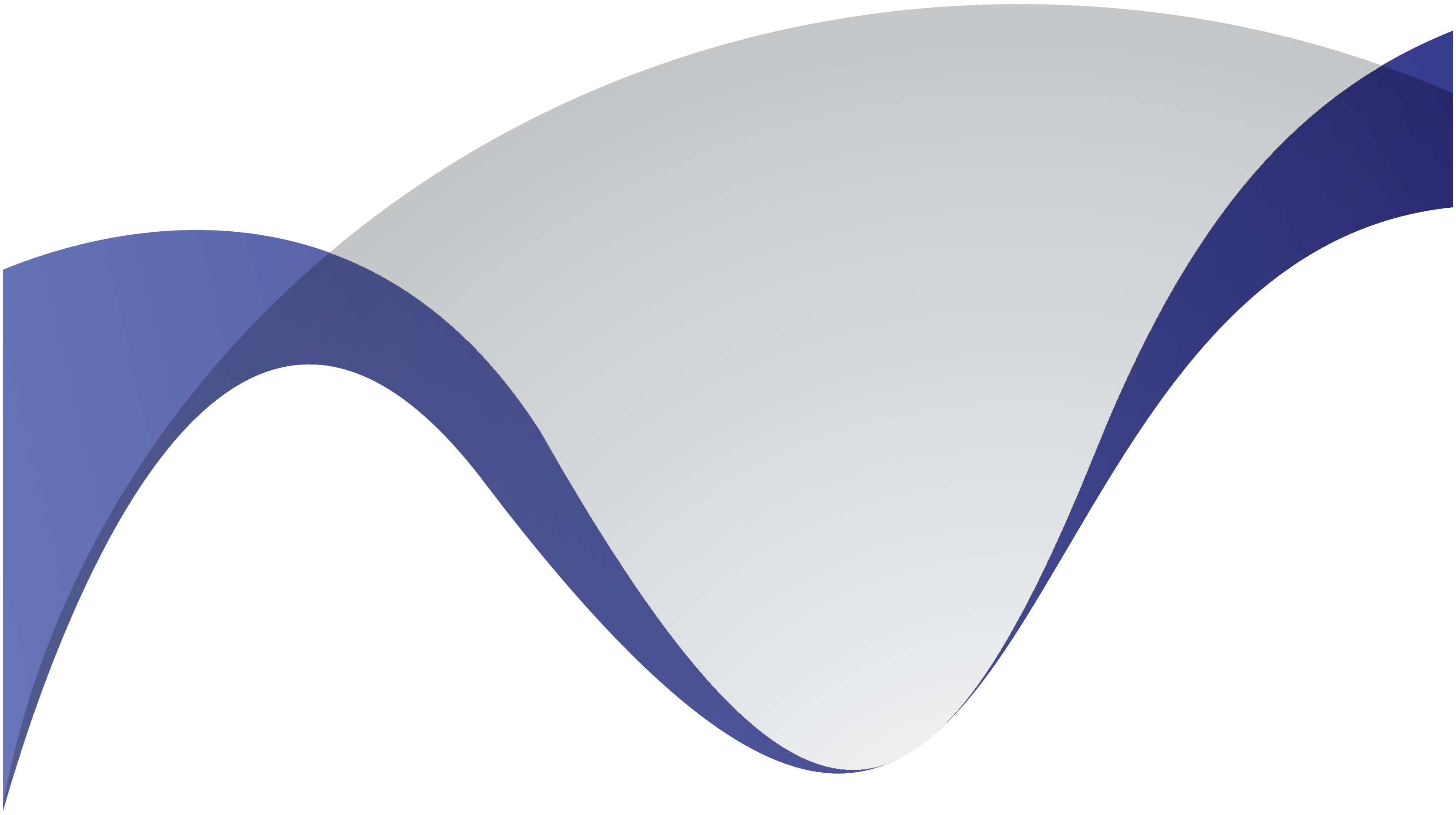
Invertebrate Zoology

An Introduction



Jean Wilkinson

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Preface

The animals which do not have a backbone are known as invertebrates. The sub-discipline of zoology which focuses on invertebrates is known as invertebrate zoology. Some of the different animals which are dealt within this discipline are tunicates, echinoderms, sponges and worms. There are various areas of study within invertebrate zoology such as arthropodology, helminthology, cnidariology and invertebrate paleontology. Different insects and spiders are studied under the subdiscipline of arthropodology. Helminthology studies parasitic worms and Cnidariology deals with the study of cnidaria such as anemones and jellyfish. Invertebrate paleontology is the study of fossil invertebrates. This book discusses the fundamentals as well as modern approaches of invertebrate zoology. Some of the diverse topics covered herein address the varied branches that fall under this category. This book will serve as a reference to a broad spectrum of readers.

A foreword of all chapters of the book is provided below:

Chapter 1 - The animals which don’t possess a vertebral column are known as invertebrates. The branch of zoology which is involved in the study of invertebrates is called invertebrate zoology. The diverse aspects of invertebrates as well as invertebrate zoology have been briefly introduced in this chapter.; **Chapter 2** - The types of invertebrate animals which have an exoskeleton, paired appendages and a segmented body are called arthropods. Arthropodology is the study of different categories of arthropods such as arachnids, crustaceans and centipedes. This chapter discusses in detail these arthropods as well as their classifications.; **Chapter 3** - The phylum of animals who are found exclusively in aquatic environments are called cnidaria. The branch of zoology which is involved in the study of cnidaria is known as cnidariology. There are four major groups within cnidarian, namely, Anthozoa, Scyphozoa, Cubozoa and Hydrozoa. The topics elaborated in this chapter will help in gaining a better perspective about these groups of cnidaria.; **Chapter 4** - The branch of study which focuses on parasitic worms is called helminthology. Some of the different categories of worms studied within this field are Platyhelminthes and Aschelminthes. This chapter has been carefully written to provide an easy understanding of the varied facets of these phyla of helminthes.; **Chapter 5** - Malacology refers to the branch of invertebrate zoology which is involved in the study of molluscs. Some of the different categories of molluscs studied within this field are Aplacophorans and Polyplacophora. The topics elaborated in this chapter will help in gaining a better perspective about these categories of molluscs.; **Chapter 6** - There are a number of invertebrate phyla, apart from the ones which have been discussed in the previous chapters. Some of these are Porifera and Annelida. The chapter closely examines these invertebrate phyla to provide an extensive understanding of the subject.

At the end, I would like to thank all the people associated with this book devoting their precious time and providing their valuable contributions to this book. I would also like to express my gratitude to my fellow colleagues who encouraged me throughout the process.

Jean Wilkinson

1

Introduction to Invertebrates and Invertebrate Zoology

The animals which don't possess a vertebral column are known as invertebrates. The branch of zoology which is involved in the study of invertebrates is called invertebrate zoology. The diverse aspects of invertebrates as well as invertebrate zoology have been briefly introduced in this chapter.

Invertebrate

Invertebrate is a term used to describe any animal without a backbone or spinal column. The group includes about 97 percent of all animal species; that is, all animals except vertebrates, (subphylum Vertebrata of the phylum Chordata), which have a backbone or spinal column. Invertebrates include simple organisms, such as sponges and flatworms, and more complex animals, such as arthropods and molluscs. Vertebrates include the familiar fish, reptiles, amphibians, birds, and mammals. Since invertebrates include all animals except a certain group, invertebrates form a paraphyletic group.

Ubiquitous and filling diverse niches, invertebrates are integral to the ecology, productivity, and harmony of all ecosystems, and central to the extraordinary diversity of life that is so cherished by humans.

Invertebrate Zoology

Invertebrate zoology is the study of animal biodiversity. "Invertebrates" include all animals exclusive of vertebrates, in an artificial division set up centuries ago. Of the 34 or so major divisions (phyla) of animal life, 33 and 2/3 are "invertebrate".

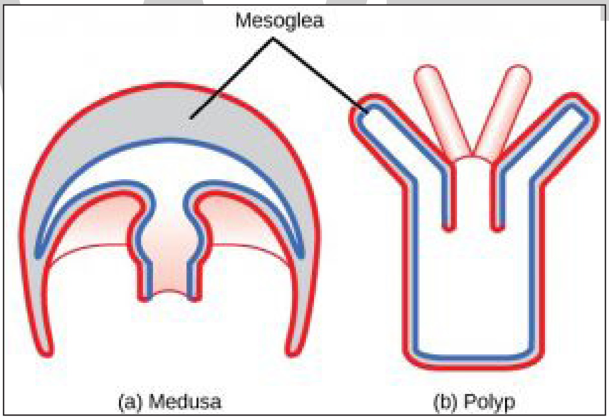
Porifera (Sponges)

The simplest of all the invertebrates, Porifera (sponges) do not display tissue-level organization, although they do have specialized cells that perform specific functions. Sponge larvae are able to swim; however, adults are non-motile and spend their life attached to a substratum. Since water is vital to sponges for excretion, feeding, and gas exchange, their body structure facilitates the movement of water through the sponge.

Cnidaria

The phylum Cnidaria contains about 10,000 described species divided into four classes: Anthozoa, Scyphozoa, Cubozoa, and Hydrozoa. The anthozoans, the sea anemones and corals, are all sessile species, whereas the scyphozoans (jellyfish) and cubozoans (box jellies) are swimming forms. The hydrozoans contain sessile forms and swimming colonial forms. The phylum Cnidaria includes animals that show radial or biradial symmetry and are diploblastic, that is, they develop from two embryonic layers. Nearly all (about 99 percent) cnidarians are marine species.

Animals in this phylum display two distinct morphological body plans: polyp or medusa. An example of the polyp form is *Hydra* spp.; perhaps the most well-known medusoid animals are the jellies (jellyfish). Polyp forms are sessile as adults, with a single opening to the digestive system (the mouth) facing up with tentacles surrounding it. Medusa forms are motile, with the mouth and tentacles hanging down from an umbrella-shaped bell. Still, some cnidarians are polymorphic, that is, they have two body plans during their life cycle (e.g., *Obelia)*.



Cnidarians have two distinct body plans, the medusa (a) and the polyp (b) All cnidarians have two membrane layers, with a jelly-like mesoglea between them.

Cnidarians contain specialized cells known as cnidocytes ('stinging cells') containing organelles called nematocysts (stingers). These cells are present around the mouth and tentacles, and serve to immobilize prey with toxins contained within the cells. The cnidarians then perform extracellular digestion in which the food is taken into the gastrovascular cavity, enzymes are secreted into the cavity, and the cells lining the cavity absorb nutrients. The gastrovascular cavity has only one opening that serves as both a mouth and an anus, which is termed an incomplete digestive system. There is no explicit excretory system nor must circulatory system, thus wastes and gases simply diffuse from the cells into the water outside the animal or in the gastrovascular cavity.

All cnidarians show the presence of two membrane layers in the body that are derived from the endoderm and ectoderm of the embryo. The outer layer (from ectoderm) is called the epidermis and lines the outside of the animal, whereas the inner layer (from endoderm) is called the gastrodermis and lines the digestive cavity. Between these two membrane layers is a non-living, jelly-like mesoglea connective layer. In terms of cellular complexity, cnidarians show the presence of differentiated cell types in each tissue layer, such as nerve cells (and a primitive nervous system. including motor and sensory neurons), contractile epithelial cells, enzyme-secreting cells, and nutrient-absorbing cells, as well as the presence of intercellular connections. However, the development of organs or organ systems is not advanced in this phylum.

Protostomes: Lophotrochozoa and Ecdysozoa

Protostomes are animal in which the blastopore, or the point of involution of the ectoderm or outer germ layer, becomes the mouth opening to the future gut. This is called protostomy or 'first mouth.' In protostomy, solid groups of cells split from the endoderm or inner germ layer to form a central mesodermal layer of cells. This layer multiplies into a band and then splits internally to form the coelom, or body cavity.

Lophotrochozoa (Flatworms, Rotifers, Worms and Molluscs)

The lophotrochozoans are having three cell layers (triploblastic), as they possess an embryonic mesoderm sandwiched between the two cell layers (ectoderm and endoderm) found in the diploblastic cnidarians. These phyla are also bilaterally symmetrical, meaning that a longitudinal section will divide them into right and left sides that are symmetrical. It also means the beginning of cephalization, the evolution of a concentration of nervous tissues and sensory organs in the head of the organism, which is where it first encounters its environment.

Phylum Platyhelminthes (Flatworms)

Most of the flatworms are classified in the superphylum Lophotrochozoa. The flatworms are acoelomate organisms that include many free-living and parasitic forms, including important parasites of humans.

A marine flatworm in East Timor.

The flatworms are acoelomates, so their bodies are solid between the outer surface and the cavity of the digestive system. There is neither a circulatory nor respiratory system, with gas and nutrient exchange dependent on diffusion and cell-cell junctions. This necessarily limits the thickness of the body in these organisms, constraining them to be flat.

Most flatworm species are monoecious, and fertilization is typically internal. Asexual reproduction is common in some groups.

Phylum Rotifera

The rotifers are a microscopic (about 100 μm to 30 mm) group of mostly aquatic organisms that get their name from the corona, a rotating, wheel-like structure that is covered with cilia at their head. Rotifers obtain their food by the current created by the movement of the corona. The rotifers are filter feeders that will eat dead material, algae, and other microscopic living organisms, and are therefore very important components of aquatic food webs.

The body form of rotifers consists of a head (which contains the corona), a trunk (which contains the organs), and the foot. Rotifers are typically free-swimming and truly planktonic organisms, but the toes or extensions of the foot can secrete a sticky material forming a holdfast to help them adhere to surfaces. The head contains sensory organs in the form of a bi-lobed brain and small eyespots near the corona.

(a) Bdelloidea

(a) Monogonota

Figure shown are examples from two of the three classes of rotifer. (a) Species from the class Bdelloidea are characterized by a large corona, shown separately from the whole animals in the center of this scanning electron micrograph. (b) *Polyarthra*, from the class Monogononta, has a smaller corona than Bdelloid rotifers, and a single gonad, which give the class its name.

Rotifers are pseudocoelomates commonly found in freshwater and some salt water environments throughout the world. Rotifers are dioecious organisms (having either male or female genitalia) and exhibit sexual dimorphism (males and females have different forms). Many species are parthenogenic and exhibit haplodiploidy, a method of sex determination in which a fertilized egg develops into a female and an unfertilized egg develops into a male. In many dioecious species, males are short-lived and smaller with no digestive system and a single testis. Females can produce eggs that are capable of dormancy for protection during harsh environmental conditions.

Phylum Annelida (Worms)

Annelida includes the segmented earthworms we typically mean of when we say ‘worm’ colloquially, but polychaete worms and leeches belong to this group as well. These animals are found in marine, terrestrial, and freshwater habitats, but a presence of water or humidity is a critical factor for their survival, especially in terrestrial habitats. Animals in this phylum show parasitic and commensal symbioses with other species in their habitat.

Annelids show protostomic development in embryonic stages and display bilateral symmetry. Key to this group, annelids have a segmented body plan wherein the internal and external morphological features are repeated in each body segment. This feature allows animals to become bigger by adding ‘compartments’ while making their movement more efficient. The overall body can be divided into head, body, and pygidium (or tail).

Although there are some exceptions, annelids generally possess many complex features:

- A true coelom, derived from embryonic mesoderm and protostomy.
- A closed circulatory system of dorsal and ventral blood vessels that run parallel to the alimentary canal as well as capillaries that service individual tissues.
- A well-developed nervous system including a nerve ring and nerve.
- Well-developed and complete digestive system is present with a mouth, muscular pharynx, esophagus, crop, and gizzard being present (in oligochaetes and many others).

However, despite many complex features, annelids lack a well-developed respiratory system; instead, gas exchange occurs across the moist body surface. Excretion is facilitated by a pair of metanephridia (a type of primitive ‘kidney’ that consists of a convoluted tubule and an open, ciliated funnel) that is present in every segment towards the ventral side.

Annelids may be either monoecious with permanent gonads (as in earthworms and leeches) or dioecious with temporary gonads that develop (as in polychaetes). However, cross-fertilization is preferred in hermaphroditic animals. These animals may also show simultaneous hermaphroditism and participate in simultaneous sperm exchange when they are aligned for copulation.

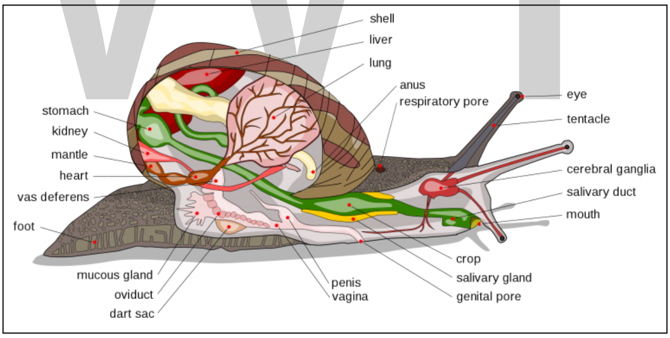
Phylum Mollusca

Phylum Mollusca is predominantly a marine group of animals; however, they are known to inhabit freshwater as well as terrestrial habitats. It is estimated that 23 percent of all known marine species are mollusks, making them the second most diverse phylum of animals. You may know them as clams, oysters, mussels, scallops, snails, slugs, conchs, as well as octopi, squids, cuttlefish, and ammonites.

Mollusks display a wide range of morphologies in each class and subclass, but share a few key characteristics: a muscular foot used for anchorage, a visceral mass containing internal organs, and a mantle that may or may not secrete a shell of calcium carbonate.


(a) (b)

(a) Snails and (b) slugs are both mollusks, but slugs lack a shell.



There are many species and variations of mollusks; this illustration shows the anatomy of an aquatic gastropod mollusk.

Mollusks are eucoelomate, but the coelomic cavity is restricted to a cavity around the heart in adult animals. These organisms possess a visceral mass containing their digestive, nervous, excretory, reproductive, and respiratory systems. Mollusk species that are exclusively aquatic have gills for respiration, whereas some terrestrial species have lungs for respiration. The mantle is the dorsal epidermis in mollusks; shelled mollusks are specialized to secrete a chitinous and hard calcareous shell.

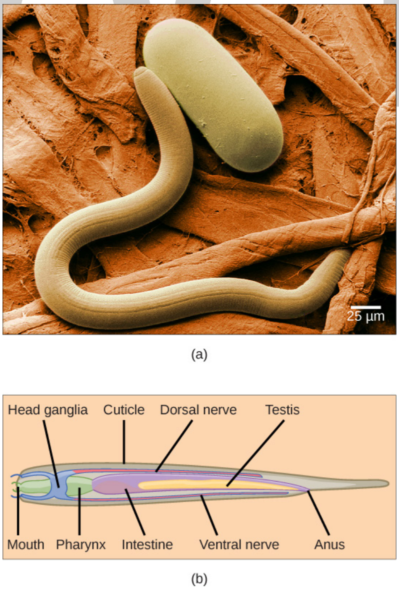
Sexual dimorphism is seen in this class of animals. Members of a species mate, and the female then lays the eggs in a secluded and protected niche. Females of some species care for the eggs for an extended period of time and may end up dying during that time period. Some species also hatch eggs which produce juvenile adults, skipping earlier life stages completely.

Ecdysozoa: Nematode Worms and Arthropods

The superphylum Ecdysozoa contains an incredibly large number of species. The name derives from the word ecdysis, which refers to the shedding, or molting, of the exoskeleton. The phyla in this group have a hard cuticle that covers their bodies, which must be periodically shed and replaced for them to increase in size. The cuticle provides a tough, but flexible exoskeleton that protects these animals from water loss, predators and other aspects of the external environment. Ecdysozoa is so large because it contains two of the most diverse animal groups: phylum Nematoda (the roundworms) and Phylum Arthropoda (the arthropods).

Phylum Nematoda (Roundworms)

The Nematoda are triploblastic and possess an embryonic mesoderm that is sandwiched between the ectoderm and endoderm. They possess a pseudocoelom and are also bilaterally symmetrical. Furthermore, the phylum includes more than 28,000 species with an estimated 16,000 being parasitic in nature. The free-living nematode, *Caenorhabditis elegans* has been extensively used as a model system in laboratories all over the world.



Scanning electron micrograph shows (a) the soybean cyst nematode (*Heterodera glycines*) and a nematode egg. (b) A schematic representation shows the anatomy of a typical nematode.

The overall morphology of these worms is cylindrical. The head is radially symmetrical. These animals show the presence of a complete digestive system with a distinct mouth and anus. This is in contrast with the cnidarians, where only one opening is present (an incomplete digestive system). The muscles of nematodes differ from those of most animals: they have a longitudinal layer only, which accounts for the whip-like motion of their movement.

Phylum Arthropoda

The name Arthropoda means ‘jointed legs’ in Greek. It is the largest phylum in Animalia containing an estimated 85 percent of known species and many arthropods yet undocumented. Phylum Arthropoda includes animals that have been successful in colonizing terrestrial, aquatic, and aerial habitats. This phylum is further classified into five subphyla: Trilobitomorpha (trilobites, all extinct), Hexapoda (insects and relatives), Myriapoda (millipedes, centipedes, and relatives), Crustaceans (crabs, lobsters, crayfish, isopods, barnacles, and some zooplankton), and Chelicerata (horseshoe crabs, arachnids, scorpions, and daddy longlegs).

The principal characteristics of all the animals in this phylum are functional segmentation of the body and presence of jointed appendages. Arthropods also show the presence of an exoskeleton made principally of chitin, which is a waterproof, tough polysaccharide. Arthropods are eucoelomate, protostomic organisms, of which insects form the single largest class.

Respiratory systems vary depending on the group of arthropod: insects and myriapods use a series of tubes (tracheae) that branch through the body, open to the outside through openings called spiracles, and perform gas exchange directly between the cells and air in the tracheae, whereas aquatic crustaceans utilize gills, terrestrial chelicerates employ book lungs, and aquatic chelicerates use book gills.

Groups of arthropods also differ in the organs used for excretion, with crustaceans possessing green glands and insects using Malpighian tubules, which work in conjunction with the hindgut to reabsorb water while ridding the body of nitrogenous waste. Generally, a central cavity, called the hemocoel (or blood cavity), is present, and the open circulatory system is regulated by a tubular or single-chambered heart.

Subphylum Hexapoda

An example of a hexapod insect, the Yellow Jacket.

The name Hexapoda denotes the presence of six legs (three pairs) in these animals as differentiated from the number of pairs present in other arthropods. Hexapods are characterized by the presence of a head, thorax, and abdomen. Many of the common insects we encounter on a daily basis, including ants, cockroaches, butterflies, and flies, are examples of Hexapoda. This is also the largest class in terms of species diversity as well as biomass in terrestrial habitats. These organisms have note that insects have developed digestive, respiratory, circulatory, and nervous systems.

Subphylum Myriapoda

Myriapoda includes arthropods with numerous legs, varying from 10 to 750. This subphylum includes 13,000 species; the most commonly found examples are millipedes and centipedes. All myriapods are terrestrial animals and prefer a humid environment.

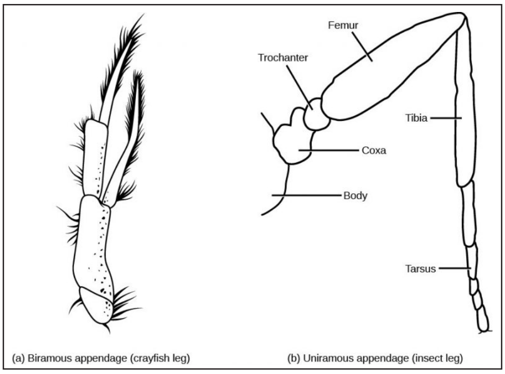
(a) The *Scutigera coleoptrata* centipede has up to 15 pairs of legs. (b) This North American millipede (*Narceus americanus)* bears many legs, although not a thousand, as its name might suggest.

Subphylum Crustacea

Crustaceans are the most dominant aquatic arthropods, since the total number of marine crustacean species stands at 67,000, but there are also freshwater and terrestrial crustacean species. Krill, shrimp, lobsters, crabs, and crayfish are examples of crustaceans. Terrestrial species like the wood lice (*Armadillidium* spp.), also called pill bugs, rolly pollies, potato bugs, or isopods, are also crustaceans, although the number of non-aquatic species in this subphylum is relatively low.

Crustaceans possess two pairs of antennae, mandibles as mouthparts, and head and thorax that is fused to form a cephalothorax. They also have a biramous (‘two branched’) appendage, which means that their legs are formed in two parts, as distinct from the uniramous (‘one branched’) myriapods and hexapods.

The exoskeletons of many species are also infused with calcium carbonate, which makes them even stronger than in other arthropods. Crustaceans have an open circulatory system where blood is pumped into the hemocoel by the dorsally located heart.



(a) Biramous appendage (crayfish leg)

(b) Uniramous appendage (insect leg)

Arthropods may have (a) biramous (two-branched) appendages or
(b) uniramous (one-branched) appendages.

Most crustaceans are dioecious, which means that the sexes are separate. Some species like barnacles may be hermaphrodites. Serial hermaphroditism, where the gonad can switch from producing sperm to ova, may also be seen in some species. Fertilized eggs may be held within the female of the species or may be released in the water. Terrestrial crustaceans seek out damp spaces in their habitats to lay eggs.

Subphylum Chelicerata

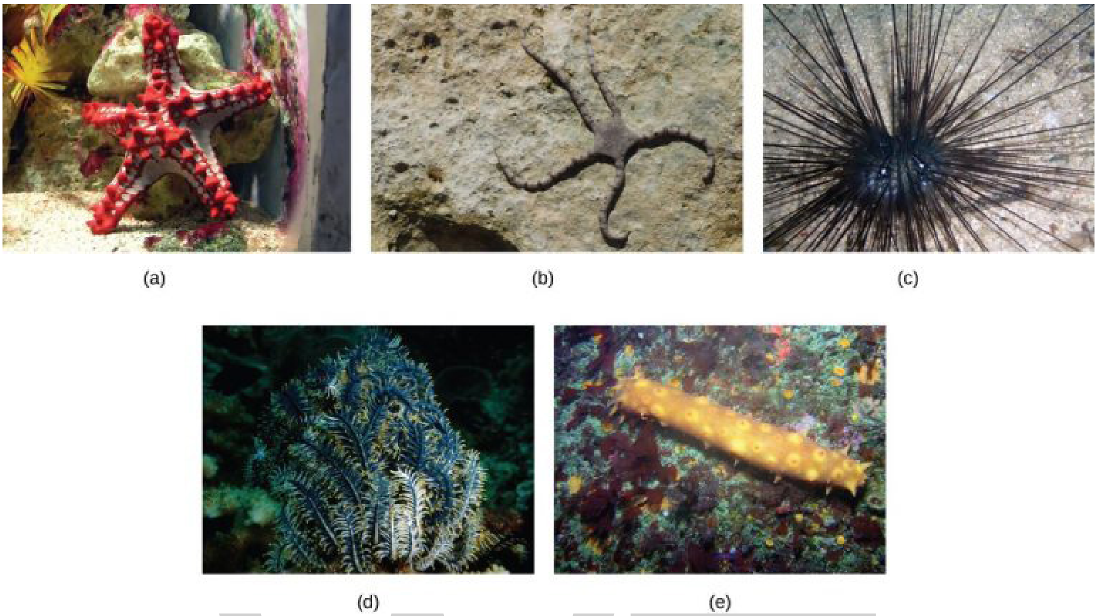
The Chelicerates include spiders, scorpions, horseshoe crabs, and sea spiders. This subphylum is predominantly terrestrial, although some marine species also exist. The phylum derives its name from the first pair of appendages: the chelicerae, which are specialized, claw-like or fang-like mouth parts. The body of chelicerates may be divided into two parts, with a relatively large abdomen and a comparatively smaller cephalothorax. These animals do not possess antennae.

Members of this subphylum have an open circulatory system with a heart that pumps blood into the hemocoel. Aquatic species have gills, whereas terrestrial species have either trachea or book lungs for gaseous exchange. Most chelicerates ingest food using a preoral cavity, but some chelicerates may secrete digestive enzymes to pre-digest food before ingesting it, or make use of evolved blood-sucking apparatuses, as in mites and ticks.

The nervous system in chelicerates consists of a brain and two ventral nerve cords. These animals use external fertilization as well as internal fertilization strategies for reproduction, depending upon the species and its habitat. Parental care for the young ranges from absolutely none to relatively prolonged care.

Invertebrate Deuterostomes: Echinodermata

Different members of Echinodermata include the (a) sea star of class Asteroidea, (b) the brittle star of class Ophiuroidea, (c) the sea urchins of class Echinoidea, (d) the sea lilies belonging to class Crinoidea, and (e) sea cucumbers, representing class Holothuroidea.



The phyla Echinodermata and Chordata (the phylum in which humans are placed) both belong to the superphylum Deuterostomia. However, echinoderms are actually invertebrates; this group broke from the branch that would later develop a vertebral column in the chordate lineage.

Echinodermata are so named owing to their spiny skin, and are exclusively marine organisms. Sea stars, sea cucumbers, sea urchins, sand dollars, and brittle stars are all examples of echinoderms.

Adult echinoderms have a calcareous endoskeleton and exhibit pentaradial symmetry, although the early larval stages of all echinoderms have bilateral symmetry. Gonads are present in each arm. These animals possess a true coelom that is modified into a unique circulatory system called a water vascular system. By using hydrostatic pressure, the animal can either protrude or retract the tube feet to pump water to move and force open mollusk shells during feeding.

The nervous system in these animals is a relatively simple structure with a nerve ring at the center and five radial nerves extending outward along the arms. Echinoderms may also undergo external fertilization, asexual reproduction, and/regeneration of body parts lost in trauma.

2

Understanding Arthropodology

The types of invertebrate animals which have an exoskeleton, paired appendages and a segmented body are called arthropods. Arthropodology is the study of different categories of arthropods such as arachnids, crustaceans and centipedes. This chapter discusses in detail these arthropods as well as their classifications.

Arthropodology is a biological discipline that focuses on the arthropods. Arthropods are invertebrates that belong to the phylum Arthropoda. This phylum is the largest among the phyla in the animal kingdom. They include the insects, the arachnids, the myriapods and the crustaceans. These animals are grouped under this phylum based on the features common to them. They have multiple paired jointed limbs and a hard chitinous exoskeleton. The exoskeleton is a hard outer casing that protects their soft internal organs. Arthropodology deals with these animals and aims to understand their evolution, anatomy, biology, and ecological importance.

Arthropodology that studies the parasitic mode of life of certain arthropods is referred to as medical arthropodology. Apart from parasitic arthropods, there are also arthropod species that act as vectors of disease. An example of that would be the mosquito. Certain species of mosquitoes serve as vectors for disease-causing viruses and parasites. Mosquito-borne viral diseases include the yellow fever, dengue fever, and zika. Mosquito-borne parasitic diseases are malaria and lymphatic filariasis.

Arthropodology may be subdivided into the following fields based on the animal groups that they study: arachnology (studies spiders and other arachnids), entomology (studies insects), carcinology (studies crustaceans), and myriapodology (studies myriapods).

Arthropod

Arthropod is any member of the phylum Arthropoda, the largest phylum in the animal kingdom, which includes such familiar forms as lobsters, crabs, spiders, mites, insects, centipedes, and millipedes. About 84 percent of all known species of animals are members of this phylum. Arthropods are represented in every habitat on Earth and show a great variety of adaptations. Several types live in aquatic environments, and others reside in terrestrial ones; some groups are even adapted for flight.

The distinguishing feature of arthropods is the presence of a jointed skeletal covering composed of chitin (a complex sugar) bound to protein. This nonliving exoskeleton is secreted by the underlying epidermis (which corresponds to the skin of other animals). Arthropods lack locomotory cilia, even in the larval stages, probably because of the presence of the exoskeleton. The body is usually segmented, and the segments bear paired, jointed appendages, from which the name arthropod ("jointed feet") is derived. About one million arthropod species have been described, of which most are insects. This number, however, may be only a fraction of the total. Based on the number of undescribed species collected from the treetops of tropical forests, zoologists have estimated the total number of insect species alone to be as high as 10,000,000. The 30,000 described species of mites may also represent only a fraction of the existing number.

The phylum Arthropoda is commonly divided into four subphyla of extant forms: Chelicerata, Crustacea, Hexapoda, and Myriapoda. Some zoologists believe that arthropods possessing only single-branched appendages, particularly the insects, centipedes, and millipedes, evolved from a separate ancestor and therefore group them within a separate phylum—the Uniramia, or Atelocerata; however, in this treatment these forms are dispersed among several subphyla. In addition, the phylum Arthropoda contains the extinct subphylum Trilobitomorpha. This group is made up of the trilobites, the dominant arthropods in the early Paleozoic seas (542 million to 251 million years ago). Trilobites became extinct during the Permian Period (299 million to 251 million years ago) at the end of the Paleozoic Era.

The myriapods (centipedes, symphylans, millipedes, and pauropods) live beneath stones and logs and in leaf mold; insects are found in all types of terrestrial habitats and some have invaded fresh water. The sea has remained the domain of the crustaceans, however, and only at its very edges are insects (subphylum Hexapoda) found.

The subphylum Crustacea contains mostly marine arthropods, though many of its members, such as the crayfish, have invaded fresh water, and one group, the pill bugs (sow bugs), has become terrestrial, living beneath stones and logs and in leaf mold. In the sea, large crustaceans such as crabs and shrimps are common bottom-dwelling arthropods. Many minute species of crustaceans (particularly the copepods) are an important component of the zooplankton (floating or weakly swimming animals) and serve as food for other invertebrates, fishes, and even whales.

Most members of the subphylum Chelicerata belong to the class Arachnida, containing the spiders, scorpions, ticks, and mites. They are largely terrestrial arthropods, living beneath stones and logs, in leaf mold, and in vegetation, but there are some aquatic mites that live in fresh water and in the sea. There are also many parasitic mites. Two small classes of chelicerates, the Merostomata, containing the horseshoe crabs, and the Pycnogonida, containing the sea spiders, are entirely marine. The merostomes are an ancient group and probably gave rise to the arachnids. Indeed, the earliest known fossil scorpions were aquatic.

General Features

Size Range

Most arthropods are small animals. Only aquatic forms are able to attain substantial sizes, because their bodies are supported in part by the surrounding water. The extinct chelicerate Eurypterida, for example, reached a length of 1.8 metres (5.9 feet), and some modern spider crabs may weigh up to 6.4 kilograms (14 pounds) and span 3.8 metres or more. Terrestrial arthropods do not grow very large. The largest adult insects and spiders do not weigh more than 100 grams (0.22 pound); however, there is evidence that larvae of *Megasoma actaeon*, a type of rhinoceros beetle, can sometimes exceed 200 grams (0.44 pound). The beetle *Goliathus regius* measures 15 centimetres (5.9 inches) in length and 10 centimetres in width, while the butterfly *Ornithoptera victoriae* of the Solomon Islands has a wing span exceeding 30 centimetres (about 1 foot). One of the longest insects is the phasmid (walkingstick) *Phryganistria chinensis*, a specimen of which measured 62.4 centimetres (about 2 feet) in length. The phasmid *Phobaeticus chani* reaches a length of more than 30 centimetres. The smallest arthropods include some parasitic wasps, beetles of the family Ptiliidae, and mites that are less than 0.25 millimetre (0.01 inch) in length, despite their complex structures.

Distribution and Abundance

Arthropods are found in almost all of the habitats that cover the Earth's surface. Minute copepods (typically less than 1 millimetre long) are among the most abundant animals on Earth, especially in marine surface waters. Many other crustaceans live in the sea at depths exceeding 4,000 metres, while the insect collembolans and jumping spiders have been found on Mount Everest at heights exceeding 6,700 metres. Collembolans and the oribatid mites are among the permanent inhabitants of Antarctica. Brine shrimp are found in some saltwater lakes, and beetles, mites, and various crustaceans have been taken from hot springs. Minute crustaceans inhabit underground waters in many parts of the world, and deserts support a large arthropod fauna, especially insects and arachnids. Arthropods are the only invertebrates capable of flight.

The numbers and diversity of arthropod insect pests are enormous. A bag filled with leaf mold from a forest floor, for example, will contain hundreds of arthropods, including mites, spiders, false scorpions, myriapods, a great variety of insects, and crustacean pill bugs. In the spring a temporary pool often teems with minute crustaceans.

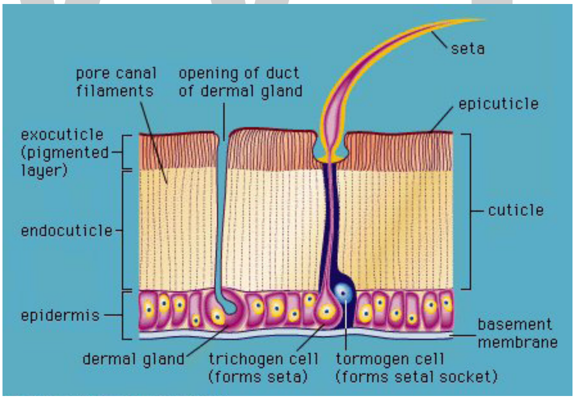
Importance

Arthropods are of great direct and indirect importance to humans. The larger crustaceans—shrimps, lobsters, and crabs—are used as food throughout the world. Small planktonic crustaceans, such as copepods, water fleas, and krill, are a major link in the food chain between the photosynthetic phytoplankton and the larger carnivores, such as many fish and whales. Although many species of insects and mites attack food crops and timber, arthropods are of enormous benefit to human agriculture. Approximately two-thirds of all flowering plants are pollinated by insects, and soil and leaf-mold arthropods, which include insects, mites, myriapods, and some crustaceans (pill bugs), play an important role in the formation of humus from decomposed leaf litter and wood.

Form And Function

The Exoskeleton and Molting

The success of arthropods derives in large part from the evolution of their unique, nonliving, organic, jointed exoskeleton, which not only functions in support but also provides protection and, with the muscle system, contributes to efficient locomotion. The exoskeleton is composed of a thin, outer protein layer, the epicuticle, and a thick, inner, chitin–protein layer, the procuticle. In most terrestrial arthropods, such as insects and spiders, the epicuticle contains waxes that aid in reducing evaporative water loss. The procuticle consists of an outer exocuticle and an inner endocuticle. In the exocuticle there is cross-bonding of the chitin–protein chains (tanning), which provides additional strength to the skeletal material. The hardness of various parts of the exoskeleton in different arthropods is related to the thickness and degree of tanning of the exocuticle. In crustaceans, additional rigidity is achieved by having the exoskeleton impregnated with varying amounts of calcium carbonate.



Diagrammatic section through the arthropod integument.

The formation of an exoskeleton required the simultaneous solution of two functional problems in the evolution of arthropods: If the animal is encased in a rigid covering, how can it grow and how can it move? The problem of growth is solved in arthropods by molting, or ecdysis, the periodic shedding of the old exoskeleton. The underlying cells release enzymes that digest the base of the old exoskeleton (much of the endocuticle) and then secrete a new exoskeleton beneath the old one. At the time of actual shedding, the old skeleton splits along specific lines characteristic of the group, and the animal pulls out of the old skeleton as from a suit of clothes. The old skeleton is usually abandoned but in some species is eaten. The new exoskeleton, which is soft and flexible, is then stretched by localized, elevated blood pressure augmented by the intake of water or air. Hardening occurs by stretching and especially by tanning within a number of hours of molting. In crustaceans, calcium carbonate is deposited into the new procuticle. (Soft-shell crabs are simply newly molted crabs.) Additional endocuticle may be added to the exoskeleton for some days or weeks following molting.

Molting is under hormonal control, and there is a long preparatory phase that precedes the process. The steroid hormone ecdysone, secreted by specific endocrine centres and circulated in the blood, is the direct initiator of molting. The actual timing of a molt, however, is regulated by other hormones and commonly by environmental factors. The interval between molts is called an instar. Because of the frequency of molts, instars are short early in life but grow longer with increasing age. Some arthropods, such as most spiders and insects, stop molting when they reach sexual maturity; others, like lobsters and crabs, molt throughout their lives. Most of the larger spiders of temperate regions, for example, molt about 10 times before reaching sexual maturity. As a result of molting, the length and volume of an arthropod display steplike increases over the life span, but internal tissue growth is continual as in other animals.

Loss of a limb is a common hazard in the life of many arthropods. Indeed, some arthropods, such as crabs, are capable of amputating an appendage if it is seized by a predator. The limb is then regenerated from a small, nipplelike rudiment formed at the site of the lost limb. The new limb develops beneath the old exoskeleton during the premolt period and then appears when the animal molts.

Muscles, Appendages and Locomotion

Arthropods are unusual among invertebrates; they lack locomotory cilia, even as larvae. The problem that a rigid external covering imposes on movement has been solved by having the exoskeleton divided into plates over the body and through a series of cylinders around the appendages. At the junction, or joints, between the plates and cylinders the exoskeleton is thin and flexible because it lacks the exocuticle and because it is folded. The folds provide additional surface area as the joints are bent. The arthropod’s exoskeleton is therefore somewhat analogous to the armour encasing a medieval knight.

Most arthropods move by means of their segmental appendages, and the exoskeleton and the muscles, which attach to the inside of the skeleton, act together as a lever system, as is also true in vertebrates. The external skeleton of arthropods is a highly efficient system for small animals. The exoskeleton provides a large surface area for the attachment of muscles and, in addition to functioning in support and movement, also provides protection from the external environment. The cylindrical design resists bending, and only a relatively small amount of skeletal material need be invested in thickness to prevent buckling. The external skeleton imposes limits on the maximum size of an arthropod, especially in those that live on land. The largest arthropods live in the sea, where they gain considerable support from the buoyance of seawater. On land, an excessive amount of skeleton would be required to support a large bulk and, in addition, the new soft skeleton might collapse following a molt.

Appendages of arthropods have been adapted for all types of locomotion—walking, pushing, running, swimming, and burrowing. In most arthropods the legs move alternately on the two sides of the body; i.e., when one leg is in a power stroke, its mate on the opposite side of the body is in the recovery stroke (the same is true of mammals when walking). The legs in front or back are a little ahead or behind in the movement sequence. Because of the lateral position of the legs, the body of an arthropod tends to hang between them. Leg interference and trunk wobble tend to be problems in an animal with a long trunk and many legs, such as a millipede or a centipede. Most arthropods have evolved more-compact bodies and a smaller number of legs. The number of pairs of legs used in walking is not more than seven in pill bugs (terrestrial crustaceans), four or five in shrimps and crabs, four in arachnids, and three in insects. This reduces the problem of mechanical interference. When a ghost crab, for example, is running rapidly across a beach or dune, only the second, third, and fourth pairs of the five pairs of legs (counting the claws) are employed. Leg interference is further reduced in most arthropods by varying limb length and placement. For example, in *Scutigera,* the centipede commonly seen in houses, the legs increase in length from front to back and thus pass over or under one another in stepping. The tendency for the trunk to wobble has been reduced in some centipedes by having overlapping dorsal plates and in millipedes by having pairs of segments fused to form double segments. Many arthropods are capable of walking on vertical surfaces. Some simply grip minute surface irregularities with the claws at the end of the legs. Others, such as certain spiders and flies, have an array of specialized gripping hairs at the ends of the legs.

Insect wings are not segmental appendages as are the legs. The paired wings arise as lateral folds of the integument, one pair above each of the last two pairs of legs. Each wing thus consists of an upper and lower sheet of exoskeleton closely applied to each other. The two skeletal sheets are separated at various places, forming tubular supporting veins. Unlike the wings of an airplane, the wings of insects are flat plates, and lift is obtained by changing the angle at which the front margin of the wing meets the oncoming air stream. The evolution of flight is one of several adaptations that have enabled insects to become the most diverse and populous group of terrestrial animals.

A burrowing habit has evolved in some insects, such as mole crickets and ants, but the largest burrowers are crustaceans. Mole crabs and box crabs are rapid burrowers in soft marine sands, and various species of mantis shrimps, mud shrimps, and snapping shrimps create elaborate burrows below the bottom surface. Crustaceans also include the largest number of arthropod tube dwellers, surpassed only by certain marine worms (polychaetes). Most of the tube-dwelling crustaceans are amphipods. Their tubes are usually composed of sand or mud particles secreted together and attached to bottom objects; there are, however, some amphipods that carry their tubes with them like a portable house.

Digestive System and Feeding

Arthropods exhibit every type of feeding mode. They include carnivores, herbivores, detritus feeders, filter feeders, and parasites, and there are specializations within these major categories. Typically, paired appendages around the mouth are used for collecting and handling food and are usually specialized in accordance with the particular diet of the animal. For example, the insect family Aphididae has mouthparts adapted for piercing vegetation and sucking out plant juices. The crustacean fiddler crabs, which emerge from burrows on sand flats at low tide, scoop up the surface sand with their small claws (only one in the male) and place the sand within their mouthparts, where it is sifted with fine hairs. The organic material is consumed, and the mineral material is ejected as a small "spitball." Where there is a large population of crabs, ejected material may cover the surface of a flat by the end of the low-tide period. The crustacean mole crabs, or sand crabs, of surf beaches use their antennae to filter plankton from the receding waves after reburying themselves. Planktonic crustacean copepods only a few millimetres long can collect up to several hundred thousand diatoms every 24 hours with certain appendages (maxillae) near the mouth. A number of carnivorous arthropods, notably spiders, pseudoscorpions, and centipedes, capture prey with poison, which is usually delivered with a pair of appendages; scorpions use a single stinger at the tip of the tail. In spiders, the poison is introduced through a pair of fangs (chelicerae) flanking the mouth, and in centipedes the poison claws lie beneath the head. Few of these species have venom that is fatal to humans.

The front and back parts of the digestive tract (foregut and hindgut) are lined with the same skeletal material that is found on the outside of the body and that is molted with the rest of the skeleton. Only the relatively small middle section (midgut) lacks a chitinous lining. The digestive tract varies greatly in structure, depending upon the diet and feeding mode of the animal. In general, however, the midgut region is the principal site of enzyme production and absorption of digested food. The enzymes may pass forward into the front part of the gut and even outside into the body of the prey, in the case of spiders.

Respiratory System

Aquatic arthropods (crustaceans and the chelicerate horseshoe crabs) possess gills for respiration. Although they vary in structure and location, the gills are always outgrowths of the integument (skin) and are therefore covered by the exoskeleton, which is thin in this area and not a barrier to the exchange of gases. Terrestrial arthropods possess tracheae and book lungs as respiratory organs. Tracheae are a system of tiny tubes that permit passage of gases into the interior of the body. In some arthropods the tracheal tubes are bathed by blood, but in insects the minute terminal endings (tracheoles) are embedded in the tissues, even within muscle cells. The tracheal tubes (but not the tracheoles) are molted along with the rest of the exoskeleton. Tracheae are a unique arthropod invention and undoubtedly evolved numerous times in the phylum, for they are found in myriapods, insects, and arachnids. Tracheal systems are highly efficient for these small, terrestrial animals. The small, external openings (spiracles) reduce water loss, the chitinous lining prevents collapse, and the small size of the arthropod and consequent short length of the tubule eliminates the need for moving gases in and out by active ventilation (diffusion usually being sufficient). Book lungs are chitin-lined internal pockets containing many blood-filled plates over which air circulates. Most spiders possess tracheae and book lungs, but large spiders (such as tarantulas) and scorpions possess book lungs alone.

Circulatory System

Arthropods possess an open circulatory system consisting of a dorsal heart and a system of arteries that may be very limited (as in insects) or extensive (as in crabs). The arteries deliver blood into tissue spaces (hemocoels), from which it eventually drains back to a large pericardial sinus surrounding the heart. A varying number of paired openings (ostia) are located along the length of the heart and permit blood to flow in when the valves are open. When the heart is contracting, closed valves prohibit the blood from flowing back and force it into the arteries of the tissues, from which it flows to other hemocoels. In the larger crustaceans, the blood then passes through the gills (where it becomes oxygenated) on its return to the heart. The blood of large arachnids and crustaceans contains the blue, oxygen-carrying pigment hemocyanin; insects lack a respiratory pigment since the tracheal system delivers oxygen directly to the tissues. A few insect larvae and some small crustaceans have blood containing hemoglobin.

Excretory System and Water Balance

Crustaceans and arachnids possess paired excretory organs (maxillary, antennal, or coxal glands) that open at the bases of certain appendages. Myriapods, insects, and some arachnids, such as spiders and mites, possess another type of excretory organ, Malpighian tubules, which open into the intestine. Thus in these animals both excretory and digestive wastes exit from the anus.

Water loss through evaporation is a major problem for animals that live on land, especially small ones like arthropods and an array of defenses against desiccation have evolved. Both arachnids and insects possess waxy compounds in the epicuticle, the outer layer of the exoskeleton, which greatly reduce evaporative water loss. Arthropods that lack a waxy epicuticle, such as the pill bugs, and very small arthropods, such as mites, pseudoscorpions, and collembolans, live in leaf mold and soil, beneath logs, under stones, and in other areas where the danger of desiccation is reduced. The waxes in the epicuticle not only reduce water loss but can also act as a water repellent, reducing the danger of submersion in droplets of rain or dew. This resistance to wetting enables aquatic insects, such as beetles, to carry below the surface a film of air, which can then be used in respiration. It also contributes to the ability of water striders to move over the surface of water without breaking through the surface film.

Both insects and spiders eliminate their nitrogenous wastes as compounds insoluble in water (uric acid, guanine), thereby not requiring that water be excreted. Insects share with birds and mammals the ability to produce urine that is saltier than the blood, which is of great value in conserving water because it permits the production of concentrated urine.

Nervous System and Organs of Sensation

The arthropod nervous system consists of a dorsal brain and a ventral, ganglionated longitudinal nerve cord (primitively paired) from which lateral nerves extend in each segment. The system is similar to that of annelid worms, from which arthropods may have evolved. The neuromuscular organization of arthropods is quite different from that of vertebrates, in which one neuron supplies a number of muscle cells, together forming a functional motor unit. The small size of the muscles prohibits such an organization in arthropods. Instead, the state of contraction of an arthropod muscle is determined by which of several different types of neurons supplying one muscle cell are fired.

The sense organs (sensilla) on the body surface involve some specialization of the exoskeleton barrier. The sensory nerve endings are lodged in cuticular hairs (setae), peg-like projections, cones, pits, or slits, which may occur in large numbers on antennae, mouthparts, joints, and leg tips. Changes in the tension of the surrounding cuticle stimulate the nerve endings. For example, the legs of spiders and scorpions possess slits in the exoskeleton that are covered by a thin membrane to which a neuronal receptor is attached below. Tension changes in the exoskeleton cause slight movements in the cuticular membrane and stimulate the receptors. Slits of varying length may be grouped together like the strings of a harp. Slit sense organs enable spiders to detect web vibrations produced by trapped insects, and they permit scorpions to detect ground vibrations produced by approaching prey. Chemoreceptive sensilla (taste and smell) have holes in the cuticle permitting the chemical substances being monitored to enter.

Most arthropods possess eyes, but in most species they function only to detect the intensity of light and the direction of the light source. The ability to detect objects is more restricted. Among arthropods the greatest visual acuity is found in the predaceous mantis shrimp, some crabs, and many insects, all of which possess compound eyes. Compound eyes are extremely effective in detecting motion. The eight eyes of spiders are not of the compound type, but in the case of the cursorial (hunting) wolf spiders and jumping spiders they are effective in locating and tracking prey.

Reproductive System and Life Cycle

With few exceptions, the sexes are separate in arthropods; i.e., there are both male and female individuals. The paired sex organs, or gonads, of each sex are connected directly to ducts that open onto the ventral surface of the trunk, the precise location depending upon the arthropod group.

In arthropods, sperm are commonly transferred to the female within sealed packets known as spermatophores. In this method of transfer the sperm are not diluted by the surrounding medium, in the case of aquatic forms, nor do they suffer from rapid desiccation on land. Among some arachnids, such as scorpions, pseudoscorpions, and some mites, the stalked spermatophore is deposited on the ground. Either the female is attracted to the spermatophore chemically or the deposition of the spermatophore occurs during the course of a nuptial dance, and the male afterward maneuvers the female into a position in which she can take up the spermatophore within her genital opening. Centipedes also utilize spermatophores with accompanying courtship behaviour. Among insects there are some primitive wingless groups, such as collembolans and thysanurans, in which the spermatophore is deposited on the ground, but in most insects the spermatophores are placed directly into the female genital opening by the male during copulation. Many other invertebrates, including several gastropods and chaetognaths, also use spermatophores. Many arthropods transfer free sperm rather than spermatophores. These include many crustaceans, millipedes, some insects (such as dipterans and hemipterans), spiders, and some mites.

Arthropod eggs are usually rich in yolk, but in all groups there are species whose eggs have little yolk. Some specialized methods of reproduction found among certain arthropods include the development of unfertilized eggs (parthenogenesis), the birth of living young (viviparity), and the formation of several embryos from a single fertilized egg (polyembryony).

The eggs of many crustaceans hatch into larvae which have fewer segments than the adult. The earliest larval hatching stage is a minute nauplius larva, which possesses only the first three pairs of appendages. Additional segments and appendages then appear at regular intervals with molting. There are several advantages of larval stages in the development of aquatic animals: Currents disperse the larvae, enabling some to settle in different locations from the parents; because many larvae are capable of feeding, less yolk is required in the egg; and, moreover, planktonic larvae do not compete with benthic adults.

In most chelicerates and insects, almost all of the segments are present at hatching, although in insects the body form may differ from that of the adult. Primitive insects, such as collembolans, have the adult form on hatching. Many insects, such as grasshoppers, crickets, and true bugs, hatch as nymphs, which superficially resemble the adult but lack wings. They gradually acquire these adult features during the nymphal instars. Other insects, such as beetles, butterflies, moths, flies, and wasps, hatch as larvae (grubs, caterpillars, maggots) that differ markedly from the adult. The larvae inhabit different environments and eat different foods than the adults. In these insects a pupal stage with metamorphosis bridges the gap between the larva and the adult form.

Myriapods have the general body form of the adult on hatching though they may lack some of the segments. Most millipedes hatch with only seven trunk segments. Some centipedes hatch with all of the adult trunk segments, but others have fewer than the adult.

The young of most arachnids are similar to the adult. The female scorpion gives birth to her young, which immediately climb onto her back. Female wolf spiders also carry their young, and prior to hatching they carry the white egg case attached to the posterior spinnerets. Unlike other arachnids, mites and ticks hatch as six-legged larvae, which acquire the fourth pair of legs at a later molt.

Arachnology

Arachnology is a biological discipline that deals with arachnids. It is one of the subfields of arthropodology.

Arachnology is concerned primarily with the study of the development, taxonomy, biology, evolution, and ecology of arachnids. Arachnids include the spiders, scorpions, pseudoscorpions, and harvestmen. Thus, arachnology may also be divided into more specific specialties, such as araneology (study of spiders), acarology (study of ticks and mites), and scorpiology (study of scorpions).

Arachnid

Arachnids are a group of animals that belong to the Chelicerata subphylum of the Arthropoda Phylum. These invertebrates are joint legged with a distinct characteristic of having eight legs although in some species, the front pair is used for sensory purposes. Some species also have appendages that have grown big enough to be confused with another pair of legs. Although there are approximately 98,000 described species of arachnids, it is possible that there is an estimated 600,000 potential species. Spiders are the most populous of the Arachnida class with 40,000 species, alongside solifuges (900 species), mites (32,000 species), scorpions (2,000 species), ticks (12,000 species), and harvestmen (6,300 species).

Physical Characteristics

Most fully grown arachnids have eight legs with two more pairs of appendages than insects have. These are the chelicerae used for feeding and protection and the pedipalps which are used for reproduction movement and feeding. Not all Arachnidae have eight legs; there are species of mites with eight legs, six legs, and even four legs. Apart from their legs, arachnids are also different from insects in that they do not have antennae or wings.

Arachnids have an exoskeleton protecting their body organs and a second layer of protection that is made up of cartilage. This layer is called the endosternite. Their bodies are divided into two segments, the cephalothorax and the abdomen. The cephalothorax is a merging of the thorax and the head, which is then covered by one carapace. The stomach is internally segmented with differences occurring in species. The main division is the preabdomen and the postabdomen.

Although most arachnids pose no threat to humans, some species possess poison glands used to pacify prey. The harmful spiders include the black widow and the brown recluse spiders.

Habitat

Arachnids are mostly terrestrial animals, living on land. Some of the class members inhabit fresh and marine water bodies. Terrestrial arachnids include spiders, false scorpions, mites, ticks, and daddy longlegs among others. Some spiders live on or near water while some ticks and mites are parasitic. Some species of mites that live in soil are important in the conversion of dead lives to humus.

Despite their chitinous exoskeleton, Arachnids are susceptible to drying up; a condition referred to as desiccation. Arachnids prefer well covered and protected microhabitats with a lot of humidity and less light. The cave dwellers have special characteristics like long detachable body parts, bright colors, and the absence of eyes.

Reproduction

Arachnids are lucky to possess two gonads which are present in the stomach area. The private opening is strategically located underneath the second abdominal section. Through very developed wooing rituals, the female is coerced into accepting the sperm package (spermatophore). The daddy longlegs is the only exclusion to this kind of sperm delivery. They instead directly deposit sperm into the female using a chitinized penis that is introduced in the female’s genital opening.

Diet and Feeding

Most arachnids are carnivorous, mostly feeding on smaller insects with a few exceptions like the parasitic ticks and mites and the daddy long legs which eat plants. Arachnids feed by either waiting and attacking or actively seeking prey. The parasitic kinds have improved mouth parts for sucking fluids from plants and animals.

Daddy long legs and house dust mites are the only arachnids that consume bits of food. The others rip up the kill into pieces and cover them with digestive a juice which then converts the victim into a nutritive fluid. The killer then keeps ingesting the fluid until only the exoskeleton is left.

Arachnid Classification

The class Arachnida includes 11 diverse sets of animals, 10 of which aren't Araneae, i.e., spiders. Three orders—Acari, Scorpiones and Opiliones—include familiar animals like mites, ticks, scorpions, and daddy longlegs.

Arachnids, Araneae and Beyond

Spiders, members of the class Araneae, are the largest group of arachnids, but they've got plenty of peers. All arachnids have six pairs of appendages, four of which are legs, no backbone and two body segments, one of which is a fused head and thorax. Arachnids are distributed across every continent except Antarctica, and appear in the fossil record more than 400 million years ago, which puts them among the first animals to make the transition from water to land. Eleven orders of arachnids are around today: Acari, Amblypygi, Araneae, Opiliones, Palpigradi, Pseudoscropionida, Ricinulei, Schizomida, Scorpiones, Solifugae and Thelyphonida. Three additional orders are extinct: Haptopoda, Phalangiotarbida and Trigonotarbida. Three of the extant orders—Acari, Scorpiones and Opiliones—represent some of the most well-known non-spider arachnids.

Acari, Ticks and Mites

It's hard to tell how many species of arachnids exist, in part because the taxonomic systems are always changing and in part because some species are so small and have yet to be documented. The second-largest documented group, behind spiders, is Acari, which includes mites and ticks. These animals have colonized nearly every land and marine environment and climate. Some of them eat plants or other small animals, while others act as parasites of plants or other larger animals. Many mites and ticks have a complex symbiotic relationship with the organisms on which they live. Some also spread disease. Most members of Acari are very small—mites, which are smaller than ticks, can be as little as 1/64 inch—and lack the primary body segmentation present in other arachnids.

Scorpiones: The Scorpions

Members of the arachnid order Scorpiones are scorpions. Their primary physical distinctions include claws and a 12-segment body that includes an upwardly curved tail. Scorpions live around the world, mostly in warm, dry regions and the tropics. Most range from half an inch to 10 inches long. The business end of their tail has a stinger that they use to instantly kill their prey—insects and spiders—which they hunt at night. They hide in burrows or under rocks during the day. Scorpions give birth to live young who are born one at a time over a period of weeks and cling to their mother's back until their first molt. All of them glow under UV light. Multiple species of arachnids look like true scorpions but in fact belong to other orders.

Opiliones, Harvestmen and Others

One of the most recognizable arachnids that are not a spider looks an awful lot like a spider: harvestmen, or daddy longlegs. These animals are members of the arachnid order Opiliones who live in temperate and tropical regions on every continent except Antarctica. The long, stilt-like legs of harvestmen cause many to mistake them for spiders, but they lack the ability to spin silk, have a less distinct waist between their primary body segments, and don't produce venom. Most eat insects and plants. Some Opiliones are likewise dull-colored but have short legs. Others are brightly colored and have bizarre eye decorations. Despite a persistent urban legend, harvestmen aren't poisonous and can't bite people. Some of them can produce a nasty-smelling substance, however, when they're disturbed.

Entomology

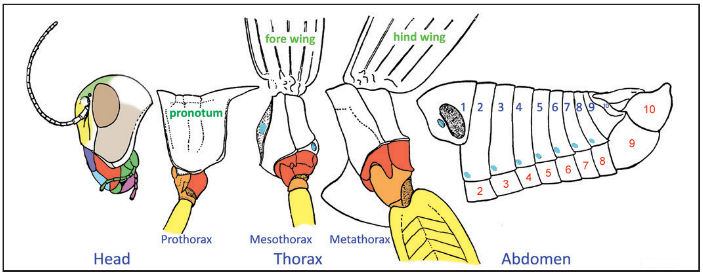
Entomology is the branch of invertebrate zoology dealing with the scientific study of insects. The zoological categories of genetics, taxonomy, morphology, physiology, behaviour, and ecology are included in this field of study. Also included are the applied aspects of economic entomology, which encompasses the harmful and beneficial impact of insects on humans and their activities. Entomology also plays an important role in studies of biodiversity and assessment of environmental quality.

Insect

Insects are the largest group in the animal kingdom. Scientists estimate there are over 1 million insect species on the planet, living in every conceivable environment from volcanoes to glaciers.

Insects help us by pollinating our food crops, decomposing organic matter, providing researchers with clues to a cancer cure, and even solving crimes. They can also harm us, such as by spreading diseases and damaging plants and structures.

Overall Body Plan



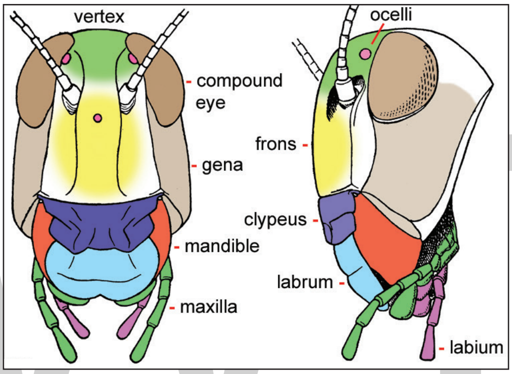
Insect Body Regions: Head, Thorax, and Abdomen.

Insects have three major body regions: head, thorax, and abdomen. The head is made of 5-7 fused segments and bears the eyes, antennae, and mouthparts.

The thorax consists of three segments called the pro-, meso-, and metathorax. Appendages used for movement are attached to the thorax. Each of the segments of the thorax bears one pair of legs and if wings are present they are found on the meso- and metathorax only. The top of the prothorax is called the pronotum.

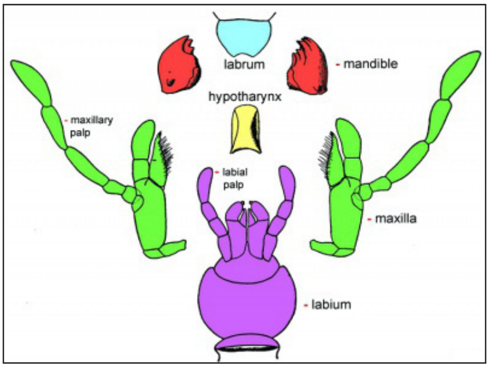
An insect's abdomen consists of 11 or fewer segments that generally do not bear any appendages, except for segments near the rear which may have appendages associated with reproduction.

Head and Mouthparts

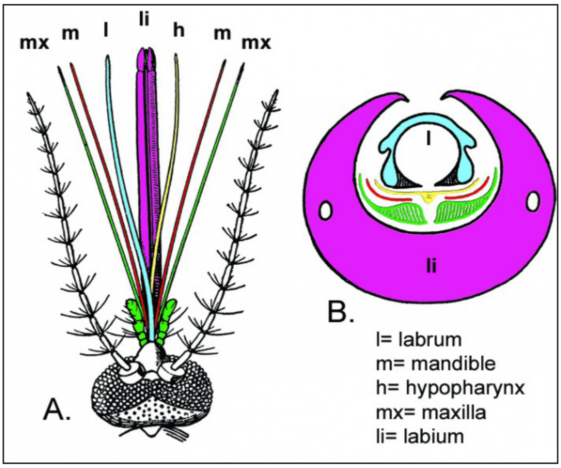


General Insect Head Regions and Mouthparts. The color of each mouthpart and region is the same throughout all the anatomy figures.

The head can be divided into general regions: The top of the head is the vertex, the side or cheeks are gena, the front of the face is the frons, and below the frons is the clypeus. These regions may be highly modified or lost in some groups of insects. Adult insects may have two types of eyes, larger compound eyes that consist of many facets (ommatidia), and eyes that occur as a single facet, ocelli. The number and placement of ocelli can be important for identification.



General Mouthparts of an insect. The color of each mouthpart is the same throughout all the anatomy figures.



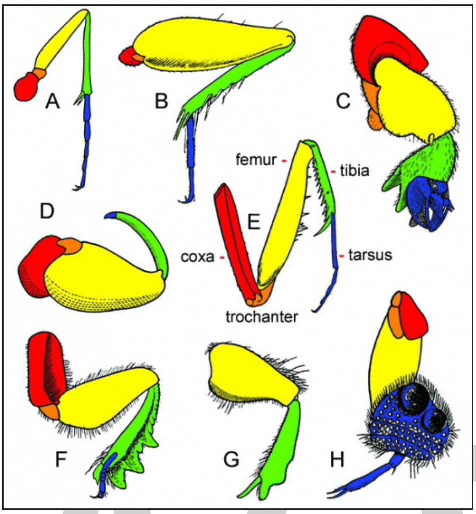
Mosquito mouthparts. The proboscis of the mosquito contains all the major mouthparts. A: Expanded mosquito proboscis. B: Cross section of proboscis. The color of each mouthpart is the same throughout all the anatomy figures.

The mouthparts of humans consist of five layers or horizons; upper lip, upper jaw, tongue, lower jaw, lower lip. Insect mouthparts also consist of five horizons and are made of appendages that have been modified for food handling. The labrum is similar to an upper lip. It is not divided but may have a notch on the outer (distal) edge. Below the labrum are the mandibles which are paired structures generally made of strong material (heavily sclerotized) and used for cutting or grinding. The specific shape and various features found on the mandibles may be very important for understanding what and how an organism eats. The hypopharynx is an internal structure located below the mandibles and has a tongue-like function. Below the mandibles (externally) are paired appendages called the maxillae. Generally each maxilla bears an appendage, the maxillary palpus that is used for food handling and may contain taste or smell organs called sensillae. The bottom horizon of insect mouthparts is the labium which is made of two fused maxilla-like structures and bears labial palps.

All insect mouthparts are modifications of this basic plan. A mosquito's proboscis contains all five mouthpart types; see the cross section in Mosquito Mouthparts. In cases of extreme modification some mouthparts may become fused, reduced, or lost. Mouthpart arrangement can be very important when studying the potential an insect has to vector a disease, access a portion of a plant, etc.

Insect Legs

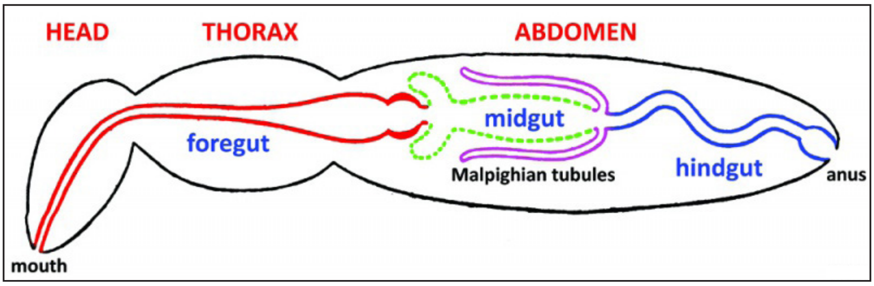
Insect have three pairs of legs, one pair on each of the three segments of the thorax and are generally called the fore-, mid-, and hind legs. Any of the pairs of legs may be heavily modified and are important for locomotion, prey capture, mating, etc. Thankfully, just like mouthparts, all insect legs contain the same basic parts. From proximal (toward or against the body) to distal (away from the body) the parts of an insect leg are: coxa, trochanter, femur, tibia, and tarsus. The tarsus almost always has one or two claws at the type used to grasp the substrate. The figure Insect Legs, right, shows legs modified for numerous purposes: A, running; B, jumping; C, digging; D, grasping; E, catching; F, walking and digging; G, reduced leg used for walking and digging; H, male leg modified for grasping females during mating.



Insect Legs. All insect legs contain the same basic parts: coxa, trochanter, femur, tibia, and tarsus, the latter of which is armed with one or two claws. The color of each leg part is the same throughout all the anatomy figures.

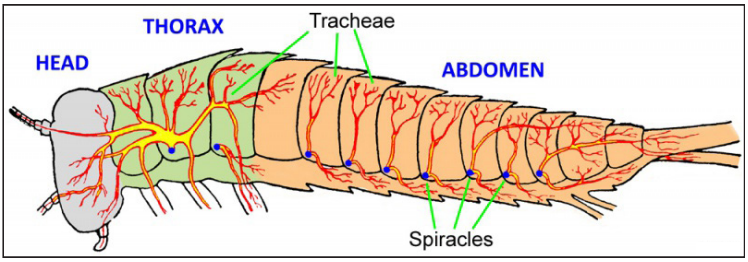
Basic Internal Anatomy

The internal anatomy of insects is amazingly complex. A good sized caterpillar has more muscles than a human. The internal anatomy of insects differs from vertebrates (including humans) in several major ways.



Digestive System. Generalized insect digestive system illustrating the three main regions.

Digestive/excretory system: Insects have a complete digestive system just like vertebrates (tube from the mouth to the anus) but it differs in a very important way. The insect digestive system has three major regions, foregut, midgut, and hindgut. The foregut and the hindgut are lined with chitin, the same stuff that makes up much of the exoskeleton of the insect. When an insect molts (sheds it's "skin",) it also sheds the internal lining of the fore- and hindguts. Loss of the gut contents is a problem if the insect relies on gut microorganisms (gut fauna) to help with digestion. The gut fauna often lives in the hind gut (termites, for example). Suddenly the gut fauna is lost and must be replenished with every molt.

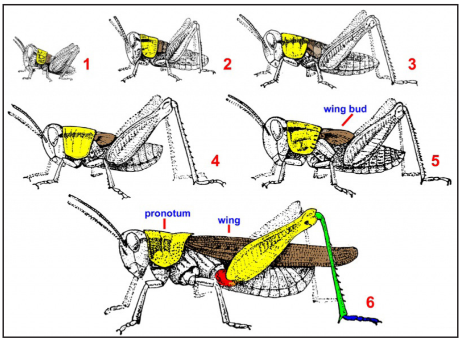


Respiratory System. Insects do not have lungs, instead they have a many tubes, tracheae, that deliver oxygen to the cells and take carbon dioxide away.

Insects do not have kidneys. Instead, metabolic wastes are removed with the Malpighian tubules.

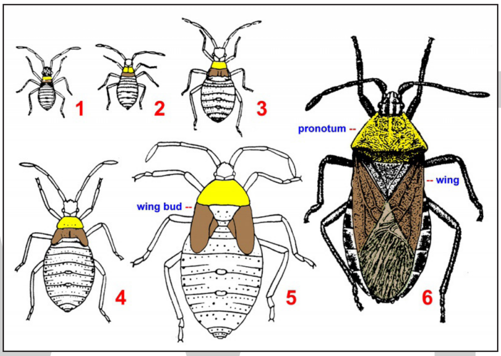
- Respiratory (ventilation) system: Insects don't have lungs. They obtain oxygen and dispel carbon dioxide through a series of tubes called tracheae. The tracheae are attached to openings on the body called spiracles. The number and placement of spiracles varies and smaller insects may not have any. Traditionally, the view has been held that respiration in insects is passive, but recent evidence has demonstrated that some insects actively expand and contract trachea to ventilate their bodies.
- Circulatory system: Insects do not have blood, or blood vessels that are part of a closed circulatory system. Instead insects have an open circulatory system where a substance called hemolymph bathes the organs directly. Some insects have a long heart-like organ along the dorsal side of the internal organs that helps circulate the hemolymph through the body. It comprises a single sheath of tissue and a series of muscles and in many insects includes a tubular portion that functions as a dorsal aorta. Hemolymph also circulates through the legs, wings, and antennae via a series of simple one-way valves.

Life Cycle



Grasshopper Life Cycle. First through fifth instars and adult grasshopper. The adult has fully formed wings, all immatures have wing buds.

Three general lifecycles occur in insects, but some insects (e.g. aphids, blister beetles, telephone-pole beetles, etc.) may have additional steps or variations. Most insects have direct internal fertilization, like mammals. This means they do not need to return to water to mate, nor do they need to worry with spermatophores like the arachnids. Most insects lay eggs, although some retain the egg inside the body until it hatches and then give "birth". Immature insect growth occurs through shedding of the skin called molting. Immature phases between molting are called instars and the growth sequence is denoted first instar, second instar, etc. Most insects grow through a specific number of instars between hatching from an egg and becoming an adult, but some insects have an indeterminate number of instars that depend on environmental temperature and food availability. In some cases appendages that were lost can be re-grown in immatures. Once an insect molts to adulthood it cannot molt again (except in some cases, such as silverfish). Adults mate (or not, many insects are parthenogenic), lay eggs (or not) and the cycle starts again.



Squash Bug Life Cycle. First through fifth instars and adult Squash bug. Note that only the adult has fully formed wings, all immatures have wing buds.

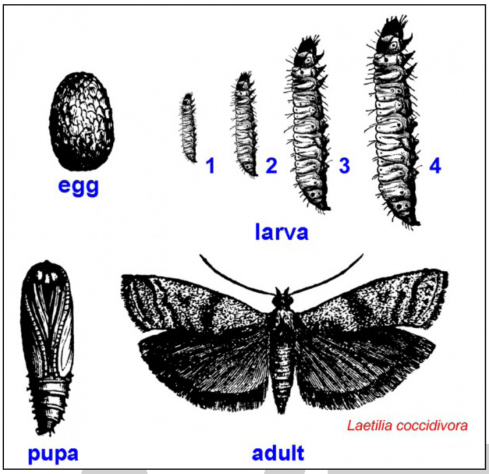
Ametabolous

Ametabolous Life Cycle: egg, multiple instars, and adult. Immatures look very similar to adults, but tend to be smaller, and lack fully formed reproductive structures. The primitively wingless orders have this life cycle: Protura, Collembola, Diplura, Microcoryphia, and Thysanura.

Hemimetabolous

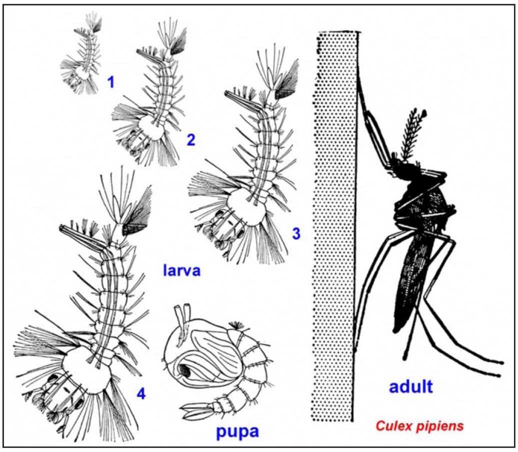
Hemimetabolous and/or Paurometabolous: egg, multiple instars, adult. "Simple metamorphosis" is the common term used to describe this life cycle. The immatures tend to look like miniature versions of the adults, except in the immature the head is larger in proportion to the body, wings are not fully formed and appear as wing buds, and reproductive structures are not developed. The Grasshopper Life Cycle and Squash Bug Life Cycle are good examples. Insect orders with this life cycle are grouped under the term Exopterygota because of visible wing buds on the immatures. Major orders of insects in this group include Orthoptera (grasshoppers and crickets), Blattodea (cockroaches), Isoptera (termites), Plecoptera (stoneflies), Thysanoptera (thrips), Hemiptera (true bugs), and Phthiraptera (lice).

Holometabolous



Laetilia coccidivora Life Cycle. The caterpillar is carnivorous and feeds on scale insects.

Holometabolous: egg, multiple instars, pupa, adult. "Complete metamorphosis" is the common term for this life cycle. The immatures look very different from the adults (e.g., caterpillar vs. butterfly, maggot vs. fly, grub vs. beetle) and never have wing buds. Insect orders with this life cycle are grouped under the term Endopterygota because immatures never had visible wing buds. The pupal stage is only found in the Endopterygota. This is typically a resting stage (e.g., the chrysalis of butterflies) where the insect undergoes a final metamorphosis from immature to adult. Major orders in the group include Coleoptera (beetles), Hymenoptera (bees, ants, and wasps), Lepidoptera (butterflies and moths), Siphonaptera (fleas), and Diptera (flies).



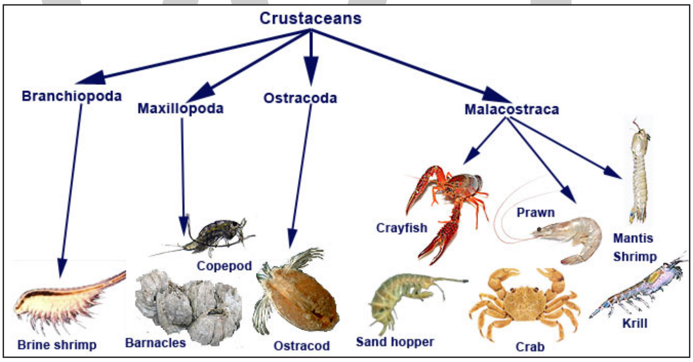
Culex pipiens Life Cycle. The larvae are commonly called "wrigglers". Unlike many holometabolous insects, the mosquito pupa can move. It is commonly called a "tumbler."

Carcinology

Carcinology is a branch of invertebrate zoology that deals with insects. Carcinology is primarily concerned with the studying of crustaceans. It attempts to study and understand various biological aspects of crustaceans, such as development, taxonomy, anatomy, physiology, genetics, evolution, distribution, and ecology of crustaceans. It has taxon-based subdivisions. An example is astacology. It is the study of crayfish. Crayfish are freshwater crustaceans characterized by their feather-like gills and morphological features similar to a lobster. Another sub-discipline is cirripedology, which is the study of barnacles. Copepodology is the sub-discipline that studies copepods.

Crustaceans

Crustaceans (make up a very large group of the Arthropods which include the crabs, lobsters, crayfish, shrimp, krill, barnacles brine shrimp, copepods, ostracods and mantis shrimp. Crustaceans are found in a wide range of habitats - most are free-living freshwater or marine animals, but some are terrestrial (e.g. woodlice), some are parasitic (e.g. fish lice) and some do not move (e.g. barnacles).



The major groups of Crustaceans.

There are over 50,000 known species of crustaceans divided into a number of major groups - the Branchiopods, the Maxillopods, the Ostracods and the Malacostraca. The Malacostraca are further divided into five groups - decapods (e.g. crabs, lobsters and shrimp), stomatopods (mantis shrimp), euphausiids (krill), amphipods (e.g. sandhoppers) and isopods (land-based) crustaceans.

Woodlouse or slater a land-living crustacean.

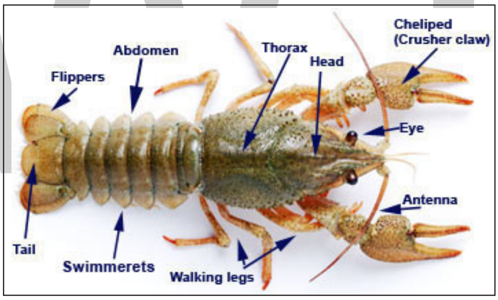
Crustaceans are invertebrates with a hard exoskeleton (carapace), a segmented body that is bilaterally symmetrical, more than four pairs of jointed appendages ("legs") and an open circulatory system (the "blood" does not flow in a closed loop). They also have eyes usually on stalks, a primitive ventral nerve cord and "brain" (ganglia near the antennae), a digestive system which is a straight tube for grinding food and a pair of digestive glands. Gills are used for respiration and they have a pair of green glands to excrete wastes (found near the base of the antennae).

Their bodies are composed of three body segments - the head, the thorax and the abdomen. In some species the head and thorax are fused together to form a cephalothorax which is covered by a single large carapace.

Each or body segment can have a pair of appendages. For example, the Malacostra have a head with 5 segments,a thorax with 8 segments and the abdomen has 6 segments.

On the segments of the head, these include two pairs of sensory antennae, one pair of mandibles (for chewing food), and two pairs of maxillae (to help the mandibles in positioning the food).

The thorax has legs, which may be specialised for use in walking or feeding. The abdomen has legs usually used for swimming (swimmerets) and ends in a fan-shaped tail (telson).



External anatomy of decapods.

Most Crustaceans are either male or female and reproduce sexually. A small number, including barnacles, are hermaphrodites. In other species, viable eggs are produced by a female without needing to be fertilised by a male.

Swimmerets

In many decapods, the first one or two pairs of swimmerets are specialised for sperm transfer by the males and the females hold the eggs until they hatch into free-swimming larvae. In many species the fertilised eggs are just released into the water or attached to objects in the water.

The larvae metamorphose through a number of stages before they become adults.

Most Crustaceans are motile (able to move about independently) and can be herbivores, carnivores or detritvores. Some are parasites and live attached to their hosts (e.g. fish lice).

Larva of a crab.

Marine crustaceans have a very wide range of predators from mammals like sea otters and seals, other crustaceans, molluscs (e.g. octopuses), sea birds, fish and humans. They protect themselves by a variety of methods - their hard exoskeletons, their chelipeds, camouflage and rapid escape (burrowing or swimming away).

Their sizes range from the Japanese spider crab with a leg span of 4.3 m to the smallest, a parasite of copepods, which is only 0.1 mm long.

A crab with its discarded, smaller exoskeleton on the right.

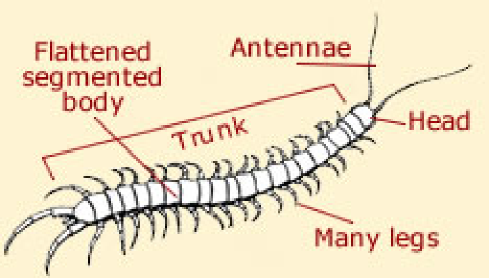
As a crustacean grows, its exoskeleton does not, so the animal must moult its old exoskeleton in order to house its expanding body. To prepare for moulting, the tissue layer under the exoskeleton detaches and secretes a new exoskeleton below the hard outer one. When the new exoskeleton is completely formed, the old exoskeleton splits along weak points and the animal pulls out, leaving its old exoskeleton intact except for the split. After a moult the animal must wait and often hide until the new exoskeleton hardens.

Myriapodology

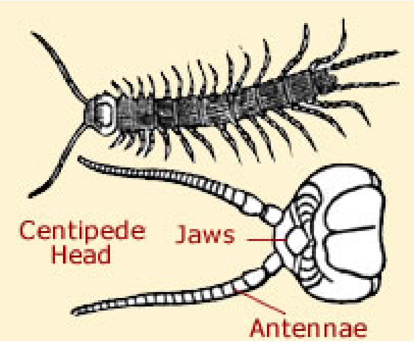
Myriapodology is a branch of invertebrate zoology that deals with myriapods. It is one of the sub-fields of arthropodology. Myriapodology deals primarily with the myriapods with the intent of understanding the myriapods' development, taxonomy, biology, evolution, distribution, and ecology. Myriapods include the millipedes, the centipedes, the symphylans, the pauropodans, and the arthropleurideans.

Centipede

Centipedes have a flattened, segmented body, long antennae, and many legs (each leg is slightly longer than the one in front of it). Centipedes have from 15 to about 177 segments (but most have about 15).



Each body segment has one pair of jointed legs attached to it. When a leg is cut off it will regenerate (grow back). The body is divided into two parts, the head and a segmented trunk. Centipedes breathe through spiracles, holes positioned along the length of the body.



The centipedes head is quite flat and covered with a round or oval shield. It carries a pair of prominent antennae, which are the animals' major sense organs, enabling it to smell and feel its way around. Many of the species are quite blind, but some carry a number of simple eyes on the front of their head shield. Even so, with a few notable exceptions, their eyesight is very poor.

The underside of the head bears a pair of stout jaws and two pairs of accessory jaws or maxillae, which hold the food whilst it is being chewed.

Curving around the sides of the head is a pair of stout poison claws with which the centipede catches and kills its prey. The poison produced by these claws is very strong and some of the large tropical centipedes can give a man a very painful and sometimes dangerous bite. Our British species however, are quite harmless, because they are all small and rarely able to pierce the skin.

Centipedes, like all arthropods, lack internal skeletons. Instead, they are covered with a hard exoskeleton made of cuticle, which protects the soft internal organs and also serves as an attachment point for the centipede’s muscles. Most of the cuticle consists of chitin, which is the same substance found in crab shells.

Most species of centipede have only one claw at the tip of their feet and run and walk on tiptoe. The house centipede has a lengthened and flattened foot, which allows it to run faster than most species.

Reproduction

Male centipedes spin a small web onto which they deposit a spermatophore for the female to take up. Sometimes this involves a courtship dance, but sometimes the males just leave the spermatophore for the females to find. In temperate areas, egg lying occurs in spring and summer, but in subtropical and tropical areas there appears to be little seasonality to centipede breeding.

Species of the Lithobiomorpha and Scutigeromorpha orders lay their eggs singly in holes in the soil, which the female then fills in and leaves. The young usually hatch with only 7 pairs of legs and gain the rest through successive molts. Scutigera coleoptera, the American house centipede, hatches with only 4 pairs of legs and in successive molts has 5, 7, 9, 11 and 15, before becoming a sexually mature adult. It takes about 3 years for S. coleoptera to achieve adulthood; however, like millipedes, centipedes are relatively long-lived when compared to their insect cousins. The European Lithobius forficatus can live for 5–6 years.

Females of the orders Geophilomorphapha and Scolopendromorpha show far more parental care. The eggs, 15–60 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, or young, or to eat them. Abandoned eggs tend to fall prey to fungi rapidly, and thus breeding is difficult to study in these species. The very large female S. gigantea centipedes, a member of the Scolopendromorpha order, exhibit parental care, guarding and tending their nests of eggs.

Millipede

Millipedes are arthropods in the class 'diplopoda'.

This class contains around 10,000 species, 15 orders and 115 families. Millipedes are found in most parts of the world from back gardens to Rainforests, on all continents except Antarctica.

The Class Diplopoda is divided into three subclasses.

Millipedes are arthropods in the class 'diplopoda'.

The subclass 'Penicillata' contains 160 species millipedes whose exoskeleton is not calcified (consisting of, or containing, calcareous matter or lime salts) and which are covered in setae (a stiff hair) or bristles.

The subclass 'Pentazonia' contains the short-bodied pill millipedes, which are capable of rolling themselves into a ball (pictured below). The subclass 'Helminthomorpha' contains the great majority of the species. Most millipedes have small distributions because they move so slowly.

Habit and Habitat of Millipedes

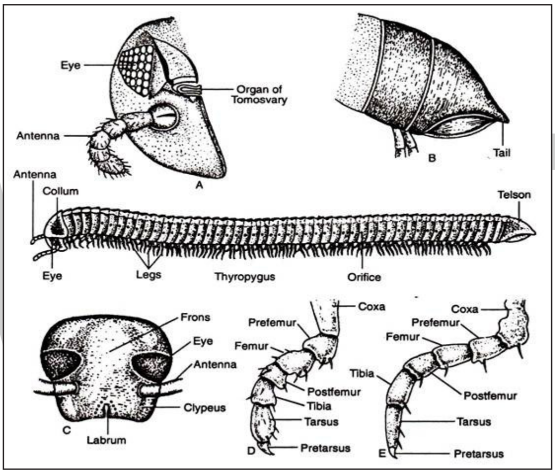
During rainy season Thyropygus lives in moist soil and during drought it lives within burrows under the upper layers of the soil. They love to stay in calcareous soil and have special attraction for sugar and manure. The secretion of stink gland from some large millipedes may produce wound on the human skin. The species described here is known as Thyropygus poseidon.

External Structures

An adult Thyropygus may be of 6 to 7 cm in length and 7-8 mm in breadth. The body is dark-brown in colour with red patches in the mid-dorsal region.

The body is divisible into:

1. A small head.
2. Extended trunk.



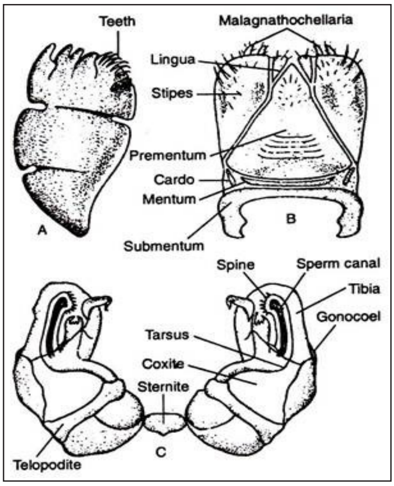
External features of the millipede. Thyropygus. A. Leteral side of the head (magnified). B. Lateral side of the posterior end (magnified). C. Frontal view of the head (magnified). D. led from one of the anterior five segments. E. leg from one of the last five segments.

Head

The head is curved anteroventrally and has powerful exoskeletal thickenings on its anterior, dorsal and lateral walls. The tergite of the first segment is called collum which fully covers the head anteriorly, dorsally and laterally to form a head capsule.

Posteriorly the head capsule remains in contact with the tergite of second segment and ventrally with a plate-like gnathochillarium. The head capsule is constituted anteriorly by a median frons, a pair of clypeo-lateral lobes. Each lobe is formed of a clypeus and labrum.

The labrum is broad, freely movable and united with the ventral side of the clypeus. On the ventral side labrum constitutes a sinus. The clypeolabral lobe extends to form a concave epipharyngeal surface in the pre- oral cavity and sets freely on the anterior margin of the mandibles.



Mandible (A), Gnathochillarium (B) and Gonopods (C) of Thyropygus.

The ventral gnathochillarium is made up of fused maxillae and is divisible into following parts:

1. Prementum: Median, triangular plate,
2. Mentum,
3. Submentum: Slender and elongated plates present posterior to prementum,
4. Stipes: One pair, one on each lateral and anterior side of prementum. Each stipe bears posteriorly a small cardo and anteriorly a pair of palps, called malagnathochillaria, carrying sensory organs, called basiconic sensillae,
5. Lingua: Present in between the apex of prementum and stipes. On each side another triangular plate, called lingua, is present with lingual lobe.

Head bears following structures:

1. Eye: Paired eyes occur one on each side of the frons. The middle of each eye is raised to a point. Each eye is an aggregation of simple eyes and is provided with skeletal ocular ridges.
2. Organ of Tomosvary: Paired sensory organs, present one on each side and slightly ventral to the eye.
3. Antenna: Paired antennae, originate one from each anterior side of the head. Each antenna is seven-segmented and placed within membranous antennal socket.

Trunk

The trunk contains nearly 47- 48 segments. All the segments are doubled and such possession of diplosegments is regarded as the characteristic feature of millipeds. Each segment has both exoskeletal and endoskeletal coverings.

The cuticle in each segment is completely ring-like. The segments are attached with one another by a thin membrane. The terminal segment or anal segment or telson is more or less triangular and bears a short upwardly directed curved tail.

The trunk region contains following structures:

1. Legs: The first five segments superficially appear to be single and carry only one pair of legs in each segment, while remaining segments have two pairs of legs in each of them. Each leg has following parts—coxa, prefemur, femur, post-femur, tibia, tarsus, pretarsus and a terminal claw. In males, the legs of the seventh trunk segment are modified as intromittent organs and known as gonopods.

2. Stink glands: The paired openings of the stink gland are present on the dorso-lateral side of each trunk segment, excepting first five and last few segments. Inside the body cavity, each stink gland is globular and sac-shaped. It has a long neck called ejaculatory duct which possesses a cuticular tongue near its opening.

   The ejaculatory duct and the tongue are provided with muscles and nerves. The secretion generally oozes out through the opening but may also be darted as a jet.

3. Stigmata: These minute opening are present ventro-laterally on each segment. The first (three segments bear one pair of stigmata while the Remaining segments have two pairs in each of them. These openings communicate with the inner tracheal pockets or pouches.

4. Anus: It is the posterior-most terminal opening of the alimentary canal and present in the last segment and directed ventrally.

Integumentary System

The integument is represented by an outer cuticle and inner epidermis. During summer cuticle may be distinctly separated into epicuticle and procuticle, but in rainy season epicuticle disappears. The procuticle is again divided into a thin homogeneous outer exocuticle and thick, lamella ted inner endocuticle. The epidermis includes one layer of large cells on a sheath of basement membrane.

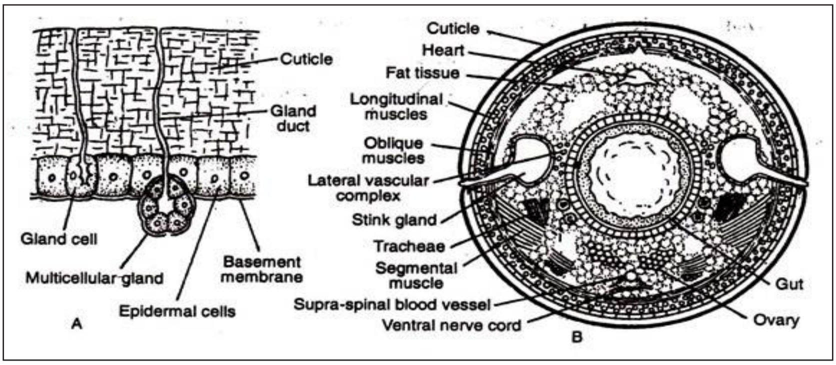
The epidermal cells perform three important functions:

1. Secrete juice which digests the old cuticle,

2. Produce the cuticle,

3. Release certain substances which stiffen the cuticle.

Numbers of unicellular and multicellular glands are present in the epidermis. Each gland has a duct of its own, which traverses through the cuticle and opens to the exterior through minute apertures.

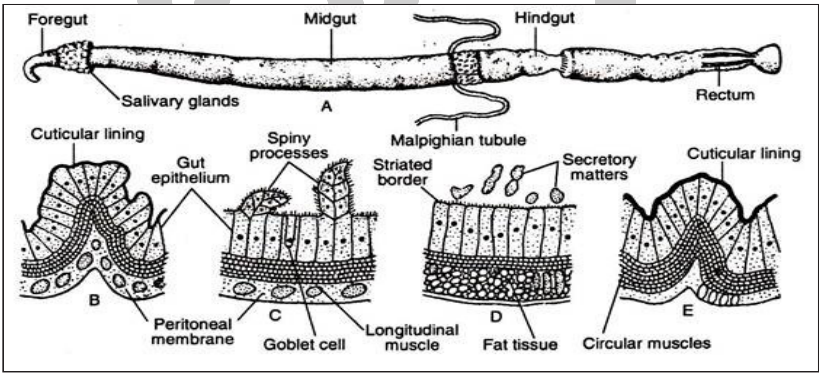


A. Transverse section of the integument of Thyropygus. B. Transverse section of Thyropygus through the mid-gut region.

Digestive System

The alimentary system includes:

1. Alimentary canal
2. Digestive glands



A. Alimentary system and associated structures of Thyropygus (only the proximal part of the Malpghian tuble is shown). B. T. S. of the wall of oesophagus. C. T. S. of the wall of the foregut (posterior end). D. T. S. of the wall of the midgut. E.T. S. of the wall of the hindgut.

Alimentary Canal

It is more or less a straight tube which is divisible into three parts:

1. Foregut,
2. Midgut,
3. Hindgut. The fore and hind guts have inner cuticular lining.

Foregut

It includes:

- Mouth,
- Mouth cavity,
- Oesophagus.

1. Mouth: This crescent-shaped opening is present at the ventral side of the head region and between epicranium and gnathochillarium. It leads into mouth or oral cavity.

2. Mouth cavity: The anterior end of the cavity is formed by the inner side of the epicranium and the posterior side by gnathochillarium. Mandibles with teeth and bristles bound its lateral sides. The cavity is divided into two chambers by the projection of the hypopharynx. The mouth cavity opens within the next part of the canal, called oesophagus.

3. Oesophagus: This short tube, immediately after originating from the mouth cavity runs dorsally, then takes a turn to the posterior direction and passes ventral to the brain. It continues up to seventh or eighth segment. The inner wall of the oesophagus is folded to form villus-like structure like the small intestine of higher animals. These projections are more extensive in the anterior part.

The inner cuticular lining is also much thicker at the anterior part but at the posterior region numerous spiny processes are present. Beneath the inner cuticular lining lies a layer of columnar epithelial cells.

This is covered by distinct layers of circular and longitudinal muscles, which in turn are enclosed within a peritoneal membrane. The longitudinal muscles are broad and placed apart from one another. This gives the characteristic appearance of the fore gut.

Midgut

It runs up to thirty to thirty- two segments. The terminal part of the mid gut is marked by a swelling of fatty tissue, from where originates the paired Malpighian tubules.

Following are the characteristics of the mid gut region:

1. It is wider but thin-walled.
2. Longitudinal muscular bands are narrow.
3. Circular muscle layer is thinner.
4. Presence of a fatty tissue beneath the peritoneal lining.
5. Inner cuticular lining is absent.

6. Epithelial cells are of various shapes and have an inner striated border.
7. Epithelial cells are secretory and absorptive in function.

Hindgut

This is the last part of the alimentary canal which terminates in an aperture, called anus. The first part of the hindgut is of same thickness as the midgut, but after a couple of segments, it becomes wider. The beginning of this wider region is marked by a constriction. The posterior part is again narrow and has thick muscles in the wall.

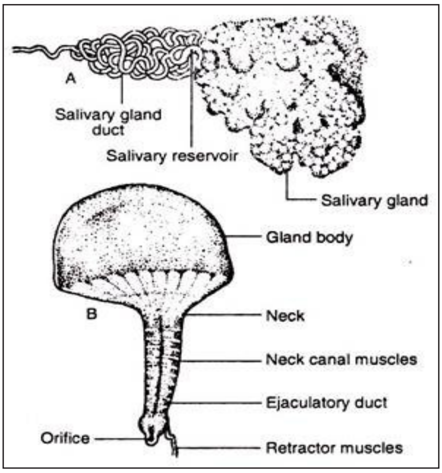
The hindgut has the following features:

1. Circular muscles are well-developed, especially at the posterior part.
2. The wall of the hind gut is internally projected into folds.
3. Epithelial cells are cubical and have no striated border.
4. Inner cuticular lining is of much lesser thickness than the foregut.

Digestive Glands

Most important gland for digestion is the salivary gland. One pair of lobular glands is present in the dorsal side of the oesophageal region. From each salivary gland, minute tubules drain into a salivary duct. The first part of the duct is sac-like and acts as reservoir.

It continues as slender and much coiled duct which runs anteriorly to open within the mouth cavity near the inner side of gnathochillarium. The details about the nature of enzymes in the saliva are not known but the products are obviously digestive in function.



A. Salivary gland with duct of Thyropygus B. Stink or Repugnatorial gland of Thyropygus.

In addition to salivary gland, the lining of mid gut contains secretory cells which also produce digestive juices.

Mechanism of Feeding and Digestion

The food includes soft parts of plants or decaying animals. It likes calcium containing leaves and prefers glucose and sucrose more than starch. The midgut is the region where digestion and absorption take place. The lining of the hindgut absorbs water from the residual food.

Circulatory System

The circulatory system of Millipedes includes:

1. Heart
2. Blood vessels
3. Blood

Heart

The heart is an elongated tubular organ which begins from the first segment and continues up to anal segment. It is present along the mid-dorsal line of the body cavity and is placed above the alimentary canal. It is enclosed within a pericardial membrane.

Heart is constricted into a number of chambers, each segment having one. In between the two chambers there is a pair of lateral openings, called ostia, through which blood enters within the heart. The wall of the heart is provided with muscles for both contraction and relaxation.

Blood Vessels

In each segment heart sends a pair of lateral arteries each of which bifurcates and each branch passes around the gut to open within a median ventral artery, called supraspinal blood vessel. Before opening into the latter, the lateral artery sends a complex of lateral vessels to supply blood to the different parts of the segments.

Anteriorly the first chamber of the heart continues as a median cephalic artery. The cephalic artery sends two pairs of lateral vessels which after sending branches to the parts around the mouth cavity finally open within the supraspinal vessel. The cephalic artery finally breaks into a number of branches to supply brain and other structures in the head region.

The ventral supraspinal vessel also sends number of segmental branches to vascularise the different parts of the body. The blood flows anteriorly through the heart and posteriorly through supraspinal vessel. Blood from arteries enters within the haemocoelomic space and bathes the tissues. From these tissue spaces blood returns through lacunae and enters within the heart through ostia.

Blood

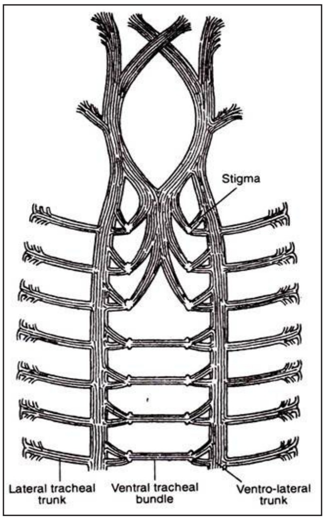
Blood contains liquid part plasma and three types of floating corpuscles or haemocytes. Various substances like protein, fat, sugars, free amino-acids, etc., are found in the plasma. Most common types of haemocytes are small in size but they possess large nuclei.

The other type of haemocyte is large, oval, with distinct nucleus and granulated cytoplasm. The third category of haemocytes is spindle-shaped. Blood in millipedes is not involved in transport of respiratory gases. It is concerned with food storage, wound repair, defence against foreign bodies and excretion.

Respiratory System

Respiratory organs of Millipedes are in the form of tracheae. In Thyropygus, the tracheae are un-branched. A major tracheal trunk includes a large number of smaller tracheal tubes and each trachea is made up of several tracheoles. The trachea has cuticular lining but the spiral thickening is not distinctly visible.

The tracheae communicate with the exterior through minute valve-fitted apertures, called stigmata. Each segment bears two pairs of stigmata, excepting the first three which possess one pair per segment. Each stigmata leads into a tracheal pouch formed by epidermal invagination.



Arrangement of tracheae at the anterior end to Thyropygus.

From each tracheal pouch, three sets of tubes originate:

1. Transverse bundle directed ventrally between the opposite pouches.

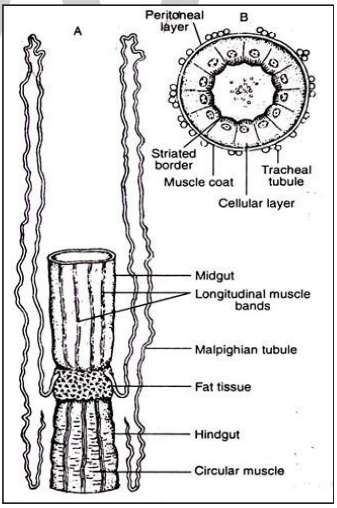
2. One lateral tube on each side running dorsolaterally to supply finer tubes to the different parts of the corresponding segment.
3. A pack of tubes which join with a common ventral tracheal trunk.

The two ventral tracheal trunks run along the entire length of the body and break up into finer vessels to supply the head region. Finer tracheolar tubules are immersed in haemolymph and open directly within the tissue. Same set of vessels convey both oxygen and carbon dioxide.

Excretory System

The cuticle and Malpighian tubules are regarded as the organs for removing metabolic wastes. The waste products like uric acids are deposited in the cuticle and are shed at the time of moulting. Malpighian tubules are two in number, originating from the ventro-lateral side of the midgut near its junction with hindgut.

The region of origin is surrounded by a ring of fat tissue. Each tubule, immediately after its origin, is directed posteriorly and then it takes a turn to run anteriorly up to the oesophagus. From there the tubule bends posteriorly and comes up to the rectum. It then again turns upward and ends blindly.



A. Malpighian tubules of Thyropygus. B. Transverse section of a Malpighian tuble.

The tubule is convoluted and capable of various movements. It remains immersed within haemolymph from where it collects excretory products in the form of uric acid and ammonia. The waste products are deposited inside the alimentary canal and are ejected with the faeces.

The transverse section of the tubule shows following structures from outside to inside:

1. Outer peritoneal layer with numerous externally placed tracheal tubule,

2. Muscular layer with striated fibres,
3. A layer of large cubical cells having striations at the inner border.

Nervous System

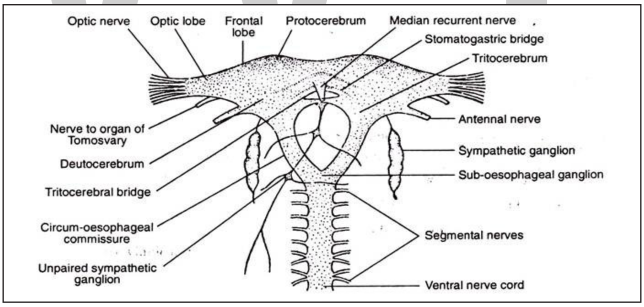
The nervous system of Millipedes includes:

1. Central nervous system,
2. Peripheral nervous system,
3. Sympathetic nervous system,
4. Sense organs.

Central Nervous System

It consists of:

1. A large supra-oesophageal ganglion or brain,
2. Paired circumoesophageal commissures,
3. Paired sub-oesophageal ganglion,
4. Elongated ventral nerve cord.



Nervous system of Thyropygus-anterior part.

Supra-oesophageal Ganglion

Though it appears to be a single large ganglion, yet it is formed by the fusion of several ganglia. It may be distinctly divided into three regions, protocerebrum, deutocerebrum and tritocerebrum. The protocerebrum contains two frontal and two lateral lobes. The deutocerebrum has a pair of antennal lobes, and tritocerebrum includes two lateral lobes.

Circum-oesophageal Commissures

From each lateral side of the supra-oesophageal ganglion a stout oesophageal commissure runs ventrally to unite with the sub- oesophageal ganglion.

Sub-oesophageal Ganglion

Paired sub-oesophageal ganglia appear to be single and the ganglionic swelling is not very prominent. It is connected posteriorly to the ventral nerve cord.

Ventral Nerve Cord

The dorsoventrally flattened ventral nerve cord is formed by two separate cords which are completely fused to be one. It runs posteriorly along the mid-ventral line. In each segment it sends two pairs of peripheral nerves but does not possess segmental ganglion.

Peripheral Nervous System

Numbers of peripheral nerves are given off from the central nervous system to the different parts of the body. The optic nerves and nerves to the organ of Tomosvary arise from the lateral lobes of the protocerebrum. The nerves to the antenna originate from antennal lobes of deutocerebrum.

The brain also sends nerves to the gnathochillarium and mandibles. In each segment ventral nerve cord sends two pairs of nerves. In each side one nerve goes to the corresponding leg and other nerve sends branches to the muscles, trachea, stigmata and wall of the heart in the same segment.

Sympathetic Nervous System

It is represented by one unpaired and one paired nerve cords. All of them originate from the brain and run posteriorly. In the paired nerves swollen ganglia are formed.

Sense Organ

Following sense organs are seen in Thyropygus:

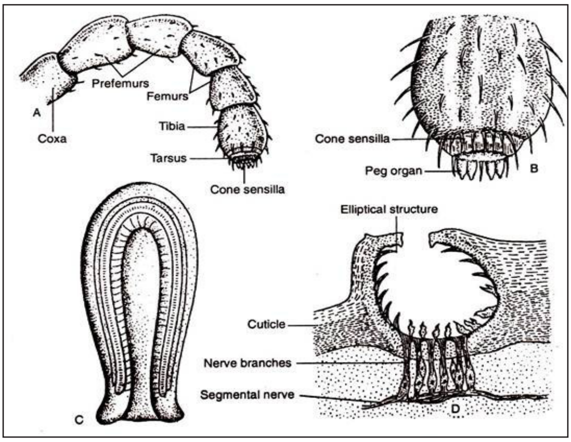
1. Antennal sense organs,
2. Gnathochillarium,
3. Organs of Tomosvary,
4. Hydroreceptor organs and
5. Eyes.

Antennal Sense Organs

Short, seven- segmented antennae bear three types of sense organs:

1. Sensory bristles,

2. Cone sensillae,
3. Peg organs.



A. Antenna of Thyropygus. B. Distal segment of the same antenna. C. Organs of Tomosvary and D. Hydroreceptor organ of Thyropygus. The hydroreceptor organ is shown in sectional view.

1. Sensory bristles: These bristles are scattered all over the antenna and contain sensory cells at their bases.
2. Cone sensillae: The two terminal segments of each antenna are transformed into conical structures containing sensory cells. These are called cone sensillae and they act both as chemoreceptor and taste organs.
3. Peg organs: The last segment bears hook-like structures, called peg organs. They also work as chemoreceptor and taste organ.

Gnathochillarium

Numerous sensory structures called basiconic sensillae are present over the distal end of the gnathochillarium. These are also gustatory in function. They may also show taste discrimination.

Organs of Tomosvary

Each of these appears as a cuticular depression with the lining of sensory cells which receive nerve supply from the optic nerve. This organ is believed to be responsible for determining vibration and also to react properly to the gravity.

Hydroreceptor Organ

These paired organs are present one on each side near the base of gnathochillarium. It is responsible for determining the water or moisture content of the soil. Structurally it resembles the tarsal organ of the spider but functionally these two are completely different.

Eyes

Each eye is made up of several simple eyes or ocelli. Each ocellus is formed by the modification of integument and in section it looks like a glass. The sides and the floor are made up of single-layer sensory epithelial cells. The cells lining the floor become pigmented and form retinal layer and the cuticles above are modified as lens and cornea.

Reproductive System

The sexes are separate and the sexual differences are noted from the structure of legs in the seventh segment of male where these legs are modified into intromittent organs or gonopods.

Male reproductive system includes testes, sperm ducts, penis and gonopods. Each testis is tubular and extends from second to fortieth segment of the body. It is placed between the alimentary canal and ventral nerve cord. The posterior-most part of the testis is tube-like, the middle part is beaded and the anterior end is convoluted.

At the anteriormost part the two testes are transversely joined by small tubes. Sperm duct originates from each testis at the third segment and runs up to the second segment and finally communicates ventrally with a small penis. The gonopods collect the sperms from the sperm duct and at the time of copulation sperms are transferred to the female genital tract.

The female reproductive system consists of an ovary, a short uterus and paired vulvae. The ovary is placed mid-ventrally above the nerve cord and is conspicuous only during maturity. It contains ovisacs, each of which holds a single egg. The ovary continues as uterus which in the third segment bifurcates into two smaller tubes. Each small tube opens externally through a vulva which is placed laterally.

Fertilization and Oviposition

During copulation sperms are transferred by the gonopods of the male within the vulvae of the female. The sperms remain viable for a considerable period in the vulvae and fertilization takes place at the uterus after certain period of copulation.

Eggs are laid in successive batches. Each egg is laid with a spherular wall formed by the secretion of the female. Eggs are generally laid at night within the chambers of burrows specially prepared for the purpose.

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3

Cnidariology: A Comprehensive Study

The phylum of animals who are found exclusively in aquatic environments are called cnidaria. The branch of zoology which is involved in the study of cnidaria is known as cnidariology. There are four major groups within cnidarian, namely, Anthozoa, Scyphozoa, Cubozoa and Hydrozoa. The topics elaborated in this chapter will help in gaining a better perspective about these groups of cnidaria.

Cnidariology is a sub-discipline of invertebrate zoology that studies the cnidarians. Cnidariology deals with studying the cnidarians. Cnidarians are those belonging to phylum Cnidaria. They include the jellyfishes, sea anemones, corals, hydras, etc. They are characterized primarily by possessing cnidae, i.e. specialized cellular structures that fire off thread-like tubules producing a stinging effect.

Cnidarian

Cnidarian, also called as Coelenterata is any member of the phylum Cnidaria (Coelenterata), a group made up of more than 9,000 living species. Mostly marine animals, the cnidarians include the corals, hydras, jellyfish, Portuguese men-of-war, sea anemones, sea pens, sea whips, and sea fans.

The phylum Cnidaria is made up of four classes: Hydrozoa (hydrozoans); Scyphozoa (scyphozoans); Anthozoa (anthozoans); and Cubozoa (cubozoans). All cnidarians share several attributes, supporting the theory that they had a single origin. Variety and symmetry of body forms, varied coloration, and the sometimes complex life histories of cnidarians fascinate layperson and scientist alike. Inhabiting all marine and some freshwater environments, these animals are most abundant and diverse in tropical waters. Their calcareous skeletons form the frameworks of the reefs and atolls in most tropical seas, including the Great Barrier Reef that extends more than 2,000 kilometres along the northeastern coast of Australia.

Only cnidarians manufacture microscopic intracellular stinging capsules, known as nematocysts or cnidae, which give the phylum its name. The alternative name, coelenterate, refers to their simple organization around a central body cavity (the coelenteron). As first defined, coelenterates included not only the animals now designated cnidarians but also sponges (phylum Porifera) and comb jellies (phylum Ctenophora). In contemporary usage, “coelenterate” generally refers only to cnidarians, but the latter term is used in order to avoid ambiguity.

General Features

Size Range and Diversity of Structure

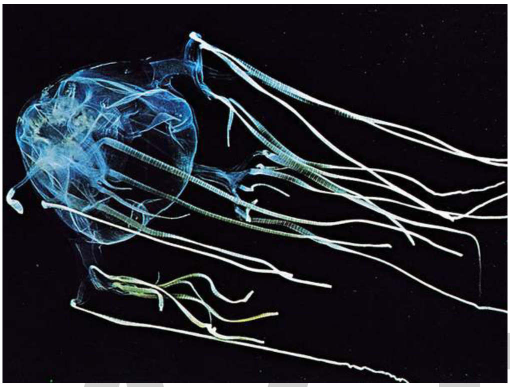
Cnidarians are radially symmetrical (i.e., similar parts are arranged symmetrically around a central axis). They lack cephalization (concentration of sensory organs in a head), their bodies have two cell layers rather than the three of so-called higher animals, and the saclike coelenteron has one opening (the mouth). They are the most primitive of animals whose cells are organized into distinct tissues, but they lack organs. Cnidarians have two body forms—polyp and medusa—which often occur within the life cycle of a single cnidarian.

Chrysaora: Sea nettle (Chrysaora fuscescens).

The body of a medusa, commonly called a jellyfish, usually has the shape of a bell or an umbrella, with tentacles hanging downward at the margin. The tubelike manubrium hangs from the centre of the bell, connecting the mouth at the lower end of the manubrium to the coelenteron within the bell. Most medusae are slow-swimming, planktonic animals. In contrast, the mouth and surrounding tentacles of polyps face upward, and the cylindrical body is generally attached by its opposite end to a firm substratum. The mouth is at the end of a manubrium in many hydrozoan polyps. Anthozoan polyps have an internal pharynx, or stomodaeum, connecting the mouth to the coelenteron.

Most species of cubozoans, hydrozoans, and scyphozoans pass through the medusoid and polypoid body forms, with medusae giving rise sexually to larvae that metamorphose into polyps, while polyps produce medusae asexually. Thus, the polyp is essentially a juvenile form, while the medusa is the adult form. In contrast, anthozoans are polypoid cnidarians and do not have a medusa stage. Commonly polyps, and in some species medusae too, can produce more of their own kind asexually.

One body form may be more conspicuous than the other. For example, scyphozoans are commonly known as true jellyfishes, for the medusa form is larger and better known than the polyp form. In hydrozoans, the polyp phase is more conspicuous than the medusa phase in groups such as hydroids and hydrocorals. Hydromedusae are smaller and more delicate than scyphomedusae or cubomedusae; they may be completely absent from the life cycle of some hydrozoan species. Some other species produce medusae, but the medusae never separate themselves from the polyps. Cubozoans have medusae commonly known as box jellyfish, from their shape. Some of these are responsible for human fatalities, mostly in tropical Australia and Southeast Asia, and include the so-called sea wasps. The polyp is tiny and inconspicuous.



Sea wasp (Chironex fleckeri).

Many cnidarian polyps are individually no more than a millimetre or so across. Polyps of most hydroids, hydrocorals, and soft and hard corals, however, proliferate asexually into colonies, which can attain much greater size and longevity than their component polyps. Certain tropical sea anemones (class Anthozoa) may be a metre in diameter, and some temperate ones are nearly that tall. Anthozoans are long-lived, both individually and as colonies; some sea anemones are centuries old. All medusae and sea anemones occur only as solitary individuals. Scyphomedusae can weigh more than a ton, whereas hydromedusae are, at most, a few centimetres across. Tentacles of medusae, however, may be numerous and extensible, which allows the animals to influence a considerably greater range than their body size might suggest. Large populations of hydroids can build up on docks, boats, and rocks. Similarly, some medusae attain remarkable densities—up to thousands per litre of water—but only for relatively brief periods.

Distribution and Abundance

Many of the world’s benthic (bottom-dwelling) ecosystems are dominated by anthozoans. Although soft and hard corals coexist in virtually all tropical areas appropriate for either, coral reefs of the tropical Indo-Pacific are built mainly by members of the anthozoan order Scleractinia (hard corals); whereas on coral reefs of the Caribbean members of the anthozoan subclass Alcyonaria (soft corals) are much more prominent. Aside from being the most numerous and covering the greatest area of any animals on the reef, the corals structure their environment, even after death. Soft corals contribute greatly to reef construction by the cementing action of the skeletal debris (spicules), filling in spaces between hard coral skeletons.

Soft-bodied anthozoans are similarly dominant in other seas. Temperate rocky intertidal zones in many parts of the world are carpeted with sea anemones. They sequester the space that is therefore made unavailable to other organisms, thus having a profound impact on community structure. The curious hemispherical anemone *Liponema* is the most abundant benthic invertebrate in the Gulf of Alaska, in terms of numbers and biomass. Parts of the Antarctic seabed are covered by anemones, and they occur near the deep-sea hot vents.

Importance

Prominent among organisms that foul water-borne vessels are sedentary cnidarians, especially hydroids. The muscles that make scyphomedusae strong swimmers are dried for human consumption in Asia. Sea anemones are eaten in some areas of Asia and North America.

Throughout the tropics where reefs are accessible, coral skeletons are used as building material, either in blocks or slaked to create cement. Another use for cnidarian skeletons is in jewelry. The pink colour known as "coral" is the hue of the skeleton of a species of hydrocoral. Other hydrocorals have purplish skeletons. Skeletons vary in hue, and those considered most desirable command a high price. The core of some sea fans, sea whips, and black corals are cut or bent into beads, bracelets, and cameos.

All cnidarians have the potential to affect human physiology owing to the toxicity of their nematocysts. Most are not harmful to humans, but some can impart a painful sting—such as *Physalia*, the Portuguese man-of-war, and sea anemones of the genus *Actinodendron*. These, and even normally innocuous species, can be deadly in a massive dose or to a sensitive person, but the only cnidarians commonly fatal to humans are the cubomedusae, or box jellyfish. Anaphylaxis (hypersensitivity due to prior exposure and subsequent sensitization) was discovered with experiments on *Physalia* toxin. Extracts of many cnidarians, mostly anthozoans, have heart-stimulant, antitumour, and anti-inflammatory properties.

Form and Function

Tissues and Muscles

Cnidarians consist of two cell layers: an outer ectoderm and an inner endoderm (the gastrodermis) that lines the coelenteron. Between these is sandwiched the mesoglea, a largely noncellular layer composed of a jellylike material permeated by a complex network of supporting fibres that may be microscopically thin or very thick. The fibres and jelly are elastic. In medusae, mesoglea comprises the bulk of the animal and forms a resilient skeleton. In polyps, the water-filled coelenteron acts as a hydrostatic skeleton, this, in concert with the mesoglea, maintains the form of these animals.

Muscles in cnidarians are extensions of the bases of ectodermal and endodermal cells. Individual muscle cells are relatively long and may occur in dense tracts in jellyfish or sea anemones. Most cnidarian muscles, however, are thin sheets at the base of ectodermal and endodermal layers.

In polyps, ectodermal muscles are oriented lengthwise along the cylindrical body and tentacles; endodermal ones are usually circular. Contraction of circular muscles against coelenteric fluid causes the polyp's body to elongate; contraction of longitudinal muscles causes it to shorten. Similar layers of muscles extend and contract the tentacles. Bending results from unequal contractions of longitudinal muscles on opposite sides of the body.

In medusae, all muscles are ectodermal, restricted to the concave oral surface (subumbrellar surface), and organized into circular and radial tracts. Contraction of circular muscles squeezes the subumbrellar space, forcing out contained water and causing the medusa to move by jet propulsion. Recovery of the elastic mesoglea re-extends contracted muscle fibres. Radial muscle contraction distorts the bell, directing the water jet at angles to the longitudinal axis of the bell, allowing the medusa to steer.

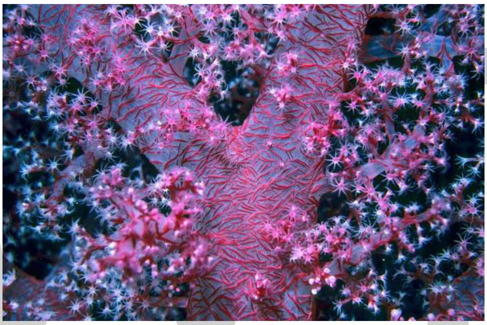
Support mechanisms and skeletons

Most members of what is usually considered a soft-bodied group have some sort of skeleton aside from the hydrostatic system. Both external and internal skeletons occur in the phylum, but only among polyps.

Most hydroid polyps secrete a horny, chitinous external skeleton that is essentially a tube around the polyp and the network of stolons that interconnect members of a colony. As well as being protective, it confers stiffness for support and has joints for flexibility. A few scyphozoan polyps have comparable chitinous skeletons. Unlike those of hydroids, hydrocoral skeletons are composed of calcium carbonate and are internal by virtue of being shallowly penetrated by channels of living tissue. Hydrocorals, which include the order Milleporina (millepores), commonly called fire coral, and the precious red coral used for jewelry, form encrusting or branching skeletons similar to those of anthozoan corals.

An anthozoan coral polyp, which resembles a sea anemone, can nearly completely retract into the calcareous cup it secrets around itself. This external skeleton underlies a continuous, superficial layer of tissue. Non-reef-forming corals typically are solitary or form small, rather delicately branched colonies, their polyps being relatively large and widely spaced. In some species of reef-forming corals, polyps are so tightly packed that their individual units share common walls. Skeletons may be encrusting, massive, or arborescent (treelike). The latter type of skeleton is delicate and typical of quiet waters at depth or in lagoons, while the former two predominate where water motion is strong. Skeleton is laid down in massive corals at a rate of about one centimetre per year; branching corals may grow considerably more rapidly. The largest corals represent cooperative efforts of up to 1,000,000 tiny individuals precipitating calcium carbonate over centuries. Few attain such proportions, however, and even the largest are eventually broken down by boring organisms such as algae, worms, sponges, and barnacles, as well as by physical processes.

The last major category of cnidarian skeletons, formed by the anthozoan subclass Alcyonaria and the order Antipatharia, are internal. Sea fan and sea whip skeletons consist of the horny protein gorgonin with calcareous spicules fused to form a solid or jointed central rod. Soft coral spicules are discrete, mostly microscopic objects of diverse shapes that vary from needle-like to club- and anchor-shaped. Located in the ectoderm, spicules stiffen the colony. In some species the several spicules that form a protective cup around each polyp may be several millimetres long. The alcyonarian *Tubipora* is known as the organ-pipe coral after the form of its red calcareous skeleton. Blue corals (the order Helioporacea) have skeletons of crystalline calcareous fibres fused into sheets, which are used for jewelry. Colonies of black coral resemble bushes and may stand more than three metres tall. Their skeletons, made entirely of proteinaceous material similar to gorgonin, are likewise used for jewelry.



Alcyonaria (soft coral), Red Sea.

Sea anemones do not produce hard skeletons, although their close relatives in the order Zoanthinaria incorporate foreign objects (sand grains, sponge spicules) into their body walls, which gives them rigidity and toughness. Small anemones that live high in the intertidal zone commonly inhabit abandoned barnacle tests (shells), thereby acquiring some of the benefits of a skeleton.

Nervous System and Organs of Sensation

Medusae have a more highly developed nerve net than do polyps, a feature that is associated with the more active way of life of medusae. Swimming is coordinated by the nervous system. Nervous systems that are capable of conducting nerve impulses both quickly and slowly give these animals’ considerable behavioral responsiveness and flexibility. Ganglia or other accumulations of nerve cell bodies are not found in cnidarians, but there are gap junctions between neurons and between neurons and effectors, which allow the transmission of nerve impulses. Statocysts, located between the tentacles or near the tentacular base, inform the animal of its orientation with respect to gravitational forces. Light-sensitive ocelli (external patches of pigment and photoreceptor cells organized in either a flat disk or a pit) occur in some medusae of each of the three classes that possess this stage. Such sensory structures are closely associated with a nerve net.

In the past nematocysts were considered independent effectors; that is, they were thought to fire upon appropriate stimulation, without mediation by the nervous system. Evidence, however, favours there being some organismal control over their firing, which may consist only of adjusting the threshold for firing, or the selectivity. Some scientists believe that nervous complexes associated with batteries (groups) of cnidae are the mechanism of control.

Digestion, Respiration and Excretion

Food is taken in and wastes are discharged through the mouth. Extracellular digestion occurs in the coelenteron, which has, in all except hydrozoans and some tiny members of the other classes, radial projections of the wall into the coelenteron that increase the surface area. Ingested material is broken down somewhat in the coelenteron and then taken up by endodermal cells for final intracellular digestion.

Respiration and excretion in cnidarians are carried on by individual cells that obtain their oxygen directly from water—either that in the coelenteron or that of the environment—and return metabolic wastes to it. Thus, all physiological functions are carried out at no more than the tissue level of differentiation.

Defense and Aggression: Nematocysts

Cnidae range from only about 10 to 100 micrometres (0.0004 to 0.004 inch) long, but they are among the most complex intracellular secretion products known. Each consists of a spherical or cigar-shaped capsule with an eversible, hollow tubule extending from one end. In the unfired state, the tubule is coiled within the capsule. When a cnidarian contacts a predator or prey item, the capsule opens and the tubule everts. The tubule may be adhesive, or it may entangle the object. Both types serve to hold food items. A third type of tubule is armed with spines that penetrate predator or prey. Toxins contained in the capsule are injected through the tubule into the object being held. Each cnida can be fired only once. Undifferentiated interstitial cells of the ectoderm and endoderm appear to be the source of the cnidoblasts (cells that produce cnidae).

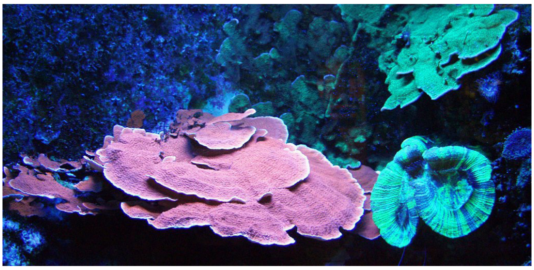
Evolution

The exact relationships between the different cnidarian groups are unknown. Among theories proposed on the evolution of the phylum Cnidaria, most treat the radial symmetry and tissue level of organization as evidence that the group is primitive (that is, it evolved before the evolution of bilateral symmetry) and hold that the medusa is the original body form, being the sexually reproductive phase of the life cycle. Another theory is that the original cnidarian was a planula-like organism that preceded both polyp and medusa. In either case, Hydrozoa is considered to be the most ancient of cnidarian classes, and Trachylina is thought to be the most primitive extant order of that group. An alternative view is that anthozoans are the stem of the phylum, which evolved from bilateral flatworms and is secondarily simplified. A corollary to this theory is that the polyp is the ancestral body form.

Speculations about the origin of the phylum are not easily resolved, for preservable skeletal structures developed relatively late in cnidarian evolution. The oldest fossilized cnidarians were soft-bodied. Representatives of all four modern classes have been identified in Ediacaran fauna of the Precambrian Period (that is, those appearing between about 635 million and 542 million years ago) known from more than 20 sites worldwide. As much as 70 percent of Ediacaran species have been considered to be cnidarians. Curiously, there are few fossil cnidarians of the Cambrian Period (542 million to 488.3 million years ago). The Conulariida, which existed from the Cambrian Period to the Triassic Period (251 million to 199.6 million years ago) are considered by some scientists to be skeletal remains of scyphopolyps, either ancestral to the coronates or without modern derivatives. Presumed fossil sea anemones are found in the lower Cambrian System. Colonies of Stromatoporoidea, considered to be an order of the class Hydrozoa that extended from the mid-Cambrian Period to the Cretaceous Period (about 145.5 million to 65.5 million years ago), produced massive skeletons. Although there were two groups of Paleozoic corals, neither of which has modern descendants, they were not great reef-builders during that era. Scleractinians arose in the mid-Triassic Period; blue corals, gorgonians, millepores, and hydrocorals have records from the Jurassic Period (199.6 million to 146 million years ago) or the Cretaceous Period to the present. Most other cnidarians are known only from the Holocene Epoch.

Anthozoa

Anthozoa is a class of marine invertebrates within the phylum Cnidaria that are unique among cnidarians in that they do not do not have a medusa stage in their development. These exclusively polypoid cnidarians are characterized by a tubular body with tentacles around the mouth and most are sedentary after the larval stage. Anthozoa includes the sea anemones, corals, sea pens, sea pansies, and sea fans, among others.



Stony corals, Scleractinia.

Anthozoa is the largest of the four classes of Cnidaria with over 6,000 species. They are found worldwide in all oceans, from the Arctic to the Antarctic. Anthozoa means "flower animals," which is descriptive of this class of invertebrates.

Anthozoans provide a number of values for human beings. Coral reefs are major tourist attractions and also provide a habitat for fish, mollusks, urchins, and crustaceans that serve as food for people. Anthozoans are used in the aquarium trade, to make coral jewelry, and scleractinian skeletons are even used as building materials and in bone grafts. Despite these values, various human activities (fishing, development, marine pollution) have had negative effects on coral reefs, with more than half of the world's coral reefs considered to be threatened.

Anthozoa is one of four classes of the invertebrate phylum, the others being Hydrozoa (Portuguese Man o' War, Obelia, etc.), Scyphozoa (true jellyfish), and Cubozoa (box jellies). All are aquatic and most are marine. The name of the phylum comes from *cnidocytes*, which are specialized cells that carry stinging secretions that are the cnidarians' main form of offense or defense and function.

The basic body shape of a cnidarian consists of a sac with a gastrovascular cavity, with a single opening that functions as both mouth and anus. It has *radial symmetry*, meaning that whichever way it is cut along its central axis (that is, by any plane that passes through its longitudinal axis), the resulting halves would always be mirror images of each other.

Theoretically, members of Cnidaria have life cycles that alternate between asexual *polyps* (the body as a vase shaped form), and sexual, free-swimming forms called *medusae* (singular medusa; the body in a bell-shaped form). However, members of Anthozoa live only as polyps. The anthozoa larva, once fusing with the substratum and developing into the polyp stage, grows benthic or sessile, meaning it no longer metamorphoses into the medusal stage. (Members of Scyphozoa live most of their life cycle as medusa, the Hydrozoa live as polyps, medusae, and species that alternate between the two and those of the class Cubozoa are named for their cube-shaped medusae, which form the dominant part of their life cycle.)

Anthozoans are essentially a tubular sac, with a mouth and tentacles position around the mouth on a flattened upper surface known as an oral disk. As with other cnidarians, the tentacles surrounding the mouth have stinging cells and the mouth is the only entry to the digestive system.

Anthozoans are only found in marine environments. They can be found in habitats from the intertidalzone to over 6,000 meters (19,500) feet deep. Species may be solitary or colonial. While solitary forms may attach to a hard substrate or burrowed into soft mud or sand on the sea bed, the colonial forms may build massive skeletons, such as the reef-building corals.

Larval forms are free moving, but most adult forms are sedentary; some groups, such as those of the orders Actiniaria (sea anemones), Ceriantharia (tube anemones), and Pennatulacea (sea pens and sea pansies) may show some movement.

Anemones and certain species of coral live in isolation, however most corals form colonies of genetically identical polyps; these polyps closely resemble anemones in structure, although are generally considerably smaller.

Behavior, Feeding, and Reproduction

Members of most species of Anthozoa are suspension feeders, capturing small planktonic invertebrates, phytoplankton, bacteria, and other suspended organic matter. Most common are passive methods of capturing prey, when it comes in contact with the tentacles. All cnidarian species can feed by catching prey with nematocysts, with large sea anemones capable of catching fish, crabs, and bivalves, and corals are capable of catching plankton.

Giant green anemone, likely *Epicystis crucifer*, Southern California.

Some of the anthozoan species harbor a type of algae, dinoflagellates called zooxanthellae, in a symbiotic relationship. The reef building corals known as hermatypic corals rely on this symbiotic relationship particularly. The zooxanthellae benefit by using nitrogenous waste and carbon dioxide produced by the host and the cnidarian gains photosynthetic capability and increased calcium carbonate production in hermatypic corals.

Various reproductive strategies are utilized by anthozoans, including production of asexual clones by fission (in longitudinal or transverse direction) and pedal laceration (where pieces of the pedal disk separate and develop new individuals) and fragmentation, and anthozoans may have separate sexes or be hermaphroditic. Gametes typically are released through the mouth for external fertilization or eggs may be retained for internal fertilization and embryos released through the mouth. The ciliated planula larvae that develop from the embryos may or may not feed. Some species can produce larvae asexually.

The synchronous release of sperm and eggs by many colonies over a coral reef is one of the most spectacular anthozoan behaviors, with such mass spawning events observed in the scleractinian corals of the Great Barrier Reef, as well as in octocorrallian and zoanthid species.

Anthozoans may exhibit aggressive behaviors in defending space from neighboring individuals of the same or different species, including using specialized, extra-long tentacles with stinging nematocysts, causing tissue death upon contact.

Some species of the subclass Alcyonaria (Octocorrallia) can produce light (bioluminescence) that may even exhibit as a wave of light across a colony.

General Anthozoa Characteristics

There are many subclasses and orders with varying characteristics under the class Anthozoa, including:

- Order Scleractinia, Stony Corals: Stony or reef-building corals form a skeleton made of calcium carbonate under the polyps to create the hard structure that most people recognize as coral. These corals are responsible for forming the base structure of coral reefs. As older polyps die off, new polyps continue to build calcifications on the old skeletons, allowing for the huge scale of reefs in the Caribbean and the Great Barrier Reef. Not all stony corals are reef-building, though, as some are not able to produce enough calcium carbonate to facilitate reef formation.
- Subclass Octocorallia, Octocorals: Despite sharing a similar appearance with stony corals, soft corals, sea pens, gorgonians and sea fans do not build the hard, calcium-carbonate skeleton of stony corals. Instead, these corals may create some internal structural supports that allow them to grow vertically but still sway with ocean currents. Soft corals are always colonial and grow with eight-fold symmetry, which means their tentacles come in groups of eight — hence the name Ocotocoral. Octocorals include the orders Alcyonacea and Helioporace.
- Order Corallimorpharia, Anemone Corals or Mushroom Corals: Members of this order are sometimes called anemone corals or mushroom corals because they resemble anemones more closely than other types of corals due to their large, flat, disc-like shape and short tentacles. They grow like wheel spokes, radiating from a center and forming concentric circles. The diameter of the circle increases as they grow. This order is extremely popular in home aquariums.
- Order Zoantharia, Zoanthids: Zoanthids have long, prominent tentacles arranged in two rows. Unlike stony and soft corals, Zoanthids incorporate sand and other substrate into their colonies for structure. They may live as individual polyps or in colonial groups.
- Order Actiniaria, Anemones: Larger anemones tend to be solitary while smaller species may use asexual reproduction to propagate and live in large concentrations

when there is suitable habitat. Anemones come in a wide range of colors, some owing their coloration to the zooxanthellae, microscopic algae, they host. Anemones have a disc-shaped bottom they use to attach themselves to rocks, in crevices and on other suitable surfaces, including the shells of other marine invertebrates.

- Subclass Ceriantharia, Tube-dwelling Anemones: This subclass looks similar to sea anemones, but tube-dwelling anemones are known for being solitary and living buried in soft sediments. They live inside tubes made of secreted mucus and organelles, and can recede into these tubes for protection. Ceriantharia includes the orders Spirularia and Penicillaria.

Scyphozoa

The class Scyphozoa includes four orders, 20 families, 66 genera, and about 200 species. The four orders are Stauromedusae, the stalked jellyfish; Coronatae, the crown or grooved jellyfish; Semaeostomeae; and Rhizostomeae.

Animals in the phylum Cnidaria may have one or both of two body forms, the benthic polyp and the pelagic medusa. The four orders within the class Scyphozoa emphasize these two forms to different degrees. Specifically, in the order Stauromedusae, there is only a benthic stage, which is considered the medusa. In the orders Coronatae, Semaeostomeae, and Rhizostomeae both stages occur in most species, with the medusa stage being the largest and most conspicuous.

The phylum Cnidaria is considered to be of early evolutionary origin, but the position of the Scyphozoa relative to other cnidarian classes (Anthozoa [corals and anemones], Cubozoa [box jellyfish], and Hydrozoa [hydroids, hydromedusae, fire corals, and siphonophores]) is uncertain. It is debated whether the polyp or the medusa form is most primitive. The scyphozoans are related most closely to cubozoans, which were placed in the same class until recently. They have similar body forms and life cycles. The scyphozoans are related least to the Anthozoa. Molecular evidence suggests that Anthozoa represents the most primitive class in the phylum Cnidaria.

The fossil record of Scyphozoa is poor. Radially symmetrical impressions have been interpreted to be casts of primitive scyphomedusae. Other fossil groups that may be ancient scyphozoan polyps are the conulariids, which were similar to modern coronate polyps and were present from the Ordovician to the late Triassic, and *Bryonia* from the Upper Cambrian and Ordovician, which is from the extinct order Bryoniida of the Scyphozoa.

Physical Characteristics

Most species in the class Scyphozoa, excluding the order Stauromedusae, have two life stages, the predominant medusa stage (up to 80 in, or 2 m, in diameter) and the small, inconspicuous polyp stage (less than 0.13 in, or 4 mm, long). The medusa, or jellyfish, stage has a saucer- to umbrella-shaped body with two epithelial layers (epidermis and gastrodermis) separated by a thick layer of mesenchyme, a gelatinous connective tissue containing cells. Near the edge of the bell in the orders Coronatae and Semaeostomeae are tentacles used in Feeding. The tentacles have millions of microscopic intracellular organelles called nematocysts that evert a hollow thread from a capsule and may inject toxin into or entangle their small prey (zooplankton, fish eggs and larvae, or other gelatinous species). In the Semaeostomeae and Rhizostomeae, there are four oral or mouth arms on the underside (concave) of the bell, which also have stinging nematocysts for feeding. The polyps, called scyphistomae, can form colonies of individuals by budding or, in the case of coronate polyps, true colonies that have a chitinous sheath. Polyps are cup-shaped, attached to the substrate by a "foot," and with the central mouth surrounded by a single ring of tentacles with nematocysts.

Stalked jellyfish in the order Stauromedusae attach to seaweed or sea grasses by an aboral stalk. The main body (calyx) is funnel- or goblet-shaped and grows to 1.2 in (3 cm) wide, with eight arms, each bearing a cluster of as many as 100 short, clubbed tentacles. In the common genus *Haliclystus,* between each arm there is an adhesive disk, by which the animal can attach to move about. The gonads extend down the arms. The mouth is located at the inside center of the funnel-shaped body. Coloration varies; it may be shades of green, brown, yellow, or maroon and often matches the color of the substrate, making these jellyfish difficult to see. This form is considered the medusa stage, and there is no polyp or swimming stage.

Jellyfish in the order Coronatae have a deep groove around the aboral surface that separates the swimming bell into a central disk and a peripheral zone, which has lappets. One thick tentacle emerges between lappets on the upper surface of the bell; depending on the species, there are between eight and 36 tentacles. The mouth opens into a large, pouchlike stomach on the underside of the bell. Most of the species are deep living, and thus the central disk is colored dark red to maroon, making it invisible at depths and presumably concealing the bioluminescence emanating from consumed prey. Most of the medusae are small, less than 2 in (5 cm) in diameter or bell height, but some species may attain 6 in (15 cm) in diameter. The known polyps are colonial and covered with a chitinous sheath.

Adult jellyfish in the order Semaeostomeae generally are large, up to 80 in (2 m) in diameter, but usually less than 12 in (30 cm). The swimming bell is flat to hemispherical in shape. The bell edge may have lappets, or it may be smooth. From eight to hundreds of tentacles are present at the bell margin or beneath the bell. In the center of the concave side of the bell are four diaphanous or frilled oral arms that lead to the central mouth. The bell ranges from translucent to opaque and from white to dark orange in color, and it may have radiating stripes in some species. The polyp stage is small and may form groups of individuals by budding.

The rhizostome medusae also are large, up to 80 in (2 m) in diameter. The swimming bell is hemispherical and very firm in texture and lacks tentacles at the edge. The bell margin has eight or 16 lappets. The four oral arms of rhizostome medusae are fused and usually very elaborate, with many tiny tentacles and small mouths for feeding. There may be clublike projections from the oral arms. The medusae are translucent to opaque, with colors ranging from white to dark red; some have patterns that include stripes and spots. The polyp stage is small and may form clusters of individuals by budding.

Distribution

Scyphozoans are found in all marine waters. Most Stauromedusae are found in cool waters along temperate to sub-polar shorelines spring through autumn. Coronate medusae generally occur at great depths, where temperatures are a cool 40–46 °F (5–8 °C), but a few species occur in subtropical to tropical waters. Semaeostome species are the predominant large medusae in polar to temperate oceans, and they also inhabit subtropical and tropical waters. The scyphistomae of those species are active only in warm months; however, they can become dormant and survive through winter months. Rhizostome species live mostly in tropical waters, with only a few species found in subtropical or temperate regions. The medusae of shallow-living scyphozoans are seen during late spring to early autumn in surface waters of temperate to polar seas. In tropical waters and among deep-dwelling species, medusae may be present all year.

Habitat

Scyphozoan medusae are found from surface waters to abyssal depths, and the polyps are attached to hard surfaces, such as pilings, shells, and rocks, at various depths, depending on the species. Most Stauromedusae are seen at intertidal down to shallow subtidal depths, usually attached to benthic plants (algae or sea grasses). One species is known from deep hydrothermal vent communities. Coronate medusae typically are found at mesopelagic depths (1,625–4,875 ft, or 500–1,500m), but a few species occur near the surface. Deep-living species may have polyps at abyssal depths, but the polyps of shallow-living species are on shallow substrates. Semaeostome and rhizostome medusae occur most abundantly near shore in surface waters above 165 ft (150 m), where food supplies are greatest. Their polyps also are found at shallow depths, often on the underside of structures away from direct light. Some semaeostome species are deep living, and their polyps generally are not known. There are no known deep-dwelling rhizostome species.

Behavior

Jellyfish behavior generally is simple, owing to their simple nervous system. Stauromedusae move around on the substrate by somersaulting, which they accomplish by alternating adhesion of the basal disc with that of tentacles or adhesive pads located between the tentacles of some genera. The most noticeable behavior of jellyfish is the rhythmic pulsation of the swimming bell, which moves them through the water for feeding and respiration. The swimming pulsations are coordinated by nerve centers around the edge of the bell. At the bell margin there also are sensory clubs (rhopalia), each consisting of a light-sensing organ (ocellus) and a gravity-sensing organ (statocyst); thus, medusae can sense light and dark and can determine their orientation in the water column. Semaeostome and rhizostome jellyfish swim continuously. This is important for oxygen exchange, which occurs over the entire body surface, and for feeding. The swimming of several species is known to be against flow in the water column; the result is that they all swim in the same direction and may become concentrated in convergences, like bales of hay stacked up to dry. Some species move up in the water column at night and down in the day ("diel vertical migration"). The scyphistomae (polyps) are able to move by the so-called foot and its extensions. They feed when prey makes contact with their tentacles, which have nematocysts; the jellyfish contract the tentacles and bring the prey to their mouths.

Feeding Ecology and Diet

All scyphozoans feed with tentacles or tentacle-like projections that have millions of microscopic intracellular organelles called "nematocysts." Some nematocysts act to Paralyze or kill the prey, whereas others entangle them. Stauromedusae catch prey by the tentacles and fold the arm inward to bring the prey to the mouth. Many coronate medusae do not swim actively while feeding but instead remain nearly motionless with their tentacles extended above the bell. For semaeostome and rhizostome medusae, the pulsations of the swimming bell force water through the tentacles and create vortices that may bring prey into contact with the tentacles and oral arms. For semaeostome medusae, when a prey item is immobilized on a tentacle, the tentacle contracts and transfers the prey to an oral arm. The prey is moved by cilia up the inside of the folded oral arm to the mouth and into one of the four gastric (stomach) pouches, where short, fingerlike projections wrap around the prey and secrete digestive enzymes. For rhizostome medusae, prey capture is by the small tentacles on the oral arms, which transfer the prey to one of the many small mouths nearby.

Most species feed on small crustaceans that predominate in most habitats. Stauromedusae consume epibenthic crustaceans, including gammarid amphipods and harpacticoid copepods. Medusae in the other orders primarily eat abundant calanoid copepods but also eat other small zooplankton, such as cladocerans, larvaceans (= appendicularians), and chaetognaths. Many semaeostome species also feed on other gelatinous species, including scyphomedusae, hydromedusae, siphonophores, and ctenophores. It is of particular interest that several species are known to consume the eggs and larvae of fish. Thus, scyphomedusae may be detrimental to fish populations, both by consuming the zooplankton foods needed by fish larvae and zooplanktivorous fish species, like herring, and by feeding on the young fish directly.

Reproductive Biology

Scyphozoans generally reproduce both asexually and sexually. The benthic forms, Stauromedusae and scyphistomae (polyps) of the other orders, reproduce asexually by budding new polyps or cysts from the body or foot. Scyphistomae, which are present in most species of all orders except Stauromedusae, also produce the medusa stage by an asexual budding process called strobilation. Strobilation typically takes place at a certain time of year and is triggered by environmental factors, which differ by species; these factors include rising (spring) or falling (autumn) temperatures or changes in light levels. During strobilation, the polyp undergoes transverse segmentation, forming one to several small medusae, called "ephyrae." The process requires days to weeks, depending on temperature.

The fully formed ephyrae break free by swimming pulsations. The ephyrae grow into sexually mature medusae over the course of a month or longer. The medusae of most species have separate sexes, but a few species are sequential hermaphrodites. The males and females are indistinguishable except by examination of the gonads. No mating occurs. Sperm strands are released into the water by males and are taken up by the females during feeding. The gonads surround the gastrovascular cavity, and eggs may be fertilized in the ovary or after they are released into the gastrovascular cavity. In most species the fertilized eggs develop into small ciliated larvae (planulae) that swim to a suitable substrate, attach, and develop into polyps. In some species, the planulae are retained (brooded) by the female before settlement. Some species lack a polyp stage.

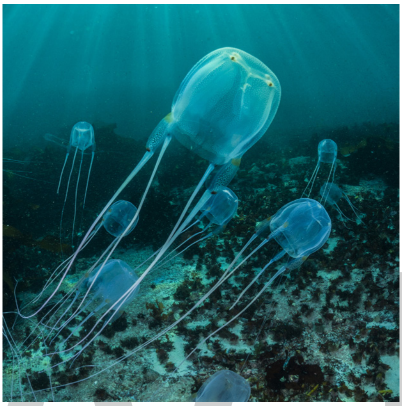
Cubozoa

Cubozoa or box jellies are one of the four groups of Cnidaria. They are named after their cube shape with four flattened sides. Most of the about 20 species are found in tropical oceans and seas and are fast, strong and agile swimmers. This swimming ability is due to the velarium, a flap under the umbrella which concentrates and increases the flow of water pushed out from the umbrella. They have four complex eyes that allow them to track moving objects and quickly respond to changes in light intensity.

The well-known cubozoan species, Chironex fleckeri, which is sometimes called the box jellyfish, is among the most venomous creatures in the world. The name sea wasp is also applied to Chironex fleckeri and some of the other cubozoan species. Members of Cubozoa, collectively, are known scientifically as cubazoans and commonly as box jellies.

With bodies shaped roughly like a square bell with tentacles dangling from the corners, box jellies are agile and active swimmers based on their ability to contract the "bell" and forcefully expel water through a constricted opening at its base. Box jellies are important components of marine ecosystems, capturing and eating fish, crustaceans, and worms, and despite their barbed and poisoned nematocysts, being eaten by large fish and sea turtles.

Box jellyfish are classified within Cnidaria, a phylum containing relatively simple invertebrate animals found exclusively in aquatic, mostly marine, environments. Cniderians comprise corals, sea anemones, jellyfish, sea pens, sea pansies, and sea wasps, as well as tiny freshwater hydra. The name of the phylum comes from *cnidocytes*—specialized cells carrying stinging "organelles," which produce specialized toxic secretory products.

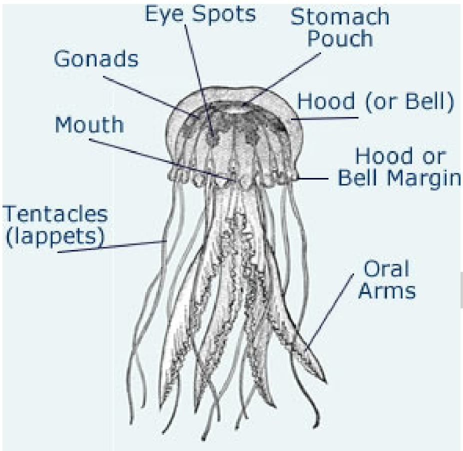


Theoretically, members of Cnidaria have life cycles that alternate between two forms—asexual *polyps* (the body as a vase-shaped form), and sexual, free-swimming forms called *medusae* (singular medusa; the body in a bell-shaped form). In reality, there is considerable variability among the four classes in the way that pattern is manifested. The class Anthozoa is characterized by the absence of medusae, living only as polyps, while the Scyphozoa live most of their life cycle as medusa. The diverse Hydrozoa species include some that live exclusively as polyps, some that live exclusively as medusae, and some species that alternate between the two. In most taxa of Hydrozoa, the polyp is the most persistent and conspicuous stage, but some lack the medusa phase, and others lack the polyp phase.

The life cycle of the class Cubozoa is dominated by the medusa form, which for them appears cube or square shaped, when viewed from above. Members of Cubozoa, Hydrozoa, and Scyphozoa are sometimes grouped together as "Medusozoa" because a medusa phase is present in all three.

The cubozoan body is shaped like a square bell, with the mouth suspended inside it on a tube (the manubrium) that leads upward to the stomach, which is inside the top part of the bell. Extending around the inside bottom of the bell is a ring of tissue called the velarium, and at the bottom corners of the bell are muscular fleshy pads (pedalia), with one or more tentacles connected to each pedalium. Four sensory structures called rhopalia are located near the center of each of the four sides of the bell. Box jellyfish have eyes that are surprisingly complex, including regions with lenses, corneas, and retinas; however, box jellyfish do not have a brain, so how the images are interpreted remains unknown. Like all cnidarians, box jellyfish possess stinging cells that can fire a barb and transfer venom.

Cubozoans are agile and active swimmers, unlike the more planktonic jellyfish. They have been commonly observed to swim a meter in just five to ten seconds, and there are unconfirmed reports of large specimens of *Chironex fleckeri* swimming as fast as two meters in one second. The high speeds are achieved through a kind of squirting action in which the medusa contracts while the velarium at the bottom contracts even more, producing a constricted opening through which the water is forcefully expelled.



Box jellies can be found in many tropical areas, including near Australia, the Philippines, Hawaii, and Vietnam.

Defense and Feeding Mechanisms

Cnidarians take their name from a specialized cell, the *cnidocyte* (nettle cell). The cnida or nematocyst is secreted by the Golgi apparatus of a cell and is technically not an organelle but “the most complex secretory product known”. Tentacles surrounding the mouth contain nematocysts. The nematocysts are the cnidarians’ main form of offense or defense and function by a chemical or physical trigger that causes the specialized cell to eject a barbed and poisoned hook that can stick into, ensnare, or entangle prey or predators, killing or at least paralyzing its victim.

Box jellyfish are voracious predators and are known to eat fish, crustacean arthropods, and worms, utilizing the tentacles and nematocysts. When the tentacles contact the prey, the nematocysts fire into the prey, with the barbs holding onto the prey and transferring venom. The tentacles then contract and pull the prey near the bell, where the muscular pedalium pushes the tentacle and prey into the bell of the medusa, and the manubrium reaches out for the prey and mouth engulfs it.

Box jellies use the powerful venom contained in epidermic nematocysts to stun or kill their prey prior to ingestion and as an instrument for defense. Their venom is the most deadly in the animal kingdom and by 1996, had caused at least 5,567 recorded deaths since 1954. Most often, these fatal envenomations are perpetrated by the largest species of box jelly, *Chironex fleckeri,* owing to its high concentration of nematocysts, though at least two deaths in Australia have been attributed to the thumbnail-sized irukandji jellyfish *(Carukia barnesi).* Those who fall victim to *Carukia barnesi* suffer several severe symptoms, known as Irukandji syndrome. The venom of cubozoans is very distinct from that of scyphozoans. Sea turtles, however, are apparently unaffected by the sting and eat box jellies.

While *Chironex fleckeri* and the *Carukia barnesi* (Irukandji) species are the most venomous creatures in the world, with stings from such species excruciatingly painful and often fatal, not all species of box jellyfish are this dangerous to humans.

Some biologists have theorized that box jellyfish actively hunt their prey, and quite effectively as they can move so quickly, instead of drifting as do true jellyfish.

Vision

Box jellyfish are known to be the only jellyfish with an active visual system, consisting of multiple eyes located on the center of each side of its bell.

The eyes occur in clusters on the four sides of the cube-like body, in the four sensory structures called rhopalia. Each rhopalia has six sensory spots, giving 24 sensory structures (or eyes) in total. Sixteen are simply pits of light-sensitive pigment (eight slit-shaped eyes and eight lens-less pit eyes), but one pair in each cluster is surprisingly complex, with a sophisticated lens, retina, iris, and cornea, all in an eye only 0.1 millimeters across.

The lenses on these eyes have been analyzed and in principle it seems they could form distortion free images. Despite the perfection of the lenses, however, the retinas of the eyes lie closer to the lens than the optimum focal distance, resulting in a blurred image. One of these eyes in each set has an iris that contracts in bright light. Four of the eyes can only make out simple light levels.

It is not currently known how this visual information is processed by Cubozoa, as they lack a central nervous system, although they seem to have four brain-like organs. Some scientists have proposed that jellies have a “nerve net” that would allow processing of visual cues.

Classification

There are two main taxa of cubozoans, Chirodropidae and Carybdeidae, containing 19 known, extant species between them. The chirodropids and carybdeids are easy to distinguish morphologically. The carybdeidae, which includes the *Carukia barnesi* (Irukandji) species, generally have only one tentacle trailing from a single pedalium at each of the four corners the bell. In the *Tripedalia* species, however, while each tentacle is connected to a single pedalium, there are two or three pedalia on each corner of the bell, giving two or three tentacles trailing from each corner. Box jellyfish of the Chirodropidae group, which contains the *Chironex fleckeri* species, are distinguished by always having only four pedalia, one at each corner, with each of the pedalia having multiple tentacles. In other words, chirodropids have multiple tentacles connected to each pedalium, while carybdeids always have just one tentacle per pedalium.

The following is a taxonomic scheme for the cubozoans, with Chirodropidae and Carybdeidae classified as families, and with 9 genera split between them:

- Phylum Cnidaria
- Family Chirodropidae
    - Chironex fleckeri
    - Chirosoides buitendijkl
    - Chirodropus gorilla
    - Chirodropus palmatus
    - Chiropsalmus zygonema
    - Chiropsalmus quadrigatus
    - Chiropsalmus quadrumanus
- Family Carybdeidae
    - Carukia barnesi
    - Manokia stiasnyi
    - Tripedalia binata
    - Tripedalia cystophora
    - Tamoya haplonema
    - Tamoya gargantua
    - Carybdea alata
    - Carybdea xaymacana
    - Carybdea sivicksi
    - Carybdea rastonii
    - Carybdea marsupialis
    - Carybdea aurifera

Distribution

Cubozoans can be found in most tropical and subtropical waters *Carybdea marsupialis* and *Carybdea rastoni* have been found in temperate waters as well. It is likely that the distribution records are incomplete as the transparent nature of these medusae makes them very difficult to locate despite their shallow and coastal distribution.

Habitat

The preferred habitat of cubozoans appears to be over sandy substrate, with box jellies located just above the bottom during the day and moving up toward the surface at night. Field observation is extremely difficult, as the jellies react to the presence of divers by rapidly moving away. *Carybdea sivickisi* possesses adhesive pads on the exumbrellar surface which enables it to attach to various substrates in the field.

Behavior

Cubozoans have the most complex behavior of any cnidarian. They are active swimmers capable of moving 9.8–19.7 ft (3–6 m) per minute. They are positively phototactic (move toward light) and are active during the day and night, although they may feed only during the night or predawn hours. Vision clearly plays a role in both feeding and reproduction. One characteristic that makes them interesting, their image forming eyes, also makes them difficult to study in the field or the laboratory because they react to the presence of their human observers by swimming away.

Reproductive Biology

Little is known about the reproductive biology of cubozoans. The life history includes a benthic stage, the polyp, which can reproduce asexually by budding, and a pelagic stage, the medusa. Eggs and sperm combine to form a ciliated larva (planula), which settles on the bottom and becomes a polyp. Unlike scyphozoans, cubozoan polyps do not undergo strobilation (asexual reproduction by division into body segments); rather, the entire polyp becomes the juvenile medusa. *C. sivickisi* uses spermatophores that can be stored by the female, and it has been hypothesized that female *C. rastoni* may collect sperm strands produced by the males. Other cubozoans may have internal fertilization as well, but most broadcast their gametes.

Hydrozoa

Hydrozoa is a diverse and wide-ranging taxonomic class (sometimes superclass) of marine and freshwater invertebrates within the phylum Cnidaria, whose members are characterized by a life cycle that always includes the presence of planula larva, and the medusa, if present, having a velum, or muscular projection from the subumbrellar margin. Hydrozoans generally display alternation of generations between polyp and medusa, although hydras exhibit only the polyp form and some species are represented only by medusae and lack the polyp stage.

Hydrozoans are carnivorous animals that can be solitary or colonial. Most are small (an umbrella of less than 50 millimeters or two inches), but some can be large (40 centimeters or 17.7 inches), and some colonies can be very large (30 meters or 98 feet). Hydrozoans include marine hydroids, freshwater hydras, some known as jellyfish and corals, and the well-known Portuguese man-of-war (or Portuguese man o’ war).

While the often small and diaphanous hydrozoa, as polpys or medusae, often go unnoticed, they are important in aquatic food chains. Hydrozoans capture crustaceans, among other appropriately sized animals, with the medusae sometimes feeding extensively on fish eggs and larva, and these invertebrates are preyed upon by various fish, crustaceans, and mollusks. While the characteristic cnidarian stinging structures known as nematocysts provide protection from many predators, some sea slugs are able to appropriate the nematocysts for their own defense.

For humans, the hydrozoans add greatly to the wonder of nature, and illustrations, such as those by Ernst Haeckel, are renowned for their beauty. Hydra is among those hydrozoans that are common in scientific research. However, some hydrozoans tend to clog the pipes of power plants, increase friction on ships they have attached to, or are pests in aquaculture. And the medusae of species like the Portuguese man o’ war (Physalia physalis)—a siphonophore colony of four kinds of specialized polpys and medusoids—can inflict severe stings on humans.

Cnidaria, the phylum to which Hydrozoa belongs, contains some 11,000 species of relatively simple invertebrate animals found exclusively in aquatic, mostly marine, environments. Cniderians include corals, sea anemones, jellyfish, sea pens, sea pansies, sea wasps, and tiny freshwater hydra. The name of the phylum comes from cnidocytes, which are specialized cells that carry stinging organelles.

In the idealized life cycle, members of Cnidaria alternate between asexual polyps and sexual, free-swimming forms called medusae (singular medusa). However, the Anthozoa live only as polyps, while Scyphozoa live most of their life cycle as medusae. The Hydrozoa live as polyps, medusae, and species that alternate between the two. Invertebrates belonging to the class Cubozoa are named for their cube-shaped medusae, which form the dominant part of their life cycle. The non-anthozoan classes may be grouped into the subphylum Medusozoa.

In the idealized life cycle, during sexual reproduction, a larva (or planula) forms from the blastula. The larva have flagella and swim until it encounters a firm substrate, on which it anchors itself and then passes through metamorphosis to the polyp stage, if present. The polyp may be solitary or form colonies by budding. Medusae are produced from the polyp and swim freely and produce eggs and sperm. However, there are many variations from this life cycle.

Hydrozoa is a very diverse class with members that vary considerably from this idealized life cycle. The life cycle does always include the presence of planula larva, which is essentially a ciliated, motile gastrula, more an embryo than larva. However, among many in Hydrozoa, the medusae remain on the polyps in a reduced form, known as gonophores. A few hydrozoans, such as the hydra, have no medusa stage whatsoever; instead the polyp itself forms male or female gametes. And in many hydrozoans, there are no polyp stages.

The main characteristic that distinguishes the medusae of members of Hydrozoa from that of other classes is the presence of the velum, which is a muscular extension of the subumbrellar margin that allows the subumbrellar cavity to be partially closed.

The umbrella of hydrozoans commonly ranges in diameter between just 0.5 millimeters (0.02 inches) and 50 millimeters (two inches), but in many species the size is larger, reaching up to ten to 20 centimeters (3.9-7.9 inches) in Aequorea and up to 40 centimeters (15.7 inches) in Rhacostoma atlanticum. The smallest polyps range from only 20 to 480 µm. Most colonies have reduced size of a few centimeters, but some can be large, such as Corymorha nutans (12 centimeters or 4.7 inches) and up to Apolemia uvaria, whose colonies reach 30 meters (98.4 feet).

Most medusae and polyps are diaphanous, but colored species exist. Often this is reddish, derived from consuming crustaceans.

Some examples of hydrozoans are the freshwater jelly (Craspedacusta sowerbyi), the freshwater polyps (Hydra), Obelia, the Portuguese man o’ war (Physalia physalis), the chondrophores (Porpitidae), “air fern” (Sertularia argenta), and the pink-hearted hydroids (Tubularia).

Distribution and Habitat

Hydrozons are found in water masses all over the world, including marine and freshwater. Medusae are mostly planktonic, but some can be benthic. Polyp stages are usually benthic, but some, such as Velella velella are planktonic.

Hydrozoans occur in all aquatic habitats, including deep sea trenches, lakes, ponds, anchialine caves, and the spaces between sand grains, and many live on other organisms such as fishes, tunicates, polychaetes, mollusks, sponges, algae, and crustaceans. These later symbiotic relationships may be parasitic or involve mutualism or commensalism.

Behavior and Diet

Polpys and medusae are both mostly carnivorous and feed on animals of appropriate size. They commonly feed on crustaceans, such as copepods. Medusae are voracious predators, which are at the apex of food chains when consuming fish eggs and larvae.

Polyps are generally more varied in diet and some feed on a wide variety of prey. Some have a symbiotic relationship with zooxanthellae and are functionally photosynthetic. Carnivores used cnidocytes to capture their food.

Most members of Hydrozoa have separate sexes and fertilization is internal, but without copulation. In some, the males spawn in the water and the sperm swim actively toward the eggs on the female (medusae or polyp colony). For many species with medusae, both females and males spawn in the water. Eggs can be small and in large numbers or large and few, depending on the species. In some species, the dominant reproduction is asexual reproduction of the polyp stage.

Medusae tend to be markedly individual and even when swarms are formed by winds or current it is not known if there is any social interaction. The colonial Hydrozoa share complex functions and have been compared to superorganisms. The zooids of a colony typically derive from a single planula.

Life Cycles

Some colonial hydrozoans have both a medusa stage and a polyp stage in their life cycle. Each colony has a base, a stalk, and one or more polyps. Hydroid colonies are usually dioecious, which means that they have separate sexes—all the polyps in each colony are either male or female, but not usually both sexes in the same colony. Hydrozoan colonies are composed of a number of specialized polyps (or “zooids”), including feeding, reproductive, and sometimes, protective zooids. In some species, the reproductive polyps, known as gonozooids (or “gonotheca” in thecate hydrozoans) bud off asexually-produced medusae. These tiny, new medusae (which are either male or female) mature and spawn, releasing gametes freely into the sea in most cases. Zygotes become free-swimming planula larvae or actinula larvae that either settle on a suitable substrate (in the case of planulae), or swim and develop into another medusae or polyp directly (actinulae). Colonial hydrozoans include siphonophore colonies, Hydractinia, Obelia, and many others.

The medusa stage, if present, is the sexually-reproductive life cycle phase (that is, in hydrozoan species that have both polyp and medusa generations). Medusae of these species of Hydrozoa are known as “hydromedusae.” Most hydromedusae have shorter life spans than the larger scyphozoan jellyfish. Some species of hydromedusae release gametes shortly after they are themselves released from the hydroids (as in the case of fire corals), living only a few hours, while other species of hydromedusae grow and feed in the plankton for months, spawning daily for many days before their supply of food or other water conditions deteriorate and cause their demise.

Systematics

Hydrozoan systematics is highly complex. Several approaches for expressing their interrelationships were proposed and heavily contested since the late nineteenth century, but in more recent times a consensus seems to be emerging.

For long, the hydrozoans were divided into a number of orders, according to their mode of growth and reproduction. Most famous among these was probably the assemblage called "Hydroida," but this group is apparently paraphyletic, united by plesiomorphic (ancestral) traits. Other such orders were the Anthoathecatae, Actinulidae, Laingiomedusae, Polypodiozoa, Siphonophora, and Trachylina.

The highly apomorphic Siphonophorae—like this Portuguese Man o' War *(Physalia physalis)*—have long misled hydrozoan researchers.

As far as can be told from the molecular and morphological data at hand, the Siphonophora, for example, were just highly specialized "hydroids," whereas the Limnomedusae—presumed to be a "hydroid" suborder—were simply very primitive hydrozoans and not closely related to the other "hydroids." Therefore, today the hydrozoans are at least tentatively divided into two subclasses, the Leptolinae (containing the bulk of the former "Hydroida" and the Siphonophora) and the Trachylinae, containing the others (including the Limnomedusae). The monophyly of several of the presumed orders in each subclass is still in need of verification.

In any case, according to this classification, the hydrozoans can be subdivided as follows, with taxon names emended to end in "-ae":

Class Hydrozoa

- Subclass Leptolinae (or Hydroidolina)
    - Order Anthomedusae (= Anthoathecata(e), Athecata(e), Stylasterina(e)) - includes Laingoimedusae but monophyly requires verification.
    - Order Leptomedusae (= Leptothecata(e), Thecaphora(e), Thecata(e)).
    - Order Siphonophorae.
- Subclass Trachylinae
    - Order Actinulidae.

  - Order Limnomedusae - Monophyly requires verification; tentatively placed here.
  - Order Narcomedusae.
  - Order Trachymedusae - Monophyly requires verification.

The Integrated Taxonomic Information System (ITIS) uses the same system but unlike here does not use the oldest available names for many groups.

In addition, there exists a unique cnidarian parasite, Polypodium hydriforme, which lives inside its host's cells. It is sometimes placed in the Hydrozoa, but actually its relationships are better treated as unresolved for the time being—a somewhat controversial 18S rRNA sequence analysis found it to be closer to Myxozoa. It was traditionally placed in its own class Polypodiozoa and this view is presently often seen to reflect the uncertainties surrounding this highly distinct animal.

Other Classifications

Some of the more widespread classification systems for the Hydrozoa are listed below. Though they are often found in seemingly authoritative Internet sources and databases, they do not agree with the currently available data. Especially the presumed phylogenetic distinctness of the Siphonophora is a major flaw that was corrected only recently.

Limnomedusae like the Flower Hat Jelly (Olindias formosa) were long allied with Anthomedusae and Leptomedusae in the "Hydroida".

The obsolete classification mentioned above was as follows:

- Order Actinulidae
- Order Anthoathecatae
- Order Hydroida
  - Suborder Anthomedusae
  - Suborder Leptomedusae
  - Suborder Limnomedusae

- Order Laingiomedusae
- Order Polypodiozoa
- Order Siphonophora

Fire corals were initially considered a separate order. They are actually a family of the Anthomedusae.

- Order Trachylina
    - Suborder Narcomedusae
    - Suborder Trachymedusae

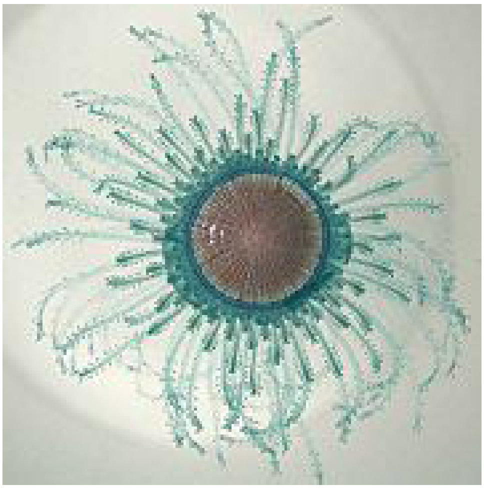
A very old classification that is sometimes still seen is:

- Order Hydroida
- Order Milleporina
- Order Siphonophorida
- Order Stylasterina (= Anthomedusae)
- Order Trachylinida

Catalogue of Life uses the following:

- Order Actinulida
- Order Anthoathecata (= Anthomedusae)
- Order Hydroida
- Order Laingiomedusae
- Order Leptothecata (= Leptomedusae)
- Order Limnomedusae
- Order Narcomedusae

- Order Siphonophora
- Order Trachymedusae



Some incorrectly place the anthomedusan family Porpitidae in a separate order "Chondrophora".

Animal Diversity Web uses the following:

- Order Actinulida
- Order Capitata
- Order Chondrophora
- Order Filifera
- Order Hydroida
- Order Siphonophora

Boero and Bouillon use the following:

- Superclass Hydrozoa
  - Class Automedusa
    - Subclass Actinulidae
    - Subclass Narcomedusae
    - Subclass Trachymedusae
  - Class Hydroidomedusa
    - Subclass Anthomedusae
    - Subclass Laingiomedusae
    - Subclass Leptomedusae

- Subclass Limnomedusae
- Subclass Siphonophorae
- Subclass Polypodiozoa

Hydra: A Freshwater Genus

The most widely-known and researched freshwater hydrozoan is Hydra, which is found in slow-moving waters.

Hydra has a pedal disc composed of gland cells that helps it attach to substrates, and like all cnidarians uses nematocysts, or “stinging cells,” to disable its prey. Hydra eat small crustaceans (such as brine shrimp), insect larvae, and annelid worms. Hydra may reproduce sexually, through the spawning of sperm (and thus insemination of eggs on the female body column), or through asexual reproduction (budding).

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4

Helminthology

The branch of study which focuses on parasitic worms is called helminthology. Some of the different categories of worms studied within this field are Platyhelminthes and Aschelminthes. This chapter has been carefully written to provide an easy understanding of the varied facets of these phyla of helminthes.

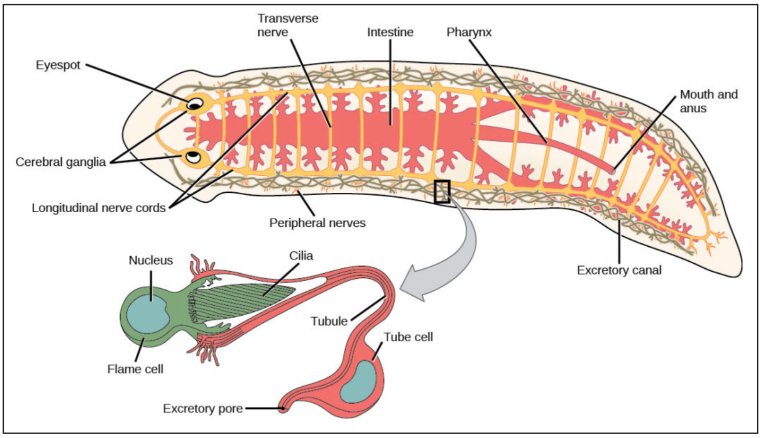
Helminthology is a sub-discipline of invertebrate zoology. Helminthology deals with studying the helminths, particularly the parasitic worms. The major groups of parasitic worms include the flatworms (Platyhelminthes), the nematodes or roundworms (Nematoda), and thorny-headed worms (Acanthocephala).

Helminthology is concerned with the studying of classification, taxonomy, distribution, ecological, and medical significance of parasitic worms.

Platyhelminthes

Flatworm, also called platyhelminth is any of the phylum Platyhelminthes, a group of soft-bodied, usually much flattened invertebrates. A number of flatworm species are free-living, but about 80 percent of all flatworms are parasitic—*i.e.,* living on or in another organism and securing nourishment from it. They are bilaterally symmetrical (*i.e.,* the right and left sides are similar) and lack specialized respiratory, skeletal, and circulatory systems; no body cavity (coelom) is present. The body is not segmented; spongy connective tissue (mesenchyme) constitutes the so-called parenchyma and fills the space between organs. Flatworms are generally hermaphroditic—functional reproductive organs of both sexes occurring in one individual. Like other advanced multicellular animals, they possess three embryonic layers—endoderm, mesoderm, and ectoderm—and have a head region that contains concentrated sense organs and nervous tissue (brain). Most evidence, however, indicates that flatworms are very primitive compared with other invertebrates (such as the arthropods and annelids). Some modern evidence suggests that at least some flatworm species may be secondarily simplified from more complex ancestors.

The phylum consists of four classes: Trematoda (flukes), Cestoda (tapeworms), Turbellaria (planarians), and Monogenea. It should be noted that some authorities consider Monogenea, which contains the order Aspidogastrea, to be a subclass within the class Trematoda. Members of all classes except Turbellaria are parasitic during all or part of the life cycle. Most turbellarians are exclusively free-living forms. More than 20,000 flatworm species have been described.



General Features

Importance

Although some platyhelminths (flatworms) are free-living and nondestructive, many other species (particularly the flukes and tapeworms) parasitize humans, domestic animals, or both. In Europe, Australia, and North and South America, tapeworm infestations of humans have been greatly reduced as a consequence of routine meat inspection. But where sanitation is poor and meat eaten undercooked, the incidence of tapeworm infestations is high. In the Baltic countries much of the population is infested with the broad tapeworm (*Diphyllobothrium latum*); in parts of the southern United States a small proportion of the population may be infested with the dwarf tapeworm (*Hymenolepis nana*). In Europe and the United States the beef tapeworm (*Taenia saginata*) is common because of the habit of eating undercooked steaks or other beef products.

Parasites in immature stages (larvae) can cause serious damage to the host. A larval stage of the gid parasite of sheep (*Multiceps multiceps*) usually lodges in the sheep brain. Fluid-filled hydatid cysts (*i.e.,* sacs containing many cells capable of developing into new individuals) of *Echinococcus* may occur almost anywhere in the body of sheep. In humans, hydatids of the liver, brain, or lung are often fatal. Infestation occurs only where people live in close association with dogs that have access to infested sheep for food.

Thirty-six or more fluke species have been reported as parasitic in humans. Endemic (local) centres of infection occur in virtually all countries, but widespread infections occur in the Far East, Africa, and tropical America. Many species are ingested as cysts, called metacercariae, in uncooked food—*e.g.,* the lung fluke *Paragonimus westermani* found in crayfish and crabs, the intestinal flukes *Heterophyes heterophyes* and

Metagonimus yokogawai and the liver fluke *Opisthorchis sinensis* in fish, and the intestinal fluke *Fasciolopsis buski* on plants. Free-swimming larvae (called cercariae) of blood flukes penetrate the human skin directly. In humans these parasites and others listed below cause much misery and death. Control of certain flukes through the eradication of their mollusk hosts has been attempted but without much success.

Schistosomiasis (bilharziasis) is a major human disease caused by three species of the genus *Schistosoma*, known collectively as blood flukes. Africa and western Asia (*e.g.,* Iran, Iraq) are endemic centres for *S. haematobium*; *S. mansoni* also is found in these areas, as well as in the West Indies and South America. In the Far East, *S. japonicum* is the important blood fluke.

Among domestic animals, the sheep liver fluke (*Fasciola hepatica*) may cause debilitating and fatal epidemics (liver rot) in sheep. These animals become infected by eating metacercariae encysted on grass. Monogenea are common pests on fish in hatcheries and home aquariums.

Size Range

Most turbellarians are less than five millimetres (0.2 inch) long, and many are microscopic in size. The largest of this class are the planarians, which may reach 0.5 metre (about 20 inches) in length. Trematodes are mostly between about one and 10 millimetres (0.04 to 0.4 inch) long; members of some species, however, may grow to several centimetres. The smallest cestodes are about one millimetre (0.04 inch) long, but members of a few species exceed 15 metres (50 feet) in length. The Monogenea range in length from 0.5 to 30 millimetres (0.02 to 1.2 inches). Aspidogastrea are from a few millimetres to 100 millimetres in length.

Distribution and Abundance

In general, free-living flatworms (the turbellarians) can occur wherever there is moisture. Except for the temnocephalids, flatworms are cosmopolitan in distribution. They occur in both fresh water and salt water and occasionally in moist terrestrial habitats, especially in tropical and subtropical regions. The temnocephalids, which are parasitic on freshwater crustaceans, occur primarily in Central and South America, Madagascar, New Zealand, Australia, and islands of the South Pacific.

Some flatworm species occupy a very wide range of habitats. One of the most cosmopolitan and most tolerant of different ecological conditions is the turbellarian *Gyratrix hermaphroditus*, which occurs in fresh water at elevations from sea level to 2,000 metres (6,500 feet) as well as in saltwater pools. Adult forms of parasitic flatworms are confined almost entirely too specific vertebrate hosts; the larval forms, however, occur in vertebrates and in invertebrates, especially in mollusks, arthropods (*e.g.,* crabs), and annelids (*e.g.,* marine polychaetes). They are cosmopolitan in distribution, but their occurrence is closely related to that of the intermediate host or hosts.

Life Cycle

Reproduction

With very few exceptions, platyhelminthes are hermaphroditic, and their reproductive systems are generally complex. Numerous testes but only one or two ovaries are usually present in these flatworms. The female system is unusual in that it is separated into two structures: the ovaries and the vitellaria, often known as the vitelline glands or yolk glands. The cells of the vitellaria form yolk and eggshell components. In some groups, particularly those that live primarily in water or have an aqueous phase in the life cycle, the eggshell consists of a hardened protein known as sclerotin, or tanned protein. Most of this protein comes from the vitellaria. In other groups, especially those that are primarily terrestrial or have a terrestrial phase in their life cycle, the eggshells are composed of another protein, keratin, a tougher material that is more resistant to adverse environmental conditions.

In the tapeworms, the tapelike body is generally divided into a series of segments, or proglottids, each of which develops a complete set of male and female genitalia. A rather complex copulatory apparatus consists of an evertible (capable of turning outward) penis, or cirrus, in the male and a canal, or vagina, in the female. Near its opening the female canal may differentiate into a variety of tubular organs. Fertilized eggs are often stored in a saclike uterus, which may become greatly distended; in tapeworms, it may fill a whole segment.

Each male and female reproductive system may have its own external opening, or gonopore, or the terminal regions of each system may join to form a common genital atrium, or passage, and a genital pore.

Either cross-fertilization (*i.e.,* involving two individuals) or self-fertilization may occur; self-fertilization is probably more common. Some free-living flatworms perform a type of copulation known as hypodermic impregnation, whereby the penis of one animal pierces the epidermis of another and injects sperm into the tissues. Some forms reproduce asexually through budding.

Development

The life cycles of the free-living forms are relatively simple. Fertilized eggs are laid singly or in batches. Frequently they are attached to some object or surface by an adhesive secretion. After a period of embryonic development, free-swimming larvae or minute worms emerge.

In contrast, parasitic platyhelminths undergo very complex life cycles, often involving several larval stages in other animals—the intermediate hosts; these hosts may be invertebrate or vertebrate.

The simplest cycle in parasitic platyhelminths occurs in the Monogenea, which have no intermediate hosts. The majority of the Monogenea are ectoparasitic (externally parasitic) on fish. The eggs hatch in water. The larva, known as an oncomiracidium, is heavily ciliated (has actively moving hairlike projections) and bears numerous posterior hooks. It must attach to a host before it can grow and mature. In some species (*e.g., Polystoma integerrimum*) parasitic in frogs, maturation of the genitalia is synchronized with maturation of the host and apparently is controlled by the endocrine system of the latter.

In the life cycle of trematode flukes of the subclass Digenea, mollusks (mostly snails) serve as the intermediate host. Fertilized eggs usually hatch in water. The first larval stage, the miracidium, generally is free-swimming and penetrates a freshwater or marine snail, unless it has already been ingested by one. Within this intermediate host, the parasite passes through a series of further stages known as sporocysts, rediae, and cercariae. Through a complex process of asexual replication, each miracidium larva gives rise to dozens, or even hundreds, of cercariae. The cercariae exit the snail and swim for a number of hours in the surrounding water. The cercariae must locate a vertebrate host to complete the life cycle. In addition, many species must first invade another intermediate host, typically a fish or amphibian. The trematode life cycle is completed only if the final, or definitive, host (such as a bird, sheep, or cow) eventually eats the intermediate host. In some species the trematode modifies the behaviour or appearance of the second intermediate host in ways that increase the likelihood that it will be eaten by the proper definitive host.

Tapeworms of the subclass Eucestoda are generally transmitted from host to host by direct ingestion of eggs; by ingestion of intermediate hosts containing larval stages; and, very rarely, by passage of a larva from an intermediate host through a skin wound into another intermediate host.

Transmission to a human host through a skin wound is most likely to occur in Asia, where frogs infested with tapeworm larvae are sometimes used to treat wounds. The tapeworm, *Hymenolepis nana*, parasitic in rodents and humans, can complete its life cycle without an intermediate host.

Regeneration

The ability to undergo tissue regeneration, beyond simple wound healing, occurs in two classes of Platyhelminthes: Turbellaria and Cestoda.

Turbellaria

Turbellarians have the greatest regenerative powers exist in species capable of asexual reproduction. Pieces from almost any part of the turbellarian *Stenostomum*, for example, can develop into completely new worms. In some cases regeneration of very small pieces may result in the formation of imperfect (*e.g.,* headless) organisms.

In other Turbellaria, regeneration of the head is limited to pieces from the anterior region or to tissues containing the cerebral ganglion (brain). The region anterior to this ganglion is incapable of regeneration, but if cuts are made posterior to it, many species can replace the entire posterior region, including the pharynx and the reproductive system. In the cut pieces, polarity is retained; *i.e.,* the anterior zone of the cut piece regenerates the head and the posterior region regenerates the tail. If a region in front of the pharynx is transplanted into the posterior region of another individual, it influences that region to form a pharyngeal zone that eventually differentiates a pharynx. This new pharyngeal zone is now said to be determined and, if removed, will regenerate again into a new pharynx.

There is evidence that a special type of cell, a neoblast, is involved in planarian regeneration. Neoblasts, rich in ribonucleic acid (RNA), which plays an essential role in cell division, appear in great numbers during regeneration. Similar cells, apparently inactive, occur in the tissues of whole organisms.

Cestoda

Regeneration, although rare in the parasitic worms in general, does occur in the cestodes. Most tapeworms can regenerate from the head (scolex) and neck region. This property often makes it difficult to treat people for tapeworm infections; treatment may eliminate only the body, or strobila, leaving the scolex still attached to the intestinal wall of the host and thus capable of producing a new strobila, which reestablishes the infestation. Cestode larvae from several species can regenerate themselves from cut regions. A branched larval form of *Sparganum prolifer*, a human parasite, may undergo both asexual multiplication and regeneration.

Ecology

Turbellaria are adapted to a wide range of environments, and many species are resistant to extreme environmental conditions. Some occur in coastal marine habitats—in sand, on or under rocks, and in or on other animals or plants. Some marine species occur at relatively great depths in the sea; others are pelagic (*i.e.,* living in the open sea). Freshwater species are found in ponds, lakes, rapidly flowing rivers, and streams. Temporary freshwater pools may contain adult forms that survive periods of dryness in an encysted state. Some aquatic species exhibit considerable tolerance to osmotic changes—*i.e.,* to differences in salt concentrations of the water; a marine species (*Coelogynopora biarmata*), for example, has also been found in freshwater springs.

Terrestrial turbellarian species occur in soil, moist sand, leaf litter, mud, under rocks, and on vegetation. Some have been found in pools in the desert and in caves. Cave-dwelling species tend to show loss of eyes and pigment.

Some species are able to stand considerable temperatures. For example, *Crenobia alpina*, which occurs in alpine streams, apparently can survive temperatures of -40° to -50 °C (-40° to -58 ° F). Remarkable heat tolerance is exhibited by *Macrostomum thermale* and *Microstomum lineare*, which are found in hot springs at 40°–47 °C (104°–117 °F). *M. lineare* can also tolerate temperatures as low as 3 °C (37 °F).

Many turbellarians live in association with plants and animals. Marine algae, for example, frequently harbour many turbellarian species, often in large numbers. Turbellarians most commonly associate with animals such as echinoderms (*e.g.,* sea stars), crustaceans (*e.g.,* crabs), and mollusks. Less commonly, associations occur with sipunculid worms, polychaete worms, arachnids (*e.g.,* spiders), cnidarians (*e.g.,* jellyfish), other turbellarians, and lower vertebrates. An interesting feature of these associations is that species within a turbellarian family tend to associate with one type of organism; for example, almost all members of the family Umagillidae associate with echinoderms.

In a few cases, the association is parasitic; *i.e.,* the turbellarians obtain all of their nourishment from the host. Most of these species belong to the order Neorhabdocoela, in which the alimentary canal is either absent or reduced.

Among the turbellaria that are parasitic or commensal (*i.e.,* living in close association with but not harmful to another organism) the Temnocephalida are best adapted for attachment to other organisms. They have a large saucer-shaped posterior adhesive organ and anterior tentacles that are also used for adhesion. All temnocephalids occur on freshwater hosts, mainly crustaceans but also mollusks, turtles, and jellyfish.

The tendency to associate with other animals apparently represents a definite evolutionary trend among the platyhelminths; permanent associations' essential to the survival of a species could develop from loose associations, which may then have given rise to parasitic forms, including the trematodes and cestodes. The free-living larval stages that frequently occur in these groups play a major role in disseminating the species.

The ecology of the parasitic groups (*i.e.,* Cestoda and Trematoda) is particularly complex, because as many as four hosts may be involved in the life cycle. In the case of the broad tapeworm, for example, humans serve as the final (or definitive) hosts, various species of fish as one intermediate host, and species of a small water crustacean (*Cyclops*) as another intermediate host. It is clear that the broad tapeworm (*Diphyllobothrium latum*) can occur only where an intimate ecological association exists among the three host groups.

In addition to adapting to the general external environment, parasites at each stage of the life cycle must adapt to the microenvironment inside the host. Adaptations include not only obvious features, such as suckers or hooks for attachment, but also those associated with the biochemical, physiological, and immunological conditions imposed by the host. Parasites frequently utilize the physiological and biochemical properties of a new host, especially those that differ markedly from the external environment, in order to trigger the next developmental stage—*e.g.,* several species of cestodes are stimulated to mature sexually by the high body temperature (40 °C) of their bird host, which contrasts sharply with the low body temperature of the cold-blooded fish host of the larval stage. The unusually intimate association of certain flukes (subclass Digenea) with mollusks suggests that flukes were originally parasites of mollusks and that they later developed an association with other hosts.

Knowledge of a platyhelminth parasite's ecology and of that of its intermediate host(s) is essential if control measures against the pest are to be effective. Humans have sometimes inadvertently modified the environment in ways that have increased the spread of infection. The Aswan High Dam in Egypt, for example, has produced conditions especially favourable for the breeding of the snail that serves as the required intermediate host of the blood fluke (*Schistosoma mansoni*). In this case, as with many trematode infestations, people exposed themselves to the disease by bathing in water containing infective larvae (cercariae) released from infested snails; the cercariae enter directly through the skin. Certain other human diseases of platyhelminth origin—such as hydatid (cyst) disease, caused by the tapeworm *Echinococcus granulosus*—owe their survival and dissemination to man's close ecological association with dogs.

In the parasitic platyhelminth species (*e.g.,* those in the Monogenea) that do not normally utilize intermediate hosts, there is a close ecological association between egg release and production of young of both the parasite and its host; infection of the next generation of host could not otherwise occur.

Many platyhelminths show highly specific adaptations to internal host environments. Many monogeneans, for example, show a marked preference for a particular gill arch in a fish. The scolex (head) of certain tapeworms of elasmobranch fishes (*e.g.,* sharks, skates, and rays) is highly specialized and can satisfactorily attach only to the gut of a fish possessing a complementary structure.

Form and Function

External Features

Some turbellarians are gray, brown, or black, with mottled or striped patterns. Others, which contain symbiotic algae in the mesenchyme, are green or brown. Parasitic flatworms usually have no pigment, but cestodes may be coloured by food (*e.g.,* bile, blood) in their gut. Some parasitic forms may show masses of dark eggs through a translucent, creamy, or whitish tissue.

The typical flatworm body is flattened and leaflike or tapelike. The head may be set off from the body or grade imperceptibly into it. The anterior (head) end can usually be distinguished from the posterior end in free-living forms by the presence of two pigment spots, which are primitive eyes. In the case of the tapeworm, the scolex is usually conspicuous for its breadth, while the strobila (body) typically consists of numerous proglottids, each of which is usually a self-sufficient reproducing unit with all of the sexual organs necessary to reproduce. The number of proglottids may vary from three in some species to several hundred in others. Organs of attachment on the scolex may, in addition to suckers, consist of hooks, spines, or various combinations of these.

The structure and function of the body covering, or tegument, differs markedly between free-living and parasitic forms. In free-living forms, the body covering is typically an epidermis consisting of one layer of ciliated cells—*i.e.,* cells with hairlike structures—the cilia being confined to specific regions in some species. In the parasitic groups—flukes, tapeworms, and monogeneans—the tegument shows striking modifications associated with the parasitic way of life. It once was thought that the tegument is a nonliving secreted layer; it is now known, however, that the tegument of parasites is metabolically active and consists of cells not separated from one another by cell walls (*i.e.,* a syncytium). The tegument itself consists of cytoplasmic extensions of tegumental cells, the main bodies of which lie in what may be described as the "subcuticular" zone, although a true cuticle is not present. A membrane separates the inner zone of the tegumental cells, the so-called perinuclear cytoplasm, from the surface syncytium, or distal cytoplasm.

The surface of tapeworms and monogeneans is drawn out into spinelike structures called microtriches, or microvilli. The microtriches probably help to attach the parasite to the gut of the host, absorb nutritive materials, and secrete various substances. In the flukes, microtriches are lacking, but spines are frequently present.

Embedded in the epidermis of turbellarians are ovoid or rod-shaped bodies (rhabdoids) of several sorts; of uncertain function, the bodies frequently are concentrated dorsally or may be clustered anteriorly as rod tracts opening at the apex. Rhabdoids are absent in flukes and tapeworms.

Internal Features

Beneath the epidermis of turbellarians is a homogeneous or lamellated basal membrane. Club-shaped mesenchymal gland cells, opening externally, generally are present in all flatworms. In turbellarians two major types of mesenchymal glands occur: one produces a slimy material upon which the organisms creep; the other secretes an adhesive substance for capture of prey, for adhesion, and for cementing egg capsules to a suitable surface. The larvae of parasitic forms generally possess similar glands whose secretions are used for adhesion, for producing cyst walls around resting stages, and for penetrating hosts; some adult parasites have glands for adhesion and, in trematodes, for softening and digesting host tissues.

The mesenchyme consists of fixed and free cells as well as a fibrous matrix. A fluid occupies the minute open spaces and serves for distribution of nutrients and wastes. The mesenchymal cells in certain groups may differentiate during growth to become sex cells or may function in asexual reproduction in repair or in regeneration.

Flatworms have no specialized respiratory system; gases simply diffuse across the body wall.

Nervous System

The main ganglia, or nerve centres, of the nervous system and the major sense organs are generally concentrated at the anterior end. Typically, the primitive brain of the flatworm consists of a bilobed mass of tissue with lateral longitudinal nerve cords connected by transverse connectives, thus forming a rather ladderlike structure or grid running the greater length of the organism. Free-living forms commonly have two longitudinal cords, but some tapeworms have as many as 10. Sensory receptors occur in all groups.

Musculature

The well-developed muscular system present in flatworms is comprised of a subcuticular musculature consisting of layers of circular, longitudinal, and diagonal muscles close to the epidermis, and a mesenchymal musculature consisting of dorsoventral, transverse, and longitudinal fibres passing through the mesenchyme. In general, platyhelminths are capable of extensive body contraction and elongation.

Digestive and Excretory Systems

The blind-ending intestine of trematodes consists of a simple sac with an anterior or midventral mouth or a two-branched out with an anterior mouth; an anus is usually lacking, but a few species have one or two anal pores. Between the mouth and the intestine are often a pharynx and an esophagus receiving secretions from glands therein. The intestine proper, lined with digestive and absorptive cells, is surrounded by a thin layer of muscles that effect peristalsis; *i.e.,* they contract in a wavelike fashion, forcing material down the length of the intestine. In many larger flukes lateral intestinal branches, or diverticula, bring food close to all internal tissues. Undigested residue passes back out of the mouth.

Cestodes have no digestive tract; they absorb nutrients from the host across the body wall. Most other flatworms, however, have conspicuous digestive systems. The digestive system of turbellarians typically consists of mouth, pharynx, and intestine. In the order Acoela, however, only a mouth is present; food passes directly from the mouth into the parenchyma, to be absorbed by the mesenchymal cells.

The excretory system consists of protonephridia. These are branching canals ending in so-called flame cells—hollow cells with bundles of constantly moving cilia.

Nutrition

Free-living Forms

Free-living platyhelminths (class Turbellaria), mostly carnivorous, are particularly adapted for the capture of prey. Their encounters with prey appear to be largely fortuitous, except in some species that release ensnaring mucus threads. Because they have developed various complex feeding mechanisms, most turbellarians are able to feed on organisms much larger than themselves, such as annelids, arthropods, mollusks, and tunicates (*e.g.,* sea squirts). In general, the feeding mechanism involves the pharynx which, in the most highly developed forms, is a powerful muscular organ that can be protruded through the mouth. Flatworms with a simple ciliated pharynx are restricted to feeding on small organisms such as protozoans and rotifers, but those with a muscular pharynx can turn it outward, thrust it through the tegument of annelids and crustaceans, and draw out their internal body organs and fluids. Turbellarians with a more advanced type of pharynx can extend it over the captured prey until the animal is completely enveloped.

Digestion is both extracellular and intracellular. Digestive enzymes (biological catalysts), which mix with the food in the gut, reduce the size of the food particles. This partly digested material is then engulfed (phagocytized) by cells or absorbed; digestion is then completed within the gut cells.

Parasitic Forms

In the parasitic groups with a gut (Trematoda and Monogenea), both extracellular and intracellular digestion occur. The extent to which these processes take place depends on the nature of the food. When fragments of the host's food or tissues other than fluids or semifluids (*e.g.,* blood and mucus) are taken as nutrients by the parasite, digestion appears to be largely extracellular. In those that feed on blood, digestion is largely intracellular, often resulting in the deposition of hematin, an insoluble pigment formed from the breakdown of hemoglobin. This pigment is eventually extruded by disintegrating gut cells.

Despite the presence of a gut, trematodes seem able to absorb glucose and certain other materials through the metabolically active tegument covering the body surface. Tapeworms, which have no gut, absorb all nutrients through the tegument. Amino acids (the structural units of proteins) and small molecules of carbohydrate (*e.g.,* sugars) cross the tegument by a mechanism called active transport, in which molecules are taken up against a concentration gradient. This process, similar to that in the vertebrate gut, requires the expenditure of energy. Cestodes may also be able to digest materials in contact with the tegument by means of so-called membrane digestion, a little-understood process.

Metabolism

Both free-living and parasitic platyhelminths utilize oxygen when it is available. Most of the parasitic platyhelminths studied have a predominantly anaerobic metabolism (*i.e.,* not dependent upon oxygen). This is true even in species found in habitats—such as the bloodstream—where oxygen is normally available.

Parasitic platyhelminths are made up of the usual tissue constituents—protein, carbohydrates, and lipids—but, compared to other invertebrates, the proportions differ somewhat; *i.e.,* the carbohydrate content tends to be relatively high and the protein content relatively low. In larval and adult cestodes, carbohydrate occurs chiefly as animal starch, or glycogen, which acts as the main source of energy for species in low oxygen habitats. The level of glycogen, like other chemical constituents, can fluctuate considerably, depending on the diet or feeding habits of the host. In some species, more than 40 percent of the worm's dried weight is glycogen.

Because carbohydrate metabolism is important in parasitic flatworms, a substantial amount of carbohydrate must be present in the host diet to assure normal growth of the parasite. Hence the growth rate of the rat tapeworm (*Hymenolepis diminuta*) is a good indicator of the quantity of carbohydrate ingested by the rat. Experiments have shown that most parasitic worms have the capability of utilizing only certain types of carbohydrate. All tapeworms that have been studied thus far utilize the sugar glucose. Many tapeworms can also utilize galactose, but only a few can utilize maltose or sucrose.

An unusual constituent of both trematodes and cestodes is a round or oval structure called a calcareous corpuscle; large numbers of them occur in the tissues of both adults and larvae. Their function has not yet been established, but it is believed that they may act as reserves for such substances as calcium, magnesium, and phosphorus.

The chief proteins in cestodes and trematodes are keratin and sclerotin. Keratin forms the hooks and part of the protective layers of the cestode egg and the cyst wall of certain immature stages of trematodes. Sclerotin occurs in both cestode and trematode eggshells, especially in those that have larval stages associated with aquatic environments.

Platyhelminth eggs hatch in response to a variety of different stimuli in different hosts. Most trematode eggs require oxygen in order to form the first larval stages and light in order to hatch. Light is thought to stimulate the release of an enzyme that attacks cement holding the lid (operculum) of the egg in place. A similar mechanism probably operates in cestodes (largely of the order Pseudophyllidea) whose life cycles involve aquatic intermediate hosts or definitive hosts, such as birds or fish.

In many cestodes, especially those belonging to the order Cyclophyllidea, the eggs hatch only when they are ingested by the host. When the host is an insect, hatching sometimes is apparently purely a mechanical process, the shell being broken by the insect's mouthparts. In vertebrate intermediate hosts, destruction of the shell depends largely on the action of the host's enzymes. Activation of the embryo within the shell and its subsequent release depend on other factors, including the amount of carbon dioxide present, in addition to the host's enzymes. Factors involving a vertebrate host are also important in establishing trematode or cestode infections after encysted or encapsulated larval stages have been ingested. Under the influence of the same factors, tapeworm larvae are stimulated to evaginate their heads (i.e., turn them inside out, so to speak), a process that makes possible their attachment to the gut lining.

Evolution

The origin of the platyhelminths and the evolution of the various classes remain unclear. There are, however, two main lines of thought. According to the more widely accepted view, the Turbellaria represent the ancestors of all other animals with three tissue layers. Other authorities have agreed, however, that flatworms may be secondarily simplified; that is, they may have degenerated from more-complex animals by an evolutionary loss or reduction of complexity.

It is generally believed that the parasitic groups are derived from the Turbellaria, many of which form close associations with other animals. These associations often show great host specificity, a characteristic of truly parasitic forms. There are a number of views regarding the evolutionary relationships among the various parasitic groups. One school of thought proposes that rhabdocoel turbellarians gave rise to monogeneans; these, in turn, gave rise to digeneans, from which the cestodes were derived. Another view is that the rhabdocoel ancestor gave rise to two lines; one gave rise to monogeneans, who gave rise to digeneans, and the other line gave rise to cestodes. A further modification of the latter view, based largely on the study of the larval forms, proposes that cestodes were derived from monogeneans.

In considering the evolution of the parasitic groups, the digeneans should be mentioned in particular. With very few exceptions, mollusks act as intermediate hosts in digenean life cycles. This condition has led to the widely accepted view that digeneans were originally commensals of mollusks that subsequently turned parasitic. Digeneans later formed an association with vertebrates; the vertebrates, in turn, became incorporated into the life cycle as definitive hosts.

Dugesia

Digesia is also as planaria and is a fresh water form of cosmopolitan distribution. Its body is elongated, flattened and some-what conical. It has a distinct head, which is triangular in form and bears a pair of semicircular ocelli and a pair of distinct auricles. These animals are acoelomate, bilaterally symmetrical and are triploblastic. Their body wall is comprised of ciliated epidermis and has rod-like bodies-the rhabdites embedded in it. Their excretory organs are protonephridia and flame cells. Their alimentary canal is having a distinct pharynx, a proboscis and an intestine, which is trifid in front and bifid behind. They reproduce through regeneration.

Habit and Habitat of Dugesia Tigrina

Dugesia tigrina is gregarious (lives in groups) found on the underside of leaves, logs, debris and rocks submerged in cool, clear and running water of streams, ponds and lakes.

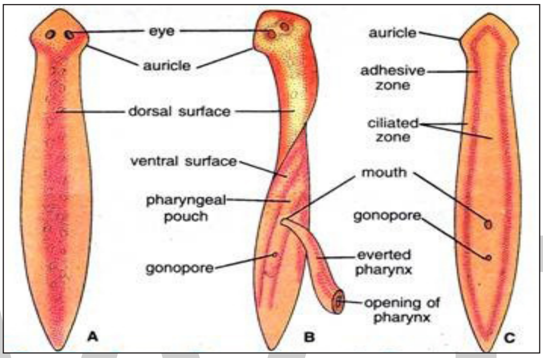
They are not easy to see unless they are moving, for they are small and flat and their dark mottled colour blends perfectly with the rocks or plants to which they cling. They live in damp surroundings as their bodies are not protected against desiccation. Dugesia tigrina is world-wide in distribution.

Structure of Dugesia Tigrina

Shape, Size and Colour

Dugesia tigrina is about 12 mm long and is dark brownish or blackish in colour.

It is a thin flattened worm with definite sides, there is an anterior end directed forwards in moving, one surface of the body is always uppermost, this is the dorsal surface, while the surface towards the substratum is ventral. The dorsal surface is darker in colour than the ventral surface. It has bilateral symmetry which is in direct correlation with progression towards the anterior end.



Dugesia: External features. A-Dorsal surface. B- Body twiseted to show a part of ventral surface; C-ventral surface.

External Morphology

The anterior end forms an obvious head which is triangular with two laterally projecting head lobes or auricles. On the head are two cup-shaped black eyes.

The head is separated from the body by a neck-like constriction. The body is elongated with the dorsal surface slightly arched and the ventral surface flat. Behind the middle of the body on the ventral side is a mouth which leads into a pharyngeal sheath containing a cylindrical pharynx which can be seen through the body wall, the pharynx can be everted through the mouth as a proboscis.

On the ventral surface encircling the margin is an adhesive zone through which an adhesive substance comes out from glands.

The animal clamps itself to the substratum by the adhesive zone. The animal when moving leaves behind a mucus trail, mucus is secreted by mucous glands opening on the ventral surface. Just a little behind the mouth aperture on the ventral surface, there is a genital aperture in sexually mature forms.

Body Wall of Dugesia Tigrina

The body wall is made of an outer epidermis and inner muscle layers. Both these layers are separated by a basement membrane. The space between muscle layer and the alimentary canal is filled with a special type of tissue called mesenchyme or parenchyma, therefore, no coelom or body cavity is found in it.

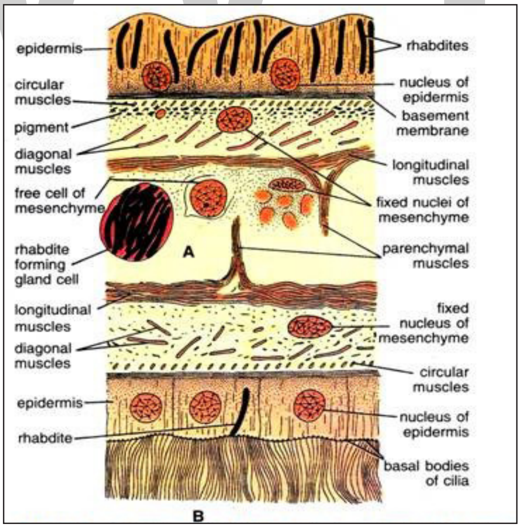
However, a detailed study of the body wall represents the following structures:

(i) Epidermis:

It is single cell-layered thick and made of cuboidal epithelial cells. The epidermis is ciliated all over in most planarians, but in Dugesia tigrina, cilia are found only on the ventral surface where they are absent from the adhesive zone. Between the epidermal cells are sensory cells and mucous gland cells in certain areas. The gland cells provide a mucus coating for the animal and they lay down a slime trail for its locomotion.

In the epidermal cells are characteristic erect hyaline rods called rhabdites, they are more abundant on the dorsal than the ventral side. Rhabdites are secreted by rhabdite gland cells usually located in mesenchyme. After the rhabdites are secreted in the rhabdite gland cells, they migrate to the epidermal cells where they lie. Rhabdites are absent in the adhesive zone.

The function of rhabdites is not known, but they form a slimy substance on discharge to the exterior which may be protective, and help in obtaining living food. Below the epidermis are granules and rods of pigment. The glands are all unicellular, some occur in the epidermis but most of them are in the mesenchyme, they have long necks opening on the surface, they secrete mucus.



Dugesia: L.S. of body wall. A-Through the dorsal body wall; B- Through the ventral body wall.

(ii) Basement Membrane:

The epidermal cells rest on a structure-less thin basement membrane to which underlying muscle layer is attached. In fact, it marks the boundary between the epidermis and muscle layers and it helps in maintaining general form of the body.

(iii) Muscle Layer:

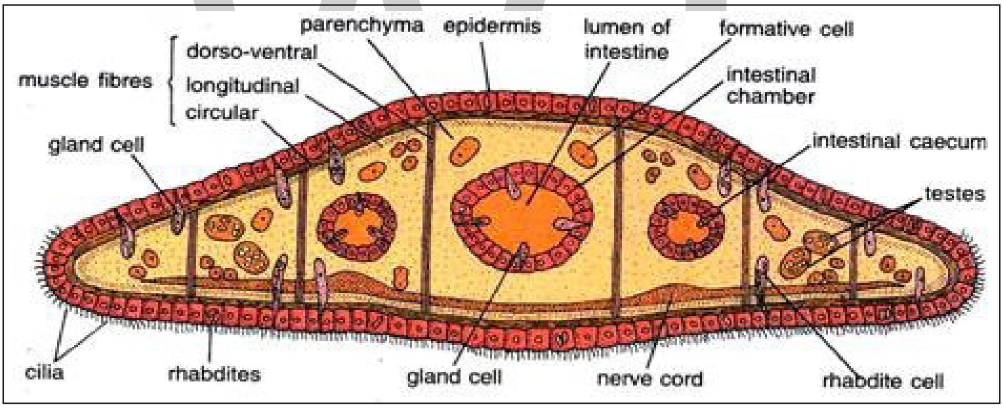
The basement membrane layer is followed by muscle layer. It contains elongated contractile muscle cells. These cells originate from myoblasts which are mesodermal in origin. The muscle layer is differentiated into an outer layer of circular muscles, middle layer of diagonal muscles and inner layer of longitudinal muscles.

The longitudinal muscle layer is more developed on the ventral side. The dorso-ventral muscles extend across the body between dorsal and ventral surfaces.

(iv) Parenchyma or Mesenchyme:

It is a special type of connective tissue of mesodermal origin. It is filled in the spaces between various internal organs and body wall. It is, in fact, a net-like syncytium containing nuclei, free wandering mesenchyme cells like neoblasts or formative cells and fluid-filled spaces.

The mesenchyme cells serve to transport digested food and excretory wastes; in fact they perform the function of circulatory system of higher animals as this system is wanting in flatworms.

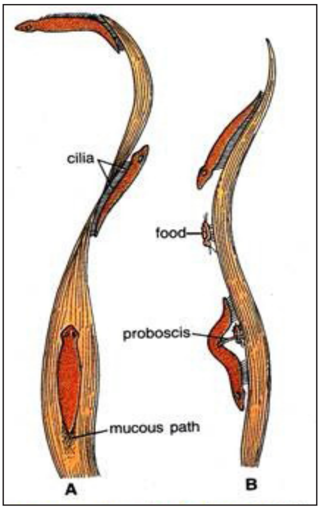


Dugesia: Diagrammatic transverse section through the body.

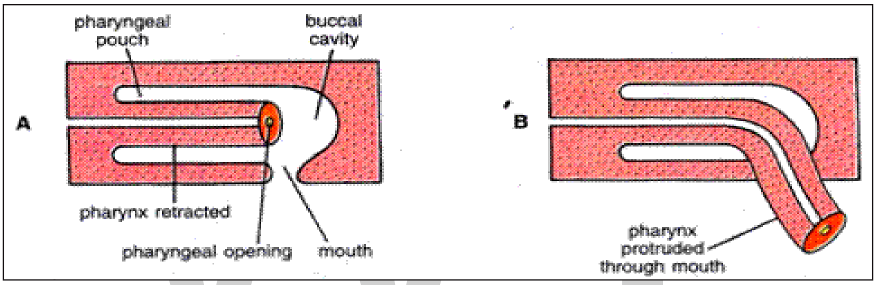
Locomotion of Dugesia Tigrina

Dugesia tigrina is aquatic but it does not swim. Dugesia tigrina moves in two ways. The usual way is gliding. In gliding, head is slightly raised, over a slime tract secreted by its marginal adhesive glands. The beating of the ventral cilia in the slime tract drives the animal along.

Rhythmic waves of movement can be seen passing backward from the head as it glides. A less common method is crawling. In crawling, Dugesia tigrina lengthens anchors its anterior end with mucus or by its special adhesive organ, and by contracting its longitudinal muscles pulls up the rest of the body. By means of its oblique muscles it can change its direction.



Dugesia: A-Locomotion; B-Feeding

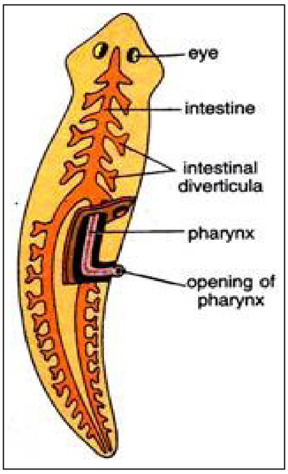


Dugesia: A-Retracted pharyna; B-Everted pharynx.

Digestive System of Dugesia Tigrina

It includes the alimentary canal, food, feeding and digestion.

(i) Alimentary Canal:



Dugesia: Digestive system.

The flatworms are the first in the animal kingdom to possess the alimentary canal which is incomplete because anus or any exit for defaecation is not found. However, the alimentary canal of Dugesia consists of mouth, pharynx and intestine.

(ii) Mouth:

It is a small oval or rounded aperture situated on the ventral side behind the middle of the body. It serves both for ingestion and egestion. It leads into a short mouth cavity which joins a cylindrical thick-walled pharynx.

(iii) Pharynx:

The pharynx lies in a pharyngeal cavity or pouch bounded by a muscular sheath called the pharyngeal sheath. The thick-walled, muscular and cylindrical pharynx in the pharyngeal pouch is attached to the anterior end of the pharyngeal sheath. The pharynx can be everted or protruded through the mouth opening as a proboscis which can be extended greatly. The eversible proboscis of Dugesia helps in feeding.

The pharynx in section is circular enclosed in a circular pharyngeal cavity. It consists of following layers from the surface to the lumen, epithelial cells, longitudinal muscle layer, circular muscle layer, outer gland cells, nerve plexus, inner gland cells, longitudinal muscle layer, circular muscle layer and an endodermal epithelial lining.

(iv) Intestine:

The attached end of the pharynx leads into an intestine which divides at once into three branches characteristic of order Tricladida to which Dugesia belongs, one extending forward in the middle line up to the head, and the other two going backwards to the posterior end, one on either side of the pharyngeal cavity.

All the three branches of intestine give off numerous branching diverticula, all ending blindly, there being no anus. The much-branched intestine is a means of increasing the surface area for digestion, absorption and distribution of food. The intestine is made of a single layer of vacuolated columnar cells containing granules, between the columnar cells are some gland cells of triangular shape containing reserve proteins.

(v) Food, Feeding and Digestion:

The animal is carnivorous. The food consists of small living worms, crustaceans and snails, and pieces of larger dead animals.

In feeding, the animal perceives the presence of food at a distance and moves towards it, living food is often entangled in the slimy secretions of mucous glands and rhabdites, then it encloses the food in the everted pharynx and digestive juices are poured into the food, the food is broken up by a pumping action of the pharynx and acted upon by extruded digestive juices for extracellular digestion, after which the food is swallowed.

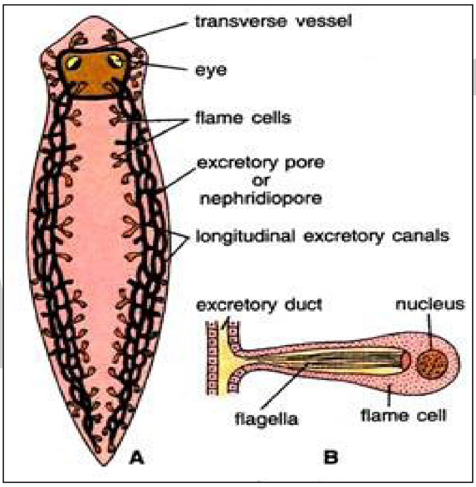
Digestion is both extracellular and intracellular; the mesenchyme helps to distribute digested food. Undigested food is egested through the mouth. Planarians can live without food for long periods, they obtain nourishment by dissolving their reproductive organs, parenchyma, and muscles, they get smaller in size. The missing parts are regenerated when they feed again.

Respiratory and Excretory System of Dugesia Tigrina

There are no respiratory organs. Exchange of gases takes through the body surface, i.e., respiratory exchange is by diffusion.

Excretory System in Dugesia

The excretory system of Dugesia tigrina consists of a system of excretory tubules having a large number of excretory cells called flame cells or protonephridia.



Dugesia: A-Excretory system; B-A flame cell.

(i) Excretory Tubules:

There is one pair of longitudinal excretory trunks running on each side of the body which open to the dorsal surface by several minute pores called nephridiopores, each pair of trunks is considerably coiled together, and the two pairs are connected together in the head by a transverse vessel.

Each longitudinal trunk divides into a number of branches; the branches divide into extremely fine capillaries which end in flame cells. The capillary is actually a part of the flame cell.

(ii) Flame Cell:

The flame cell is nucleated and has a number of protoplasmic processes reaching into the mesenchyme. The flame cell has an intracellular space which is continued into the capillary. In the space of the flame cell are a number of flagella which vibrate giving the appearance of a flickering candle flame, hence, the name.

The flame cells occur in large numbers placed along the length of the body on each side. The flame cells are excretory units and work like nephridia of annelids. Since, these are very simple in structure and function like nephridia, hence, also referred to as protonephridia.

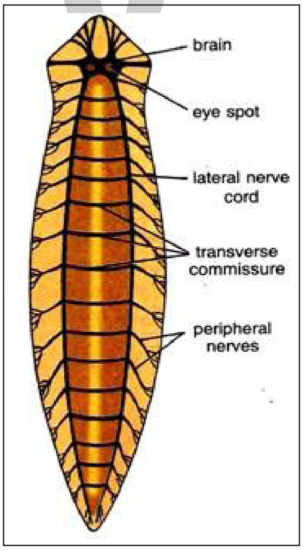
(iii) Physiology:

Excretory substance is collected from the mesenchyme and is transferred into the cavities of flame cells. The beating of flagella of flame cells causes hydrostatic pressure by which fluid waste passes into longitudinal trunks and goes out of nephridiopores.

The excretory system is spoken of as a protonephridial system. But more important than removal of excretory matter, the system brings about elimination of excess water from the animal; it functions as an osmoregulatory system.

Nervous System of Dugesia

The nervous system of Dugesia tigrina represents the primitive type of centralised nervous system of higher animals. It consists of the brain, nerve cords and peripheral nerves.



Dugesia: Nervous system.

Brain

In the head is a brain made of bilobed cerebral ganglia in the shape of an inverted V, with limbs near the eyes and the rest lying parallel to the head margin. From the brain numerous nerves extend forward and laterally to the head and auricles.

Nerve Cords and Peripheral Nerves

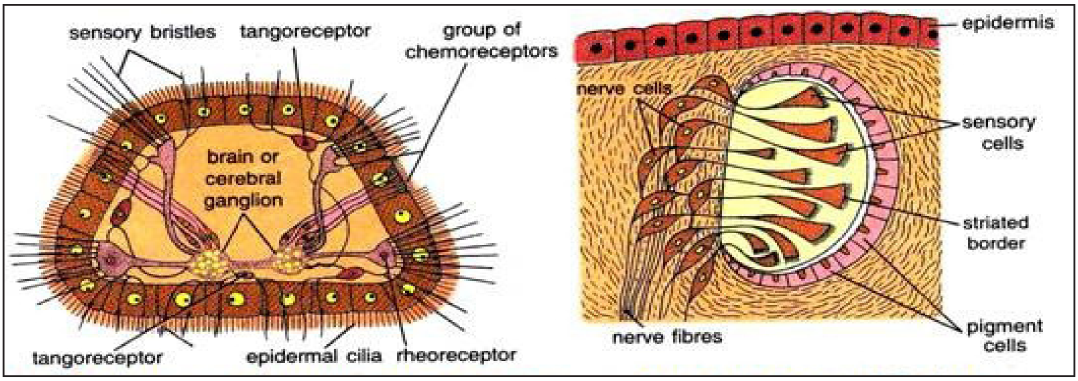
The brain is continued into two ventral nerve cords which run to the posterior end, each lying about one-third of the distance from the margin. The nerve cords give off transverse branches on both sides; the two cords are joined by some transverse commissures. The nervous system acts as a coordinating centre for nerve impulses.

In addition to the central nervous system there is a sub-epidermal plexus or nerve net just below the epidermis, and a deeper sub- muscular plexus in the mesenchyme below the muscle layers of the body wall, both are joined to the nerve cords. In fact, the brain and nerve cords constitute the central nervous system, while the various nerves originating from central nervous system constitute the peripheral nerves.

Sense Organs of Dugesia Tigrina

In Dugesia tigrina, sense organs consist of chemoreceptors, auricular organ, tango-receptors, rheoreceptors and eyes or ocelli.

1. Chemoreceptors: Chemoreceptors are found on the head, they are ciliated pits and grooves in which the epidermis has sunken cells having cilia but no rhabdites, and they are supplied by a sensory nerve. They enable the animal to find food by means of water current which passes over them.
2. Auricular Organ: On each side of the head is a whitish groove called an auricular organ lying near the base of the auricle. The grooves are ciliated and are provided with nerves, they are organs of chemical sense for smelling and tasting.
3. Tango Receptors: These are sensory cells for touch stimuli and found distributed at the anterior end most abundantly on the ventral surface around the mouth opening.
4. Rheoreceptors: These are sensitive to water currents; their sensory processes project much beyond the level of body cilia.



Dugesia: Diagrammatic T.S. of anterior end to show various receptors (left). Dugesia: V.S. of eye (rught).

Eyes or Ocelli

Eyes are two round dark spots on the dorsal surface of the head. The eye has a pigment cup with its open mouth facing laterally forward. Projecting into the pigment cup are several retinal cells, they are bipolar nerve cells with expanded inner ends which are striated, and outer ends joined to the brain.

Eyes are capable of a crude discrimination of the direction of light. The pigment cup serves as a shield and light can enter only through its opening to stimulate the photosensitive expanded ends of retinal cells, thus, the animal can detect the direction of light. The animal is negatively phototactic and is most active at night.

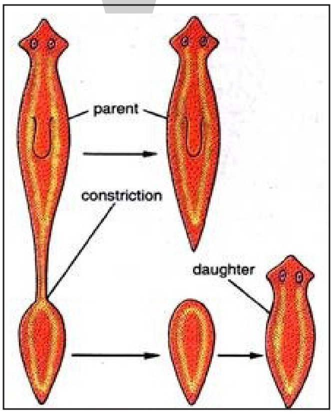
Reproduction of Dugesia Tigrina

Dugesia tigrina reproduces both asexually and sexually.

(i) Asexual Reproduction:

Dugesia tigrina exists in asexual and sexual strains. The asexual form has no reproductive organs, it reproduces by fission. Fission occurs when the animal has attained maximum size; the posterior end adheres firmly, while the anterior region advances forward so that the animal ruptures into two behind the pharynx.

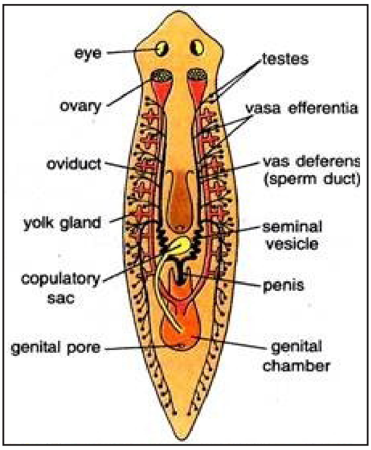
Each new animal regenerates its missing parts. The separated anterior part regenerates the posterior region and the rear end grows into a complete worm. Locomotion and adhesion are essential for fission.



Dugesia: Asexual reproduction by fission.

(ii) Sexual Reproduction:

Reproductive organs are temporary in Dugesia tigrina, they are formed during the breeding season, after which the reproductive organs degenerate and the animal becomes an asexual strain which will reproduce by fission till early summer of the following year. The sexual strain develops hermaphrodite organs and it reproduces sexually every year in early summer.



Dugesia. Reproductive system.

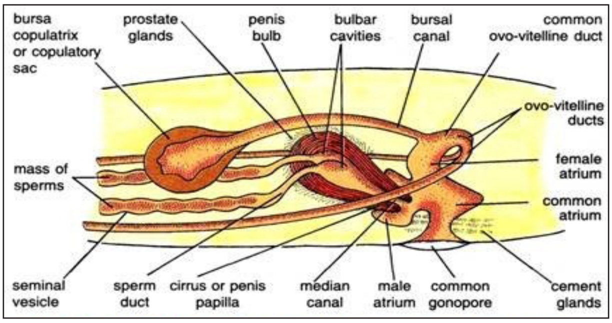
Male Reproductive Organs

Male reproductive organs consist of two rows of testes, vasa efferentia, a pair of vas deferens and a penis. The testes are numerous, small and round. They are situated on the right and left borders of the body. Each testis is connected to the vas deferens of its side by a tiny duct, the vas efferens.

Each vas deferens enlarges posteriorly to form a seminal vesicle where the sperms are stored until discharged posteriorly through the muscular penis. The right and left vaas deferens unite at the middle of the body and form a median duct which passes through a muscular penis. The penis opens into a genital atrium, a cavity that terminates in the genital pore through which the penis extends during the copulation.

Female Reproductive Organs

There is one pair of small ovaries lying laterally behind the head. From each ovary arises a long oviduct which runs laterally. At the commencement of each oviduct where it arises from the ovary, is a small dilated seminal receptacle. On each side of body there are numerous small yolk glands which join the oviducts, yolk cells from yolk glands pass into oviducts, hence, called ovo-vitelline duct.



Dugesia: A part of the reproductive system in lateral view.

Opening into the genital atrium is large club- shaped copulatory sac. Numerous small cement glands open into the genital atrium and oviduct. The genital atrium opens externally by a genital pore situated on the ventral side behind the mouth.

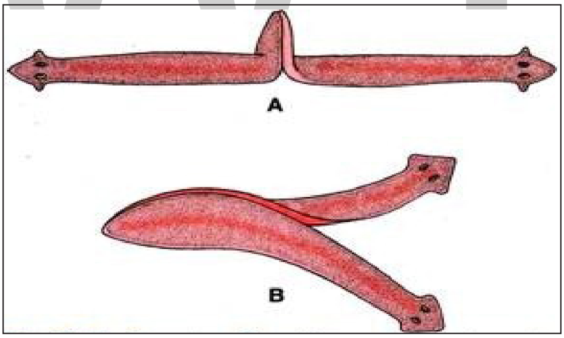
Copulation, Fertilisation and Development of Dugesia Tigrina

During copulation, the two worms come together by their ventral surfaces facing in the same direction. The penis papilla of each emerges by elongation through the genital pore and is inserted into the copulatory sac of the other worm by which mutual insemination occurs.

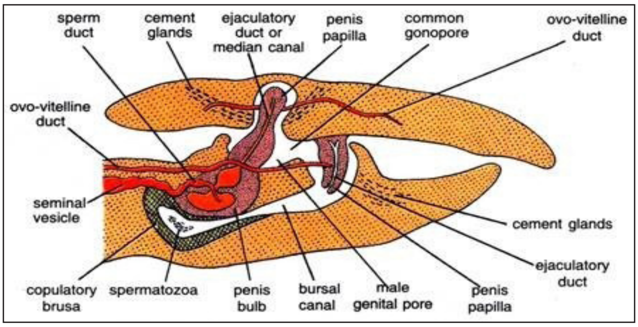
The sperms are discharged into the copulatory sac where they stay only a short while, they travel up the oviducts to reach the seminal receptacles. As the eggs come out of the ovary they are fertilised, and they pass down the oviducts becoming mingled with yolk cells from yolk glands.

The eggs and yolk cells collect in the genital atrium a capsule or cocoon is formed around from yolk cells. The capsule contains several fertilised eggs, and it is laid through the genital pore under stones.

While passing out the capsule receives the secretion of cement glands, this adhesive secretion forms a stalk on the capsule. The capsules get attached to stones by their stalk. One animal copulates several times during the breeding season and lays a cocoon every few days.



Dugesia: Copulation. A-Head ends facing in opposite direction;
B-Head ends facing in the same direction.



Dugesia: A copulating pair in section.

The development is direct, i.e., without any larval form. Each zygote in capsule develops into a young worm in about two weeks, finally the capsule ruptures and the young worms hatch out. These resemble their parents except that they are smaller in size and without reproductive organs which has not yet developed. They feed, grow and develop sex organs to reproduce again.

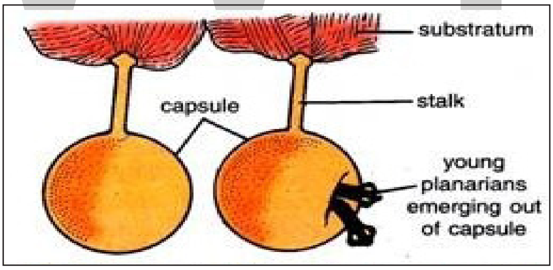
Regeneration of Dugesia Tigrina

Dugesia tigrina has great powers of regeneration. Regeneration is a process of restitution and involves the development of lost part of the body automatically. If it is cut into two, each part will form the lost portion. A cut piece of moderate size from any part of the body will form a new worm. Some pieces taken from posterior side form animals with reduced heads or no head at all.

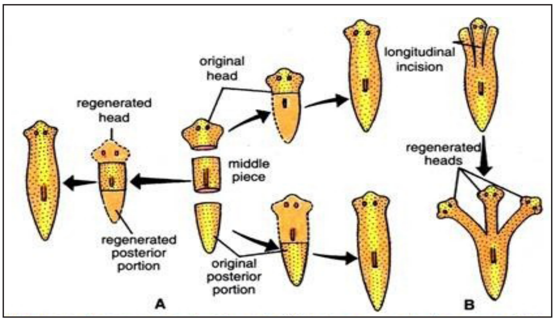
The ability of a piece to regenerate into a complete worm depends upon the regeneration of head at the anterior cut surface, because the head controls the morphological pattern.

If a sexually mature planarian is cut into two between the pharynx and the copulatory apparatus, then the reproductive organs degenerate, and each piece will regenerate into an asexual worm. Longitudinal cuts can be made to produce double heads or tails.

It was thought that interstitial cells are responsible for regeneration. But recently it has been shown that on cutting a planarian free cells from the mesenchyme called neoblasts migrate to the cut surface and give rise to a bud-like structure called blastemas which differentiate into the lost part.



Dugesia: Young planarians hatching from and egg capsule.



Dugesia: Regeneration. A-There individuals regenerate from an individual cut into three parts; B-Formation of a heteromorphy with three heads.

In fact, the process of regeneration is completed by two processes occurring together. These processes are epimorphosis, which is related to the formation of lost part, and morphollaxis, which is related to the adjustment and coordination between the old tissue and regenerated tissues.

Aschelminthes

Aschelminths can be free-living or parasitic. The free-living organisms are extremely abundant in soils and sediments and they feed on bacteria. While some others are plant parasites and can cause disease in crops that are economically important. The others are parasites that can be found in animals and human beings. Some of the parasitic worms include hookworms, pinworms, Guinea worms, and intestinal roundworms.

Ascaris lumbricoides is the Giant Intestinal Roundworm that is an endoparasite living in the human intestine. They are very common in children. These worms cause a disease called ascariasis. Many adult roundworms live inside the intestine, causing obstruction to the intestinal passage. This causes abdominal discomfort, colic-like pain, impaired digestion, diarrhea, and vomiting. Generally, deworming medicines are given to get rid of these roundworms from the body.

Characteristic Features of Phylum Aschelminthes

- The body of these organisms is unsegmented and triploblastic.
- They have a pseudocoeloem, where the body cavity is not lined by the mesodermal layer.
- They are bilaterally symmetric.
- The body is cylindrical or thread like with elongated, slender worm-like appearance and tapering at both ends.

- Body wall has epidermis, muscle layer and is covered by cuticle.
- The body size of these organisms varies from microscopic to several centimetres in length.
- These organisms are mostly parasitic, with a few free-living.
- They exhibit an organ system level of organization.
- Externally, there is little differentiation between the anterior and posterior regions. But internal cephalization is present.
- There is no distinct head. However, the mouth is present in the anterior.
- The digestive system is complete, with a mouth and anus.
- The mouth in these organisms is terminal and is surrounded by lips bearing sense organ.
- Amphids and papillae are the main sensory organs.
- The nervous system consists of a nerve-ring that encircles the oesophagus. From it, nerves extend out anteriorly and posteriorly.
- Respiratory organs are absent. Respiration occurs through the general body surface. It is aerobic in free-living forms and anaerobic in parasitic organisms.
- The excretory system has canals and gland-like.
- Sexes are separate and are unisexual, exhibiting sexual dimorphism.
- Fertilization is internal.
- They are ovo-viviparous, oviparous or viviparous.
- The life cycle of these organisms is complicated. It may be with or without an intermediate host.

Examples:

- Ascaris lumbricoides – Round Worm
- Enterobius vermicularis – Pinworm
- Ancylostoma duodenale – Hookworm
- Wuchereria bancrofti – Filarial worm
- Loa loa – Eye Worm

Ascaris Lumbricoides

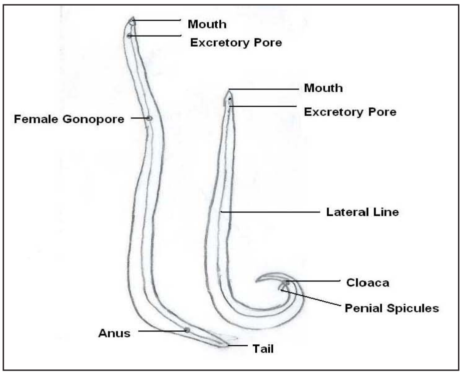
Ascaris is a common roundworm found in the small intestine of various vertebrates like chicken, pig, cattle, horse and man. Among the roundworms the genus Ascaris is of the larger size. There can be roughly one thousand to four thousand adult Ascaris in a single man. Ascaris is more common in the children.

Morphology

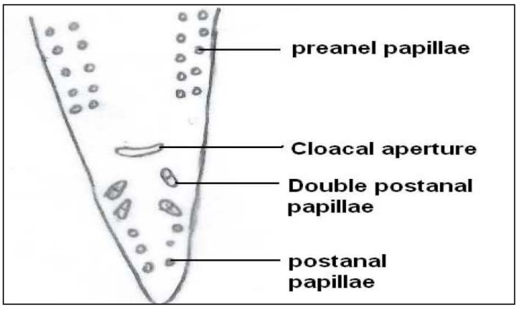
Ascaris lumbricoides is an elongated, cylindrical, endoparastic and bisexual worm. It exhibit marked sexual dimorphism. The female measures 20-41 cms and the male 15-31cms. The tail of the female is straight while that of the male is curved like a hook. They are generally white or yellow in colour. The body is covered by tough and elastic cuticle. The mouth lies at the anterior end of the body surrounded by three lips. One is drosal in position and the other two are ventro-lateral, so the mouth is triradiate. Ventrally, little behind the mouth is the excretory pore. Ventrally, little before the hind end is anus in female and the cloacal aperture in male. The female has a separate gonopore placed ventrally nearly one-third length from the anterior side.

Body Wall

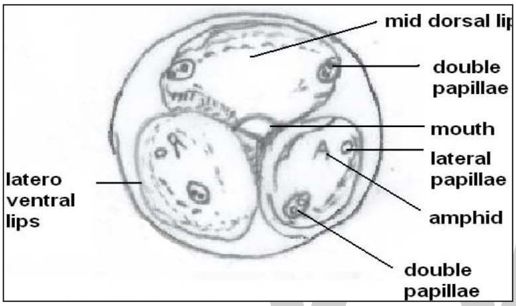
The body wall is covered by thick tough non-chitinous cuticle resistant to the host's digestive enzymes but it is permeable to the salts and water. The cuticle is continuous with the cuticular lining of the pharynx foregot and rectum hindgut. The cuticle is not smooth; it has wrinkles or transverse striations. The cuticle is shed four times during the lifetime and is secreted by the, the underlying epidermis secretes cuticle. Below the cuticle is syncytial epidermis meaning that the epidermis is having many nuclei but no cell membrane i.e. the cells limits are not marked. The epidermis is thickened internally into ridges at four regions, commonly called cords or ridges. The lateral cords are more conspicuous and contain the longitudinal excretory canals along with lateral new card. The dorsal and the ventral thickenings contain the dorsal and the ventral nerve cords respectively. The longitudinal muscles lie in four groups, which is separated by four thickenings of the epidermis. There are no circular muscles present. Each cord has nearly 150 muscles cells. The muscle cell has two distinct portions. An outer and towards the epidermis is the fibrillar portion, which is contractile, and the inner cytoplasmic portion, which has non-contractile supporting fibrils. The cytoplasmic zone is extended into a long narrow process, the muscle tail. The muscle tails of the dorsal side extend dorsally to get inserted into the dorsal epidermal cord. The muscle tails of the ventral side gets inserted into the ventral epidermal cord. Body cavity is the space between the gut and the body wall. As it is not lined by mesodermal epithelium,so it is not a coelom but a pseudocoelom. The body cavity has pesudocoelomic fluid, which distributes the digested food and collects the waste material in it. The pesudocoel has five giant cells the pseudocoelocytes. Their position is fixed in the epidermal cords. The pesudocoelocytes on the pharynx extend as membrane having delicate fibrous strands covering the internal structures and organ of the pseudocoel.



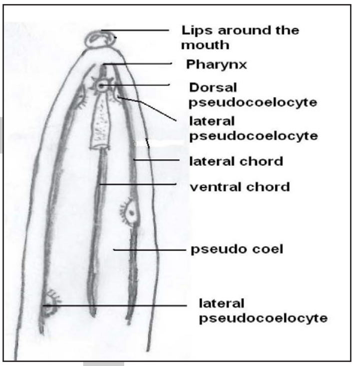
Ascaris: Female and Male.



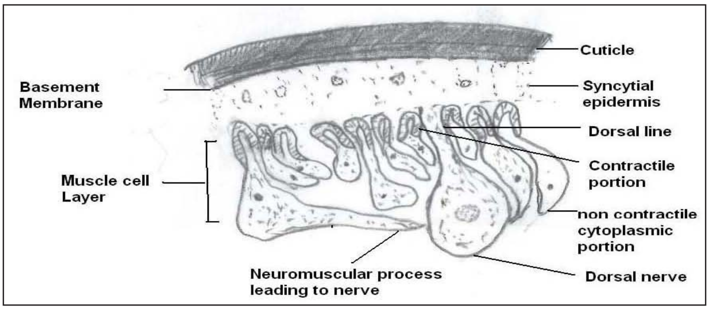
Posterior Part of male in Ventral view showing Papillae.



Enface view of mouth and lips.



Position of pseudocoelocyte in the pseudocoel.



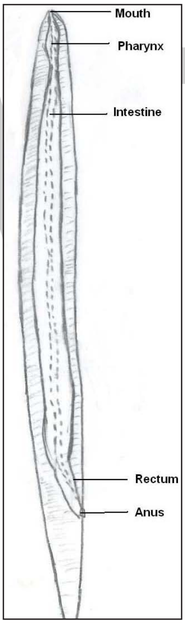
Transverse Section Body Wall.

Digestive System

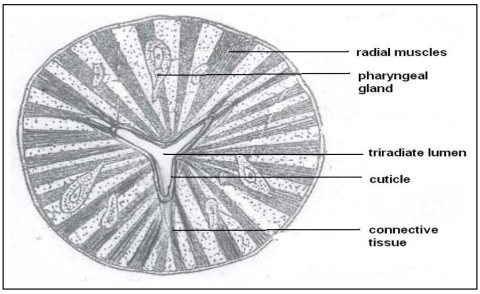
The alimentary canal is complete divided into three parts foregut or pharynx, mid gut or the intestine and hindgut or the rectum. The pharynx and the rectum are lined by the cuticle and are ectodermal in origin. The mouth is tri-radiate in shape. In nematodes six lips or labia surround the mouth. However in two Ascaris the mouth is surrounded by only three lips because of the fusion of lips each, one is mid dorsal, the other two are latero ventral in position. The lips have sensory structures on them.

The pharynx or oesophagus is short, thick walled, having tri-radiate lumen, which is lined by cuticle continuous with the body wall. The wall of the pharynx has radial muscles. Posteriorly pharynx opens into the intestine, which is dorso-ventrally flattened and thin walled as it is made up of a single layer of columnar epithelial cells. The free margin of the cells is produced into microvilli to increase the surface area for absorption. The intestine opens into the rectum, which is flattened dorsally and is lined by cuticle. The hindgut wall has tall columnar cells, and few muscle fibers. In female the rectum opens into a transverse slit the anus but in male it opens out by cloaca aperture because the male reproductive duct also joins the rectum.

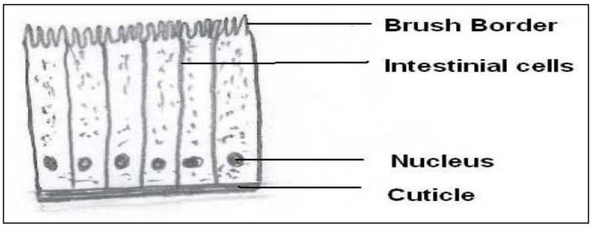
The food of the Ascaris contains blood and partly or fully digested food of the host. The muscular pharynx sucks the food. Digestion in the intestine is mainly extra cellular, facilitated by proteases, amylase and lipase. Some intracellular digestion also takes place. The digested food is absorbed by the intestinal cells from there it diffuses into the pseudocoelomic fluid, and distributed to the entire body cells.



Alimentary canal.



Transverse section of Pharynx.



Vertical section of intestinial wall.

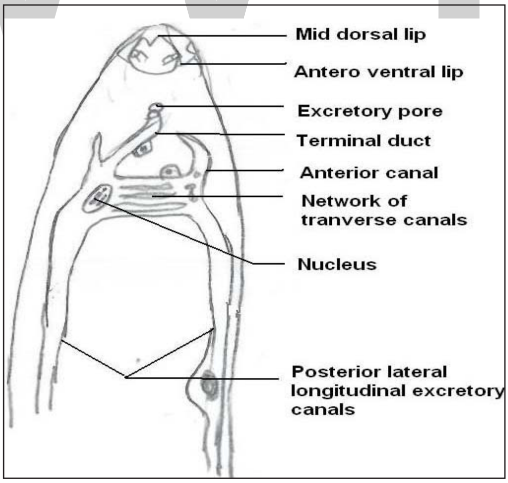
Respiration

There are no respiratory structures. The oxygen concentration of the host's intestine is very low so anaerobic respiration takes place. Ascaris obtains energy by breaking down glycogen into carbon dioxide and fatty acids. Whenever sufficient oxygen is present it goes for aerobic respiration.

Excretory System

There is no protonephridia. The excretory system consists of two long longitudinal canals, which are connected to each other by the transverse canalicular network below the pharynx. A short terminal duct arises from the transverse canal and opens out as a minute excretory pore on ventral side just behind the lips. The anterior canals are quite short and the posterior longitudinal excretory canals run the entire length and are closed at both the ends.

It was earlier thought that the entire excretory system is formed by the cytoplasm of a single giant cell whose nucleus lies on the left side of the transverse canaliculi. A firm membrane lines the entire system; there being no cilia or flagella. With the discovery of two more nuclei in the excretory system it is now believed that the entire excretory system is made up of more than one cell. The entire longitudinal excretory canals are intracellular excavations. The excretory waste material is ammonia and urea and it is pushed forward towards the excretory pore probably by the muscular undulations of the body of the Ascaris.



Anterior part of the excretory system.

Nervous System

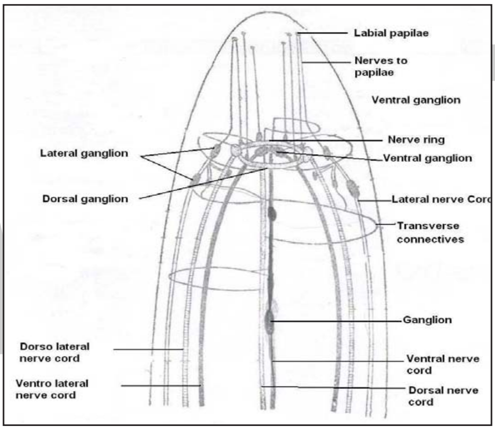
Nervous System is very well developed and quite complicated. The nerve cells are fixed in number and position. Around the pharynx is circumpharnygeal nerve ring from which arise the nerves.

Associated with the nerve rings are:

- A Median dorsal ganglion,
- A pair of sub-dorsal ganglia,
- A pair of lateral ganglia each divided into six smaller ganglia,
- A large ventral ganglion.

Anteriorly the nerve ring gives off eight nerves:

- Six papillary nerves, which innervate sensory papillae of the lips. Two of these nerves are dorso-lateral, two laterals, and two ventro-laterals in position. Each papillary nerve forms small papillary ganglia very near to its origin.
- The two-amphidial nerves of each side arise from one of the six lateral ganglia and innervate the sensory structure the amphids.



Anterior part of the nervous system.

Posteriorly the nerve ring gives eight nerve or cords:

1. A dorsal nerve cord lying in the dorsal line.
2. Ventral ganglionated nerve cord lying in the ventral line, it is the main nerve cord.
3. A pair of lateral nerve cards.
4. A pair of dorsolateral nerve cards.
5. A pair of ventrolateral nerve cards.

Various Transerverse connectives and commissures connect the eight nerves.

Sense Organs

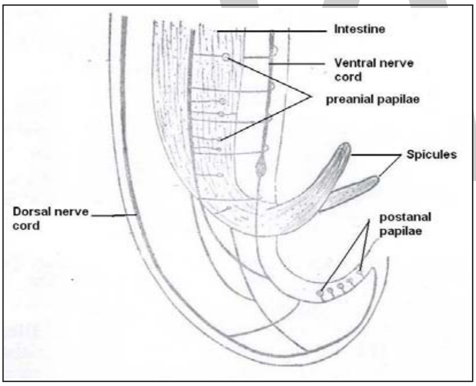
The sense organs are very simple because Ascaris is an endoparasite. The sensory structures are Papillae, Amphids and the Phasmids. The papillae are of three kinds labial, cervical and genital.

The papillae are projections of the cuticle. It is an elongated structure having fine sensory fibers with some expansion below the cuticle, surrounded by supporting cells. The dorsal lip has two double sensory structures the papilla, one on either end. Only one double sensory structure is present on one side of the ventro lateral lip. On the other side of the lip there is a single papilla and an amphid.

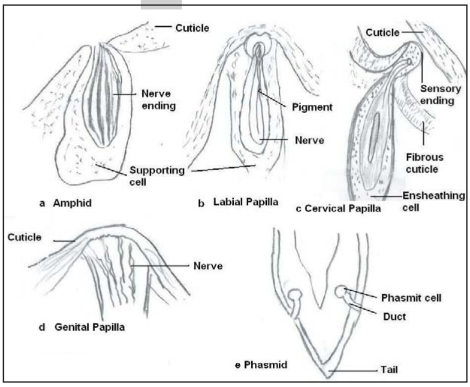
Each double sensory structure has a labial papilla & a cephalic papilla. First narrow and then widens and ends below the surface of the cuticle. Genital papillae are present only in males. There are fifty pairs of preanal and five pairs of post anal genital papillae. They help during copulation.

The papillae are tango receptors.

- Amphids: Each ventro-lateral lip has small pit just above the labial papillae containing sensory cells. These are called amphids. They are chemoreceptors.
- Phasmids are a pair of unicellular glands, which open out as a small pit one on each side of the tail behind the anus they are chemoreceptors.



Lateral View of the posterior part of the male nervous system.



Sensory receptors.

Reproductive System

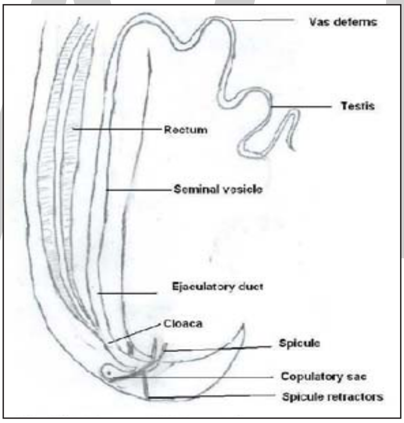
The gonads are thin, long and their walls are made up of single layer of cuboidal cells. It has a central rachis, which is surrounded by large number of amoeboid cells. These are developing gametes. The gonads are telogenic i.e. gametogonia are shed from the proximal part of the gonad from a terminal cell.

Sexes are separate and sexual dimorphism is quite evident. The male has a curved tail and female's tail is straight. Female has a separate anus and a genital opening whereas male has a cloaca and papillae around the cloaca.

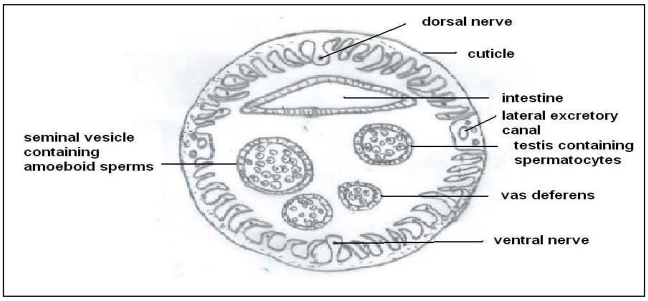
1. Male Reproductive System: It consists of testis, vas deferens, seminal vesicle, ejaculatory duct and penial setae confined to the posterior part of the body. The male reproductive system occurs in single set i.e. monorchis. The single testis is long thread like convoluted having central rachis. The posterior part of testis continues as vas deferens, which is thick, short and twisted, The vas deferens does not have the central rachis. The vas deferens opens into more thicker, straight and muscular seminal vesicle.

The seminal vesicle opens into a narrow, short and muscular ejaculatory duct, which opens into posterior part of the rectum to form the cloaca. The wall of the ejaculatory duct has a number of prostate glands whose secretions help in copulation. The cloaca opens out ventrally by a transverse cloacal apertune, little in front of the hind end.

Penial Setae: The cloaca evaginates on the dorsal side to form a pair of muscular penial sacs or spicule pouches. The two spicule pouches join together and open into the cloaca. Each penial sac secretes a cuticular spicule having a cytoplasmic core. The spicules sacs have protractor and retractor muscles to protreude and withdraw the spicules from and into the cloacal aperture respectively. The spicules serve to open the female genital pore during copulation to deposit the sperms.



Male reproductive system.



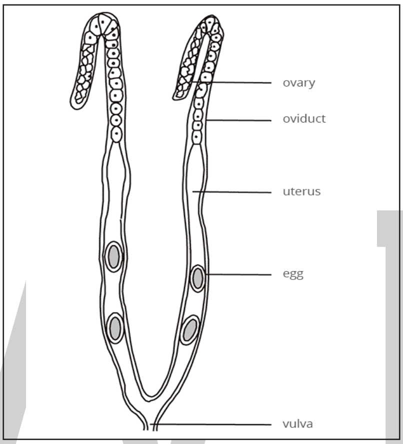
Transverse section of a mature male.

2. Female Reproductive System: Ascaris has a pair of long twisted ovaries lying in the posterior two third of the pseudocoel. Each ovary continues posteriorly into a thicker and twisted oviduct having a lumen. Each oviduct opens into a thicker and muscular

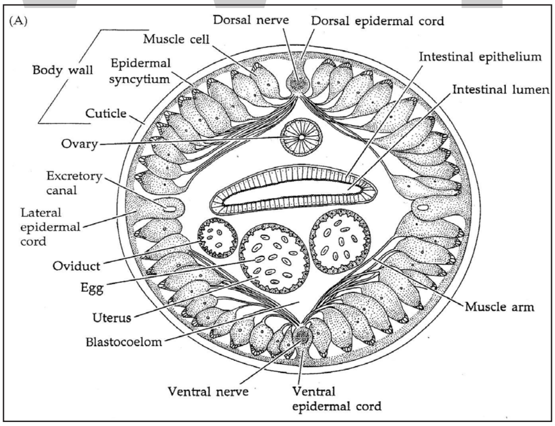
uterus. The uterus is, lined by cuticle. The first part of the uterus is called seminal receptacle, which store the sperms after copulation.

It is here that fertilization of eggs takes place. The distal part of the uterus store fertilized eggs. The wall of the uterus has gland cells, which secretes yolk and material for eggshell.

The two uteri join together to form the vagina in the anterior third of the body. The vagina is short and a highly muscular tube, which is entirely lined by the cuticle. The vagina opens out mid ventrally as a female genital pore or vulva. Vulva is a transverse slit with lips and is present near about one third of the body length from the anterior side.



Female reproductive organs.



Transverse section of a mature female.

Life History

Mature male and female worms copulate in the small intestine of the host, during copulation the penial setae open the vulva and the motile amoeboid sperms move into the vagina and then to seminal receptacle of the female Ascaris by amoeboid movement. Fertilization takes place in the seminal receptacle where oocytes are also present. The unfertilized egg contains fat and glycogen globules. After fertilization glycogen forms a fertilization membrane around the fertilized egg, which hardens into a chitinous shell, the fat globules accumulate below the shell and form a lipoid layer. The distal part of the uterus forms thick, heavy protein membrane on the shell. This wavy protein membrane is characteristic of Ascaris eggs. The fertilized eggs are elliptical in shape measuring 60-70u by 40-50u.

The uteri of a single female may contain as many as 2,70,00,000 eggs. A female may lay as many as 15,000 to 2,00,000 unsegmented eggs in a day. In the moist soil the eggs can remain alive for several months but dry conditions can kill the eggs.

The eggs require a period of incubation before entering the human body. For further development they require a temperature lower than human body. Favorable temperature is 85 degree F (about 30˚C) oxygen and moisture. The cleavage starts in the soil.

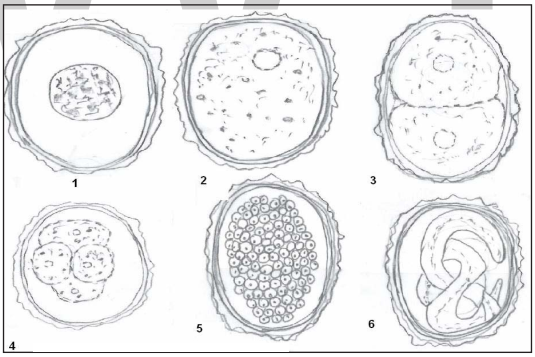
The cleavage is spiral and determinate. The sixteen-cell stage is like a hollow ball. This is the blastula stage and the inner cavity the blastocoel. Blastula by invagination forms a gastrula. A juvenile develops in 10-14 days. The juvenile has an alimentary canal, a lateral excretory system and a nerve ring. This stage is called rhabditiform larva or rhabditoid (because of its resemblance to a soil nematode called Rhabditis). The larva grows for a week and then moults within the shell to become the second stage juvenile. This is the infectious stage of Ascaris and further development requires high temperature which therefore can occur in the host's intestine only. Egg containing second stage juvenile enters the body of the host along with contaminated food and water. The egg membranes are dissolved in the intestine and the juveniles are free within few hours. The 0.02 - 0.03mm juvenile bores the intestinal wall and enters the blood vessels (branches of hepatic portal). It moves along with the blood in the body for nearly ten days and vein finally is large enough to damage the pulmonary capillary and reach the alveolar spaces. Here it moults for the second time, and after growing for few days moults for the third time. The fourth stage juvenile takes an upward journey passing through bronchus, trachea and then the pharynx. It remains in the pharynx till it is coughed out through the nostrils or mouth or moves down to enter the oesophagus. It then moves downward and reaches the intestine and measures 2-3 mm long. In the intestine the juvenile moults for the fourth and final time, becomes the adult, and attains sexual maturity. The total period taken for the whole journey in host is about 25 days. Generally it lives in the intestine for 9 –12 months.

Pathogenicity

The disease caused by Ascaris is called Ascariasis. Degree of pathogenesis depends upon the number of worms present in the intestine. It causes more harm to the children than adult.

Pathogenesis caused by adult Ascaris:

1. Abdominal discomforts like vomiting and colic pains, interferes in protein digestion.
2. Absorb host's digested food resulting in malnutrition and hence shunted growth.
3. Irritation of mucous membrane results in involuntary muscular contractions. Acute infection can cause coma and death.
4. Can cause appendicitis and hepatitis.
    - Larva: It may prove to be more harmful than the adult by causing hemorrhages. The circulating juveniles can cause, serious damage to any vital organ like kidney, brain, eye, particularly to lungs, which can result in pneumonia leading to death.
    - Treatment: Use of anti-helminth drugs like mixture of tetrachlorethylene and the oil of chenopoduim is very effective; other drugs are hetrazan, pierazine hydrate dilhiazanine, tetraezole etc.
    - Prevention: An effective sanitary system to dispose of the faeces. Vegetables should be thoroughly washed or boiled before consuming them. Nails should be cut so that no dirt and eggs collect below them. Always wash the hands with soap before eating.

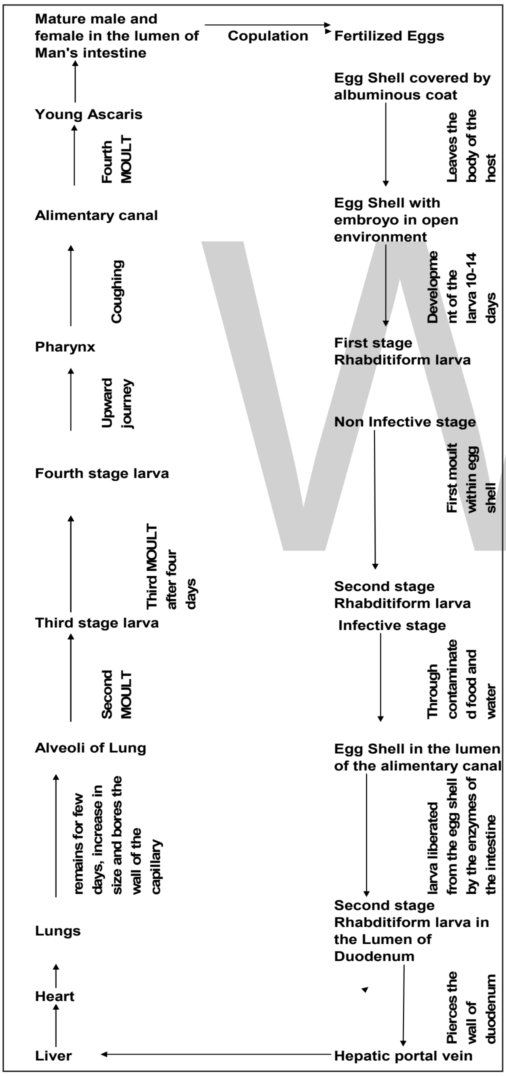


Stages in the development of the egg.

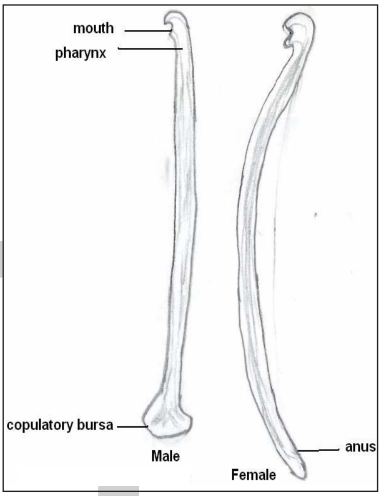
Parasitic Adaptations

1. Long and elongated body of the allows to accommodate many Ascaris in the small intestine of the host.
2. The cuticle protects the inner organs, and the antienzymes, counter act the digestive enzymes and toxins of the host.
3. Muscular pharynx helps in the ingestion of the food.
4. The pseudocoelomic fluid helps in the distribution of food to various parts of the body and transfer of waste substances to the excretory canal.

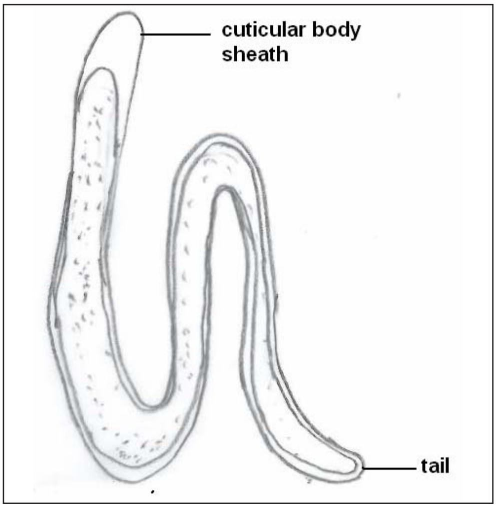
5. Anaerobic respiration enables the worm to service in oxygen free intestinal medium.
6. Production of large number of small sized eggs to continue the race.
7. The capsule protects the juvenile from all unfavorable environmental conditions.
8. Direct infection by the juvenile has higher chances of dispersal.
9. No intermediate host.



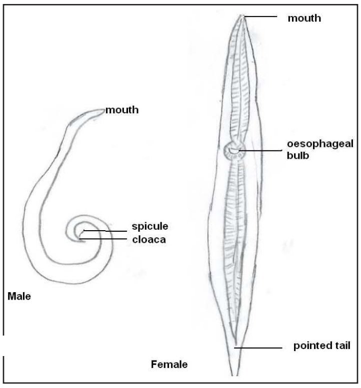
Life Cycle of Ascaris.



Ancylostoma



Wuchereria bancrofti (microfiaria).



Enteronbius vermicularis.

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5

Malacology

Malacology refers to the branch of invertebrate zoology which is involved in the study of molluscs. Some of the different categories of molluscs studied within this field are Aplacophorans and Polyplacophora. The topics elaborated in this chapter will help in gaining a better perspective about these categories of molluscs.

The study of molluscs is called Malacology. Animals falling in mollusca phylum include snails, slugs, octopus, squid, and bivalves generally, such as clams and mussels. Most of these animals have shells. The scientists who study molluscs are called malacologists.

Mollusk, also spelled mollusc is any soft-bodied invertebrate of the phylum Mollusca, usually wholly or partly enclosed in a calcium carbonate shell secreted by a soft mantle covering the body. Along with the insects and vertebrates, it is one of the most diverse groups in the animal kingdom, with nearly 100,000 (possibly as many as 150,000) described species. Each group includes an ecologically and structurally immense variety of forms: the shell-less Caudofoveata; the narrow-footed gliders (Solenogastres); the serially valved chitons (Placophora or Polyplacophora); the cap-shaped neopilinids (Monoplacophora); the limpets, snails, and slugs (Gastropoda); the clams, mussels, scallops, oysters, shipworms, and cockles (Bivalvia); the tubiform to barrel-shaped tusk shells (Scaphopoda); and the nautiluses, cuttlefishes, squids, and octopuses (Cephalopoda).

General Features

Size Range and Diversity of Structure

Typical molluscan features have been substantially altered, or even lost, in many subgroups. Among the cephalopods the giant squids (*Architeuthis*), the largest living invertebrates, attain a body length of eight metres (more than 26 feet); with the tentacle arms extended, the total length reaches to 22 metres. Other cephalopods exceed a length of one metre. Many of the remaining molluscan classes show a large variation in size: among bivalves the giant clam (*Tridacna*) ranges up to 135 centimetres (four feet) and the pen shell (*Pinna*) from 40 to 80 centimetres; among gastropods the sea hares (*Aplysia*) grow from 40 to 100 centimetres and the Australian trumpet, or baler (*Syrinx*), up to 60 centimetres; among placophores the gumshoe, or gumboot chiton (*Cryptochiton*), achieves a length up to 30 to 43 centimetres; and, among solenogasters, *Epimenia* reaches a length of 15 to 30 centimetres. Finally, gastropods of the family Entoconchidae, which are parasitic in echinoderm sea cucumbers, may reach a size of almost 1.3 metres. In contrast, there are also minute members, less than one millimetre (0.04 inch) in size, among the solenogasters and gastropods.

Distribution and Abundance

The mollusks have adapted to all habitats except air. Although basically marine, bivalves and gastropods include freshwater species. Gastropods have also adapted to land, with thousands of species living a fully terrestrial existence. Found on rocky, sandy, and muddy substrata, mollusks burrow, crawl, become cemented to the surface, or are free-swimming.

Mollusks are found worldwide, but there is a preponderance of some groups in certain areas of the world. The close association of many molluscan groups with their food source—whether by direct dependence on a specific food supply (*e.g.,* plant-eating, or herbivores) or by involvement in food chains—limits their geographic distribution; for example, bivalves of the family Teredinidae (shipworms) are associated with wood. In general, cold-water regions support fewer species.

Importance to Humans

Mollusks are of general importance within food chains and as members of ecosystems. Certain species are of direct or indirect commercial and even medical importance to humans. Many gastropod species, for example, are necessary intermediate hosts for parasitic flatworms (class Trematoda, phylum Platyhelminthes), such as the species that cause schistosomiasis in humans. Most bivalves contribute to the organic turnover in the intertidal (littoral) zones of marine and fresh water because, as filter feeders, they filter up to 40 litres (10 gallons) of water per hour. This filtering activity, however, may also seriously interfere with the various populations of invertebrate larvae (plankton) found suspended and free-swimming in the water. One species, the zebra mussel (*Dreissena polymorpha*), is regarded as a particularly harmful exotic invader. Carried from Europe in ship ballast water, zebra mussels were taken to the Great Lakes in 1986. To date, they have caused millions of dollars in commercial damage by clogging the water pipes of power plants and cooling systems. They are driving many native freshwater bivalve species to extinction.

Many gastropods, bivalves, and cephalopods are a source of food for many cultures and therefore play an important role in the fishing industries of many countries. Many shell-bearing molluscan species are also used to fabricate ornaments and are harvested for the pearl and mother-of-pearl industries.

Reproduction and Life Cycles

Mollusks are primarily of separate sexes, and the reproductive organs (gonads) are simple. Reproduction via an unfertilized gamete (parthenogenesis) is also found among gastropods of the subclass Prosobranchia. Most reproduction, however, is by sexual means. Eggs and sperm are released into the water by members of some (primitive) species, and fertilization occurs there. In prosobranch gastropods, water currents may cause a simple internal fertilization within the mantle cavity, or males may fertilize eggs internally using a muscular penis. Both male and female reproductive organs may be present in one individual (hermaphroditism) in some species, and various groups' exhibit different adaptations to this body form. For example, in hermaphroditic bivalves and prosobranch gastropods, male and female gonads are functional at separate times and in rhythmic and consecutive patterns (successive hermaphroditism). Conversely, male and female gonads are functional at the same time (simultaneous hermaphroditism) in solenogasters and many other gastropods.

Fertilization by transfer of capsules containing sperm (spermatophores) typically occurs in cephalopods and some gastropods. In cephalopods, transfer of spermatophores is usually combined with copulation by a modified arm, or hectocotylus. Copulation in solenogasters, often by means of a special genital cone, may be supported by copulatory stylets. Various penis formations, in part with copulatory stylets, or darts, are widely found in gastropods.

Eggs are deposited singly or in groups, generally on some hard surface and often within jelly masses or leathery capsules. Squids of the suborder Oegopsida and some gastropods have eggs that are suspended in the water. Fertilized eggs commonly undergo spiral cleavage, as in annelids and a number of other "protostome" phyla. The eggs of cephalopods, on the other hand, possess a large amount of yolk, which displaces the dividing cells and causes a characteristic type of development.

Many mollusks develop into free-swimming larvae; these larvae are either feeding (planktotrophic) or nonfeeding (lecithotrophic). The larva in primitive bivalves is a pericalymma (test cell) larva in which the embryo is protected below a covering (test) of cells provided with one to four girdles of cilia, at the apex of which is a sensory plate of ciliated cells. After the developing juvenile has grown out apically of the test (which then is lost), the animal settles and develops into an adult. The test in other lecithotrophic larvae is restricted to a preoral girdle of ciliated cells (the prototrochus) and is called the trochophore larva. Trochophores are encountered in the development of many marine annelid species (phylum Annelida). In more advanced mollusks (such as in marine gastropods and bivalves), the trochophore larva develops into a veliger larva. In these generally planktotrophic larvae, the girdle of ciliated cells widens to form a velum that entraps food and also propels the microscopic mollusk through the water. As the larva continues to develop, the shell, mantle cavity, tentacles, and foot appear. After a specific amount of time, which varies according to species and environmental conditions, the larva loses the velum and metamorphoses into an adult. A substantial change in shell morphology usually marks the transition to adult form.

Secondary (newly evolved) larvae have developed among some freshwater bivalves and some cephalopods. Maternal protection of the developing eggs (brood) is not unexceptional behaviour in solenogasters, bivalves, and certain gastropod adults. Direct development without a larval stage or the bearing of live young from a yolky egg, or both, are typical in cephalopods and most nonmarine (and many marine) gastropods. Many species go through two breeding seasons per year, whereas in some cephalopod species mating or egg lying appears to be rapidly followed by death effected by hormones.

Habitats, Feeding Habits and Associations

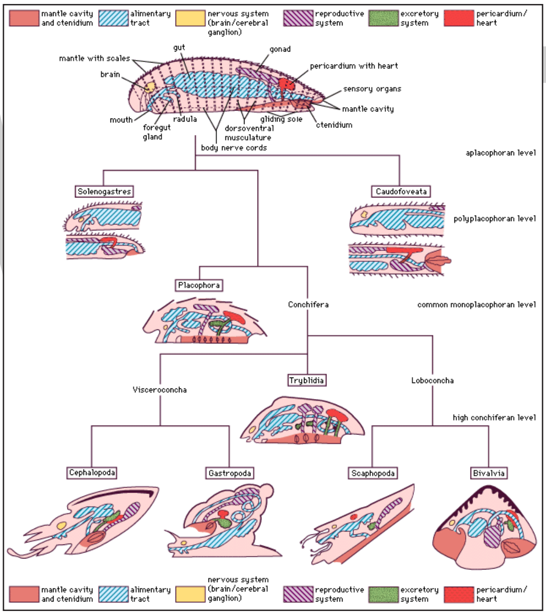
Caudofoveates (subclass Chaetodermomorpha, class Aplacophora) burrow in muddy sediments at depths of 10 to more than 7,000 metres (33 to 23,000 feet) and consume microorganisms and loose organic material (detritus). In contrast, solenogasters (subclass Neomeniamorpha, class Aplacophora) prey on some members of the class Cnidaria (*e.g.,* hydroids and corals) in five to 6,850 metres of water, on clay or muddy sand, or directly upon hydroid or coral colonies. Chitons (class Polyplacophora) cling to hard bottoms of the intertidal zone, scraping algae from the rock surfaces by using their strong rasping teeth (radula); several members of the polyplacophoran family Lepidopleuridae consume detritus found at depths down to 7,000 metres, and Hanleyidae as well as Hopaliidae even depend on animal food. The few extant members of the class Monoplacophora inhabit secondary hard bottoms at depths of 175 to 6,500 metres and capture detritus by means of head appendages (velum) around the mouth. The scaphopods dwell in sand or sandy mud down to 7,000 metres and nourish themselves on protozoa, crustaceans, or small mollusks captured by the filamentous head tentacles (captacula). Except for the carnivorous septibranch anomalodermata, all bivalves are ciliary suspension feeders, using food-sorting organs near the mouth (labial palps) and respiratory gills modified to assist in feeding (ctenidia). Found in marine and fresh water, most bivalves burrow into sediments to depths of 10,700 metres or attach themselves to hard surfaces by means of tough threads secreted by the byssus gland in the foot. The members of some species may even bore into wood or rock. Cephalopods are generally carnivores, feeding on crustaceans and fishes, but some have adapted a microvorous diet of detritus and microscopic organisms and plants. Some cephalopods are offshore (pelagic) jet swimmers, moving from the surface to depths of 5,400 metres, while others dwell near the bottom (benthic) at depths of 8,100 metres.

The greatest ecological diversity is shown by the gastropods. The marine members are found from the spring-tide line to deep-sea trenches (10,500 metres deep) and inhabit nearly all possible habitats, even floating weeds. Both shelled and naked gastropods have pelagic members that spend their entire lives swimming in the water; others penetrate marine hot vents or interstices between sand grains. Some gastropods are parasitic, while others are predatory. Freshwater snails also are found in groundwaters and may inhabit hot springs. Widely distributed throughout all terrestrial habitats, various members of the gastropod order Stylommatophora are adapted to certain regions.

Some littoral bivalves, such as *Tridacna*, as well as some sea slugs, such as *Aeolidia*, share an obligatory symbiosis with zooxanthellae (a group of algae). Another metabolic association exists between certain bacteria and several bivalves and gastropods of deep-sea hot vents or other sulfide systems. There are several parasitic mollusks.

Locomotion

Mollusks have a wide range of locomotory patterns. Solenogasters and various smaller gastropods glide upon cilia that beat rapidly against a pathway of mucus secretions. This pattern of movement is supported or replaced in larger mollusks by the propulsive waves that run along the surface of the foot and are controlled by the actions of the dorsoventral musculature. Burrowing occurs as an interaction between musculature and the hydrostatic skeleton; it is performed in caudofoveates and several sea slugs by the whole anterior body but is restricted to the foot in scaphopods, bivalves, and some specialized gastropods.



Organizational levels and body diagrams of the eight classes of mollusks evolved from a hypothetical generalized ancestor (archi-mollusk).

Various bivalves (*e.g.*, cockles) and snails may perform rapid twists or jumps through violent flexion of the foot. Buoyancy floating and jet propulsion are found in cephalopods; floating is also known in gastropods, and swimming of a different kind is practiced by some opisthobranch and prosobranch gastropods as well as in scallops and related bivalves. Octopods use their arms to crawl or even to swim or float with the help of the body skin interconnecting the arms (interbrachiate web). Some bivalve groups bore into hard surfaces by secreting strong chemicals that dissolve the substrate or by drilling, using the shell and radula. A sedentary (sessile) way of life has been adopted by many bivalves and some gastropods.

Features of Defense

The external cover that extends over the mantle may consist of a hardened epithelial layer called a cuticle, separate calcareous plates, or a shell. Another defense includes the ability of most solenogasters and chitons to roll the body up. Chitons, neopilinids, and limpets can adhere firmly to the substrate by a powerful suction pad foot. Protection is also afforded if the animal is able to withdraw into its shell; a snail has the added advantage of having a hardened plate (operculum) on the foot that blocks the shell opening (auricle) once the animal has withdrawn. Burrowing by caudofoveates, scaphopods, many bivalves, and some gastropods also offers protection from predators.

In many gastropods, slippery mucus is secreted from mantle extensions, or parapodia, as a defense against larger predators, such as sea stars (starfish). In scaphopods, mucus is secreted against an aggressor from the anterior mantle. Certain molluscan subgroups secrete noxious chemicals either as a poisonous secretion of the salivary glands or as distasteful acids in mantle cells. Glandular secretions by solenogasters or the gastropod superfamily Eolidacea prevent the stinging nettle capsules (nematocysts) of cnidarians, when consumed, from expulsing the stingers; moreover, some gastropods are able to store and then use the capsules in their own defense when attacked by a predator. Some mollusks secrete fluids to divert or frighten a predator, to provide camouflage, or to inhibit the predator's sense of smell. For example, the ink in cephalopods, the luminous cloud secreted by some deep-sea squids, and the purple fluid from the sea hare (*Aplysia*; a gastropod of the subclass Opisthobranchia) distract and confuse the predator and conceal the prey. Camouflage or frightening coloration is effective in protecting cuttlefishes, octopuses, and sea slugs, as well as other gastropods.

Blue-ringed octopus (genus hapalochlaena).

Form and Function

The highly varied evolutionary development of basic molluscan features has left only a few characters that may be taken as typical. As a result, molluscan form varies much among levels and subgroups.

External Features

The most obvious external molluscan features are the dorsal epidermis called the mantle (or pallium), the foot, the head (except in bivalves), and the mantle cavity. The mantle in caudofoveates and solenogasters is covered by cuticle that contains scales or minute, spinelike, hard bodies (spicules), or both (aplacophoran level). The chitons (class Polyplacophora) develop a series of eight articulating plates or valves often surrounded by a girdle of cuticle with spicules; in all other mollusks, the mantle secretes an initially homogeneous shell. The mantle and shell are laterally compressed in scaphopods and bivalves; in gastropods and cephalopods the head is free of the mantle and shell. In bivalves a dorsal hinge ligament joins two shell valves, which are further held together by two adductor muscles with attachment points on the inner aspect of each valve.

The molluscan body, which contains all the visceral elements (such as the digestive tract, gonads, and heart), is connected to the mantle by dorsoventral musculature. The head, when present, has tentacles called captacula in scaphopods, labial palps in bivalves, head tentacles in gastropods, and arms in cephalopods. The primitive ciliary gliding surface with forward pedal and sole glands is reduced in caudofoveats and some gastropods, as well as in some bivalves, and it is narrowed to a ridged tract in solenogasters as well as some members of the placophore genus *Cryptoplax*. The foot forms an anteriorly elongated and slendered burrowing organ in scaphopods, is ax-shaped to vermiform in bivalves, and is modified to a siphon or funnel in cephalopods. Among gastropods of the subclass Opisthobranchia, the foot may be extended laterally to form swimming lobes (parapodia), or even flapping wings (in pteropods, or sea butterflies).

The mantle, or pallial, cavity is found between the mantle rim and the body. The pallial complex is a collection of structures at the roof of the mantle cavity and typically contains at least one pair of lamellate gills (ctenidia), a thick layer of glandular epithelium called mucus tracts or hypobranchial glands, and the outlets for the digestive, excretory, and reproductive systems. A loss of the ctenidia (along with the mucus tracts) is seen in scaphopods, advanced gastropods, septibranch bivalves, and solenogasters.

Internal Features

Muscles and Tissues

The internal molluscan organization is almost entirely soft-bodied. The body cavity is filled with fibrous tissue or fluid-filled spaces (hemocoel), or both. When filled with fluid, the hemocoel expands against the body wall and fibrous tissues, providing a rigid framework and stretching opposing muscles. This same fluid pressure, generated by contraction of other muscles, allows the foot to extend from the shell and penetrate the sediment for burrowing. Conversely, extrusion of the head and foot from the shell in gastropods and cephalopods, shell elevation in gastropods, and the rapid expansion and contraction of the mantle required for jet propulsion in squid and other cephalopods are the result of muscle contractions in the mantle tissue.

The basic sets of muscle systems, fully retained only in solenogasters, include the subintegumental musculature below the mantle; a pair of longitudinal muscle bundles below the mantle margins, which roll the body up and which are almost disintegrated in conchiferans; and the dorsoventral musculature, which is reduced in caudofoveates and shell-less gastropods and which in shelled gastropods forms the columellar muscles that attach the animal to its shell.

Nervous System and Organs of Sensation

In the nervous system typical of mollusks, a pair of cerebral ganglia (masses of nerve cell bodies) innervate the head, mouth, and associated sense organs. From the dorsal cerebral ganglia, two pairs of longitudinal nerve cords arise: a pair of lateral (pleural) nerve cords, often forming pleural ganglia (which innervate the mantle), and a ventral pair of pedal nerve cords, often forming pedal ganglia (which innervate the foot). In primitive forms both cords are interconnected by lateral branches of nerve fibres. A buccal nerve loop with paired ganglia generally supplies the radular apparatus in the head. Posterior paired visceral ganglia, when present, innervate the viscera. Other mollusks have various grades of ganglia, all of which may be concentrated anteriorly. Because of torsion (that is, a twisting of the body during development), special nerve configurations are found in gastropods; in cephalopods a cartilaginous capsule encloses the concentrated mass of ganglia.

Supplied by the most posterior aspect of the lateral nerve cords, a chemoreceptive sense organ (the osphradium) monitors the water currents entering the mantle cavity. This organ has regressed in scaphopods, some cephalopods, and some gastropods. Pluricellular mantle papillae, which penetrate the cuticle, the valves, and the shell in some conchifers, are differentiated in placophores as photoreceptors. Aside from the well-developed, vertebrate-like eyes of cephalopods, there are photoreceptors on the mantle margins of scallops and related bivalves. Orientation in different gastropods is evidenced by reaction to polarized light, which in part serves for homing. Homing in other gastropods and in the chitons that flee from light appears to be performed by chemoreception along their mucus trails.

Digestive System

The primitive alimentary tract is straight, and the foregut contains glands and chitinized teeth, called the radula, upon a tough membrane or ribbon underlain by a mass of compact tissue as a support and operated by musculature. In bivalves and some other mollusks the whole radular apparatus is reduced or absent. The radula is used to bite, tear, and scrape various food materials. The different structural aspects of the radula in caudofoveates, solenogasters, and gastropods serve in classification. The differentiation of a more flexible radular structure among the primitive archaeogastropods subsequently enabled successful radiation into diverse habitats.

The midgut in caudofoveates (class Aplacophora) divides into a hindgut and a large ventral sac for enzyme production. In contrast, the midgut in placophores and conchifers is subdivided into a slender esophagus with a pair of glandular pouches, a distinct stomach with a pair of digestive glands, and a slender, often looped intestine. In primitive conchifers the stomach is of the so-called style sac type. The esophagus opens into an anterior elaboration of the stomach into which the enzymes from the style sac, an area separated by ridges, also are released; the tapered end of the stomach leads to the intestine. Cilia that line the style sac churn the stomach contents and form a long food-laden mucous mass called a protostyle, which abuts a chitinous area of epithelium in the stomach. Usually found within the style sac is a rod, called the crystalline style. The protostyle or the crystalline styles are fully retained in the bivalves and gastropods that subsist on small microorganisms and detritus. The protostyle or crystalline style may vary in form among the bivalves. Digestion in primitive forms appears to have been both intracellular and extracellular, such as is still the case in solenogasters (class Aplacophora), many bivalves, and most gastropods. In advanced levels either intracellular or extracellular digestion appears to be exclusively elaborated—*e.g.,* advanced crystalline style and intracellular.

Circulatory System

Mollusks possess an open circulatory system in which body fluid (hemolymph) is transported largely within sinuses devoid of distinct epithelial walls. The posteriodorsal heart enclosed in a pericardium typically consists of a ventricle and two posterior auricles. Hemolymph is drained from ctenidia, gills, or other specialized respiratory epithelia into the respective auricles. The ventricle pumps the hemolymph through a middorsal sinus (in solenogasters and scaphopods) or vessel (aorta) into the body tissues. Hemolymph drains from the tissues into the gills, whence it returns to the auricles.

The respiratory pigment is commonly dissolved in the fluid, either as hemoglobin (as is especially the case in bivalves) or more generally as hemocyanin, which contains copper rather than iron; in more-advanced forms, hemoglobin is bound to blood cells. In chitons and monoplacophorans (but not in the caudofoveates and the solenogasters) the heart is also the site of the purifying ultrafiltration, and the waste products are then discharged into the pericardium and via a pair of pericardial outlets modified to excretory organs (emunctoria, such as false kidneys or nephridia).

Reproductive System

In adult cephalopods and some other representatives the paired dorsal gonad retains the developmental connection with the pericardium. In caudofoveates and solenogasters, eggs or sperm are discharged into the pericardial cavity, and from there the pericardial outlets transport them to the environment, where fertilization takes place. In more-advanced mollusks there are usually separate ducts to transport the gametes (gonoducts): a pair of gonoducts, called oviducts for the female gametes and spermiducts, or vas deferens, for the male gametes, leads the egg and sperm, respectively, to the mantle cavity. Glands to secrete protective coatings around the egg may be present. In gastropods the left gonad is reduced, and after torsion only the right gonad is operational, leaving the internal body asymmetrical; similar asymmetries are also found in some other molluscan subgroups.

Endocrine System

Hormone production is not well documented in mollusks other than gastropods and cephalopods. Antagonistic neurohormonal control of reproductive activity and metabolic processes is performed in the gastropods through cerebral dorsal bodies and lateral lobes or juxtaposed organs and in the cephalopods through optic glands. In some cephalopods, the hormones also affect death by starvation after the mollusk has deposited its eggs or has mated. Neurosecretions by cells outside the nerve cell bodies (ganglia) have been described in gastropods and cephalopods, the released hormones diffusing through the tissues rather than being concentrated in special organs.

Heart rate in mollusks plays a crucial role in many metabolic processes, including excretion; hormones that affect the heart are released from the wall of veins in cephalopods or, in gastropods, from the subesophageal ganglia, the junction between the auricles and the ventricle. Insulin-like hormones shed from gastropods and bivalves by certain midgut cells control the amount of glucogen (a storage form of sugar) kept as a reserve nutrient.

Classification of Phylum Mollusca

Phylum Mollusca is a very diverse (85,000 species) group of mostly marine species. Mollusks have a dramatic variety of form, ranging from large predatory squids and octopus, some of which show a high degree of intelligence, to grazing forms with elaborately sculpted and colored shells. This phylum can be segregated into seven classes: Aplacophora, Monoplacophora, Polyplacophora, Bivalvia, Gastropoda, Cephalopoda, and Scaphopoda.

This chiton from the class Polyplacaphora has the eight-plated shell that is indicative of its class.

Class Aplacophora ("bearing no plates") includes worm-like animals primarily found in benthic marine habitats. These animals lack a calcareous shell but possess aragonite spicules on their epidermis. They have a rudimentary mantle cavity and lack eyes, tentacles, and nephridia (excretory organs). Members of class Monoplacophora ("bearing one plate") possess a single, cap-like shell that encloses the body. The morphology of the shell and the underlying animal can vary from circular to ovate. A looped digestive system, multiple pairs of excretory organs, many gills, and a pair of gonads are present in these animals.

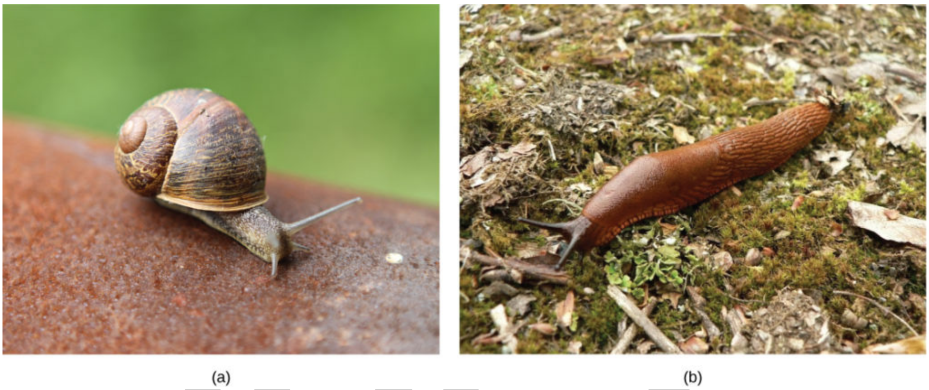
Animals in the class Polyplacophora ("bearing many plates") are commonly known as "chitons" and bear an armor-like eight-plated shell. These animals have a broad, ventral foot that is adapted for suction to rocks and other substrates, and a mantle that extends beyond the shell in the form of a girdle. Calcareous spines may be present on the girdle to offer protection from predators. Respiration is facilitated by ctenidia (gills) that are present ventrally. These animals possess a radula that is modified for scraping. The nervous system is rudimentary with only buccal or "cheek" ganglia present at the anterior end. Eyespots are absent in these animals. A single pair of nephridia for excretion is present.

These mussels, found in the intertidal zone in Cornwall, England, are bivalves.

Class Bivalvia ("two shells") includes clams, oysters, mussels, scallops, and geoducks. Members of this class are found in marine as well as freshwater habitats. As the name suggests, bivalves are enclosed in a pair of shells (valves are commonly called "shells") that are hinged at the dorsal end by shell ligaments as well as shell teeth. The overall morphology is laterally flattened, and the head region is poorly developed. Eyespots and statocysts may be absent in some species. These animals are suspension feeders—they eat material, such as plankton, that is suspended in the water around them. Due to their diet, this class of mollusks lacks a radula. Respiration is facilitated by a pair of ctenidia, whereas excretion and osmoregulation are brought about by a pair of nephridia. Bivalves often possess a large mantle cavity. In some species, the posterior edges of the mantle may fuse to form two siphons that serve to take in and exude water.

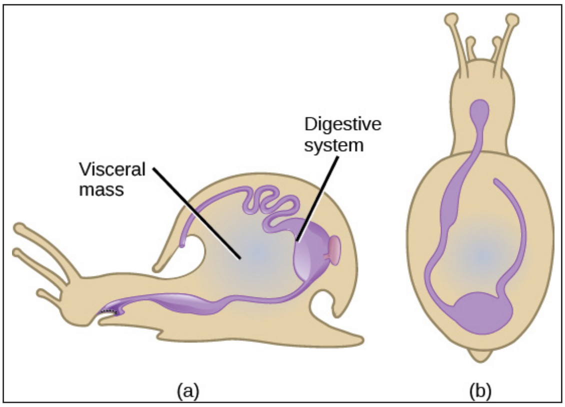
One of the functions of the mantle is to secrete the shell. Some bivalves like oysters and mussels possess the unique ability to secrete and deposit a calcareous nacre or “mother of pearl” around foreign particles that may enter the mantle cavity. This property has been commercially exploited to produce pearls.

Animals in class Gastropoda (“stomach foot”) include well-known mollusks like snails, slugs, conchs, sea hares, and sea butterflies. Gastropoda includes shell-bearing species as well as species with a reduced shell. These animals are asymmetrical and usually present a coiled shell. Shells may be planospiral (like a garden hose wound up), commonly seen in garden snails, or conispiral, (like a spiral staircase), commonly seen in marine conches.



(a) Snails and (b) slugs are both gastropods, but slugs lack a shell.

The visceral mass in the shelled species displays torsion around the perpendicular axis on the center of the foot, which is the key characteristic of this group, along with a foot that is modified for crawling. Most gastropods bear a head with tentacles, eyes, and a style. A complex radula is used by the digestive system and aids in the ingestion of food. Eyes may be absent in some gastropods species. The mantle cavity encloses the ctenidia as well as a pair of nephridia.



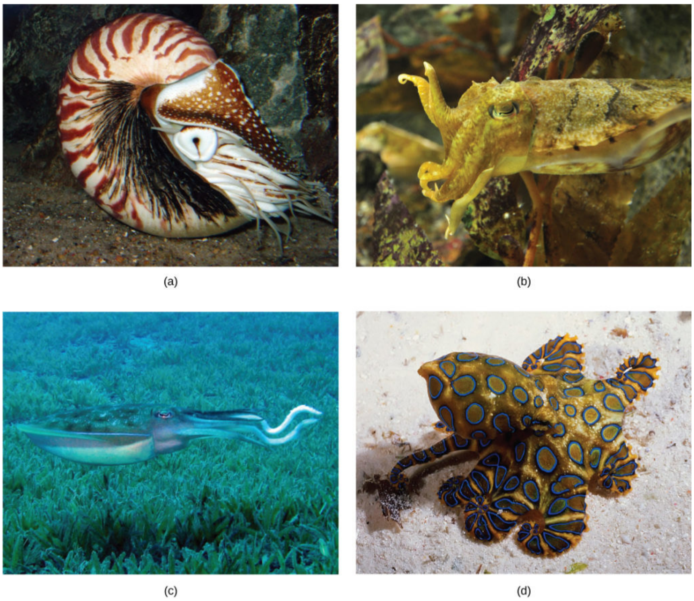
During embryonic development of gastropods, the visceral mass undergoes torsion, or counter clockwise rotation of anatomical features. As a result, the anus of the adult animal is located over the head. Torsion is an independent process from coiling of the shell.

Class Cephalopoda ("head foot" animals), include octopi, squids, cuttlefish, and nautilus. Cephalopods are a class of shell-bearing animals as well as mollusks with a reduced shell. They display vivid coloration, typically seen in squids and octopi, which are used for camouflage. All animals in this class are carnivorous predators and have beak-like jaws at the anterior end. All cephalopods show the presence of a very well-developed nervous system along with eyes, as well as a closed circulatory system. The foot is lobed and developed into tentacles, and a funnel, which is used as their mode of locomotion. Suckers are present on the tentacles in octopi and squid. Ctenidia are enclosed in a large mantle cavity and are serviced by large blood vessels, each with its own heart associated with it; the mantle has siphonophores that facilitate exchange of water.

Locomotion in cephalopods is facilitated by ejecting a stream of water for propulsion. This is called "jet" propulsion. A pair of nephridia is present within the mantle cavity. Sexual dimorphism is seen in this class of animals. Members of a species mate, and the female then lays the eggs in a secluded and protected niche. Females of some species care for the eggs for an extended period of time and may end up dying during that time period. Cephalopods such as squids and octopi also produce sepia or a dark ink, which is squirted upon a predator to assist in a quick getaway.

Reproduction in cephalopods is different from other mollusks in that the egg hatches to produce a juvenile adult without undergoing the trochophore and veliger larval stages.

In the shell-bearing *Nautilus* spp., the spiral shell is multi-chambered. These chambers are filled with gas or water to regulate buoyancy. The shell structure in squids and cuttlefish is reduced and is present internally in the form of a squid pen and cuttlefish bone, respectively. Examples are shown in figure.



The (a) nautilus, (b) giant cuttlefish, (c) reef squid, and (d) blue-ring octopus are all members of the class Cephalopoda.

Members of class Scaphopoda ("boat feet") are known colloquially as "tusk shells" or "tooth shells," as evident when examining *Dentalium*, one of the few remaining scaphopod genera.

Antalis *vulgaris* shows the classic Dentaliidae shape that gives these animals their common name of "tusk shell."

Scaphopods are usually buried in sand with the anterior opening exposed to water. These animals bear a single conical shell, which has both ends open. The head is rudimentary and protrudes out of the posterior end of the shell. These animals do not possess eyes, but they have a radula, as well as a foot modified into tentacles with a bulbous end, known as captaculae. Captaculae serve to catch and manipulate prey. Ctenidia are absent in these animals.

Aplacophorans

Aplacophorans, which are also called solenogasters, are worm-shaped mollusks covered with spicules or sharp needle-like projections. The body shape varies from almost spherical to elongated and slender. These mollusks are usually less than 2 in (5 cm) in length, but adult individuals may vary from 0.039-0.078 in (1-2 mm) to 3.9 in (10 cm) or more in length.

The exterior of an aplacophoran may be spiny, smooth, or rough. The head is poorly developed, and the typical mollusk shell and foot are absent. The exoskeleton is represented only by a cuticular (horny secreted) layer that bears spicules in a variety of forms. The spicules and integument (covering) together form a character that links genera or families in this class to one another. Most aplacophorans have some specialized spicules at the entrance to the mantle cavity; these are presumably used in copulation. The cuticle and epidermis may be either thick or thin relative to the size of the species: a thick cuticle may occur together with a thin epidermis; a thin cuticle may occur with a thick epidermis; or they may be the same thickness. Glandular cells on the epidermis known as papillae may have either long stalks or no stalks at all.

Aplacophorans have a midventral longitudinal groove containing one or more ridges, which are similar in structure to the foot of other mollusks. The mantle covers the upper surface, the sides, and the greater part of the lower surface of the animal. A large gland that secretes mucus opens into the groove toward the front.

The mouth at the front of the animal opens into a muscular pharynx lined by a thick cuticle. The pharynx typically receives the products of one or two pairs of salivary glands and the radula sac. Some genera lack salivary glands. Neomenioid species creep by ciliary action of the “foot” along a sticky track of mucus produced from the ciliated, eversible pedal pit at the anterior end of the pedal groove. Both the pedal groove and the pedal pit are supplied by many mucus-secreting glands. The radula is highly variable in form. It is situated where the pharynx joins the midgut unless an esophagus is present; it may have two teeth per row, one tooth per row, or many teeth per row. The radula is lacking in 20% of known species.

The posterior end of the body contains a cavity into which one or two gametopores open as well as the anus, the copu-latory spicule sacs, and the folds of respiratory tissue or papillae. The posterior cavity is believed to represent a mantle cavity. Burrowing species have a pair of gills. In Neomenia and in several other genera there is a circlet of laminar gills in the mantle cavity; in other genera, however, there are no gills.

Evolution and Systematics

The class Aplacophora contains two subclasses: Neome-niomorpha (also called Solenogastres) and Chaetodermo-morpha (also called Caudofoveata). Most neomenioids creep by means of a narrow foot with a ventral groove that begins as a pedal pit toward the front of the animal. They have a sensory vestibule above the mouth; a single midgut organ combining stomach and digestive gland; and serial sets of muscle bands running along their sides and lower surface. Neomenioids are simultaneous hermaphrodites; they also lack ctenidia in their mantle cavities. A ctenidium is a finger-shaped or comb-like structure that functions in respiration. The subclass of Neomeniomorpha comprises three orders (Pholidoskepia, Neomeniomorpha, and Cavibelonia); 24 families; 75 genera; and fewer than 250 species. The subclass Chaetodermomorpha contains six families and 15 genera. Aplacophorans in this subclass have a midgut separated into a stomach and a digestive organ, and one pair of ctenidia in their mantle cavities.

It is uncertain to what extent aplacophorans are specialized and to what extent they are primitive mollusks, but there is no evidence that they ever had shells. Their specialized features include the reduction or loss of the foot; the absence of a shell; sometimes the lack of a radula (a specialized organ unique to mollusks that allows them to scrape food from the ocean floor); and modifications of the nephridia (simple organs for excreting wastes) in certain genera to form accessory sexual organs. The possession of well-defined cerebral and pleural ganglia (groups of nerve cells) indicates that the Apla-cophora are more advanced than the Polyplacophora mollusks in this respect at least. It seems probable that aplacophorans represent a secondary simplification of an ancestral form.

Distribution

Aplacophorans are found in all oceans of the world; some genera have worldwide distribution. Although they have been sampled at depths ranging from 16 to 17,390 ft (5-5,300 m), the greatest diversity of species occurs at depths greater than 656 ft (200 m).

Habitat

Neomenioids live on hydroids, corals, or surface sediment. Caudofoveatans construct burrows in marine sediments, which they inhabit head downward.

Feeding Ecology and Diet

Neomenioids feed on cnidarians—stony and soft corals, hydrozoans, zooantharians, or gorgonians. Some species prey only on specific cnidarians. Caudofoveatans ingest sediment or may be selective carnivores or scavengers. They feed mostly on faraminifera.

Reproductive Biology

Aplacophorans are hermaphrodites and have paired go-nads. Copulation probably occurs in those with the former condition, and spawning in the latter. Researchers have inferred from the presence of seminal receptacles, the structure of introsperm (sperm that never contact the water), and observation of living specimens of Epimenia australis that fertilization takes place internally.

Polyplacophora

Chitons are distinct in possessing eight (sometimes seven) overlapping transverse shell plates (hence, the name Polypla-cophora, which means “bearer of many plates”) that permit the ovoid, dorsoventrally reduced body to conform to the irregular, rocky shores on which they are most often found. Strong, paired pedal retractor muscles extend from the foot to each shell valve, which is often wing-like or butterfly-like in shape, with two lateral, anterior extensions where these muscles attach. The shell plates are composed of four layers: an outer, organic periostracum; an inner tegmentum composed of calcium carbonate and proteinaceous material (con-chiolin); an inner articulamentum below the tegmentum, comprised of pure calcium carbonate (aragonite) that extends laterally, free of the tegmentum layer to form the insertion plates of each valve; and the innermost hypostracum, lying against the mantle.

A juvenile chiton on a cone shell.

The mantle, a thick, stiff tissue layer that secretes the shell, extends beyond the shell plates (and sometimes over them, such as in Cryptochiton stelleri). This tissue layer secretes a thin glycoprotein cuticle on the dorsal surface of the body. This cuticle may bear scales, bristles, or calcareous spicules similar to those in the class Aplacophora.

Ventrally, a broad muscular foot is bordered laterally on each side of the body by a pallial groove between the edge of the foot (medially) and the edge of the mantle (laterally), forming a chamber in which the gills (or ctenidia) are located. Within these mantle cavities, anywhere from six to 88 pairs of ciliated, bipectinate gills are located. A current of water enters alongside the anterior end of the body, ventrally, on both sides of the body near the head, and travels through each of these grooves posteriorly, exiting out of the body beyond the tail end of the digestive track (the anus). This water current carries oxygenated seawater, and rids the animal of egested feces (released from the anus) as well as urine released out of a pair of nephridiopores that open laterally in the posterior mantle cavity. The nephridiopores represent the exit points of two large nephridia that filter out wastes within the coelomic cavity surrounding the heart, which is filled with blood (and often termed a heomocoel).

Most chitons feed on microalgae, scraping the surface of the rocks on which they sit with a long radular belt of 17 recurved teeth, arranged in transverse rows that are capped with magnetite (an iron-containing hardening material) in some species. Some variation in feeding exists. Species such as Katharina tunicata feed on large macroalgae, including kelps (Hedophyllum). Other species possess spectacular modifications of the anterior portion of the girdle to trap small crustacean prey, allowing the evolution of carnivory in an otherwise completely herbivorous (or omnivorous) group.

The chiton nervous system consists of a circumenteric nerve ring around the gut, leading to ladder-like nerve cords that radiate posteriorly towards the end of the body along four lines: two paired pedal cords and two paired visceral cords. These four nerve cords are connected by a series of transverse rung-like commissures, yielding the ladder-like form of the overall system.

Reproduction in chitons involves a single gonad, formed in the dorsal hemocoel, which empties gametes (either eggs or sperm, depending on the sex of the individual) by way of two gonoducts into the mantle cavity just anterior to the openings of the nephridiopores on both sides of the foot. Eggs (which are coated with a spiny envelope) are released either singly or in strings, and are fertilized externally in the water column. Development usually leads to a lecithotrophic (yolk-filled) trochophore larva. There is no veliger stage. Some species have larger, direct-developing eggs that are brooded in the female's mantle cavity, from which a juvenile chiton is formed. The shell gland develops with seven regions on the dorsum of the juvenile; the seventh band divides later to form an eighth. Thus, eight shell plates are formed.

Evolution and Systematics

The earliest fossil chitons occur in the Upper Cambrian, dating the group back nearly half a billion years. The fossil record of this group of mollusks is relatively sparse, with approximately 350 described fossil species. Chitons diversified more rapidly in recent (Cenozoic) times, and today there are approximately 1,000 living species worldwide. One-fifth of the species are found on the Pacific coast of North America, distributed from Alaska to Southern California, more than on any coast of comparable length in the world. Roughly half of all living species live in the intertidal or shallow subtidal zones.

Within the phylum Mollusca, the chitons are unique in possessing eight shell valves. However, the class Monopla-cophora, with a single shell, shares several characteristics with the chitons, including eight pairs of dorsoventral pedal retractor muscles. Repeated pairs of many organs, including one to three pairs of gonoducts, three to seven pairs of excretory nephridiopores, three to six pairs of gills, and two paired atria in monoplacophorans may suggest that mollusks as a whole evolved from a segmented ancestor not unlike the chitons. Larval aplacophorans, larval polyplacophorans, and adult polyplacophorans possess seven or eight transverse dorsal rows of spicules, further strengthening the link between these two classes of mollusks. Finally, recent analyses of 18S rDNA gene sequences suggest that the mollusks are united with other eu-trochozoans that possess a trochophore larva, including the annelids. The analyses also support the theory that mollusks arose from a segmented ancestor.

Nevertheless, other theories currently lean toward a non-segmented ancestor for the phylum Mollusca, based on the unsegmented coelom (unlike that of annelids), the lack of agreement in the number of paired organs in basal mollusks (e.g., aplacophorans versus polyplacophorans), and the lack of evidence of segmentation in many other classes within the phylum. These theories support the placement of the apla-cophorans, with a vermiform body that lacks a shell (and often lacks a foot, radula, and most gills), as near the base of the phylogenetic tree of mollusks.In addition, apparent differences between the shell valves of polyplacophorans and the so-called dorsal plates found in aplacophorans suggest that chitons stand alone as a uniquely derived group that arose early in the evolution of mollusks.

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It is unclear where, within the spiralian protostomes (including numerous phyla such as the Platy-helminthes, Nemertea, Sipuncula, Echiura, Annelida, Ony-cophora, and Arthropoda), the mollusks arose, although the presence of a reduced coelomic area surrounding the heart (the pericardial space) suggests a coelomate (rather than acoelomate) ancestor.

Distribution

Chitons are common rocky intertidal inhabitants, occurring particularly in the temperate zone.

Habitat

Chitons are found primarily on hard substrates, molding their body to the contours of the rock. They are found from the high intertidal zone to depths of more than 13,123 ft (4,000 m), and occur in tropical, temperate, and cold polar seas. Most abundant on hard substrates, especially rocks, chitons graze on surface microalgae and encrusting organisms.

Behavior

Cryptochitons and other chitons roll up when dislodged from a rock, about the only defensive trick these animals have. Several species, such as the mossy chiton (Mopalia muscosa), have "home scars", or areas on a rock that they return to following excursions for feeding; these place are often particularly well situated for the chiton to grasp onto to avoid dislodgement by waves as the tide comes in. Except for the predatory chiton, Placiphorella velata, which can quickly trap prey with its "head-flap", most chitons are highly sedentary animals that remain stationary when the tide is out, mostly feeding at night when low tides or full water submergence keeps them moist.

Feeding Ecology and Diet

The radula, a chitonous ribbon covered with many rows of hard, recurved teeth, is used for feeding, most frequently on the microalgae that coat the rocks on which chitons are found. In some species, this radula contains iron, part of it as magnetite, the only known example of biological production of this common mineral. Magnetite greatly strengthens the radula, allowing many chitons to feed on hard, encrusted coralline algae.

Besides the microscopic and macroscopic algae, chitons are also known to feed on other encrusting organisms (such as bryozoans). One genus (Placiphorella) has evolved the remarkable ability to capture live prey such as worms and small crustaceans by using an expanded "head-flap" created by an anterior extension of the girdle, which is held above the substrate until unwary victims wander in, at which time the head-flap is rapidly closed down over the prey.

Reproductive Biology

The reproductive system of chitons consists of a gonad located in front of the heart dorsally, with a pair of ducts that open into the mantle cavity at the posterior end of the body. The sexes are always separate, with sperm shed into the sea. Eggs are either shed into the sea or retained in the female's mantle cavity, where sperm that enter with the respiratory currents fertilize them. The eggs are then brooded until embryos become well-developed young chitons.

Gastropod

Gastropod is any member of more than 65,000 animal species belonging to the class Gastropoda, the largest group in the phylum Mollusca. The class is made up of the snails, which have a shell into which the animal can generally withdraw, and the slugs, which are snails whose shells have been reduced to an internal fragment or completely lost in the course of evolution.

Gastropods are among the few groups of animals to have become successful in all three major habitats: the ocean, fresh waters, and land. A few gastropod types (such as conch, abalone, limpets, and whelks) are used as food, and several different species may be used in the preparation of escargot. Very few gastropod species transmit animal diseases; however, the flukes that cause human schistosomiasis use gastropods as intermediate hosts. The shells of some species are used as ornaments or in making jewelry. Some gastropods are scavengers, feeding on dead plant or animal matter; others are predators; some are herbivores, feeding on algae or plant material; and a few species are external or internal parasites of other invertebrates.

General Features

Size Range and Diversity of Structure

Some adult marine snails (*Homalogyra*) and forest-litter snails (*Stenopylis*, *Punctum*) are less than one millimetre (0.04 inch) in diameter. At the other extreme, the largest land snail, the African *Achatina achatina*, forms a shell that is almost 20 centimetres (eight inches) long. The largest freshwater snails, *Pomacea* from South America, reach nearly 10 centimetres in diameter, and the largest marine snail, the Australian *Syrinx aruanus*, occasionally grows to more than 0.6 metre (two feet). The longest snail probably is *Parenteroxenos doglieli*, which lives as a parasite in the body cavity of a sea cucumber: it grows to be almost 130 centimetres (50 inches) in length, although it is only 0.5 centimetre (0.2 inch) in diameter. Most snails are much smaller; probably 90 percent of all adult snails are less than one inch in maximum dimension.

Snails show a tremendous variety of shapes, based primarily upon the logarithmic spiral. They can be coiled flatly in one plane, as in *Planorbis*; become globose with the whorls increasing rapidly in size, as in *Pomacea*; have the whorls become elongate and rapidly larger, as in *Conus* and *Scaphella*; have a few flatly coiled whorls that massively increase in width, as in *Haliotis*; become elongated and spike-shaped, as in *Turritella*; or be humped to form a limpet shape, as in *Fissurella*. Often a number of such shell shapes can be found among species within a single family, but such marine families as the Terebridae, Conidae, and Cypraeidae are conservative in shape. Shells of different species vary markedly in thickness, and those of many species bear conspicuous spines and ridges, probably as an evolutionary adaptation to predation.

Traditionally, the three main gastropod groups are the prosobranchs (subclass Prosobranchia), the opisthobranchs (subclass Opisthobranchia), and the pulmonates (subclass Pulmonata); however, many authorities classify the pulmonates as a subgroup within subclass Opisthobranchia. The prosobranchs generally secrete a substantial shell into which the animal can withdraw. The operculum, an often calcified disk situated on the rear part of the foot, fills the shell aperture when the snail is inside the shell, protecting the animal against predation and desiccation. Opisthobranchs are marine species that often have a reduced or absent shell and very colourful bodies. The pulmonates are snails and slugs that lack an operculum but show complex and highly varied body structures. They have a "lung" or pulmonary cavity that serves also as a water reservoir. Gastropods have a fossil record that extends back over 500 million years.

Distribution and Abundance

Of the more than 65,000 species, about 30,000 are marine, 5,000 live in fresh water, and 30,000 live on land. In general, oceanic gastropods are most diverse in number of species and in variety of shell structures in tropical waters; several hundred species (each represented by a small number of individuals) can be found in a single coral reef habitat. This is in contrast to the Arctic or subarctic coasts, where the few species present are represented by many individuals. A number of deep-sea species are known, and a significant snail fauna is associated with hydrothermal vents. Most marine species have large ranges.

Freshwater snails are common in ponds, streams, marshes, and lakes. Usually only a few species are found at one place, but each species will have a rather wide range. Most species are common and feed on algae or dead plant matter. In a few relatively old river systems and lakes—in particular, Lake Baikal in Siberia, Lake Titicaca in South America, Lake Ohrid on the North Macedonia–Albania border, the Mekong basin in Southeast Asia, and the African Rift lakes—extensive and complex radiations of snails have occurred in recent geologic time, producing a large number of species.

Land snails are marginally, but very successfully, terrestrial. When actively moving, they continuously lose water. During periods when water is unavailable, they retreat into their shells and remain inactive until conditions improve. They hibernate during winter periods, when water is locked into snow or ice, and estivate during periods of summer drought. Land snails have been found above the snow line; species of *Vitrina* crawl on snowbanks in Alpine meadows. Other species inhabit barren deserts where they must remain inactive for years between rains.

Fewer than 10 species live in the same area together across most of North America. On the other hand, in such favourable areas as New Zealand, Jamaica, northeastern India, and the wet forests of Queensland (Australia) 30 to 40 different species can be found together. In some parts of Western Europe 20 species can be found together. Only one or two species are found in many desert regions, and they have dramatic feeding specializations.

The local abundance of snails and slugs can be spectacular. Millions of some brackish-water and freshwater species can live on small mud flats. An acre of British farmland may hold 250,000 slugs, and a Panamanian montane forest was estimated to have 7,500,000 land snails per acre. Despite this abundance, snails and slugs often pass unobserved. Land and freshwater species often stay hidden during the day and are active at night. Most marine species as well are nocturnal, and the shells of many of these species are so heavily covered with algae and other encrusting organisms that they may be mistaken for bits of rock.

Importance to Humans

From earliest times, humans have used many snail species as food. Periwinkles (*Littorina*) in Europe and South Africa, queen conchs (*Strombus gigas*) in the West Indies, abalones (*Haliotis*) in California and Japan, and turban shells (*Turbo*) in the Pacific are the most frequently eaten marine snails. Occasionally limpets and whelks are used for food, but they are more commonly used as fish bait. Freshwater snails rarely are eaten. Land snails of the family Helicidae have been eaten in the Middle East and Europe since prehistoric times. Today many tons of the European edible snails *Helix aspersa* and *H. pomatia* (the most common species used to prepare escargot) are raised on snail farms or collected wild. Several species of *Otala* and *Eobania* from Morocco and Algeria are exported for food.

Edible snail (Helix pomatia).

In some places, introductions of *Achatina* and *Helix* have resulted in damage to crops and gardens by these rapidly multiplying snails. On the other hand, habitat degradation, the introduction of predatory rats and land snails, and shell collecting by humans have caused the extinction of about 50 percent of all *Achatinella* species in Hawaii. Eighteen of the remaining 19 native species have been pushed to the brink of extinction.

California orange groves are plagued by *H. aspersa*. Many slugs accidentally introduced from Europe to both the West Coastal and the Eastern to Midwestern United States are a continual nuisance in home gardens. Freshwater snails of the family Bythinidae sometimes become so numerous that they clog the filter systems of pumping stations.

Shells of certain snails are highly prized by collectors. The operculum of some *Turbo* species is used in making earrings; cameos are cut from the shell of the Red Sea snail *Cassis rufa*. Abalone shells are used in many cultures for decorative purposes; the shell of the golden cowrie (*Cypraea aurantium*) served at one time as a badge of a chief in Fiji. Strings of shells have been used as money.

Serious medical problems are caused by the few freshwater snails (*Pomatiopsis*, *Bulinus*, *Biomphalaria*) that serve as intermediate hosts for flatworms that parasitize humans. Schistosomiasis is a disease caused by minute blood flukes (schistosomes). Both snails and flukes are most common in areas where fields are irrigated. Schistosomes also parasitize birds and mammals. A skin rash called swimmer's itch results from bird schistosomes trying, only partly successfully, to penetrate human skin. They die in the upper skin layers, and their decomposition causes local infection. Other health problems are caused by several snails and slugs (e.g., *Bradybaena*, *Angustipes*, *Veronicella*) that serve as intermediate hosts for the rat lungworm. If an infected land snail or slug is inadvertently chopped up in a salad and eaten, the worm can migrate to the brain and encyst, causing moderate to severe damage.

Most gastropods, however, are useful to humans in that they help decompose dead plants and animals into substances that can be used by plants to manufacture new organic compounds. In both field and forest, as in ponds, rivers, and oceans, gastropods are an important part of the decomposer community, and some are significant predators.

The colonization of freshwater and terrestrial habitats by gastropods is due to the plasticity of their body and organ systems. Most major groups of organisms primarily inhabit only one of the three great biospheres (ocean, fresh water, or land); the gastropods are well represented in all three.

Reproduction and Life Cycles

Gastropods originated in the oceans, and relics of this fact are preserved in the early life history of freshwater and land species. Only in the most primitive prosobranchs (such as abalone) are the gametes released into the water for fertilization to take place outside the female. The fertilized egg hatches into a free-swimming form (trochophore larva). Upon the expansion of the ciliary girdle of the trochophore larva into large, heavily ciliated lobes (vela), the larva, called a veliger, undergoes torsion, a 180° twisting of the body that brings the posterior part of the body to an anterior position behind the head. Torsion is unique to the gastropods.

In some species the swimming veliger stage persists for weeks or even months. The veliger has a small shell into which the velar lobes and head can be withdrawn and a larval heart that seems to exist solely to provide circulation in the velar lobes. Food consists of diatoms (an algae group) and other small plankton collected by ciliary currents of the velum and channeled by the currents into the mouth. Special excretory cells located on either side of the mouth and the larval heart disappears when the veliger leaves the plankton and metamorphoses into a crawling snail. After metamorphosis, the juvenile snail starts a typical pattern of rapid growth until sexual maturity, at which point growth either ceases or is greatly slowed as energy is diverted to the production of the next generation. In opisthobranchs and many pulmonates, the life span is about one year, although there are notable exceptions. Prosobranchs in general seem to have a much longer life span, with some species of the freshwater Vivipara living 20 years in captivity. Some Sonoran Desert snails from California have been revived after eight years in estivation. Such desert species may live 20 to 50 years.

Several trends are evident in gastropod life-history evolution from the basic pattern. First, there is a tendency toward the development of structures to permit internal fertilization. In some species, pallial reproductive tubes of male and female become closed tubes, and a male copulatory organ develops on the right side of the head for transmission of sperm to the female. In many species the trochophore and veliger stages are passed within an egg mass or capsule provided with a food supply, rather than as free-swimming immature organisms that must find their own food. At first, provision of nutriment for the young probably involved laying eggs in a mucous mass. As evolution progressed, more rigid capsules containing yolk and with a protective cover might have been laid singly or in masses. Some species currently provide parental care of the eggs or egg mass. Finally the eggs are retained inside a brood pouch or the uterus of some species until the young are ready to hatch (ovoviviparity). An additional evolutionary trend involves sex reversal and the development of hermaphroditism—the presence of both male and female sex organs in one animal; the members of nearly all opisthobranch and pulmonate species are hermaphrodites.

Such changes occurred more than once during gastropod evolution, and there is no pattern of changes that would suggest clear evolutionary relationships. The differences correlate with habitat and frequently are seen within species of one genus. *Littorina* is a classic example: in England *L. neritoides* lives in crevices of exposed rocks above normal high water but releases floating (pelagic) egg capsules during fortnightly high tides or storms; *L. littorea*, on the lower half of the shore, also has pelagic egg capsules, which hatch six days later into veligers; *L. littoralis*, which lives on seaweeds that are rarely exposed by the tides, deposits gelatinous egg masses on the seaweeds, and the larvae pass through the veliger stage in the egg mass, emerging in two to three weeks as crawling young; and *L. saxatilis*, which extends from midtide level to several feet above the high-water mark, retains the eggs inside the female until they hatch as crawling young.

In the most primitive prosobranchs the duct carrying eggs or sperm (gonoduct) opens into the kidney or renopericardial duct; in more-advanced archaeogastropods it opens into the ureter. Separation of the excretory and reproductive ducts occurred later in evolution and is evident in the orders Mesogastropoda and Neogastropoda. The females of these latter forms have the upper portion of the oviduct specialized for secreting nutritive material around the fertilized eggs and the lower portion for encapsulating the egg and nutritive material.

Prosobranchs such as *Cerithiopsis*, *Janthina*, and *Turritella* have extremely large, modified sperm that carry thousands of smaller, normal sperm from the male into the oviduct of the female; the large sperm swim the substantial distance between individuals. More frequently a penis is used to insert a stream of sperm into a special storage organ or the oviduct. In the opisthobranch *Limapontia* the penis stylet injects sperm through the body wall into a storage organ (bursa) of the mate.

Not surprisingly, land gastropods exhibit internal fertilization. The more primitive species directly transfer a stream or gelatinous mass of sperm by insertion of the penis. One individual can act as a male and the other as a female, or copulation can be reciprocal. During evolution, loosely adherent masses of sperm gave rise to enclosed packets of sperm and then to horny or calcareous sperm bundles (spermatophores) with elaborately ornamented exteriors. It is not uncommon for there to be as many as 12 such spermatophores inside the bursa of one female. Closely related species show clear differences in the number and spacing of exterior spikes. Undoubtedly, this difference provides a method of species recognition among these snails. Other pulmonates depend on explicit courtship patterns (such as the slugs from the family Limacidae) or structural differences in the penis (as in the land snails of the family Endodontidae) to distinguish members of their own species.

Most members of the prosobranch family Calyptraeidae begin life as fully functional males but, after a transitional phase, spend their remaining life span as females. *Crepidula* species, for example, form stacks of as many as 19 individuals. The younger ones on top are male, the old ones on the bottom female, and those in the middle are intermediate in sex. Isolated young individuals function as males for only a week or two, but young males in a stack remain male for a longer period, through some unidentified influence of the larger females underneath. Some limpets also undergo sex reversal.

Egg production is correlated with the degree of care given the eggs or young. On one extreme, some species produce hundreds of thousands or even millions of eggs. These eggs receive no care and suffer massive mortality (less than 1 percent survive). On the other extreme, some species produce only one or two eggs, which receive intensive parental care. There are also many gradations between the extremes. Many members of the orders Mesogastropoda and Neogastropoda produce egg capsules that may contain from one to more than 1,000 eggs. In *Busycon*, for example, each capsule may contain up to 1,000 eggs, but extensive cannibalization occurs upon unhatched eggs in the capsule and among the early hatched young. *Strombus* can lay a tubular string of eggs 23 metres (75 feet) long, with up to 460,000 eggs. Many snails in the genus *Conus* cement up to 1.5 million eggs in capsules on the undersides of rocks. Opisthobranchs weave delicate ribbons of eggs in colourful gelatinous sheets—sometimes up to 50 millimetres (two inches) of ribbon per hour—that contain many millions of eggs. In these cases, the eggs hatch into swimming veligers. Freshwater snails frequently deposit fertilized eggs in capsules on plant leaves or rocks, but the number of eggs deposited is much less than in the marine gastropods.

Direct care of the embryos is given in different ways. A small trochid, *Clanculus bertheloti*, deposits its eggs in grooves on the shell surface and covers them with a sheet of mucus to hold them in place; many *Neptunea* simply cement the egg capsules to their shell surface. Many *Crepidula* species deposit a mass of 5,000 to 20,000 eggs under the shell edge just in front of the female's foot, brooding them until they hatch as veligers. Freshwater viviparids and thiarids have either uterine or neck brood pouches, in which the fertilized eggs develop to a crawling stage. The vermetid *Stephopoma* and the acmaeid *Acmaea rubella* brood their young in the mantle cavity between the fleshy body and the shell. A number of endodontid land snails on Pacific islands deposit their eggs in the umbilicus, an opening in the shell base. In one species, *Libera fratercula*, the young gnaw their way out through the apex of the maternal shell. One pteropod, *Hydromeles*, has an internal brood chamber that apparently ruptures, freeing the young into the body cavity of the parent; the escape of the young may cause the parent's death.

Even without direct care of the eggs, land snails generally lay fewer than 200 eggs at a time. This reflects the different problems encountered on land and the lower mortality of larvae that are protected within the egg coverings. Many slugs and some snails bury egg masses in soil or under moist pieces of bark. Others, such as *Discus*, scatter their eggs singly over bark and decaying wood. One tropical genus (*Amphidromus*) rolls a leaf into a tube, seals one end with mucus, and lays its eggs in the cylinder thus formed. The South American *Strophocheilus* lays one large egg about four centimetres (1.5 inches) long. Among the many ways in which land snails minimize losses from drying is the adoption of ovoviviparity, or the hatching of eggs within the parent's body.

The evolutionary trend from the simple release of eggs and sperm into the surrounding seawater toward the provision of a large quantity of nutritive materials and protective encapsulation of each fertilized egg has resulted in an increase in the size of the organs that provide these abilities as well as a reduction in the sizes of the ovary and testis. The shift to direct transfer of sperm masses has led to evolution of both complex structures and complex behaviours for species recognition.

Ecology and Habitats

Although all levels of the ocean are inhabited by snails, they are in greatest abundance in and just below the tidal zones, where the most abundant quantities of food may be found. The extent of their effect on a coastline is indicated by the estimate that an average population of 860 million *Littorina* (periwinkles) on one square mile of rocky shore ingests 2,200 tons of material each year, only about 55 tons of which is organic matter. Limpets of all types are even more influential in such habitats, browsing and grazing on the algae and sessile animals. One interesting characteristic of limpets is that of homing. Numerous species have the tendency to settle on one spot and to feed on regular pathways radiating from this home base, to which they return for rest or under stressful conditions.

Some larger prosobranchs are selective herbivores, cutting off one- to two-centimetre (0.4- to 0.8-inch) strips of seaweed for swallowing. More characteristic of the sand and mud flats are scavengers that indiscriminately take in surface debris; scavengers are found in various groups, including limpets, strombids, and nassariids. Carnivores include both surface hunters and burrowing forms such as the naticids (moon snails). Some carnivorous species (e.g., moon snails and dog whelks) have evolved specialized glands that secrete a complex combination of acids and enzymes, enabling the snails to bore through the shells of other mollusks. As an adaptation to sedentary life, snails in several families have adopted mucociliary feeding by collecting food particles from water currents. Sensory reception to detect prey is highly developed in many carnivores.

Heteropods swim either by undulations of the foot or by the action of fleshy fins. Pelagic opisthobranchs show almost every conceivable type of swimming mechanism and are at times extremely abundant on the ocean surface. Among pteropods (sea butterflies), the foot has become divided and elongated into two thin muscular wings that can be used to propel the snail through the water. Many opisthobranchs and most small freshwater pulmonates can glide on the underside of the surface film of the water but are not able to swim.

Diversity of mollusks in the ocean has resulted in part from specialization in food resources. Temperature and salinity are the prime physical factors limiting range extensions, usually by preventing successful breeding rather than by preventing settlement and growth of young.

The evolutionary migration of snails from marine habitats into fresh water and onto land required a number of new adaptations. Snails had extra problems to solve, relating to their basic feeding and reproductive patterns. In the ocean, dispersal can take place by way of a veliger stage transported passively by currents and waves. In streams and rivers such a means of dispersal would result in downstream spread only. Probably because of this, along with the osmotic problems faced by tiny embryos developing in fresh water, the veliger stage was suppressed; instead, many freshwater prosobranchs brood the young inside the female, and pulmonates attach egg capsules to rocks, to vegetation, or to other snail shells. This essentially restricts snail dispersal to individual movement or occasional transport by birds and other vertebrates. In prosobranchs with separate sexes, the freshwater distributions closely follow drainage systems, because, in order to colonize a new body of water, either a pregnant female must be transported or both a male and a female must arrive at about the same time. The majority of pulmonates in fresh water are hermaphrodites and are capable of self-fertilization as well as cross-fertilization with other individuals. As a result, any pulmonate entering a new body of water can establish a considerable population of that species in a short time. For this reason, isolated ponds often have several species of pulmonates but only rarely prosobranch gastropods. In crawling over waterweeds, the pulmonates frequently come in contact with the feet or feathers of wading birds, to which they adhere accidentally by mucus secretion and are carried to a new pond.

Land snails avoid desiccation in several ways. Prosobranchs retreat into their shells, and the operculum effectively seals the opening against the exterior. In the tropics, land operculates have developed elaborate breathing tubes to allow gas exchange during dry periods and yet minimize water loss. Pulmonates lack an operculum, but a great number of the forms secrete either simple mucous covering (epiphragms) across the shell aperture or, in some of the more arid areas, a calcium-impregnated seal that can be almost as thick as the shell itself. Most land snails, however, have adjusted to life on land primarily through behaviour patterns. They stay in areas of high moisture or retreat into damp niches during short dry spells. A few burrow into soil. *Sonorella* species survive by remaining dormant during the years between rains; the genital structures of many individuals are reduced or lost to minimize use of energy in reproductive activities.

Only in the wet and warm tropics have tree snails been able to evolve. These species have brightly coloured shells that usually are much thinner than those of their terrestrial counterparts. In the humid mountain regions of the world, where a constant supply of moisture is available throughout the year, there has been a marked tendency toward reduction of the shell and the evolution of slugs. This tendency probably results from two different selective pressures that reinforce each other. The shell, which is useful primarily in providing protection against desiccation, is no longer needed when moisture is plentiful. Secondly, construction of the shell requires calcium, which is generally in short supply on the slopes of volcanic mountains. With the need for the shell lessened and the primary constituent in short supply, any mutation favouring shell reduction is advantageous. Although most species of slugs seem to have evolved in mountain areas, their spread into lowlands has been greatly aided by crop irrigation and garden watering.

Most land snails occupy the surface litter and upper soil zone. This microhabitat is generally moist, and food is plentiful in the form of decaying animals and plants as well as fungi. Most land snails have shells that are drab in colour and inconspicuous. Frequently, the shell surface is highly sculpted. The minute species (less than three millimetres [0.1 inch] in diameter) are preyed upon by small arthropods. The normal instinct of a snail to withdraw into its shell is of no help, since the predator simply follows the snail into its shell. Elaborate barriers that narrow the shell opening and tiny spines along the opening must provide some protection, since this construction occurs among species in more than 12 pulmonate families.

Most land snails feed directly on decaying plant matter, which is a simple shift in feeding behaviour from the primitive browsing of their marine ancestors. The carnivorous habit probably evolved through a transition period of carrion eaters. Many slugs feed on dead animal matter as well as plants. Pursuit and capture of other snails or earthworms demand increased sensory equipment and more rapid motion. Most carnivores, such as *Euglandina*, have greatly elongated bodies that allow them to reach farther into the shells of their victims.

Locomotion

The foot is the organ of locomotion in land gastropods. In swimming and sessile forms, however, the foot is greatly reduced or greatly modified. The normal progression of a snail is by muscular action, with a series of contraction waves proceeding from the posterior to the anterior end of the gliding portion of the foot. A few groups have the foot divided into right and left halves, with separate waves moving on each side. When the foot is narrow, as in *Strombus* and *Aporrhais*, the animal moves in fits and starts, tumbling along by a digging action of the foot and the pointed operculum. Certain small gastropod species move by the beating action of cilia of the foot on the mucous sheet secreted by the anterior part of the foot. Most prosobranchs are slow-moving, with a speed of less than eight centimetres (about three inches) per minute, although *Haliotis* has been reported to move at almost 10 times that rate.

Many opisthobranchs use foot musculature to move, but some glide on the underside of water-surface films through ciliary action. Swimming has been achieved in a number of ways. Body undulations propel such large snails as *Dendronotus* and *Melibe*. Pteropods, *Gastropteron*, *Akera*, and others move foot flaps (parapodia) to provide motion, and some species swim by undulating their entire bodies.

Freshwater pulmonates use ciliary action on a bed of mucus secreted by the snail.

Land pulmonates depend upon a combination of muscular action and cilia for locomotion. In many of these species the foot is divided longitudinally into three parts, with locomotor activity being confined to the central section, which glides on a mucous track. An additional use of slime by slugs is in the act of mating. A slime rope is secreted from which the mating pair of slugs is able to suspend themselves. If irritated, slugs can secrete copious quantities of slime. This reaction is the basis for one of the most effective methods of controlling slugs: spreading enough ashes in slug-infested areas causes exhaustion and death of the animals through the overproduction of slime.

Some of the small, tropical, brightly coloured sluglike species will, when disturbed, travel at a very high rate of speed with the anterior half of the foot lifted off the ground. They can continue moving at this pace for a distance of almost a metre at a rate faster than one metre per minute in snails less than two to three centimetres (or about one inch) in body length. Large gastropods, such as *Achatina* or *Strophocheilus*, are much slower, although carnivores are usually relatively fast-moving.

Food and Feeding

As in all molluscan groups except the bivalves, gastropods have a firm odontophore at the anterior end of the digestive tract. Generally, this organ supports a broad ribbon (radula) covered with a few to many thousand “teeth” (denticles). The radula is used in feeding: muscles extrude the radula from the mouth, spread it out, and then slide it over the supporting odontophore, carrying particles or pieces of food and debris into the esophagus. Although attached at both ends, the radula grows continuously during the gastropod’s life, with new rows of denticles being formed posteriorly to replace the worn denticles cast off at the anterior end. Both form and number of denticles vary greatly among species—the differences correlating with food and habitat changes. Radular morphology is an important tool for species identification.

Evidently, the most primitive type of gastropod feeding involved browsing and grazing of algae from rocks. Some species of the order Archaeogastropoda still retain the basic rhipidoglossan radula, in which many slender marginal teeth are arranged in transverse rows. During use, the outer, or marginal, denticles swing outward, and the radula is curled under the anterior end of the odontophore. The latter is pressed against the feeding surface, and, one row at a time, the denticles are erected and scrape across the surface, removing fine particles as the odontophore is withdrawn into the mouth. As the marginals swing inward, food particles are carried toward the midline of the radula and collected into a mucous mass. By folding the teeth inward, damage to the mouth lining is avoided and food particles are concentrated. Mucus-bound food particles are then passed through the esophagus and into the gut for sorting and digestion.

From this basic pattern, numerous specializations have developed, involving changes in the numbers, sizes, and shapes of radular teeth that correspond to dietary specializations. Prosobranch gastropods include herbivores, omnivores, parasites, and carnivores, some of which drill through the shells of bivalves, gastropods, or echinoderms to feed. Some gastropods, for example, possess a “toxoglossate” radula that has only two teeth, which are formed and used alternately. Most toxoglossate gastropods inject a poison via the functional tooth. Prey selection usually is highly specific. Although many cones hunt polychaete worms, others prey on gastropods or fishes, using the radular tooth as a harpoon, with poison being injected into the prey through the hollow shaft of the tooth. Several of the large fish-eating cones, which produce a variety of potent nerve poisons, have been known to kill humans.

Some other gastropods, such as the opisthobranch *Dolabella*, have as many as 460 teeth per row with a total of 25,000 denticles. In terms of feeding, opisthobranchs are extremely varied. Besides the algae-sucking sacoglossans, *Aplysia* cuts up strips of seaweed for swallowing, and a number of the more primitive species feed on algae encrusted on rocks. Perhaps the majority of opisthobranchs, including the sea slugs, are predators on sessile animals, ascidians and coelenterates being especially favoured. Pyramidellids are ectoparasites on a variety of organisms. Some of the pteropods are ciliary feeders on microorganisms.

Pulmonate gastropods are predominantly herbivores, with only a few scavenging and predatory species. Primitively, the pulmonate radular tooth has three raised points, or cusps (i.e., is tricuspid), but modifications involving splitting of cusps or reductions to one cusp are numerous. The modification of the radular tooth reflects dietary differences between species. In particular, with each successive appearance of a carnivorous type during evolution, the teeth have been reduced in number, each tooth usually having one long, sickle-shaped cusp.

Much of the diversity achieved by the gastropods relates to the evolutionary shifts in radular structure, which have led to exploitation of a variety of food sources. Predators capable of swimming, surface crawling, and burrowing to capture prey have evolved among the prosobranchs and opisthobranchs; predators that produce chemical substances for entering the shells of their prey have evolved among the mesogastropods (family Naticidae and superfamily Tonnacea), the neogastropods (family Muricidae), and a nudibranch opisthobranch (Okadaia); and, in the pulmonates, predation and thus a carnivorous diet have evolved at least 12 times.

Form and Function

Gastropods present such a variety of structures and adaptations that few all-encompassing characteristics can be presented. The following survey focuses on variety in the external shell and the body.

The Shell

The typical snail has a calcareous shell coiled in a spiral pattern around a central axis called the columella. Generally, the coils, or whorls, added later in life are larger than those added when the snail is young. At the end of the last whorl is the aperture, or opening. The shell is secreted along the outer lip of the aperture by the fleshy part of the animal called the mantle, first by outward additions to the shell lip and then by secretion of inner thickening layers. The outer layer, or periostracum, is a mixture of proteins known as conchin. Inner layers of calcium carbonate interlace with a network of conchin and are impregnated with a variety of mineral salts. The calcium usually is in the form of calcite crystals in marine species and aragonite crystals in terrestrial species, but mixtures of crystal types do occur. New shell is secreted by specialized mantle tissue.

Modifications and ornamentations of the basic shell are widely variable among species. Frequently, the shell is altered into a nonspiral cap or a cup-shaped limpet form as an adaptation to life in swift currents (the freshwater family Ancylidae) or amid pounding waves on rocks (the marine families Acmaeidae, Patellidae, Fissurellidae, and Calyptraeidae). In many groups, such as the abalones (the family Haliotidae), only traces of spiral coiling are evident, because the rate of successive whorl widths is so large that the last, or body, whorl occupies more than 90 percent of the shell volume. Elaborate surface sculpture, including knobs and spines, has evolved to serve as protection against predation. In a few species of the genera Leucozonia and Acanthina, a spine on the lip edge is used to wedge open clam valves so that the snail can feed. As implied earlier, land gastropods in dry regions tend to have very thick shells; on the other hand, those in very humid mountain situations have thin shells or none at all. Many carnivorous snails have the calcareous part of the shell greatly reduced.

The Body

The gastropod body consists of four main parts: visceral hump, mantle, head, and foot. The body is attached to the shell either by one columellar muscle or by a series of muscles. Typical snails can withdraw the head and foot into the shell, but numerous species have shells so reduced in size as to be unable to contain the body; slugs, of course, have either an internal shell vestige or no shell at all.

The Visceral Hump

The visceral hump, or visceral mass, of gastropods is always contained within the shell; it generally holds the bulk of the digestive, reproductive, excretory, and respiratory systems. A significant part of the visceral hump consists of the mantle, or pallial, cavity. In both prosobranchs and shelled opisthobranchs this is a cavity completely open anteriorly; in pulmonates it is closed except for a narrow pore. The mantle tissue at the forward edge of the cavity secretes the shell. The upper surface of the mantle cavity serves a respiratory function. In marine species the ciliated lining of the mantle cavity helps produce water current that passes posteriorly across the gill, or ctenidium, and the osphradium, which is thought to be a sensory receptor that can detect chemical changes in the environment. Both organs lie on the left anterior side of the cavity. The water current sweeps across the posterior part of the mantle cavity, where the nephridiopore, or kidney opening, lies; the water current then passes anteriorly along the right margin past the anus, through which undigested particles of food are eliminated, and usually moves past the gonopore, through which sexual products are released. Cilia on the gill play an important role in water flow through the mantle cavity; they also help some species (e.g., Crepidula) capture food particles.

The mantle cavity serves as a space for the head and foot when these organs are retracted. Many land pulmonates apparently also use the mantle cavity to retain water. Prosobranchs use the operculum, the horny or calcareous disk located on the back of the foot at the posterior end, to seal the shell opening after the head and body have been retracted.

The Mantle

The mantle is the fleshy lining of the outer wall of the shell; it roofs the mantle cavity. At its anterior end lie glandular tissues that deposit the various shell layers. In terrestrial forms with reduced shells, various lobes and laps extend anteriorly over the neck and head or are reflected back over the shell surface. These are highly vascularized and probably serve both in respiration and in water balance of the body. Many carnivorous marine forms have the mantle collar extended forward and rolled into a muscular siphon, which functions in both food location and chemoreception by allowing the snail to sample water in different directions.

The Head

Generally, the head is bilaterally symmetrical, bearing one or two pairs of tentacles, often with accessory palps, and the mouth in the middle of the ventral margin. In stylommatophoran land snails the upper tentacles, or ommatophores, are invaginable (capable of being rolled in), and the eyes are borne at the tips. In freshwater basommatophorans and most prosobranchs the eyes are located at the base of the tentacles, although in such forms as Strombus the eyes are elevated onto an accessory stalk. Prosobranchs have contractile (not invaginable) tentacles. In carnivorous snails the lateral lips of the mouth form lobes called labial palps, which help to locate prey. The mouth itself frequently is prolonged into a proboscis that extends well in front of the tentacles. Carnivorous species often have a proboscis capable of great extension, either invaginable or contractile.

The Foot

Although the basic form of the foot is a flat, broadly tapered, muscular organ, which is highly glandularized and usually ciliated, numerous modifications occur in various groups. Frequently there is an anterior-posterior division into a propodium and a metapodium, with the former capable of being reflexed over the shell. In Strombus the foot is greatly narrowed; in limpets and abalones it is broadly expanded and serves as an adhesive disk. In pelagic gastropods, especially the heteropods and pteropods, the foot is a swimming organ. Many prosobranchs and some opisthobranchs have lateral projections of the foot called parapodia; they are used in swimming or else are reflexed over the shell surface. An unusual feature found in several kinds of land slugs, some nudibranchs, and the neogastropod marine family Harpidae is the ability to self-amputate the posterior portion of the foot, which remains wriggling violently to distract a predator while the anterior foot and visceral mass creep slowly away to safety.

Nervous System and Sense Organs

A series of paired ganglia (knotlike masses of nerve cell bodies that collectively function as the central nervous system) are connected by nerve cords, which are bilaterally arranged in the primitive forms. The process of torsion has twisted the visceral cords into the form of a figure eight. In more-advanced gastropods there are secondary modifications to a more nearly bilateral state, and in many groups there has been detorsion. Water-dwelling mollusks depend primarily upon ciliary water currents passing across chemoreceptors for information from the environment. The primary chemoreceptors in the gastropod body are scattered over the skin surface, protruding from tentacles or palps, and housed inside the mantle cavity in the form of the osphradium, an olfactory organ connected to the respiratory system. Sense organs are more highly developed in carnivores than in herbivores. Eyespots, located at the base (most gastropods) or tip (land pulmonates) of the eye tentacles, are primarily light-sensitive rather than image-forming. A pair of statocysts, thought to be balancing organs, is present in nonsessile taxa.

Digestive System

The radular motion conveys food particles into the mouth, and ciliary currents move the food through the digestive tract, except in carnivores, where muscular action plays an important role. Various salivary and digestive glands secrete enzymes into either or both the buccal cavity and the stomach, where digestion takes place. The apical digestive gland, or “liver,” can store digested food for use during periods of inactivity.

Excretory System

There are two kidneys, or nephridia, in primitive gastropods, such as the archaeogastropods, while, in the advanced forms, one kidney is small or lost. The kidney plays different roles, depending upon the environment in which the snail lives. Most marine gastropods have the same total concentrations of solutes as in the surrounding seawater, and thus a small osmotic differential (i.e., equilibrium) exists between the water leaving and that entering the cell. Little energy is needed therefore to prevent the cells from losing or gaining too much water. Freshwater gastropods, however, have a higher total solute concentration than that of the surrounding water. The kidney must expend energy to control water balance (osmoregulation). The flow of water through the mantle cavity is restricted in freshwater species by the closure of the mantle cavity by the mantle collar. Land prosobranchs have an open mantle cavity and, in order to conserve water, secrete nearly crystalline urine. Land pulmonates have a ureteric groove or closed ureter that resorbs water from the urine. In both marine and freshwater species, ciliary water currents sweep the excreted matter out of the mantle cavity.

Respiration

In marine and freshwater gastropods, respiration takes place as water currents pass across the gill surfaces within the mantle cavity in most species with spiral shells, across gill elements along the sides of the bodies in most limpets, or through projections from the body surface in sea slugs or other taxa with reduced shells. The upper surface of the mantle cavity is heavily vascularized in land snails, which use muscular contractions to pump air in and out of the small respiratory pore at the anterior edge of the mantle cavity. In some land slugs or tropical snails with reduced shells, a respiratory function have shifted either to external projections from the mantle collar or to the skin as the area of mantle roof available for respiration has decreased in size.

Reproductive System

The primitive archaeogastropods retain two nephridia; the right nephridium provides the passage for eggs or sperm from the ovary or testis to the mantle cavity. The sexes are separate in nearly all prosobranchs, although in a few taxa, such as *Crepidula*, an animal begins life as a male and then changes to a female later. Opisthobranch and pulmonate species are hermaphroditic and often protandrous (male gonads maturing first); however, in many taxa, adults become simultaneous hermaphrodites (male and female gonads are functional at the same time). Internal fertilization is common in the more advanced marine species but mandatory in the freshwater and terrestrial groups.

A very few gastropod species are parthenogenetic (gametes developing without fertilization); the progeny of these species are clones of the parent.

Features of Defense

Warning coloration is found in some of the brilliantly coloured shells and bodies of carnivorous marine snails that produce highly toxic poisons. Similar bright colours characterize some land snails and slugs that secrete noxious chemicals and thus will be sampled only once by a predator. Camouflage coloration provides partial protection against predation by some European land snails.

Evolution and Paleontology

The basic trends in snail evolution (aside from changes in radular and shell morphology) involve a loss of organs, a change from an herbivorous to a carnivorous diet, a shift from the ocean to freshwater and terrestrial life, and the adoption of a sluglike form through reduction or loss of the shell and visceral hump. Each change has occurred independently several times in the course of gastropod evolution.

Prosobranch gastropods are the most primitive. One group, the Diotocardia, which retains two sets of mantle organs, is nearest the generalized gastropod in structure. Gradual loss of the set of mantle organs on the right side of the body occurs in the primitive archaeogastropod superfamilies Trochacea and Neritacea, thus providing a transition to the more highly developed order Monotocardia, with only one set of mantle organs. Among the numerous changes in the Monotocardia are fewer radular teeth and a shift from grazing on algae and fungi to predation and the consumption of larger sessile organisms. The two main divisions of the Monotocardia show different evolutionary patterns. Although most mesogastropods have remained coastal marine, a number of species have invaded freshwater environments. Others crossed to land directly from the tidal zone, rather than passing through a freshwater transitional period. At the peak of prosobranch evolution is the order Neogastropoda, all marine predators with highly modified radular teeth and often well-developed poison glands to aid in capturing prey. Reduction and loss of the right mantle organs are correlated with more efficient respiration and sensory apparatuses, in which a water current crosses over the sensory organs and gills on the left side, then out on the right side, together with excretory and fecal deposits. Gill cilia are largely responsible for creating these water currents.

Opisthobranchs probably arose from an unknown group of primitive prosobranchs and have evolved extensively into different lines showing a reduction of the visceral hump and shell. In certain forms the foot is shortened, and external cerata develop to provide a respiratory surface to replace the lost mantle-cavity surface and ctenidia. Members of family Pyramidellidae (order Heterostropha) contain a mixture of prosobranch and opisthobranch characteristics.

Pulmonates show varying degrees of adjustment to freshwater and land life, with increasing union of the male and female gonoducts characterizing the more advanced groups. Similarly, the highly advanced suborder Holopoda and superfamily Limacacea show complex accessory organs on the genitalia and a more sophisticated means of water conservation through development of a closed secondary ureter and resorption of water from the excretory products. More than a dozen different groups of pulmonates have become predators, usually upon other snails or earthworms.

Fossil gastropods are known from Cambrian deposits. Since the shell is often very similar in unrelated families, fossil gastropods more than 350 million years old are not usually placed in the classification outlined below but instead are treated separately. Most neogastropod prosobranchs appeared near the end of the Mesozoic (65.5 million years ago), and many groups of land snails are known from Eocene formations (roughly 56 million to 34 million years old). Snails had their adaptive radiation early in geologic history. Living genera of marine, freshwater, and land snail families are known from Oligocene to Miocene deposits (33.9 million to 5.3 million years old). Unlike mammals, which have undergone great evolutionary change in the last 50 million years, gastropods have shown little progressive evolution during that time.

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6

Other Invertebrate Phyla

There are a number of invertebrate phyla, apart from the ones which have been discussed in the previous chapters. Some of these are Porifera and Annelida. The chapter closely examines these invertebrate phyla to provide an extensive understanding of the subject.

Porifera

This group of animals is probably considered as the oldest animal group. They are also called as Sponges. These are by far the simplest multicellular animals. Even though they are multicellular, they do not have any tissues or organs. Sponges live in an aquatic habitat as they have to have an intimate contact with water. Water plays a major role in the feeding, exchange of gases and as well as excretion. The body of the sponges has many holes or pores called ostia. The body structure of sponges is designed in such a way that water moves through the body, where it can filter out food and also absorb the dissolved oxygen, along with eliminating waste material.

Organisms belonging to this phylum do not have specialised digestive, nervous or circulatory system. Instead, they have a water transport or canal system, which achieves the functions of digestion, excretion and also an exchange of gases.

Their bodies do not show any symmetry and their shape is adapted so as to allow maximum efficiency of water flow through the central cavity that is present inside. They generally feed on bacteria and other food particles that are present in the water. Their bodies have a large central cavity called the spongocoel. Water enters through the ostia into the spongocoel and goes out through the osculum. Cells called as Choanocytes or collar cells line up the spongocoel and canals, with their flagellum protruding out. It is the beating of this flagellum from all choanocytes that moves the water all through the body of the sponge.

Characteristic Features of Phylum Porifera

- They are generally marine aquatic organisms, with a few freshwater species.
- Their bodies are asymmetrical.
- Body shape can be cylindrical, vase-like, rounded or sac-like.

- They are diploblastic animals with two layers, the outer dermal layer and the inner gastral layer. There is a gelatinous, non-cellular mesoglea, in between these two layers. This contains many free amoeboid cells.
- The body has many pores called the ostia and a single large opening called osculum at the top.
- Spongocoel is the body cavity that is present.
- They have the characteristic canal system for the flow of water through the body.
- Sense organs are absent.
- There is an endoskeleton present with calcareous spicules (calcium carbonate) or siliceous spicules (silica) or sponging fibres (protein).
- Sexes are not separate.
- Asexual reproduction is seen through budding, fragmentation. Sexual reproduction is seen in certain species, through gametic fusion.

Examples:

- Sycon (Scypha).
- Spongilla (Freshwater sponge).
- Euspongia (Bath sponge).

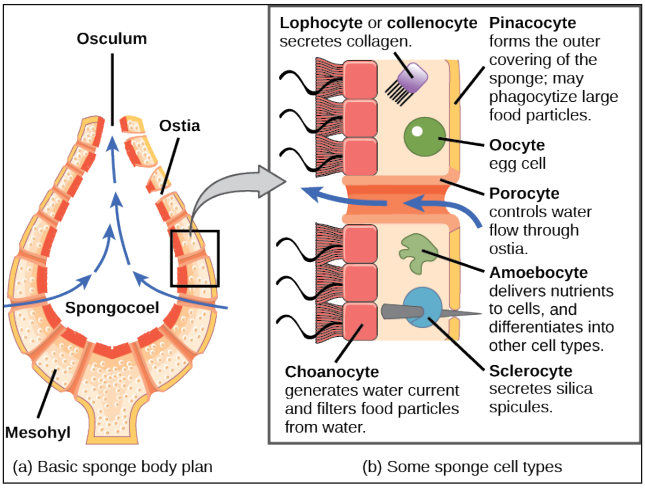
Morphology of Sponges

The morphology of the simplest sponges takes the shape of a cylinder with a large central cavity, the spongocoel, occupying the inside of the cylinder. Water can enter into the spongocoel from numerous pores in the body wall. Water entering the spongocoel is extruded via a large common opening called the osculum. However, sponges exhibit a range of diversity in body forms, including variations in the size of the spongocoel, the number of osculi, and where the cells that filter food from the water are located.

While sponges (excluding the hexactinellids) do not exhibit tissue-layer organization, they do have different cell types that perform distinct functions. Pinacocytes, which are epithelial-like cells, form the outermost layer of sponges and enclose a jelly-like substance called mesohyl. Mesohyl is an extracellular matrix consisting of a collagen-like gel with suspended cells that perform various functions. The gel-like consistency of mesohyl acts like an endoskeleton and maintains the tubular morphology of sponges. In addition to the osculum, sponges have multiple pores called ostia on their bodies that allow water to enter the sponge. In some sponges, ostia are formed by porocytes, single tube-shaped cells that act as valves to regulate the flow of water into the spongocoel. In other sponges, ostia are formed by folds in the body wall of the sponge.

Choanocytes (“collar cells”) are present at various locations, depending on the type of sponge, but they always line the inner portions of some space through which water flows (the spongocoel in simple sponges, canals within the body wall in more complex sponges, and chambers scattered throughout the body in the most complex sponges). Whereas pinacocytes line the outside of the sponge, choanocytes tend to line certain inner portions of the sponge body that surround the mesohyl. The structure of a choanocyte is critical to its function, which is to generate a water current through the sponge and to trap and ingest food particles by phagocytosis. Note the similarity in appearance between the sponge choanocyte and choanoflagellates (Protista). This similarity suggests that sponges and choanoflagellates are closely related and likely share a recent common ancestry. The cell body is embedded in mesohyl and contains all organelles required for normal cell function, but protruding into the “open space” inside of the sponge is a mesh-like collar composed of microvilli with a single flagellum in the center of the column. The cumulative effect of the flagella from all choanocytes aids the movement of water through the sponge: drawing water into the sponge through the numerous ostia, into the spaces lined by choanocytes, and eventually out through the osculum (or osculi). In the meantime, food particles, including waterborne bacteria and algae, are trapped by the sieve-like collar of the choanocytes, slide down into the body of the cell, are ingested by phagocytosis, and become encased in a food vacuole. Lastly, choanocytes will differentiate into sperm for sexual reproduction, where they will become dislodged from the mesohyl and leave the sponge with expelled water through the osculum.

The second crucial cells in sponges are called amoebocytes (or archaeocytes), named for the fact that they move throughout the mesohyl in an amoeba-like fashion. Amoebocytes have a variety of functions: delivering nutrients from choanocytes to other cells within the sponge, giving rise to eggs for sexual reproduction (which remain in the mesohyl), delivering phagocytized sperm from choanocytes to eggs, and differentiating into more-specific cell types. Some of these more-specific cell types include collencytes and lophocytes, which produce the collagen-like protein to maintain the mesohyl, sclerocytes, which produce spicules in some sponges, and spongocytes, which produce the protein spongin in the majority of sponges. These cells produce collagen to maintain the consistency of the mesohyl. The different cell types in sponges are shown in figure.

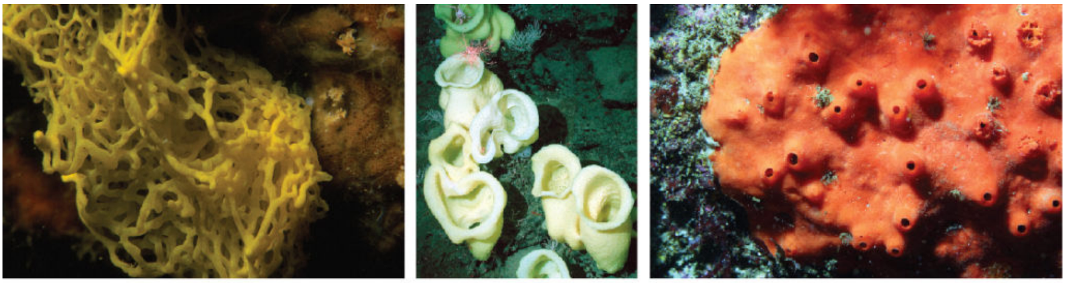


(a) Basic sponge body plan (b) Some sponge cell types

The sponge's (a) basic body plan and (b) some of the specialized cell types found in sponges are shown.

In some sponges, sclerocytes secrete small spicules into the mesohyl, which are composed of either calcium carbonate or silica, depending on the type of sponge. These spicules serve to provide additional stiffness to the body of the sponge. Additionally, spicules, when present externally, may ward off predators. Another type of protein, spongin, may also be present in the mesohyl of some sponges.

The presence and composition of spicules/spongin are the differentiating characteristics of the three classes of sponges: Class Calcarea contains calcium carbonate spicules and no spongin, class Hexactinellida contains six-rayed siliceous spicules and no spongin, and class Demospongia contains spongin and may or may not have spicules; if present, and those spicules are siliceous. Spicules are most conspicuously present in class Hexactinellida, the order consisting of glass sponges. Some of the spicules may attain giant proportions (in relation to the typical size range of glass sponges of 3 to 10 mm) as seen in Monorhaphis chuni, which grows up to 3 m long.


(a) (b) (c)

(a) Clathrina clathrus belongs to class Calcarea, (b) Staurocalyptus spp. (common name: yellow Picasso sponge) belongs to class Hexactinellida, and (c) Acarnus erithacus belongs to class Demospongia.

Physiological Processes in Sponges

Sponges, despite being simple organisms, regulate their different physiological processes through a variety of mechanisms. These processes regulate their metabolism, reproduction, and locomotion.

Digestion

Sponges lack complex digestive, respiratory, circulatory, reproductive, and nervous systems. Their food is trapped when water passes through the ostia and out through the osculum. Bacteria smaller than 0.5 microns in size are trapped by choanocytes, which are the principal cells engaged in nutrition, and are ingested by phagocytosis. Particles that are larger than the ostia may be phagocytized by pinacocytes. In some sponges, amoebocytes transport food from cells that have ingested food particles to those that do not. For this type of digestion, in which food particles are digested within individual cells, the sponge draws water through diffusion. The limit of this type of digestion is that food particles must be smaller than individual cells.

All other major body functions in the sponge (gas exchange, circulation, excretion) are performed by diffusion between the cells that line the openings within the sponge and the water that is passing through those openings. All cell types within the sponge obtain oxygen from water through diffusion. Likewise, carbon dioxide is released into seawater by diffusion. In addition, nitrogenous waste produced as a byproduct of protein metabolism is excreted via diffusion by individual cells into the water as it passes through the sponge.

Reproduction

Sponges reproduce by sexual as well as asexual methods. The typical means of asexual reproduction is either fragmentation (where a piece of the sponge breaks off, settles on a new substrate, and develops into a new individual) or budding (a genetically identical outgrowth grows from the parent and eventually detaches or remains attached to form a colony). An atypical type of asexual reproduction is found only in freshwater sponges and occurs through the formation of gemmules. Gemmules are environmentally resistant structures produced by adult sponges wherein the typical sponge morphology is inverted. In gemmules, an inner layer of amoebocytes is surrounded by a layer of collagen (spongin) that may be reinforced by spicules. The collagen that is normally found in the mesohyl becomes the outer protective layer. In freshwater sponges, gemmules may survive hostile environmental conditions like changes in temperature and serve to recolonize the habitat once environmental conditions stabilize. Gemmules are capable of attaching to a substratum and generating a new sponge. Since gemmules can withstand harsh environments, are resistant to desiccation, and remain dormant for long periods, they are an excellent means of colonization for a sessile organism.

Sexual reproduction in sponges occurs when gametes are generated. Sponges are monoecious (hermaphroditic), which means that one individual can produce both gametes (eggs and sperm) simultaneously. In some sponges, production of gametes may occur throughout the year, whereas other sponges may show sexual cycles depending upon water temperature. Sponges may also become sequentially hermaphroditic, producing oocytes first and spermatozoa later. Oocytes arise by the differentiation of amoebocytes and are retained within the spongocoel, whereas spermatozoa result from the differentiation of choanocytes and are ejected via the osculum. Ejection of spermatozoa may be a timed and coordinated event, as seen in certain species. Spermatozoa carried along by water currents can fertilize the oocytes borne in the mesohyl of other sponges. Early larval development occurs within the sponge, and free-swimming larvae are then released via the osculum.

Locomotion

Sponges are generally sessile as adults and spend their lives attached to a fixed substratum. They do not show movement over large distances like other free-swimming marine invertebrates. However, sponge cells are capable of creeping along substrata via organizational plasticity. It must be noted, however, that this pattern of movement has been documented in laboratories, but it remains to be observed in natural sponge habitats.

Leucosolenia

Leucosolenia, also spelled Leucoselenia is the genus of tubular branched sponges of the class Calcispongiae (phylum Porifera). Found in tide pools and on wharves and represented by numerous species, the widespread genus includes most of the asconoids, structurally the simplest sponges.

Most species of Leucosolenia are 2.5 centimetres (one inch) or less in length. They grow as a colony of slender individuals connected by a common stolon—i.e., a rootlike process—which also attaches the group to the bottom or to some other surface. Water—which enters the central cavity (spongocoel) of the animal through numerous tiny perforations—is expelled through one large opening, the osculum, at the tip. The water current is created by flagella attached to choanocytes. Choanocytes are cells that line the spongocoel (that is, the central cavity of the sponge). The outer body wall consists of thin, flat cells called pinacocytes. Between the two cell layers is a jellylike matrix, the mesoglea, which usually contains freely moving cells (amoebocytes) and skeletal spicules often shaped like slender three- or four-pointed stars. The spicules, which provide support for the body tube, are produced by special amoebocytes.

New individuals usually develop as free-swimming flagellated larvae from eggs produced by amoebocytes. These larvae are released through the osculum of the parent. They eventually attach themselves permanently to new surfaces and metamorphose into tiny sponges. Some leucosolenids—for example, L. botryoides—also may reproduce by budding, a process in which a fingerlike extension of the parent body breaks off. The tip of the extension becomes the lower end of the new individual when it attaches to a new site.

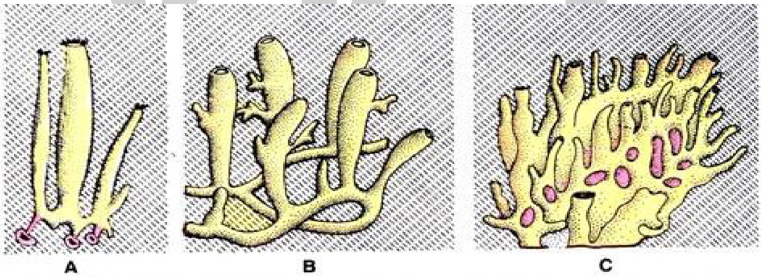
Habit, Habitat and Distribution of Leucosolenia

Leucosolenia is a small, delicate branching, colonial marine sponge. It grows in shallow water below low tide mark on sea shore rocks where wave action is intense and is not found in calm water. Leucosolenia is found abundantly along the northern Atlantic coast and is supposed to be very sensitive to external conditions.

About 100 species of Leucosolenia have been reported from different seas all over the world. However, L. botryoides, L. complicata and L. variabilis are common species.

Structure of Leucosolenia

The colony of Leucosolenia is whitish yellow in colour. In the simplest species of Leucosolenia, the colony consists of few simple vase-like, cylindrical individuals each terminating in an osculum and united at their bases by irregular horizontal tubes. Most species are more complicated, consisting of a confused network of branching tubes from which stand out a few larger erect cylinders bearing an osculum at their summit.



Types of Leucosolenia: A- Simple, B-Branching, C-Reticulate.

Leucosolenia-a branched colony.

Leucosolenia complicata.

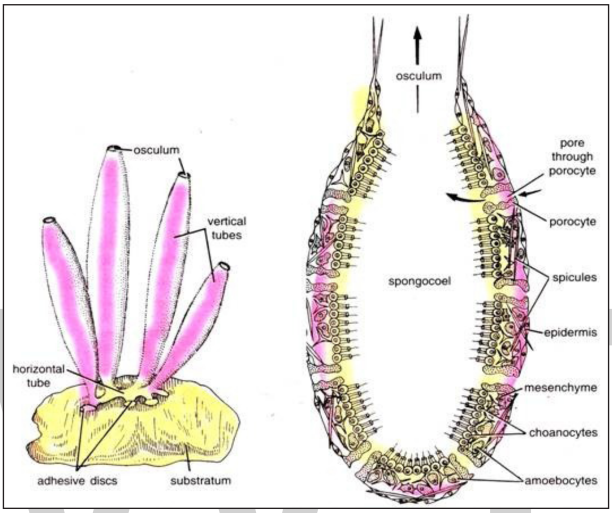
Osculum of leucosolenia.

Leucosolenia variabilis.

Leucosolenia botryoides.

Finally, in the most complicated species, the outermost tubes fuse together forming a false surface or pseudoderm leaving a few large openings or pseudo pores so that the sponge appears solid and simulates a higher type of sponge; but sections show the network of ascon tubes in the interior.

Each tube of the colony may reach up to 25 mm in height and also produces a number of buds. Each main tube opens to the exterior by an aperture called osculum at the summit. The cavity of the tube is known as spongocoel or paragastric cavity.



Leucosolenia colony (left). Leucosolenia:Longitudinal section(right).

Body Wall

The body wall is thin and consists of an outer epidermis,the pinacoderm and an inner endodermis, the choanoderm separated by a jelly-like non-cellular layer of mesenchyme or mesogloea, enclosing a central cavity, the spongocoel. The wall of each tube is perforated by numerous pores through which water enters the spongocoel and passes out by osculum.

(i) Pinacoderm: The outer epidermis consists of thin, scale-like, flattened cells, called pinacocytes, which lie with the edges touching and forming a single layer of cells, the pinacoderm. This layer forms the outer protective covering of the tube. A pinacocyte has thin highly contractile margins and contains a central bulging having nucleus.

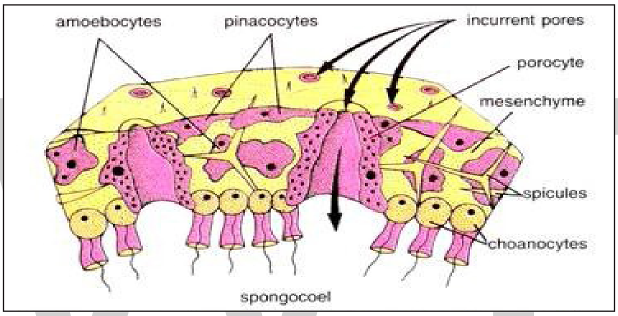
(ii) Choanoderm: The inner epithelium consists of a single layer of choanocyte cells and forms the lining of the spongocoel and also referred to as gastrodermis. A choanocyte is an oval cell having a flagellum which arises from basal granule and is surrounded at its base by a contractile transparent protoplasmic collar.

The nuclei of choanocytes lie at the bases of cells. The beating of the flagella of choanocyte cells maintains water current in the body of sponge.

(iii) Mesenchyme or Mesogloea: Mesenchyme is the intermediate layer between the pinacoderm and choanoderm. Mesenchyme is a thin layer and is in the form of gel. It is secreted by the choanocytes and it holds the skeletal elements of $CaCO_3$ called spicules or sclerites in place. In the mesenchyme are some amoebocytes which are amoeboid cells, they wander about freely. These cells contain RNA and self- replicating in nature.

These cells can give rise to different types of cells, hence, totipotent in action; they may give rise to pinacocytes, choanocytes, collencytes, sclerocytes or scleroblasts and reproductive cells. The spicules are crystalline; needle-like which are monaxons, tetraxons (having four rays) or triaxons.

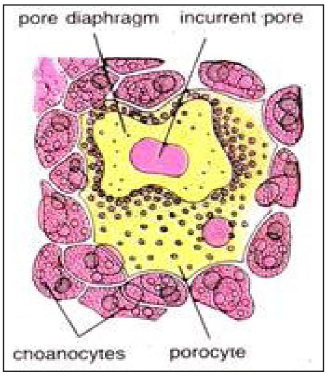
The spicules are scereted by scleroblast cells and remain embedded in the mesenchyme and some monaxon spicules project out of the pinacoderm. A few monaxon spicules form a scanty fringe around the osculum.



Leucosolenia: Diagrammatic cross section of a portion of body wall highly magnified to show the cellular structure.

Ostia

The wall of each tube is pierced or perforated by numerous pores called ostia or incurrent pores which pass through a space or lumen of cells called porocytes. The porocytes are supposed to be modified pinacocytes. Each ostium or incurrent pore is intracellular, i.e., it is a canal through a single, large, tubular and highly contractile porocyte cell communicating outside with the spongocoel.



Leucosolenia: Porocyte with sourounding choanocytes.

Physiology of Leucosolenia

No adult sponge is capable of locomotion, and some are quite devoid of contractile powers, except for changes in the porocytes. Most do have at least local contractile powers that appear to be restricted to within 3 or 4 mm of the point of strong stimulus. Reactions are most noticeable when stimuli are applied to the region of the osculum.

All reactions are slow and one to several minutes elapses before the responses become noticeable. Sponges are devoid of sensory or nerve cells, the contractile responses mentioned above are, therefore, direct reactions to stimuli.

Under normal conditions all the apertures (ostia and oscula) of a sponge are widely open and a current of water flows in through the incurrent openings or ostia and out through the osculum. The water currents are caused by the beating of the flagella of the choanocytes.

This flow brings food and provides opportunity for gaseous exchange and the elimination of metabolic wastes. The structure of sponge is such that the flow of water passes the choanocyte areas quite slowly.

The food comprises the plankton—microscopical animals and plants and bits of organic matter. It appears that food particles adhere to the collars or are caught between the collars of adjacent choanocytes. The food particles are ingested into the choanocytes or passed directly into underlying amoebocytes. Some observers think that food particles are also taken in through the epidermal cells.

Digestion is always intracellular, as in Protozoa, occurring in food vacuoles which are acidic at first and alkaline later. Un-digestible particles are ejected from the amoebocytes and find their way into the outgoing currents.

Several enzymes have been identified in sponge extracts: Protein-digesting enzymes similar to trypsin, pepsin, rennin and erepsin; lipase; invertase; and amylase in some cases.

Since sponges usually contain bacteria and other organisms, it is not clear that the enzymes in question really come from the cells of sponge. Digested food is stored in certain amoebocytes as glycogen, glycoproteins and lipoproteins. Respiration and elimination of metabolic wastes are accompanied by osmosis without the aid of special structures.

Reproduction of Leucosolenia

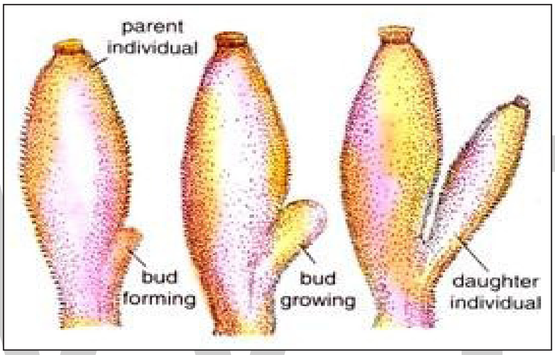
Leucosolenia reproduces both asexually and sexually.

(i) Asexual Reproduction: Leucosolenia reproduces asexually by budding. In budding, Leucosolenia sprouts new horizontal branches which grow over rocks and other substrata and give rise to erect vase-shaped individuals. When the upright branches attain sufficient size their tops break through as oscula.

Leucosolenia has also remarkable power of regeneration. Any piece of broken Leucosolenia is capable of growing into a complete individual. This process is slow, and months or even years may be required before size is attained.

(ii) Sexual Reproduction: Sexual reproduction takes place by the formation of gametes, i.e., ova and sperms. Leucosolenia is hermaphrodite, because both the gametes are formed in the body of same individual, though gonads are altogether absent. The gametes are, however, formed by the differentiation (say, gametogenesis) of amoebocyte cells.

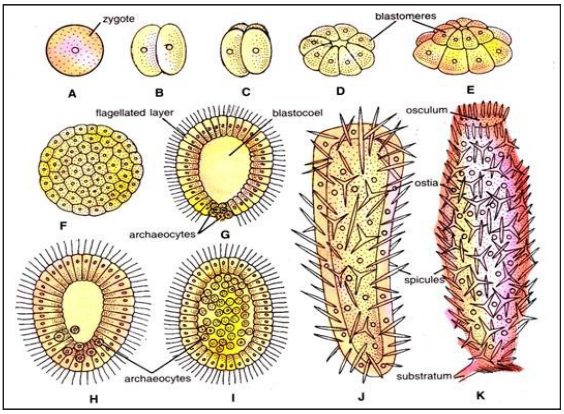
Cross-fertilisation occurs, which is internal. The sperms are drawn in the body of Leucosolenia with the water current which fertilize the ova. The development of Leucosolenia have been described by Metschnikoff and Minchin.



Leucosolenia: Diagram showing stages in budding.

Development of Leucosolenia

The fertilised egg undergoes equal and holoblastic cleavage to form an oval hollow blastula, called coeloblastula. The coeloblastula is composed entirely of a narrow flagellated cell except at the posterior pole, where there is a group of rounded non-flagellated cells. These are believed to be archaeocytes which form all future archaeocytes of the sponge.



Leucosolenia: Stages in development. A-Zygote; B to E-cleaving stages; F-Early blastula; G and H-Coeloblastula; I-Parenchymula; J-Young sponge; K-Adult sponge.

These together with adjacent flagellated cells (which thereupon lose their flagella) wander into the interior and fill it with a mass of cells. The resulting larva is, thus, a stereogastrula or parenchymula and ah inner mass of amoeboid cells.

The parenchymula swims freely for some hours. Then it attaches by the anterior pole and develops into a flat plate with an irregular outline. The amoeboid cells (interior cells) migrate to the external surface and form the epidermis (pinacoderm) and mesenchyme.

The flagellated cells are, thus, enclosed and become the choanocytes. A central spongocoel appears, an osculum breaks through, and spicules are secreted. After a few days of attachment, the larva is converted into the adult asconoid sponge.

Scypha

Scypha, also called sycon is the Scypha, also called sycon, genus of marine sponges of the class Calcarea (calcareous sponges), characterized by a fingerlike body shape known as the syconoid type of structure. In the syconoid sponges, each “finger,” known as a radial canal, is perforated by many tiny pores through which water passes into a single central cavity. The water exits through an oscule, or larger opening, at the tip. Water is driven through the sponge by the beating of many hairlike cilia lining the central cavity. Scypha species grow to only about 2 or 3 cm (about 1 inch) in length.

Habit, Habitat and Distribution of Scypha

Scypha, also known as crown sponge, is a small, marine sponge found attached by a sticky secretion to some submerged solid object like rocks, shells of molluscs and corals. It is found in shallow water up to a depth of 50 fathoms (1 fathom = 6 feet) where waves provide the animal with plenty of food and well oxygenated water.

It is a branching colonial sponge, though solitary individuals are also found. Scypha is widely distributed and found in abundance near North Atlantic shores. The different species of Scypha are S. ciliatum, S. elegans, S. coronata, S. lingua, S. gelatinosum and S. raphanus.

External Features of Scypha

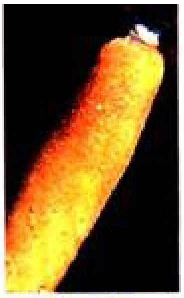
Scypha is vase-shaped and is 2.5 to 7.5 cm in length. It has several cylinders; all the cylinders are connected at the base by which it is attached by a sticky secretion to some submerged solid object in the sea. It is grey or light brown in colour. The distal or free end of each cylinder has a single large opening, the osculum or exhalent or ex-current pore.

The osculum is encircled by an upstanding collar of long monaxon spicules termed the oscular fringe looking like a crown; hence, the name crown sponge is given to it. It prevents the entry of other animals into the sponge; below the osculum is a short, narrow collar region.

The body of the sponge is covered externally by a thin dermal epithelium or ectoderm. The surface of a cylinder has polygonal elevations, and between the elevations are depressed lines, in the depressions are groups of ostia which are inhalant or incurrent pores. These are intercellular apertures and not intracellular as in Leucosolenia.

Inside each cylinder is a spongocoel (Gr., spongos = sponge; koilos = hollow) or Para gastric cavity which is not digestive cavity. The wall of the cylinder is thick due to increase in the amount of mesogloea, the wall has folded in such a way as to form two types of canals, the incurrent canals and radial canals, they lie alternately and radially around the spongocoel,but ostia and canals are absent from the collar and basal regions.

Scypha ciliata.

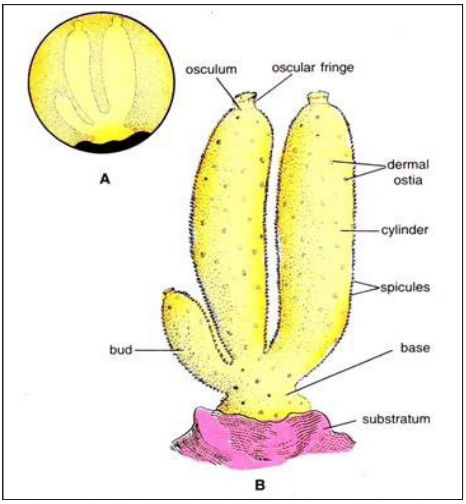


Scypha.

Scypha lingua.

Canal System of Scypha

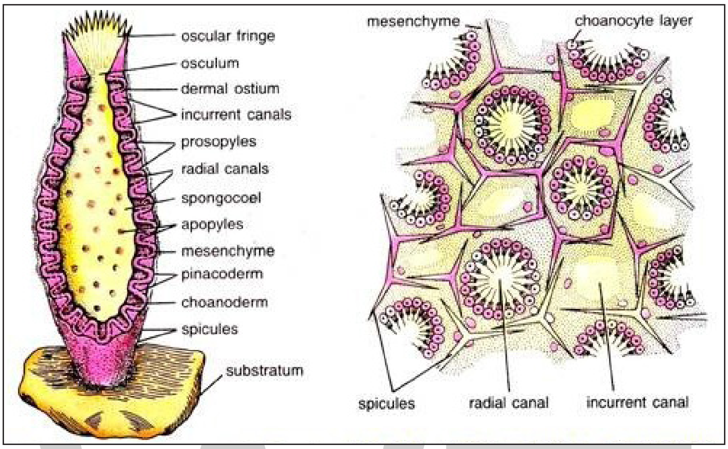
Scypha, like all other sponges, possesses the characteristic peculiarity-the canal system. The sponge body is traversed by numerous canals of several types' which together form the canal system. It plays a very important role in the life of Scypha like those of other sponges. The particular type of canal system found in Scypha is known as syconoid type which is more advanced than the asconoid type.



Scypha: A-Colony in natural size; B-Colony magnified.

It consists of the following:

(i) Spongocoel: If the cylindrical body of Scypha is cut open longitudinally, it shows that osculum leads into a narrow tubular cavity called the Para gastric cavity or spongocoel. The spongocoel is lined with thin, gastral ectodermal cells called, pinacocytes.

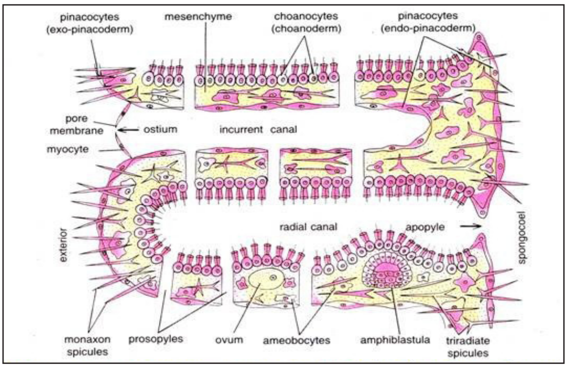


Scypha: A diagrammatic L.S. of a cylinder showing gross internal structure (left).
Scypha cylinder. Diagrammatic V.S. thorugh the wall (right).

(ii) Radial or Flagellated Canals: The thick body wall lining the spongocoel contains many finger-like, straight outpushings at regular intervals called radial or flagellated canals. The radial canals are lined with flagellated collar cells or choanocytes. Each radial canal appears octagonal in cross section.

The radial canals are closed at their outer ends towards the surface of cylinder but at their inner ends each communicates with a small wide ex-current canal by an aperture called apopyle or internal ostia which joins the spongocoel.

(iii) Ex-Current Canal: The ex-current canal is a short and wide passage between the radial canal and spongocoel. It leads radial canal into the spongocoel. The ex-current canals are lined with flat ectodermal cells like the spongocoel. The broad connection between the ex-current canal and the spongocoel is called the gastric ostium.



Scypha: A diagrammatic sectional view of the body wall showing one incurrent and one radial canal.

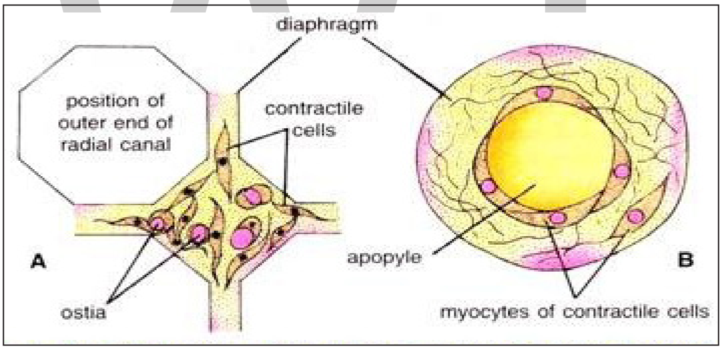
Between the radial canal and ex-current canal is a thin diaphragm perforated by large hole called apopyle. The apopyle is surrounded by contractile myocytes due to which it can contract or dilate.

(iv) Incurrent Canals: In between the two successive radial canals, a tubular space called incurrent canal is present. Thus, radial canals and incurrent canals are arranged alternately.

The incurrent canals are narrow passages somewhat square in section. The incurrent canals open to the exterior between the blind outer ends of the radial canals by apertures termed dermal ostia (L., ostium = door) or dermal pores. Incurrent canals are lined by flat ectodermal cells called pinacocytes like the spongocoel.

Externally an incurrent canal is covered by a pore membrane pierced by 3 or 4 ostia which are intercellular (in Leucosolenia the ostia are intracellular). The incurrent canals end blindly, at their inner ends, not reaching the spongocoel. Between the incurrent canal and spongocoel, the mesogloea is specially thickened to form the gastral cortex.

The incurrent and radial canals run side by side. The wall between the incurrent and radial canals is pierced by numerous minute pores called prosopyles (Gr., pros = near, pyle = gate). The prosopyles are perforations in porocytes. The porocytes are tubular contractile cells formed from modified pinacocytes.



Scypha: A-Magnified surface view of pore membrane showing ostia;
B-An apopyle surrounded by its diaphragm.

The circulation of water in Scypha takes place in the following way. The water enters into the incurrent canals through the ostia, passes into the radial canals through prosopyles and from radial canals into the spongocoel by apopyles and leaves the spongocoel by terminal osculum.

In other way, the course of water into the canal system can be represented as water from outside → dermal ostia → incurrent canals prosopyles → radial canals → apopyles → spongocoel → osculum → outside.

Histology (Microscopic Structure) of Scypha

All sponges are diploblastic, i.e., their body wall is composed of two layers with an intermediate mesenchyme or mesohyl. The pinacoderm consisting of exopinacoderm covering the body surface except ostia and osculum and endopinacoderm lining the incurrent canals and spongocoel.

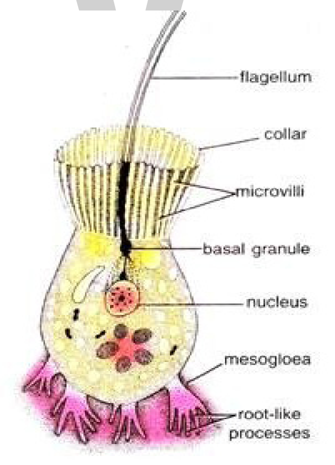
It is made of thin, large and polygonal, scale-like pinacocytes. Pinacocytes are ectodermal in origin and lie with their edges touching so that they form a loose layer and also line the incurrent canals.

The choanoderm forming gastral epithelium, lining the radial canals, consists of single layer of large choanocytes or collar cells which are endodermal in origin and were discovered by James Clark.

The choanocytes are rounded or oval cells whose base rests upon the mesenchyme, while the free end bears a transparent contractile collar encircling the base of the single long flagellum. A choanocyte also contains a nucleus, a contractile vacuole and food vacuoles.

The electron microscopic structure of a choanocyte reveals the presence of all cellular organelles like mitochondria, Golgi apparatus, endoplasmic reticulum, ribosomes, etc., in it. Its collar is formed by 20-30 cytoplasmic processes called microvilli which are contractile in nature.

The microvilli are often connected together side by side. The flagellum consists of usual pattern of fibrils in 9 + 2 and originates from basal granule or kinetosome. The choanocyte cell has root-like processes embedded in the mesenchyme.



A Choanocyte cell as seen under electron microscope.

Between the dermal epidermis and endoderm is an intermediate layer, the mesenchyme. The mesenchyme consists of a gelatinous transparent matrix, commonly called mesogloea or mesohyl, presumably of a protein nature, in which free amoeboid cells or amoebocytes wander about.

When there are much mesogloea and relatively few cells, the mesenchyme is termed collenchyma; when the cells are numerous, the name parenchyma is applied. The mesenchyme is like a gel and holds the spicules in place.

Sponge Cells or Cellular Elements of Scypha's Body

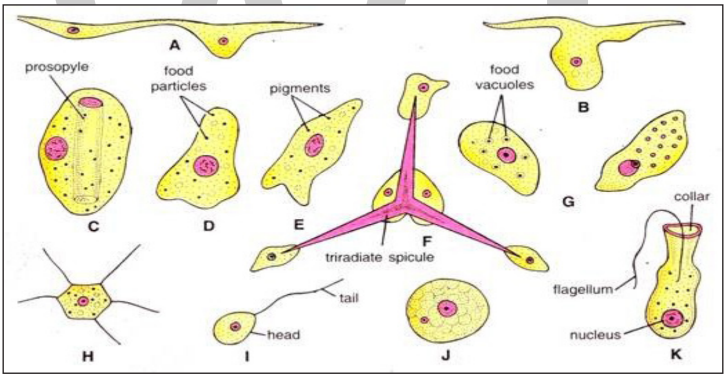
There are several types of cells found in sponges which are not organised into well-defined tissues, the cells form loose collections and they act more or less independently of each other.

The sponge cells are as follows:

1. Pinacocytes are thin polygonal scale-like cells, they are large and flat with a central nucleus, they lie with their edges touching, and they are highly contractile. Contractions or expansions of the edges of pinacocytes can slightly decrease or increase the size of the entire sponge.

Pinacocytes form the external dermal layer, they line the incurrent canals, and in some they also line the spongocoel. The external pinacocytes are spoken of as "ectoderm" and those lining the spongocoel as "endoderm".

2. Porocytes or pore cells are modified pinacocytes, they are large-size contractile cells; through the porocyte runs a large perforation called prosopyle which connects an incurrent canal to a radial canal or to a flagellated chamber.



Scypha: Cellular elements. A-Pinacocytes; B-Myocyte; C-Porocyte; D-Thesocyte; E-Chromocyte; F-Scleroblast; G-Archeocytes; H-Collencyte; I-Sperm; J-Ovum; K-Choanocyte.

3. Choanocytes or flagellate endoderm cells are large, oval, nucleated cells, each with a contractile vacuole and some food vacuoles; at one end is a long flagellum arising from a basal granule, the basal granule is joined to centriole and the two together are called a centroblepharoplast which controls the movements of the flagellum. Below this is a parabasal body joined by a fibril to the centroblepharoplast and the nucleus.

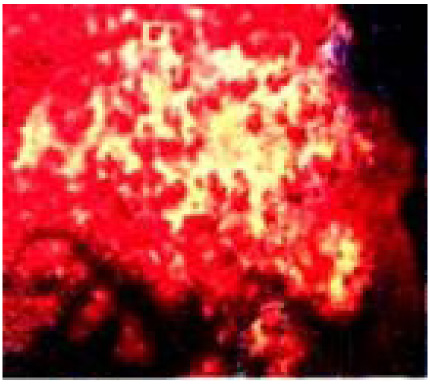
The flagellum has two central fibrils and nine double peripheral fibrils; it is surrounded at its base by a transparent contractile collar made of a ring of erect and closely set microvilli which project from the cell. Choanocytes form a layer of adjacent cells in radial canals or flagellated chambers of sponges; the movement of their flagella causes a current of water. Choanocytes are endodermal in origin.

4. Amoebocytes are amoeboid cells with pseudopodia, they wander about freely in the mesogloea, they are modified to form the following types of cells:

1. Collencytes have several slender, long, branching pseudopodia; the branches are like connective tissue cells in the mesogloea.
2. Archeocytes are large amoebocytes, they have a few blunt pseudopodia, the nucleus is large, they are generalized cells and they transport food and waste substances. They can give rise to other types of amoebocytes, and they form sperms, eggs and asexual reproductive bodies called gemmules, such cells which can change into almost any kind of cell within an animal are said to be totipotent.
3. Chromocytes are pigmented amoebocytes having lobose pseudopodia. They probably impart colouration to the body of sponge.
4. Thesocytes are amoebocytes having lobose pseudopodia like chromocytes but filled with food reserves. Thus, these cells work as storage cells.
5. Trophocytes are found loaded partly or completely with digested food and serve to transfer it; from one place to other.
6. Phagocytes collect food from choanocytes through their pseudopodia and also engulf excreta and damaged tissues.
7. Myocytes are fusiform contractile cells, they form a sphincter around apertures, such as oscula and apopyles where they act like muscles to open or close these apertures, they show some similarity to involuntary muscles in shape and contractility.
8. Scleroblasts are amoebocytes in the act of secreting the skeleton of a sponge. They are called calcoblasts if they secrete calcareous spicules or silicoblasts if they secrete siliceous spicules or spongioblasts if they secrete spongin fibres.
9. Gland cells are amoeboid with a long strand at one end, they are found attached by their strands to the surface of a sponge, and they secrete slime.
10. Germ cells are male and female gametes (sperm and ova) differentiate from archeocytes cells. In some cases, the germ cells are said to be differentiated from choanocytes.

Skeleton of Scypha

In Scypha the skeleton consists of calcareous spicules. The spicules or sclerites are definite bodies, having a crystalline appearance and consisting in general of simple spines or of spines radiating from a point. They have an axis of organic material around which is deposited the inorganic substance either calcium carbonate or hydrated silica. Spicules present a great variety of shape.

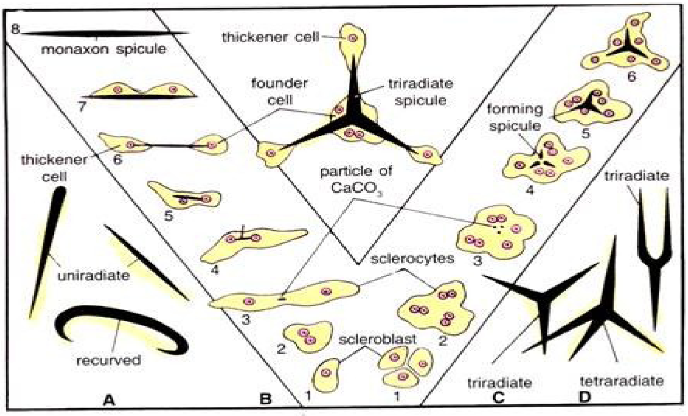


Calcareous spicules.

In Scypha the spicules have a definite arrangement with regard to its canal system and are of the following types:

1. Large one rayed needle-like monaxon spicules are arranged in a circlet around the osculum.
2. Simple spear-like monaxon spicules project from dermal cortex opposite the outer ends of the radial canals.
3. Three rayed or triaxon spicules are present along the radial canals with their one end pointing towards the distal ends of the canals.
4. Four rayed or tetraxon spicules are present, along with triaxon spicules in the thick gastral cortex surrounding the spongocoel. In the body of Scypha, the monaxon spicules project from the body surface and may be needle-like or spear-like, while the triradiate spicules lie embedded inside forming a network.

On the outer surface the monaxon spicules project in masses from the polygonal elevations where they partly conceal and protect the ostia, each group of these spicules is collectively called oxeote spicules.



Scypha: Structure and development of spicules. A-kinds of monaxon spicules'; B-Development of monaxon spicules; C-Development of triaxon spicules; D-king of triradiate spicules.

Water Current of Scypha

Water current plays a very important role in the physiology of the sponges. The current of water brings in food and oxygen and it takes away waste products. Under normal conditions all the apertures of a sponge are widely open and a current of water flows through the animal and out at the oscula.

The water current is caused by the beating of the flagella of the choanocytes, but as the flagella do not beat in coordination, the way in which a current of water is produced is not clearly understood. The most plausible explanation is that of Van Tright based on observations of thin expansion of freshwater sponges.

The flagellar movement consists of a spiral undulation passing from base to tip and creating a water current in the same direction.

As the choanocytes in each flagellated chamber are grouped near the prosopyle with their collars more or less pointed towards the apopyle, the water currents tend to flow from the flagellar tips towards the apopyle. The mechanism will obviously be more effective when the apopyles are larger than prosopyles, as is usually the case in sponges, since the water will tend to seek the larger outlet.

The water current enters the body of Scypha through its ostia into the incurrent canals, then through the prosopyles it goes to the radial canals lined by choanocytes. From the radial canals the water enters the ex-current canals through the apopyles from where it enters the spongocoel, then the water goes out through the large osculum.

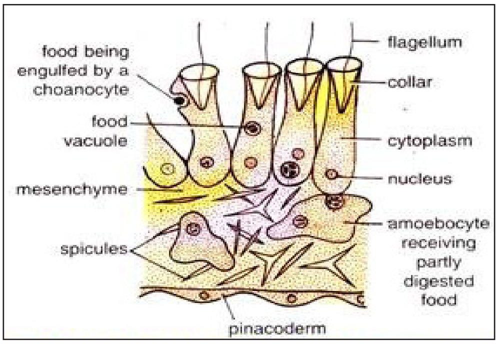
Nutrition of Scypha

Scypha feeds on particles of organic matter and small living organisms, such as bacteria, diatoms and Protozoa; they are drawn in with the water current. Food is ingested partly by porocytes but mainly by choanocytes either through the side of the cell or through its collar. In the cell a food vacuole is formed in which digestion occurs. Digestion is entirely intracellular, as in Protozoa.

The contents of the food vacuoles are first acidic, and then they become alkaline. Several enzymes have been identified in sponge extracts. Partly digested food is taken up by amoebocytes in which digestion is completed, the amoebocytes transport and supply the digested food to all parts of the body.

Digested food is stored as reserves, chiefly glycogen, fat and glycoproteins, and lipoproteins in amoebocytes which are termed as the socytes.

Undigested remains of food are cast out through the collars of choanocytes from where they pass out with the current of water. But in non-calcareous sponges the food is transferred from choanocytes to amoebocytes or amoebocytes engulf the food directly, digestion v occurs only in amoebocytes which also egest the undigested particles.



Scypha: Ingestion of food by choanocyes and its digestion.

Respiration in Scypha

Special respiratory organs are wanting in sponges. Gaseous exchange occurs by simple diffusion, between the cells of sponge and the current of water. Oxygen dissolved in water is taken in by diffusion through the general body surface by the pinacocytes and internally by the choanocytes. Amoebocytes distribute the oxygen throughout the mesenchyme and take away the carbon dioxide.

The process of respiration is entirely intracellular as in Protozoa. Sponges prefer places where water contains plenty of oxygen. If kept in foul water or water deficient in oxygen contents or if their dermal pores become clogged with silt,the sponges die or undergo reduction.

The rate of consumption of Scypha was found to range from 0.16 ml. of oxygen per gram of fresh weight per hour in the smaller specimens to 0.04 in the larger ones. The upper half just above the osculum consumes 10 to 50 per cent more oxygen per gram per hour than the basal half.

Excretion in Scypha

Egested wastes and excretory matter (largely ammonia) leave the body with the current of water. Some observers claim that amoebocytes containing excretory granules and inclusions are discharged by sponges.

Nervous System and Behaviour of Scypha

Sponges are devoid of sensory or nerve cells. The sponge body displays only very slight powers of conductivity. Strong stimuli such as cuts or sharp blows are transmitted not at all or only 3 or 4 mm at the most. Conductivity is the best developed at the osculum where transmission occurs more readily away from than toward opening. The oscular rim appears to be the most sensitive part of the sponge.

However, Tuzet and Pavans de Ceccatty believe that the collencytes are nervous in function; some of them behave like neurons and constitute a diffused nerve net connecting the pinacoderm, choanoderm and myocytes. Thus, these cells acting as neurons are believed to receive and conduct the various types of stimuli.

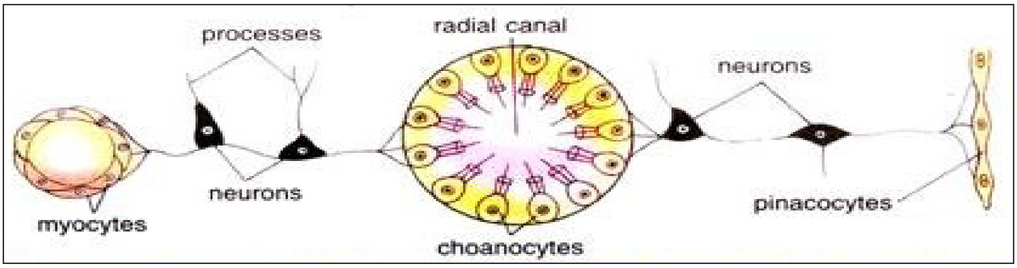


Diagram illustrating the probable mechanism of reception and conduction of nerve impulses in a sponge.

Reproduction of Scypha

Scypha reproduces both asexually and sexually.

(i) Asexual Reproduction: In Scypha asexual reproduction takes place by budding and regeneration.

- Budding: A small bud appears at the base of an adult Scypha and grows into full size. It may adhere to the parent and, thus, help to form a colony, or it may break free and forms a new individual and leads an independent life.
- Regeneration: Regenerative power of sponges is very high. Any piece of the body of Scypha is capable of growing into a complete sponge, if kept in a suitable environment.

(ii) Sexual Reproduction: Scypha is monoecious (hermaphrodite). Both sperms and ova are produced from the archaeocytes which are present in the mesogloea.

Oogenesis

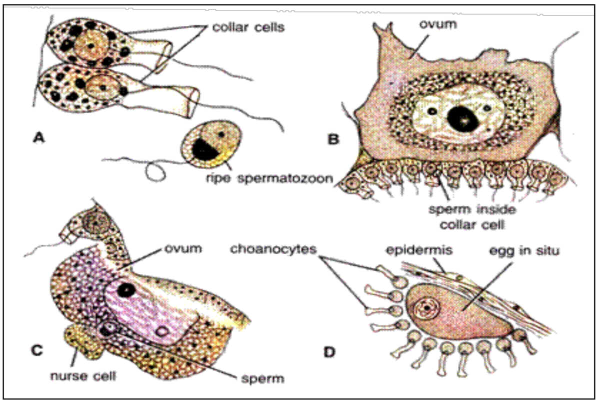
The egg mother cell or ovocyte is first derived from an enlarged amoebocyte with a large nucleus and conspicuous nucleolus.

It grows and acquires food stores by engulfing or fusing with other similar amoebocytes or may receive supplies from special trophocytes. Upon attaining full size it undergoes the usual maturation divisions to form the ovum which lies in the wall of the radial canal, ready to be fertilised by a sperm from another sponge.

Spermatogenesis

The sperm mother cell or spermatogonium is described as an enlarged amoebocyte that soon becomes enveloped by one or more flattened cover cells derived by the division of the mother cell or consisting of other amoebocytes. The whole is called spermatocyst.

The spermatogonium divides two or three times into the spermatocytes which give rise to sperm. The sperm comprises a rounded nucleated head and vibratile long tail. Other authors state that spermatogonia are transformed choanocytes, and Gatenby has described the transformation of an entire flagellated chamber into spermatozoa.

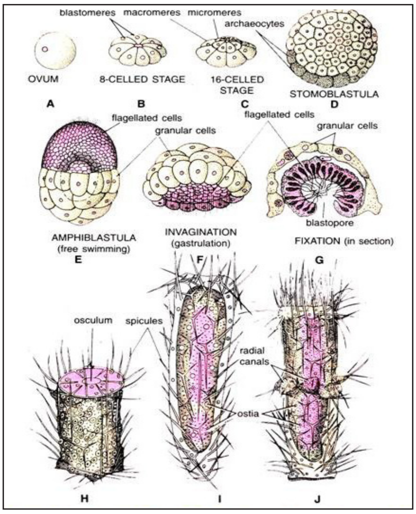


Fertilisation in Grantia: A-A ripe spermatozoon near two choancocytes; B- Sperm enters a collar cell adjacent to an ovum; C-Nurse cell giving up sperm into ovum; D-Fertilized egg in situ.

Fertilisation

Due to protogynous condition cross fertilisation occurs which is internal and the eggs are fertilised in situ.

The sperm does not enter directly in the ovum but reaches a radial canal and is dispersed by the water currents. The sperm enters a choanocyte adjacent to ripe ovocyte. The choanocyte loses its collar and flagellum, becomes amoeboid, and plasters itself to the surface of the ovocyte, which forms a conical depression to receive it.



Scypha: Development: A-Ovum; B-8celled stage; C-16celled stage; D-Biastula; E-Amphiblastula; F-beginning of invagination; G- Gastrula showing fixation; H-young sponge; I-Asconoid (olynthus) stage; J-Syconoid stage.

The sperm in the meantime has lost its tail, and its swollen head becomes surrounded by a capsule. The capsule carrying the sperm head penetrates into the ovocyte. According to Gatenby and others the sperm enters a choanocyte, which acts as a nurse cell and then fuses with the egg but according to Duboscq and Tuzet the sperm carrying choanocyte departs after the transfer of the sperm into the ovocyte.

Early Embryonic Development

The fertilised egg undergoes maturation and holoblastic cleavage and develops in situ into a blastula. The first three cleavages are vertical and produce a disc of eight pyramidal cells or blastomeres. A horizontal cleavage then divides the blastomeres unequally, yielding eight large cells macromeres produce the future epidermis and eight small cells micromeres give rise to future choanocytes.

At the 16 cell stage the embryo lies just beneath the maternal choanocyte layer as a flattened disc-shaped body.

The micromeres (small cells) increase rapidly, elongate and each acquires a flagellum on its inner end facing the blastocoel. The large cells remain undivided for some time, become rounded and granular and in their middle an opening forms that functions as a mouth to ingest adjacent maternal cells. This stage is called stomoblastula by Duboscq and Tuzet.

The stomoblastula, thus, is the blastula stage of Scypha consisting of many small, elongated and flagellated micromeres and 8 spherical granular macromeres. It bears a blastocoel which opens out by an aperture, the mouth which is formed in the macromeres.

The mouth is used for engulfing the surrounding maternal cells for nutrition. The stomoblastula undergoes a process of inversion in which the embryo turns out through its mouth, so that the flagella become directed towards the outside. Now, the embryo is called amphiblastula larva.

Amphiblastula Larva

The amphiblastula larva occurs in the development of most of the Calcarea. It is more or less oval in shape and consists of one-half of small, narrow flagellated cells and the other half large rounded granular cells. The amphiblastula larva forces its way into the adjacent radial canal and escapes through the osculum of the parent to swim for some hours with the flagellated cells directed forward.

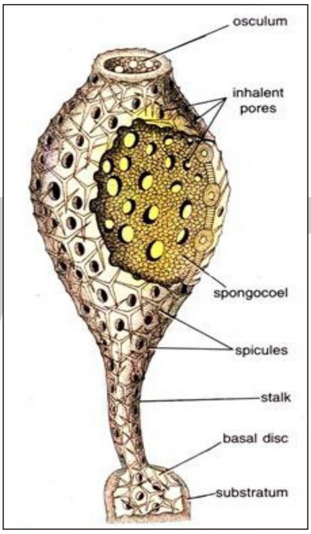
After swimming for a few hours gastrulation takes place by the invagination of the flagellated cells. Now the larva becomes a typical gastrula with a blastopore at the invaginated side.

Post-embryonic Development (Metamorphosis)

The gastrula soon gets attached to some substratum like rock, sea weed, etc., by its blastoporal end and develops into a cylinder.

At the free end of the cylinder an opening, the osculum is formed. A large number of small perforations are formed on the cylinders which are the ostia. The non-flagellated granular cells give rise to the dermal epithelium, scleroblasts and porocytes. The flagellated cells give rise to the choanocytes, archaecocytes and amoebocytes. The mesenchyme arises from both the layers.

The young Scypha now reaches the olynthus stage resembling the asconoid type of sponge. The adult or syconoid stage develops from the olynthus stage by pushing out of the wall, first at the middle, into radial canals. The choanocytes are shifted in these radial canals and the body wall increases in thickness. Thus, the adult Scypha is formed and its colony develops later on by further branching.



Oylnthus stage of Clathrina (a calcareus sponge) with a portion of the wall cut to show spongocoel.

Annelida

The phylum Annelida is made up of segmented worms such as earthworms. Segmented worms are divided into many repeating segments. There are roughly 15,000 species of annelids. Most belong to one of three classes. A species in each class is pictured in figure.

Polychaete: Marine worm

Oligochate: Earthworm

Hirudinean: Leech

Classes of Annelids: The majority of annelids are polychaetes. They live on the ocean floor, so you may not be familiar with them.

Structure and Function of Annelids

Annelids range in length from less than 1 millimeter to over 3 meters. They never attain the large size of some mollusks. Like mollusks, however, they have a coelom. In fact, the annelid coelom is even larger, allowing greater development of internal organs. Annelids have other similarities with mollusks, including:

- A closed circulatory system (like cephalopods).
- An excretory system consisting of tubular nephridia.
- A complete digestive system.
- A brain.
- Sensory organs for detecting light and other stimuli.
- Gills for gas exchange (but many exchange gas through their skin).

The segmentation of annelids is highly adaptive. For one thing, it allows more efficient movement. Each segment generally has its own nerve and muscle tissues. Thus, localized muscle contractions can move just those segments needed for a particular motion. Segmentation also allows an animal to have specialized segments to carry out particular functions. This allows the whole animal to be more efficient. Annelids have the amazing capacity to regrow segments that break off. This is called regeneration.

Annelids have a variety of structures on the surface of their body for movement and other functions. These vary, depending on the species. Several of the structures are described in figure.

Bristles (setae)
Tiny chitin bristles, called setae, help worms cling to and move along surfaces.

Paired Appendages
Pairs of paddle-shaped appendages are used for swimming and gas exchange.

Feeding Tentacles
Tentacles are used for sensing and feeding. The feeding tentacles of the worm shown here make it look like a feather duster.

Suckers
Leeches lack both bristles and appendages. Instead, they have a sucker at each end of the body that they use for locomotion.

Annelid External Structures: Many annelids have bristles and other types of external structures. Each structure is not present in all species.

Annelid Reproduction

Most species of annelids can reproduce both asexually and sexually. However, leeches can reproduce only sexually. Asexual reproduction may occur by budding or fission. Sexual reproduction varies by species.

- In some species, the same individual produces both sperm and eggs. But worms mate to exchange sperm, rather than self-fertilizing their own eggs. Fertilized eggs are deposited in a mucous cocoon. Offspring emerge from the cocoon looking like small adults. They grow to adult size without going through a larval stage.
- In polychaete species, there are separate sexes. Adult worms go through a major transformation to develop reproductive organs. This occurs in many adults at once. Then they all swim to the surface and release their gametes in the water, where fertilization takes place. Offspring go through a larval stage before developing into adults.

Ecology of Annelids

Annelids live in a diversity of freshwater, marine, and terrestrial habitats. They vary in what they feed on and how they obtain their food.

- Earthworms are deposit feeders. They burrow through the ground, eating soil and extracting organic matter from it. Earthworm feces, called worm casts, are very rich in plant nutrients. Earthworm burrows help aerate soil, which is also good for plants.
- Polychaetes live on the ocean floor. They may be sedentary filter feeders, active predators, or scavengers. Active species crawl along the ocean floor in search of food.
- Leeches are either predators or parasites. As predators, they capture and eat other invertebrates. As parasites, they feed off the blood of vertebrate hosts. They have a tubular organ, called a proboscis, for feeding.

Polychaete

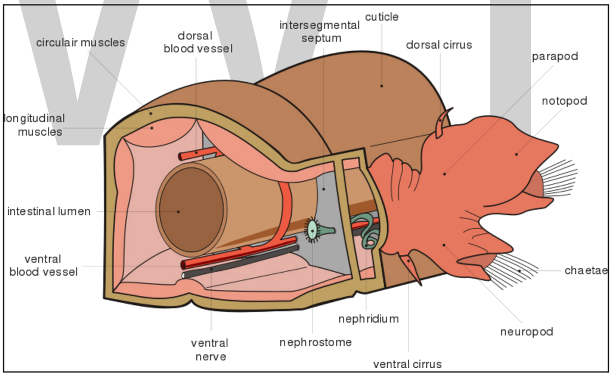
Polychaete or polychete is any of the diverse, mostly marine segmented worms of the annelid class Polychaeta, characterized by having most segments with one pair of lateral, fleshy, lobelike appendages called parapodia, with numerous bristles (setae) projecting from them. The facts that segments have bundles of setae have led to polychaetes sometimes being referred to as bristle worms. Some sessile forms may have the parapodia reduced or absent.

Polychaeta is a very large and diverse class, with more than 10,000 described species. They range in length from less than two millimeters to greater than three meters, and include mobile and sessile forms, and pelagic, surface dwelling, and benthic forms, including burrowers and tube dwellers. Feeding behaviors include raptorial (carnivorous, herbivorous, omnivorous, scavenger), deposit feeding, filter feeding, and suspension feeding. Some forms are brightly colored. Common representatives include the lugworm *(Arenicola marina)* and the sandworm or clam worm *(Nereis)*.

Polychaetes are found worldwide, in all marine habitats, from polar to tropical regions, and some live in freshwater or brackish environments; a few inhabit land environments that are completely inundated with water.

Because of their abundance in marine environments, polychaetes play an important role in marine food chains, and are preyed upon by other invertebrates, fish, and birds. Those polychaetes that are part of the benthos not only are important in benthic food chains, but also help in the recycling of organic matter. For humans, polychaetes are used as bait for recreational fishing and as indicators for monitoring the health of environments. The striking colors, iridescent forms, and unique shapes of some species add greatly to the wonder of nature.

Description



General anatomy of a polychaete.

As annelids, polychaetes have true segments. Anterior to the true segments lie the prostomium and peristomium. This head region of two segments typically contains two pairs of eyes, three antennae, several tentacles, a pair of palps, and the mouth (Carmack). Polychaeta have well-developed heads compared to other annelids. Posterior to the true segments is the pygidium. This last segment, or tail, is where the anus is located. Growth takes place by adding segments just in front of the pygidium (Carmack).

Typically, each body segment between the head and the tail (the trunk) has a pair of fleshy, lateral protrusions called parapodia. These parapodia bear many bristles, called setae (chaetae), which are made of chitin. The parapodia may be uniramous (with one branch) or biramous (with two branches), the later having an upper division or dorsal lobe (notopodium) and lower division or ventral lobe (neuropodium). In some sessile forms that live in tubes or permanent burrows, the parapodia may be reduced or absent.

Christmas tree worms (Spirobranchus giganteus) from East Timor.
These are small, tube-building polychaete worms.

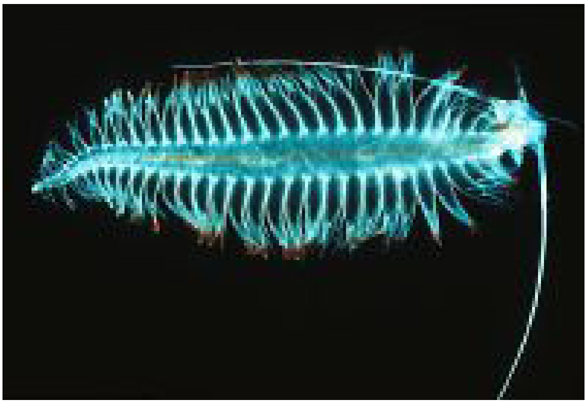
The polychaetes' paddle-like and highly vascularized parapodia are used for movement and act as the annelid's primary respiratory surfaces. (Parapodia can be thought of as kinds of external gills that are also used for locomotion.) The chitinous setae may be used for such purposes as to help the worm move, by fixing the non-moving sections of the worm in place, or by excreting poison for self-defense (Carmack).

The length of polychaetes range from less than 0.078 inches (less than two millimeters) to greater than 9.8 feet (greater than three meters). Most are less than 3.9 inches (ten centimeters) and between 0.078 to 0.39 inches (two to ten millimeters) wide. Most are elongated and cylindrical, with many segments, but they may also be short, compact, and with few segments.

The body of polychaetes varies from light tan to opague, including red, pink, green, yellow, and combinations of colors. Some forms are iridescent or luminescent.

Polychaetes can regenerate such body parts as tentacles, parapodia, cirri, and palps, as well as posterior ends. Such regeneration is used by many polychaetes during asexual reproduction, as new individuals develop from an isolated fragment or a bud that grows from an individual. The majority of polychaetes are sexually reproducing and are dioecious (with male or female sexual parts), with hermaphroditism in only a few species.

Distribution and Ecology

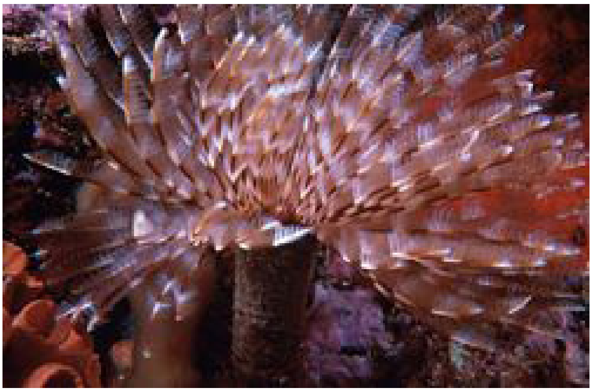


Tomopteris from plankton.

Polychaetes are found worldwide, mostly in marine environments, but also include some species that live in brackish and freshwater environments. A few groups have evolved to live in terrestrial environments, like Namanereidinae with many terrestrial species, but these are restricted to inundated or humid areas. Some of these have cutaneous invaginations for aerial gas exchange.

In marine environments, polychaetes are found from the intertidal zone to the deepest depths of the ocean, and from the Polar Regions to tropical regions. One notable polychaete, the Pompeii worm *(Alvinella pompejana)*, is endemic to the hydrothermal vents of the Pacific Ocean. Pompeii worms are thought to be the most heat-tolerant complex animals known.

Polychaetes occupy a wide variety of habitats. Some live among the plankton, having adaptations to swim and spending their lives in the water column. Most burrow or build temporary or permanent tubes on the bottom, or crawl on the surface of the substrate. Some live in the surface area of the water. They are found in reefs, crevices of rocks, and so forth. Although most are free-living, a few are parasitic, and some live as commensals, associating with another animal either for attachment, protection, or food.



Sabellastarte indica.

The mobile forms or Errantia tend to have well-developed sense organs and jaws, while the Sedentaria (or stationary forms) lack them but may have specialized gills or tentacles used for respiration and deposit or filter feeding, e.g., fanworms.

Polychaetes include such remarkable forms as the recently discovered genus *Osedax*, which includes the Bone-eating snot flower. Another remarkable polychaete is *Hesiocaeca methanicola*, which lives on methane clathrate deposits. *Lamellibrachia luymesi* is a cold seep tube worm that reaches lengths of over three meters and may be the longest lived animal at over 250 years old.

The feeding ecology of polychaetes includes raptorial forms (carnivores, herbivores, omnivores, scavengers), suspension feeders, filter feeders, and surface and subsurface deposit feeders.

Fossil Record

The fossil record for polychaetes is poor, given that they are soft-bodied worms and do not fossilize well. Being soft bodied, the fossil record of polychaetes is dominated by their fossilized jaws, known as scolecodonts, and the mineralized tubes that some of them secrete.

The oldest crown group polychaetes fossils come from the Sirius Passet Lagerstatte, which is tentatively dated to the lower-middle Atdabanian (early Cambrian) (Conway and Peel 2008). Many of the more famous Burgess Shale organisms, such as *Canadia* and *Wiwaxia*, may also have polychate affinites. An even older fossil, *Cloudina*, dates to the terminal Ediacaran period; this has been interpreted as an early polychaete, although consensus is absent.

Taxonomy and Systematics

Taxonomically, the polychaetes are thought to be paraphyletic, meaning that as a group it contains its most recent common ancestor, but does not contain all the descendants of that ancestor. Groups that may be descended from the polychaetes include the earthworms, the leeches, sipunculans, and echiurans. The Pogonophora and Vestimentifera were once considered separate phyla, but are now classified in the polychaete family Siboglinidae.

Oligochaeta (Earthworms)

Earthworms belong to a well-defined clade, the Clitellata, which includes leeches, branchiobdellids, many aquatic and small terrestrial worms with a single cell-layered clitellum, and the earthworms, most of which have a multi-layered clitellum. However, earthworms as a group lack a defining characteristic unique to earthworms. This is because they include the Moniligastridae, a south and east Asian earthworm family, which have a single-layered clitellum and prosoporous (male genital openings in front of the female genital openings). All other earthworms have a multi-layered clitellum and male genital openings behind the female pores (opisthoporous) and are called the Crassiclitellata. As soft-bodied invertebrates, earthworms lack a fossil record, other than burrow traces that may or may not have been created by earthworms. Their phylo-genetic relationships have been a matter of controversy since the early twentieth century. Based on analysis of DNA sequence data, Jamieson et al. concluded that the large family Megascolecidae (in the broad sense, including the Acan-thodrilidae and Octochaetidae, of some authors) is the sister-group of the Ocnerodrilidae, and that these in turn are together the sister-group of a clade composed of several families: Sparganophilidae, Komarekionidae, Almidae, Lutodrili-dae, Hormogastridae, Lumbricidae, and Microchaetidae. The remaining two numerically important families, Glossoscoleci-dae and Eudrilidae, form a third major clade of Crassiclitel-lata, but relationships to the other two were not clear. Several small families, plus the Moniligastridae, were not included in the analysis. These families complete the family list of the Crassiclitellata: Ailoscolecidae, Alluroididae, Biwadrilidae, Di-porochaetidae, and Kynotidae. Overall, there are 17 families, one order, and more than 4,000 species.

Physical Characteristics

Earthworms have a “tube within a tube” construction, an outer muscular body wall surrounding a digestive tract that begins with the mouth in the first segment and ends with the anus in the last segment. Body wall musculature consists of an outer circular layer and inner longitudinal layers, which respectively extend and shorten the body. Between the body wall and the gut is the body cavity, within which various other organs are arranged, generally segmentally. Segments are repeated units of the body, externally manifested as rings and internally separated by septa. In earthworms, each segment except the first bears setae, small chitinous bristles used for traction in the burrow.

A typical earthworm gut consists of the mouth, a muscular pharynx for taking in food, a gizzard for reducing food particles to smaller sizes, an esophagus, and an intestine. In the family Lumbricidae, the gizzard is located after the esophagus, just prior to the expansion of the intestine. Intestinal gizzards have evolved independently in other families and genera. The esophageal wall may secrete digestive enzymes, and in some earthworms, parts of the esophagus are modified as glands for the secretion of calcium carbonate into the gut contents. The intestine may be differentiated into digestive and absorptive regions, and often has a dorsal in-folding of the intestinal wall, called the typhlosole.

Small excretory organs, the nephridia, are arranged seg-mentally, from two per segment to many small nephridia per segment. Urine is excreted through nephropores to the outside, or is collected via systems of tubules and excreted into the intestine. In some families, nephridia of the anterior segments have been modified as glands for digestive secretions.

Close-up of worm casts in a lawn.

Earthworms are hermaphrodites. Reproductive organs are located in the anterior segments. The female reproductive system consists of paired ovaries in the 13 th segment, ovarian funnels leading from the ovaries to an external female genital pore on the 14th segment, and depending on the family, there may be sperm receptacles called spermathecae. If present, these will generally be in some of segments 5-10. Sper-mathecae receives sperm from the mate during copulation. Alternatively, sperm may be deposited in packets called sper-matophores, which will be found clinging to the exterior of the worm. The clitellum provides an outer casing for the ova and also secretes food used by the developing embryo.

Male organs consist of testes in one or both of segments 10 and 11, testicular funnels leading to sperm ducts through which sperm passes to the male genital openings, seminal vesicles in segments adjacent to the testicular segments (one or more of segments nine, 11, 12), and in some families, prostate glands that secrete fluids associated with the male genital pores. In other families, there are often glands associated with setae modified for use in copulation.

Distribution

Earthworms are globally distributed, but do not occur in deserts or regions where there is permafrost or permanent snow and ice. They may also be absent from the taiga biome and other cold climate vegetation types where soils are strongly acid (pH below 4). It has been shown that during the last 20,000 years, many glaciated areas have lacked the presence of earthworms, but in these and other places where they do not occur naturally, some species have been introduced by human activity. The Megascolecidae have the widest natural distribution, being present on all continents, except Europe. The Glossoscolecidae are confined to tropical South America, Central America, and a few Caribbean islands, while the Eudrilidae are found only in sub-Saharan Africa. The Lum-bricidae are mainly in Europe, with a few species native to North America. Australian indigenous species are exclusively megascolecids. A few species have attained global temperate or tropical distributions with human assistance.

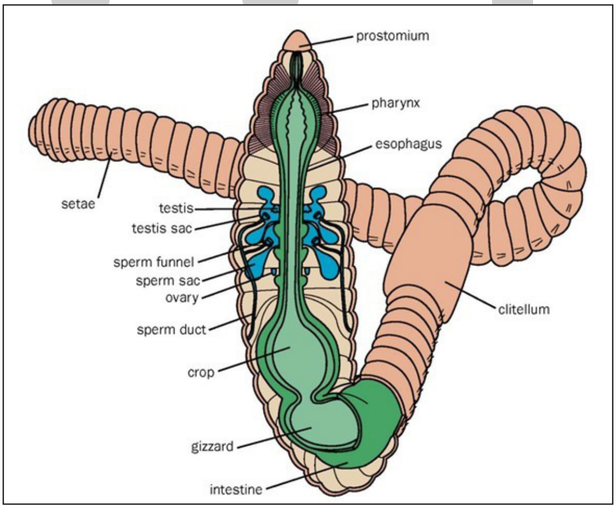
Habitat

The typical earthworm habitat is soil, but there are species living in freshwater mud, saltwater shorelines, and in suspended soils of tropical forests. The soil habitat can be divided into litter layer, topsoil, and deeper soil horizons, with different earthworms utilizing each.

Behavior

The three ecological categories of earthworms have very different behavior patterns. The anecic feeding behavior has been described. Their primary escape tactic is to rapidly withdraw into the burrow. Epigeic species crawl or burrow through organic matter deposits and feed on it. They have well-developed escape behavior that includes rapid motions, even the ability to jump and thrash about randomly, and to drop tail segments for the predator. Endogeics have little escape behavior, may just writhe or coil in the hand, and may exude some body cavity fluids. In some instances, these fluids may be noxious.

Feeding Ecology and Diet



Earthworm anatomy.

Earthworms feed on dead and decomposing organic material such as fallen leaves, decaying roots, and soil organic matter. Epigeic worms are those feeding at or near the surface, or within accumulations of organic matter on or above the soil surface (e.g., logs, epiphyte root mats in trees, etc.). These will consume relatively freshly dead plant matter, as do anecic worms. Anecic earthworms maintain a deep burrow from which they emerge to ingest plant matter from the soil surface; the best known is the European night crawler, Lum-bricus terrestris. Endogeic worms operate deeper in the soil and utilize organic matter that has already been somewhat or extensively modified from its original condition. Body size, coloration, and gut morphology are consistently different among these three categories. Epigeics are typically small, darkly colored, and have little secondary development of gut surface area. Anecics are large, colored only in the head, and have gut morphology similar to epigeics. Endogeic worms may be small or very large, but are usually un-pigmented, and show the greatest degree of gut surface area development.

Reproductive Biology

Most earthworms are simultaneous hermaphrodites and exchange sperm during copulation. Sperm transfer may be external, in which the seminal fluid flows from male genital openings to the spermathecae, or there may be penis-like organs to insert the seminal fluid directly into the spermathecal openings. Sperm transfer by spermatophores is also known to occur. After copulation, fertilization takes place in the egg case. The case, or cocoon, is formed by the clitelum and passes over the female pores to receive one or more ova. It is then worked forward over the spermathecal pores, from which sperm are expelled into the case, and fertilization results. The cocoon is deposited in the soil or other substrate. The developing embryo feeds on clitellar and/or prostatic secretions, passes through larval stages, and emerges as a miniature earthworm. Growth and maturation may take months or years, depending on the species. In temperate zones, mating and cocoon deposition generally take place in the spring, with a secondary period possible in the autumn. In tropical areas, the peak of activity occurs during rainy seasons. However, the details of mating seasons in tropical earthworms are poorly known.

Some species of earthworms are clonal and reproduce by parthenogenesis. In this case, a diploid ovum is produced that is a genetic copy of the parent. No fertilization is necessary, so a single individual can reproduce unaided. This is important among the many species that have attained wide artificial distributions. In other instances, hermaphroditic species have been observed self-fertilizing.

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This book was conceptualized with the vision of imparting up-to-date and integrated information in this field. To ensure the same, a matchless editorial board was set up. Every individual on the board went through rigorous rounds of assessment to prove their worth. After which they invested a large part of their time researching and compiling the most relevant data for our readers.

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The publisher and the editorial board hope that this book will prove to be a valuable piece of knowledge for students, practitioners and scholars across the globe.

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