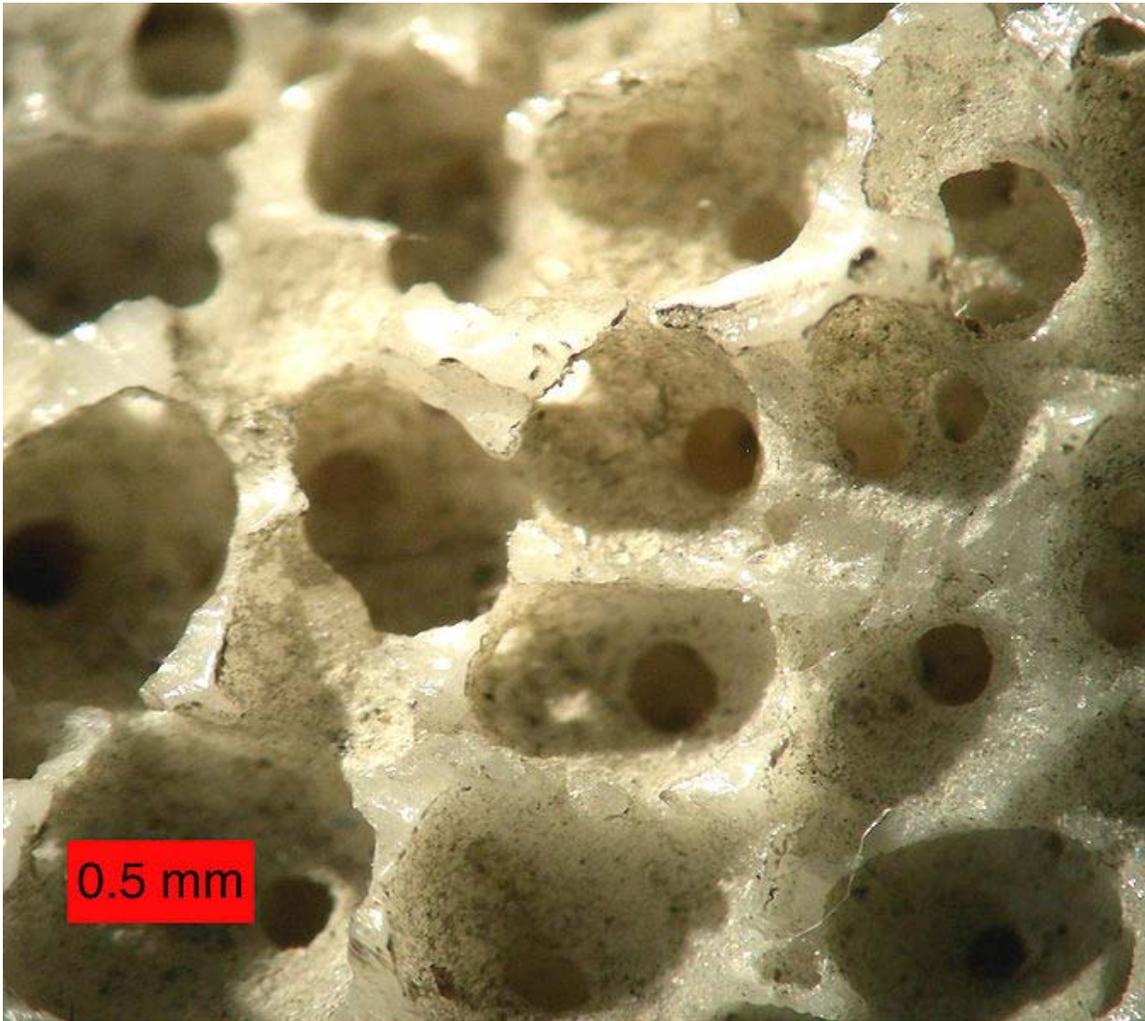
As primary producers

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 Clionidae, 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.

Chapter- 3

Arthropod



Extinct and modern arthropods

Scientific classification

Domain:	Eukaryota
Kingdom:	Animalia
Subkingdom:	Eumetazoa
Superphylum:	Ecdysozoa
Phylum:	Arthropoda Latreille, 1829

Subphyla and Classes

- **Subphylum Trilobitomorpha**
 - Trilobita – trilobites (extinct)
- **Subphylum Chelicerata**
 - Arachnida – spiders, scorpions, etc.
 - Xiphosura – horseshoe crabs, etc.
 - Pycnogonida – sea spiders
 - Eurypterida – sea scorpions (extinct)
- **Subphylum Myriapoda**
 - Chilopoda – centipedes
 - Diplopoda – millipedes
 - Pauropoda
 - Symphyla
- **Subphylum Hexapoda**
 - Insecta – insects
 - Entognatha
- **Subphylum Crustacea**
 - Branchiopoda – brine shrimp etc.
 - Remipedia
 - Cephalocarida – horseshoe shrimp
 - Maxillopoda – barnacles, fish lice, etc.
 - Ostracoda – seed shrimp
 - Malacostraca – lobsters, crabs, shrimp, etc.

An **arthropod** is an invertebrate animal having an exoskeleton (external skeleton), a segmented body, and jointed appendages. Arthropods are members of the phylum **Arthropoda** (from Greek ἄρθρον *arthron*, "joint", and ποδός *podos* "foot", which together mean "jointed feet"), and include the insects, arachnids, crustaceans, and others. Arthropods are characterized by their jointed limbs and cuticles, which are mainly made of α -chitin; the cuticles of crustaceans are also biomineralized with calcium carbonate. The rigid cuticle inhibits growth, so arthropods replace it periodically by molting. The arthropod body plan consists of repeated segments, each with a pair of appendages. It is so versatile that they have been compared to Swiss Army knives, and it has enabled them to become the most species-rich members of all ecological guilds in most environments. They have over a million described species, making up more than 80% of all described living animal species, and are one of only two animal groups that are very successful in

dry environments – the other being the amniotes. They range in size from microscopic plankton up to forms a few meters long.

Arthropods' primary internal cavity is a hemocoel, which accommodates their internal organs and through which their blood circulates; they have open circulatory systems. Like their exteriors, the internal organs of arthropods are generally built of repeated segments. Their nervous system is "ladder-like", with paired ventral nerve cords running through all segments and forming paired ganglia in each segment. Their heads are formed by fusion of varying numbers of segments, and their brains are formed by fusion of the ganglia of these segments and encircle the esophagus. The respiratory and excretory systems of arthropods vary, depending as much on their environment as on the subphylum to which they belong.

Their vision relies on various combinations of compound eyes and pigment-pit ocelli: in most species the ocelli can only detect the direction from which light is coming, and the compound eyes are the main source of information, but the main eyes of spiders are ocelli that can form images and, in a few cases, can swivel to track prey. Arthropods also have a wide range of chemical and mechanical sensors, mostly based on modifications of the many setae (bristles) that project through their cuticles.

Arthropods' methods of reproduction and development are diverse; all terrestrial species use internal fertilization, but this is often by indirect transfer of the sperm via an appendage or the ground, rather than by direct injection. Aquatic species use either internal or external fertilization. Almost all arthropods lay eggs, but scorpions give birth to live young after the eggs have hatched inside the mother. Arthropod hatchlings vary from miniature adults to grubs and caterpillars that lack jointed limbs and eventually undergo a total metamorphosis to produce the adult form. The level of maternal care for hatchlings varies from zero to the prolonged care provided by scorpions.

The versatility of the arthropod modular body plan has made it difficult for zoologists and paleontologists to classify them and work out their evolutionary ancestry, which dates back to the Cambrian period. From the late 1950s to late 1970s, it was thought that arthropods were polyphyletic, that is, there was no single arthropod ancestor. Now they are generally regarded as monophyletic. Historically, the closest evolutionary relatives of arthropods were considered to be annelid worms, as both groups have segmented bodies. This hypothesis is by now largely rejected, with annelids and molluscs forming the superphylum Lophotrochozoa. Many analyses support a placement of arthropods with cycloneuralians (or their constituent clades) in a superphylum Ecdysozoa. Overall however, the basal relationships of Metazoa are not yet well resolved. Likewise, the relationships between various arthropod groups are still actively debated.

Although arthropods contribute to human food supply both directly as food and more importantly as pollinators of crops, they also spread some of the most severe diseases and do considerable damage to livestock and crops.

Description

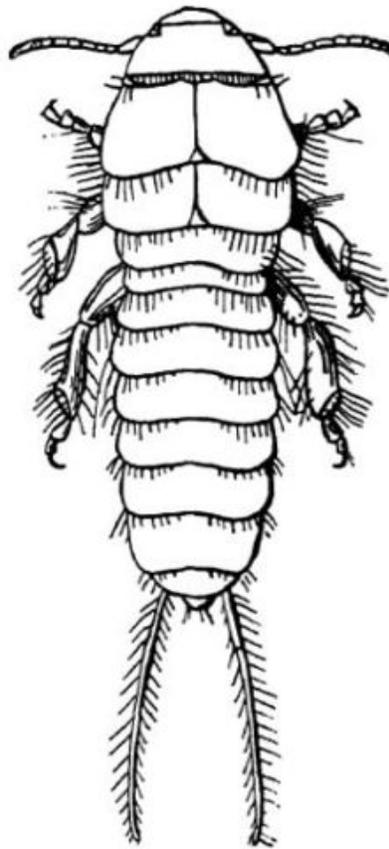
Arthropods are invertebrates with segmented bodies and jointed limbs. The limbs form part of an exoskeleton, which is mainly made of α -chitin, a derivative of glucose. One other group of animals, the tetrapods, has jointed limbs, but tetrapods are vertebrates and therefore have endoskeletons.

Diversity

One estimate indicates that arthropods have 1,170,000 described species, and account for over 80% of all known living animal species. Another study estimates that there are between 5 to 10 million extant arthropod species, both described and yet to be described. Estimating the total number of living species is extremely difficult because it often depends on a series of assumptions in order to scale up from counts at specific locations to estimates for the whole world. A study in 1992 estimated that there were 500,000 species of animals and plants in Costa Rica alone, of which 365,000 were arthropods.

They are important members of marine, freshwater, land and air ecosystems, and are one of only two major animal groups that have adapted to life in dry environments; the other is amniotes, whose living members are reptiles, birds and mammals. One arthropod subgroup, insects, is the most species-rich member of all ecological guilds (ways of making a living) in land and fresh-water environments. The lightest insects weigh less than 25 micrograms (millionths of a gram), while the heaviest weigh over 70 grams (2.5 oz). Some living crustaceans are much larger, for example the legs of the Japanese spider crab may span up to 4 metres (13 ft).

Segmentation



Hemimerus Hanseni.

(After Hansen.)

Segments and tagmata of an arthropod

The embryos of all arthropods are segmented, built from a series of repeated modules. The last common ancestor of living arthropods probably consisted of a series of undifferentiated segments, each with a pair of appendages that functioned as limbs. However all known living and fossil arthropods have grouped segments into tagmata in which segments and their limbs are specialized in various ways; The three-part appearance of many insect bodies and the two-part appearance of spiders is a result of this grouping; in fact there are no external signs of segmentation in mites. Arthropods also have two body elements that are not part of this serially repeated pattern of segments, an acron at the front, ahead of the mouth, and a telson at the rear, behind the anus. The eyes are mounted on the acron.

The original structure of arthropod appendages was probably biramous, with the upper branch acting as a gill while the lower branch was used for walking. In some segments of all known arthropods the appendages have been modified, for example to form gills, mouth-parts, antennae for collecting information, or claws for grasping; arthropods are

"like Swiss Army knives, each equipped with a unique set of specialized tools." In many arthropods, appendages have vanished from some regions of the body, and it is particularly common for abdominal appendages to have disappeared or be highly modified.

The most conspicuous specialization of segments is in the head. The four major groups of arthropods – Chelicerata (includes spiders and scorpions), Crustacea (shrimps, lobsters, crabs, etc.), Tracheata (arthropods that breathe via channels into their bodies; includes insects and myriapods), and the extinct trilobites – have heads formed of various combinations of segments, with appendages that are missing or specialized in different ways. In addition some extinct arthropods, such as *Marrella*, belong to none of these groups, as their heads are formed by their own particular combinations of segments and specialized appendages. Working out the evolutionary stages by which all these different combinations could have appeared is so difficult that it has long been known as "the Arthropod head problem". In 1960 R.E. Snodgrass even hoped it would not be solved, as trying to work out solutions was so much fun.

Exoskeleton

Arthropod exoskeletons are made of cuticle, a non-cellular material secreted by the epidermis. Their cuticles vary in the details of their structure, but generally consist of three main layers: the epicuticle, a thin outer waxy coat that moisture-proofs the other layers and gives them some protection; the exocuticle, which consists of chitin and chemically hardened proteins; and the endocuticle, which consists of chitin and unhardened proteins. The exocuticle and endocuticle together are known as the procuticle. Each body segment and limb section is encased in hardened cuticle. The joints between body segments and between limb sections are covered by flexible cuticle.

The exoskeletons of most aquatic crustaceans are biomineralized with calcium carbonate extracted from the water. Some terrestrial crustaceans have developed means of storing the mineral, since on land they cannot rely on a steady supply of dissolved calcium carbonate. Biomineralization generally affects the exocuticle and the outer part of the endocuticle. Two recent hypotheses about the evolution of biomineralization in arthropods and other groups of animals propose that it provides tougher defensive armor, and that it allows animals to grow larger and stronger by providing more rigid skeletons; and in either case a mineral-organic composite exoskeleton is cheaper to build than an all-organic one of comparable strength.

The cuticle can have setae (bristles) growing from special cells in the epidermis. Setae are as varied in form and function as appendages. For example, they are often used as sensors to detect air or water currents, or contact with objects; aquatic arthropods use feather-like setae to increase the surface area of swimming appendages and to filter food particles out of water; aquatic insects, which are air-breathers, use thick felt-like coats of setae to trap air, extending the time they can spend under water; heavy, rigid setae serve as defensive spines.

Although all arthropods use muscles attached to the inside of the exoskeleton to flex their limbs, some still use hydraulic pressure to extend them, a system inherited from their pre-arthropod ancestors; for example, all spiders extend their legs hydraulically and can generate pressures up to eight times their resting level.

Molting

The exoskeleton cannot stretch and thus restricts growth. Arthropods therefore replace their exoskeletons by molting, or shedding the old exoskeleton after growing a new one that is not yet hardened. Molting cycles run nearly continuously until an arthropod reaches full size.

In the initial phase of molting, the animal stops feeding and its epidermis releases molting fluid, a mixture of enzymes that digests the endocuticle and thus detaches the old cuticle. This phase begins when the epidermis has secreted a new epicuticle to protect it from the enzymes, and the epidermis secretes the new exocuticle while the old cuticle is detaching. When this stage is complete, the animal makes its body swell by taking in a large quantity of water or air, and this makes the old cuticle split along predefined weaknesses where the old exocuticle was thinnest. It commonly takes several minutes for the animal to struggle out of the old cuticle. At this point the new one is wrinkled and so soft that the animal cannot support itself and finds it very difficult to move, and the new endocuticle has not yet formed. The animal continues to pump itself up to stretch the new cuticle as much as possible, then hardens the new exocuticle and eliminates the excess air or water. By the end of this phase the new endocuticle has formed. Many arthropods then eat the discarded cuticle to reclaim its materials.

Because arthropods are unprotected and nearly immobilized until the new cuticle has hardened, they are in danger both of being trapped in the old cuticle and of being attacked by predators. Molting may be responsible for 80 to 90% of all arthropod deaths.

Internal organs



- = heart
- = gut
- = brain, nerve cord, ganglia
- = eye

Basic arthropod body structure

Arthropod bodies are also segmented internally, and the nervous, muscular, circulatory and excretory systems have repeated components. Arthropods come from a lineage of animals that have a coelom, a membrane-lined cavity between the gut and the body wall that accommodates the internal organs. The strong, segmented limbs of arthropods

eliminate the need for one of the coelom's main ancestral functions, as a hydrostatic skeleton, which muscles compress in order to change the animal's shape and thus enable it to move. Hence the coelom of the arthropod is reduced to small areas around the reproductive and excretory systems. Its place is largely taken by a hemocoel, a cavity that runs most of the length of the body and through which blood flows.

Arthropods have open circulatory systems, although most have a few short, open-ended arteries. In chelicerates and crustaceans, the blood carries oxygen to the tissues, while hexapods use a separate system of tracheae. Many crustaceans, but few chelicerates and tracheates, use respiratory pigments to assist oxygen transport. The most common respiratory pigment in arthropods is copper-based hemocyanin; this is used by many crustaceans and a few centipedes. A few crustaceans and insects use iron-based hemoglobin, the respiratory pigment used by vertebrates. As with other invertebrates and unlike among vertebrates, the respiratory pigments of those arthropods that have them are generally dissolved in the blood and rarely enclosed in corpuscles.

The heart is typically a muscular tube that runs just under the back and for most of the length of the hemocoel. It contracts in ripples that run from rear to front, pushing blood forwards. Elastic ligaments, or small muscles, connect the heart to the body wall and expand sections that are not being squeezed by the heart muscle. Along the heart run a series of paired ostia, non-return valves that allow blood to enter the heart but prevent it from leaving before it reaches the front.

Arthropods have a wide variety of respiratory systems. Small species often do not have any, since their high ratio of surface area to volume enables simple diffusion through the body surface to supply enough oxygen. Crustacea usually have gills that are modified appendages. Many arachnids have book lungs. Tracheae, systems of branching tunnels that run from the openings in the body walls, deliver oxygen directly to individual cells in many insects, myriapods and arachnids.

Living arthropods have paired main nerve cords running along their bodies below the gut, and in each segment the cords form a pair of ganglia from which sensory and motor nerves run to other parts of the segment. Although the pairs of ganglia in each segment often appear physically fused, they are connected by commissures (relatively large bundles of nerves), which give arthropod nervous systems a characteristic "ladder-like" appearance. The brain is in the head, encircling and mainly *above* the esophagus. It consists of the fused ganglia of the acron and one or two of the foremost segments that form the head – a total of three pairs of ganglia in most arthropods, but only two in chelicerates, which do not have antennae or the ganglion connected to them. The ganglia of other head segments are often close to the brain and function as part of it. In insects these other head ganglia combine into a pair of subesophageal ganglia, under and behind the esophagus. Spiders take this process a step further, as *all* the segmental ganglia are incorporated into the subesophageal ganglia, which occupy most of the space in the cephalothorax (front "super-segment").

There are two different types of arthropod excretory systems. In aquatic arthropods, the end-product of biochemical reactions that metabolise nitrogen is ammonia, which is so toxic that it needs to be diluted as much as possible with water. The ammonia is then eliminated via any permeable membrane, mainly through the gills. All crustaceans use this system, and its high consumption of water may be responsible for the relative lack of success of crustaceans as land animals. Various groups of terrestrial arthropods have independently developed a different system: the end-product of nitrogen metabolism is uric acid, which can be excreted as dry material; Malpighian tubules filter the uric acid and other nitrogenous waste out of the blood in the hemocoel, and dump these materials into the hindgut, from which they are expelled as feces. Most aquatic arthropods and some terrestrial ones also have organs called nephridia ("little kidneys"), which extract other wastes for excretion as urine.

Senses

The stiff cuticles of arthropods would block out information about the outside world, except that they are penetrated by many sensors or connections from sensors to the nervous system. In fact, arthropods have modified their cuticles into elaborate arrays of sensors. Various touch sensors, mostly setae, respond to different levels of force, from strong contact to very weak air currents. Chemical sensors provide equivalents of taste and smell, often by means of setae. Pressure sensors often take the form of membranes that function as eardrums, but are connected directly to nerves rather than to auditory ossicles. The antennae of most hexapods include sensor packages that monitor humidity, moisture and temperature.



Head of a wasp with three ocelli (centre), and compound eyes at the left and right

Most arthropods have sophisticated visual systems that include one or more usually both of compound eyes and pigment-cup ocelli ("little eyes"). In most cases ocelli are only capable of detecting the direction from which light is coming, using the shadow cast by the walls of the cup. However the main eyes of spiders are pigment-cup ocelli that are capable of forming images, and those of jumping spiders can rotate to track prey.

Compound eyes consist of fifteen to several thousand independent ommatidia, columns that are usually hexagonal in cross section. Each ommatidium is an independent sensor, with its own light-sensitive cells and often with its own lens and cornea. Compound eyes have a wide field of view, and can detect fast movement and, in some cases, the polarization of light. On the other hand the relatively large size of ommatidia makes the images rather coarse, and compound eyes are shorter-sighted than those of birds and mammals – although this is not a severe disadvantage, as objects and events within 20 centimetres (7.9 in) are most important to most arthropods. Several arthropods have color vision, and that of some insects has been studied in detail; for example, the ommatidia of bees contain receptors for both green and ultra-violet.

Most arthropods lack balance and acceleration sensors, and rely on their eyes to tell them which way is up. The self-righting behavior of cockroaches is triggered when pressure sensors on the underside of the feet report no pressure. However many malacostracan crustaceans have statocysts, which provide the same sort of information as the balance and motion sensors of the vertebrate inner ear.

The proprioceptors of arthropods, sensors that report the force exerted by muscles and the degree of bending in the body and joints, are well understood. However, little is known about what other internal sensors arthropods may have.

Reproduction and development



Compsobuthus wernerii female with young (white)

A few arthropods, such as barnacles, are hermaphroditic, that is, each can have the organs of both sexes. However, individuals of most species remain of one sex all their lives. A few species of insects and crustaceans can reproduce by parthenogenesis, for example, without mating, especially if conditions favor a "population explosion". However most arthropods rely on sexual reproduction, and parthenogenetic species often revert to sexual reproduction when conditions become less favorable. Aquatic arthropods may breed by external fertilization, as for example frogs also do, or by internal fertilization, where the ova remain in the female's body and the sperm must somehow be inserted. All known terrestrial arthropods use internal fertilization, as unprotected sperm and ova would not survive long in these environments. In a few cases the sperm transfer is direct from the male's penis to the female's oviduct, but it is more often indirect. Some crustaceans and spiders use modified appendages to transfer the sperm to the female. On the other hand, many male terrestrial arthropods produce spermatophores, waterproof packets of sperm, which the females take into their bodies. A few such species rely on females to find spermatophores that have already been deposited on the ground, but in most cases males only deposit spermatophores when complex courtship rituals look likely to be successful.



The nauplius larva of a prawn

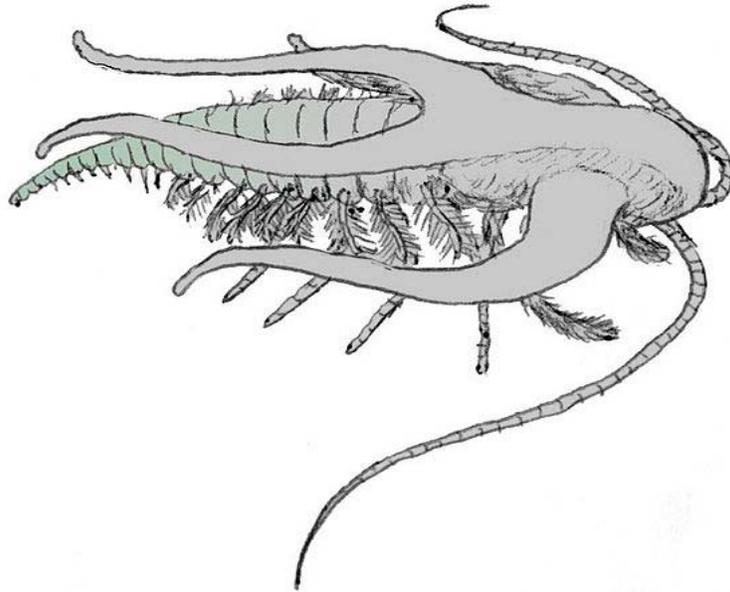
Most arthropods lay eggs, but scorpions are viviparous: they produce live young after the eggs have hatched inside the mother, and are noted for prolonged maternal care. Newly born arthropods have diverse forms, and insects alone cover the range of extremes. Some hatch as apparently miniature adults (direct development), and in some cases, such as silverfish, the hatchlings do not feed and may be helpless until after their first molt. Many insects hatch as grubs or caterpillars, which do not have segmented limbs or hardened cuticles, and metamorphose into adult forms by entering an inactive phase in which the larval tissues are broken down and re-used to build the adult body. Dragonfly larvae have the typical cuticles and jointed limbs of arthropods but are flightless water-breathers with extendable jaws. Crustaceans commonly hatch as tiny nauplius larvae that have only three segments and pairs of appendages.

Evolution

Last common ancestor

The last common ancestor of all arthropods is reconstructed as a modular organism with each module covered by its own sclerite (armor plate) and bearing a pair of biramous limbs. Whether the ancestral limb was uniramous or biramous is far from a settled debate, though. This Ur-arthropod had a ventral mouth, pre-oral antennae and dorsal eyes at the front of the body. It was a non-discriminatory sediment feeder, processing whatever sediment came its way for food.

Fossil record



Marrella, one of the puzzling arthropods from the Burgess Shale

It has been proposed that the Ediacaran animals *Parvancorina* and *Spriggina*, from around 555 Mya, were arthropods. Small arthropods with bivalve-like shells have been found in Early Cambrian fossil beds dating 541 to 539 million years ago in China. The earliest Cambrian trilobite fossils are about 530 million years old, but the class was already quite diverse and worldwide, suggesting that they had been around for quite some time. Re-examination in the 1970s of the Burgess Shale fossils from about 505 million years ago identified many arthropods, some of which could not be assigned to any of the well-known groups, and thus intensified the debate about the Cambrian explosion. A fossil of *Marrella* from the Burgess Shale has provided the earliest clear evidence of molting.

The earliest fossil crustaceans date from about 513 million years ago in the Cambrian, and fossil shrimp from about 500 million years ago apparently formed a tight-knit procession across the seabed. Crustacean fossils are common from the Ordovician period onwards. They have remained almost entirely aquatic, possibly because they never developed excretory systems that conserve water.

Arthropods provide the earliest identifiable fossils of land animals, from about 419 million years ago in the Late Silurian, and terrestrial tracks from about 450 million years ago appear to have been made by arthropods. Arthropods were well pre-adapted to colonize land, because their existing jointed exoskeletons provided protection against desiccation, support against gravity and a means of locomotion that was not dependent on water. Around the same time the aquatic, scorpion-like eurypterids became the largest ever arthropods, some as long as 2.5 metres (8.2 ft).

The oldest known arachnid is the trigonotarbid *Palaeotarbus jerami*, from about 420 million years ago in the Silurian period. *Attercopus fimbriunguis*, from 386 million years ago in the Devonian period, bears the earliest known silk-producing spigots, but its lack of spinnerets means it was not one of the true spiders, which first appear in the Late Carboniferous over 299 million years ago. The Jurassic and Cretaceous periods provide a large number of fossil spiders, including representatives of many modern families. Fossils of aquatic scorpions with gills appear in the Silurian and Devonian periods, and the earliest fossil of an air-breathing scorpion with book lungs dates from the Early Carboniferous period.

The oldest definitive insect fossil is the Devonian *Rhyniognatha hirsti*, dated at 396 to 407 million years ago, but its mandibles are of a type found only in winged insects, which suggests that the earliest insects appeared in the Silurian period. The Mazon Creek lagerstätten from the Late Carboniferous, about 300 million years ago, include about 200 species, some gigantic by modern standards, and indicate that insects had occupied their main modern ecological niches as herbivores, detritivores and insectivores. Social termites and ants first appear in the Early Cretaceous, and advanced social bees have been found in Late Cretaceous rocks but did not become abundant until the Mid Cenozoic.

Evolutionary family tree



The velvet worm (Onychophora) is closely related to arthropods

From the late 1950s to the late 1970s, Sidnie Manton and others argued that arthropods are polyphyletic, in other words, they do not share a common ancestor *that was itself an arthropod*. Instead, they proposed that three separate groups of "arthropods" evolved separately from common worm-like ancestors: the chelicerates, including spiders and scorpions; the crustaceans; and the uniramia, consisting of onychophorans, myriapods and hexapods. These arguments usually bypassed trilobites, as the evolutionary relationships of this class were unclear. Proponents of polyphyly argued the following: that the similarities between these groups are the results of convergent evolution, as natural consequences of having rigid, segmented exoskeletons; that the three groups use different chemical means of hardening the cuticle; that there were significant differences in the construction of their compound eyes; that it is hard to see how such different

configurations of segments and appendages in the head could have evolved from the same ancestor; and that crustaceans have biramous limbs with separate gill and leg branches, while the other two groups have uniramous limbs in which the single branch serves as a leg.

Further analysis and discoveries in the 1990s reversed this view, and led to acceptance that arthropods are monophyletic, in other words they do share a common ancestor *that was itself an arthropod*. For example Graham Budd's analyses of *Kerygmachela* in 1993 and of *Opabinia* in 1996 convinced him that these animals were similar to onychophorans and to various Early Cambrian "lobopods", and he presented an "evolutionary family tree" that showed these as "aunts" and "cousins" of all arthropods. These changes made the scope of the term "arthropod" unclear, and Claus Nielsen proposed that the wider group should be labelled "Panarthropoda" ("all the arthropods") while the animals with jointed limbs and hardened cuticles should be called "Euarthropoda" ("true arthropods").

A contrary view was presented in 2003, when Jan Bergström and Xian-Guang Hou argued that, if arthropods were a "sister-group" to any of the anomalocarids, they must have lost and then re-evolved features that were well-developed in the anomalocarids. The earliest known arthropods ate mud in order to extract food particles from it, and possessed variable numbers of segments with unspecialized appendages that functioned as both gills and legs. Anomalocarids were, by the standards of the time, huge and sophisticated predators with specialized mouths and grasping appendages, fixed numbers of segments some of which were specialized, tail fins, and gills that were very different from those of arthropods. This reasoning implies that *Parapeytoia*, which has legs and a backward-pointing mouth like that of the earliest arthropods, is a more credible closest relative of arthropods than is *Anomalocaris*. In 2006, they suggested that arthropods were more closely related to lobopods and tardigrades than to anomalocarids.

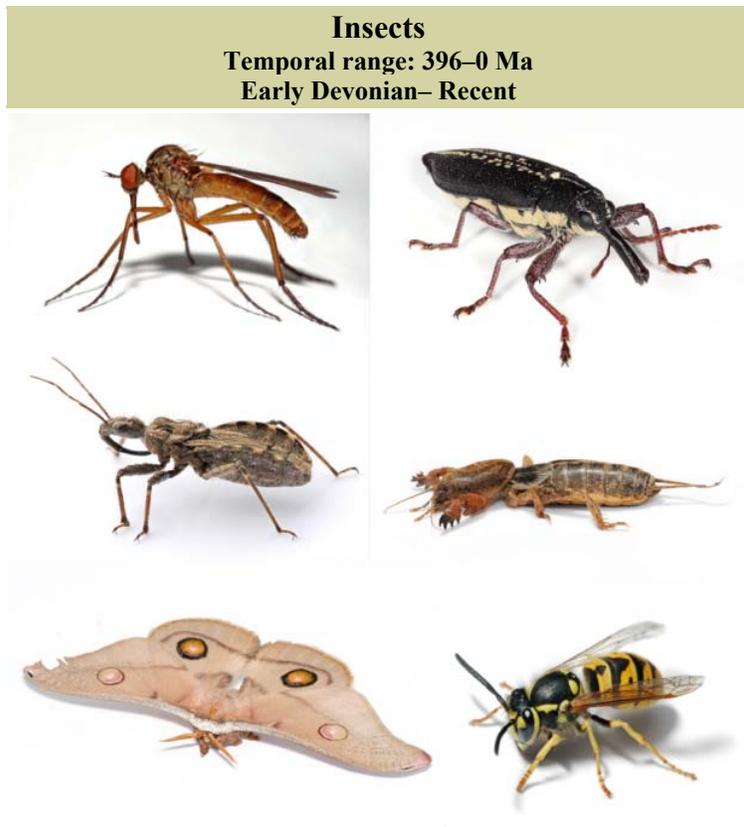
Higher up the "family tree", the Annelida have traditionally been considered the closest relatives of the Panarthropoda, since both groups have segmented bodies, and the combination of these groups was labelled Articulata. There had been competing proposals that arthropods were closely related to other groups such as nematodes, priapulids and tardigrades, but these remained minority views because it was difficult to specify in detail the relationships between these groups.

In the 1990s, molecular phylogenetic analyses of DNA sequences produced a coherent scheme showing arthropods as members of a superphylum labelled Ecdysozoa ("animals that molt"), which contained nematodes, priapulids and tardigrades but excluded annelids. This was backed up by studies of the anatomy and development of these animals, which showed that many of the features that supported the Articulata hypothesis showed significant differences between annelids and the earliest Panarthropods in their details, and some were hardly present at all in arthropods. This hypothesis groups annelids with molluscs and brachiopods in another superphylum, Lophotrochozoa.

If the Ecdysozoa hypothesis is correct, then segmentation of arthropods and annelids either has evolved convergently or has been inherited from a much older ancestor and subsequently lost in several other lineages, such as the non-arthropod members of the Ecdysozoa.

Chapter- 4

Insect



Clockwise from top left: dancefly (*Empis livida*), long-nosed weevil (*Rhinotia hemistictus*), mole cricket (*Gryllotalpa brachyptera*), German wasp (*Vespula germanica*), emperor gum moth (*Opodiphthera eucalypti*), assassin bug (Harpactorinae)

Scientific classification

Kingdom: Animalia
Phylum: Arthropoda
Subphylum: Hexapoda

Class: **Insecta**
Linnaeus, 1758

Subclasses

- Monocondylia (Archaeognatha)
- Dicondylia

Apterygota
Pterygota

Insects (from Latin *insectum*, a calque of Greek ἔντομον [*éntomon*], "cut into sections") are a class within the arthropods that have a chitinous exoskeleton, a three-part body (head, thorax, and abdomen), three pairs of jointed legs, compound eyes, and two antennae. They are among the most diverse group of animals on the planet and include more than a million described species and represent more than half of all known living organisms. The number of extant species is estimated at between six and ten million, and potentially represent over 90% of the differing metazoan life forms on Earth. Insects may be found in nearly all environments, although only a small number of species occur in the oceans, a habitat dominated by another arthropod group, the crustaceans.

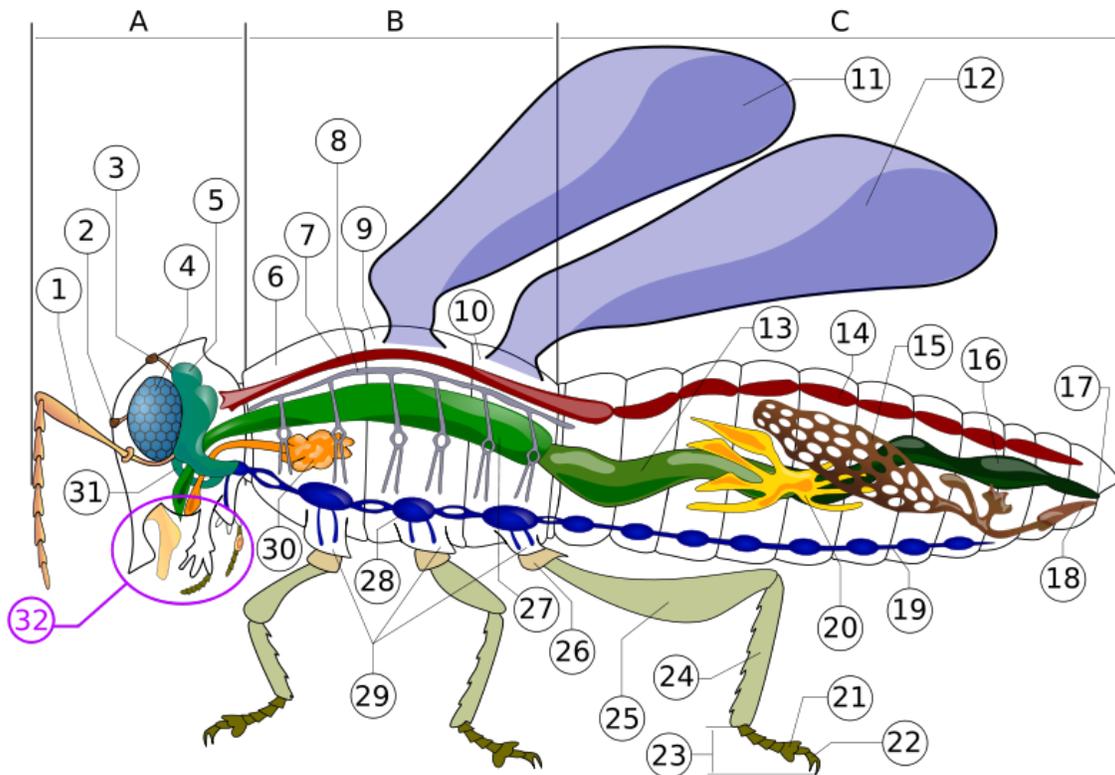
The life cycles of insects vary but most hatch from eggs. Insect growth is constrained by the inelastic exoskeleton and development involves a series of molts. The immature stages can differ from the adults in structure, habit and habitat and can include a passive pupal stage in those groups that undergo complete metamorphosis. Insects that undergo incomplete metamorphosis lack a pupal stage and adults develop through a series of nymphal stages. The higher level relationship of the hexapoda is unclear. Fossilized insects of enormous size have been found from the Paleozoic Era, including giant dragonflies with wingspans of 55 to 70 cm (22–28 in). The most diverse insect groups appear to have coevolved with flowering plants.

Insects typically move about by walking, flying or occasionally swimming. Because it allows for rapid yet stable movement, many insects adopt a tripedal gait in which they walk with their legs touching the ground in alternating triangles. Insects are the only invertebrates to have evolved flight. Many insects spend at least part of their life underwater, with larval adaptations that include gills and some adult insects are aquatic and have adaptations for swimming. Some species, like water striders, are capable of walking on the surface of water.

Insects are mostly solitary, but some insects, such as certain bees, ants, and termites are social and live in large, well-organized colonies. Some insects, like earwigs, show maternal care, guarding their eggs and young. Insects can communicate with each other in a variety of ways. Male moths can sense the pheromones of female moths over distances of many kilometers. Other species communicate with sounds: crickets stridulate, or rub their wings together, to attract a mate and repel other males. Lampyridae in the beetle order Coleoptera communicate with light.

Humans regard certain insects as pests and attempt to control them using insecticides and a host of other techniques. Some insects damage crops by feeding on sap, leaves or fruits, a few bite humans and livestock, alive and dead, to feed on blood and some are capable of transmitting diseases to humans, pets and livestock. Many other insects are considered ecologically beneficial and a few provide direct economic benefit. Silkworms and bees have been domesticated by humans for the production of silk and honey, respectively.

Morphology and physiology



Insect morphology

A- Head **B-** Thorax **C-** Abdomen

1. antenna
2. ocelli (lower)
3. ocelli (upper)
4. compound eye
5. brain (cerebral ganglia)
6. prothorax
7. dorsal blood vessel
8. tracheal tubes (trunk with spiracle)
9. mesothorax
10. metathorax
11. forewing
12. hindwing
13. mid-gut (stomach)

14. dorsal tube (Heart)
15. ovary
16. hind-gut (intestine, rectum & anus)
17. anus
18. oviduct
19. nerve chord (abdominal ganglia)
20. Malpighian tubes
21. tarsal pads
22. claws
23. tarsus
24. tibia
25. femur
26. trochanter
27. fore-gut (crop, gizzard)
28. thoracic ganglion
29. coxa
30. salivary gland
31. subesophageal ganglion
32. mouthparts

General body plan

Insects have segmented bodies supported by an exoskeleton, a hard outer covering made mostly of chitin. The segments of the body are organized into three distinctive but interconnected units, or tagmata: a head, a thorax, and an abdomen. The head supports a pair of sensory antennae, a pair of compound eyes, and, if present, one to three simple eyes (or ocelli) and three sets of variously modified appendages that form the mouthparts. The thorax has six segmented legs—one pair each for the prothorax, mesothorax and the metathorax segments making up the thorax—and, if present in the species, two or four wings. The abdomen consists of eleven segments, though in a few species of insects these segments may be fused together or reduced in size. The abdomen also contains most of the digestive, respiratory, excretory and reproductive internal structures. There is considerable variation and many adaptations in the body parts of insects especially wings, legs, antenna, mouth-parts etc.

Exoskeleton

Insect outer skeleton, the cuticle, is made up of two layers: the epicuticle, which is a thin and waxy water resistant outer layer and contains no chitin, and a lower layer called the procuticle. The procuticle is chitinous and much thicker than the epicuticle and has two layers: an outer layer known as the exocuticle and an inner layer known as the endocuticle. The tough and flexible endocuticle is built from numerous layers of fibrous chitin and proteins, criss-crossing each others in a sandwich pattern, while the exocuticle is rigid and hardened. The exocuticle is greatly reduced in many soft-bodied insects (e.g., caterpillars), especially during their larval stages.

Insects are the only invertebrates to have developed active flight capability, and this has played an important role in their success. These muscles are able to contract multiple times for each single nerve impulse, allowing the wings to beat faster than would ordinarily be possible. Having their muscles attached to their exoskeletons is more efficient and allows more muscle connections; crustaceans also use the same method, though all spiders use hydraulic pressure to extend their legs, a system inherited from their pre-arthropod ancestors. Unlike insects, though, most aquatic crustaceans are biomineralized with calcium carbonate extracted from the water.

Nervous system

The nervous system of an insect can be divided into a brain and a ventral nerve cord. The head capsule is made up of six fused segments, each with a pair of ganglia, or a cluster of nerve cells outside of the brain. The first three pairs of ganglia are fused into the brain, while the three following pairs are fused into a structure of three pairs of ganglia under the insect's esophagus, called the subesophageal ganglion.

The thoracic segments have one ganglion on each side, which are connected into a pair, one pair per segment. This arrangement is also seen in the abdomen but only in the first eight segments. Many species of insects have reduced numbers of ganglia due to fusion or reduction. Some cockroaches have just six ganglia in the abdomen, whereas the wasp *Vespa crabro* has only two in the thorax and three in the abdomen. Some insects, like the house fly *Musca domestica*, have all the body ganglia fused into a single large thoracic ganglion.

At least a few insects have nociceptors, cells that detect and transmit sensations of pain. This was discovered in 2003 by studying the variation in reactions of larvae of the common fruitfly *Drosophila* to the touch of a heated probe and an unheated one. The larvae reacted to the touch of the heated probe with a stereotypical rolling behavior that was not exhibited when the larvae were touched by the unheated probe. Although nociception has been demonstrated in insects, there is not a consensus that insects feel pain consciously.

Digestive system

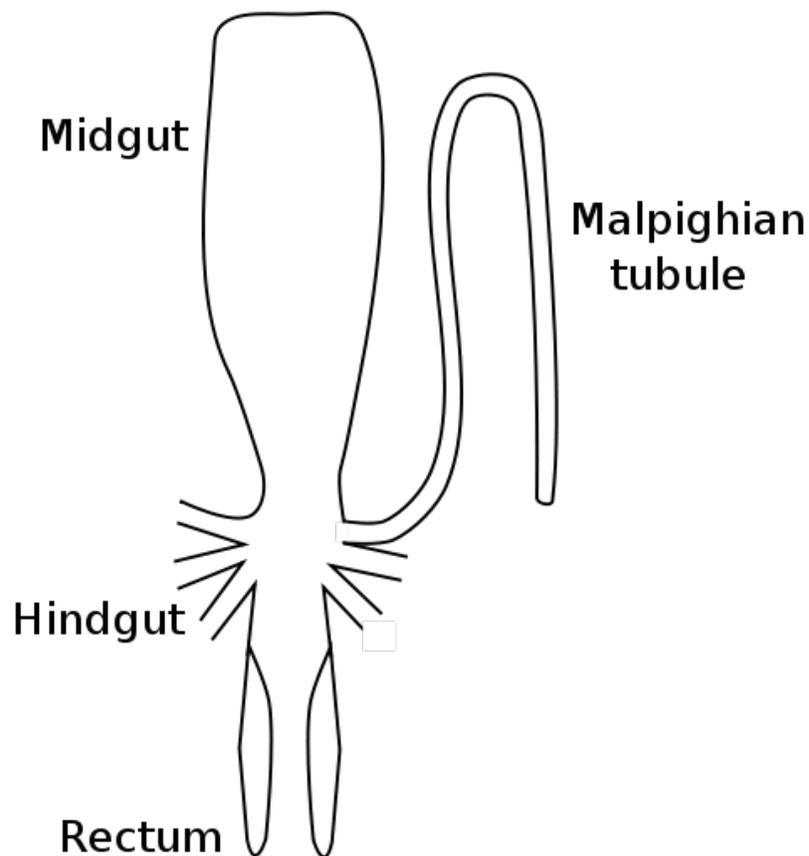
An insect uses its digestive system to extract nutrients and other substances from the food it consumes. Most of this food is ingested in the form of macromolecules and other complex substances like proteins, polysaccharides, fats, and nucleic acids. These macromolecules must be broken down by catabolic reactions into smaller molecules like amino acids and simple sugars before being used by cells of the body for energy, growth, or reproduction. This break-down process is known as digestion.

The main structure of an insect's digestive system is a long enclosed tube called the alimentary canal, which runs lengthwise through the body. The alimentary canal directs food unidirectionally from the mouth to the anus. It has three sections, each of which performs a different process of digestion. In addition to the alimentary canal, insects also

have paired salivary glands and salivary reservoirs. These structures usually reside in the thorax, adjacent to the foregut.

The salivary glands (element 30 in numbered diagram) in an insect's mouth produce saliva. The salivary ducts lead from the glands to the reservoirs and then forward through the head to an opening called the salivarium, located behind the hypopharynx. By moving its mouthparts (element 32 in numbered diagram) the insect can mix its food with saliva. The mixture of saliva and food then travels through the salivary tubes into the mouth, where it begins to break down. Some insects, like flies, have extra-oral digestion. Insects using extra-oral digestion expel digestive enzymes onto their food to break it down. This strategy allows insects to extract a significant proportion of the available nutrients from the food source. The gut is where almost all of insects' digestion takes place. It can be divided into the foregut, midgut and hindgut.

Foregut



Stylized diagram of insect digestive tract showing malpighian tubule, from an insect of the order Orthoptera.

The first section of the alimentary canal is the foregut (element 27 in numbered diagram), or stomodaeum. The foregut is lined with a cuticular lining made of chitin and proteins as protection from tough food. The foregut includes the buccal cavity (mouth), pharynx, esophagus, and Crop and proventriculus (any part may be highly modified) which both store food and signify when to continue passing onward to the midgut. Here, digestion starts as partially chewed food is broken down by saliva from the salivary glands. As the salivary glands produce fluid and carbohydrate-digesting enzymes (mostly amylases), strong muscles in the pharynx pump fluid into the buccal cavity, lubricating the food like the salivarium does, and helping blood feeders, and xylem and phloem feeders.

From there, the pharynx passes food to the esophagus, which could be just a simple tube passing it on to the crop and proventriculus, and then on ward to the midgut, as in most insects. Alternately, the foregut may expand into a very enlarged crop and proventriculus, or the crop could just be a diverticulum, or fluid filled structure, as in some Diptera species.



Bee defecating. Note the contraction of the anus which provides internal pressure.

Midgut

Once food leaves the crop, it passes to the midgut (element 13 in numbered diagram), also known as the mesenteron, where the majority of digestion takes place. Microscopic projections from the midgut wall, called microvilli, increase the surface area of the wall and allow more nutrients to be absorbed; they tend to be close to the origin of the midgut. In some insects, the role of the microvilli and where they are located may vary. For example, specialized microvilli producing digestive enzymes may more likely be near the end of the midgut, and absorption near the origin or beginning of the midgut.

Hindgut

In the hindgut (element 16 in numbered diagram), or proctodaeum, undigested food particles are joined by uric acid to form fecal pellets. The rectum absorbs 90% of the water in these fecal pellets, and the dry pellet is then eliminated through the anus (element 17), completing the process of digestion. The uric acid is formed using hemolymph waste products diffused from the Malpighian tubules (element 20). It is then emptied directly into the alimentary canal, at the junction between the midgut and hindgut. The number of Malpighian tubules possessed by a given insect varies between species, ranging from only two tubules in some insects to over 100 tubules in others.

Respiration and circulation

Insect respiration is accomplished without lungs. Instead, the insect respiratory system uses a system of internal tubes and sacs through which gases either diffuse or are actively pumped, delivering oxygen directly to tissues that need it via their trachea (element 8 in numbered diagram). Since oxygen is delivered directly, the circulatory system is not used to carry oxygen, and is therefore greatly reduced. The insect circulatory system has no veins or arteries, and instead consists of little more than a single, perforated dorsal tube which pulses peristaltically. Toward the thorax, the dorsal tube (element 14) divides into chambers and acts like the insect's heart. The opposite end of the dorsal tube is like the aorta of the insect circulating the hemolymph, arthropods' fluid analog of blood, inside the body cavity. Air is taken in through openings on the sides of the abdomen called spiracles.

There are many different patterns of gas exchange demonstrated by different groups of insects. Gas exchange patterns in insects can range from continuous and diffusive ventilation, to discontinuous gas exchange. During continuous gas exchange, oxygen is taken in and carbon dioxide is released in a continuous cycle. In discontinuous gas exchange, however, the insect takes in oxygen while it is active and small amounts of carbon dioxide are released when the insect is at rest. Diffusive ventilation is simply a form of continuous gas exchange that occurs by diffusion rather than physically taking in the oxygen. Some species of insect that are submerged also have adaptations to aid in respiration. As larvae, many insects have gills that can extract oxygen dissolved in water, while others need to rise to the water surface to replenish air supplies which may be held or trapped in special structures.

Reproduction and development



A pair of *Simosyrphus grandicornis* hoverflies mating in flight.

The majority of insects hatch from eggs. The fertilization and development takes place inside the egg, enclosed by a shell (chorion). Some species of insects, like the cockroach *Blattella germanica*, as well as juvenile aphids and tsetse flies, are ovoviviparous. The eggs of ovoviviparous animals develop entirely inside the female, and then hatch immediately upon being laid. Some other species, such as those in the genus of cockroaches known as *Diploptera*, are viviparous, and thus gestate inside the mother and are born alive. Some insects, like parasitic wasps, show polyembryony, where a single fertilized egg divides into many and in some cases thousands of separate embryos.



The different forms of the male (top) and female (bottom) tussock moth *Orgyia recens* is an example of sexual dimorphism in insects.

Other developmental and reproductive variations include haplodiploidy, polymorphism, paedomorphosis or peramorphosis, sexual dimorphism, parthenogenesis and more rarely hermaphroditism. In haplodiploidy, which is a type of sex-determination system, the offspring's sex is determined by the number of sets of chromosomes an individual receives. This system is typical in bees and wasps. Polymorphism is the where a species may have different *morphs* or *forms*, as in the oblong winged katydid, which has four different varieties: green, pink, and yellow or tan. Some insects may retain phenotypes that are normally only seen in juveniles; this is called paedomorphosis. In peramorphosis, an opposite sort of phenomenon, insects take on previously unseen traits after they have matured into adults. Many insects display sexual dimorphism, in which males and females have notably different appearances, such as the moth *Orgyia recens* as an exemplar of sexual dimorphism in insects.

Some insects use parthenogenesis, a process in which the female can reproduce and give birth without having the eggs fertilized by a male. Many aphids undergo a form of parthenogenesis, called cyclical parthenogenesis, in which they alternate between one or many generations of asexual and sexual reproduction. In summer, aphids are generally female and parthenogenetic; in the autumn, males may be produced for sexual reproduction. Other insects produced by parthenogenesis are bees, wasps, and ants, in which they spawn males. However, overall, most individuals are female, which are produced by fertilization. The males are haploid and the females are diploid. More rarely, some insects display hermaphroditism, in which a given individual has both male and female reproductive organs.

Insect life-histories show adaptations to withstand cold and dry conditions. Some temperate region insects are capable of activity during winter, while some others migrate to a warmer climate or go into a state of torpor. Still other insects have evolved mechanisms of diapause that allow eggs or pupae to survive these conditions.

Metamorphosis

Metamorphosis in insects is the biological process of development all insects must undergo. There are two forms of metamorphosis: incomplete metamorphosis and complete metamorphosis.

Incomplete metamorphosis

Insects that show hemimetabolism, or incomplete metamorphosis, change gradually by undergoing a series of molts. An insect molts when it outgrows its exoskeleton, which does not stretch and would otherwise restrict the insect's growth. The molting process begins as the insect's epidermis secretes a new epicuticle. After this new epicuticle is secreted, the epidermis releases a mixture of enzymes that digests the endocuticle and thus detaches the old cuticle. When this stage is complete, the insect makes its body swell by taking in a large quantity of water or air, which makes the old cuticle split along predefined weaknesses where the old exocuticle was thinnest. Other arthropods have a much different process and only molt; though must accommodate for the difference in exoskeleton structure and make up with other enzymes.

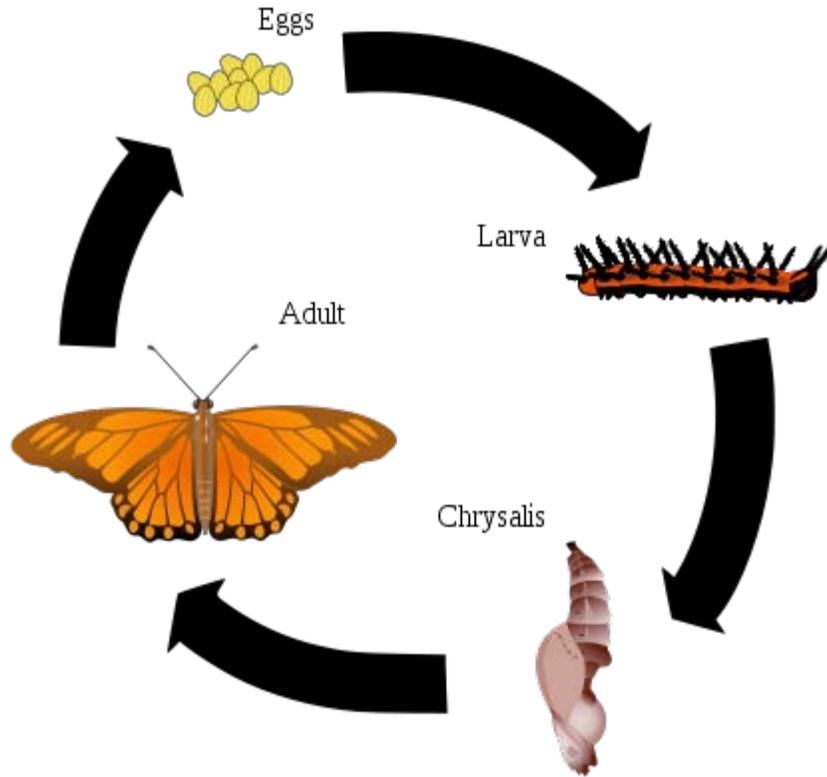
Immature insects that go through incomplete metamorphosis are called nymphs or in the case of dragonflies and damselflies as naiads. Nymphs are similar in form to the adult except for the presence of wings, which are not developed until adulthood. With each molt, nymphs grow larger and become more similar in appearance to adult insects.



Like other insects that develop through incomplete metamorphosis, this Southern Hawker dragonfly molts its exoskeleton (shown above) several times during its pre-adult life.

Complete metamorphosis

Gulf Fritillary Life Cycle



Gulf Fritillary life cycle, an example of holometabolism.

Holometabolism, or complete metamorphosis, is where the insect changes all in four stages, an egg or embryo, a larva, a pupa, and the adult or imago. In these species, egg hatches to produce a larva, which is generally worm-like in form. This worm-like form can be one of several varieties: eruciform (caterpillar-like), scarabaeiform (grub-like), campodeiform (elongated, flattened, and active), elateriform (wireworm-like) or vermiform (maggot-like). The larva grows and eventually becomes a pupa, a stage marked by reduced movement and often sealed within a cocoon. There are three types of pupae: obtect, exarate or coarctate. Obtect pupae are compact, with the legs and other appendages enclosed. Exarate pupae have their legs and other appendages free and extended. Coarctate pupae develop inside the larval skin. Insects undergo considerable change in form during the pupal stage, and emerge as adults. Butterflies are a well known example of an insects that undergo complete metamorphosis, although most insects use this life cycle. Some insects have evolved this system to hypermetamorphosis.

Some of the oldest and most successful insect groups, such Endopterygota, use a system of complete metamorphosis. Strangely though, complete metamorphosis is unique to

certain insect orders, like Diptera, Lepidoptera, and Hymenoptera, and no other arthropods undergo it, but incomplete metamorphosis.

Senses and communication

Many insects possess very sensitive and/or specialized organs of perception. Some insects such as bees can perceive ultraviolet wavelengths, or detect polarized light, while the antennae of male moths can detect the pheromones of female moths over distances of many kilometers. There is a pronounced tendency for there to be a trade-off between visual acuity and chemical or tactile acuity, such that most insects with well-developed eyes have reduced or simple antennae, and vice-versa. There are a variety of different mechanisms by which insects perceive sound, while the patterns are not universal, insects can generally hear sound if they can produce it. Different insect species can have varying hearing, though most insects can hear only a narrow range of frequencies related to the frequency of the sounds they can produce. Mosquitoes have been found to hear up to 2 MHz., and some grasshoppers can hear up to 50 MHz. Certain predatory and parasitic insects can detect the characteristic sounds made by their prey or hosts, respectively. For instance, some nocturnal moths can perceive the ultrasonic emissions of bats, which helps them avoid predation. Insects that feed on blood have special sensory structures that can detect infrared emissions, and use them to home in on their hosts.

Some insects display a rudimentary sense of numbers, such as the solitary wasps that prey upon a single species. The mother wasp lays her eggs in individual cells and provides each egg with a number of live caterpillars on which the young feed when hatched. Some species of wasp always provide five, others twelve, and others as high as twenty-four caterpillars per cell. The number of caterpillars is different among species, but always the same for each sex of larva. The male solitary wasp in the genus *Eumenes* is smaller than the female, so the mother of one species supplies him with only five caterpillars; the larger female receives ten caterpillars in her cell.

Light production and vision



Insects have compound eyes and two antennae.

A few insects, such as members of the families Poduridae and Onychiuridae (Collembola), Mycetophilidae (Diptera), and the beetle families Lampyridae, Phengodidae, Elateridae and Staphylinidae are bioluminescent. The most familiar group are the fireflies, beetles of the family Lampyridae. Some species are able to control this light generation to produce flashes. The function varies with some species using them to attract mates, while others use them to lure prey. Cave dwelling larvae of *Arachnocampa* (Mycetophilidae, Fungus gnats) glow to lure small flying insects into sticky strands of silk. Some fireflies of the genus *Photuris* mimic the flashing of female *Photinus* species to attract males of that species, which are then captured and devoured. The colors of

emitted light vary from dull blue (*Orfelia fultoni*, Mycetophilidae) to the familiar greens and the rare reds (*Phrixothrix tiemanni*, Phengodidae).

Most insects, except some species of cave dwelling crickets, are able to perceive light and dark. Many species have acute vision capable of detecting minute movements. The eyes include simple eyes or ocelli as well as compound eyes of varying sizes. Many species are able to detect light in the infrared, ultraviolet and the visible light wavelengths. Color vision has been demonstrated in many species and phylogenetic analysis suggests that UV-green-blue trichromacy existed from at least the Devonian period between 416 and 359 million years ago.

Sound production and hearing

Insects were the earliest organisms to produce and sense sounds. Insects make sounds mostly by mechanical action of appendages. In grasshoppers and crickets, this is achieved by stridulation. Cicadas make the loudest sounds among the insects by producing and amplifying sounds with special modifications to their body and musculature. The African cicada *Brevisana brevis* has been measured at 106.7 decibels at a distance of 50 cm (20 in). Some insects, such as the hawk moths and Hedylid butterflies, can hear ultrasound and take evasive action when they sense that they have been detected by bats. Some moths produce ultrasonic clicks that were once thought to have a role in jamming bat echolocation. The ultrasonic clicks were subsequently found to be produced mostly by unpalatable moths to warn bats, just as warning colorations are used against predators that hunt by sight. Some otherwise palatable moths have evolved to mimic these calls.

Very low sounds are also produced in various species of Coleoptera, Hymenoptera, Lepidoptera, Mantodea, and Neuroptera. These low sounds are simply the sounds made by the insect's movement. Through microscopic stridulatory structures located on the insect's muscles and joints, the normal sounds of the insect moving are amplified and can be used to warn or communicate with other insects. Most sound-making insects also have tympanal organs that can perceive airborne sounds. Some species in Hemiptera, such as the corixids (water boatmen), are known to communicate via underwater sounds. Most insects are also able to sense vibrations transmitted through surfaces. For example, an insect is caught in a spider web and struggles to escape. The vibrations it produces are sensed by the spider, who is alerted to its presence. Through these vibrations, the spider can tell where on the web the insect is located, as well as how big it is.

Communication using surface-borne vibrational signals is more widespread among insects because of size constraints in producing air-borne sounds. Insects cannot effectively produce low-frequency sounds, and high-frequency sounds tend to disperse more in a dense environment (such as foliage), so insects living in such environments communicate primarily using substrate-borne vibrations. The mechanisms of production of vibrational signals are just as diverse as those for producing sound in insects.

Some species use vibrations for communicating within members of the same species, such as to attract mates as in the songs of the shield bug *Nezara viridula*. Vibrations can

also be used to communicate between entirely different species; lycaenid (gossamer-winged butterfly) caterpillars which are myrmecophilous (living in a mutualistic association with ants) communicate with ants in this way. The Madagascar hissing cockroach has the ability to press air through its spiracles to make a hissing noise as a sign of aggression; the Death's-head Hawkmoth makes a squeaking noise by forcing air out of their pharynx when agitated, which may also reduce aggressive worker honey bee behavior when the two are in close proximity.

Chemical communication

In addition to the use of sound for communication, a wide range of insects have evolved chemical means for communication. These chemicals, termed semiochemicals, are often derived from plant metabolites include those meant to attract, repel and provide other kinds of information. Pheromones, a type of semiochemical, are used for attracting mates of the opposite sex, for aggregating conspecific individuals of both sexes, for deterring other individuals from approaching, to mark a trail, and to trigger aggression in nearby individuals. Allomonea benefit their producer by the effect they have upon the receiver. Kairomones benefit their receiver instead of their producer. Synomones benefit the producer and the receiver. While some chemicals are targeted at individuals of the same species, others are used for communication across species. The use of scents is especially well known to have developed in social insects.

Chapter- 5

Mollusca

Mollusca

Temporal range: Cambrian–Recent



Tonicella lineata, a polyplacophoran or chiton, anterior end towards the right

Scientific classification

Kingdom:	Animalia
Superphylum:	Lophotrochozoa
Phylum:	Mollusca Linnaeus, 1758

Diversity

85,000 recognized living species

The **Mollusca**, common name **molluscs** or **mollusks**, is a large phylum of invertebrate animals. There are around 85,000 recognized extant species of molluscs. This is the largest marine phylum, comprising about 23% of all the named marine organisms. Numerous molluscs also live in freshwater and terrestrial habitats. Molluscs are highly diverse, not only in size and in anatomical structure, but also in behaviour and in habitat.

The phylum Mollusca is typically divided into nine or ten taxonomic classes, of which two are extinct. The gastropods (snails and slugs) include by far the most classified species, accounting for 80% of the total. Cephalopod molluscs such as squid, cuttlefish and octopus are among the most neurologically advanced invertebrates. Either the giant squid or the colossal squid is the largest known species of animal without a backbone.

The two most universal features of the body structure of molluscs are a mantle with a significant cavity used for breathing and excretion, and the organization of the nervous system. Because of the great range of anatomical diversity, many textbooks base their descriptions on a hypothetical "generalized mollusc", with features common to many but not all classes within the Mollusca.

There is good evidence for the appearance of gastropods, cephalopods and bivalves in the Cambrian period 542 to 488.3 million years ago. However, the evolutionary history both of the emergence of molluscs from the ancestral group Lophotrochozoa, and of their diversification into the well-known living and fossil forms, is still vigorously debated. The most abundant metallic element in molluscs is calcium.

Molluscs have for many centuries been the source of important luxury goods, notably pearls, mother of pearl, Tyrian purple dye, and sea silk. Their shells have also been used as money in some pre-industrial societies.

There is a risk of food poisoning from toxins that accumulate in molluscs under certain conditions, and many countries have regulations that aim to minimize this risk. Blue-ringed octopus bites are often fatal, and the bite of *Octopus rubescens* can cause necrosis that lasts longer than one month if untreated, and headaches and weakness persisting for up to a week even if treated. Stings from a few species of large tropical cone shells can also kill. However, the sophisticated venoms of these cone snails have become important tools in neurological research and show promise as sources of new medications.

Schistosomiasis (also known as bilharzia, bilharziosis or snail fever) is transmitted to humans via water snail hosts, and affects about 200 million people. A few species of snails and slugs are serious agricultural pests, and in addition, accidental or deliberate introduction of various snail species into new territory has resulted in serious damage to some natural ecosystems.

Taxonomy

The phylum Mollusca is monophyletic and is typically divided into nine or ten taxonomic classes, of which two are extinct. The gastropods (snails and slugs) include by far the most classified species, accounting for 80% of the total. Cephalopod molluscs such as squid, cuttlefish and octopus are among the most neurologically advanced invertebrates. Either the giant squid or the colossal squid is the largest known species of animal without a backbone.

Opinions vary about the number of classes of molluscs—for example the table below shows eight living classes, and two extinct ones. However some authors combine the Caudofoveata and solenogasters into one class, the Aplacophora. Two of the commonly recognized classes are known only from fossils

Synonymy has been a great problem. The phylum Mollusca is certainly the marine group where the number of names, given in the last 250 years, and number of valid names of species are most at odds with each other. The great number of scientific journals and publications, most of which can only be consulted on payment, makes it difficult for the taxonomist to know whether or not a newly described species has actually been described before in the relevant literature. This causes many synonymies to remain unrecognized for decades. It is currently believed that synonyms represent at most 10-20% of the 1,635 new marine species (many of which are mollusks) that are on average being described each year.

Class	Major organisms	Described living species	Distribution
Caudofoveata	worm-like organisms	120	seabed 200–3,000 metres (660–9,800 ft)
Aplacophora	solenogasters, worm-like organisms	200	seabed 200–3,000 metres (660–9,800 ft)
Polyplacophora	chitons	1,000	rocky tidal zone and seabed
Monoplacophora	An ancient lineage of molluscs with cap-like shells	31	seabed 1,800–7,000 metres (5,900–23,000 ft); one species 200 metres (660 ft)
Gastropoda	All the snails and slugs including abalone, limpets, conch, nudibranchs, sea hares, sea butterfly	70,000	marine, freshwater, land
Cephalopoda	squid, octopus, cuttlefish, nautilus	900	marine
Bivalvia	clams, oysters, scallops, geoducks, mussels	20,000	marine, freshwater
Scaphopoda	tusk shells	500	marine 6–

			7,000 metres (20–23,000 ft)
Rostroconchia †	fossils; probable ancestors of bivalves	extinct	marine
Helcionelloida †	fossils; snail-like organisms such as <i>Latouchella</i>	extinct	marine

Distinguishing features

The two most universal features of the body structure of molluscs are a mantle with a significant cavity used for breathing and excretion, and the organization of the nervous system. Because of the great range of anatomical diversity, many textbooks base their descriptions on a hypothetical "generalized mollusc", with features common to many but not all classes within the Mollusca.

Diversity



About 80% of all known mollusc species are gastropods (snails and slugs), including the cowry (a sea snail) pictured here.

Estimates of accepted described living species of molluscs vary from 50,000 to a maximum of 120,000 species. In 2009 Chapman estimated the number of described living species at 85,000. Haszprunar in 2001 estimated about 93,000 named species, which include 23% of all named marine organisms. Molluscs are second only to

arthropods in numbers of living animal species—far behind the arthropods' 1,113,000 but well ahead of chordates' 52,000. It has been estimated that there are about 200,000 living species in total, and 70,000 fossil species, although the total number of mollusc species that ever existed, whether or not preserved, must be many times greater than the number alive today.

Molluscs have more varied forms than any other animal phylum. They include snails, slugs and other gastropods; clams and other bivalves; squids and other cephalopods; and other lesser-known but similarly distinctive sub-groups. The majority of species still live in the oceans, from the seashores to the abyssal zone, but some form a significant part of the freshwater fauna and the terrestrial ecosystems. Molluscs are extremely diverse in tropical and temperate regions but can be found at all latitudes. About 80% of all known mollusc species are gastropods. Cephalopoda such as squid, cuttlefish and octopus are among the neurologically most advanced of all invertebrates. The giant squid, which until recently had not been observed alive in its adult form, is one of the largest invertebrates. However a recently caught specimen of the colossal squid, 10 metres (33 ft) long and weighing 500 kilograms (0.49 LT; 0.55 ST), may have overtaken it.

Freshwater and terrestrial molluscs appear exceptionally vulnerable to extinction. Estimates of the numbers of non-marine molluscs vary widely, partly because many regions have not been thoroughly surveyed. There is also a shortage of specialists who can identify all the animals in any one area to species. However, in 2004 the IUCN Red List of Threatened Species included nearly 2,000 endangered non-marine molluscs. For comparison, the great majority of molluscs species are marine but only 41 of these appeared on the 2004 Red List. 42% of recorded extinctions since the year 1500 are of molluscs, almost entirely non-marine species.

Definition

The words *mollusc* and mollusk are both derived from the French *mollusque*, which originated from the Latin *molluscus*, from *mollis*, soft. *Molluscus* was itself an adaptation of Aristotle's τὰ μαλάκια, "the soft things", which he applied to cuttlefish. The scientific study of molluscs is known as malacology.

Molluscs have developed such a varied range of body structures that it is difficult to find synapomorphies (defining characteristics) that apply to all modern groups. The most general characteristic of molluscs is that they are unsegmented and bilaterally symmetrical. The following are present in all modern molluscs:

- The dorsal part of the body wall is a mantle (or pallium) which secretes calcareous spicules, plates or shells. It overlaps the body with enough spare room to form a mantle cavity.
- The anus and genitals open into the mantle cavity.
- There are two pairs of main nerve cords.

Other characteristics that commonly appear in textbooks have significant exceptions:

A "generalized mollusc"

Because of the enormous variations between groups of molluscs, many text books start the subject by describing a "generalized mollusc", which some suggest *may* resemble very early molluscs and which is rather similar to modern monoplacophorans.

The generalized mollusc has a single, "limpet-like" shell on top. The shell is secreted by a mantle that covers the upper surface. The underside consists of a single muscular "foot". The visceral mass, or visceropallium, is the soft, non-muscular metabolic region of the mollusc. It contains the body organs.

Mantle and mantle cavity

The mantle cavity is a fold in the mantle that encloses a significant amount of space. It is lined with epidermis. It is exposed, according to habitat, to sea, fresh water or air. The cavity was at the rear in the earliest molluscs but its position now varies from group to group. The anus, a pair of osphradia (chemical sensors) in the incoming "lane", the hindmost pair of gills and the exit openings of the nephridia ("kidneys") and gonads (reproductive organs) are in the mantle cavity. The whole soft body of bivalves lies within an enlarged mantle cavity.

Shell

The mantle edge secretes a shell (secondarily absent in a number of taxonomic groups, such as the nudibranchs) that consists of mainly chitin and conchiolin (a protein) hardened with calcium carbonate), except that the outermost layer in almost all cases is all conchiolin. Molluscs never use phosphate to construct their hard parts, with the questionable exception of *Cobcrephora*. While most mollusc shells are composed mainly of aragonite, those gastropods that lay eggs with a hard shell use calcite (sometimes with traces of aragonite) to construct the eggshells.

The shell consists of three layers : the outer layer (the periostracum) made of organic matter, a middle layer made of columnar calcite and an inner layer consisting of laminated calcite, that is often nacreous.

Foot

The underside consists of a muscular foot, which has adapted to different purposes in different classes. The foot carries a pair of statocysts, which act as balance sensors. In gastropods, it secretes mucus as a lubricant to aid movement. In forms that have only a top shell, such as limpets, the foot acts as a sucker attaching the animal to a hard surface, and the vertical muscles clamp the shell down over it; in other molluscs, the vertical muscles pull the foot and other exposed soft parts into the shell. In bivalves, the foot is adapted for burrowing into the sediment; in cephalopods it is used for jet propulsion, and the tentacles and arms are derived from the foot.

Chapter- 6

Annelid

Annelida

Temporal range: Early Ordovician–Recent



Glycera sp.

Scientific classification

Kingdom:	Animalia
Superphylum:	Lophotrochozoa
Phylum:	Annelida Lamarck, 1809

Classes and subclasses

- Class Polychaeta (paraphyletic?)
- Class Clitellata
 - Oligochaeta – earthworms, etc.
 - Branchiobdellida
 - Hirudinea – leeches
- Class Myzostomida
- Class Archiannelida (polyphyletic)

The **annelids** (also called "ringed worms"), formally called **Annelida** (from French *annelés* "ringed ones", ultimately from Latin *anellus* "little ring"), are a large phylum of segmented worms, with over 17,000 modern species including ragworms, earthworms and leeches. They are found in marine environments from tidal zones to hydrothermal vents, in freshwater, and in moist terrestrial environments. Although most textbooks still use the traditional division into polychaetes (almost all marine), oligochaetes (which include earthworms) and leech-like species, research since 1997 has radically changed this scheme, viewing leeches as a sub-group of oligochaetes and oligochaetes as a sub-group of polychaetes. In addition, the Pogonophora, Echiura and Sipuncula, previously regarded as separate phyla, are now regarded as sub-groups of polychaetes. Annelids are considered members of the Lophotrochozoa, a "super-phylum" of protostomes that also includes molluscs, brachiopods, flatworms and nemerteans.

The basic annelid form consists of multiple segments, each of which has the same sets of organs and, in most polychaetes, a pair of parapodia that many species use for locomotion. Septa separate the segments of many species, but are poorly-defined or absent in some, and Echiura and Sipuncula show no obvious signs of segmentation. In species with well-developed septa, the blood circulates entirely within blood vessels, and the vessels in segments near the front ends of these species are often built up with muscles to act as hearts. The septa of these species also enable them to change the shapes of individual segments, which facilitates movement by peristalsis ("ripples" that pass along the body) or by undulations that improve the effectiveness of the parapodia. In species with incomplete septa or none, the blood circulates through the main body cavity without any kind of pump, and there is a wide range of locomotory techniques – some burrowing species turn their pharynges inside out to drag themselves through the sediment.

Although many species can reproduce asexually and use similar mechanisms to regenerate after severe injuries, sexual reproduction is the normal method in species whose reproduction has been studied. The minority of living polychaetes whose reproduction and lifecycles are known produce trochophore larvae, which live as plankton and then sink and metamorphose into miniature adults. Oligochaetes are full hermaphrodites and produce a ring-like cocoon round their bodies, in which the eggs and hatchlings are nourished until they are ready to emerge.

Earthworms support terrestrial food chains both as prey and by aerating and enriching soil. The burrowing of marine polychaetes, which may constitute up to a third of all species in near-shore environments, encourages the development of ecosystems by enabling water and oxygen to penetrate the sea floor. In addition to improving soil fertility, annelids serve humans as food and as bait. Scientists observe annelids to monitor the quality of marine and fresh water. Although blood-letting is no longer in favor with doctors, some leech species are regarded as endangered species because they have been over-harvested for this purpose in the last few centuries. Ragworms' jaws are now being studied by engineers as they offer an exceptional combination of lightness and strength.

Since annelids are soft-bodied, their fossils are rare – mostly jaws and the mineralized tubes that some of the species secreted. Although some late Ediacaran fossils may represent annelids, the oldest known fossil that is identified with confidence comes from about 518 million years ago in the early Cambrian period. Fossils of most modern mobile polychaete groups appeared by the end of the Carboniferous, about 299 million years ago. Scientists disagree about whether some body fossils from the mid Ordovician, about 472 to 461 million years ago, are the remains of oligochaetes, and the earliest certain fossils of the group appear in the Tertiary period, which began 65 million years ago.

Classification and diversity

There are over 17,000 living annelid species, ranging in size from microscopic to the Australian giant Gippsland earthworm, which can grow up to 3 metres (9.8 ft) long. Although research since 1997 has radically changed scientists' views about the evolutionary family tree of the annelids, most textbooks use the traditional classification into the following sub-groups:

- **Polychaetes** (about 12,000 species). As their name suggests, they have multiple chetae ("hairs") per segment. Polychaetes have parapodia that function as limbs, and nuchal organs ("nuchal" means "on the neck") that are thought to be chemosensors. Most are marine animals, although a few species live in fresh water and even fewer on land.



An earthworm's clitellum

- **Clitellates** (about 5,000 species). These have few or no chetae per segment, and no nuchal organs or parapodia. However, they have a unique reproductive organ, the ring-shaped clitellum ("pack saddle") round their bodies, which produces a cocoon that stores and nourishes fertilized eggs until they hatch. The clitellates are sub-divided into:
 - **Oligochaetes** ("with few hairs"), which includes earthworms. Oligochaetes have a sticky pad in the roof of the mouth. Most are burrowers that feed on wholly or partly decomposed organic materials.
 - **Hirudinea**, whose name means "leech-shaped" and whose best known members are leeches. Marine species are mostly blood-sucking parasites, mainly on fish, while most freshwater species are predators. They have

suckers at both ends of their bodies, and use these to move rather like inchworms.

The Archannelida, minute annelids that live in the spaces between grains of sediment, were treated as a separate class because of their simple body structure, but are now regarded as polychaetes. Some other groups of animals have been classified in various ways, but are now widely regarded as annelids:

- Pogonophora / Siboglinidae were first discovered in 1914, and their lack of a recognizable gut made it difficult to classify them. They have been classified as a separate phylum, Pogonophora, or as two phyla, Pogonophora and Vestimentifera. More recently they have been re-classified as a family, Siboglinidae, within the polychaetes.
- The Echiura have a checkered taxonomic history: in the 19th century they were assigned to the phylum "Gephyrea", which is now empty as its members have been assigned to other phyla; the Echiura were next regarded as annelids until the 1940s, when they were classified as a phylum in their own right; but a molecular phylogenetics analysis in 1997 concluded that Echiurans are annelids.
- Myzostomida live on crinoids and other echinoderms, mainly as parasites. In the past they have been regarded as close relatives of the trematode flatworms or of the tardigrades, but in 1998 it was suggested that they are a sub-group of polychaetes. However, another analysis in 2002 suggested that myzostomids are more closely related to flatworms or to rotifers and acanthocephales.

Description

Segmentation

Most of an annelid's body consists of segments that are practically identical, having the same sets of internal organs and external chaetae (Greek *χαιτα*, meaning "hair") and, in some species, appendages. However, the frontmost and rearmost sections are not regarded as true segments as they do not contain the standard sets of organs and do not develop in the same way as the true segments. The frontmost section, called the prostomium (Greek *προ-* meaning "in front of" and *στομα* meaning "mouth") contains the brain and sense organs, while the rearmost, called the pygidium (Greek *πυγιδιον*, meaning "little tail") contains the anus, generally on the underside. The first section behind the prostomium, called the peristomium (Greek *περι-* meaning "around" and *στομα* meaning "mouth"), is regarded by some zoologists as not a true segment, but in some polychaetes the peristomium has chetae and appendages like those of other segments.

The segments develop one at a time from a growth zone just ahead of the pygidium, so that an annelid's youngest segment is just in front of the growth zone while the peristomium is the oldest. This pattern is called teloblastic growth. Some groups of annelids, including all leeches, have fixed maximum numbers of segments, while others add segments throughout their lives.

The phylum's name is derived from the Latin word *annelus*, meaning "little ring".

Body wall, chetae and parapodia

Annelids' cuticles are made of collagen fibers, usually in layers that spiral in alternating directions so that the fibers cross each other. These are secreted by the one-cell deep epidermis (outermost skin layer). A few marine annelids that live in tubes lack cuticles, but their tubes have a similar structure, and mucus-secreting glands in the epidermis protect their skins. Under the epidermis is the dermis, which is made of connective tissue, in other words a combination of cells and non-cellular materials such as collagen. Below this are two layers of muscles, which develop from the lining of the coelom (body cavity): circular muscles make a segment longer and slimmer when they contract, while under them are longitudinal muscles, usually four distinct strips, whose contractions make the segment shorter and fatter. Some annelids also have oblique internal muscles that connect the underside of the body to each side.

The chetae ("hairs") of annelids project out from the epidermis to provide traction and other capabilities. The simplest are unjointed and form paired bundles near the top and bottom of each side of each segment. The parapodia ("limbs") of annelids that have them often bear more complex chetae at their tips – for example jointed, comb-like or hooked. Chetae are made of moderately flexible β -chitin and are formed by follicles, each of which has a chaetoblast ("hair-forming") cell at the bottom and muscles that can extend or retract the cheta. The chaetoblasts produce chetae by forming microvilli, fine hair-like extensions that increase the area available for secreting the cheta. When the cheta is complete, the microvilli withdraw into the chaetoblast, leaving parallel tunnels that run almost the full length of the cheta. Hence annelids' chetae are structurally different from the setae ("bristles") of arthropods, which are made of the more rigid α -chitin, have a single internal cavity, and are mounted on flexible joints in shallow pits in the cuticle.

Nearly all polychaetes have parapodia that function as limbs, while other major annelid groups lack them. Parapodia are unjointed paired extensions of the body wall, and their muscles are derived from the circular muscles of the body. They are often supported internally by one or more large, thick chetae. The parapodia of burrowing and tube-dwelling polychaetes are often just ridges whose tips bear hooked chetae. In active crawlers and swimmers the parapodia are often divided into large upper and lower paddles on a very short trunk, and the paddles are generally fringed with chetae and sometimes with cirri (fused bundles of cilia) and gills.

Nervous system and senses

The brain generally forms a ring round the pharynx (throat), consisting of a pair of ganglia (local control centers) above and in front of the pharynx, linked by nerve cords either side of the pharynx to another pair of ganglia just below and behind it. The brains of polychaetes are generally in the prostomium, while those of clitellates are in the peristomium or sometimes the first segment behind the peristomium. In some very mobile and active polychaetes the brain is enlarged and more complex, with visible

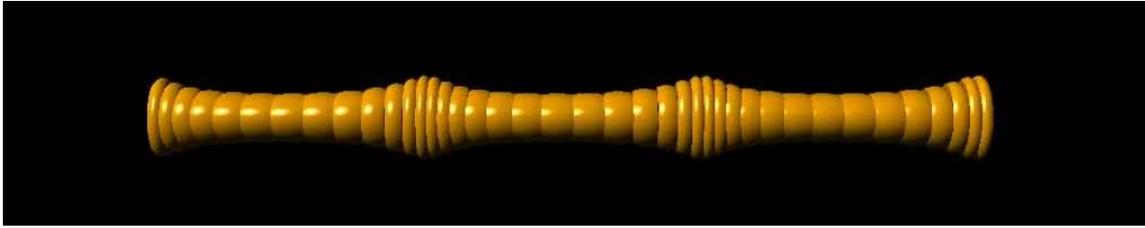
hindbrain, midbrain and forebrain sections. The rest of the central nervous system is generally "ladder-like", consisting of a pair of nerve cords that run through the bottom part of the body and have in each segment paired ganglia linked by a transverse connection. From each segmental ganglion a branching system of local nerves runs into the body wall and then encircles the body. However, in most polychaetes the two main nerve cords are fused, and in the tube-dwelling genus *Owenia* the single nerve chord has no ganglia and is located in the epidermis.

As in arthropods, each muscle fiber (cell) is controlled by more than one neuron, and the speed and power of the fiber's contractions depends on the combined effects of all its neurons. Vertebrates have a different system, in which one neuron controls a group of muscle fibers. Most annelids' longitudinal nerve trunks include giant axons (the output signal lines of nerve cells). Their large diameter decreases their resistance, which allows them to transmit signals exceptionally fast. This enables these worms to withdraw rapidly from danger by shortening their bodies. Experiments have shown that cutting the giant axons prevents this escape response but does not affect normal movement.

The sensors are primarily single cells that detect light, chemicals, pressure waves and contact, and are present on the head, appendages (if any) and other parts of the body. Nuchal ("on the neck") organs are paired, ciliated structures found only in polychaetes, and are thought to be chemosensors. Some polychaetes also have various combinations of ocelli ("little eyes") that detect the direction from which light is coming and camera eyes or compound eyes that can probably form images. The compound eyes probably evolved independently of arthropods' eyes. Some tube-worms use ocelli widely spread over their bodies to detect the shadows of fish, so that they can quickly withdraw into their tubes. Some burrowing and tube-dwelling polychaetes have statocysts (tilt and balance sensors) that tell them which way is down. A few polychaete genera have on the undersides of their heads palps that are used both in feeding and as "feelers", and some of these also have antennae that are structurally similar but probably are used mainly as "feelers".

Coelom, locomotion and circulatory system

Most annelids have a pair of coeloms (body cavities) in each segment, separated from other segments by septa and from each other by vertical mesenteries. Each septum forms a sandwich with connective tissue in the middle and mesothelium (membrane that serves as a lining) from the preceding and following segments on either side. Each mesentery is similar except that the mesothelium is the lining of each of the pair of coeloms, and the blood vessels and, in polychaetes, the main nerve cords are embedded in it. The mesothelium is made of modified epitheliomuscular cells, in other words their bodies form part of the epithelium but their bases extend to form muscle fibers in the body wall. The mesothelium may also form radial and circular muscles on the septa, and circular muscles around the blood vessels and gut. Parts of the mesothelium, especially on the outside of the gut, may also form chloragogen cells that perform similar functions to the livers of vertebrates: producing and storing glycogen and fat; producing the oxygen-carrier hemoglobin; breaking down proteins; and turning nitrogenous waste products into ammonia and urea to be excreted.



Peristalsis moves this "worm" to the right

Many annelids move by peristalsis (waves of contraction and expansion that sweep along the body), or flex the body while using parapodia to crawl or swim. In these animals the septa enable the circular and longitudinal muscles to change the shape of individual segments, by making each segment a separate fluid-filled "balloon". However, the septa are often incomplete in annelids that are semi-sessile or that do not move by peristalsis or by movements of parapodia – for example some move by whipping movements of the body, some small marine species move by means of cilia (fine muscle-powered hairs) and some burrowers turn their pharynges (throats) inside out to penetrate the sea-floor and drag themselves into it.

The fluid in the coeloms contains coelomocyte cells that defend the animals against parasites and infections. In some species coelomocytes may also contain a respiratory pigment – red hemoglobin in some species, green chlorocruorin in others – and provide oxygen transport within their segments. Respiratory pigment is also dissolved in the blood plasma. Species with well-developed septa generally also have blood vessels running all long their bodies above and below the gut, the upper one carrying blood forwards while the lower one carries it backwards. Networks of capillaries (fine blood vessels) in the body wall and around the gut transfer blood between the main blood vessels and to parts of the segment that need oxygen and nutrients. Both of the major vessels, especially the upper one, can pump blood by contracting. In some annelids the forward end of the upper blood vessel is enlarged with muscles to form a heart, while in the forward ends of many earthworms some of the vessels that connect the upper and lower main vessels function as hearts. Species with poorly-developed or no septa generally have no blood vessels and rely on the circulation within the coelom for delivering nutrients and oxygen.

However, leeches and their closest relatives have a body structure that is very uniform within the group but significantly different from that of other annelids, including other members of the Clitellata. In leeches there are no septa, the connective tissue layer of the body wall is so thick that it occupies much of the body, and the two coeloms are widely separated and run the length of the body. They function as the main blood vessels, although they are side-by-side rather than upper and lower. However, they are lined with mesothelium, like the coeloms and unlike the blood vessels of other annelids. Leeches generally use suckers at their front and rear ends to move like inchworms. The anus is on the upper surface of the pygidium.

Respiration

In some annelids, including earthworms, all respiration is via the skin. However, many polychaetes and some clitellates (the group to which earthworms belong) have gills associated with most segments, often as extensions of the parapodia in polychaetes. The gills of tube-dwellers and burrowers usually cluster around whichever end has the stronger water flow.

Feeding and excretion

Feeding structures in the mouth region vary widely, and have little correlation with the animals' diets. Many polychaetes have a muscular pharynx that can be everted (turned inside out to extend it). In these animals the foremost few segments often lack septa so that, when the muscles in these segments contract, the sharp increase in fluid pressure from all these segments everts the pharynx very quickly. Two families, the Eunicidae and Phyllodoceidae, have evolved jaws, which can be used for seizing prey, biting off pieces of vegetation, or grasping dead and decaying matter. On the other hand some predatory polychaetes have neither jaws nor eversible pharynges. Selective deposit feeders generally live in tubes on the sea-floor and use palps to find food particles in the sediment and then wipe them into their mouths. Filter feeders use "crowns" of palps covered in cilia that wash food particles towards their mouths. Non-selective deposit feeders ingest soil or marine sediments via mouths that are generally unspecialized. Some clitellates have sticky pads in the roofs of their mouths, and some of these can evert the pads to capture prey. Leeches often have an eversible proboscis, or a muscular pharynx with two or three teeth.

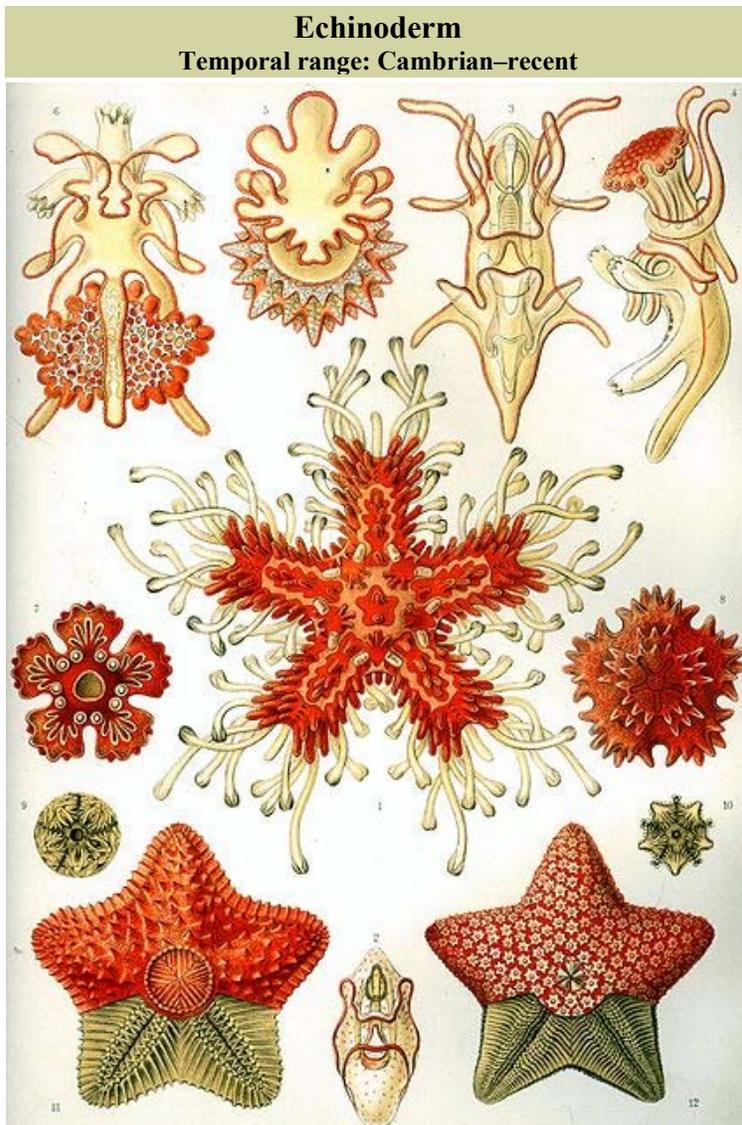
The gut is generally an almost straight tube supported by the mesenteries (vertical partitions within segments), and ends with the anus on the underside of the pygidium. However, in members of the tube-dwelling family Siboglinidae the gut is blocked by a swollen lining that houses symbiotic bacteria, which can make up 15% of the worms' total weight. The bacteria convert inorganic matter – such as hydrogen sulfide and carbon dioxide from hydrothermal vents, or methane from seeps – to organic matter that feeds themselves and their hosts, while the worms extend their palps into the gas flows to absorb the gases needed by the bacteria.

Annelids with blood vessels use metanephridia to remove soluble waste products, while those without use protonephridia. Both of these systems use a two-stage filtration process, in which fluid and waste products are first extracted and these are filtered again to re-absorb any re-usable materials while dumping toxic and spent materials as urine. The difference is that protonephridia combine both filtration stages in the same organ, while metanephridia perform only the second filtration and rely on other mechanisms for the first – in annelids special filter cells in the walls of the blood vessels let fluids and other small molecules pass into the coelomic fluid, where it circulates to the metanephridia. In annelids the points at which fluid enters the protonephridia or metanephridia are on the forward side of a septum while the second-stage filter and the nephridiopore (exit opening in the body wall) are in the following segment. As a result

the hindmost segment (before the growth zone and pygidium) has no structure that extracts its wastes, as there is no following segment to filter and discharge them, while the first segment contains an extraction structure that passes wastes to the second, but does not contain the structures that re-filter and discharge urine.

Chapter- 7

Echinoderm



Haeckel's diagrams of Asteroidea specimens

Scientific classification

Kingdom:	Animalia
Subkingdom:	Eumetazoa
Superphylum:	Deuterostomia
Phylum:	Echinodermata Klein, 1734

Subphyla & Classes

- Homalozoa † Gill & Caster, 1960
 - Homostelea †
 - Homoiostelea †
 - Stylophora †
 - Ctenocystoidea † Robison & Sprinkle, 1969
- Crinozoa
 - Crinoidea
 - Paracrinoidea † Regnéll, 1945
 - Cystoidea † von Buch, 1846
- Asterozoa
 - Ophiuroidea
 - Asteroidea
- Echinozoa
 - Echinoidea
 - Holothuroidea
 - Ophiocystioidea †
 - Helicoplacoidea †
 - ?*Arkarua* †
- Pelmatozoa †
 - Edrioasteroidea †
- Blastozoa †
 - Blastoidea †
 - Eocrinoidea † Jaekel, 1899

† = Extinct

Echinoderms (Phylum **Echinodermata**) are a phylum of marine animals. Echinoderms are found at every ocean depth, from the intertidal zone to the abyssal zone. Aside from the problematic *Arkarua*, the first definitive members of the phylum appeared near the start of the Cambrian period.

The phylum contains about 7,000 living species, making it the second-largest grouping of deuterostomes, after the chordates. Echinoderms are also the largest phylum that has no freshwater or terrestrial representatives.

The word is derived from the Greek *ἔχينوδέρματα* (*echinodermata*), plural of *ἔχινόδερμα* (*echinoderma*), "spiny skin" from *ἔχινός* (*echinos*), "sea-urchin", originally "hedgehog," and *δέρμα* (*derma*), "skin".

The echinoderms are important both biologically and geologically: biologically because few other groupings are so abundant in the biotic desert of the deep sea, as well as the shallower oceans, and geologically as their ossified skeletons are major contributors to many limestone formations, and can provide valuable clues as to the geological environment. Further, it is held by some that the radiation of echinoderms was responsible for the Mesozoic revolution of marine life.

Taxonomy

Two main subdivisions of echinoderms are traditionally recognised: the more familiar, motile Eleutherozoa, which encompasses the Asterozoa (starfish), Ophiurozoa (brittle stars), Echinozoa (sea urchins and sand dollars) and Holothurozoa (sea cucumbers); and the sessile Pelmatozoa, which consists of the crinoids and extinct Paracrinoids. Some crinoids, however, namely the feather stars, are also highly motile.

A fifth class of Eleutherozoa consisting of just three species, the Concentricyclozoa (sea daisies), were recently merged into the Asterozoa. The fossil record contains a host of other classes which do not appear to fall into any extant crown group.

Anatomy and physiology

Echinoderms evolved from animals with bilateral symmetry. Although adult echinoderms possess pentaradial, or five-sided, symmetry, echinoderm larvae are ciliated, free-swimming organisms that organize in a bilaterally symmetric fashion that makes them look like embryonic chordates. Later, the left side of the body grows at the expense of the right side, which is eventually absorbed. The left side then grows in a pentaradially symmetric fashion, in which the body is arranged in five parts around a central axis.

They exhibit fivefold radial symmetry in portions of their body at some stage of life, even if they have secondary bilateral symmetry. Many crinoids and some seastars exhibit symmetry in multiples of the basic five, with seastars such as *Helicoilaster* known to possess up to 50 arms, and the sea-lily *Comanthina schlegelii* boasting 200.

Skin and skeleton

Echinoderms have a mesodermal skeleton composed of calcareous plates or ossicles. Despite the robustness of the individual skeletal modules, complete echinoderm skeletons are rare in the fossil record. This is because they quickly disarticulate once the encompassing skin rots away, and in the absence of tissue there is nothing to hold the plates together. The modular construction is a result of the growth system employed by echinoderms, which adds new segments at the centre of the radial limbs, pushing the existing plates outwards in the fashion of a trachea. The spines of sea urchins are most readily lost, as each spine can be moved individually and is only loosely attached in life. A walk above a rocky shore will often reveal a large number of spineless but otherwise complete sea urchin skeletons.

Skeletal elements are also deployed in some specialised ways, such as the "Aristotle's lantern" of sea urchins, crinoids' stalks, and the supportive "lime ring" of sea cucumbers.

The epidermis itself consists of cells responsible for the support and maintenance of the skeleton, as well as pigment cells, mechanoreceptor cells, which detect motion on the animal's surface, and sometimes gland cells which secrete sticky fluids or even toxins.



Echinoderms exhibit a wide range of colours.

The varied and often vivid colors of echinoderms are produced by the action of skin pigment cells. These may be light sensitive, and as a result many species change

appearance completely as night falls. The reaction can happen very quickly — the sea urchin *Centrostephanus longispinus* changes from jet black to grey-brown in just 50 minutes when exposed to light. The colours are produced by a variable combination of coloured pigments, such as the dark melanin, red carotinoids, and carotin proteins, which can be blue, green, or violet.

The water vascular system

Echinoderms possess a unique water vascular or "ambulacral" system. This is a network of fluid-filled canals that function in gas exchange, feeding, and secondarily in locomotion. This system is derived from both the hydrocoel and axocoel. This system may have allowed echinoderms to function without the gill slits found in other deuterostomes.

The system comprises a central ring, the hydrocoel, and radial ambulacra stretching along the body or arms. As well as assisting with the distribution of nutrients through the animal, the system is most obviously expressed in the tube-feet of most echinoderms. These are extensions of the water vascular system which poke through holes in the skeleton and can be extended or contracted by the redistribution of fluid between the foot and internal sac.

In the crinoids, the tube feet waft food particles captured on the radial limbs towards the central mouth; in the asteroids, the same wafting motion is employed to move the animal across the ground. Sea urchins use their feet to prevent the larvae of encrusting organisms from settling on their surfaces; potential settlers are moved to the urchin's mouth and eaten. Some burrowing sea stars poke their tube feet through the surface of the sand or mud above them into the water column and use them to attain oxygen from the water column.

Other organs

Although echinoderms possess a complete digestive gut, it is very simple, often simply leading directly from mouth to anus. It can generally be divided into a pharynx, stomach, intestine and anus or cloaca.

Echinoderms also have a haemal system, and often also a *perihæmal system*. Both are derived from the coelom, and form an open and reduced circulatory system. This usually consists of a central ring and five radial vessels, although there is no true heart, and the blood often lacks any respiratory pigment.

Gaseous exchange occurs by *dermal branchae* or *papulae* in seastars, *peristominal gills* in sea urchins, *genital bursae* in brittle stars and *cloacal trees* in holothurians. Exchange of gases also takes place through tube feet.

Echinoderms lack specialized excretory organs and so nitrogenous waste, chiefly in the form of ammonia diffuses out through the respiratory surfaces.

They have a simple radial nervous system that consists of a modified nerve net — interconnected neurons with no central brain (although some do possess ganglia). Nerves radiate from central rings around the mouth into each arm or along the body; the branches of these nerves coordinate the movements of the organism.

The gonads occupy the entire body cavities of sea urchins and sea cucumbers, while the less voluminous crinoids, brittle stars, and seastars have two gonads per arm. While the primitive condition is considered to be one genital aperture, many organisms have multiple holes through which eggs or sperm may be released.

Reproduction

Sexual reproduction

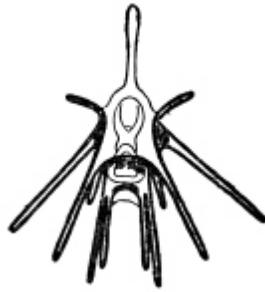
Echinoderms become sexually mature after approximately two to three years, depending on the species and the environmental conditions. The eggs and sperm cells are released into open water, where fertilization takes place. The release of sperm and eggs is coordinated temporally in some species, and spatially in others. Internal fertilization has currently been observed in three species of sea star, three brittle stars and a deep water sea cucumber.

In some species of feather star, the embryos develop in special breeding bags, where the eggs are held until sperm released by a male happen to find them and fertilize the contents. This can also be found among sea urchins and sea cucumbers, where exhibit care for their young can occur, for instance in a few species of sand dollars who carry their young between the pricks of their oral side, and heart urchins possess breeding chambers. With brittle stars, special chambers can be developed near the stomach bags, in which the development of the young takes place. Species of sea cucumbers with specialized care for their offspring may also nurse the young in body cavities or on their surfaces. In rare cases, direct development without passing through a bilateral larval stage can occur in some sea stars and brittle stars. Another strategy that has evolved in some sea stars and brittle stars is the ability to reproduce asexually by dividing in two halves while they are small juveniles, while turning to sexual reproduction when they have reached sexual maturity.

Asexual reproduction

Many echinoderms have remarkable powers of regeneration. Some sea stars are capable of regenerating lost arms. In some cases, lost arms have been observed to regenerate a second complete sea star. Sea cucumbers often discharge parts of their internal organs if they perceive danger. The discharged organs and tissues are quickly regenerated. Sea urchins are constantly losing their spines through damage — all parts are replaceable. Some seastar populations can reproduce entirely asexually purely by the shedding of arms for long periods of time.

Larval development



The "pluteus larva" of a sea urchin

The development of an echinoderm begins with a bilaterally symmetrical embryo, with a coeloblastula developing first. Gastrulation marks the opening of the "second mouth" that places them within the deuterostomes, and the mesoderm, which will host the skeleton, migrates inwards. The secondary body cavity, the coelom, forms by the partitioning of three body cavities.

Upon metamorphosis, each taxon produces a distinct planktonic larva, which varies in shape among the classes. Larval stages with prominent "arms" are often referred to as pluteus larvae (often with a prefix to denote taxon).

The left hand side of the larva develops into the adult organism while the right hand side eventually being absorbed; the left hand side typically becomes the oral plate.

Distribution and habitat

Echinoderms are globally distributed in almost all depths, latitudes and environments in the ocean. They reach highest diversity in reef environments but are also widespread on shallow shores, around the poles — refugia where crinoids are at their most abundant — and throughout the deep ocean, where bottom-dwelling and burrowing sea cucumbers are common — sometimes accounting for up to 90 % of organisms. While almost all echinoderms are benthic — that is, they live on the sea floor — some sea-lilies can swim at great velocity for brief periods of time, and a few deep-sea sea cucumbers are fully floating. Some crinoids are pseudo-planktonic, attaching themselves to floating logs and debris, although this behaviour was exercised most extensively in the Paleozoic, before competition from such organisms as barnacles restricted the extent of the behaviour. Some sea cucumbers employ a similar strategy, hitching lifts by attaching to the sides of fish.

The larvæ of many echinoderms, especially starfish and sea urchins, are pelagic, and with the aid of ocean currents can swim great distances, reinforcing the global distribution of the phylum.

Chapter- 8

Centipede

Centipedes

Fossil range: 418–0 Ma
Late Silurian to Recent



Scolopendra sp. (Scolopendromorpha: Scolopendridae)

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Myriapoda
Class:	Chilopoda Latreille, 1817

Orders and Families

Scutigleromorpha

- Psellioididae
- Scutigerae
- Scutigerae

Lithobiomorpha

- Henicopidae
- Lithobiidae

Craterostigmomorpha

- Craterostigmidae

Scolopendromorpha

- Cryptopidae
- Scolopendridae
- Scolopocryptopidae

Geophilomorpha

- Mecistocephalidae
- Neogeophilidae
- Geophilidae
- Geophilidae
- Linotaeniidae

Centipedes (from Latin prefix *centi-*, "hundred", and *pes, pedis*, "foot") are arthropods belonging to the class **Chilopoda** of the subphylum Myriapoda. They are elongated metameric animals with one pair of legs per body segment. Despite the name, centipedes can have a varying number of legs from under 20 to over 300. Centipedes have an odd number of pairs of legs, e.g. 15 or 17 pairs of legs (30 or 34 legs) but never 16 pairs (32 legs). A key trait uniting this group is a pair of venom claws or "forcipules" formed from a modified first appendage. Centipedes are a predominantly carnivorous taxon.

Centipedes normally have a drab coloration combining shades of brown and red. Cavernicolous (cave-dwelling) and subterranean species may lack pigmentation and many tropical scolopendromorphs have bright aposematic colours. Size can range from a few millimetres in the smaller lithobiomorphs and geophilomorphs to about 30 cm (12 in) in the largest scolopendromorphs. Centipedes can be found in a wide variety of environments.

Worldwide there are estimated to be 8,000 species of centipede, of which 3,000 have been described. Centipedes have a wide geographical range, reaching beyond the Arctic

Circle. Centipedes are found in an array of terrestrial habitats from tropical rainforests to deserts. Within these habitats centipedes require a moist micro-habitat because they lack the waxy cuticle of insects and arachnids, and so lose water rapidly through the skin. Accordingly, they are found in soil and leaf litter, under stones and dead wood, and inside logs. Centipedes are among the largest terrestrial invertebrate predators and often contribute significantly to the invertebrate predatory biomass in terrestrial ecosystems.

Description

Centipedes have a rounded or flattened head, bearing a pair of antennae at the forward margin. They have a pair of elongated mandibles, and two pairs of maxillae. The first pair of maxillae form the lower lip, and bear short palps. The first pair of limbs stretch forward from the body to cover the remainder of the mouth. These limbs, or maxillipeds, end in sharp claws and include venom glands that help the animal to kill or paralyse its prey.

Centipedes possess a variable number of ocelli, which are sometimes clustered together to form true compound eyes. Even so, it appears that centipedes are only capable of discerning light and dark, and not of true vision. Indeed, many species lack eyes altogether. In some species the final pair of legs act as sense organs similar to antennae, but facing backwards. An unusual sense organ found in some groups are the organs of Tömösvary. These are located at the base of the antennae, and consist of a disc-like structure with a central pore surrounded by sensory cells. They are probably used for sensing vibrations, and may even provide a sense of hearing.



Underside of *Scolopendra cingulata*, showing the forcipules

Forcipules are a unique feature found only in centipedes and in no other arthropods. The forcipules are modifications of the first pair of legs, forming a pincer-like appendage always found just behind the head. Forcipules are not true mouthparts, although they are used in the capture of prey items, injecting venom and holding onto captured prey. Venom glands run through a tube almost to the tip of each forcipule.

Behind the head, the body consists of fifteen or more segments. Most of the segments bear a single pair of legs, with the maxillipeds projecting forward from the first body segment, and the final two segments being small and legless. Each pair of legs is slightly longer than the pair immediately in front of it, ensuring that they do not overlap, and therefore reducing the chance that they will collide with each other while moving swiftly.

In extreme cases, the last pair of legs may be twice the length of the first pair. The final segment bears a telson and includes the openings of the reproductive organs.

Centipedes are predators, and mainly use their antennae to seek out their prey. The digestive tract forms a simple tube, with digestive glands attached to the mouthparts. Like insects, centipedes breathe through a tracheal system, typically with a single opening, or spiracle on each body segment. They excrete waste through a single pair of malpighian tubules.

Scolopendra gigantea, also known as the **Amazonian giant centipede**, is the largest existing species of centipede in the world, reaching over 30 cm (12 in) in length. It is known to eat lizards, frogs, birds, mice, and even bats, catching them in midflight, as well as rodents and spiders. The now extinct *Euphoberia* was the largest centipede, growing up to 1 m (39 in) in length.

Life cycle



A centipede protecting her eggmass

Centipede reproduction does not involve copulation. Males deposit a spermatophore for the female to take up. In one clade, this spermatophore is deposited in a web, and the male undertakes a courtship dance to encourage the female to engulf his sperm. In other cases, the males just leave them for the females to find. In temperate areas egg laying occurs in spring and summer but in subtropical and tropical areas there appears to be little

seasonality to centipede breeding. It is also notable that there are a few known species of parthenogenetic centipedes.

The Lithobiomorpha, and Scutigleromorpha lay their eggs singly in holes in the soil, the female fills the hole in on the egg and leaves it. The number of eggs laid ranges from about 10 to 50. Time of development of the embryo to hatching is highly variable and may take from one to a few months. Time of development to reproductive period is highly variable within and among species. For example, it can take 3 years for *S. coleoptera* to achieve adulthood, whereas under the right conditions Lithobiomorph species may reach a reproductive period in 1 year. In addition, centipedes are relatively long-lived when compared to their insect cousins. For example: the European *Lithobius forficatus* can live for 5 or 6 years. The combination of a small number of eggs laid, long gestation period, and long time of development to reproduction has led authors to label Lithobiomorph centipedes as K-selected.

Females of Geophilomorpha and Scolopendromorpha show far more parental care, the eggs 15 to 60 in number are laid in a nest in the soil or in rotten wood, the female stays with the eggs, guarding and licking them to protect them from fungi. The female in some species stays with the young after they have hatched, guarding them until they are ready to leave. If disturbed the females tend to either abandon the eggs of their young or eat them; abandoned eggs tend to fall prey to fungi rapidly. Some species of Scolopendromorpha are matrifagic, meaning that the offspring eat their mother.

Little is known of the life history of Craterostigmomorpha.

Anamorph vs. epimorph

Centipedes grow their legs at different points in their development. In the primitive condition, exhibited by the L, Scutigleromorpha and Craterostigmomorpha, development is anamorphic. That is to say, more pairs of legs are grown between moults; for example, *Scutigera coleoptrata*, the American house centipede, hatches with only 4 pairs of legs and in successive moults has 5, 7, 9, 11, 15, 15, 15 and 15 before becoming a sexually mature adult. Life stages with fewer than 15 pairs of legs are called larval stadia (~5 stages). After the full complement of legs is achieved, the now post-larval stadia (~5 stages) develop gonopods, sensory pores, more antennal segments, and more ocelli. All mature Lithobiomorph centipedes have 15 leg-bearing segments.

The Craterostigmomorpha only have one phase of anamorph, with embryos having 12 pairs, and moults 15.

The clade Epimorpha, consisting of orders Geophilomorpha and Scolopendromorpha, derived epimorph. Here, all pairs of legs are developed in the embryonic stages, offspring do not develop more legs between moults. It is this clade that contains the *longest* centipedes; the maximum number of thoracic segments may also vary intra-specifically, often on a geographical basis; in most cases, females bear more legs than males. The number of leg-bearing segments varies widely, from 15 to 191, but the

developmental mode of their creation means that they are always added in pairs – hence the total number of pairs is always odd.

Ecology



A centipede being eaten by a European roller

Centipedes are a predominantly predatory taxon. They are known as generalist predators which means that they have adapted to eat a variety of different available prey items. Examination of centipede gut contents suggest that plant material is an unimportant part of their diet although centipedes have been observed to eat vegetable matter when starved during laboratory experiments.

Centipedes are also known to be nocturnal. Studies on centipede activity rhythms confirm this, although there are a few observations of centipedes active during the day and one species *Strigamia chinophila* that is diurnal. What centipedes actually eat is not well known because of their cryptic lifestyle and thorough mastication of food. Laboratory feeding trials support that they will feed as generalists, taking most anything that is soft-bodied and in a reasonable size range. It has been suggested that earthworms provide the bulk of diets for Geophilomorphs, since Geophilomorphs burrow through the soil and earthworm bodies would be easily pierced by their poison claws. Observations suggest

that Geophilomorphs cannot subdue earthworms larger than themselves, and so smaller earthworms may be a substantial proportion of their diet. Scolopendromorphs, given their size, are able to feed on vertebrates as well as invertebrates. They have been observed eating reptiles, amphibians, small mammals, bats and birds. Collembola may provide a large proportion of Lithobiomorph diet. Little is known about Scutigermorph or Craterostigmomorph diets. All centipedes are potential intraguild predators. Centipedes and spiders may frequently prey on one another.

Centipedes are eaten by a great many vertebrates and invertebrates, such as mongooses, mice, salamanders, beetles and snakes. They form an important item of diet for many species and the staple diet of some such as the African ant *Amblyopone pluto*, which feeds solely on geophilomorph centipedes, and the South African Cape black-headed snake *Aparallactus capensis*.

Centipedes are found in moist microhabitats. Water relations are an important aspect of their ecology, since they lose water rapidly in dry conditions. Water loss is a result of centipedes lacking a waxy covering of their exoskeleton and excreting waste nitrogen as ammonia, which requires extra water. Centipedes deal with water loss through a variety of adaptations. Geophilomorphs lose water less rapidly than Lithobiomorphs even though they have a greater surface area to volume ratio. This may be explained by the fact that Geophilomorphs have a more heavily sclerotized pleural membrane. Spiracle shape, size and ability to constrict also have an influence on rate of water loss. In addition, it has been suggested that number and size of coxal pores may be variables affecting centipede water balance.

Centipedes live in many different habitat types; forest, savannah, prairie, and desert to name a few. Some Geophilomorphs are adapted to littoral habitats, where they feed on barnacles. Species of all orders excluding Craterostigmomorpha have adapted to caves. Centipede densities have been recorded as high as 600/m² and biomass as high as 500 mg/m² wet weight. Small geophilomorphs attain highest densities, followed by small Lithobiomorphs. Large Lithobiomorphs attain densities of 20/m². One study of scolopendromorphs records *Scolopendra morsitans* in a Nigerian savannah at a density of 0.16/m² and a biomass of 140 mg/m² wet weight.

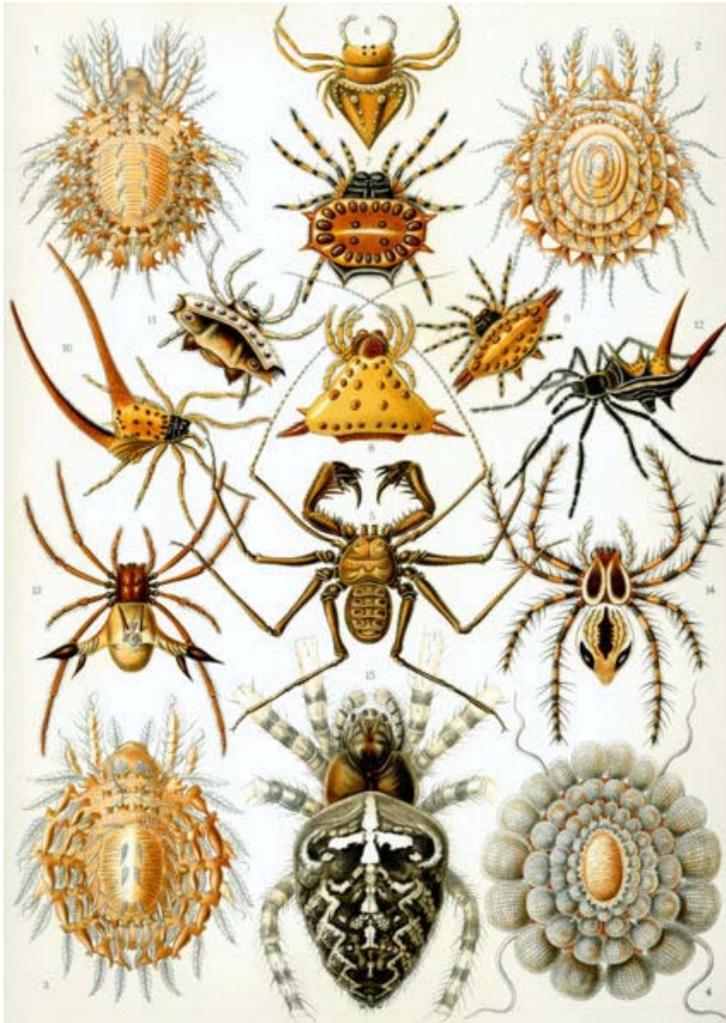
Hazards to humans

Some species of centipede can be hazardous to humans because of their bite. Although a bite to an adult human is usually very painful and may cause severe swelling, chills, fever, and weakness, it is unlikely to be fatal. Bites can be dangerous to small children and those with allergies to bee stings. The bite of larger centipedes can induce anaphylactic shock in such people. Smaller centipedes usually do not puncture human skin.

Chapter- 9

Arachnid

Arachnida
Temporal range: 420–0 Ma
Silurian to Recent



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

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Chelicerata
Class:	Arachnida Cuvier, 1812

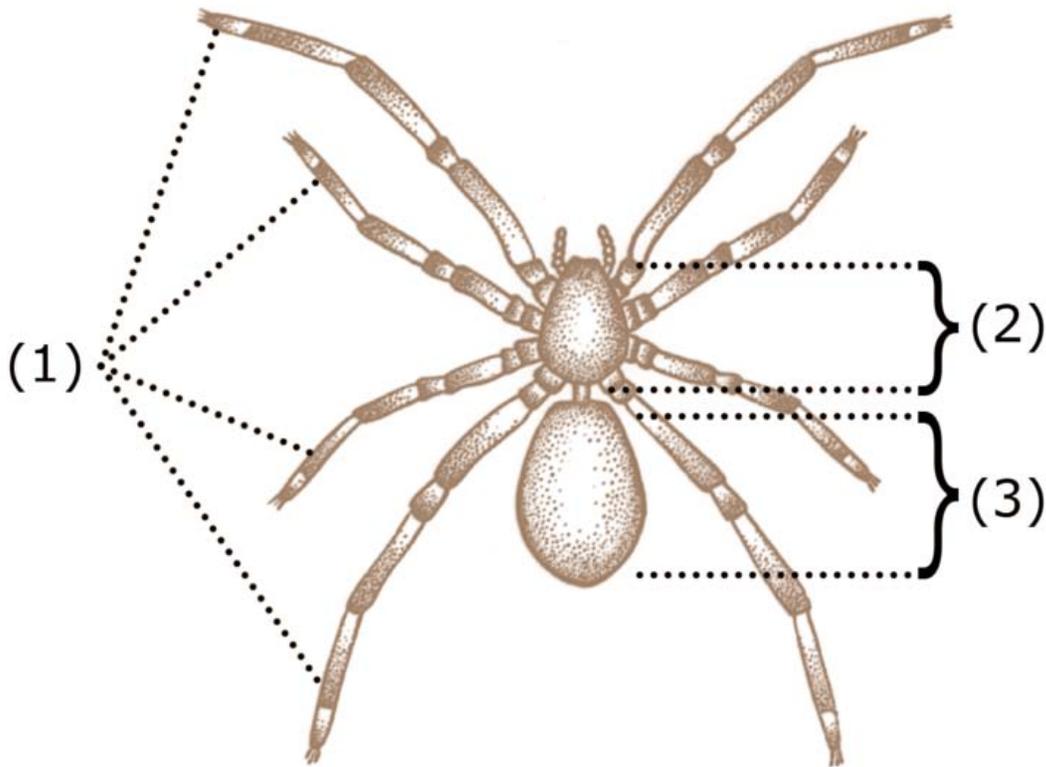
Extant orders

Acarina
Amblypygi
Araneae
†Haptopoda
Opiliones
Palpigradi
†Phalangiotarbida
Pseudoscorpionida
Ricinulei
Schizomida
Scorpiones
Solifugae
Thelyphonida
†Trigonotarbida

Arachnids are a class (**Arachnida**) of joint-legged invertebrate animals in the subphylum Chelicerata. All arachnids have eight legs, although in some species the front pair may convert to a sensory function. The term is derived from the Greek word ἀράχνη (*aráchnē*), meaning "spider".

Almost all extant arachnids are terrestrial. However, some inhabit freshwater environments and, with the exception of the pelagic zone, marine environments as well. They comprise over 100,000 named species, including spiders, scorpions, harvestmen, ticks, mites and Solifugae.

Anatomy



Basic characteristics of arachnids include four pairs of legs (1) and a body divided into two segments: the cephalothorax (2) and the abdomen (3).

Almost all adult arachnids have eight legs, and arachnids may be easily distinguished from insects by this fact, since insects have six legs. However, arachnids also have two further pairs of appendages that have become adapted for feeding, defense, and sensory perception. The first pair, the chelicerae, serve in feeding and defense. The next pair of appendages, the pedipalps have been adapted for feeding, locomotion, and/or reproductive functions. In Solifugae, the palps are quite leg-like, so that these animals appear to have ten legs. The larvae of mites and Ricinulei have only six legs; the fourth pair appears when they moult into nymphs. However, there are also adult mites with six, or even four legs.

Arachnids are further distinguished from insects by the fact they have no antennae or wings. Their body is organized into two tagma called the prosoma, or cephalothorax, and the opisthosoma, or abdomen. The cephalothorax is derived from the fusion of the cephalon (head) and the thorax, and is usually covered by a single, unsegmented carapace. The abdomen is segmented in the more primitive forms, but varying degrees of fusion between the segments occur in many groups. It is typically divided into a

preabdomen and postabdomen, although this is only clearly visible in scorpions, and in some orders, such as the Acari, the abdominal sections are completely fused.

Like all arthropods, arachnids have an exoskeleton, and they also have an internal structure of cartilage-like tissue called the endosternite, to which certain muscle groups are attached. The endosternite is even calcified in some Opiliones.

Physiology

There are some characteristics that are particularly important for the terrestrial lifestyle of an arachnid, such as internal respiratory surfaces in the form of tracheae, or modification of the book gill into a book lung, an internal series of vascular lamellae used for gas exchange with the air. While the tracheae are often individual systems of tubes, similar to those in insects, ricnuleids, pseudoscorpions, and some spiders possess sieve tracheae, in which several tubes arise in a bundle from a small chamber connected to the spiracle. This type of tracheal system has almost certainly evolved from the book lungs, and indicates that the tracheae of arachnids are not homologous with those of insects.

Further adaptations to terrestrial life are appendages modified for more efficient locomotion on land, internal fertilisation, special sensory organs, and water conservation enhanced by efficient excretory structures as well as a waxy layer covering the cuticle.

The excretory glands of arachnids include up to four pairs of coxal glands along the side of the prosoma, and one or two pairs of Malpighian tubules, emptying into the gut. Many arachnids have only one or the other type of excretory gland, although several do have both. The primary nitrogenous waste product in arachnids is guanine.

The blood of arachnids is variable in composition, depending on the mode of respiration. Arachnids with an efficient tracheal system do not need to transport oxygen in the blood, and may have a reduced circulatory system. In scorpions and some spiders, however, the blood contains haemocyanin, a copper-based pigment with a similar function to haemoglobin in vertebrates. The heart is located in the forward part of the abdomen, and may or may not be segmented. Some mites have no heart at all.

Diet and digestive system

Arachnids are mostly carnivorous, feeding on the pre-digested bodies of insects and other small animals. Only in the harvestmen and among mites, such as the house dust mite, is there ingestion of solid food particles, and thus exposure to internal parasites, although it is not unusual for spiders to eat their own silk. Several groups secrete venom from specialized glands to kill prey or enemies. Several mites are parasites, some of which are carriers of disease.

Arachnids pour digestive juices produced in their stomachs over their prey after killing it with their pedipalps and chelicerae. The digestive juices rapidly turn the prey into a broth of nutrients which the arachnid sucks into a pre-buccal cavity located immediately in

front of the mouth. Behind the mouth is a muscular, sclerotised pharynx, which acts as a pump, sucking the food through the mouth and on into the oesophagus and stomach. In some arachnids, the oesophagus also acts as an additional pump.

The stomach is tubular in shape, with multiple diverticula extending throughout the body. The stomach and its diverticula both produce digestive enzymes and absorb nutrients from the food. It extends through most of the body, and connects to a short sclerotised intestine and anus in the hind part of the abdomen.

Senses

Arachnids have two kinds of eyes, the lateral and median ocelli. The lateral ocelli evolved from compound eyes and may have a tapetum, which enhances the ability to collect light. The median ocelli develop from a transverse fold of the ectoderm. The ancestors of modern arachnids probably had both types, but modern ones often lack one type or the other. The cornea of the eye also acts as a lens, and is continuous with the cuticle of the body. Beneath this is a transparent vitreous body, and then the retina and, if present, the tapetum. In most arachnids, the retina probably does not have enough light sensitive cells to allow the eyes to form a proper image.

In addition to the eyes, almost all arachnids have two other types of sensory organs. The most important to most arachnids are the fine sensory hairs that cover the body and give the animal its sense of touch. These can be relatively simple, but many arachnids also possess more complex structures, called trichobothria.

Finally, slit sense organs are slit-like pits covered with a thin membrane. Inside the pit, a small hair touches the underside of the membrane, and detects its motion. Slit sense organs are believed to be involved in proprioception, and possibly also hearing.

Reproduction

Arachnids may have one or two gonads, which are located in the abdomen. The genital opening is usually located on the underside of the second abdominal segment. In most species, the male transfers sperm to the female in a package, or spermatophore. Complex courtship rituals have evolved in many arachnids to ensure the safe delivery of the sperm to the female.

Arachnids usually lay yolky eggs, which hatch into immatures that resemble adults. Scorpions, however, are either ovoviviparous or viviparous, depending on species, and bear live young.

Systematics

- † Trigonotarbida — extinct
- Amblypygi — "blunt rump" tailless whip scorpions with front legs modified into whip-like sensory structures as long as 25 cm or more (140 species)

- Araneae — true spiders (40,000 species)
 - Mesothelae — very rare, basal spiders, with abdomen segmented and spinnerets median
 - Opisthohelae — spiders with abdomen unsegmented and spinnerets located posteriorly
 - Araneomorphae — most common spiders
 - Mygalomorphae — tarantulas and tarantula-like spiders
- † Phalangiotarbida — extinct
- Opiliones — phalangids, harvestmen or daddy-long-legs (6,300 species)
- Palpigradi — microwhip scorpions (80 species)
- Pseudoscorpionida — pseudoscorpions (3,000 species)
- Ricinulei — ricinuleids, hooded tickspiders (60 species)
- Schizomida — "split middle" whip scorpions with divided exoskeletons (220 species)
- Scorpiones — scorpions (2,000 species)
- Solifugae — solpugids, windscorpions, sun spiders or camel spiders (900 species)
- † Haptopoda — extinct
- Thelyphonida — vinegarroons or whip scorpions (formerly uropygida) forelegs modified into sensory appendages and a long tail on abdomen tip (100 species)
- Acarina — mites and ticks (30,000 species)
 - Acariformes
 - Sarcoptiformes
 - Trombidiformes
 - Opilioacariformes
 - Parasitiformes — holothyran, ticks and mesostigmatic mites

It is estimated that a total of 98,000 arachnid species have been described, and that there may be up to 600,000 in total, including undescribed species.

Acarina



Ixodes hexagonus, a tick

Acarina or **Acari** is a taxon of arachnids that contains mites and ticks. Its fossil history goes back to the Devonian period, although there is also a questionable Ordovician record. The Devonian period was the time frame in which certain species of animals developed legs. In most modern treatments, the Acari is considered a subclass of Arachnida and is composed of 2–3 orders or superorders: Acariformes, Parasitiformes, and Opilioacariformes. Most acarines are minute to small (e.g. 0.080–1.00 mm), but the giants of the Acari (some ticks and red velvet mites) may reach lengths of 10–20 mm. It is estimated that over 50,000 species have been described (as of 1999) and that a million or more species are currently living. The study of mites and ticks is called acarology.

Only the faintest traces of primary segmentation remain in mites, the prosoma and opisthosoma being insensibly fused, and a region of flexible cuticle (the circumcapitular furrow) separates the chelicerae and pedipalps from the rest of the body. This anterior body region is called the gnathosoma (or capitulum) and is also found in the Ricinulei. The remainder of the body is called the idiosoma and is unique to mites. Most adult mites have four pairs of legs, like other arachnids, but some have fewer. For example, gall mites like *Phyllocoptes variabilis* (superfamily Eriophyoidea) have a wormlike body with only two pairs of legs; some parasitic mites have only one or three pairs of legs in the adult stage. Larval and prelarval stages have a maximum of three pairs of legs; adult mites with only three pairs of legs may be called 'larviform'.

Acarine ontogeny consists of an egg, a prelarval stage (often absent), a larval stage (hexapod except in Eriophyoidea, which have only 2 pairs of legs), and a series of nymphal stages. Larvae (and prelarvae) have a maximum of 3 pairs of legs (legs are often reduced to stubs or absent in prelarvae); legs IV are added at the first nymphal stage.

Acarines live in practically every habitat, and include aquatic (freshwater and sea water) and terrestrial species. They outnumber other arthropods in the soil organic matter and detritus. Many are parasitic, and they affect both vertebrates and invertebrates. Most parasitic forms are external parasites, while the free living forms are generally predaceous and may even be used to control undesirable arthropods. Others are detritivores that help to break down forest litter and dead organic matter such as skin cells. Others still are plant feeders and may damage crops. Damage to crops is perhaps the most costly economic effect of mites, especially by the spider mites and their relatives (Tetranychidae), earth mites (Pentaleidae), thread-footed mites (Tarsonemidae) and the gall and rust mites (Eriophyoidea). Some parasitic forms affect humans and other mammals, causing damage by their feeding, and can even be vectors of diseases such as scrub typhus and rickettsial pox. A well-known effect of mites on humans is their role as an allergen and the stimulation of asthma in people affected by the respiratory disease. The use of predatory mites (e.g. Phytoseiidae) in pest control and herbivorous mites that attack weeds is also important. An unquantified, but major positive contribution of the Acari is their normal functioning in ecosystems, especially their roles in the decomposer subsystem.

Amblypygi



An amblypygid

Amblypygids are also known as **tailless whip scorpions** or **cave spiders**. Approximately 5 families, 17 genera and 136 species have been described. They are found in tropical and subtropical regions worldwide. Some species are subterranean; many are nocturnal. During the day, they may hide under logs, bark, stones, or leaves. They prefer a humid environment. Amblypygids may range from 5 to 40 mm. Their bodies are broad and highly flattened and the first pair of legs (the first walking legs in most arachnid orders) are modified to act as sensory organs. (Compare solifugids, uropygids, and schizomids.) These very thin modified legs can extend several times the length of body. They have no silk glands or venomous fangs, but can have prominent pincer-like pedipalps. Amblypygids often move about sideways on their six walking legs, with one "whip" pointed in the direction of travel while the other probes on either side of them. Prey are located with these "whips", captured with pedipalps, then torn to pieces with chelicerae. Fossilised amblypygids have been found dating back to the Carboniferous period.

Amblypygids, particularly the species *Phrynus marginemaculatus* and *Damon diadema*, are thought to be one of the few species of arachnids that show signs of social behavior. Research conducted at Cornell University by entomologists suggests that mother amblypygids comfort their young by gently caressing the offspring with her feelers. Further, when two or more siblings were placed in an unfamiliar environment, such as a cage, they would seek each other out and gather back in a group.

Araneae



Araneus diadematus

Araneae, or spiders, are the most familiar of the arachnids, and the most numerous, if only described species are counted. All spiders produce silk, a thin, strong protein strand extruded by the spider from spinnerets most commonly found on the end of the abdomen. Many species use it to trap insects in webs, although there are many species that hunt freely. Silk can be used to aid in climbing, form smooth walls for burrows, build egg sacs, wrap prey, temporarily hold sperm, and even fly, among other applications.

All spiders except those in the families Uloboridae and Holarachaeidae, and in the suborder Mesothelae (together about 350 species) can inject venom to protect themselves or to kill and liquefy prey. Only about 200 species, however, have bites that can pose

health problems to humans. Many larger species' bites may be painful, but will not produce lasting health concerns.

Spiders are found all over the world, from the tropics to the Arctic, with some extreme species even living underwater in silken domes that they supply with air, and on the tops of the highest mountains.

Chapter- 10

Flatworm (Platyhelminthes)

Platyhelminth worms Temporal range: 40–0 Ma



Bedford's flatworm, *Pseudobiceros bedfordi*

Scientific classification

Kingdom:	Animalia
(unranked):	Protostomia
(unranked):	Spiralia
(unranked):	Platyzoa
Phylum:	Platyhelminthes Gegenbaur, 1859

Classes

Cestoda
Monogenea
Trematoda
Turbellaria

The **flatworms**, known in scientific literature as **Platyhelminthes** or **Plathelminthes** (from the Greek *πλατύ*, *platy*, meaning "flat" and *ἕλμινθ* (root: *ἔλμινθ*-), *helminth*-, meaning worm) are a phylum of relatively simple bilaterian, unsegmented, soft-bodied invertebrate animals. Unlike other bilaterians, they have no body cavity, and no specialized circulatory and respiratory organs, which restricts them to flattened shapes that allow oxygen and nutrients to pass through their bodies by diffusion.

In traditional zoology texts Platyhelminthes are divided into Turbellaria, which are mostly non-parasitic animals such as planarians, and three entirely parasitic groups: Cestoda, Trematoda and Monogenea. Turbellarians are mostly predators, and live in water or in shaded, humid terrestrial environments such as leaf litter. Cestodes (tapeworms) and trematodes (flukes) have complex life-cycles, with mature stages that live as parasites in the digestive systems of fish or land vertebrates, and intermediate stages that infest secondary hosts. The eggs of trematodes are excreted from their main hosts, whereas adult cestodes generate vast numbers of hermaphroditic, segment-like proglottids which detach when mature, are excreted and then release eggs. Unlike the other parasitic groups, the monogeneans are external parasites infesting aquatic animals, and their larvae metamorphose into the adult form after attaching to a suitable host.

Because they do not have internal body cavities, for over a century Platyhelminthes were regarded as a primitive stage in the evolution of bilaterians (animals with bilateral symmetry and hence with distinct front and rear ends). However, analyses since the mid-1980s have separated out one sub-group, the Acoelomorpha, as basal bilaterians, in other words closer to the original bilaterians than to any other modern groups. The remaining Platyhelminthes form a monophyletic group, in other words one that contains all and only descendants of a common ancestor that is itself a member of the group. The redefined Platyhelminthes is part of the Lophotrochozoa, one of the three main groups of more complex bilaterians. These analyses have also concluded that the redefined Platyhelminthes, excluding Acoelomorpha, consists of two monophyletic sub-groups, Catenulida and Rhabditophora, and that Cestoda, Trematoda and Monogenea form a monophyletic sub-group within one branch of the Rhabditophora. Hence the traditional platyhelminth sub-group "Turbellaria" is now regarded as paraphyletic since it excludes the wholly-parasitic groups although these are descended from one group of "turbellarians".

Over half of all known flatworm species are parasitic, and some do enormous harm to humans and their livestock. Schistosomiasis, caused by one genus of trematodes, is the second most devastating of all human diseases caused by parasites, surpassed only by malaria. Neurocysticercosis, which arises when larvae of the pork tapeworm *Taenia solium* penetrate the central nervous system, is the major cause of acquired epilepsy worldwide. The threat of platyhelminth parasites to humans in developed countries is rising because of organic farming, the popularity of raw or lightly-cooked foods, and imports of food from high-risk areas. In less developed countries, people often cannot afford the fuel required to cook food thoroughly, and poorly-designed water-supply and irrigation projects increase the dangers presented by poor sanitation and unhygienic farming.

Two planarian species have been used successfully in the Philippines, Indonesia, Hawaii, New Guinea and Guam to control populations of the imported giant African snail *Achatina fulica*, which was displacing native snails. However, there is now concern that these planarians may themselves become a serious threat to native snails. In North-west Europe there are concerns about the spread of the New Zealand planarian *Arthurdendyus triangulatus*, which preys on earthworms.

Description

Distinguishing features

Platyhelminthes are bilaterally symmetrical animals, in other words their left and right sides are mirror images of each other; this also implies that they have distinct top and bottom surfaces and distinct head and tail ends. Like other bilaterians they have three main cell layers, while the radially symmetrical cnidarians and ctenophores "(comb jellies)" have only two cell layers. Beyond that, they are "defined more by what they do not have than by any particular series of bodily specializations." Unlike other bilaterians, platyhelminthes have no internal body cavity and are therefore described as acoelomates. They also lack specialized circulatory and respiratory organs. Their bodies are soft and unsegmented.

	Cnidarians and Ctenophores	Platyhelminthes	More "advanced" bilaterians
Bilateral symmetry	No		Yes
Number of main cell layers	Two, with jelly-like layer between them		Three
Distinct brain	No		Yes
Specialized digestive system	No		Yes
Specialized excretory system	No		Yes
Body cavity containing internal organs		No	Yes
Specialized circulatory and respiratory organs		No	Yes

Features common to all sub-groups

The lack of circulatory and respiratory organs limits platyhelminths to sizes and shapes that enable oxygen to reach and carbon dioxide to leave all parts of their bodies by simple diffusion. Hence many are microscopic and the large species have flat ribbon-like or leaf-like shapes. The guts of large species have many branches, so that nutrients can diffuse to all parts of the body. Respiration through the whole surface of the body makes platyhelminthes vulnerable to fluid loss, and restricts them to environments where

dehydration is unlikely: sea and freshwater; moist terrestrial environments such as leaf litter or between grains of soil; and as parasites within other animals.

The space between the skin and gut is filled with mesenchyme, a connective tissue that is made of cells and reinforced by collagen fibers that act as a type of skeleton, providing attachment points for muscles. The mesenchyme contains all the internal organs and allows the passage of oxygen, nutrients and waste products. It consists of two main types of cell: fixed cells, some of which have fluid-filled vacuoles; and stem cells, which can transform into any other type of cell, and are used in regenerating tissues after injury or asexual reproduction.

Most platyhelminths have no anus and regurgitate undigested material through the mouth. However, some long species have an anus and some with complex branched guts have more than one anus, since excretion only through the mouth would be difficult for them. The gut is lined with a single layer of endodermal cells which absorb and digest food. Some species break up and soften food first by secreting enzymes in the gut or pharynx (throat).

All animals need to keep the concentration of dissolved substances in their body fluids at a fairly constant level. Internal parasites and free-living marine animals live in environments that have high concentrations of dissolved material, and generally let their tissues have the same level of concentration as the environment, while freshwater animals need to prevent their body fluids from becoming too dilute. Despite this difference in environments, most platyhelminths use the same system to control the concentration of their body fluids. Flame cells, so called because the beating of their flagella looks like a flickering candle flame, extract from the mesenchyme water that contains wastes and some re-usable material, and drive it into networks of tube cells which are lined with flagella and microvilli. The tube cells' flagella drive the water towards exits called nephridiopores, while their microvilli re-absorb re-usable materials and as much water as is needed to keep the body fluids at the right concentration. These combinations of flame cells and tube cells are called protonephredia.

In all platyhelminths the nervous system is concentrated at the head end. This is least marked in the acoels, which have nerve nets rather like those of cnidarians and ctenophores, but densest around the head. Other platyhelminths have rings of ganglia in the head and main nerve trunks running along their bodies.

Major sub-groups

Early classification divided the flatworms into four groups: Turbellaria, Trematoda, Monogenea and Cestoda. It had long been recognized that this classification was artificial, and in 1985 Ehlers proposed a phylogenetically more correct classification where the massively polyphyletic "Turbellaria" was split into a dozen orders, and Trematoda, Monogenea and Cestoda were joined in the new order Neodermata. However, the classification presented here is the early, traditional, classification, as it still is the one used everywhere except in scientific articles.

Turbellaria



The turbellarian *Pseudoceros dimidiatus*



Two turbellarians mating by penis fencing. Each has two penises, the white spikes on the undersides of their heads.

These have about 4,500 species, are mostly free-living, and range from 1 mm (0.039 in) to 600 mm (24 in) in length. Most are predators or scavengers, and terrestrial species are mostly nocturnal and live in shaded humid locations such as leaf litter or rotting wood. However, some are symbiotes of other animals such as crustaceans, and some are parasites. Free-living turbellarians are mostly black, brown or gray, but some larger ones are brightly colored. The Acoela and Nemertodermatida were traditionally regarded as turbellarians, but are now regarded as members of a separate phylum, the Acoelomorpha, or as two separate phyla. *Xenoturbella*, a genus of very simple animals, has also been re-classified as a separate phylum.

Turbellarians have no cuticle (external layer of organic but non-cellular material). In a few species the skin is a syncytium, a collection of cells with multiple nuclei and a single shared external membrane. However the skins of most species consist of a single layer of cells, each of which generally has multiple cilia (small mobile "hairs"), although in some large species the upper surface has no cilia. These skins are also covered with microvilli between the cilia. They have many glands, usually submerged in the muscle layers below the skin and connect to the surface by pores through which they secrete mucus, adhesives and other substances.

Small aquatic species use the cilia for locomotion, while larger ones use muscular movements of the whole body or of a specialized sole to creep or swim. Some are capable of burrowing, anchoring their rear ends at the bottom of the burrow and then stretching the head up to feed and then pulling it back down for safety. Some terrestrial species throw a thread of mucus which they use as a rope to climb from one leaf to another.

The acoel *Convoluta roscoffensis* swallows cells of the green alga *Tetraselmis* and does not feed as an adult, presumably relying on the alga to provide nourishment as endosymbionts. In other acoels the gut is lined by a syncytium. These and some other turbellarians have a simple pharynx lined with cilia and generally feed by using cilia to sweep food particles and small prey into their mouths, which are usually in the middle of the underside. Most other turbellarians have a pharynx that is eversible, in other words can be extended by being turned inside-out, and the mouths of different species can be anywhere along the underside. The freshwater species *Microstomum caudatum* can open its mouth almost as wide as its body is long, to swallow prey about as large as itself.

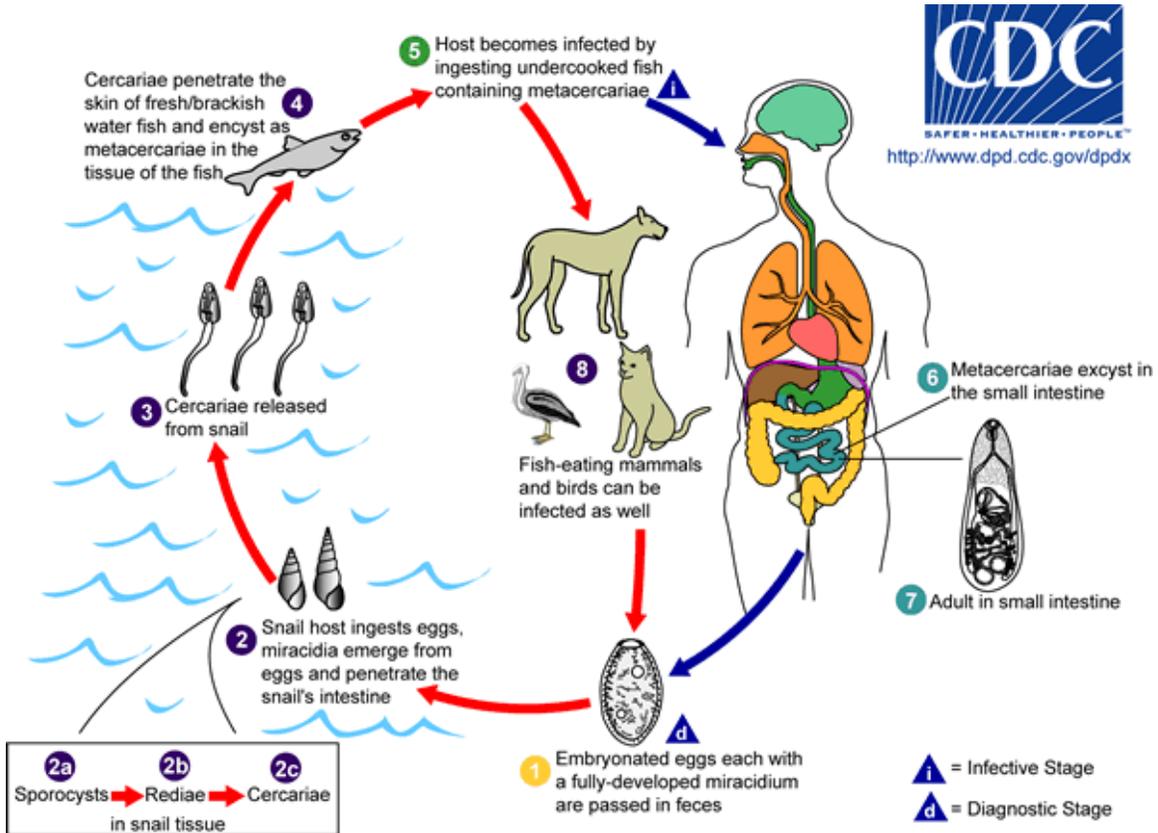
Most turbellarians have pigment-cup ocelli ("little eyes"), one pair in most species but two or even three pairs in some. A few large species have many eyes in clusters over the brain, mounted on tentacles, or spaced uniformly round the edge of the body. The ocelli can only distinguish the direction from which light is coming and enable the animals to avoid it. A few groups – mainly catenulids, acoelomorphs and seriates – have statocysts, fluid-filled chambers containing a small solid particle or, in a few groups, two. These statocysts are thought to be balance and acceleration sensors, as that is the function they perform in cnidarian medusae and in ctenophores. However, turbellarian statocysts have no sensory cilia, and it is unknown how they sense the movements and positions of the solid particles. On the other hand most have ciliated touch-sensor cells scattered over

their bodies, especially on tentacles and around the edges. Specialized cells in pits or grooves on the head are probably smell-sensors.

Planaria, a sub-group of seriates, are famous for their ability to regenerate if divided by cuts across their bodies. Experiments show that, in fragments that do not already have a head, a new head grows most quickly on those that were closest to the original head. This suggests that the growth of a head is controlled by a chemical whose concentration diminishes from head to tail. Many turbellarians clone themselves by transverse or longitudinal division, and others, especially acoels, reproduce by budding.

All turbellarians are hermaphrodites, in other words have both female and male reproductive cells, and fertilize eggs internally by copulation. Some of the larger aquatic species mate by penis fencing, a duel in which each tries to impregnate the other, and the loser adopts the female role of developing the eggs. In most species "miniature adults" emerge when the eggs hatch, but a few large species produce plankton-like larvae.

Trematoda



Life-cycle of the diogenean *Metagonimus*

These parasites' name refers to the cavity in their holdfasts (Greek τρήμα, hole), which resemble suckers and anchor them within their hosts. The skin of all species is a

syncytium, a layer of cells that shares a single external membrane. Trematodes are divided into two groups, Digenea and Aspidogastrea (also known as Aspodibothrea).

Digenea

These are often called flukes as most have flat rhomboid shapes like that of a flounder (Old English *flóc*). They have about 11,000 species, more than all other platyhelminthes combined, and second only to roundworms among parasites on metazoans. Adults usually have two holdfasts, a ring round the mouth and a larger sucker midway along what would be the underside in a free-living flatworm. Although the name "Digeneans" means "two generations", most have very complex lifecycles with up to seven stages, depending on what combinations of environments the early stages encounter – most importantly whether the eggs are deposited on land or in water. The intermediate stages transfer the parasites from one host to another. The definitive host in which adults develop is a land vertebrate, the earliest host of juvenile stages is usually a snail that may live on land or in water, and in many cases a fish or arthropod is the second host. For example, the adjoining illustration shows the life cycle of the intestinal fluke metagonimus, which hatches in the intestine of a snail; moves to a fish where it penetrates the body and encysts in the flesh; then moves to the small intestine of a land animal that eats the fish raw; and then generates eggs that are excreted and ingested by snails, thereby completing the cycle. Schistosomes, which cause the devastating tropical disease bilharzia, belong to this group.

Adults range between 0.2 mm (0.0079 in) and 6 mm (0.24 in) in length. Individual adult digeneans are of a single sex, and in some species slender females live in enclosed grooves that run along the bodies of the males, and partially emerge to lay eggs. In all species the adults have complex reproductive systems and can produce between 10,000 and 100,000 times as many eggs as a free-living flatworm. In addition the intermediate stages that live in snails reproduce asexually.

Adults of different species infest different parts of the definitive host, for example the intestine, lungs, large blood vessels, and liver. The adults use a relatively large, muscular pharynx to ingest cells, cell fragments, mucus, body fluids or blood. In both the adults and the stages that live in snails, the external syncytium absorbs dissolved nutrients from the host. Adult digeneans can live without oxygen for long periods.

Aspidogastrea

Members of this small group have either a single divided sucker or a row of suckers that cover the underside. They infest the guts of bony or cartilaginous fish and of turtles, and the body cavities of marine and freshwater bivalves and gastropods. Their eggs produce ciliated swimming larvae, and the life-cycle has one or two hosts.

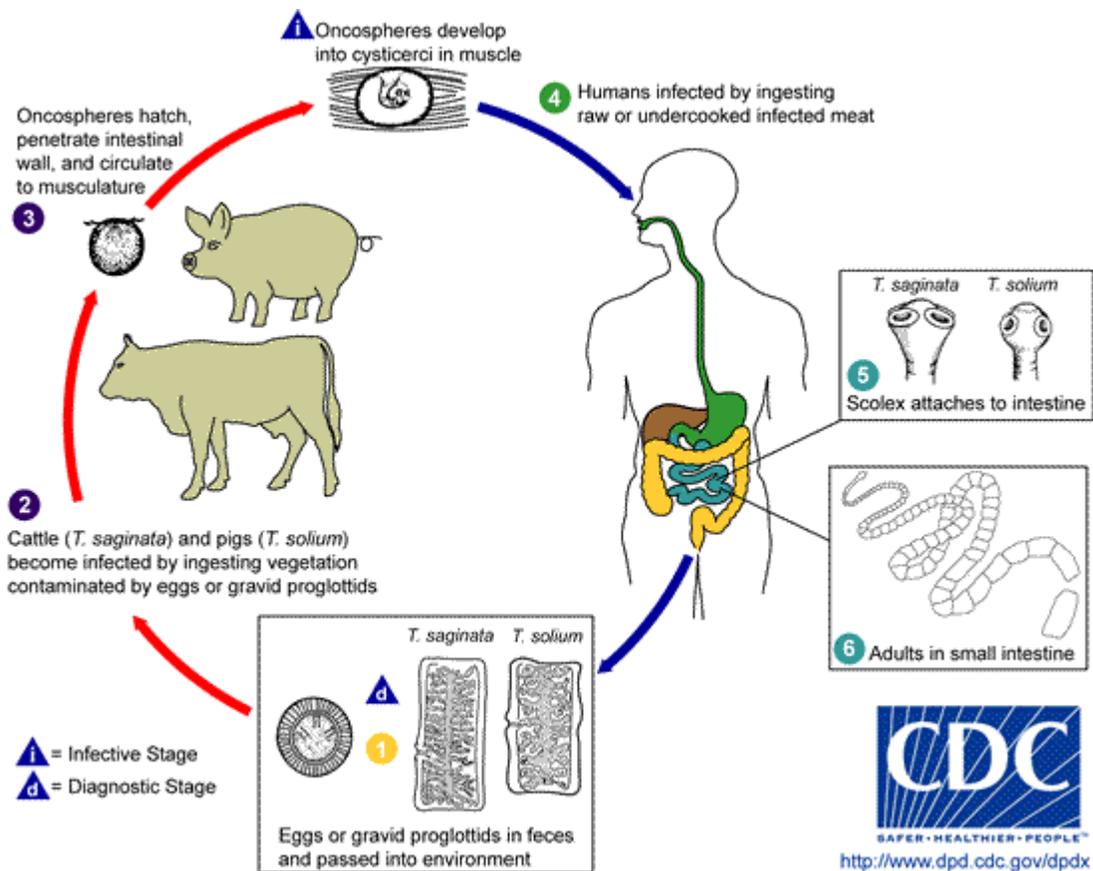
Cercomeromorpha

This group of parasites attach themselves to the host by means of disks that bear crescent-shaped hooks. They are divided into Monogenea and Cestoda.

Monogenea

There are about 1,100 species of monogeneans. Most are external parasites that require particular host species, mainly fish but in some cases amphibians or aquatic reptiles. However, some are internal parasites. Adult monogeneans have large attachment organs at the rear, haptors (Greek ἅπτειν, haptain, means "catch"), which have suckers and hooks. To minimize water-resistance they have flattened bodies. In some species the pharynx secretes enzymes that digest the host's skin, allowing the parasite to feed on blood and cellular debris. Others graze externally on mucus and flakes of the host's skin. The name "Monogenea" is based on the fact that these parasites have only one non-larval generation.

Cestoda



Lifecycle of the eucestode *Taenia*. Inset 5 shows the scolex, which has 4 suckers round the sides and, in *Taenia solium*, a disk with hooks on the end. Inset 6 shows the

tapeworm's whole body, in which the scolex is the tiny round tip in the top left corner, and a mature proglottid has just detached.

These are often called tapeworms because of their flat, slender but very long bodies – the name "cestode" is derived from the Latin word *cestus*, which means "tape". The adults of all 3,400 cestode species are internal parasites in the organs of vertebrates, including fish, cats, dogs and humans. The head is generally tiny compared to the size of the whole animal, and forms a scolex that attaches the parasite to the lining of the host's gut. The commonest type of scolex has four suckers round the sides and a disk equipped with hooks at the end. However, some species have more complex arrangements, for example *Myzophyllobothrium*'s scolex looks rather like a part-peeled banana, with four sucker-like flaps on the sides and a group of four small suckers on short stalks at the end.

Cestodes have no mouths or guts, and the syncitial skin absorbs nutrients – mainly carbohydrates and amino acids – from the host, and also disguises it chemically to avoid attacks by the host's immune system. Shortage of carbohydrates in the host's diet stunts the growth of the parasites and kills some. Their metabolisms generally use simple but inefficient chemical processes, and the parasites compensate by consuming large amounts of food relative to their size.

In the majority of species, known as eucestodes ("true tapeworms"), the neck produces a chain of segments called proglottids by a process known as strobilation. Hence the most mature proglottids are furthest from the scolex. Adults of *Taenia saginata*, which infests humans, can form proglottid chains over 20 metres (66 ft) long, although 4 metres (13 ft) is more typical. Each proglottid has both male and female reproductive organs. If the host's gut contains two or more adults of the same cestode species, they generally fertilize each other; but proglottids of the same worm can fertilize each other and even fertilize themselves. When the eggs are fully developed, the proglottids separate and are excreted by the host. The eucestode life-cycle is less complex than that of digeneans, but varies depending on the species. For example:

- Adults of *Diphyllobothrium* infest fish, and the juveniles use copepod crustaceans as intermediate hosts. Excreted proglottids release their eggs into the water, and the eggs hatch into ciliated swimming larvae. If a larva is swallowed by a copepod, it sheds the cilia and the skin becomes a syncitium and the larvae makes its way into the copepod's hemocoel (internal cavity that is the main part of the circulatory system) and attached itself with three small hooks. If the copepod is eaten by a fish, the larva metamorphoses into a small, unsegmented tapeworm, drills through to the gut and becomes an adult.
- Various species of *Taenia* infest the guts of humans, cats and dogs. The juveniles use herbivores – for example pigs, cattle and rabbits – as intermediate hosts. Excreted proglottids release eggs that stick to grass leaves and hatch after being swallowed by a herbivore. The larva makes its way to the herbivore's muscles and metamorphoses into an oval worm about 10 millimetres (0.39 in) long, with a scolex that is kept inside. When the definitive host eats infested and raw or

undercooked meat from an intermediate host, the worm's scolex pops out and attaches itself to the gut, and the adult tapeworm develops.

A smaller group, known as Cestodaria, have no scolex, do not produce proglottids, and have body shapes like those of diogeneans. Cestodarians parasitize fish and turtles.