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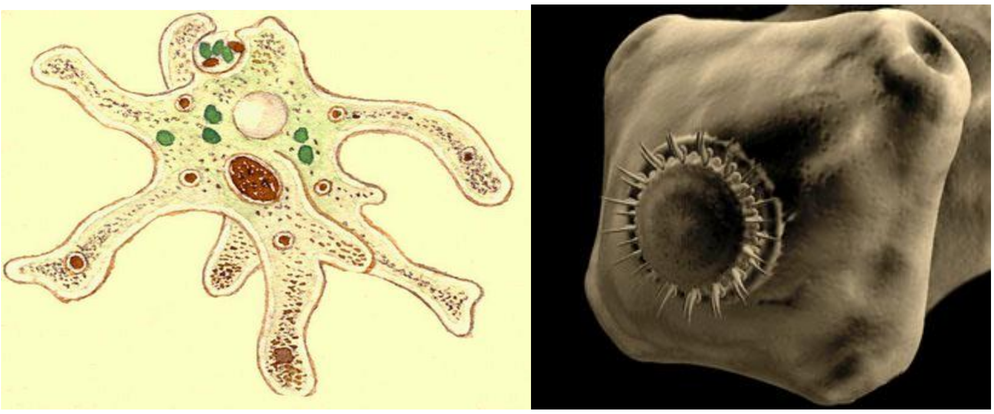
Кафедра загальної зоології та іхтіології



GENERAL ZOOLOGY

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PROTOZOA

Protozoa are microscopic animals that consist either of a single cell or of a colony of nearly identical cells. They include:

- asymmetrical, amoeboid blobs;
- floating forms with perfect spherical symmetry;
- and forms with bilateral symmetry similar to that of flatworms.

Typically they range between 10 and 100 microns in length or diameter, but both smaller and larger examples are found. The malaria parasite, for example, may measure about 3 microns and fit comfortably inside a red blood cell, while some fossil shelled amoebae exceeded 15 cm in diameter.

Protozoa are highly successful animals. Well over 50,000 species have been described, and they are distributed in most natural habitats throughout the world.

- They occur commonly in both freshwater and marine environments.
- Some are found typically in soil, interacting with other microorganisms and with resident plants.
- Some live as symbionts attached to the bodies of aquatic plants and animals, while others live inside the bodies of invertebrate and vertebrate hosts. Some symbiotic protozoa help their hosts digest foods containing cellulose.
- Some cause serious diseases, including malaria, amoebic dysentery, African sleeping sickness, and coccidiosis (in domesticated animals).

Protozoa have three main distinguishing features:

- their bodies are composed of single cells without surrounding cell walls, or loosely organized colonies of such cells;
- free-living forms move by means of flagella, cilia, Or amoeboid protrusions termed pseudopodia; and
- they feed by ingesting particles of food (including whole microorganisms)

Main taxons of Protozoa

Phylum Sarcomastigophora
  Class Sarcodina
    Subclass Rhizopoda
    Subclass Radiolaria
    Subclass Heliozoa
  Class Mastigophora
    Subclass Phytomastigina
    Subclass Zoomastigina

Phylum Sporozoa
  Class Gregarinina
  Class Coccidiomorpha

Phylum Cnidosporidia

Phylum Microsporidia

Phylum Ciliophora
  Class Ciliata
  ClassSuctoria

General Structure of Protozoa

Internally, protozoa contain the typical structures found in all **eucaryotic** cells. In contrast to the **procaryotic** cells of bacteria and blue-green algae, they have a well-defined **nucleus** with its set of **chromosomes** and a mass of **cytoplasm** filling out the space inside the **cell membrane**. The cell membrane is a typical three-ply unit membrane such as encloses all eucaryotic cells, but in ciliates and some other protozoa multiple membranes of this type strengthen the body surface. The cytoplasm contains the usual cellular metabolic machinery and in addition has systems of **vacuoles**, including **food vacuoles** for digestion of particulate food and **contractile vacuoles** in free-living protozoa to regulate the water balance of their cytoplasm.

Locomotion. Protozoan locomotion shares some of the same basic mechanisms of molecular contraction encountered in the functioning of the **flagella** and **cilia** of higher animals, in the amoeboid movement of white blood cells, and in muscular contraction. The individual flagella and cilia of protozoa have the same basic structure, possessing an inner fibrous core (axoneme) and an outer sheath, which is an extension of the cell membrane. The axoneme has a remarkably constant arrangement consisting of a central pair of fibrils surrounded by nine pairs of fibrils. The differential contraction of these fibrils causes the lashing or beating of the organelles against the water and results in propulsion.

Cilia, which are relatively shorter than flagella, usually are held stiffly, like paddles, in the backward thrust against the medium. In their recovery stroke they become limp and offer less resistance to the medium. The movement of ciliates is complicated by the necessity of coordinating the beating of hundreds of cilia.

Amoeboid movement is by means of **pseudopods**. The protoplasm of amoebae consists of a more fluid central region (plasmasol) and a more rigid outer wall region (plasmagel), which are interconvertible. At the advancing end of the body, plasmasol flows into a forming pseudopod, where it is partly converted into a stiffened wall of plasmagel. At the opposite end, plasmagel is being converted at the same time into plasmasol, which then flows forward into the pseudopod.

Sensory Equipment. Most protozoa respond to light, heat, chemical agents, and other environmental stimuli, without special sensory equipment. The cell surface and the irritable protoplasm directly underneath receive stimuli and mediate responses by the locomotor organelles or other contractile elements. Algal flagellates, however, have a light-sensitive organelle called the stigma that enables them to seek light for photosynthesis. Also, some cilia and flagella are specialized as tactile bristles.

Defensive and Offensive Behavior. Protozoa, like other motile forms, readily move toward or away from stimuli. These movements respond to slight differences in intensity. In the case of ciliates, distinctive avoidance behavior is elicited by such unfavorable conditions as toxic substances or excessive light or heat.

Some flagellates and ciliates have arrays of small sacs (**trichocysts**) at the body surface from which fibrous threads are discharged into the medium. There are two general kinds of trichocysts. Those of some predatory forms, such as *Didinium,* are toxic and immobilize or lyse the prey. Those of forms like *Paramecium* are presumed to have a defensive function.

How Protozoa Get Food. Different groups of protozoa exhibit all the basic modes of nutrition, from the photosynthetic algal flagellates to the predatory ciliates and amoebae's and intracellular malaria parasites. Food is taken in either by **absorption** of soluble compounds through the cell membrane or by being packaged as particles or macromolecules in vacuoles that are pinched off the cell membrane. Protozoan food vacuoles take the place of the digestive tract of animals. Enzymes are added to the vacuolar contents, and the food is dissolved for assimilation.

Most protozoa do not possess permanent mouth openings. Food particles are first drawn into contact with the cell surface, a cuplike depression is formed, and a food vacuole is pinched off into the cytoplasm, with a portion of the cell membrane serving as the vacuolar wall. This process is termed ***phagocytosis***. In the case of forms with localized mouths, or **cytostomes**, as food particles are guided through the opening they are enclosed in vacuoles from a reserve supply of membrane material in the vicinity.

A modified form of phagocytosis termed **pinocytosis**, or "cell drinking," is used to take in soluble organic compounds such as proteins.

Reproduction—Asexual The basic reproductive process in protozoa is a form of **cell division**, usually without leaving any trace of the parental body. The simplest case is production of two equal-sized daughters *(**binary fission**),* as seen among most flagellates, amoebae, and ciliates.

Budding differs from binary fission in that two unequal-sized offspring are produced. In the case of attached forms like the stalked ciliate *Vorticella,* a small bud migrates to a new attachment site, while the larger offspring retains the parental stalk and the original site.

In the case of ***multiple fission****,* or ***schizogony****,* repeated nuclear divisions occur in a common mass of cytoplasm, followed by cleavage into numerous offspring each with a nucleus. Schizogony is especially well developed in some Sporozoa.

Sexual. Sexual reproduction occurs in all major groups of protozoa. In its simplest form — as in the algal flagellate *Chlamydomonas* or myxamoebae of the slime mold *Physarum* — two individuals functioning as **gametes** fuse in a process called ***syngamy***. The two gametic individuals may be morphologically identical *(**isogamy**)* or may be differentiated into a motile sperm-like individual and a stationary egg-like cell (***anisogamy***). Unlike higher forms, in which two distinct sexes occur, some protozoan species produce multiple mating types.

Ciliate protozoa display a unique kind of sexual reproduction called ***conjugation***. In (hit process a pair of individuals from different mating types join temporarily, with a cytoplasm bridge connecting them. Each partner donates across the bridge a gametic micronucleus, which fuses with a host gametic nucleus to form a zygote micronucleus in each conjugant. Each partner thus acquires a new diploid micronucleus and a new genetic combination.

Life Cycles. Protozoan life cycles are highly diverse. Some forms *(Amoeba proteus* and many flagellates) exhibit only periods of **growth and asexual reproduction**. Many—but not A. *proteus*—form resistant stages (**cysts**) as temporary reactions to unfavorable conditions.

In forms with sexual reproduction, meiosis (reduction from the diploid to the haploid chromosome number) may occur just prior to gamete formation, as in, higher animals, or reduction may occur with the first cell division following zygote formation. In the latter case all stages except the zygote have the haploid chromosome number, as in many algal flagellates and in all sporozoans. The foraminiferans are unique among animals in showing true alternation of generations, as in lower plants, with two balanced generations differing in shape and chromosome number.

PHYLUM SARCOMASTIGOPHORA

This group embraces the closely related amoeboid protozoans and flagellates in two classes: Sarcodina and Mastigophora.

Class Sarcodina includes the protozoa with pseudopodia as the dominant means of locomotion. Skeletal structures are especially prominent in marine forms, exemplified by the remarkable tests (shells) of foraminifera and radiolaria. Subgroups are distinguished by different types of pseudopods, used for food capture as well as locomotion. About 10,000 species belong to this class.

Mostly dwell at the marine environment, but amount of freshwater species is also significant. Not a lot of species inhabit in wet soil, some species are represented by parasitic organisms.

Subclass Rhizopoda

Cell form is very various, pseudopods are good-developed and active.

3 orders: Amoebina, Testacea, Foraminifera.

Order Amoebina

Includes probably the simplest rhizopoda, which have no exoskeleton. Mostly inhabitants of freshwater environment; some species dwell in marine environment, wet soil or parasites.

Amoebas' range is between 10-15 microns and 2-3 mm in cell size. Typically they are uninucleate, but multinucleate also exist.

Amoeba proteus is the most common freshwater amoeba (Fig. 1).

Reproduction

Asexual cell division (mitosis). The basic reproductive process in protozoa is a form of cell division, usually without leaving any trace of the parental body. The simplest case is production of two equal-sized daughters (binary fission).

Intestinal amoeba

A lot of parasitic amoebas dwell into intestine of vertebrates including human. They normally feed with intestine contents especially bacteria and do not disturb the host organism (*Entamoeba coli*). But dysenteric amoeba *Entamoeba histolytica* dwelling in the **large intestine** can causes the serious contagious disease dysentery when penetrates into the mucous membrane of large intestine.

Spreading of parasitic amoeba happens by cysts (resistant stages); they get to the environment with feces.

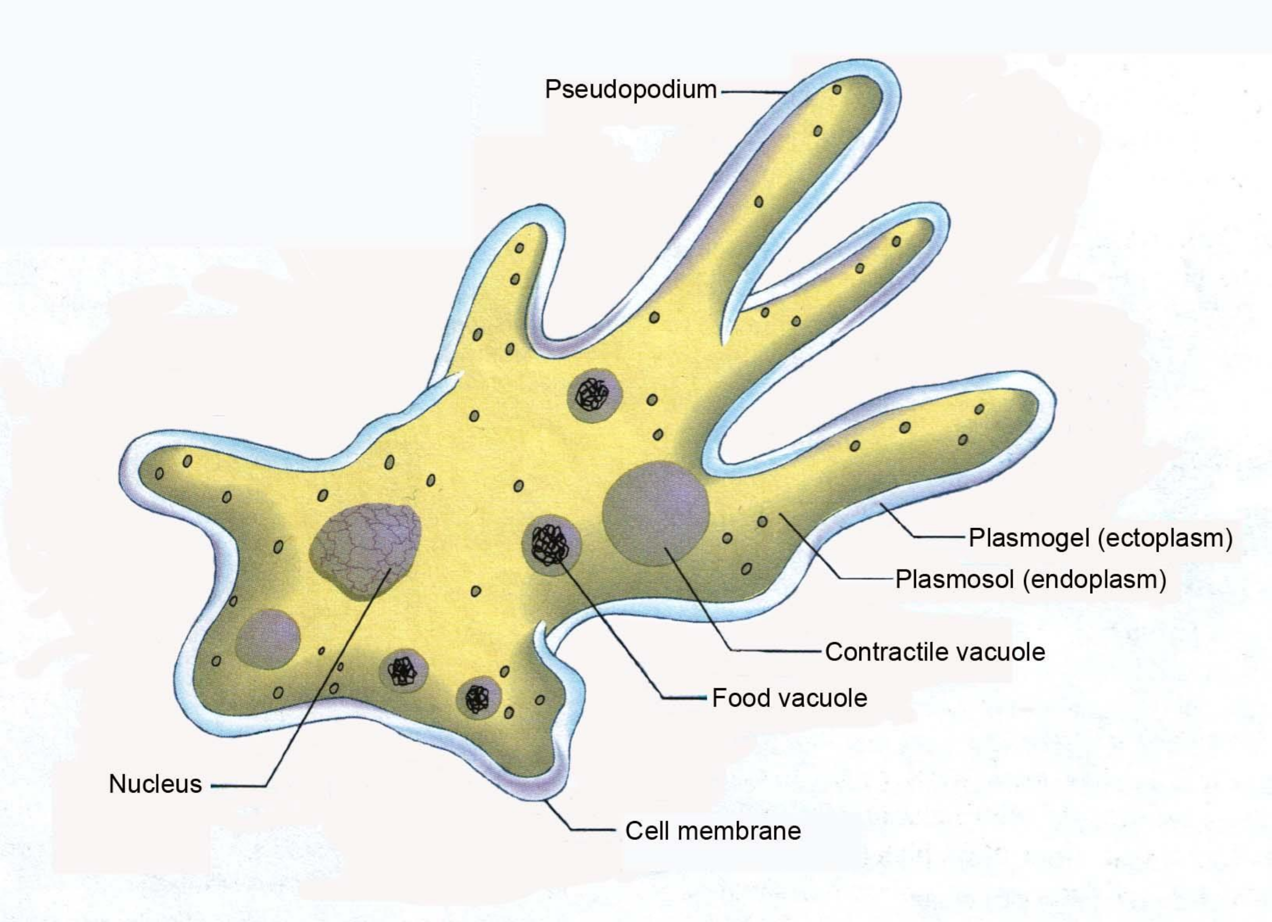


Fig. 1. *Amoeba proteus*

Order Testacea

They care the tests (shells) consist of organic mater, or microscopic inorganic particles glued together by cytoplasm secret. Normally test is round or oval, pseudopods protrude from the special aperture. Reproduction is analogous to the reproduction of amoebas; one of the new cells accepts the parent test, and another forms the new test around it.

Testacea dwell in freshwater environment mostly associated with aquatic plantation, they are also numerous in peat bogs.

Order Foramimifera

They are obligatory marine protozoa. Test (shell) consists of organic mater pseudochitin, or calcium carbonate.

The foraminiferans are unique among animals in showing true alternation of generations, with two balanced generations differing in shape and chromosome number.

Subclasses Radiolaria and Heliozoa – for student presentations

Class Mastigophora

The Class Mastigophora includes all protozoa with flagella as the primary locomotor organelles. Normally flagella locate at the front part of the cell, but some species have the hole body covered with flagella.

Reproduction is mostly asexual as cell duplication.

Chlorophyll-bearing flagellates and close relatives are combined in the subclass Phytomastigophora ("plant flagellates") (Fig. 2).

These are distinguished by their photo-synthetic pigments, which impart green, brown, and golden colors to the bodies. Algal flagellates play an important ecological role as primary producers in freshwater and marine plankton. Dinoflagellates like Gonyaulax occasionally bloom as "red tides" that cause extensive mortality of fishes, and may poison humans who eat shellfish that ingest the protozoa.

The remaining flagellates, which have no chlorophyll and are structurally distinct, are placed in the subclass Zoomastigophora. This is an artificial grouping of diverse forms, ranging from ubiquitous, simple flagellates in polluted waters and soil, such as Oikomonas, to highly complex, multiflagellated forms, such as Trichonympha, that have evolved as intestinal symbionts of termites and related insects and supply the enzymes with which the insects digest cellulose. Important parasites are also included in this subclass. Some flagellates invade human tissues, causing serious diseases, such as African sleeping sickness (fever) (*Trypanosoma rhodesiense*) and Leishmaniasis (*Leishmania*).

Trypanosoma is the blood parasitic protozoa. Antelopes are the host organisms. Tsetse fly is the carrier of the disease.

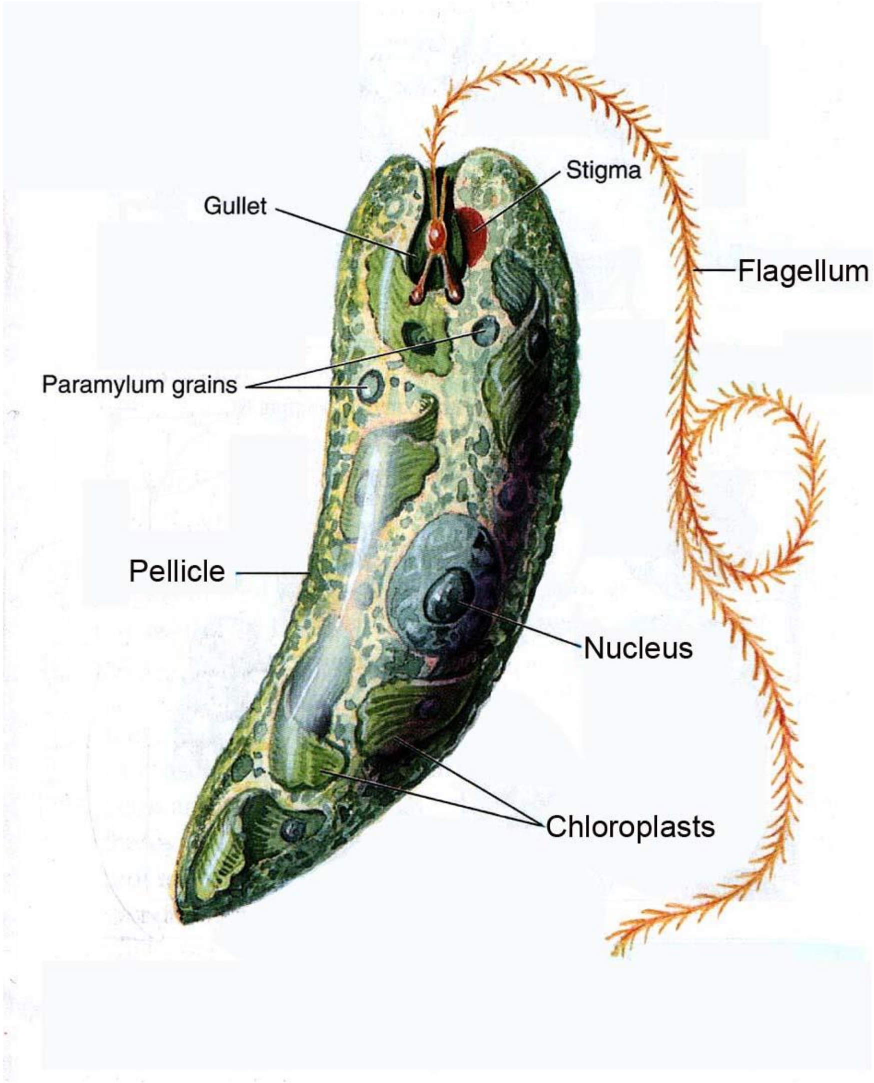


Fig. 2 *Euglena sp.*

PHYLUM SPOROZOA

All members of this assemblage are highly specialized internal parasites lacking special locomotor organelles. Their complex life cycles begin with a liberated spore (sporozoite) that penetrates into cells of an animal host.

The class Gregarinia is restricted to invertebrate hosts. At one stage gregarines leave their host's cells to develop in a body cavity, where they continue to grow and acquire a complex structure, but do not reproduce asexually.

Members of the class Coccidia, on the other hand, develop inside host cells of vertebrates as well as invertebrates, remaining small and having the capacity to undergo schizogony. In the case of multiple fission, or schizogony, repeated nuclear divisions occur in a common mass of cytoplasm, followed by cleavage into numerous offspring each with a nucleus. The numerous asexual offspring re-infect new host cells and intensify the infection. This accounts for the destructiveness of diseases that are caused by many Coccidia, such as malaria (Plasmodium) and coccidiosis *(Eimeria* and others).

PHYLUM CILIOPHORA

This group includes the most animal-like protozoa with highly coordinated movements and special oral devices to capture food. Characteristic features include:

- cilia as locomotor organelles,
- the presence of macro- and micronuclei, and
- conjugation as the typical form of sexual reproduction.

Conjugation: in this process a pair of individuals from different mating types join temporarily, with a cytoplasm bridge connecting them. Each partner donates across the bridge a gametic micronucleus, which fuses with a host gametic nucleus to form a zygote micronucleus in each conjugant. Each partner thus acquires a new diploid micronucleus and a new genetic combination.

The ciliary apparatus shows much greater variation than do flagella.

Class **Ciliata** includes the most generalized ciliates, such as *Paramecium* (Fig. 3) or Tetrany-mena, for example, with simple, uniform distribution of cilia and without specialized ciliary structures leading to the cytostome (mouth). Symbiotic associations are well developed among holotrichs. For example, beneficial ciliates in the rumens of herbivorous mammals digest cellulose like termite flagellates.

Class **Suctoria** is highly specialized for food capture. Adult stages of Ephelota, for example, have no cilia or cytostome. They are anchored to the substrate by noncontractile stalks and have tentacles that attach to prey and suck out its contents.

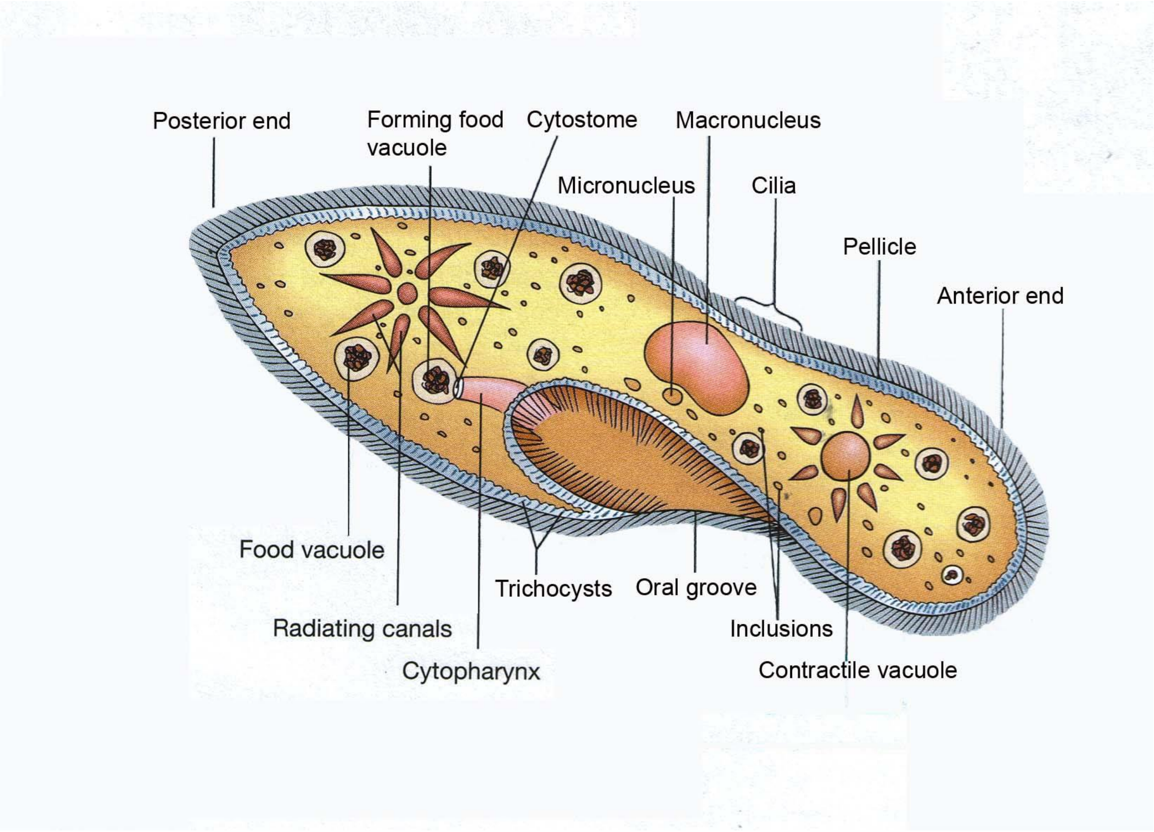


Fig. 3 *Paramecium caudatum*

SUBKINGDOM METAZOA

The fundamental difference, which distinguishes the Metazoa from Protozoa is that metazoan cells belonging to the single organism are different both in structure and in functions. Cells of the similar structure and functioning form tissues, and tissues form the units of higher structural and functional level – organs.

On this way two main stages are recognized:

Diploblastic stage: the tissue grade.

The simplest type of bodily architecture in this subkingdom. The body consists of a sac with one opening, and with the wall composed of two cellular layers and a layer of secreted jelly between them. The inner layer is the ***endoderm***. It consists of cells specialized for the processes of digestion, and the cavity which it lines is for the reception of food. The outer layer is the ectoderm*:* by its cells relations with the environment are regulated. Some of these cells form a protective and retaining sheet; among them stand others which are sensitive; others—**nerve-cells**—lying below the sheet. From certain undifferentiated cells at the base of the ectoderm there are formed the generative cells.

Triploblastic stage: the organ grade.

In triploblastic metazoan phyla there is between ectoderm and endoderm a third layer, the *mesoderm*. From the mesoderm appearance the real organogenesis started in the Kingdom Animalia. The main organ systems of mesodermal origination are:

- Muscular system;
- Vascular system, including blood;
- Internal skeleton

With the mesoderm forming the origination of body cavities is also related:

- Primary body cavity (haemocoel);
- Secondary body cavity (coelom).

PHYLUM PORIFERA (Sponges)

Sponges (Fig. 4) are multicellular organisms; invariably sessile and aquatic; with a single cavity in the body, lined in part or almost wholly by collared flagellate cells; with numerous pores in the body wall through which water passes in, and one or more larger openings through which it passes out; and generally with a skeleton, calcareous, siliceous, or horny.

The skeleton of sponges may be mineral in nature (calcareous CaCO3 or siliceous SiO2) or composed of protein and other components (spongin). The mineral skeleton is formed for the most part by units called spicules, either scattered throughout the sponge or united to form fibres; spicules are classified as megascleres, which function in support, and microscleres, which function in protection and also aid in support.Structure: Sponges are shapeless organisms, or they got tube-like or barrel-like shape. The Porifera are unusual animals in that they lack definite organs to carry out their various functions. The most important structure is the system of canals and chambers, called a water-current system, through which water circulates to bring food to the sponge (Fig 4).

Body consists of a sac with one opening, and with the wall composed of two cellular layers and a layer of secreted jelly between them. The inner layer is the **endoderm**. It consists of cells specialized for the processes of digestion, and the cavity which it lines is for the reception of food. The outer layer is the **ectoderm**: by its cells relations with the environment are regulated. The jelly substance in between is called **mesohyl**, in which cells of various types are scattered:

- **Collencytes** – star-like cells served for shape support;
- **Scleroblasts** (spicule cells) – skeleton-forming sells;
- **Amoebocytes** – reserve cells which can be transmuted into any type mentioned above or form sexual cells.

The essential elements of the water-current system include the pores, or ostia, through which water enters the sponge (incurrent system); the **choanocytes**, or collar cells, which are flagellated cells that capture food; and the **oscula**, openings through which water is expelled (excurrent system).

Three types of water-current systems of increasingly complex structure may be distinguished by the arrangement of choanocytes and the development of canals:

The simplest, or **ascon**, type, is characterized by an arrangement of **choanocytes** around a central cavity that directly communicates with the **osculum**. The walls of these sponges are thin, lack canals, and are perforated by pores, which actually are openings through cells (**porocytes**).

The **sycon** type of water-current system, is at first characterized by choanocytes that surround fingerlike projections called radial canals of the sponge wall. Water enters the radial canals directly through pores, makes its way into the central cavity, or spongocoel, and leaves by way of an osculum.

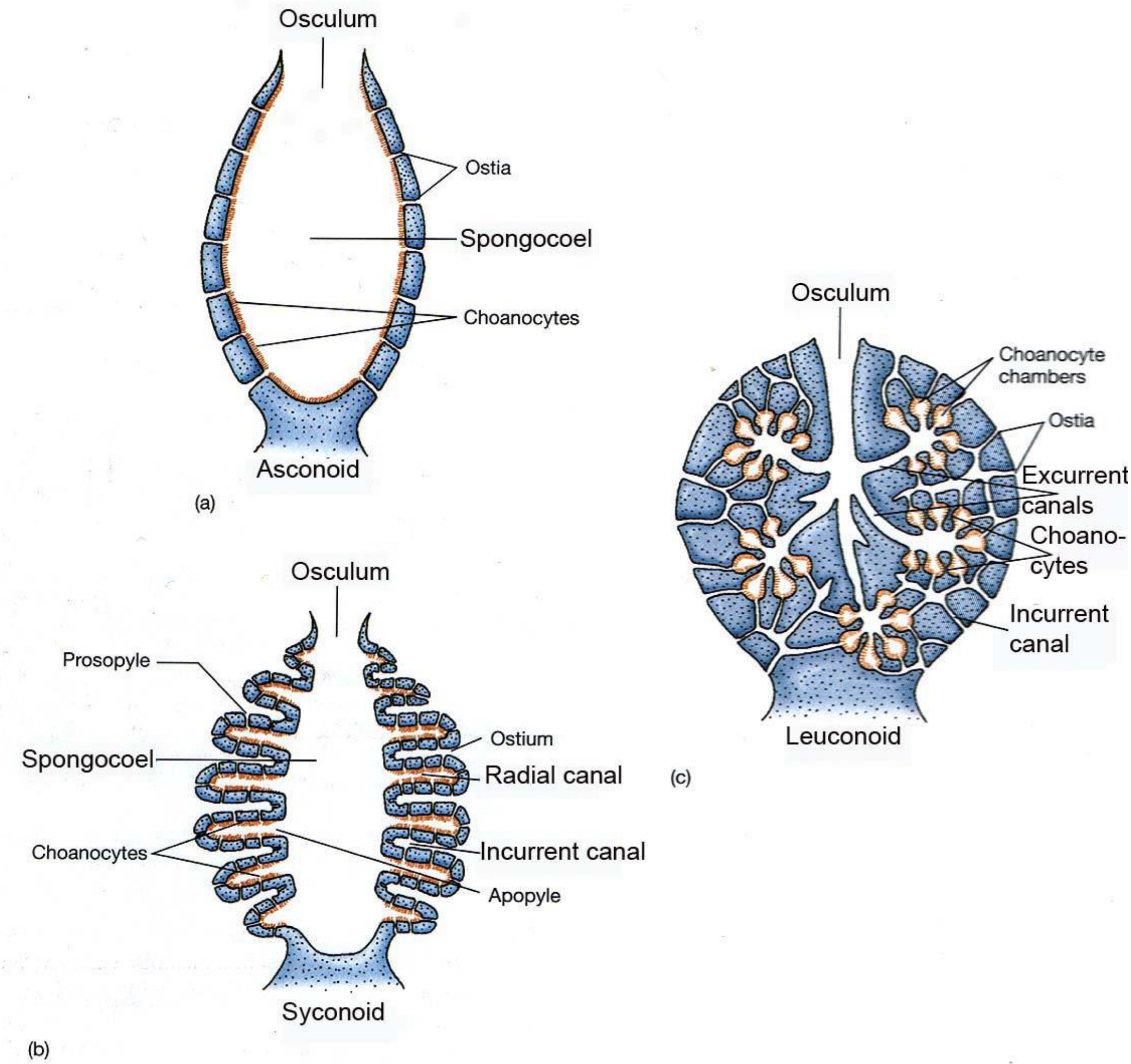


Fig. 4 Body types in Sponges

In the **leucon** type the radial canals are replaced by numerous small flagellated chambers in which the choanocytes are localized; the chambers, scattered throughout the body of the sponge, have pores through which water passes into a complex system of incurrent canals, then into a **spongocoel** (internal cavity) (**paragaster**) by way of excurrent canals. Water enters very small pores found among the cells (pinacocytes), which line the outer surface of the sponge. After passing through a system of incurrent canals and cavities, also lined with pinacocytes, the water reaches the flagellated chambers, enters them through openings (prosopyles), and leaves through other openings (apopyles). The water is expelled through the osculum after passing through a system of excurrent canals and cavities lined with pinacocytes.

In Phylum Porifera digestion takes place within cells (intra-cellular digestion). Spongocoel does not take part in digestion.

Life cycle: Most sponges reproduce sexually, although asexual reproduction may occur. Sponges are generally **hermaphroditic** (male and female germ cells in one animal); sometimes **dichogamy**, in which male and female germ cells develop at different times in the same animals, occurs.

Sexual reproduction: The fertilization of an egg by a spermatozoan is peculiar in sponges in that a spermatozoan, after its release from a sponge, is carried by the water current until it is captured by a specialized cell called a **choanocyte**, or collar cell, in another sponge.

A larva swims for a period of time that may vary from a few hours to a few days before it descends to find a surface suitable for attachment. After attachment, the larva undergoes developmental changes (metamorphosis) becoming a young individual, and the young individual gradually develops into an adult sponge.

Asexual reproduction: Asexual reproduction occurs in sponges in various ways; the best known method is called gemmulation. Gemmulation begins when aggregates of cells become isolated at the surface of a sponge and are then called gemmules. These are expelled from the adult sponge and, in some marine species, serve as a normal reproductive process or, sometimes, as a means to carry the sponges over periods of unfavourable conditions when the adults degenerate; e.g., drought, temperature extremes.

Regeneration: The extraordinary capacity of sponges to regenerate is manifested not only by restoration of damaged or lost parts but also by complete regeneration of an adult from fragments or even single cells. Sponge cells may be separated by mechanical methods (e.g., squeezing a piece of sponge through fine silk cloth) or by chemical methods (e.g., elimination of calcium and magnesium from seawater).

Distribution and abundance: The Porifera are present at all water depths, from the tidal zone to the deepest regions (abyss). They occur at all latitudes and are particularly abundant in Antarctic waters. Calcispongia and Demospongia are found mainly on the rocky bottoms of the continental shelf; the Hyalospongia are characteristic of the deepest muddy bottoms of oceans and seas. In some environments, sponges are the dominating organisms; sometimes they cover wide areas, especially on rocky overhangs and in the caves of the littoral, or shore, zone. A restricted number of species are adapted to brackish waters; and members of the family Spongillidae (class Demospongiae) populate the fresh waters of rivers and lakes.

Classification

PHYLUM PORIFERA (Sponges): about 5,000 species.

Class Calcispongia

Skeleton of spicules of calcium carbonate; species either vase-shaped compact structures, loose networks of thin tubes, or irregular massive colonies; mostly small in size; inhabit shallow waters of all seas, from intertidal regions to depths of 200 m (660 ft); a few species to 800 m (2,600 ft); about 300 species.

Class Hyalospongia

Skeleton basically of hexactinal (6-rayed) siliceous spicules and lacking in spongin; exclusively marine, in deeper waters of all seas, depths from 25 to 8,500 m (80-29,000 ft); commonly fixed firmly to a hard surface, some species anchored in soft bottom sediments; about 500 species.

Class **Demospongia** Skeleton of either 1- or 4-rayed siliceous spicules, spongin fibres, or both; skeleton lacking in a few primitive genera; most abundant and widely distributed group of sponges (about 4,200 species); occur from intertidal regions to depths of about 5,500 m (18,000 ft) in seas; Spongillidae the freshwater sponge family.

PHYLUM COELENTERATA (CNIDARIA)

Cnidarians are invariably aquatic organisms, mostly dwelling in seas, but some species also inhabit in brackish and fresh waters. Metazoa, either sedimentary of free-swimming, with primary radial structure.

Features:

1. The body wall (Fig. 5) composed of two layers of cells, the ectoderm and endoderm, and between these a layer secreted by them (mesogloea).
Within the body wall a single cavity, having a single opening for ingestion and egestion, and often complicated by canals.
2. Digestion is both intracellular and extracellular.
3. The nervous system is as the network of cells.
4. Nematocysts are present in this group.
5. Both sexual and asexual reproduction takes place. Special cnidarian larvae – planula.
6. Life cycle includes polype and medusoid forms; some polyps can form colonies.

This phylum includes about 9.000 species.

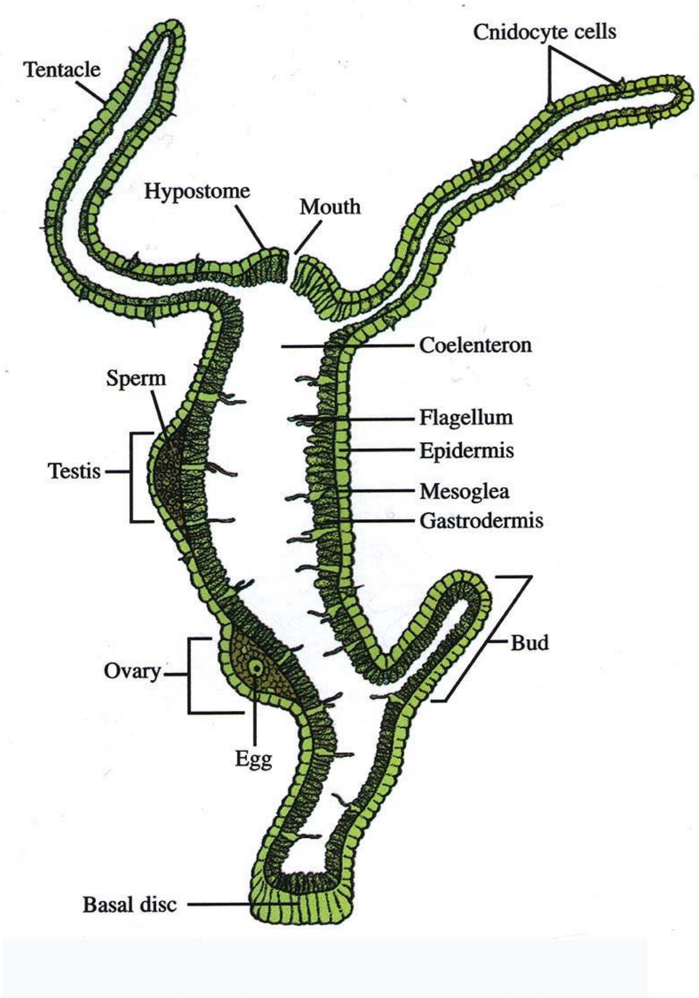


Fig. 5 *Hydra*, body construction

Classification

Class **Hydrozoa** (Fig. 6)**:** Cnidaria with both polyp and medusoid forms in their living cycle.

Class **Scyphozoa:** Cnidaria with medusoid stage as the main stage in the life cycle.

Class **Anthozoa:** Cnidaria with only polyp stage represented in their life cycle.

Class **Ctenophora:** Coelenterates without nematocysts; development is simple, without metamorphose

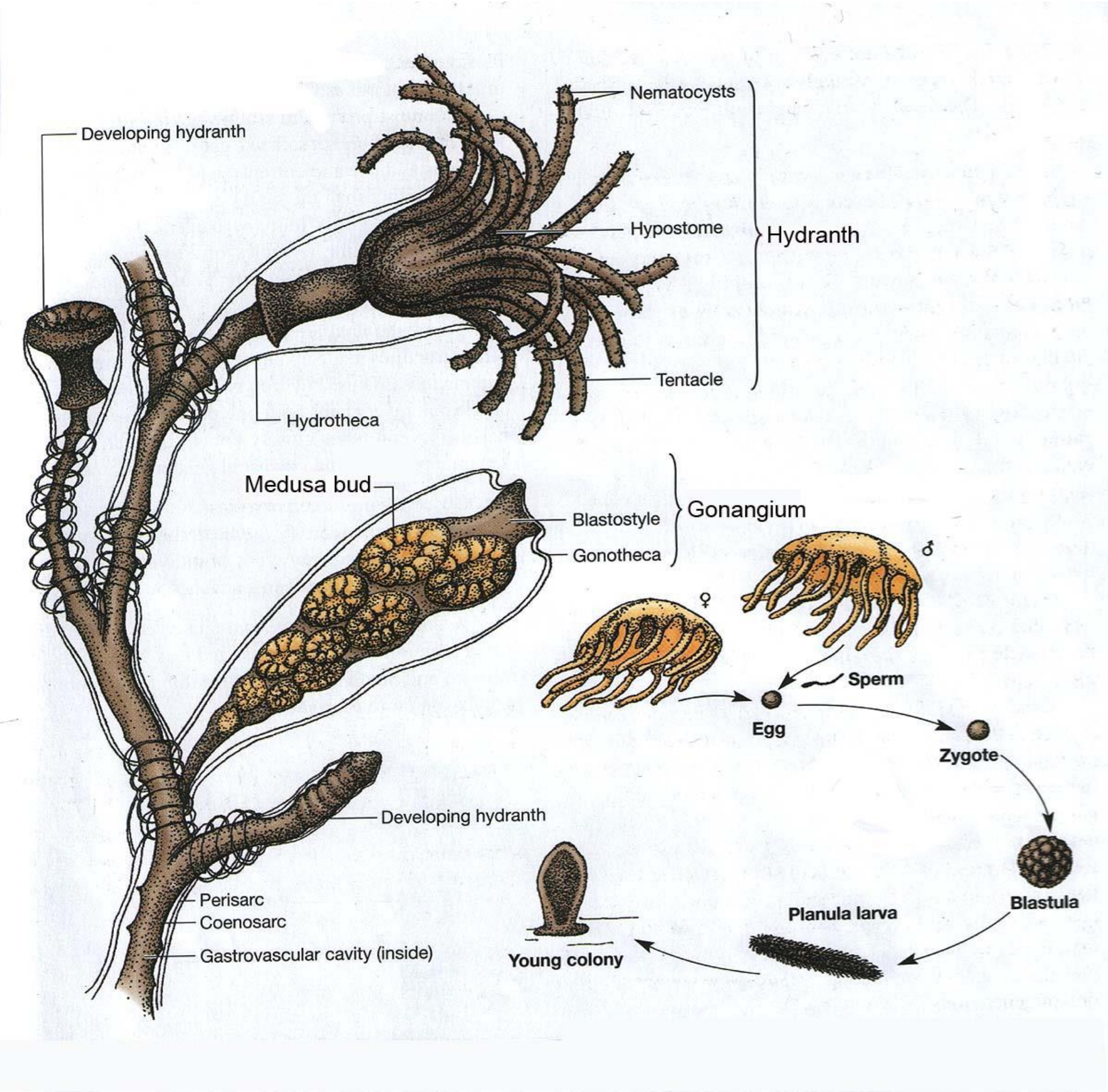


Fig. 6 *Orbelia* (Hydrozoa), life circle

THE ACOELOMATA

Under this title are grouped the phyla **Platyhelminthes, Nemertea, Rotifera, Nematoda, Gastrotricha, Acanthocephala** and **Nematomorpha** (the last three of which are very small groups). The animals contained in these are unsegmented forms with mesenchyme and the space between the gut and the body wall (when it exists) is a primary body cavity filled with fluid (e.g. **Rotifera**). The turgor of the body cavity fluid when present has a determining role in the preservation of the form of the body (e.g. **Nematoda** and **Rotifera**). Generally speaking this space with its contained fluid plays the part of a circulatory system, but in the Nemertea the body cavity is reduced to a series of canals which constitute the first vascular system in the animal kingdom. I his primary body cavity has no definite epithelial boundaries and so can be easily distinguished from a true coelorn. It tends to be invaded by mesenchyme cells; in the Platyhelminthes these completely fill it, forming a characteristic tissue (parenchyma), and in the Nematoda the cavity appears to be completely occupied by a very few enormous vacuolated cells whose vacuoles simulate a body cavity.

The excretory organ is of nephridial type (or it may be derived from this as in **Nematoda**). It is a canal, closed at the internal end, intracellular or intercellular, with some hydromotor arrangement which maintains a flow of fluid to the exterior. In the simplest cases there is a continuous ciliation of the inner wall of the canal (some **Turbellaria**). Usually, however, the ciliation has disappeared over most of the canal but is strengthened and differentiated in others; the characteristic units of the system, the flame cells, being now found. Flame cells may be situated in the course of the canal in some forms but usually constitute the *terminal organ*. This system, though usually spoken of as 'excretory', is primarily concerned with the regulation of fluid content and is often absent in marine forms (e.g**. Turbellaria Acoela**). A nerve net is usually present and from this are differentiated an anterior ' brain' and some longitudinal nerves. The reproductive system is that in which differences between and within the groups principally occur: these differences are to be regarded as adaptations to the varying conditions of life.

PHYLUM PLATYHELMINTHES

DIAGNOSIS. Free-living, and parasitic, bilaterally symmetrical, triploblastic Metazoa; usually flattened dorsoventrally; without anus, coelom or haemocoele; with a flame-cell system; and with complicated, usually hermaphrodite, organs of reproduction.

VERMES. The name Platyhelminthes is given to a division of that heterogeneous collection of animals which in Linnaeus's time were called Vermes. The Vermes included everything that looked like a worm, but appearances have since been found to be deceptive and the collection has been broken up into separate phyla, one of which is the Platyhelminthes or flatworms. Of all the worm-like animals the flat-worms are undoubtedly the most primitive, for they alone show relationships to the Coelenterata. Some authors have suggested that the Turbellaria are the most primitive of the Metazoa, and that the Coelenterates are derived from the Platyhelminthes.

CLASSIFICATION

Class **1. TURBELLARIA.** Free-living platyhelminthes, with a gut, a cellular ciliated outer covering to the body, usually havingrhabdites, not forming proglottides. Suckers are rarely present. The system-atics are based primarily on the arrangement and structure of the gut.

Order **1. Acoela.** The gut is not hollow but is a syncytium formed by the union of endodermal cells. There is no muscular pharynx. *Convoluta, Otocelis*

Order 2**. Rhabdocoela.** The gut is straight with the mouth at the anterior end. *Microstomum, Rhynchoscolex, Dalyellia*

Order **3. AIloiocoela.** The gut has small diverticula arising from it. *Plagiostomum, Hofstenia, Otoplana*

Order 4. **Tricladida.** Gut with three branches, one directed forwards, two directed backwards.

Suborder 1. **Maricola.** Marine forms. *Procerodes, Bdelloura Suborder*

2. **Paludicola.** Fresh-water forms.

Phagocata, Polycelis, Planaria Suborder

3. **Terricola.** Terrestrial forms. *Bipalium, Cotyloplana*

Order 5. **Polycladida.** Gut has many branches radiating out from central mouth.

Suborder **1. Acotylea.** No sucker. *Euplana, Leptoplana*

***Suborder 2*.** **Cotylea.** Have a sucker. *Thysanozoon, Yungia*

Order **6. Temnocephalea.** Ectocommensals on fresh-water crustaceans, reduced ciliation, develop prolongations on the anterior end, have suckers. *Temnocephala, Actinodactylella*

Class **2**. **TREMATODA.** Parasitic platyhelminthes with a gut, a thick cuticle, and suckers that may be thickened by a series of chitinous ridges.

Order **1. Heterocotylea** *or* **Monogenea.** Oral suckers usually absent or poorly developed, posterior suckers usually well developed and complex. No alternation of hosts. *Polystomum, Octobothrium*

Order 2. **Malacocotylea *or* Digenea.** Anterior sucker well developed, alternation of hosts. *Distomum, Schistosoma*

Class **3**. **CESTODA.** Endoparasitic platyhelminthes, no gut, adult has lost ciliated ectoderm and replaced it by a thick cuticle; proglottides usually formed.

Order **1. Cestodaria.** Tapeworms with undivided bodies, do not form proglottides. *Amphilina*

Order 2. **Eucestoda.** Tapeworms with body divided into proglottides. *Taenia, Diphyllobothrium, Moniezia*

GENERAL ACCOUNT

Of these the Turbellaria are with few exceptions free-living, while the I rcinatoda and Cestoda are all, without exception, parasites. It is in the I ii rbellaria that we see most clearly the typical organization of a platyhelminth, lor in the Trematoda and Cestoda the parasitic habit has induced a consider-.iNc departure from the structure of the free-living ancestor.

In shape the Platyhelminthes are flattened, they are not segmented and do not possess a coelom. The ectoderm is ciliated in the Turbellaria, but the filiation is lost in the two parasitic groups and there are further modifications.
The gut, which is present only in the Turbellaria and Trematoda, has but iine opening which serves both as mouth and anus, and in this respect icminds us of the Coelenterata. Between the ectoderm and the endoderm which constitutes the lining of the gut there exist a large number of star-shaped cells with large intercellular spaces forming a mass of *parenchymatous tissue.*

The nervous system consists essentially of a network as in the Coelenterata, with the important difference that there is an aggregation of nerve cells at the .interior end which, in the free-living forms almost always takes the form of a pair of *cerebral ganglia,* and that certain of the strands of the network stretching backwards from these cerebral ganglia are often more distinct than others .ind merit the name of nerve cords. There is, therefore, the beginning of a definite central nervous system. There are no ganglia other than lie cerebral, but in the general nervous network nerve cells and nerve fibres ,irc mixed together.

LICTODERM. The outer covering of a platyhelminth differs according to the r.i oup to which it belongs. In the Turbellaria the outer covering is formed of cctodermal cells. These are usually large and flat, sometimes with peculiar II ranched nuclei as in *Mesostomum,* or smaller and with round nuclei as in the majority of forms. Externally the cells are ciliated, the cilia being arranged in 11 acts over the surface of the body. Inside the cells are seen a number of i. -rystalime, rod-shaped bodies, known as *rhabdites.* Although much has been written about rhabdites their function remains obscure. They are a secretion, more or less firm, which dissolves and becomes liquid in contact with water. I 'hey are formed in special cells, lying either between the ectoderm cells or just beneath them in the parenchyma, and distributed thence to the ectoderm i.-clls. Rhabdites are usually absent from the ectoderm cells in the neighbourhood of sense organs. It will be noticed that when Turbellaria are placed for preservation in an irritant fluid such as acetic acid the body becomes covered with an opaque white layer. Whether this opaque layer is produced from the rhabdites or from the slime glands which occur in certain regions of the body is not certain.

BASEMENT MEMBRANE. Immediately below the ectoderm lies the basement membrane. This is a thin transparent structureless layer, which probably assists in preserving the general shape of the body and serves as an attachment for the muscles which lie immediately beneath it.

The basement membrane is continuous over the body except where it is penetrated by the openings of gland cells. It is absent beneath the ectoderm, overlying the sensory areas. In certain parts of the ectoderm, notably in the pharynx of the Tricladida, the nuclei of the ectoderm cells sink through the basal membrane and its underlying muscle layer and come to lie in the parenchyma attached to the cells by long strands of protoplasm. In the Trematoda and the Cestoda, the ectoderm cells have all sunk into the parenchyma, and the body is covered by a thick cuticle secreted by the ectoderm cells.

PARENCHYMA. The parenchyma (also called the *mesenchyme),* which fills the interior of the body, is of very different structure in different Platyhelminthes. It is generally formed of cells with long irregular processes and much intercellular space. Within these cells are small granules and particles, which slain readily. Their appearance and number vary according to the state of health of the animal, whether it is starved or fed, and they are probably, therefore, products of secretory activity formed after the assimilation of food and destined eventually to be converted into rhabdites or the slime which flows from the slime glands. The parenchyma is no mere padding tissue. It probably serves for the transport of food materials, and certain cells in it provide for the repair of lost parts of the body. These free cells of the parenchyma retain their embryonic condition and do not become vacuolated or branched. They are smaller than the branched cells of the parenchyma and scattered among them in normal circumstances, but when an injury occurs they migrate to the cut surface, where they collect in large numbers and proceed to regenerate the tissues lost by injury.

MUSCLES. Passing through the parenchyma and running dorsoventrally are strands of muscle which are attached at either end to the dorsal and the ventral muscle layers. The muscles themselves consist of fibres formed of a homogeneous transparent material that shows no trace of any structure. These fibres are produced by a special cell, the *myoblast,* which is often to be seen lying alongside the fibre it has produced.

DIGESTIVE SYSTEM. The digestive system of the platy helminth differs entirely from that of the higher animals in that it is a sac with one opening only, which serves both for the entry of the food and the exit of the faeces, and not a tube with a mouth and anus serving separately for the entry and exit of food. In the simplest forms, in many of the Rhabdocoela, the sac is a straight wide tube with no diverticula, while in others the gut is branched. In the Tricladida the gut has three main branches. A muscular structure lined by an inturning of the ectoderm surrounding the mouth forms the *pharynx.* The pharynx itself may lie in a pit of the ventral body wall, called the *pharynx pouch,* from which it can be protruded or withdrawn. The epithelial lining of the gut cavity consists of large cells without cilia, the cell walls of which are often difficult to distinguish. A muscular wall to the gut is present, but is so exiguous as to avoid identification in many forms, and it appears therefore as if nothing separates the cells of the gut from the parenchyma. It is possible for food substances to pass not only from the lumen of' the gut into the cells lining it, but also from the parenchyma. Thus when Turbellaria are starved they can consume certain organs lying in the parenchyma (ovaries, testes, etc.) by passing these into the gut cells or into the lumen i 'I' the gut for digestion.

The Turbellaria are carnivorous and will eat small living Crustacea or worms which are caught by the protrusion of the pharynx. A sticky secretion, derived from the slime glands and perhaps the rhabdites, is immediately poured over t lie prey, which is thus wrapped up in slime. If the object is small enough it is ingested whole into the gut. Here digestion proceeds. Fat is digested in the lumen of the gut, but the digestion of other substances takes place in vacuoles in the cells of the gut wall. Animals which have recently died are also eaten by Turbellaria, and an effective trap can be made by placing a freshly killed worm or a *Gammarus* or two in a jampot and lowering it to the bottom of the stream or pond. The Turbellaria are able to 'scent out' the food, and all those within a wide area collect in the pot for the feast. When the animal is too large to be ingested whole, the pharynx is attached to the prey and worked backwards and forwards with a pumping motion, while at the same time a disintegrating digestive fluid is poured out from the walls of the pharynx. Particles of food are thus pumped up into the gut cavity and digested in the same way as the living prey. In the Trematoda, also, the cells lining the gut have a certain limited power of amoeboid movement at their exposed edges, and intracellular digestion is apparently the usual method.

STARVATION AND REJUVENATION. The Turbellaria are able to go without food for long periods, but during starvation they grow smaller and smaller. Stoppenbrink starved *Planaria alpina,* keeping them entirely without food, while as a control he kept a similar collection supplied with food. His results are given in the table below. The measurements are in millimetres.

This reduction in size is accompanied by the absorption and digestion of the internal organs, which disappear in a regular order, the animal using these as food in the manner already described. The first things to go are the eggs which are ready for laying, then follow the yolk glands and the remainder of the generative apparatus. Finally the ovaries and the testes disappear, so that the animal is reduced to sexual immaturity. Next the parenchyma, the gut and the muscles of the body wall are reduced and consumed. The nervous system alone holds out and is not reduced so that starved planarians differ in shape from the normal forms in having a disproportionately large head end, the bulk of which is the unreduced cerebral ganglion. On feeding these starved forms will regenerate all the lost organs and return to the normal size, like Alice when she ate the right half of the mushroom.

NERVOUS SYSTEM. The nervous system consists essentially of a network as in the coelenterates with the important difference that there is an aggregation of nerve cells at the anterior end which, in the free-living forms, almost always takes the form of a pair of cerebral ganglia, and that certain of the strands Stretching backwards from these cerebral ganglia are often more distinct than Others and merit the name of nerve cords. There is, therefore, the beginning of a definite central nervous system. There are no ganglia other than the cerebral but in the general nervous network nerve cells and nerve fibres are mixed together.

By operating on the animals in different ways it is possible to show what functions the different parts of the nervous system have. If the cerebral ganglion of a Polyclad is removed, the body of the animal remains permanently quiescent after the operation. This state of quiescence is not, however, due to a loss of co-ordination in the motor system. Stimulation of the anterior end can evoke all the normal forms of locomotion, and this shows that the nerve net and not the cerebral ganglion is responsible for the correlation of the different parts of the musculature. The primitive central nervous system which here takes the form of a cerebral ganglion is best regarded as a development In connexion with the special sense organs, from which it receives stimuli. The cerebral ganglion functions as a relay system in which the stimuli received from the special sense organs are reinforced, often extended in time, and then passed on to the nerve net. When this sensory relay has been destroyed by removing the cerebral ganglia, the nerve net is no longer excited to bring the muscular system into action, although this may still be done by artificial stimuli.

SENSE ORGANS. Sense organs occur in adults only in the free-living Turbellaria, where they may take the form of eyes, otocysts, tentacles and ciliated pits in the ectoderm. They may also occur in the free stages in the life history of the Trematoda and Cestoda. The *eyes* occur on the dorsal surface where they are visible as dark spots. The retina is formed of cup-shaped cells, which are heavily pigmented. The interior of the cup is filled with special nerve cells, varying in number from two to thirty, the fibrillae of which touch the retina, and the fibres at the other end are joined together to form an optic nerve leading to the brain. There is no lens, but the ectoderm over the eye is not pigmented and so permits light to pass through it. It should be noted that in this simple eye, as in the extremely complicated organ found in the vertebrates, the light has to pass through the sensory cells of the nervous system before it reaches the retina, for they are in front of, not behind, the retina. This type of eye is easily seen and studied in the common fresh-water planarians. In *Planaria lugubris*, the eye has only two sight cells, while in *Planaria lactea* there are thirty.

Special sensory cells which act as receptors for the appreciation of changes In the composition of the surrounding medium (chemo-sensory receptors) or to changes in the flow of water past the surface of the body (rheotactic receptors) are situated just below the ectoderm. Their endings project through the ectoderm and form the actual receptor organ. The taste receptors are spread uniformly over the surface of the body in the Rhabdocoelida, but tend to be more numerous near the mouth. The endings of the taste receptors project among the cilia and are of the same length as these. The rheotactic receptors are confined to certain areas; their endings project among the cilia and are slightly longer than these. Special chemo-sensory receptors with short nerve endings that project only just above the surface of the ectoderm occur in definite areas or grooves on the head. Here the cilia and rhabdites are absent. These areas are known as auricular organs. These sensory organs may also be sunk into pits which, as they are provided with long cilia for driving the water into them, are known as *ciliated pits*.

The *tentacles* are projections of the body wall near the anterior end. They are found in the Turbellaria only, but are not present in all these. When present they are quite distinct and have very long cilia which, by their motion, set up currents which pass the water over special sensory areas and so lead us to suppose that their use is for water-testing, or searching for food. Occasionally these tentacles may be sunk into pits.

A statocyst occurs in primitive forms of the Turbellaria. It is situated above the brain and suggests a connexion with the Coelenterata where such sense organs are common, but as we know nothing of its nervous supply it is difficult to make a proper comparison.

LOCOMOTION. Movement in the Platyhelminthes is effected in two ways. The animal may creep over a surface by the motion of the ectodermal cilia, the surface being freely lubricated when necessary, as is the case in land forms by the discharge of slime from the ectodermal slime glands. More rapid movement is effected by the general musculature of the body which causes a series of undulations to pass backwards along the flat body and urges it forward. The *musculature* of a platyhelminth consists of a covering of muscle lying just below the ectoderm and composed of two layers, an outer circular and an inner longitudinal layer, except in the Cestoda and in the pharynx of the Turbellaria where the outer muscles are the longitudinal and the inner the circular.

EXCRETORY SYSTEM. An excretory system exists in nearly all Platyhelminthes. In the Acoela, however, it is absent. The excretory system usually consists of main canals, running down either side of the body. The position of the openings of these main canals to the exterior varies. The main canals are fed by smaller branches which are ciliated, while the main canals are not. These smaller branches again branch many times and finally end in an organ known as *a. flame cell*. The large canals are often quite easily visible in living specimens, but the flame cell is exceedingly small and can only be seen in transparent forms as in the cercaria larvae of the Trematoda. The flame cell itself consists of a cell with branched processes extending amongst the parenchyma cells. Attached to the cell are a number It is from this flickering motion that the cell derives its name. It is generally believed that excretion of substances into the lumen of the tube is performed by the cells forming the wall of the tube itself. The flame cells represent concentrations of the originally complete ciliary lining of the canal and their function is to maintain a hydrostatic pressure which will cause the excreted substances to move down the lumen of the tube to the exterior (cilia in the flame cells work against the colloid osmotic pressure of the body fluids and let water, salts and sugars into the flame cells. The required materials are later readsorbed in the proximal tubules and it is possible though not proven that specific excretory materials may be secreted into the tubules. In this way the animals are definitely able to osmoregulate and possibly excrete via their nephridia. It is conceivable that the lack of excretory organs In some of the Acoela is correlated with the presence of a symbiotic protistan.

REPRODUCTIVE ORGANS. Itisin the generative organs that the Platyhelminthes show the greatest complexity of organization. With rare exceptions the Platyhelminthes are hermaphrodite. The *generative pore* is variably placed but it is usually to be found in the middle line of the ventral surface not nearer to the anterior or posterior end than one-quarter or one-fifth the length of the body. This pore leads into a space known as the *genital atrium.* Into the genital atrium open the separate ducts leading from the male and female portions of the generative system, together with other accessory organs. The homologies of the various accessory portions of the generative organs in the three different groups are difficult to ascertain. Names are often used which were applied to organs before their homologies were ascertained, and this increases the confusion.

In studying the generative systems in actual specimens elaborate reconstruction from sections is often necessary, as the heavy pigmentation obscures them when the animal is viewed by transmitted light. In transparent specimens careful staining will bring to light most of the parts, but it often requires considerable skill and practice to identify these parts.

The organization of the platyhelminth generative system may be reduced to a general plan as follows. The *testes* are round bodies, often very numerous, having a lining of cells which give rise to the spermatozoa. From the testes lead out ducts, the *vasa efferentia,* which, uniting, form the *vas deferens.* There are usually two vasa deferentia collecting the sperm from the testes on either side of the body. The ends of the vasa deferentia are often distended and act as *vesiculae seminales.* The vasa deferentia unite and lead into a pear-shaped bag with very muscular walls. This is *the penis.* At rest it opens into the genital atrium, but during copulation it is extruded through the genital pore to the exterior and pushed into the genital pore of another individual. The penis is usually seen very easily, being one of the most conspicuous parts of the genital apparatus.

The female portion of the generative system consists of the *ovary,* which produces the ova, and the *vitellarium,* which supplies the ova with yolk and a shell. The shell substance is liquid and hardens later. This division into ovarium and vitellarium (or 'yolk gland' as it is sometimes called) occurs throughout the Platyhelminthes, but it is probably an elaboration of the more usual arrangement of forming the yolk in the ovary, an arrangement which occurs in the primitive Acoela and in the Polycladida. The ovaries discharge their ova into an *oviduct* which is enlarged near the point of this discharge and thus forms a *receptaculum seminis.* Here fertilization occurs. The oviduct nexl receives the opening of the *vitelline ducts.* After the opening of the vitellinc ducts the duct continues as the *ductus communis,* and leads into the genital atrium. At the junction of the oviducts and vitelline ducts there is a thickeniny of the walls of the duct and certain glands, the 'shell' glands, pour a secretion on to the egg which probably assists in hardening the shell. This thickening is indistinct in the Turbellaria but is very marked in the Trematoda, and the structure there receives the name of *ootype,* because it is the place where the egg is shaped before being passed into the uterus for storage. In the Trematoda the ductus communis is long and coiled and serves for the storage of eggs. It is called the 'uterus', but it is not of course homologous with the ‘'uterus' of the Rhabdocoela which will be described shortly, nor with the 'uterus' of the Cestoda which is again probably a different organ.

The genital atrium receives not only the openings of the male and female organs but also certain accessory organs. **In** the Rhabdocoela, of which *Mesostoma* is an example, there open out from the genital atrium on either side the paired *uteri* in which the eggs are stored before laying. In *Dalyellia* the fertilized eggs pass into the parenchyma. There is another opening which leads into a short muscular receptacle, the *bursa copulatrix.* The bursa copulatrix receives the penis of another individual during copulation. Sperm is deposited here but remains only for a short time before being expelled by muscular contractions and received into the oviduct where it is collected near the ovary in the true receptaculum seminis. In the Tricla-dida the uterus and the bursa copulatrix are replaced by organs, the homologies of which are doubtful. These are the unpaired *stalked gland organ* and the unpaired *muscular gland organ.* The stalked gland organ is often called the 'uterus' but it has not been observed to contain eggs. It is regularly present, whereas the muscular gland organ is often absent. It has recently been shown that the stalked organ serves as a bursa copulatrix and receives temporarily the penis and the sperm of another individual.

COPULATION. During copulation the ventral surfaces of two animals are applied together so that the genital openings lie opposite to each other. The penes are extruded through the genital opening of one copulant into the genital opening of the other. There is a mutual exchange of sperm. Since the ova are ripe at the same time as the sperm, and as, in many forms, there is only one common genital opening to the exterior, special precautions are necessary to prevent self-fertilization. To ensure that cross-fertilization shall take place a great elaboration of the structures surrounding the genital atrium has occurred, resulting in that complication of the genitalia which is **so** characteristic of the Platyhelminthes.

In fresh-water Tricladida copulation occurs fairly freely among animals kept in glass jars, where they are easily observed. When the penis is retracted its lumen is closed so that sperm cannot escape into the genital atrium, whence it might find its way up the oviduct. When the penis is thrust out through the genital opening during copulation it is dilated on extrusion, so that the lumen is opened. This dilation also causes the penis to fill completely the genital atrium and opening, so that the opening of the oviduct into the genital atrium is blocked and no sperm can enter or ova escape. At copulation the penis of one animal is squeezed past the penis of the other into the genital atrium. It cannot enter the oviduct, since this is blocked and so it is received into the stalked gland organ, where the sperm is temporarily deposited. After copulation is finished, the penes are withdrawn and the sperm is transferred from the stalked gland organ to the oviduct. The arrangement of the organs round the genital atrium in the Tricladida varies considerably. In *Bdell-cephala*, for example, the penis is reduced and, when extruded, does not fill the genital atrium sufficiently to block the opening of the oviduct. In this case a flap of skin has developed which is drawn over the opening of the oviduct when the penis is extruded.

After the sperm is transferred to the oviduct, it moves up to the receptaculum seminis at the top, near to the point of discharge of the ova. The ova are fertilized in the oviduct and then move down towards the genital atrium, receiving on the way the products of the vitellaria. On arrival in the genital atrium a cocoon is shaped and made ready to be deposited. When laid it is usually attached to weeds, sometimes by a stalk.

EGGS. The parasitic Trematoda and Cestoda are unaffected by the seasons and are perpetually producing eggs. But in the Turbellaria the season of egg-laying varies. In some, for example *Dendrocoelum lacteum,* the generative system is in full working order all the year round, in others, for example *Planaria alpina,* the eggs are only produced during the winter months. *Mesostoma* produces two kinds of eggs which are called 'summer' and 'winter' eggs. The 'winter' eggs have a thick shell and are well supplied with yolk; they remain in the uterus and escape only with the death of the parent. The 'winter' egg can remain dormant for a long period. The 'summer' egg is very thin-shelled and has very little yolk. The development is very rapid and the young embryos are seen moving in the uterus of the parent seventy-two hours after the appearance of the eggs. They escape by the genital pore and their formation does not involve the death of the parent. The term 'winter' and 'summer' egg is not entirely apposite, for 'winter' eggs are often found in midsummer. The 'winter' egg is a method of carrying the species over unfavourable conditions which may develop in winter or in summer. The ' summer' egg is a means for rapid multiplication when conditions are favourable.

EMBRYOLOGY. With the exception of the Acoela and the Polycladida the eggs are provided with special cells that look after the nutrition of the developing embryos, but in the Acoela and Polycladida the yolk is enclosed in the egg, the egg being endolecithal. The egg divides into four blastomeres which then divide to form a total of eight cells. This division is unequal in that there are four large cells and four small ones, the macromeres and micromeres. The micromeres do not lie immediately above the macromeres, instead they lie above and at an angle of 45° to the macromeres. This type of cleavage is called spiral cleavage in contrast to the radial cleavage seen in echinoderms and the bilateral cleavage found in ctenophores.

The development of the turbellarian embryo is very much like that of the annelids and reference should be made to p. 291 for details of the development and the terms used to describe the development. The cells of the first quartet give rise to the main body ectoderm as do also 3A-3D; 4of forms the body of the mesoderm and also the endoderm, the situation being similar to that found in the annelid trochoblast cell *4d.* In addition, during the early stages of development it is possible to pick out a small rosette and quartet much like that seen in the polychaetes. The larva develops a temporary frontal tuft homologous with the apical tuft of the trochophore; this disappears at a later »tage of development.

Gastrulationis epibolic, forming small gastrulae with no enteron. Near the blastopore a small invagination arises that gives rise to the pharynx and intestinal cells, the latter moving to form a small cavity, the gut. The embryo then develops to become a small planarian. This is the direct development.

In some Polyclads, i.e. *Hoploplana,* and in all the Cotylea, instead of direct development into an adult the embryo develops into a pelagic larva,' Miiller's larva'. This larva has eight ciliated lappets by which it swims for a few days. These lappets are then absorbed and the larva stops being planktonic and settles down to a life of crawling on the sea bottom. In *Stylochus* the embryo only develops four lappets and the larval form is then called ' Gotte's larva'. It is interesting to note that *Planocerareticulata* goes through a Miiller's larva stage whilst still retained within the egg case.

As mentioned on p. 143, projecting processes forming arms and bands of cilia are common and belong to many different phyla. Their presence is probably an adaptive feature and it is unwise to base phylo-genetic speculations on them. Muller's larva is planktonic and acts as a distributive phase in the life of the animal.

ASEXUAL REPRODUCTION AND REGENERATION. Asexual reproduction occurs commonly in the Turbellana. In *Microstomum lineare* the hinder end buds off new individuals which remain attached for some time so that chains of three or four individuals in different stages of development are often seen. Planarians undergo autotomy, cutting themselves in two by a ragged line which traverses the middle of the body. Lost parts are easily regenerated in the Tricladida and the group is a favourite one for experimental work on regeneration.

The interstitial cells play an important role in regeneration of planarians. If one takes a white planarian and cuts off its head a new head will soon be regenerated. If one repeats the experiment but this time irradiates the body with X-rays then a new head will not grow. If one takes such an irradiated decapitated animal and implants a small piece of tissue from a black non-irradiated animal, the white animal starts to regenerate a new head. The tissue in the head is largely formed from the black implanted tissue as can be seen from its pigmentation. The cells that are most responsible are the interstitial cells, and it will be recollected that these cells are important in regeneration of the coelenterates too.

Having thus provided the reader with a general account of the organization of a platyhelminth it will now be possible for us to follow the systematic arrangement of the phylum, to define the divisions and to point out features of interest in various forms and life histories.

CLASS 1. TURBELLARIA

The Turbellaria may be defined as Platyhelminthes which are nearly all free living and not parasitic, which retain the enteron; which have a cellular, ciliated outer covering to the body; which usually have rhabdites; and which do not form proglottides. Suckers are very rarely present.

The systematic arrangement of the Turbellaria is based primarily on the structure of the gut. There are six orders: (1) Acoela, (2) Rhabdocoela, (3) Alloiocoela, (4) Tricladida, (5) Polycladida, (6) Temnocephalea

CLASS 2. TREMATODA

DIAGNOSIS. The Trematoda may be defined as Platyhelminthes which are parasitic; which retain the enteron; which in the adult have outside the ecto-derm a thick cuticle; which have suckers; usually, but not always, a sucker on the ventral surface in addition to one surrounding the mouth; the ventral sucker is subdivided in some forms and may also be stiffened with a ring-like chitinous skeleton.

The Trematoda are all parasitic but they resemble in general shape the Turbellaria. They have retained the mouth, which is anteriorly placed, and the gut, which, however, is bifid—a shape not found in the Turbellaria. As in the Turbellaria, the gut may have lateral diverticula which branch freely. The Trematoda have, however, lost the external ciliation of the Turbellaria. The ectoderm is represented by cells sunk into the parenchyma in much the same way as nuclei of the ectodermal cells in the pharynx of the Tricladida. But the outer portion of the cell is lost in the Trematoda and its place is taken by a thick *cuticle*, which is often armed with spines. Suckers are always present for attachment to the host and are of large size. The presence of these suckers and their shape makes it possible to divide the Trematoda proper into two orders: (1) Heterocotylea, (2) Malacocotylea.

CLASSIFICATION

1. *Order* **Heterocotylea.** Trematodes with only one host; suckers stiffened with chitinous supports. *Octobothrium, Polystomum.*

2. *Order* **Malacocotylea.** Trematodes with two or more hosts in their life cycls; suckers simple. *Fasciola, Schistosoma, Wedlia.*

1. *Order* Heterocotylea (Monogenea.)

DIFFERENCES BETWEEN HETEROCOTYLEA AND MALACOCOTYLEA.

` In the Heterocotylea there is a large posterior sucker stiffened with chitinous ipports. It is often subdivided, as in *Octobothrium* or *Polystomum*. In the Malacocotylea the sucker is not always posterior, it often moves forward on the ventral surface so that, as in *Fasciola,* it comes to lie one-third of the body-length from the anterior end. It is never provided with chitinous supports. All the Heterocotylea are ectoparasites with the single exception of *Piilystomum* which occurs in the bladder of the common frog, of which from 3 to 10% are infected by it. They are confined to one host only. The Malacocotylea are all internal parasites nd pass from one host to another at certain stages in their life history. In the Heterocotylea the excretory pores are paired and lie near the anterior end of the body, whereas in the Malacocotylea the excretory system discharges to the exterior through a single median pore placed at the posterior end of the body. In the Heterocotylea there arc separate openings for the male and female portions of the generative •yiitom, while in the Malacocotylea there is but one common opening. In the Heterocotylea there is a pair of ducts leading from the ootype to the exterior ndependently from the male and female ducts, usually called the *vaginae*. The vaginae are inconspicuous as a rule, but in *Polystomum* their openings are very clearly marked by two prominences on either side of the body about one-fifth of the body-length from the anterior end. Corresponding ducts do not occur in the Malacocotylea. The nervous system of the Heterocotylea is more primitive than that of the Malacocotylea, but in both groups it is stereotyped and does not vary as it does in the Turbellaria. In both groups it consists of a cerebral ganglion th six cords leading posteriorly. In the Heterocotylea there are irregular missures between the cords, while in the Malacocotylea the commissures are few in number and regular.

LIFE HISTORY OF THE HETEROCOTYLEA. The habitat of this order is on the gills of fishes where they often live isolated. Self-fertilization must therefore be practised, ut copulation has been observed in *Polystomum* and also in *DIphzoon*, where it is permanent. The members of this order probably cause considerable inconvenience to their hosts, but the numbers infesting one host is seldom very considerable and y have no economic importance as parasites. The eggs when laid are normally attached to the body of the host.

Polystomum is exceptional in laying the eggs in the bladder whence they pass out to the exterior into water. The egg hatches as a larva with eyespots nd a large ventral posterior sucker. It swims by means of cilia which are arranged in bands round the body. These larvae make their way to some particular spot on the host after being free- swimming for a time. As soon as they attach themselves the ciliary covering is cast off and the generative organs develop. The larva of *Polystomum* seeks out a tadpole, dying within twenty-four hours if one is not found. If a tadpole is reached, the parasite fastens itself on to the gills, where its ciliary covering is cast and it then creeps into the bladder to wait for three years efore becoming sexually mature. The larvae may, however, attach themselves to the external gills, where a copious supply of nourishment induces such rapid growth that the animal becomes sexually mature in five weeks and produces eggs. But it dies when the tadpole metamorphoses, and thus it never reaches the bladder.

In *Diplozoon,* which lives attached to the gills of the minnow, the larvae attach themselves to the gills of the host, but they do not develop generative organs ntil they meet another larva. If such a meeting occurs the larvae fuse across the middle. After fusion the generative organs develop and the animals grow in such a manner that the vas deferens of one form is permanently connected to the genital atrium of the other. They thus remain throughout their lives in permanent copulation.

nother form which displays a variation of the usual type of history is *Gyrodactylus* which occurs in the gills of fresh-water fish. In *Gyrodactylus* the ovary and the vitellarium are not separated, as is the general rule in the Trematoda, but constitute one organ. A single egg ripens at a time and, after fertilization, develops into an embryo in the uterus. Before the first embryo leaves the mother a second younger one appears inside it so that we thus have a condition of three generations one inside the other, and the conditions are such that the youngest embryo must develop without fertilization. This feature of the development of one larva with another without the agency of fertilization is common in the life histories of the Malacocotylea but *Gyrodactylus is* the one member of the Heterocotylea in which it occurs.

2. *Order* Malacocotylea (Digenea.)

The life history of *Fasciola* may be taken as the type of life history commonly found in the group. For details of this life history the reader is referred to elementary text-books.

In the Malacocotylea the adult is always, with rare exceptions, parasitic in some vertebrate host, the sporocyst and redia stages are always parasitic in a mollusc. Two hosts are always, and three may be, necessary for complete development. Divergence from the typeoflife history recorded for *Fasciola* may come about by (I) a generation, the redia stage, being omitted, (2) the sporo-cyst forming by budding a second generation of sporocysts within which the cercariae arise, (3) the cercaria requiring to encyst in a host and to await this host being eaten by the final host before reaching sexual maturity as in the case of *Gasterostomum fimbriatum,* where the sporocyst develops in the liver of *Anodonta,* the cercaria encysts in the roof of the mouth of the roach and only reaches sexual maturity when the roach is swallowed by a perch.

In *Distomum macrostomum,* which is parasitic in the gut of thrushes, there is no free-living stage in the life history. The eggs, passed out with the faeces of the bird, are eaten by a snail, inside which the sporocyst develops. The sporouyst finds its way into one of the tentacles. It there develops pigment, being brightly coloured in bands of green and red, while its presence stops the snail from withdrawing this tentacle. Presumably this brightly coloured object attracts the bird which devours the snail and infects itself by setting free the cercariae from the sporocyst.

Schistosoma (=Bilharzia) is a parasite of man, living as an adult in the abdominal veins. It is long and thin and well adapted for this habitat. It is one of the rare examples of dioecious trematodes. The male, however, does not lose touch with the female once he has found her, but carries her permanently in a fold of the ventral body wall. The eggs are laid in the blood vessels and, being provided with a sharp spike, they lacerate the walls of the capillaries and pass into the bladder. Immediately the urine is diluted the miracidia hatch, but they wait for dilution before hatching. The second host is a water-snail. The cercariae swim freely in the water, and in districts in China and Egypt where the disease is common they swarm. Bathing, washing or drinking the infected water allows the cercaria to enter the final host. The cercariae penetrate the skin with great rapidity and, entering the blood system, make their way to the abdominal veins where they become mature. The disease can be prevented by strict sanitary measures in regard to water, and it can be cured by the administration of compounds of antimony to infected patienls. That the disease is a very old one in Egypt is shown by the discovery of *Schistosoma* eggs in the kidneys of mummies of the twentieth dynasty (1250-1000 B.C.).

The hatching of miracidia from the egg of *Schistosoma* is dependent on the dilution of the urine by fresh water and this serves to emphasize the fact that the stages in the life history of all parasites are ultimately connected with environmental conditions. The egg of *Fasciola hepatica* (Fig 7,8) does not hatch unless the pH of the water in which it is deposited is below 7-5, the optimum point apparently being about pH 6-5. If the eggs are kept in water more alkaline than pH 7-5 the embryo remains within the shell and eventually dies.

The identification of a cercaria with an adult is a task which requires great patience, and many cercaria are known which have not been as yet connected with an adult. Almost any mollusc, if dissected carefully under a hand lens, will provide specimens of rediae and cercariae, although infected specimens may be more common in some localities than in others. The tail of a cercaria is often an elaborate structure. Some have rings and chitinous stiffenings, while the well-known Bucephalus larva of *Gasterostomum* is a cercaria with a forked tail.

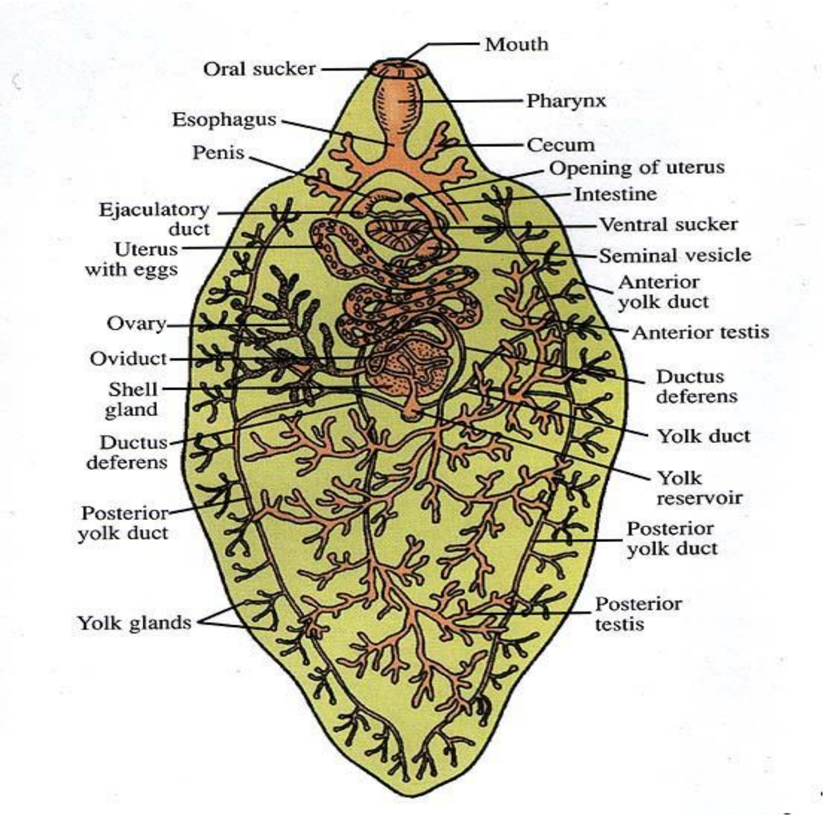


Fig. 7 *Fasciola*, whole mount

Other examples of the Malacocotylea are *Wedlia,* which is parasitic on fish and has the male carried in the female, *Diplostomum*, parasitic in birds, and *Phyllodislomum,* parasitic in amphibia.

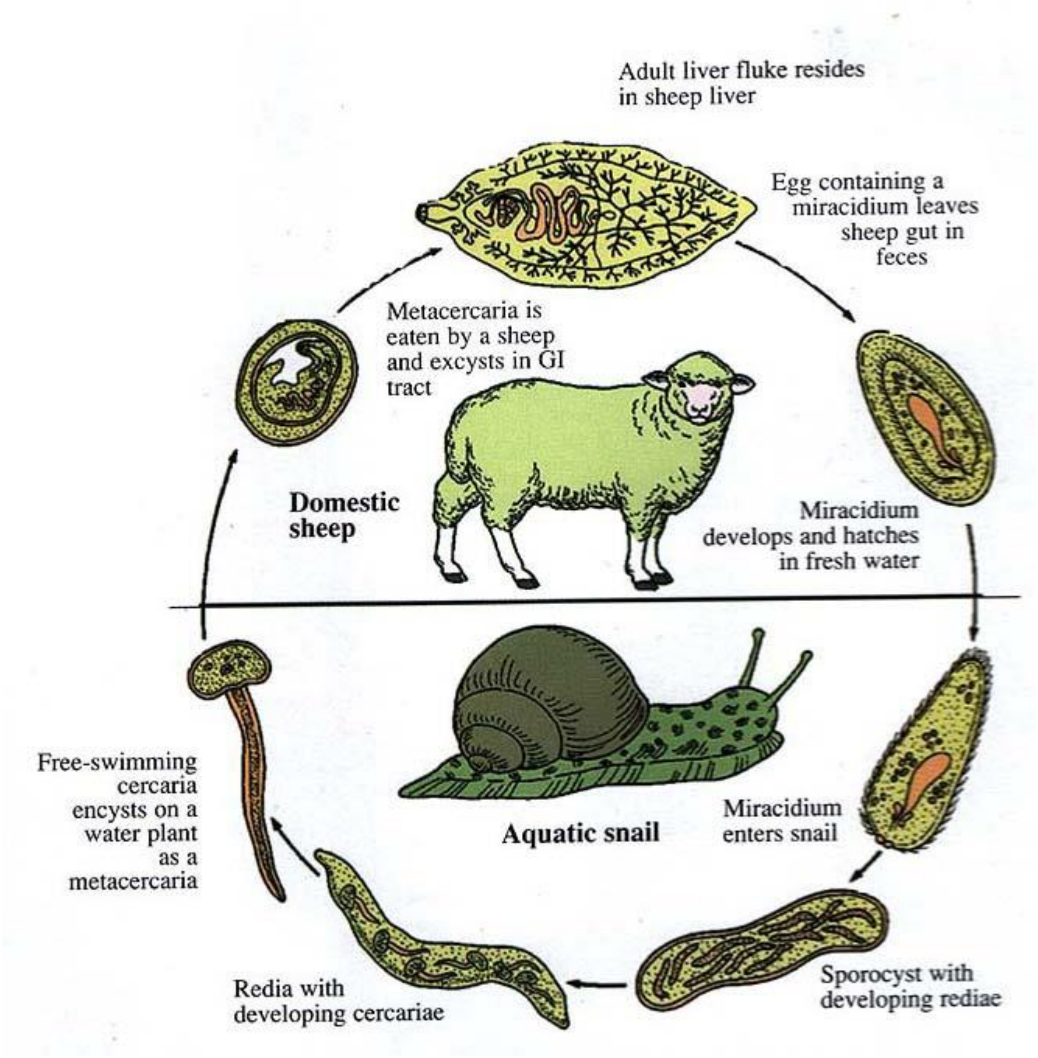


Fig. 8 *Fasciola,* sheep liver fluke, life circle

CLASS 3. CESTODA

The Cestoda (Fig. 9) may be defined as endoparasitic Platyhelminthes in which the enteron is absent and the ciliated ectoderm has, in the adult, been replaced by a thick cuticle. In the parenchyma lime cells occur. Proglottides are usually formed.

The Cestoda as a group have felt the influence of the parasitic habit more than the Trematoda. They have dispensed altogether with a gut, there is no mouth, and they absorb their food through the skin. As they live always in the alimentary canal of vertebrates they are conveniently situated for this purpose and the amount of food available to them probably counterbalances the difficulties attendant on dispensing with the usual method of digesting and assimilating food. The ectoderm cells have sunk into the parenchyma after secreting a cuticle as in the Trematoda, but this cuticle is thicker and divided into layers. Immediately beneath the cuticle are the longitudinal muscles. The circular muscles are incomplete at the edges. In transverse sections the circular muscles appear to divide the parenchyma into two regions, an outer cortical zone, where occur the cut ends of the longitudinal muscle together with calcareous bodies, and an inner or medullary zone, where the generative system lies.

The Cestoda may be divided into two orders: (1) Cestodaria, (2) Eucestoda

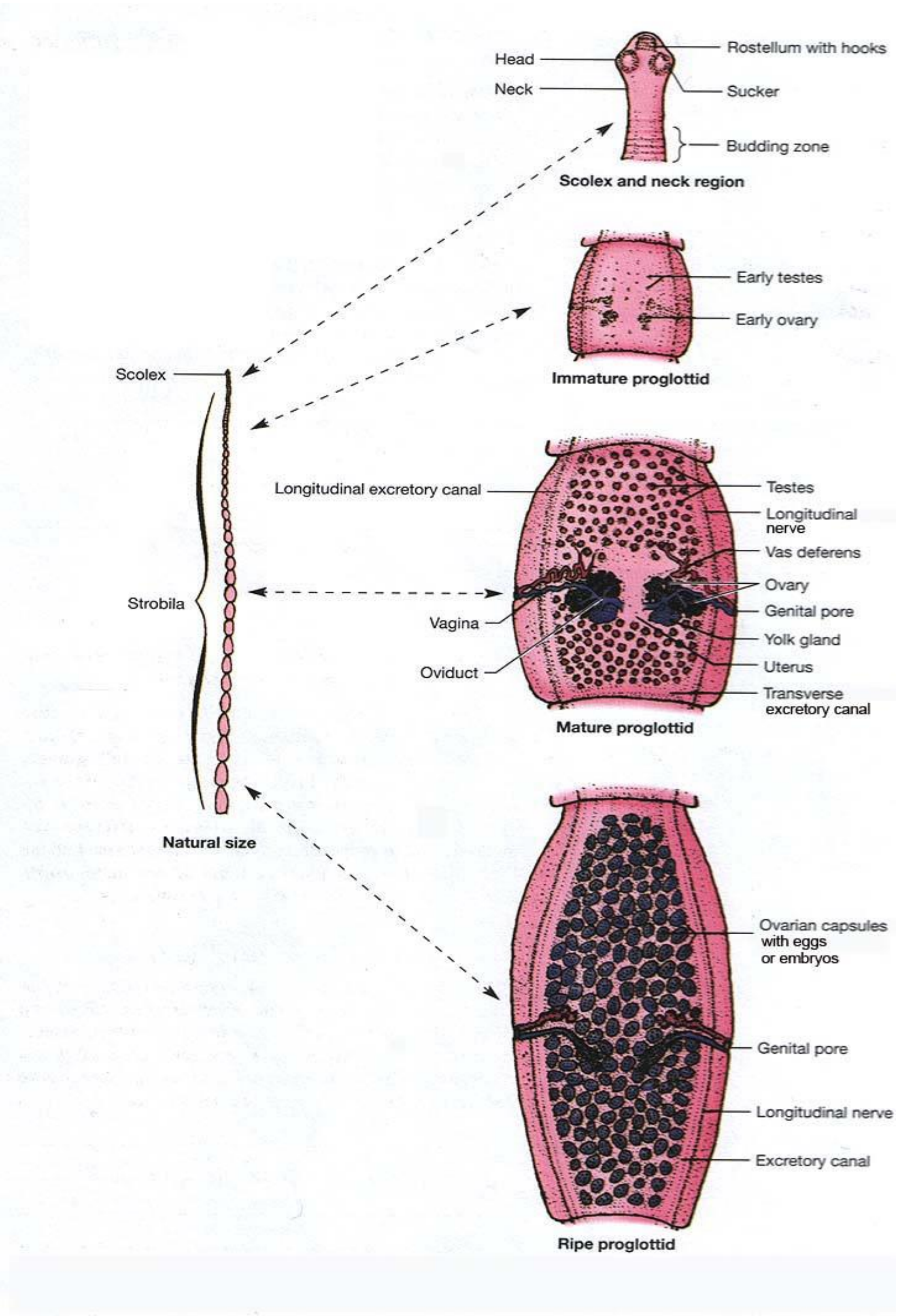


Fig. 9 *Dipylidium* (Cestoda), representative section of body

1. *Order* Cestodaria

These are small forms which live in the gut of fishes, usually Elasmobranchs. They resemble a trematode in shape and in the fact that they do not form proglottides, but they have no gut. They have at one end a 'frilled' organ which serves for attachment, and a small sucker at the other end. Examples of this order are *Amphilina* and *Gyrocotyle.* It is difficult from the structure to say which end is the anterior and which the posterior, for the nervous system consists of two cords running down either side of the body with a single similar commissure at either end. But when the animal moves it has the lulled' organ in front so that is spoken of as the anterior end.

2. Order Eucestoda

There are distinguished from the Cestodaria by the fact that they all have the power of budding and so reproducing asexually, resembling in this respect the turbellarian *Microstomum lineare.*

The adult worm has a *scolex* which is provided with organs of fixation such as. hooks, suckers or folds. The scolex is usually buried in the intestinal mucosa of the host. Behind the scolex comes the *neck*, the most slender portion of the body, which may or may not be sharply marked off from the scolex. It is in the neck that asexual reproduction occurs, fresh segments being continually cut off and, as they grow larger, pushed by the formation of new segments away from the scolex. The segment so formed is called *a. proglottis.* The proglottis is not truly comparable with the new individuals produced in *Microstomum lineare.* Through each proglottis run the excretory canals and the nervous strands which are common to all. The proglottis when first cut off from the neck region is devoid of generative organs, but these develop as it becomes more mature. When the generative organs are mature, fertilization of the ova occurs, the ovaries and the testes disappear, and the uterus alone remains to store the eggs. When the proglottis reaches this stage it is 'ripe' and breaks off to pass out with the faeces. Despite its connection with'the scolex, each proglottis must be regarded as an individual for it contains a full set of generative organs both male and female.

SCOLEX . The structure of the scolex is of importance, for it forms the basis of the classification of the Eucestoda. In the tape-worms occurring in the gut of fishes the scolex may have two or four suckers and the neck may be sharply separated from the region where budding occurs. In these tape-worms the scolex is often armoured with chitinous projections and hooks, and the number of the proglottides is usually small. The tape-worms occurring in the mammals *(Cyclophyllided)* are, with one exception, characterized by a head which bears four suckers at the sides, and, on a projection at the top, called the rostellum, is a crown of hooks.

PRIMITIVE CESTODES. As a general rule the more primitive cestodes are found in the lower vertebrates, while the advanced types are found in the mammals. The evolutionary stage of the parasite is therefore closely related to that of its host. A notable exception to this rule is *Diphyllobothrium latum*, the Broad Tape-worm of man, which belongs to a group of tape-worms occurring more commonly in the guts of fishes. The scolex of *Diphyllobothrium* has two suckers on either side of the head. These suckers are of the nature of flabby folds sharply distinct from the well-defined cuplike suckers of the Cyclophyllidea.

REPRODUCTIVE SYSTEM. The generative organs are of the same type as is found generally throughout the Platyhelminthes. There is a single opening for both male and female organs. From the ootype there leads out a duct which is called the *uterus* and is used for the storage of eggs, but it is doubtful whether it is homologous with the uterus of the Trematoda.

LIFE HISTORY. The life history of a cestode is a complicated combination of sexual and asexual reproduction. One, two or three hosts may be necessary. The egg passes to the exterior with the faeces. It contains inside it an embryo armed with six hooks called an 'onchosphere'. The egg case takes different shapes; in *Diphyllobothrium latum*, which is a more primitive type of cestode, the covering of the embryo is ciliated. In the Cyclophyllid tape-worms, which constitute the most advanced group of the Cestoda, the ciliary covering is lost. In *Dipylidium caninum,* the adult of which occurs in the alimentary canal of the cat or dog, it is replaced by an albuminous coat with a chitinous lining iside, while in most of the other forms only the chitinous covering persists. The egg hatches as an onchosphere after being swallowed by the first host. 'he onchosphere then penetrates the wall of the alimentary canal using its hooks for this purpose and lodges somewhere in the peritoneal cavity of the host. Here it develops suckers and a scolex.

In primitive forms, such as *Diphyllobothrium,* the larval cestode rests inside the first host, a *Cyclops,* at a stage of its development known as the plerocercoid stage. This stage is ovate in shape and the generative organs are undeveloped and there are no signs of proglottides. The *Cyclops* is then eaten by fresh-water fish, after which the larva, or plerocercus, bores through the wall f the alimentary canal and rests in the body cavity where it grows still further, ;aching the metacestode stage. Proglottides can be distinguished in the metacestode stage but the generative organs are not fully mature. Growth now ceases but the metacestode stage is often inconveniently large for the body cavity, causing it to bulge. Sticklebacks thus infected with the metacestode of *Schistocephalus gastcrostei* arc commonly found. The adult in this case reaches maturity when eaten by a bird. Man acquires *Diphyllobothrium latum,* a nearly related form, by eating pike infected with the metacestode.

In the Cyclophyllidea the resting stage in the first host is the ' bladder-worm' (or cysticercus). The onchosphere on reaching its resting place becomes hollowed out into a ball filled with fluid. A depression then forms in the wall of the sphere and becomes an inverted scolex. In *Taenia serrata,* the common tape-worm of the dog, the bladder stage in the rabbit (to which the name *Cysticercus pisiformis* was given before the connexion with the adult was discovered) has but one head inverted into the cyst. In the bladder-worm stage of *Taenia coenurus,* which is found in the brain of the sheep and causes the disease known as 'gid' or 'staggers', many heads are formed and in-vaginated into the cyst so that multiple infection may occur when a sheep is devoured and torn to pieces by dogs or wolves. In *Taenia echinococcus,* the adult of which lives in the alimentary canal of the dog and is remarkable for having but three proglottides, the cysticercus stage is found in domestic animals and also in man in countries where men live in close association with dogs. The cyst stage is very large and the bladder may contain a gallon or more of fluid. Such a cyst, known as a 'hydatid', rapidly proves to be fatal. It is particularly dangerous and difficult to eradicate because the walls of the cyst have the power of budding off asexually daughter cysts. A still further development of asexual budding in the cysticercus stage occurs in *Staphylo-cystis,* where the onchosphere imbeds itself in the liver and then develops a stalk or stolon which buds off cysts which are detached and fall into the body cavity of the host.

Where the cysticercus is swallowed by the final host the head is everted from the bladder, the bladder is digested and proglottides forthwith make their appearance from the neck region of the scolex. So far as is known the production of proglottides continues for the duration of the life of the host.

The subdivision of the Eucestoda depends on the shape of the scolex. There are five divisions, the last of which contains the forms commonly found as adults in the alimentary canal of the Mammalia and is the only group of economic importance.

1. **Tetraphyllidea.** The four suckers are usually stalked outgrowths of the scolex. Parasitic in fish, amphibia and reptiles. Onchosphere enters a copepod and develops into a larva known as a plerocercoid, in which condition it remains until the copepod is eaten, when it develops into the adult. Size moderate, usually 20-30 cm. long, but occasionally as small as 1 cm. or as large as 1 m. An example is *Anthobothrium*.

2. **Diphyllidea.** There are two suckers only and the scolex has a long neck armed with spines. There is only one family and one genus, *Echinobothrium,* which is found in the spiral intestine of Selachians. The larva, which is of cysticercoid form, is found in the prawn *Hippolyte.*

3. Tetrarhynchidea. These have four suckers each provided with a long spiniferous rectractile process. The adult is parasitic in the alimentary canal of Elasmobranchs and especially Ganoids. The larva, which may be of either the procercoid or cysticercoid type, occurs in marine invertebrates of many kinds, fish and occasionally reptiles.

4. Pseudophyllidea. The scolex has two suckers which may be absent in some forms, there is no clearly marked neck and hooks are usually absent. Occasionally as in *Trianephorus,* a common parasite of fresh-water fish, the external divisions between the proglottides are indistinct and these are only indicated by the regularly placed openings of the uterine birth pores. The majority of these are parasitic as adults in fresh-water fishes, but *Diphyllobothrium latus* occurs in man and *Bothriotaenia* in birds. *Archigetes* is parasitic as an adult in body of *Tubifex,* an oligochaete worm living in fresh water. The larva is a plerocercoid which in some forms, *Caryophyllaceus* and *Archigetes,* develops gonads paedogenetically so that there is no adult with proglottides. These paedogenetic forms closely resemble the Cestodaria in appearance.

5. Cyclophyllidea. The scolex bears four cup-shaped suckers and has a rostellum with a crown of hooks.

The Cyclophyllidea comprise the majority of the common tape-worms. Those infesting the gut of mammals all have a scolex closely resembling that of *Taenia,* with four well-defined suckers and a circlet of hooks. Those found in the gut of fish have a more elaborate scolex. The number of proglottides varies considerably, the smallest number is found in the genus *Echino-coccus,* while many forms have hundreds of proglottides and are several yards in length. The proglottides never drop off before they are mature, as they may do in the other groups, and develop generative organs later, consequently the separated proglottides always contain fully developed onchospheres. Two interesting forms may be mentioned. *Dipylidium caninum* is a tape-worm infesting the alimentary canal of dogs and cats. Each proglottis has a double set of generative organs with two separate generative openings, a feature which gives the animal its name, but which may occur in other forms. The first host is the flea, and puppies and kittens are early infected by catching and eating these insects. *Hymenolepis nana* is one of the smallest tape-worms. The adult has ten to twenty proglottides and only measures half an inch in length. It occurs in children in certain places, particularly Lisbon and New York, where it is said to be increasing. It is remarkable among tape-worms for being the only one known to go through all its life history in one host. The embryos bore into the intestinal wall where they pass through the cysticercus stage and emerge again into the alimentary canal when adult.

GENITALIA HOMOLOGIES. The homologies of the various ducts of the genitalia of the Platyhelminthes present great difficulties. While one or two, the oviduct and the vas deferens for example, are quite clearly homologous throughout, the homologies of others, particularly the accessory organs such as uterus, bursa copulatrix, vagina, are very doubtful. The 'uterus' of the Trematoda is clearly the ductus communis of the Turbellaria greatly elongated and used for egg storage, while the vagina of the Cestoda is the same, but the relation of the 'vagina' of the Heterocotylea or the 'uterus' of the Cestoda remains at present obscure.

If the vagina of the Cestoda is homologous with the uterus of the Trematoda, the uterus of the Cestoda, which is a single duct, may correspond to the vagina of the Trematoda, which is, however, a paired structure. The homologies of the ducts in the Trematoda are further complicated by the presence of Laurer's canal, a duct leading out of the ductus communis and opening to the exterior in the Malacocotylea but into the gut in the Heterocotylea. The bursa copulatrix and the muscular pear-shaped organ, which open into the genital atrium in the Turbellaria, are accessory reproductive organs which are probably not represented in the parasitic forms.

PHYLUM NEMATHELMINTHES

DIAGNOSIS.

- Unsegmented worms, with an elongated body
- Primary body cavity
- Ectoderm represented by a thin sheet of non-cellular hypodermis, secreting an elastic cuticle, made of protein, not chitin, usually moulted four times in the life of the individual;
- Cilia absent from both external und internal surfaces;
- A single layer of muscle cells underneath the hypodermis, divided into four quadrants, each muscle cell being elongated in the same direction as the body
- Excretory system consisting of two intracellular tubes running in the lateral lines;
- Nervous system made up of a number of nerve cells rather diffusely arranged but forming a circumpharyngeal ring and a number of longitudinal cords of which the mid dorsal and mid ventral are the most important;
- Sense organs of the simplest type;
- Sexes usually separate, gonads continuous with ducts, fertilization internal;
- Alimentary canal straight and composed of two ectodermal parts, the suctorial fore gut and the hind gut and an endodermal mid gut without glands or muscles;
- Development direct, larvae only differing slightly from adult.

AFFINITIES. The nematodes appear to occupy an isolated position, but ninny of their characters, though more specialized, resemble those of the Platyhelminthes and Rotifera. They are certainly closely related to the Acmithocephala, Gastrotricha, and the Nematomorpha. One of their peculiar features is certainly secondary, namely the absence of cilia. There are in some nematodes cilium-like processes to the internal border of the endoderm cells; in one case active movement has been reported. The excretory canals, when the nhscncc of flame cells is taken into account, are seen to resemble those of the t'ltityhelminthes. Nearly all the other characters may be called primitive. 1'he simplicity of organization, the absence of segmentation at all stages and a vttucular system, the diffuse nature of the nervous system and the structure of I lie muscle cells are all signs of a lowly origin. But it is still maintained by some (hut these features are not primitive but degenerate and that the origin of the phylum is to be sought in the arthropods, probably in the parasitic forms of that group (the degenerate arachnids called linguatulids). If this view is taken it must be supposed that the parasitic nematodes are the most primitive members of the phylum and that some of their descendants became less and less parasitic, until entirely free-living forms came into existence. This would be an extraordinary reversal of evolution for assuming which, at present, there are no grounds.

The view taken in this book is that the free-living nematodes are ancestral to the parasitic forms and that there is no real connection between the arthropods and the nematodes. Not only do the nematodes present no indications of segments or appendages at any point of the life history but also the cuticle is of an entirely different chemical composition in the two phyla, and the loss of cilia most likely a phylogenetically recent phenomenon in the nematodes as in the parasitic platyhelminthes.

CLASSIFICATION

Class 1. **APHASMIDIA.** No phasmids (caudal sensory organs), excretory system rudimentary or poorly developed. Males have one spicule.

Order **1. Trichurata.** Have a long fine oesophagus. *Trichuris, Capillaria*

Order 2. **Dioctophymata.** Oesophagus cylindrical. *Dioctophyma*

Class 2. **PHASMIDIA.** Have phasmids, excretory system present and well developed. Males usually have two spicules.

Order **1. Rhabditata.** Small, mainly free-living worms, oesophagus with one or two bulbs, simple mouth or may have six papillae. *Rhabditis, Strongyloides*

Order 2. **Ascaridata.** Oesophagus bulbed or cylindrical, long vagina, mouth with 3-6 papillae; males usually have two spicules but no true bursa, tail curls ventrally. *Ascaris, Enterobius*

Order 3. **Strongylata.** Simple mouth with no papillae. Males with two spicules and a true bursa. Oesophagus club-shaped or cylindrical. *Ancylostoma, Strongylus*

Order **4. Spirurata.** Oesophagus cylindrical, often partly muscular and partly glandular; males have two spicules with well-developed alae and papillae; vagina elongate and tubular;
require an intermediate host.

Wuchereria, Onchocerca, Gnathostoma

Order 5. **Caniallanata.** Mouth simple or with lateral jaws, posterior part of oesophagus has from one to three large nuclei; requires an intermediate host. *Dracunculus*

Class 1. **APHASMIDIA.** No phasmids (caudal sensory organs), excretory system rudimentary or poorly developed. Males have one spicule.

Class 2. **PHASMIDIA.** Have phasmids, excretory system present and well developed. Males usually have two spicules.

ANATOMY. The anatomy of the nematodes is best known from the study of *Ascaris* which is one of the largest members of the group and the only one adapted for dissection in class. Full accounts of this form are given elsewhere, but the following points must be emphasized. In *Ascaris* there appears to be a wide space between the muscle layer and the endoderm cells, with no epithelial boundary walls, but on closer examination it is seen to be occupied by a very small number of greatly vacuolated cells, and what appears to be a continuous cavity is really the confluent vacuoles of adjacent cells, and so the term 'intracellular' may be applied to it. This arrangement has not been verified in many other nematodes but connective tissue cells can usually be demonstrated in the space. They may be phagocytic; the enormous branched cells of *Ascaris*, lying on the lateral lines, take up in their tiny corpuscle-like divisions such substances as carmine and indigo which are injected into the body.

A striking feature of the histology of *Ascaris* (Fig. 10) is the presence of greatly enlarged cells. Not only do the body cavity cells show this, but in the excretory system the greater part of the canal is contained in the body of one cell which divides into two limbs each running the whole length of the body on opposite titles.

As a simple type of nematode the genus *Rhabditis* will be described, as it is seen alive as a transparent object under the microscope. Most species are free-living. They are obtained by allowing small pieces of meat to tl»c»»y in moist earth. The larvae, which exist in an 'encysted' condition in the •nil, lire attracted by the products of decay, and in a few days become sexually mature. Great numbers of adults and young can then be scraped off the lurfnce of the meat in the liquefied matter formed by bacterial decomposition.

The cuticle in *Rhabditis* is smooth and bears no protuberances. In other Hf»mnlodes there is often considerable sculpturing and lobing of the cuticle. Even in *Rhabditis* the mouth is surrounded with six oral lobes or papillae. In *Enoplus* each of these lobes possesses a sensory bristle, there being, in all, three rings of sensory bristles around the mouth. Sometimes, as in *Wilsonema,* the oral lobes have marked forked protuberances. *Greeffiella* has a series of cuticular spines covering the whole of the body. Spines are present in *Desmoscolex,* and in the draconematids they are used in locomotion.

with great rapidity through the alimentary canal by the pumping action of the oesophagus.

SENSE ORGANS. The nematodes have poorly developed sense organs. Papillae of a sensory nature are commonly present on the surface of the cuticle. In addition there are spines and scales present in some of the free-living marine forms. There are a pair of specialized sense organs, the amphids, present on the head of most nematodes; though their function is not clear they are probably chemoreceptors. The amphids are reduced in the purasitic forms. Posteriorly there are a pair of unicellular glands called phasmids. These are best developed in the parasitic worms. Fresh-water and iiuirinc nematodes often have a pair of eyes.

NERVOUS SYSTEM. This consists of a circum-enteric ring en-uicling the pharynx, a pair of lateral ganglia, a dorsal and a ventral ganglion. I'11 >in these ganglia emerge a dorsal, ventral and several lateral nerves which Kin tlic length of the body. Cross connexions between these nerves occur along I he length of the body. Anteriorly from the nerve ring run six nerves to the mill .

EXCRETORY SYSTEM. There are two types of excretory systems, the glandular type and the H-type. The glandular type is found in the free-living nematodes where there is a single large cell on the ventral part of the junction of the pharynx and mid gut. The duct from this cell runs forwards and opens into the mid line of the cuticle. In other forms such as *Rhabdias* there are two such kidney-shaped cells. These cells may have their posterior part extended to run the length of the body, the two cells forming an H. In *Ascaris* such an H-system is present but there is only one cell body.

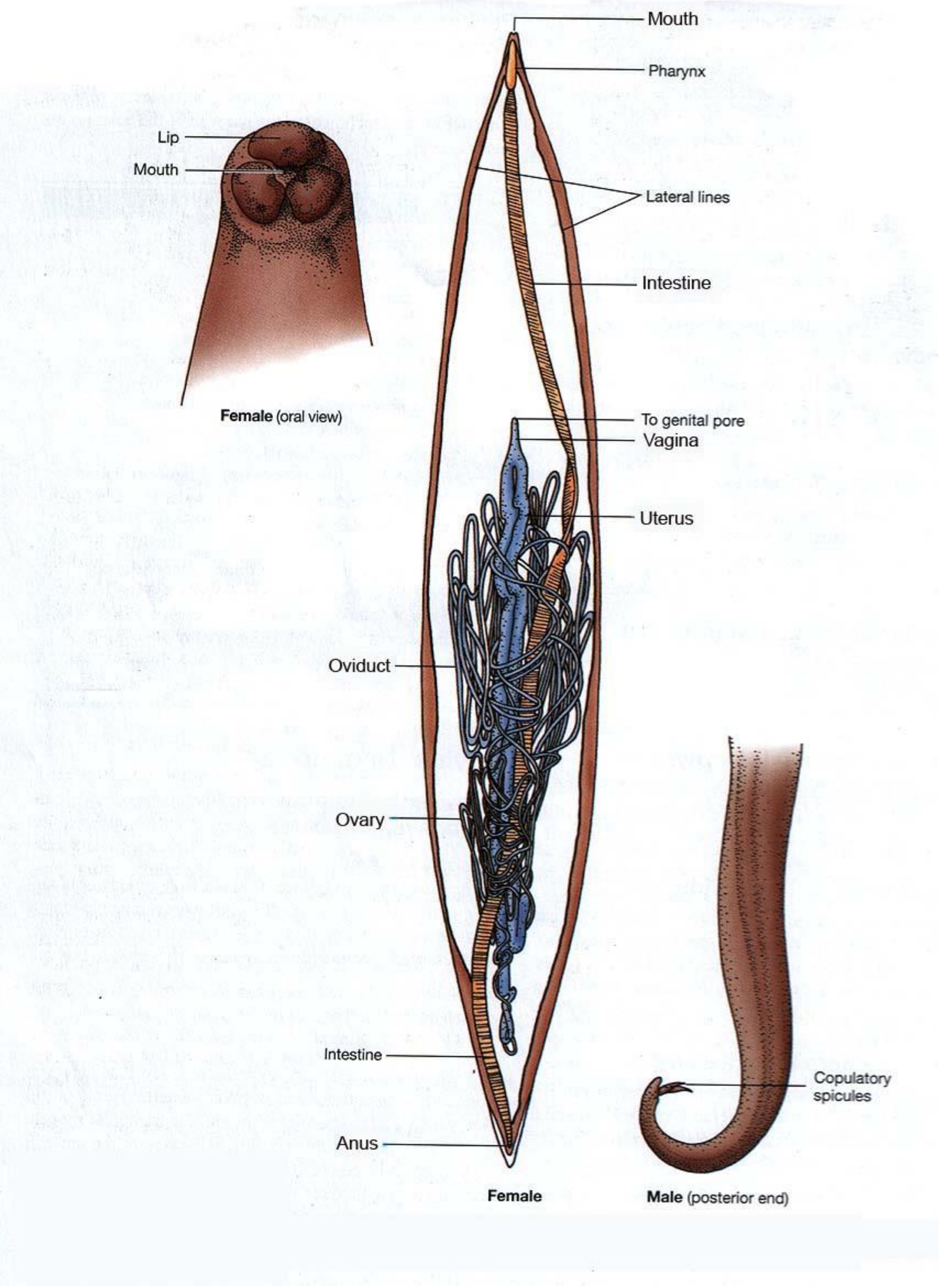


Fig. 10 *Ascaris sp*., internal anatomy

GENITALIA. The genital organs are of the type seen in *Ascaris* but simpler. In the female there are two tubular gonads bent once on themselves, discharging by a single genital aperture, situated about half-way between the head and the tail. The *ovary* is a short syncytial tube, the nuclei becoming larger and larger and the centre of more definite and larger aggregations of cytoplasm and yolk nearer the uterus. Finally, there is a single ovum discharged at a time into the *oviduct;* as soon as this happens another ripens in its, place. To reach the uterus the egg has first to pass through a portion of the oviduct *(receptaculum seminis)* filled with the amoeboid spermatozoa of the 111.ilc. Fertilization takes place, a shell is formed and at the same time maturation proceeds. The two uteri join to form the median *vagina.* In this the fertilized egg develops and the young larva is formed and may hatch within i In- vagina. The stages of segmentation are seen nowhere with such ease or .clearness as in a small transparent nematode of this kind.

The male, on the other hand, has only a single gonad. The apical testis is syncytial like the ovary. Nearing the vas deferens a zone may be seen of free spermatocytes and in the vas deferens itself can be seen large numbers of rounded spermatozoa. The genital duct opens into the gut to form a *cloaca.* This contains a dorsal pocket in which is secreted a chitinous apparatus consisting of two converging rods, the *copulatory spicules,* with a grooved connecting, piece to hold the points together. The pocket has a special muscle which protrudes the spicules from the anus (cloacal aperture). To each side of 11 us aperture is a lateral cuticular flange, supported by ribs, which meets its irllnw at the root of the drawn-out tail. This acts as a sucker *(copulatory),* by which the male retains its position on the body of the female until 11 ic spicules are thrust through the female aperture and keep the female and 111.1 If apertures both apposed and open. Then by the contraction of the muscles "i i lie cloaca the spermatozoa are expelled and passed into the vagina of the i< male. Here they become amoeboid and travel up the uteri so that they can nirci the ova as the latter are discharged.

LIFE CYCLES. In the majority of nematodes, there are four moults. After the second moult the animal may remain within the loosely lining skin as a so-called' encysted' larva which possesses, however, the power. They feed on the intestinal tissues and only accidentally rupture the blood vessels, causing anaemia in the host. The females are fertilized *in situ* and eggs are laid, which begin to segment before they pass out into the faeces. The rest .of the life history may be shown as follows:

(1) First larval form *(rhabditoid)* with a buccal cavity like *Rhabditis.* This lives in the soil for three days before the first moult.

(2) Second larval form which moults after two days, the skin remaining as •i i vst round this *strongyloid* larva.

(3) In this stage the animal becomes negatively geotropic and thigmotropic, ascending through the soil and being specially attracted to the moist skin of human beings. This they penetrate by way of the hair follicles, though occasionally the larva enters the gut by the mouth. In the former event, the minute larva is able to make its way through the skin to lymph spaces and to blood vessels, eventually being swept into the circulation by the vena cavae to the right auricle, thence to the right ventricle and then to the lung. In the pulmonary capillaries this career is ended and the larvae make their way into the alveolar cavities of the lung. They then travel by the bronchi and the trachea to the oesophagus and so to the intestine. Here the animal is freed from the second skin, producing the larva *without buccal capsule.* The third moult produces the last larval stage towards the fifth to seventh day and this is termed the larva *with provisional buccal capsule* (4). Finally, about the fifteenth day the fourth moult produces the worm with *the definitive buccal capsule (5),* and in three to four weeks from hatching the parasite has become sexually mature and is attached to the epithelium of the intestine.

This most important human parasite shows in its earliest stages the structure and the free-living habit of the primitive form *Rhabditis,* and it is noteworthy that there are many species of the latter genus which have already become parasites. It may, however, be supposed that a less specialized life history is that of the species of *Eterobius* in which the egg is swallowed by the host and the remaining stages of development take place in the gut. It is said that several successive generations of the parasite may occur within the same host.

On the other hand, the wandering habit of nematodes is a fundamental character and even forms in the first stage of parasitism (facultative) may penetrate host tissues.

The life histories of the principal nematode parasites of man and domestic animals. They arearranged inadefinite order passing from the simplest type in *Haemonchus* to the most specialized life histories in *Wuchereria (Filaria), Loa* and *Dracunculus.*

Two other classes of nematode parasites merit particular attention. They are, respectively, parasites of plants and insects.

PLANT PARASITES. Nematodes are particularly fitted for a parasitic life in plants by reason of their form and activity and their capacity (at the end of the second larval stage) for resisting desiccation and other unfavourable conditions. They are small enough, as larvae, to obtain entrance through the stomata of leaves, and sometimes possess dart-like projections of the buccal lining which enable them to penetrate the cell walls of plants. They feed on cell sap and by their interference with the life of the host plant cause the formation of galls, wilting and withering of the leaves, and stunting of the plant.

Tyienchus tritici passes through a single generation in the course of the year, and infects wheat. The animal becomes adult when the grain is ripening and a pair, inhabiting a single flower, produce several hundred larvae. Instead of the grain a brown gall is produced, and in this the larvae (after moulting twice) may survive for at least twenty years. If the grain falls to the ground the larvae may remain there over the winter or may escape into the soil. When the corn begins to grow in the spring they enter the tissues of the plant and make their way up the stem to the flower, where they speedily mature. The great interest of this life history lies in the easy adaptation of the parasitic life history to the annual cycle of the wheat plant and the extreme capacity for survival in a dormant and desiccated condition until the right plant host becomes available.

Tyienchus devastatrix, on the other hand, may pass through several generations in the year and attacks indiscriminately clover, narcissi bulbs and onions, and many other useful plants. *Heterodera* is a parasite of the roots of tomatoes, cucumbers and beets, and is remarkable because the female attaches herself in larval life to a rootlet from which she sucks a continuous flow of sap. She is fertilized by wandering males and grows enormously, becoming lemon-shaped. Inside the body thousands of larvae are produced, which escape into the soil and live there until the opportunity arises for infection of fresh roots.

INSECT PARASITES. Four of these may be mentioned, though other life histories are also of great interest.

In *Mermis* a curious reversal of the typical nematode life cycle occurs. The sexual forms are all free-living either in the soil or fresh water. On summer days after showers the sexual forms of *Mermis nigrescens* exhibit a curious tropism, leaving their haunts two or three feet in the ground and crawling up Ihe stems of plants, but disappearing when the sun grows warm. The eggs are laid in the ground and when the larvae hatch they pierce the skin of insect larvae and wander into the body cavity where they nourish themselves by absorbing fluid food through the cuticle. The mid gut has become a solid body, having no connexion with the mouth and anus, and in it fat is stored up which serves as raw material for the production of eggs. When the animals 1'ccome sexually mature they escape into the soil.

In *Tyienchus dispar* (a form which is thus placed in the same genus as the well-known plant parasites) the adult female and innumerable larvae are found in the body cavity of the bark-beetle, *Ips,* during the winter. *Allanto-nema* has similar relations to another bark-beetle, *Hylobius.* The female is enormously developed; the uterus and other female organs occupy the whole of the body, the gut having entirely disappeared. In the spring the larvae (having undergone two moults) bore through the walls of the end gut and undergo further development in the 'frass' (faeces of the beetle). The male develops precociously and fertilizes the female which, when it becomes mature, is still of normal proportions. After fertilization the females (only) infect the beetle larvae which by this time have appeared. Entrance is obtained by means of a 'dart' exactly like the similar organ in the plant parasites. In the body cavity the female *Allantonema* grows rapidly, and when metamorphosis occurs and the mature bark-beetle seeks another tree to form a new colony, it is full of larvae.

Spherularia is a parasite of the humble-bee. In the summer the moss and soil near the bee's nest is inhabited by the sexually mature worms, and after fertilization has taken place the female wanders into the body cavity of the insect, as in the preceding life histories. Though the number of cells in the somatic tissues of the bee is said not to increase in number, there is an enormous growth in size of the vagina which becomes prolapsed and forms eventually an organ many times the size of the rest of the body, which remains attached for some time but eventually disappears. The parasitized humble bees, after passing the winter in their nests, tend to emerge early. In the spring very often inactive bees may be caught which prove, on dissection, to contain one or more of these enormous sausage-shaped bodies, each of them full of eggs and larvae, which escape through the gut wall and become free-living.

Atractonema , a parasite of the Cecidomyidae, has a similar life history.

PHYLUM ANNELIDA

DIAGNOSIS. Segmented worms in which the perivisceral cavity is coelomic; with a single preoral segment (prostomium); with a muscular body wall in which externally the elongated muscle cells are arranged with their longitudinal axes across the width of the worm (circular layer) while internally their axes are parallel to the length of the worm (longitudinal layer); with a central nervous system consisting of a pair of preoral ganglia connected by commissures with a pair of ventral cords which usually expand in each segment to form a pair of ganglia from which run nerves to all parts of the segment; with nephridia and coelomoducts; and the larva, if present, of the trocho-sphere type.

While the above definition is the only one that can be applied to all the annelids, typical representatives of the phylum can also be described as possessing a definite cuticle and bristles or *chaefae* composed of chitin, arranged segmentally, imbedded in and secreted by pits of the ectoderm. The cuticle is thin and not composed of chitin, thus differing from that of the Arthropoda.

CLASSIFICATION

There are six classes of which the first three are the most important in the phylum.

CLASS 1. POLYCHAETA

Well-segmented annelids with chaetae and a spacious perivisceral coelom usually divided by intersegmental septa. The chaetae arise from special prominences of the body wall called parapodia. The animals usually have a distinct head which bears a number of appendages. They are nearly always dioecious and the gonads extend throughout the body. There is external fertilization and the fertilized egg gives rise to a free-swimming larva, the trochosphere. The group is mainly marine though there are some estuarine forms. Typical examples are *Arenicola, Sabella, Nereis.*

CLASS 2. OLIGOCHAETA

Well-segmented annelids with chaetae and a spacious perivisceral coelom usually divided by intersegmental septa. The chaetae are fewer in number than in the polychaetes and they are not situated on parapodia. There is usually a distinct prostomium in front of the mouth but it does not bear appendages. The animals are hermaphrodite, the male and female gonads being few in number (one or two pairs), the male always being anterior to the female. The special genital ducts, the coelomoducts, open by funnels into the coelom; spermathecae and a clitellum are present at sexual maturity. Reproduction is by copulation and cross-fertilization, eggs being laid in cocoons and titveluping directly without a larval stage. The group has terrestrial and fresh-water forms. Typical examples are *Allolobophora, Tubifex.*

CLASS 3. HIRUDINEA

Annelids with a somewhat shortened body and a fixed number of segments.The segments are broken up externally into a number of rings or annuli. The animals are without chaetae or parapodia. The anterior and posterior ends of the body have suckers. The coelom is very much invaded by the growth of mesenchymatous tissue and is usually reduced to several longitudinal spaces (sinuses) with transverse communications. One primitive form *Acanthobdella* has chaetae and a spacious perivisceral coelom in its anterior segments. The animals are hermaphrodite and develop a clitellum at sexual maturity. Reproduction is by copulation and cross-fertilization; eggs being laid in a cocoon and developing directly without a larval stage. The group is represented by a few genera on land and in the sea, most genera are fresh-water forms. Typical examples are *Hirudo, Glossiphonia.*

A small group of worms with a ciliated epidermis, little or no evidence of segmentation and only rarely possessing chaetae as in *Saccocirrus.* The animals are mostly marine. Typical examples are *Protodrilus, Polygordius, Saccocirrus.*

CLASS 5. ECHIUROIDEA

Marine burrowing annelids that have lost almost all traces of segmentation in the adult though the trochosphere larva shows mesoblastic somites or ganglionic rudiments. The chaetae are lost except in a few forms. The animals have a well-developed preoral lobe and a spacious coelom. Typical examples are *Echiurus, Bonellia.*

CLASS 6. SIPUNCULOIDEA

Annelids of doubtful affinities. They have a well-developed spacious coelom and a single pair of nephridia but the adult shows no sign of segmentation. The larva, however, shows three pairs of somites that quickly disappear. They are sessile sand dwellers and they have a coiled intestine so that the anus IN dorsal and anterior. Typical examples are *Sipunculus, Phascolosoma.* POLYCHAETA, OLIGOCHAETA AND HIRUDINEA. The linking of these classes into subphyla presents several interesting problems. The classes are closely related, with the Oligochaeta possessing characters intermediate between those of the Polychaeta and the Hirudinea. One classification groups (he Polychaeta and the Oligochaeta together as a class Chaetopoda with the common characters of chaetae and a well-developed coelom. On the other hand it is possible to link the Oligochaeta and the Hirudinea together to form I he group Clitellata; both possess a clitellum during sexual maturity, are hermaphrodite, and show many close resemblances during embryonic development. The nervous system of the Polychaeta develops from two distinct centres whilst those of the Oligochaeta and Hirudinea develop from one centre. The mesoderm in the Polychaeta arises from the *4d* cells whilst in the Oligochaeta and Hirudinea the mesoderm develops from 3D or *3d,* but not *4d.*

Two suggested groupings of the major classes of the annelids:

Polychaeta Oligochaeta

(1) Chaetopoda **(1) Clitellata**

\ \ Oligochaeta Hirudinea

(2) Hirudinea **(2) Polychaeta**

The remaining groups, Archiannelida, Echiuroidea and Sipunculoidea present a greater problem in deciding their affinities. The archiannelids are probably simplified polychaetes though through their simplification they ihow many apparently primitive characters. There is no clear indication that Hie different genera of the archiannelids are closely related; it is more probable Unit their similarities are due to convergence and not due to close phylogenetic iclutionship.

The Echiuroidea and Sipunculoidea used to be grouped together as the (icphyrea mainly on the fact that they were both burrowing animals that had loNt their segmentation and showed certain common nephridial characters, nil of which are features of doubtful phylogenetic significance. The Echiuroi-ilon have more annelid affinities than do the Sipunculoidea though both »how their annelid affinities more closely during their embryonic phase. (lie two groups have on occasions each been placed in a separate distinct phylum.

CLASS 1. POLYCHAETA

Diagnosis. Well-segmented Annelida, with a spacious perivisceral coelom, usually divided by intersegmental septa; marine; numerous chaetae arising from special prominences of the body wall called parapodia; usually with a distinct head which bears a number of appendages; nearly always dioecious, with gonads extending throughout the body and external fertilization; with a free-swimming larva, the *trochosphere.*

GENERAL ACCOUNT. In a typical polychaete (Fig. 11) there is a distinct preoral region or *prostomium* and a postoral body composed of many segments. Each segment owes its distinctness to the development in the larva of a pair of mesoblastic somites which join round the gut, the cavities which develop in them becoming the peri-visceral cavity of the adult segment. At the same time the larval ectoderm (epiblast) develops segmentally repeated organs: the *ganglia,* swellings in the continuous ventral nerve cords, the *nephridia* or excretory organs and the *chaetae.* The chaetae are borne in groups upon processes known *as parapodia,* whose projection from the body wall is due to the development of special muscles for moving the chaetae.

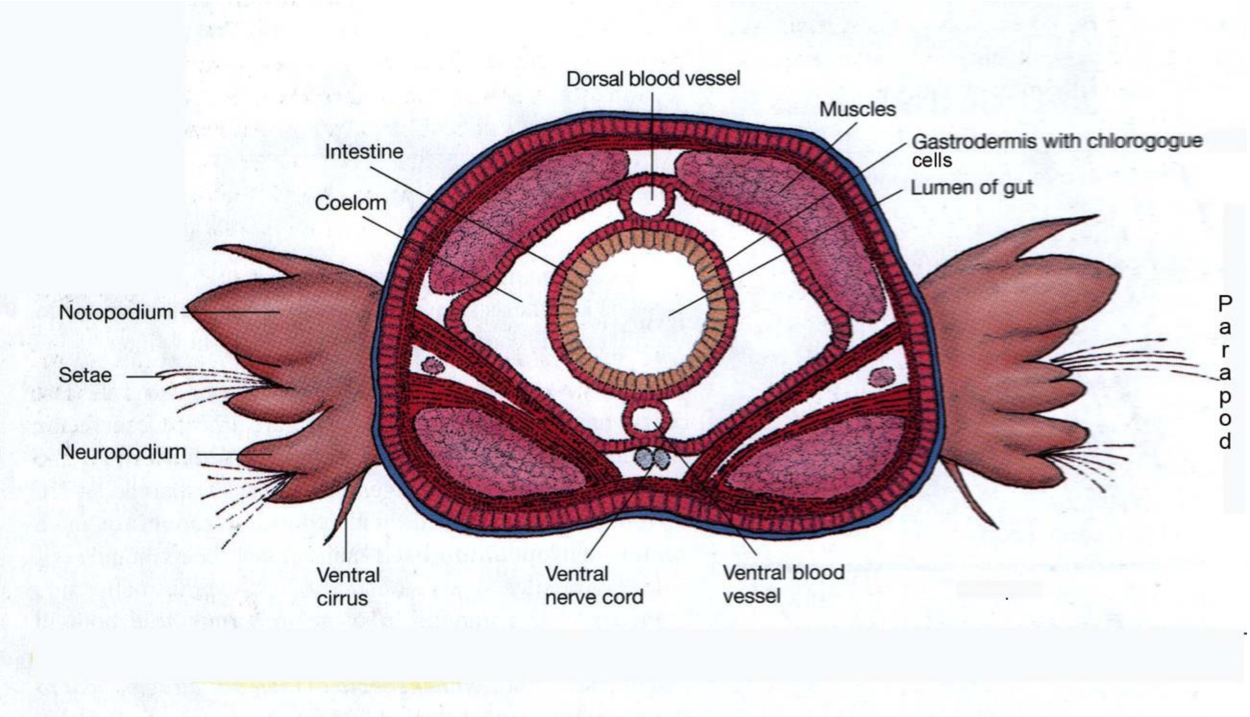


FIG 11. POLYCHAETA, INTERNAL ANATOMY

NERVOUS SYSTEM. The chief feature of the nervous organization is that the musculature of all parts of the body is co-ordinated by metamerically repeated intra- and intersegmental reflexe. In each segment there is, for example, a correlation of the circular and longitudinal muscles by the segmental nerves which acts so that contraction of one brings about automatically relaxation of the other. Then there are nervous connexions between adjacent segments which act so that excitation of a muscle layer in one segment leads to excitation of the same layer in the other segment. By the working together of the inter- and intrasegmental reflexes the normal peristaltic movement of the body is brought about.

There may also be a system of giant fibres running along the whole length of the ventral nerve cord. These are responsible for the reactions which require immediate co-ordination of the whole body in response to excitation of the higher centres, the supra- and subpharyngeal ganglia. The rapid contraction of the whole of the longitudinal musculature in response **to** a noxious stimulus is an example of this kind of reaction. A nereid, which has had the suprapharyngeal ganglia removed, moves about ceaselessly, showing that a function of the ganglia In the normal animal is the inhibition of movement. If the supra- and mibpharyngeal ganglia are both removed then the animal is permanently quiescent, a condition like that of a polyclad turbellarian when the cerebral ganglia are removed.

The head and accompanying sense organs may be well developed, for Distunce, in some of the pelagic Polychaeta where the eyes are remarkably complex. In such cases the brain (prostomial ganglia) may attain a structure almost as complicated as in the higher arthropods. The head processes (tentacles, palps) vary greatly. While they may be very complicated in the irriint Polyehaeta, they are frequently absent in burrowing members of that group.

COELOM. The coelom is bounded by an epithelial layer, the *peritoneum,* which gives rise to the *gonads* (which are usually developed in most of the segments), to the *yellow cells,* which play a part in the work of nitrogenous ncrction, and to the *coelomoducts* by which the eggs and sperm pass from the riiolom to the exterior. In most of the polychaetes the eggs are fertilized externally, forming a *trochosphere* larva, the method of reproduction thus conforming to that of other marine groups.

In some forms the coelom may be very spacious and have a ciliary circulation, as in *Aphrodite* where it develops at the expense of the blood system.

SKELETAL SYSTEMS. The annelids like the coelenterates, platyhelminthes, Mini molluscs have a hydraulic skeleton; the longitudinal muscles being extended due to an increase in the hydraulic pressure when the circular muscles contract. The longitudinal muscles are attached to a lattice-work of inextensible collagen fibres in the basement membrane. In *Arenicola,* where there are few septa dividing the coelomic cavity, the importance of the coelomic fluid during locomotion is shown by the following experiment. *Arenicola* normally takes about three minutes to burrow into the sand. If 0-38 ml. of coelomic fluid are removed with a hypodermic syringe, then the animal takes eight minutes to burrow. This indicates that the reduced coelomic pressure makes ll men; difficult for the circular and longitudinal muscles to co-ordinate. On the other hand if *Arenicola* is cut in half it takes four to five minutes to burrow. This is due to the contraction of the circular muscles at the cut surface which takes place and prevents the loss of the coelomic fluid.

In *Lumbricus* there are septa between each segment and each septum has a foramen through which the nerve cord passes. Injection of dyes and X-ray opaque substances show that there is no passage of coelomic fluid from one segment to the next during locomotion. The circular muscles of the septum around the nerve cord contract and so make each segment a closed discrete unit. It is possible that the development of small hydraulic units increases the efficiency of the locomotor system in the annelids.

BLOOD SYSTEMS. The blood system varies greatly. In small forms it is absent altogether. Typically it consists of a dorsal vessel in which the blood moves forward, and a ventral vessel in which it moves backward and from which the skin is supplied with venous blood. The whole of the dorsal vessel is usually contractile: there may also be vertical segmental contractile vessels which are usually called 'hearts'. In some forms, for example *Pomatoceros,* there are no separate dorsal and ventral vessels but a *sinus* round the gut: the peristalsis of the latter brings about the movements of the blood. While the whole of the skin is sometimes richly supplied with blood vessels and usually performs an important part in the aeration of the blood there are often branched segmented processes which may rightly be called *gills*: the alimentary canal is probably a respiratory organ too. While haemoglobin is often present in the blood, usually in solution, a related pigment, chlorocruorin, which is green, occurs in many tubicolous polychaetes. The variable state of the mechanism of respiration is shown by the fact that one species of a genus (the polychaete, *Polydrrus)* may possess haemoglobin while another has no respiratory pigment.

It is not clear to what extent the haemoglobin in annelids has the same function as haemoglobin in mammals. In many annelids the haemoglobin under normal conditions remains in an oxygenated condition and so does not help in oxygen transport. An alternative suggestion is that the haemoglobin acts as an oxygen store in emergencies such as prolonged periods of tidal exposure. In *Lumbricus* there does appear reasonable evidence that the pigment plays a part in oxygen conduction.

NEPHRIDIA. The nephridia are essentially tubes developed from the ectoderm which push their way inwards so that they project into the body cavity. In some polychaetes they end blindly—this is the primitive condition. In most annelids they have acquired an opening (nephrostome) into the body cavity itself. In some cases there is a partial fusion with a mesodermal element, the coelomoduct, so that a compound tube consisting mainly of ectoderm but partly of mesoderm exists *(nephromixium).* Nephromixia may take on the functions of coelomoducts where these do not exist independently. All types of tubes are termed here *segmental organs.*

CLASS 2. OLIGOCHAETA

DIAGNOSIS. Annelids, with a comparatively small number of chaetae, not situated on parapodia, with prostomium distinct but usually without appendages; always hermaphrodite, the male and female gonads being few in number (one or two pairs), situated in fixed segments of the anterior region. the male always anterior to the female; with special genital ducts (coelonio ducts) opening by funnels into the coelom, *spermatherae*, and a *rlitrlliiin* present at sexual maturity; with reproduction by copulation and cross-fertilization; eggs being laid in a cocoon, developing directly without a larval stage.

Order **1. Terricolae.** Oligochaetes living on land. *Lumbrlcus, Allolobophora, Eutyphoeus.*

Order 2. **Limicolae.** Oligochaetes living in water. *Tubifex, Sfylaria, Aeolosoma.*

GENERAL ACCOUNT. The pharynx is not eversible and pharyngeal teeth (such as frequently occur In the Polychaeta) are absent, except in one small family, the Branchio-bdellidae, which have ectoparasitic habits similar to the leeches and resemble them in some particulars of structure.

Though the chaetae are not bome on parapodia they are usually divided Into two bundles or groups on each side which roughly correspond to the noto- and neuropodia. They may be classified into hair chaetae which are long and fine (dorsal chaetae of *Stylarid)* and shorter chaetae which are rod-like *(Lumbricus)* or needle-like. The point of the needle is single- or double-pronged. There is not, however, the great variety found in the Polychaeta.

Certain main features of the reproductive system are the salient characters of the group. Its members are, without exception, hermaphrodite, and with a single possible exception cross-fertilization only is possible. The restriction of the gonads to a few segments occurs also in some sabellids umong the Polychaeta and in some archiannelids. The sexual cells are shed Into the coelom either into the general coelomic cavity as in the Polychaeta or into special parts of it divided off from the rest *(seminal vesicles* of *Lumbricus)* where they mature. Spermathecae are usually present to contain the »pcrmatozoa received from another worm in copulation. The clitellum is a Npccial glandular development of the epidermis whose principal function is

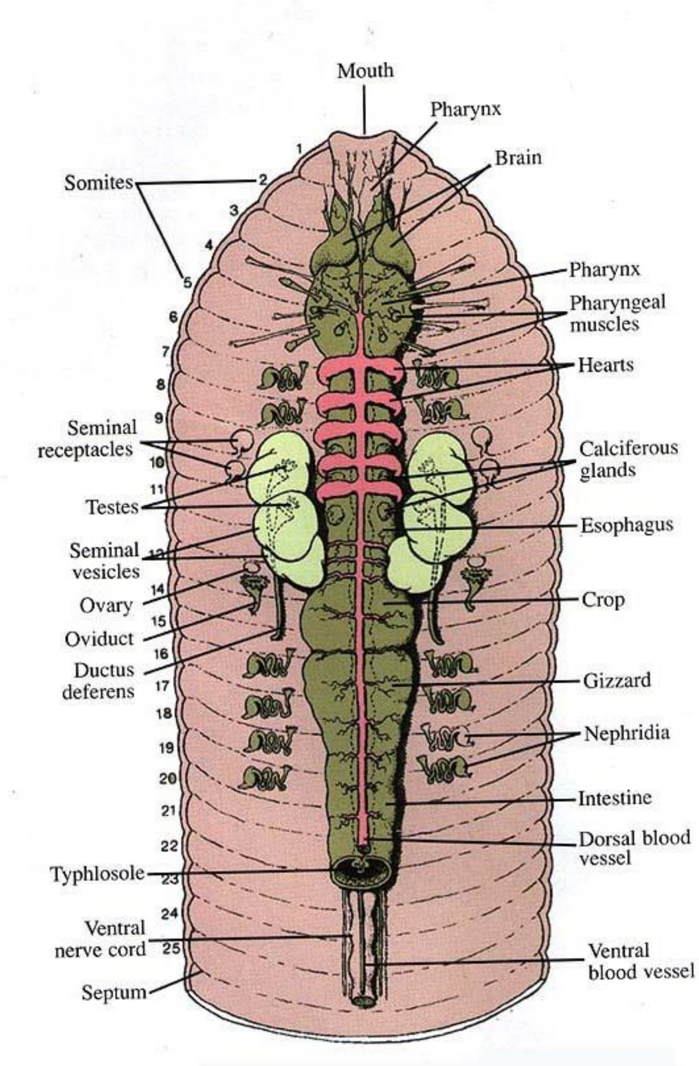
I lie secretion of the substance of the cocoon and the albuminoid material which nourishes the embryo. It is a secondary sexual character which is only present in the reproductive season in most Oligochaeta, but the earthworms

(Allolobophora) used in zoological laboratories in this country nlwuys possess it. Both the clitellum and the cocoon produced by it are found In the Hirudinea. It may also be mentioned that many Oligochaetes have upccial copulatory chaetae, sometimes hooked for grasping the other worm in with a sharp point for piercing it.

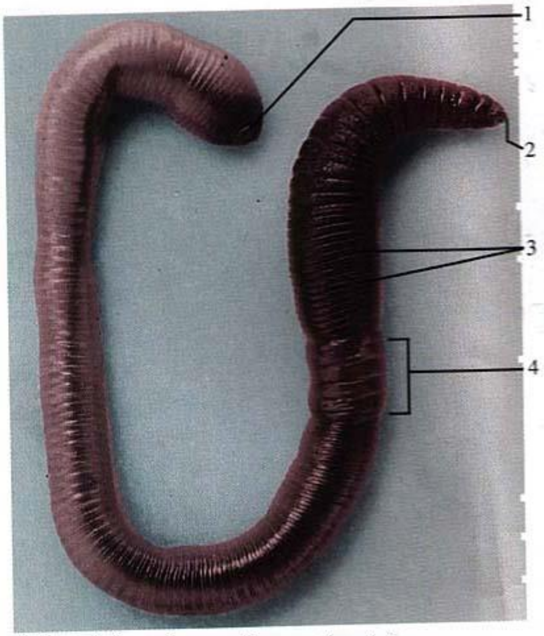
I 'or the purposes of the elementary student it is probably best to recognize that the Oligochaeta contain two well-marked ecological types, the 'earth-worm', a larger burrowing terrestrial form, and the aquatic oligochaete which In much smaller and simpler in structure. It is probable that the former type In the more primitive; the aquatic oligochaete shows many characters which iCNCinble those of the archiannelids and are most likely due to a process of simplification. The reasons for the conclusion that the aquatic oligochaetes are not the oldest of these groups are given below.

Earthworms. These are divided into a number of families of which the most important are the Lumbricidae, containing *Lumbricus* (Fig. 12) and *Allolobophora,* and the Mega-scolecidae which is the largest of all.

The primitive forms in all families resemble *Lumbricus* in the following characters. There are a large number of segments and each one is furnished with eight chaetae arranged in pairs and all on the ventral side of the worm. A series of *dorsal pores* is found along the back in the intersegmental grooves. The alimentary canal is characterized by a large muscular *pharynx* by which the food is sucked in, with many glands, the secretion of which is used in external digestion. The oesophagus in one part of its length gives rise to one or more pairs of diverticula, the cells of which secrete calcium carbonate *(oesophageal pouches* and *glands).* At the end of the oesophagus or the beginning of the intestine there is a thick-walled *gizzard* in which the food is masticated with the aid of the soil particles. The intestine has a dorsal ridge, the *typhlosole,* to increase the absorptive surface. The nervous, muscular and circulatory systems exist throughout the earthworms with little variation from the condition in *Lumbricus.*



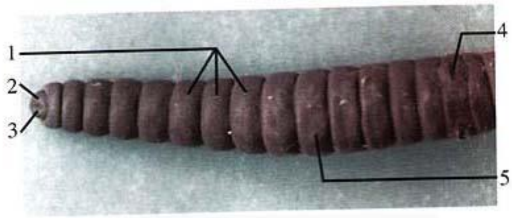
A diagram of the anterior end of the earthworm, *Lumbricus*



A dorsal view of an earthworm, *Lumbricus*

Lumbricus.

1. Pygideum	3. Segments
2. Prostomium	4. Clitellum



The anterior end of an earthworm, *Lumbricus*

Lumbricus.

1. Setae	4. Opening of ductus (vas) deferens
2. Mouth	5. Segment 10
3. Prostomium	

Fig. 12 Oligochaeta, construction

The variations which occur in more specialized members of all families are as follows. The chaetae may increase in number and come to be arranged in a complete ring round the body *(perichaetine).* The dorsal pores may disappear. The oesophagus may lose its calciferous glands and the gizzard may be absent or develop into several. The reproductive organs vary in small but important particulars. There are nearly always two pairs of *testes* in segments 10 and 11 and one pair of *ovaries* in segment 13, but the testes may be reduced to a single pair. There are usually two pairs of *spermathecae* but the number varies and occasionally they are absent altogether. The *prostate glands* (ol' unknown function) are nearly always present in earthworms except in the Lumbricidae.

REPRODUCTION. The reproductive system consists essentially of two pairs of *testes* in segments 10 to 11 and one pair of *ovaries* in segment 13, followed by ducts which open by large funnels just behind the gonads and discharge to the exterior in the next segment in the case of the oviduct, anil several segments behind in the ease of the sperm duct. The testes, at least, arc enveloped by *sperm sacs* (vesiculae seminales) which are outgrowths of tin-septa, and in the cavity of these the sperm undergo development. In somr earthworms there are no sperm sacs and this condition, resembling that in the Polychaeta, is probably the earliest in the group. There are two pairs ol *spermathecae* in the region in front of the testes. In the neighbourhood ol the male external aperture there are *spermiducal (prostate) glands* which do not actually open into the sperm duct. A single pair of segmental org.uis (open nephridia) is present in each segment.

The simplest method of copulation in earthworms is that found in *Eutyphoeus*, where the end of the sperm duct can be everted to form a *penis*. Tlir. is inserted into the spermathecal apertures and the spermatozoa thus p.iss directly from one worm to another. **It** is obvious that the mechanism of copulation is far more complicated in the Lumbricidae. Here the worms come Into contact along their ventral surfaces and each becomes enveloped in a mucous sheath. Close adhesion is secured between the clitellum of one worm and the segments 9 and 10 of the other, partly by embracing movements of the clitellum and partly by the chaetae of the same region being thrust far into the body wall of the partner. The sperm passes out of the male aperture and along the *seminal groove* to the clitellum; how it enters the spermathecae of I he other worm has never been determined.

The cocoons are formed some time after copulation. The worm forms a mucous tube as in copulation. The cocoon is then secreted round the clitellum uiul finally the albuminous fluid which nourishes the embryo is formed between the cocoon and the body wall and the worm frees itself from the cocoon by a series of jerks. All three products, mucus, cocoon substance and albumen, are secreted by the clitellum and each probably by a distinct type of cell. The eggs are sometime extruded and passed backwards into the cocoon while it is still in position on te clitellum but the spermathecae eject the spermatozoa when the cocoon passes he embryo of *Eisenia* is illustrated in Fig. 200. The prototroch is absent but the gut and stomodaeum are developed early to absorb the albumen in the cocoon. There are two mesoblast pole cells at the hinder end which bud off the mesodermal strips: there are three ectodermal pole cells on each side, the most ventral a *neuroblast* forming half the nerve cord and the two others *nephroblasts* giving rise to longitudinal rows of cells which divide up to form the nephridia.

In *Lumbricus* the larva goes through a type of metamorphosis within the cocoon. Larval excretory organs, musculature, and cilia around the mouth develop at an early stage only to be broken down at a later stage and replaced by the adult organs. A similar situation is seen in the development of some leeches. In fact there are many similarities in the development of the Oligo chaeta and Hirudinea which mark them off from the Polychaeta. The Oligo. chaeta and Hirudinea like the Polychaeta show spiral cleavage. But whilst the mesoderm in the Polychaeta comes from the *4d* cell, in the Oligochaeta and Hirudinea it may come from the 3D, 4o or *3d,* but never *4d.* Another difference is seen in the development of the nervous system. The central nervous system of the Polychaeta arises from two sites, one in the prostomium the other in the body. In the Oligochaeta and Hirudinea the central nervous system arises from only one site. These and other similarities link the Oligochaeta and Hirudinea into one group, the Clitellata.

SEGMENTAL ORGANS. The Oligochaeta like the Hirudinea but unlike the Polychaeta have their nephridia and coelomoducts separate. The nephridia tire metanephridia and are usually present in each segment of the body whilst the coelomoducts are restricted to a few reproductive segments. The nephridia din cither open to the outside of the body (exonephric) as in *Lumbricus* or they can open into the gut (enteronephric) as in *Pheretima.* When the original lurgc pair of nephridia are still present in each segment they are called Imloncphridia. In other cases the nephridia may divide to form many small nephridia which are called meronephridia. In the development of the excretory system of *Megascolidrs* the segmental organs first appear as cords of rclls, tine p;iir in each segment. These holonephridia are later thrown into loops and each loop becomes separated off from the next to form a mero-nephridium. *Lumbricus* has a pair of exonephric holonephridia in each segment. *Allolobophora* has a pair of holonephridia in each segment but these open into a longitudinal duct that discharges into the hind end of the intestine. In the Indian earthworm *Pheretima,* there are three different types of nephridia.

(1) In segments 4, 5, and 6 there are many enteronephric meronephridia opening into the pharynx. These are called peptonephridia and may have a digestive function.

(2) Each segment posterior to segment 6 has a number of exonephric meronephridia.

(3) In addition to these many exonephric meronephridia, segment 15 and all those posterior to it have 40-50 pairs of small meronephridia. These open into a pair of ducts that run along the dorsal wall of the intestine. These ducts huvc segmental openings into the intestine.

It has been suggested that the enteronephridia are of use in water conservation since *Pheretima* can survive drought conditions better than most earthworms.

CIRCULATION. There is a well-developed blood circulation. Blood flowing 111 rough the parietal and dorse-intestinal vessels of each segment is collected In the dorsal vessel. It is prevented from returning by an elaborate system of vulvcs. Waves of peristaltic contraction beginning at the hind end of the dorsal vessel and continued by the 'hearts' press it forwards and vcntralwards into the ventral vessel which is the main distributing channel.

Aquatic Oligochaeta

As ii type of these, *Stylaria,* belonging to the family Naididae, will be shortly dficribcd. This is a transparent worm rather less than a centimetre long found crawling on water weed. The prostomium bears minute eyes and is produced into a long filiform process. In most of the segments there are **two** bundles of chaetae on each side, the dorsal consisting of hair chaetae and needle chaetae, while the ventral has only 'crotchets' with a double point. The first four segments have no dorsal bundles (incipient cephalization).

The alimentary canal is simpler in character than that of *Lumbricus,* a gizzard being absent. The intestine is ciliated and the action of the cilia brings In from the anus a current of water which probably assists respiration. The testes develop in segment 5 and the ovaries in segment 6, while a pair of spermathecae is found in the testis segment. The sexual cells develop In the seminal vesicle and the ovisac, which are unpaired backward pouchings ol' septa 5/6 and 6/7 respectively. The male ducts open by a funnel on septa 5/6 and discharge into an *atrium,* which is lined by the cells *of the prostate.* While sexual individuals are often met with and can be recognized at once by the appearance of the opaque clitellum in segments 5-7, individuals reproducing asexually are much commoner. Chains of worms attached to one another may be found, and the existence of one or more *zones of fission,* where new segments are being formed and separation of two individuals will take place, is easily observed under the microscope.

Stylaria is a delightful object of study. The operation of many of the organs can be easily observed with a low power and the results form a useful suppir ment to work with *Lumbricus* in understanding oligochaete organization.

From the above account it will be seen that *Stylaria* differs from *Lumhi •icn* not only in its small size and transparency but also in the number and appc.i i ance of the chaetae—which give it a certain resemblance to the Polychaeta. The reproductive organs, however, are entirely different from those of the latter group and it is in this system that the real contrast between polychaete and oligochaete lies.

The aquatic oligochaetes when they are of small size often show reduction of the vascular system, ciliation of the under-surface (in one form, *Aeolosoma),* and a nervous system of embryonic type. These are characters which may be primitive but, as in the archiannelids, so here, they are probably the results of simplification; it is generally agreed that the replacement of sexual by asexual reproduction is a secondary feature, and the frequency with which it is found in the aquatic Oligochaeta shows them to be, on the whole, specialized types.

Two common genera, *Tubifex* and *Lumbriculus,* are larger worms which in their appearance have more resemblance to earthworms. A brief description of them follows.

Tubifex. A. small red worm with rather numerous chaetae in the dorsal and ventral bundles belonging to various types; without gizzard; testes and ovaries in segments 10 and 11 respectively.

It lives in the mud at the bottom of ponds and lakes with its head buried and its tail waving in the water; the latter movements are respiratory. They draw water from upper layers which contain more oxygen: when the oxygen content of the water in general falls a greater length of the worm is protruded and its movements become more vigorous. A great deal of detritus passes through its alimentary canal so that *Tubifex* plays the same sort of part in fresh water that the earthworms play on land.

Lumbriculus resembles *Tubifex* superficially but has only eight chaetae in a segment, placed as in *Lumbricus;* chaetae double-pointed; not often met with in sexual state but reproduces habitually by breaking up into pieces each of which regenerates the missing segments.

At the posterior end there is a continuous *sinus* round the gut, in the middle region this becomes resolved into a dense plexus of capillaries and at the anterior end there is the beginning of a segmental arrangement.

CLASS 3. HIRUDINEA

DIAGNOSIS. Annelida with a somewhat shortened body and small, fixed number of segments, broken up into annuli and without chaetae (except in *Actinlhohilella)* or parapodia; at the anterior and posterior ends several segments modified to form suckers; coelom very much encroached upon by the growth of mesenchymatous tissue and usually reduced to several longitudinal tubular spaces (sinuses) with transverse communications. Hermaphrodite, with clitellum. Embryo develops inside cocoon.

CLASSIFICATION. The Hirudinea may be divided as follows:

Acanthobdellidae. A group intermediate between the Oligochaeta and the Hirudinea, containing the single genus *Acanthobdella.*

Rhynchobdellidae. Marine and fresh-water forms, with colourless blood, protrusible proboscis and without jaws. *Glossiphonia.*

Gnathobdellidae. Fresh-water and terrestrial forms, with red blood and without a protrusible proboscis but usually with jaws. *Hirudo.*

GENERAL ACCOUNT.

In the typical leeches the *constitution of the body* is remarkably constant. There is a prostomium and thirty-two body segments; an anterior sucker (in the centre of which is the mouth) is formed from the prostomium and the first two segments, and a posterior from the last seven. Both suckers are directed ventrally. The subpharyngeal' ganglion' is composed of four single ganglia fused together and the posterior 'ganglion' of seven. Between them lie twenty-one free ganglia, and the number of segments is estimated by summation of all the ganglia. The number of annuli to a segment varies in different forms.

ALIMENTARY CANAL. The alimentary canal is highly characteristic and consists of the following parts. (1) A muscular *pharynx* with unicellular salivary glands. In the Gnathobdellidae, which includes *Hirudo,* there are three chitinous plates or jaws. In the Rhynchobdellidae there is a protrusible *proboscis* surrounded by *a. proboscis sheath.* (2) A short *oesophagus* follows, leading into (3) the *mid gut* (crop) which is often provided with lateral caeca, varying in number, and is used for storing up the blood or other juices of the host. This is kept from coagulating by the ferment (anticoagulin) contained in the salivary secretion *(Hirudo).* In the mid gut a very slow digestion takes place, the blood appearing almost unchanged even after several months. (4) An *intestine,* which is also endodermal, and has, in *Hirudo,* a pair of diverticula. (5) A very short ectodermal *rectum* discharging by the anus, which is dorsal to the posterior sucker.

BODY WALL. The body wall consists of a single layer of ectodermal cells between which blood capillaries penetrate, a dermis with pigment cells and blood vessels, and an outer circular and inner longitudinal layer of muscles. The muscle fibres have a characteristic structure, consisting of a cortex of rlriuted contractile substance and a medulla of unmodified protoplasm. Inside the musculature are masses of mesenchymatous tissue: in the Gnathobdellidae this is pigmented and forms the *botryoidal tissue,* the cells ill' which are arranged end to end and contain intracellular capillaries filled with a red fluid.

The mesenchyme almost completely occupies the space which is the perivisceral cavity in the earthworm. There are, however, longitudinal canals, constituting the *sinus system,* and these represent the remnants of the coelomic spaces; there are always dorsal and ventral and often two lateral sinuses, and there are numerous transverse canals in each segment. Into this reduced coelom the nephrostomes open and the gonads are found in it. The blood system consists of two contractile lateral vessels (and in the Rhynchobdellidae of dorsal and ventral vessels running inside the corresponding coelomic spaces). These vessels all communicate with one another. They also communicate with the sinuses of the coelom and with the capillaries of the botryoidal tissue, as has been shown by careful injection. This astonishing condition is unique, but a parallel may be drawn with the vertebrate in which the lymphatic system communicates both with the coelom and the blood system. The peculiar functions of the lymphatic system are not shared by the botryoidal vessels which have no particular connexion with the gut.

NERVOUS SYSTEM. The nervous system is of the usual annelidan type but characterized by the fusion of ganglia anteriorly and posteriorly.

There are segmental sense organs in the form of papillae, and on the head some of these are modified to form eyes and the so-called 'cup-shaped organs'.

NEPHRIDIA. The nephridia are much like the metanephridia of the Oligochaeta except that they are more specialized due to the reduction of the coelom and the masking of the primary segmentation. The nephrostome is the only ciliated part and projects into a ventral coelomic chamber. The nephrostome leads into an expansion called the capsule. The capsule is usually filled with phagocytes and as a rule does not communicate with the following intracellular canal. This nephridial canal is much coiled and branched and in the Ichthyobdellidae the branches link up to form a network. This is the plectonephric condition, the canals leading to the outside.

REPRODUCTION. The testes, of which there are often several pairs (nine in *Hirudo),* and the single pair of ovaries are also present as closed vesicles in the sinuses and are derived from the coelomic epithelium, but in distinction from the rest of the annelids they are continuous with their ducts. The separation of the genital part of the coelom from the rest, begun in the Oligochaeta, here becomes complete. The testes discharge into a common vas deferens on each side; the two vasa unite anteriorly to form a median penis. Similarly the two oviducts join and the eggs pass through a single albumen gland and vagina to the exterior. The spermatozoa, united in bundles, are deposited on the body of another leech and appear to make their way through the skin to the ovaries where fertilization occurs. The eggs are laid in cocoons, the case of which is formed by clitellar glands in the same way as in *Lumbricus.*

Family **Acanthobdellidae**

Acanthobdella, a parasite of salmon, is a link with the Oligochaeta. In it the specialized hirudinean characters are only partly developed. There is no anterior sucker but a well-developed posterior sucker formed from four segments. The total number of segments is twenty-nine compared with thirty-two in the rest of the group. There are dorsal and ventral pairs of chaetae in the first five body segments and the coelomic body cavity is a continuous perivisceral space, interrupted only by segmental septa as in the Oligochaeta. It is, however, restricted by the growth of mesenchyme in the body wall and split up into a dorsal and ventral part in the clitellar region. The so-called testes (really vesiculae seminales) are tubes running through several segments, filled with developing spermatozoa and their epithelial wall is continuous with that of the perivisceral coelom, another primitive feature. The vasa deferentia, moreover, open into the testes by typical sperm funnels.

It is interesting to find that in the Branchiobdellidae, a family of the Oligochaeta, parasitic on crayfish, there is the same sort of leech-like structure: a posterior sucker, annulated segments, absence of chaetae and presence of jaws. But the condition of the coelom, nephridia and generative organs is so like that of the Oligochaeta that the family must remain in that group.

Family **Rhynchobdcllidae**

Pontobdella, parasitic on elasmobranch fishes. *Glossiphonia*, a fresh-water leech feeding on molluscs such as *Limnaea* and *Planorbis* and on the larvae of *Chironomus;* body ovate and flattened; hind gut with four pairs of lateral caeca; eggs laid in the spring, the young when hatched attaching themselves to the ventral surface of the body of the mother.

Family **Gnattiobdellidae**

Hirudo, the medicinal leech, at one time a common British species but now rare, jaws armed with sharp teeth.

Haemopis, the horseleech, common in streams and ponds, which it leaves to deposit its cocoons and in pursuit of prey; jaws armed with blunt teeth, which cannot pierce the human skin; a single pair of caeca in the mid gut.

This leech is carnivorous, devouring earthworms, aquatic larvae of insects, tadpoles and small fish. The land leeches of the tropics, of which *Haemadipsa* may serve as an example, live in forests and swamps and, mounted on leaves and branches, wait until a suitable mammalian prey presents itself.

PHYLUM MOLLUSCA

DIAGNOSIS.

1. Bilaterally symmetrical animals, but sometimes body can be asymmetrical.
2. Unsegmented coelomate animals, but the most primitive forms have methameric organs. Coelom varying in development, but always represented by pericardium, the cavity of the kidneys (which communicates with the pericardium), and the cavity of the gonads.
3. Body consists of a head (usually well developed), a ventral muscular foot and a dorsal visceral hump; with soft skin, that part covering the visceral hump (the mantle) often secreting a shell which is largely calcareous, and produced into a free flap or flaps to enclose partially a mantle cavity into which open the anus and the mesoblastic kidneys (usually a single pair);
4. A pair of ctenidia (organs composed of an axis with a row of leaf-like branches on each side, contained in the mantle cavity, originally used for breathing);
5. Alimentary canal usually with a buccal mass, radula and salivary glands, and always a stomach into which opens a *digestive gland* or *hepatopancreas*,
6. Blood system consisting of a heart, a median ventricle and two lateral auricles, arterial system and venous system often expanding into a more or less extensive haemocoele, with haemocyanin as respiratory pigment;
7. Nervous system consisting of a circumoesophageal ring, often concentrated into cerebral and pleural ganglia, pedal cords or ganglia and visceral loops;
8. Development of mollusks are very similar to the polychaet development. Larvae mostly of the **trochosphere** (trochophore) type.

CLASSIFICATION

There are five classes in the Mollusca.

Class 1. AMPHINEURA. Molluscs with an elongated bilaterally symmetrical body, without tentacles or eyes; nervous system without ganglia.

Order 1. Polyplacophora. Well-developed flat foot, shell made up from many units. Chiton

Order 2. Monoplacophora. Well-developed flat foot, shell made from one unit, have an internal metamerism. Neopilina

Order 3. Aplacophora. Foot reduced. Neomenia

Class 2. GASTROPODA. Molluscs possessing a head, tentacles, and at some stage of their development show torsion.

Order 1. Prosobranchiata. Gasteropods in which the adult shows torsion; the visceral loop is in a figure of eight, the gills are anterior to the heart. Haliotis, Patella, Buccinum, Pterotrachea

Order 2. Opisthobranchiata. Gasteropods in which the adults show detorsion by a process of untwisting. Aplysia, Doris

Order 3. Pulmonata. Gasteropods in which the adult's nervous system becomes symmetrical following torsion by a process of shortening of the abdominal commissures. Limnaea, Helix

Class 3. SCAPHOPODA. Bilaterally symmetrical molluscs living in a tubular shell open at both ends, reduced foot, tentaculate, no gills. Dentalium, Cadulus

Class 4. BIVALVIA (LAMELLIBRANCHIATA). Molluscs with a bilaterally symmetrical body laterally compressed and enclosed by a shell that develops as two valves. The head is rudimentary, tentacles are absent.

Order 1. Protobranchiata. Lamellibranchs with flat, non-reflected gill filaments. Nucula, Yoldia

Order 2. Filibranchiata. Lamellibranchs with reflected gill filaments, the filaments being joined by ciliary junctions. Mytilus, Anomia

Order 3. Eulamellibranchiata. Lamellibranchs with reflected filaments, the filaments being connected by vascular tissue. Anodonta, Cardium

Order 4. Septibranchiata. Lamellibranchs with gills no longer respiratory but, instead, forming a muscular septum. Poromya, Cuspidaria

Class 5. CEPHALOPODA. Bilaterally symmetrical molluscs; the head is well developed and surrounded by a crown of tentacles representing the foot; develops a siphon, typically have a chambered shell; nervous system greatly centralized, eyes usually well developed.

Order 1. Dibranchiata. Cephalopods with a single pair of gills and kidneys; shell internal. Sepia, Loligo, Octopus

Order 2. Tetrabranchiata. Cephalopods with two pairs of gills and kidneys; shell external. Nautilus, Baculites

DETAILED ACCOUNT

BASIC MOLLUSCAN PATTERN. While we do not know exactly what the ancestral molluscs looked like, we can make a very shrewd guess at their structure. They had a head with tentacles, a flat creeping foot, a conical visceral hump covered by a mantle which possibly contained numerous calcareous spicules and not a complete shell, and a posterior mantle cavity into which opened the median terminal anus and the common apertures of the kidneys and the gonads, and which also contained the ctenidia. In the alimentary canal the fore gut formed a muscular body, the buccal mass, and a radula and the mid gut an oesophagus, stomach and digestive glands and intestine. The heart had a median ventricle and a pair of auricles. The perivisceral coelom reduced by the development of an extensive haemocoele is represented by the pericardium with which communicates in front the cavity of the gonads and at the sides the two coelomoducts ('kidneys'). In the nervous system there were, as in annelids and arthropods, a circumoeso-phageal commissure or brain which may or may not have been ganglionated, ventral pedal cords, a visceral commissure coming from the pleural part of the brain, and a pallial commissure in the mantle edge. From this beginning diverged the different groups which we know today.

MAIN VARIANTS ON PATTERN. The chitons (Amphineura), which have departed least from the ancestral structure, became elongated but limpet-like forms, their visceral hump being protected by eight shell plates, their mantle cavity extended^ll round the foot, while instead of a single pair of ctenidia many such pairs arose. The Gasteropoda remained as short creeping forms; they are characterized by the growth of the visceral hump dorsally, but unequally so that it has coiled in a spiral (which is covered by a single shell). This caused a readjustment of the visceral hump which has revolved (usually to the right) on the rest of the body through 180° (torsion) and the mantle cavity is now anterior. The Bivalvia are flattened from side to side, the whole body being covered by two mantle lobes secreting two shell valves united by a median hinge. The ctenidia inside the greatly enlarged mantle cavity have developed into huge organs of automatic food collection and so the head, rendered unnecessary and withdrawn into the mantle cavity, has become vestigial. Similarly the foot has lost its flat sole and has to be extended out between the valves to move the animal. In the Cephalopoda, though there is an unequal growth of the visceral hump relative to the rest of the body, as in gastropods, it is coiled in a plane spiral, but there is no torsion, the mantle cavity remaining posterior. The primitive forms in the group have an external shell which is divided into chambers, and those behind the body chamber contain gas. This has had a great effect on the development of the group, for by diminishing the specific gravity of the animals it has enabled them to become more or less free-swimming. They have tended, with the loss of the shell, to become more and more efficient swimmers, and this is associated with the development of their predatory habits. The anterior regions shows a kind of transformation new to the molluscs in its partial modification into circum-oral prehensile tentacles for seizing food. Lastly, and in connexion with all these changes, the brain and sense organs have become enormously developed and the cephalopods are seen to be one of the most progressive groups of invertebrates.

THE SHELL. Characteristically the ectodermal epithelium of the mantle secretes a shell in the Mollusca and in most of them the method of secretion is the same. The original shell is laid down by the mantle of the veliger larva, but all extension takes place by secretion at its edge. The outer shell layer, periostracum, formed of homy conchiolin, is first produced in a groove and then the prismatic layer, largely consisting ofcalcite or arra-gonite, is secreted underneath it by the cells of the thickened edge. The innermost nacreous layer (also mostly calcium carbonate) is, however, formed by the cells of the whole of the mantle, and under such conditions as occur in the formation of pearls this general epithelium is capable of secreting any of the three shell layers.

THE COELOM. The coelom is primitively represented as three pairs of cavities, the renocoele, the gonocoele and the pericardium, though they do not develop in a manner suggestive of mesodermal segmentation. Originally these three cavities intercommunicated and the reproductive cells discharged through the renocoele. In the more advanced molluscs there is a progressive separation of the renal and the gonadial products till they each discharge through their own duct. A similar separation of the renal and gonadial systems is seen in the development of the vertebrate urino-genital system.

GILLS. The molluscs are mainly an aquatic group respiring by means of gills. These gills are usually supplied with cilia which bring a current of water flowing over the respiratory surface. Oxygen will diffuse most efficiently into a gill if the direction of water flowing over the gill is opposite to the direction of blood flowing inside the gill. This is referred to as 'the principle of counter-flow' and it ensures efficient oxygenation of the blood. This has been of some importance in the evolution of the gill structure and their position in the mantle cavity. The arterial blood vessel always lies upstream to the venous vessel. In addition there is a special development of supporting tissue to hold the gill in position.

THE MOLLUSCAN STOMACH. The stomach in the molluscs shows considerable variation in form and function correlated with the different feeding habits. The primitive molluscs were microphagous feeders, animals feeding on minute particles which they scraped off rocks by means of a well-developed radula. They also secreted a large amount of mucus; food particles and mucus were sent down to the stomach which had a complex series of folds that sorted out the food particles and prevented them from blocking the ducts leading to the digestive and absorbing gland. The stomach has three distinct areas. (1) A series of ciliary sorting areas that filter-off the different food particles. (2) A cuticular lined gastric shield which protects the stomach against the action of sharp particles and also helps to crush large particles. (3) A small sac with strong cilia. These cilia seize the mucus string coming in from themouth and rotate it and its contained food towards the intestine. The sac thus acts as a capstan. In the primitive animals the sac becomes full of stiff mucus imbedded with faeces; this is called the protostyle. The coarse foods go straight through the stomach to the intestine; the smaller particles are separated out by the ciliary fields and carried to the openings of the absorptive and digestive gland. This type of stomach is seen in Diodora. Other primitive gasteropods such as Trochus still have the faecal style sac but the mucus strings that come from the oesophagus, instead of going to the sac, go to a specially developed caecum. The style sac still acts as a capstan and receives the mucus after it has been to the caecum and passes it on to the intestine. The more intensive herbivores show an interesting modification of the style sac. Though it still retains some of its capstan-like action, it becomes filled with a crystalline material which contains an amylase which helps to digest the starches present in the food. In addition the style contains many spiro-chaetes which may secrete a cellulase also found in the style. The crystalline style and its associated enzymes have been evolved independently several times in the molluscs. It is found in the advanced herbivorous gasteropods such as Crepidula, Cavolinia, Lambis, as well as in several lamellibranchs. In the carnivorous gasteropods the gut becomes muscular and loses its mechanical sorting areas, style sac and gastric shield. Instead there is a complex development of a muscular buccal mass and gut so that a well-developed peristaltic wave can occur. One usually imagines that a carnivorous animal tan eat worms and other molluscs, but it should be remembered that animals feeding on coelenterates and polyzoans are also carnivores. Some molluscs have very specialized feeding methods. Vermetus gigas, a gasteropod, traps its prey by releasing a series of mucus threads from the pedal gland. Small animals become trapped in these threads and at intervals the threads are swallowed and the animals passed to the stomach. Other gasteropods feed on molluscs. Natica bores holes in mollusc shells by applying its mouth to the shell and releasing sulphuric acid from a special gland on the snout. The acid dissolves a hole in the shell and Natica then inserts its radula into the hole and scoops out the animal's soft entrails. Purpura uses a mechanical method of boring into a shell, the radula slowly scraping away successive layers of the shell. Philene swallows small lamellibranchs whole and crushes them up in a muscular gizzard. Chrysallida, an opisthobranch pyramellid, is a parasite on sedentary polychaetes. It has no true radula but has developed a special hollow tooth in a proboscis that is also furnished with a sucker. The animal approaches a polychaete, extends the proboscis, grasps its prey with the sucker and then suddenly inserts the tooth through the body wall. The blood is then sucked out of the host by means of a muscular suction pump. Calma, a small opisthobranch living on the yolk of fish eggs, has a very reduced stomach, no gizzard, and no anus. The faecal material accumulates in the liver throughout the whole of the animal's life.

EMBRYOLOGY. In general the embryology of the molluscs closely resembles that of the polychaetes. To simplify matters the account given here will be restricted to the Gasteropoda amongst the molluscs. Most of the gasteropods are oviparous though viviparity is fairly common, being found in Littorina rudis, several species of Helix, and in Paludina to mention a few species. Those that lay eggs may either do so singly as in the case of *Haliotis* and

Acmea or they may lay them in cocoons. The mortality in the cocoons is high though most of the cells that are laid in the cocoon are not true eggs; many function as nurse cells and provide the developing embryos with food. In *Buccinum* the development of the nurse cells has been particularly studied. The fertilized eggs start to cleave. Cleavage is total and spiral and is to some extent affected by the amount of yolk in the egg. The spiral cleavage is very much the same as that described for the polychaetes. The first two divisions bring about the ABCD cells which then divide to form the four micro-meres which sit in between the large macromeres. Further left and right division leads to the development of the four quartets of cells. During these cleavages the cells form the two structures noticed in the polychaetes, the apical cross and the rosette. It is important to note that though these two structures are found in both polychaetes and molluscs there are certain definite differences in the formation of the two groups. In the polychaetes the branches of the cross lie in line with the cells of the first macromeres A-D. In the gastero-pods the branches of the cross lie between the cells of the first macromeres. Another difference is that in the gasteropods the cells Ia^{112}-l</$^{11!}$ are not incorporated in the cross though they are in the annelid cross. The gasteropods on the other hand have in the cross the cells *2a-2d*, which do not take part in the annelid cross.

In general the fate of the molluscan quartets is very similar to that of the annelid cells. The main supply of the mesoderm arises from the *4d* cells though some of the mesoderm arises from mesenchyme cells that migrate into the embryo. Gastrulation can occur by several methods. *Littorina* gastrulates by simple invagination, *Crepidula* by epiboly and *Patella* by ingression. The *4d cell* migrates internally and forms the mesoderm rudiment, the coelom arising as a separation of the mesoderm cells. The mesoderm does not show segmentation, though at times there may be a very regular disposition of the mesoderm cells as a band on either side of the gut.

LARVAE. In the Mollusca the development of the trochosphere takes place in a fashion identical with that described for the annelid. In the diagram given here for *Patella,* we see the completion of gastrulation and the appearance of the ciliated rings of the trochosphere; also the single large cell which gives rise to the mesoderm. Then, the early *veliger* with an internal organization similar to the annelid, with apical organ, larval nephridia and prototroch. The figure shows, however, organs which are not present in the annelid. On the dorsal side between the prototroch and the anus the larval ectodermal epithelium forms the rudiment of the *mantle* and even at this early age secretes the first *shell.* On the ventral side, there is a prominence which is the *foot* (formed by the union of two rudiments). The single mesoderm cell gives rise first of all to two regular mesoderm bands; and by the development of a cavity in each of these, right and left coelomic sacs are formed; then instead of segmenting as in the annelid, these largely break up into single cells, some elongating and becoming muscle cells. It is because there is never any commencement of segmentation in the embryonic mesoderm in molluscs that we have the strongest grounds for believing that molluscs never had segmented ancestors. The trochosphere is followed by a second free-swimming stage, the veliger, in which the prototroch develops into an organ, the *velum,* of increased importance, which serves not only for locomotion but also for feeding, the cilia creating a current, which brings particles into the mouth. In the veliger stage the foot increases in size and the shell often becomes coiled in the Gastropoda.

INTERNAL ANATOMY of mollusks is presented at Figeres 13-16.

Fig. 13 *Helix* (Gastropoda), internal construction

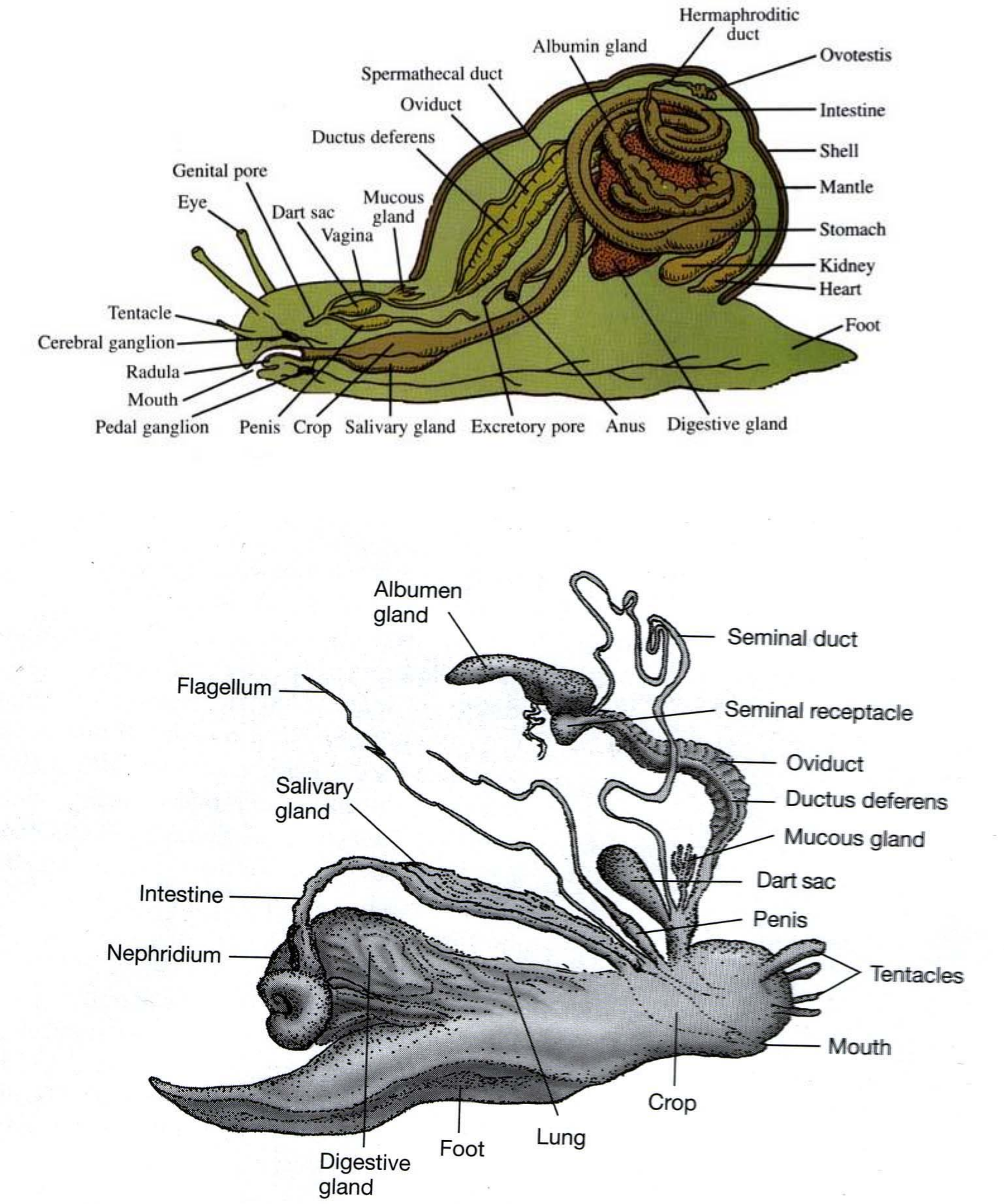


Fig. 14 *Helix* (the garden snail), internal organs

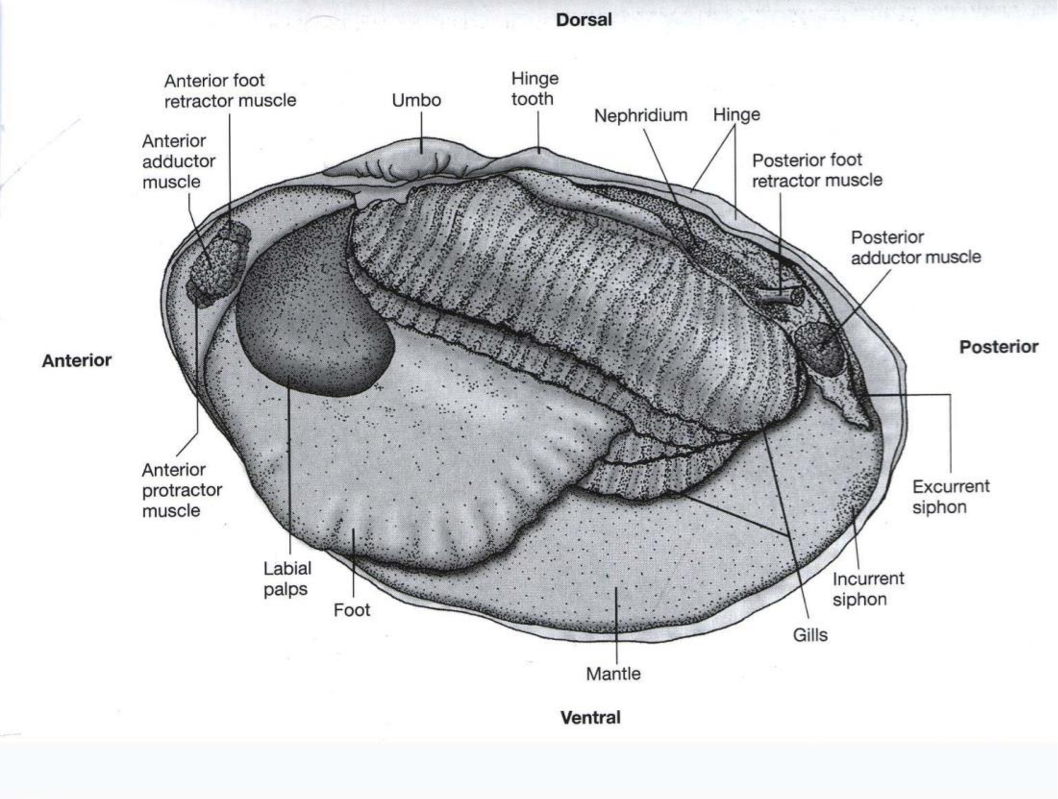


Fig. 15 Freshwater mussel, partly dissected, lateral view

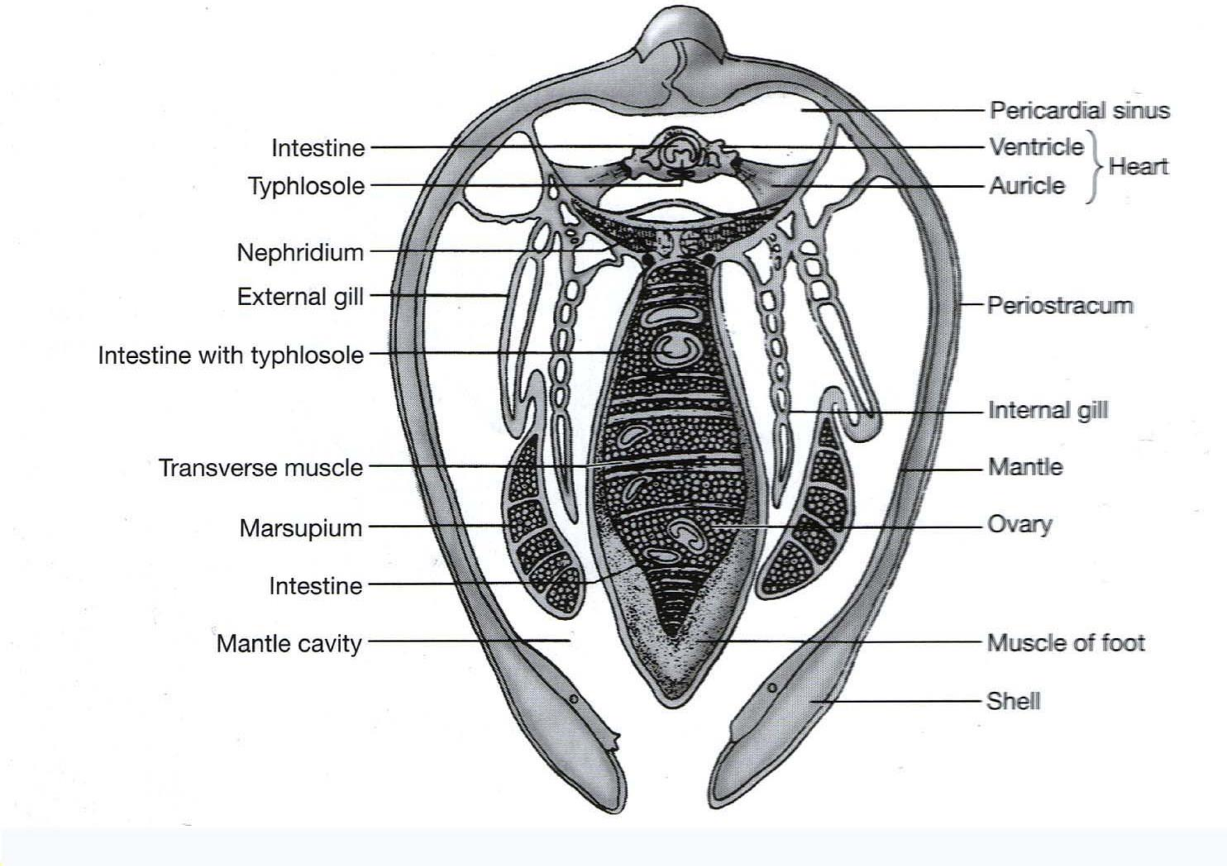


Fig. 16 Freshwater mussel, cross section trough heart region

PHYLUM ARTHROPODA

CLASS CRUSTACEA

DEFINITION. Arthropoda, for the most part of aquatic habit and mode of respiration; whose second and third somites bear antennae; and their fourth somite a pair of mandibles.

FACTORS IN THE EVOLUTION OF THE CRUSTACEA. (1)

(1)Specialization of limbs

The Crustacea are essentially aquatic arthropods. That fact alone makes it possible that in them the same appendages should combine the functions of locomotion (by swimming), feeding (by gathering particles from the water), respiration (by exposing a thinly covered surface to the medium), and the reception of sensory stimuli. There is perhaps no extant crustacean in which all four functions are thus combined—unless we may regard the trunk limbs of the Branchiopoda (see below) as sense organs in a minor degree—but not uncommonly three, and perhaps usually two, are performed by the same limb. In the lowest members of the class—the phyllopod Branchiopoda (such creatures as the fairy shrimp, *Chirocephalus)*a long series of somites of the trunk bear similar appendages which all function alike in swimming, respiration, and the gathering of food. Evolution within the crustacean group appears to have proceeded mainly by the specialization, for particular functions, of particular appendages of an ancestor which possessed along the whole length of the body a numerous series of limbs, of which all, except probably the first pair (antennules), were as much alike and capable of at least as many functions as those which the Branchiopoda now possess upon the trunk. Such a condition existed in the Trilobita, but in all modern Crustacea the appendages of the head are already specialized for various uses, and in most members of the group the specialization has gone farther. Moreover, it has taken place in more than one way. Limbs which in one crustacean are adapted to some particular function are in others specialized for quite different services.

(2) Shortening of the body. Two other factors, added to, or perhaps consequent upon, the specialization of limbs, have taken part in bringing about the great variety of organization which exists in the Crustacea. One is a shortening of the body. As the efficiency of the limbs increases by specialization, there occurs a lessening of their number, and finally the reduction or loss of the somites whose limbs have thus disappeared. The reduction, which has occurred independently in every class, has taken place in the hinder part of the body, though as a rule the extreme hind end (telson) is relatively unaffected.

(3) Development of carapace. The other factor is the development, from the hinder part of the head, of a skin fold—the *carapace*—by which the important anterior region of the body is overhung and protected, and the setting up in the surrounding water of currents for purposes of respiration and feeding is facilitated. Not all crustaceans possess the carapace: in some it has perhaps never existed, others have discarded it. In those which have it, its extent varies: in extreme cases it encloses the whole body.

The transformation of the external make-up of the body is of course reflected in the internal organization, which shows corresponding concentrations of function and differentiation of the contents of somites.

CLASSIFICATION

Subclass 1. BRANCHIOPODA. Free crustaceans with compound eyes; usually a carapace; at least four pairs of trunk limbs which are in most cases broad, lobed and fringed on the inner edge with bristles.

Order **1. Anostraca.** No carapace; stalked eyes; antenna of fair size but not biramous; trunk limbs numerous and all alike; caudal rami unjointed. *Chirocephalus, Artemia*

Order 2. **Lipostraca.** Fossil order represented by *Lepidocaris.*

Order 3. **Notostraca.** Carapace a broad shield above trunk; compound eyes sessile and close together; trunk limbs numerous, the first pairs differing considerably from the rest; multi-articulate caudal rami. *Apus, Lepiduris*

Order **4. Diplostraca.** Compressed carapace enclosing trunk and limbs; compound eyes sessile and apposed or fused; antenna large and biramous; 4-27 pairs of trunk limbs usually considerably differentiated.

Suborder **1. Conchostraca.** 10-27 pairs of trunk limbs. *Estheria Suborder* 2. **Cladocera.** 4-6 pairs of trunk limbs.

Daphnia, Sida, Leptodora, Polyphemus

***Subclass* 2**. OSTRACODA. Free crustaceans with a bivalve shell and an adductor muscle; and not more than two recognizable pairs of trunk limbs, these not being phyllopodia. *Cypris, Cypridina*

Subclass 3. COPEPODA. Free or parasitic crustaceans without compound eyes or carapace, typically six pairs of thoracic limbs of which the first is always and the sixth is often, uniramous, the rest biramous. No limbs situated on the abdomen.

Calanus, Chondracanthus, Lernaea, Cyclops

Subclass 4. **BRANCHIURA.** Crustacea temporarily parasitic on fishes, with compound eyes, a suctorial mouth, carapace-like expansions of the head, unsegmented limbless abdomen. •*Argulus*

Subclass 5. CIRRIPEDIA. Fixed, for the most part hermaphrodite, crustaceans, without compound eyes in the adult, with a carapace (except in rare instances) as a mantle which encloses the trunk;
usually with a mandibular palp and typically six pairs of thoracic limbs.

Order 1. **Thoracica.** Cirripedia with alimentary canal, six pairs of thoracic limbs, no abdominal somites, permanently attached by the preoral region. *Lepas*

Order 2. **Acrothoracica.** Separate sexes; have an alimentary canal, less than six pairs of thoracic limbs, no abdominal somites. Permanently sessile. *Alcippe*

Order 3. **Apoda.** Hermaphrodite, no mantle, no thoracic limbs, no anus, the body divided T^y constrictions into rings. *Proteolepas*

Order 4. **Rhizocephala.** Parasitic on decapod crustaceans; never have an alimentary canal; adult has no appendages, develops fungus-like roots which penetrate into host.

Sacculina, Thompsonia

Order 5. **Ascothoracica.** Parasitic, with alimentary canal and six pairs of thoracic appendages. *Laura*

Subclass 6. MALACOSTRACA. Crustacea with compound eyes, usually stalked; typically a carapace covering the thorax; a thorax of eight somites; an abdomen of six somites (rarely seven); all except the rare seventh abdominal somite bear appendages.

*Order **1.*** **Leptostraca.** Have seven abdominal somites; phyllopodia, large carapace not fused to any thoracic somite. *Nebalia*

Order 2. **Hoplocarida.** Shallow carapace fused to three thoracic somites. First five thoracic limbs subchelate. *Squilla*

Order 3. **Syncarida.** No carapace. *Anaspides, Bathynella*

Order **4. Peracarida.** Carapace does not fuse with more than four thoracic segments. **Have** oostegites.

Suborder **1. Mysidacea.** Carapace covers most of thoracic segments. *Mysis Suborder* 2. **Cinnacea.** Carapace covers only three or four segments. *Diastylis Suborder* 3. **Tanaidacea.** Carapace small, covers only two thoracic segments. *Apseudes, Tanais Suborder* **4. Isopoda.** No carapace, body dorso-ventrally flattened.

Ligia, Armadillidium, Idotea Suborder 5. **Amphipoda.** No carapace, body laterally flattened.

Gammarus, Caprella, Phronima

Order 5. **Eiicarida.** Carapace fused to all the thoracic segments. No oostegites. *Suborder* **1. Euphausiacea.** Small scaphognathite, no statocyst.

Nyctiphanes Suborder 2. **Decapoda. Big** scaphognathite, statocysts present.

1. **Macrura.** Abdomen hard, long and extended. *Astacus*
2. **Anomura.** Abdomen soft. *Eupagurus*
3. **Brachyura.** Abdomen hard, short and folded beneath the body. *Carcinus*

GENERAL CLASSIFICATION OF CRUSTACEA. The specialization of the limbs, shortening of the body and development of the carapace has given rise to six subclasses of Crustacea. We must now briefly survey them.

(1) BRANCHIOPODA. In the Branchiopoda feeding is performed by the limbs of the trunk. In the 'phyllopod' groups of this subclass, mentioned above, it is only on the head that differentiation among the appendages has proceeded to any considerable extent. Of the head limbs each, as we have seen, is specialized for some particular function, such as the service of the senses or the manducation of food. On the trunk the limbs, which are numerous, are still similar and all subserve at least the functions of feeding and respiration. In the order *Anostraca,* to which *Chirocephalus* belongs, there is no carapace, and the trunk limbs, whose similarity is very strong, retain the function of swimming. In the order *Notostraca*, also phyllopodous, there is a carapace but it is wide and shallow and does not enclose the trunk limbs, and they are still used for swimming. A certain degree of differentiation exists between these limbs, the anterior pairs for instance being capable of clasping objects. In both the foregoing orders limbs have been dispensed with on some of the hinder somites. The remaining phyllopod group, the *Conchostraca*, are united with the non-phyllopod group Cladocera as the order *Diplostraca.* In the members of that order (except a few aberrant Cladocera) the carapace encloses the trunk limbs, which are not used for swimming, that function being taken over by the antennae. The Conchostraca alone among branchiopods retain limbs on all their trunk somites like the trilobites, but as in the Notostraca there is a certain degree of

differentiation between the members of the series. In the *Cladocera,* the highest group of the Branchiopoda, a compact and very efficient feeding apparatus is formed by some half-dozen pairs of limbs; the trunk is correspondingly shortened, and even so some of the hinder somites are limbless. In certain members of this group, such as the water-flea *Daphnia,* there is a high degree of differentiation between the trunk limbs.

(2) OSTRACODA. A similar habit of body is even more strongly developed in the subclass Ostracoda which are very short-bodied and completely enclosed in a bivalve shell formed by the carapace. Whereas, however, in the Cladocera it is by trunk limbs that food is gathered, in the Ostracoda that function is performed by limbs of the head. The trunk limbs, which have lost the functions of swimming and respiration as well as that of feeding, serve relatively unimportant subsidiary purposes, and are reduced, at most, to two pairs. Some members of the class carry shortening to an extreme pitch by contriving to dispense with one or both of these pairs.

(3) The members of the subclass COPEPODA also feed by means of appendages on the head, though they use these differently from the Ostracoda. In contrast to that group they have no carapace, and they have retained a trunk of some ten somites, of which the first half-dozen bear limbs which are specialized organs of swimming. The hinder part of the trunk is without appendages, save a pair of styles on the telson, often shows coalescence of somites, and may become a mere stump. Some of those members of this class which are parasitic lose in the adult female the segmentation and most, or even all, of the appendages.

(4) In the small subclass of parasites known as BRANCHIURA which are sometimes placed in the Copepoda, but differ from that group in possessing compound eyes and in other important respects, there are carapace-like lobes at the sides of the head, but these do not enclose the trunk, and the general build of the body and the form and function of the thoracic limbs simulate those of a copepod. The abdomen is much reduced.

(5) The subclass CIRRIPEDIA or barnacles, which as larvae attach themselves by their antennules to some object upon which they henceforward lead a sedentary life under the protection of a large, mantle-like carapace, bear, upon the same trunk somites as do the Copepoda, limbs which, like those of the latter group, are biramous. These appendages, however, are used, not for swimming, but for gathering food-particles from the water; while of the head appendages the antennae are absent and the others are much reduced and not used in gathering food. The least specialized members of this subclass are, in respect of segmentation and appendages, on a par with the best-segmented of the Copepoda. Most cirripedes, however, have lost the whole of the hinder (abdominal) region of the trunk. Others are deficient in the appendages of further somites, and the series ends with the sac-like parasites of the order *Rhizocephala*.

(6) The subclass MALACOSTRACA (the highest crustaceans, including various 'shrimps', slaters, sandhoppers, crayfishes, etc.) obtain their food with the limbs on the anterior region (thorax) of the trunk, and, in primitive cases in which it is gathered as particles, strain it from the water with the last pair of appendages of the head (the maxillae). The thoracic limbs retain also the function of locomotion and normally are adapted for respiration by the presence upon them of gills, which are usually protected by a carapace of moderate size. Thus this region of the body of the Malacostraca is, in its own ways, as many-functioned as the corresponding part of the trunk of *Chirocephalus.* The Malacostraca maintain in typical cases the swimming function of the limbs on the hinder portion (abdomen) of the trunk, and some of the subclass have found other uses (ovigerous, copulatory, etc.) for these appendages. Accordingly there is seldom any reduction in the fixed number of fourteen (or fifteen) trunk somites which, arranged always in a thorax of eight and an abdomen of six (or seven), characterizes the class. Nevertheless in all but one of the orders the abdomen has lost a somite, in the crabs and

some others of the highest suborder *(Decapoda)* it is reduced, and in a few members of the subclass it is a limbless and unsegmented stump.

ENTOMOSTRACA. The name Entomostraca was formerly used in the classification of the class, to distinguish from the Malacostraca a division containing all the other subclasses. Since, however, these differ from one another as widely as each of them does from the Malacostraca, the name is no longer used in classification but is only a convenient designation for the lower crustacean subclasses as a whole.

GENERAL STRUCTURE.

CUTICLE. The cuticle of a crustacean is, save for the joints, usually stout relative to the size of the animal, but is thinner and flexible in many parasitic genera. It is often strengthened by calcification, and in certain ostracods, barnacles and crabs this gives it a stony hardness. In each somite there may or may not be distinguishable the dorsal plate or *tergite (tergum)* and ventral *sternite (sternum)* usual in arthropods. The tergite may project at each side as a *pleuron*.

SOMITES. There are embryological indications that the *body* should be regarded as containing, besides the *somites,* an anterior *presegmental region,* to which the eyes belong, corresponding to the prostomium of a worm, and a *postsegmentalregion* or *telson,* on which the anus opens. Each somite, except the first, which is purely embryonic, may bear a pair of *appendages,* though it is rarely that the appendages of all the somites are present at the same time. The somites never all remain distinct in the adult. Always some of them are fused together and with the presegmental region so as to form a head, and often there is also fusion of them elsewhere.

TAGMATIZATION: HEAD. Nearly always the somites are grouped into three tagmata, differentiated by peculiarities of their shape or appendages, and known as the head, thorax, and abdomen. These, however, are not morphologically equivalent in different groups.

The *head* always contains, besides the region of the eyes and the embryonic first somite, the somites of five pairs of appendages—two, the antennules and antennae, preoral; and three, the mandibles, maxillules, and maxillae, postoral. More somites are often included in the actual head, but as the additional appendages (maxillipeds) then usually show features of transition to those behind them, and as the fold of skin which forms the carapace first arises from the maxillary somite, the true head is held to consist only of the anterior portion of the body as far as that somite inclusive. There is evidence of an earlier head, carrying only the first three pairs of limbs which alone exist in the *Nauplius* larva, and still indicated in some cases, by a groove which crosses thecheek immediately behind the mandible. This *mandibular groove* is distinct from the true *cervical groove* which often (as in *Astacus*)marks the boundary between head and thorax: the two grooves may co-exist, as in *Apus* and in *Nephrops.* The Crustacea, indeed, admirably illustrate the way in which the process of 'cephalization' tends, in arthropods as in vertebrates, to extend backwards and to involve more and more segments. With it has gone a backward shifting of the mouth, which in the Crustacea now stands behind the third somite, with two pairs of appendages (antennules and antennae) in front of it. The commissure which unites the ganglia of the antennae still passes behind the mouth, and may usually be seen, as in *Astacus*, crossing from one of the circumoesophageal commissures to the other. The head of the Crustacea is unlike, and less specialized than, those of other arthropods in that its limbs are not entirely restricted to sensory and alimentary functions but often have also other uses, such as swimming, the setting up of currents, or prehension.

THORAX AND ABDOMEN. The head, though it varies in extent, is of the same nature throughout the group, being primarily, like the heads of other animals, the seat of the principal organs of special sense and of manducation. On the other hand, the two tagmata known as the *thorax* and *abdomen,* which usually can be recognized in, and together compose, the post-cephalic part of the body or *trunk*, vary rrnach more in extent, and each of them has in the several groups no constant feature save its position relative to the other. The precise boundary between thorax and abdomen is sometimes difficult to fix. The names, as they are commonly used, are in this respect inconsistently applied, denoting in some groups limb-bearing and limbless regions, in others the sections of the trunk which lie before and behind the genital openings. For the sake of consistency we shall adopt the convention that the somite which bears the genital openings (or the hinder such somite when, as sometimes happens, the male opening is on a somite behind that of the oviduct) is always the last somite of the true thorax. In this sense, in certain cases (copepods, cladocera), somites which are commonly called abdominal are strictly to be reckoned as thoracic. In respect of segmentation the trunk varies from the condition of a limbless stump in certain ostracods to the possession of more than sixty somites in some of the Branchiopoda.

CARAPACE. A structure very commonly found in crustaceans is the *shell* or carapace, a dorsal fold of skin arising from the hinder border of the head and extending for a greater or less distance over the trunk. Its size varies greatly. In the Ostracoda and most conchostracans it encloses the whole body, extending forwards at the sides so as to shut in the head. In other cases, it only leaves part or the whole of the head uncovered. In typical malacostraca it covers the thorax, but in some it is a short jacket, leaving several thoracic somites uncovered, and in some (the Syncarida, Isopoda, and Amphipoda) it has disappeared. In the Anostraca and Copepoda it was perhaps never present. It may be a broad, flat shield over the back, as in *Apus*, but is usually compressed, and in the Conchostraca and Ostracoda becomes truly bivalve, with a dorsal hinge. In the Cirripedia it is an enveloping mantle, usually strengthened by shelly plates. In the Conchostraca, Ostracoda, Leptostraca, and Cirripedia it has an adductor muscle, but the adductors of these groups vary in position and are not homologous. The carapace may fuse with the dorsal side of some or all of the thoracic somites (the Cladocera, most of the Malacostraca): such somites are not on that account alone to be regarded as included in the head, though they may become so. The *chamber* enclosed by the carapace is known in various cases by various names as gill chamber, mantle cavity, etc., and performs important functions in sheltering gills or embryos, directing currents of water which subserve feeding or respiration, etc. In front, the carapace is continuous with the dorsal plate which represents the terga of the head, the cervical groove, if present, marking the boundary between them. We shall apply the term *dorsal shield* to the structure composed of the dorsal plate of the head with the carapace, if the latter be present. These terms have been used in various senses. In the usage here proposed, when there is no carapace fold, the dorsal shield is the dorsal plate of the head together with the terga of the somites that are fused with the head.

The dorsal plate of the head may be prolonged in front as a projection which is called the *rostrum*.

DORSAL ORGAN. A glandular patch or patches on the dorsal surface of the head, near its hinder limit, in many of the Branchiopoda, in *Anaspides,* and in the young stages of various other crustaceans, is known as the *dorsal organ* or *neck gland.* It is used by cladocera and conchostraca for temporary fixation. In other cases its function is not known. Possibly the organs to which this name is given are not all homologous. They must not be confused with the 'neck organ' of branchiopods.

APPENDAGES. Of the appendages or *limbs* of the Crustacea, the first, or antennule, is a structure *sui generis,* not comparable in detail with any of the others. Typically it is uniramous, and though in many of the Malacostraca it has two rami, these are probably not homologous with the rami, described below, of other appendages. The remaining limbs may all be reduced to one or other of two types—the' biramous' limb usually so-called, to which most of them more or less clearly conform, and the *phyllopodium,* to which belong the trunk limbs of the Branchiopoda and some other appendages, chiefly maxillules and maxillae and notably the maxilla of the Decapoda. The name by which the first of these types is generally known refers to the fact that limbs which best represent it fork distally into two rami. Since, however, the phyllopodium possesses the same two rami, and bears them, though not as a distal fork, yet in the same way as a great number of limbs of the first type, it is well not to use a name which might imply that there is a constant difference in respect of the rami between the limbs of the two types. We shall therefore call the first type the *stenopodium,* referring to its usually slender form (Greek *arnvos,* narrow).

STENOPODIUM. In the stenopodium the two rami—an inner *endopodite* and an outer *exopodite*—are set upon a common stem, the *proto-podite.* In many cases the protopodite bears also, on its outer side, one or more processes known as *epipodites*. In limbs in which the type is most perfectly developed the two rami are subequal and are borne distally upon the protopodite but in most cases the endopodite is the larger, and forms with the protopodite an axis, the *corm,* on which the exopodite stands laterally. In a few instances the exopodite is the larger.

PHYLLOPODIUM. The phyllopodium, is a broader and flatter limb than the majority of stenopodia. Its cuticle is usually thin, and then the shape of the limb is maintained largely by the pressure of blood within it. In these cases the flexibility is such that no joints are needed. There is in this limb an axial portion or corm which bears on the median side a row of lobes known as *endites,* and on the outer side one or more lobes known as *exiles.* Of the latter the more distal, standing usually opposite the third or fourth endite from the base and often known as the *flabellum,* is the homo-logue of the exopodite of the biramous limb. Exites proximal to this are epipodites. Of the *endites,* that which stands at the base of the limb is usually different in form from the rest and used in one way or another for manipulating the food. It is known as the *gnathobase.*

A limb of either type may vary by the lack of any of its parts. Notably the loss of the exopodite is liable to produce from either a *uniramous limb.* More-over, though the two types are very distinct in cases in which they are perfectly developed, as in the swimmerets of *Astacus* and the trunk limbs of *Apus*, there are many limbs which depart more or less from either type in the direction of the other—as, for instance, from the stenopodial type in the shape of the exopodite, or, as stated above, in the relation of the latter to the rest of the limb, or from the phyllopodium in the proportions of the rami or the reduction of the endites.

PRIMITIVENESS OF THE PHYLLOPODIUM AND STENOPODIUM. The comparison just made between the phyllopodium and the stenopodium leaves untouched the question which of them is the more primitive, that is, more resembles the limbs of the ancestral crustacean. On this point there is an old and as yet unsettled controversy. As proof of the primitiveness of the stenopodium it is pointed out (1) that this limb is more widespread than the phyllopodium, (2) that it occurs in the *Nauplius* larva, the early phyllopod *Lepidocaris*, and the trilobites, in all of which it is likely to be primitive, (3) that it more nearly approaches the form of the majority of pnrapodia of the Annelida, from which the Crustacea are held to have taken origin. In demonstration of the ancestral nature of the phyllopodium it is urged (1) that typical stenopodia with subequal rami borne distally upon a protopodite are comparatively rare and usually occur in highly specialized crustiiccans (Copepoda, Cirripedia; Malacostraca) (2); that the biramous limbs of the *Nauplius* and *Lepidocaris* are not primitive but adaptive, the relations of the rami of the limbs of trilobites are problematical, and the admittedly primitive Branchiopoda possess phyllopodia; (3) that the unjointed, turgid, lobed phyllopodium more nearly resembles the parapodia of certain annelids in which the neuropodium is axial, than the stenopodium resembles the normal biramous parapodium.

FUNCTIONS OF LIMBS. Concerning the functions of particular members of the series of limbs, and the corresponding modifications of their structure, little can be said that would hold good throughout the subphylum. There is an immense variety in these respects. The *antennules* and *antennae* are primarily sensory, and perhaps usually possess something of that function when they are also capable of swimming, prehension, attachment, etc. In the nauplius larva the antennules are uniramous and the antennae biramous, and they normally retain these conditions in the adult. The *mandibles* always play, by means of their strong gnathobase, some part in preparing the food, whether by chewing or by piercing for suction, but the distal part of the limb *(palp)* may aid in locomotion or set up feeding currents. They generally lose in the adult the biramous condition which they have in the nanplius. The *maxillules* and *maxillae* tend to be phyllopodia. The maxillules have usually the function of passing food to the mouth but may serve other ends. The maxillae have various functions in connexion with feeding and respiration. The *limbs of the thorax* perform in various cases practically every function for which appendages are used. If a crustacean walks, it is usually by means of these limbs. Often in one or more of them the last joint can be opposed to the joint which precedes it, forming a *chela* (or a *subchela),* so that the appendage is adapted for grasping. Modification of the hinder thoracic or anterior abdominal limbs in connexion with reproduction is common. *Abdominal limbs* are lacking save in certain of the Branchiopoda and most 01 the Malacostraca. When they are present they are commonly used for swimming, for setting up currents of water, or for carrying eggs and young.

FEEDING METHODS. When feeding is restricted to a few limbs it is often, though not always, accomplished in some other way than by the original habit of gathering food in small particles. Continuous and automatic strain-ing-out of such particles, which is practised (though in different modes) by the most primitive members of all classes except the Branchiura, is superseded in various members of different classes by the intermittent seizure, by particular limbs, of particles of some size, and this by the grasping of larger objects, which may lead to a predatory habit. Finally, either of these modes of feeding may be replaced in parasites by suction or absorption, through organs which do not always represent appendages at all. (Parasites, however, are not known among the Branchiopoda or Ostracoda.) Needless to say, each change in the mode of obtaining nutriment has entrained numerous alterations in organs other than those by which the food is actually taken, as in the means of locomotion, sense organs, weapons of offence, etc. On the other hand, adaptations to mere differences of habitat, in the Crustacea, as in other arthropods, are, as a rule, strikingly small. There is, for instance, remarkably little difference between a land crustacean and its nearest marine relatives. Pelagic genera, however, are sometimes considerably modified.

ACCESSORY APPENDAGES. Three elements of minor importance complete the external make-up of the Crustacea. In front of the mouth is a *lahrum* or upper lip; behind the mandibles is a lower lip or *metastoma,* usually cleft into a pair of lobes known as *paragnatha;* and on the telson usually (but in no adult malacostracan except the Leptostraca)is a pair of *caudal rami* forming the caudal *furca.*

Appendages which are lost are *regenerated* at subsequent moults; and the highest members of the group possess an elaborate mechanism for *autofomy*—the breaking-off of limbs which have been injured or which have been seized by enemies.

INTERNAL SKELETON. An internal skeleton is usually present in the form of ingrowths of the cuticle, known as *apodemes,* which serve for the insertion of muscles. Sometimes (notably in the Decapoda) they unite to form a framework, the *endophragmal skeleton.* In the Notostraca, a mesodermal tendinous plate, the *endosternite,* lies under the anterior part of the ttliincntary canal.

NERVOUS SYSTEM. The nervous systems of Crustacea exhibit a very complete series of stages from the ideal arthropod condition to the extremes! concentration. That of the Branchiopoda is in a very primitive state, having the antennal ganglia behind the mouth as the first pair of the ventral ladder, distinct ganglia for the following somites, and widely separated ventral cords. In the lower members of the Malacostraca *(Nebalia,* some mysids, etc.), the antennal ganglia have joined the brain and the ventral cords are closer together, but otherwise the primitive condition is retained. In other crustaceans various degrees of concentration of the ventral ladder are found, beginning with the establishment of a suboesophageal ganglion for the somites of the mouth parts, and ending in the formation, in the crabs and some other forms, of a single ventral ganglionic mass. In the Rhizocephala one ganglion supplies the whole body. The brain contains ganglia for the eyes *(optic lobes),* for the first or preantennulary somite *(protocerebrum),* and for the antennules *(deuto-* or *mesocerebrum).*

As in other arthropods, the name *procerebrum* is given to the anterior part of the brain, composed of the protocerebrum, the optic lobes, and sometimes other ganglia which are not connected with paired limbs.

Except in the Branchiopoda it also contains the antennal ganglia *(trito-* or *metacerebruni).* A *visceral* ('sympathetic') system is present. In its main features the functioning of the nervous system resembles that of insects (p. 458).

SENSE ORGANS. Sense organs are well developed in the free members of the group. *Eyes* are of two kinds, the *compound* eyes, of which a pair is usually present except in the Copepoda and adult cirripedes, and the *median* eye. Details of the structure of the compound eyes have been given above. They may be sessile or stalked, and the latter condition has given rise to a theory that they represent a pair of appendages. Since, however, there are no somites corresponding to their ganglia and since at their first appearance in the embryo they are sessile, this view is not generally accepted. The median eye is the eye of the *Nauplius* larva, and it persists in most adults, though it is generally vestigial in the Malacostraca. It consists of three pigmented cups, one median and two lateral, each of which is filled with retinal cells whose outer ends are continued as nerve fibres. Thus the sense cells are inverted, as in the eyes of vertebrata. Sometimes each cup has a lens. In some of the Copepoda the lateral cups are removed from the median one and developed as a pair of lateral eyes. Senses other than sight are subserved by various modifications of the bristles which exist on the surface of the body and contain nerve fibrils in their protoplasmic contents. Most of these bristles are branched in various ways and have *tactile* functions, including that of appreciating the resistance of the water to movements. In the Decapoda and Syncarida on the basal joint of the antennule and in the Mysidae on the endopodite of the sixth abdominal appendage there is a pit whose wall bears such hairs while the hollow usually contains sand grains (most decapods) or a calcareous body formed by the animal (Mysidae). These organs are *statocysts* for the sense of balance. *Olfactory hairs* or *aesthetascs* with delicate cuticle stand on most antennules and on many antennae. A pair of groups of cells, sometimes surmounted by setae, standing on the front of the head and known as *frontal organs,* are found in many crustaceans and are supposed to be sensory. They are present as two papillae in the *Nauplius* larva. The *nuchal sense organ* or 'neck organ' of many branchiopods is a group of cells on the upper side of the head containing refractive bodies and connected to the brain by a special nerve. **Its** function is unknown.

PIGMENTATION. Asis well known, most crustaceans are pigmented. The pigments are of various colours—red, orange, yellow, violet, green, blue, hrown, black, etc., though not all are found in any one species. The majority of them are lipochromes, though the brown and black are melanins. For the most part they are contained in branched cells (chromatophores), but some of the blue, and perhaps certain others, are diffused in the tissues. The chromatophores may lie in the epidermal layer, in the dermis, or in the connective tissue of deeper organs. Their behaviour has been studied in various malacostracans. The pigment is often caused to expand or contract, which it does by flowing into and out of their processes. In this it is affected by light, responding both to intensity of illumination and to the nature of the background, but only rarely to colour (wave-length). In light of high intensity or on a light-absorbing (e.g. dull black) background it expands; in light of low intensity or on a light-dispersing (e.g. dull white) background it contracts. Different pigments are affected to different degrees, and thus both the degree and the pattern of the coloration of a sensitive species (notably, for instance, of many prawns), changes with its surroundings—

usually, in nature, in such a way as to render the animal inconspicuous. The response to intensity of illumination is due to direct action of the light upon the chromatophores and will thus take place even in blinded animals; the response to background ALIMENTARY CANAL. The alimentary canal is with very rare exceptions straight, save at its anterior end, where it ascends from the ventral mouth. *The/ore gut* and *hind gut* (stomodaeum and proctodaeum), lined with cuticle intumed at the mouth and anus, leave a varying length of *mid gut* (mesenteron) between them. The intrinsic musculature, sometimes supplemented by extrinsic muscles running to the body wall, is strongest in the fore gut, whose lining sometimes develops teeth or hairs. In the Malacostraca these elements become a more complex proventriculus ('stomach'), with a 'gastric mill' and a filtering apparatus of bristles which strains particles from the juices of the food, the mill and filter being often in separate 'cardiac' and 'pyloric' chambers. The mid gut usually bears near its anterior end one or more pairs of diverticula ('hepatic caeca') which serve for secretion and absorption and may branch to form a 'liver'. This gland, however, unlike the liver of vertebrates, forms all the enzymes necessary for the digestion of the food and absorbs from its lumen the products of digestion. It stores the reserves in the form of glycogen and fat. Occasionally there is an anterior median dorsal caecum. Caeca are also sometimes found at the hinder end of the mid gut: these are more often median. In a few cases the hind gut is absent and the mesenteron ends blindly. In the Rhizocephala and the monstrillid copepods the alimentary canal is absent throughout life, for these animals absorb through the skin during the parasitic period enough nutriment to last through an entire life history.

DIGESTION is extracellular. The fore gut is frequently the seat of mechanical processes, and sometimes of chemical action by juices secreted by the mid gut diverticula, but never of absorption. The latter process as well as most of the chemical work is performed by the mid gut, including the hepatic diverticula. In the hind gut the faeces are passed to the anus, being in some entomostraca sheathed in a so-called 'peritrophic membrane' composed of a mucoid substance secreted by certain cells of the epithelium.

EXCRETION. The principal excretory organs of the Crustacea are two pairs of glands, known as the *ante final* and *maxillary glands,* which open at the bases of the appendages from which they take their names. They are very rarely (Lophogastridae) both well developed at the same stage in the name species, but one may succeed the other as a functional organ in the course of the life history: the antennal gland, for instance, is the larval excretory organ of the Branchiopoda, but the maxillary gland is that of the adult; and the Decapoda, whose adult kidney is the antennal gland, sometimes use as larvae the maxillary gland instead. The maxillary gland is the more widespread as an adult organ, the antennary gland being functional in the adult only in certain of the Malacostraca. In the Ostracoda and Leptostraca both are vestigial in the adult. Each of these glands has an *end sac* and a *duct* leading from the end sac to the exterior. The end sac is always mesodermal and doubtless represents a vestige of the coelom. The duct is sometimes (in the Malacostraca probably always) a multicellular, mesodermal structure, and sometimes intracellular and of ectodermal origin. At the junction of end sac and duct there is often a sphincter. The antennal gland of the Decapoda is usually very complicated. That of the crayfish lacks extensions of the bladder which lie among the viscera in many other genera as in crabs. All the parts of the organs are excretory, and the function of the sphincter of the end sac is perhaps to prevent the passage back into that vesicle of poisonous products excreted in the duct.

These glands are probably the remaining members of a series of segmental excretory organs. Their mesodermal portions are no doubt coelomoducts, homologous with those of the Annelida; their ectodermal portions probably are not the homologues of nephridia but represent ectodermal glands such as are common in the Crustacea. Various other glands, mostly of doubtful morphological significance, which occur in different crustaceans have been shown, or are suspected, to have an excretory function. Thus, in *Nebalia,* eight pairs of ectodermal glands at the bases of the thoracic limbs are excretory, while in ostracods a pair of rather complex glands, also of ectodermal origin, which lie between the folds of the shell in the antennal region, may have a similar function. Excretion appears also sometimes to be performed by caeca of the mid gut—as by some of those of the barnacles and by the posterior pair of amphipods—or by cells of the epithelium of the mid gut itself.

RESPIRATION in many of the smaller crustaceans, notably in the Cope-poda, takes place through the general surface of the body. In forms with stouter cuticle or more bulky bodies this is supplemented or replaced by the use of special organs upon which the cuticle remains thin. The most important of such organs are the lining of the carapace, if that structure be present, and certain epipodites which are known as gills and in many of the Malacostraca have their surface increased by branching or folding. In the Decapoda incorporation of the precoxa with the flank of the body has brought it about that some of the gills (proepipodites. Fig. 250 c) stand in that position and not upon the actual limbs. Such gills are known as 'pleurobranchiae'. In the Isopoda respiration is effected by the broad rami of the abdominal limbs. Renewal of the water upon the respiratory surfaces may be brought about by the movements of the limbs upon which they are located, but often certain appendages bear special lobes adapted to set up a current under the carapace and thus to flush the chamber in which the gills and the carapace lining are situated.

Some land crustaceans have no special adaptations for respiration in air. In others the gill chamber is adapted, by the presence of vascular tufts of the lining of the carapace, for use as a lung. The woodlice, which are terrestrial members of the Isopoda, are remarkable in approaching in their respiration the principle employed by normally terrestrial arthropods, for the integument of their abdominal limbs is invaginated to form branching tubes which resemble tracheae.

VASCULAR SYSTEM. The vascular system is seen in its most primitive condition in the Branchiopoda Anostraca *(Chirocephalus)* Here the *heart* runs the whole length of the trunk, situated above the gut in a blood sinus known as the *pericardium,* with which it communicates by a pair ofostia in each somite except the last. In front it is continued into the only *artery,* a short aorta, from which the blood flows direct into the *sinuses* of the head and thence through those of the trunk to the pericardium, eddies from a main ventral sinus supplying the limbs. In all other Crustacea, except the Stomato-poda, the heart, if it be present, is in some degree shortened, and in the Malacostraca a system of arteries interposes between the heart and the sinuses, leaving the former by several vessels, which conduct the blood to the organs. In the Eucarida (Euphausiacea and Decapoda) the heart is shortened to a compact shape and has three pairs of ostia; in most of the Cladocera it is a sac with only one pair. In the Cirripedia and many of the Copepoda and Ostracoda the heart is absent and the blood is kept in movement only by the movements of the body and alimentary canal. In the parasitic copepod *Lernanthropus* and some related genera there is a remarkable system of closed blood vessels without a heart.

The *blood* is a pale fluid, which bears leucocytes except in ostracods and most copepods. It contains in the Malacostraca the copper-containing respiratory pigment *haemocyanin*. In various entomostraca, notably in *Lernanthropus,* just mentioned, haemoglobin has been found.

REPRODUCTIVE SYSTEM. As is usual with animals that are free and active, the *sexes* are separate in the great majority of the Crustacea, though the Cirripedia, which are sessile, certain of the parasitic Isopoda, and a few exceptional species in other groups, are hermaphrodite. Parthenogenesis takes place in many of the Branchiopoda and Ostracoda, and in these it is often only at more or less fixed intervals that sexual reproduction occurs. The male is usually smaller than the female and in some parasites is minute and attached to her body. He has often clasping-organs for holding his partner, and these may be formed from almost any of the appendages. He may also possess organs for the transference of sperm: these may be modified appendages or protrusible terminal portions of the vasa deferentia. The *gonads* of both sexes are hollow organs from which ducts lead directly to the exterior. Primarily there is one gonad on each side, but they often unite more or less completely above the alimentary canal. The ducts usually open near the middle of the body, though the male openings of Cirripedia and some Cladocera are almost terminal and the female opening of Cirripedia Is on the first thoracic somite. Save in the Cirripedia, the Malacostraca, and •oine of the Cladocera, the ducts of the two sexes open upon the same somite.

SPERM AND OVA. The spermatozoa are very varied in form and often of complex structure; usually, but not always, they are immobile. They are transferred to the female, often in packets *(spermatophores).* The *ova* have usually much yolk, and meroblastic, centrolecithal cleavage, but sometimes are less yolky and undergo total cleavage. Gastrulation may be by invagination, or by immigration. Occasionally the eggs are set free at laying, but in the great majority of cases they are retained for a time by the mother, either in some kind of brood pouch or adhering in some way to her body or appendages. *Development* is not infrequently direct, but in most cases involves a larval stage or stages.

LARVAL FORMS. Typically, the crustacean hatches as a *nauplius* larva, a minute creature, egg-shaped with the broad end in front, unseg-mented, but provided with three pairs of appendages—the antennules, which are uniramous, and the antennae and mandibles, which are biramous and should each bear a gnathobasic process or spine directed towards the mouth, though those of the mandibles are often not developed at first. The antennal ganglia are as yet postoral. The median eye is the only organ of vision. A pair of frontal organs are present as papillae or filaments. There is a large labrum. Fore, mid and hind guts can be recognized in the alimentary canal. Antennal glands may be present. This larva is found in some members of every class of the Crustacea, though among the Mala-costraca only certain primitive genera possess it, and in the Ostracoda it is modified by having already at hatching a precociously developed bivalved carapace. In every class, however, it is also often passed over, and becomes an embryonic stage within the egg membrane or in a brood pouch, the animal hatching at a later stage, such as the *metanauplius* and *zoaea* mentioned below, or even almost as an adult.

In the Branchiopoda and Ostracoda the nauplius is transformed gradually into the adult, adding somite after somite in order from before backwards by budding in front of the telson, much as somites are added to the trochosphere in the development of annelids, while by degrees the other features of the adul t develop. The early stages of this process, which possess more somites than the nauplius, but have not yet the adult form, are known as metanauplii. The carapace is often foreshadowed quite early by a dorsal shield, which later grows out behind and at the sides to assume the form which it has in the adult, and the appendages, at first mere buds, gradually take on their final shapes.

VARIATIONS IN LIFE CYCLE. In most cases, however, the process just described is modified. (1) It makes a sudden great advance at one moult. In the Cirripedia the late nauplius passes with a leap to the so-called *cypris* larva, which has many of the features of the adult: a similar leap takes the copepod metanauplius to the first *cyclops* stage and those of Malacostraca to the *zoaea.* (2) Certain structures may be precociously developed. In those of the Malacostraca which have nauplii, the metanauplius is followed by stages, known as *zoaeae,* in which the abdomen is well developed, while the thorax, though it already possesses in front a few pairs of biramous appendages, is still rudimentary in its hinder part. In these larvae also the last pair of abdominal limbs usually appears, or comes to functional development, before the others. Zoaeae, however, most often are not preceded by ;a free nauplius but appear as the first free stage. (3) Temporary ret regression of certain organs takes place during the development of some nf the Millucostraca: this affects some of the thoracic limbs in certain Stomatopoda and the prawn *Sergestes,* abdominal swimmerets and the antennule In the prawn *Panaeus.*

INTERNAL ANATOMY of Crustaceans is shown at Fig 17.

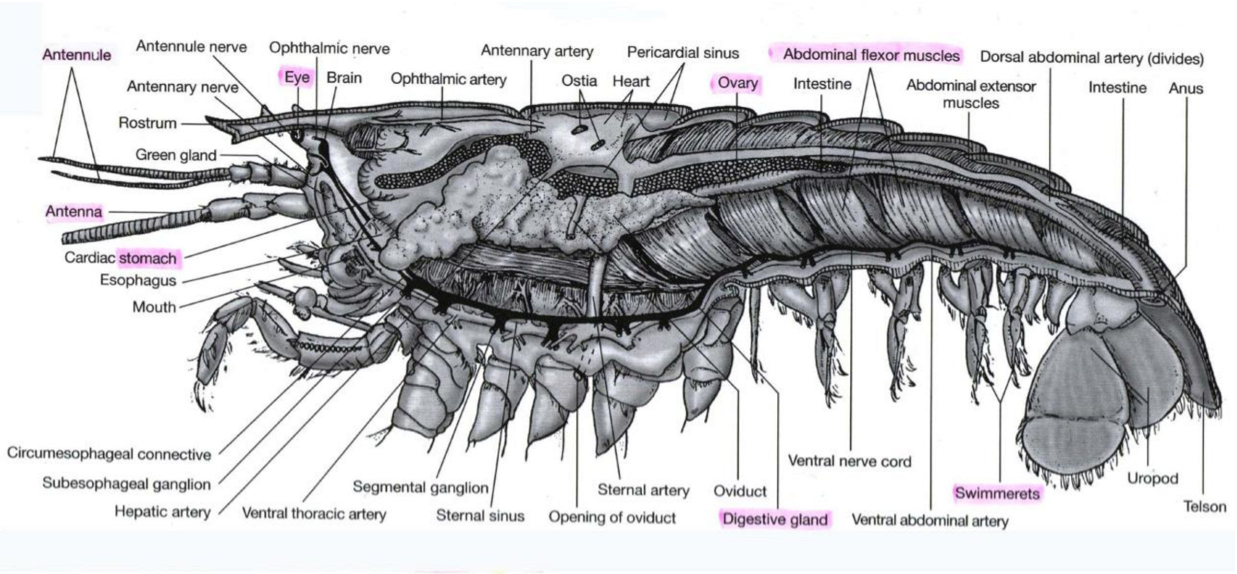


Fig. 17 Crayfish, internal anatomy, female

Class Chelicerata

Anatomy features of Chelicerata are presented at Fig. 18.

Class Insecta

Diagnosis

1. Body is divided into three distinct regions:
    - head (6 segments; single pair of antennae; single pair of mandibles; 2 pairs of maxillae)
    - thorax (3 segmenrs with 3 pairs of legs and usually 2 pairs of wings)
    - abdomen (typically 11 segments, no limbs).
2. Alimentary system: typical for arthropods.
3. Circulatory system: typical open system. There is a dorsally placed heart, primitively consisting of 13 chambers, each corresponding to a segment. Aorta opens into the body cavity and blood bathes all the organs
4. Respiration: by trachea

5. Excretion: the principal excretory organs – Malpighian tubules – ectodermal structures openeng into the anterior end of the hind gut

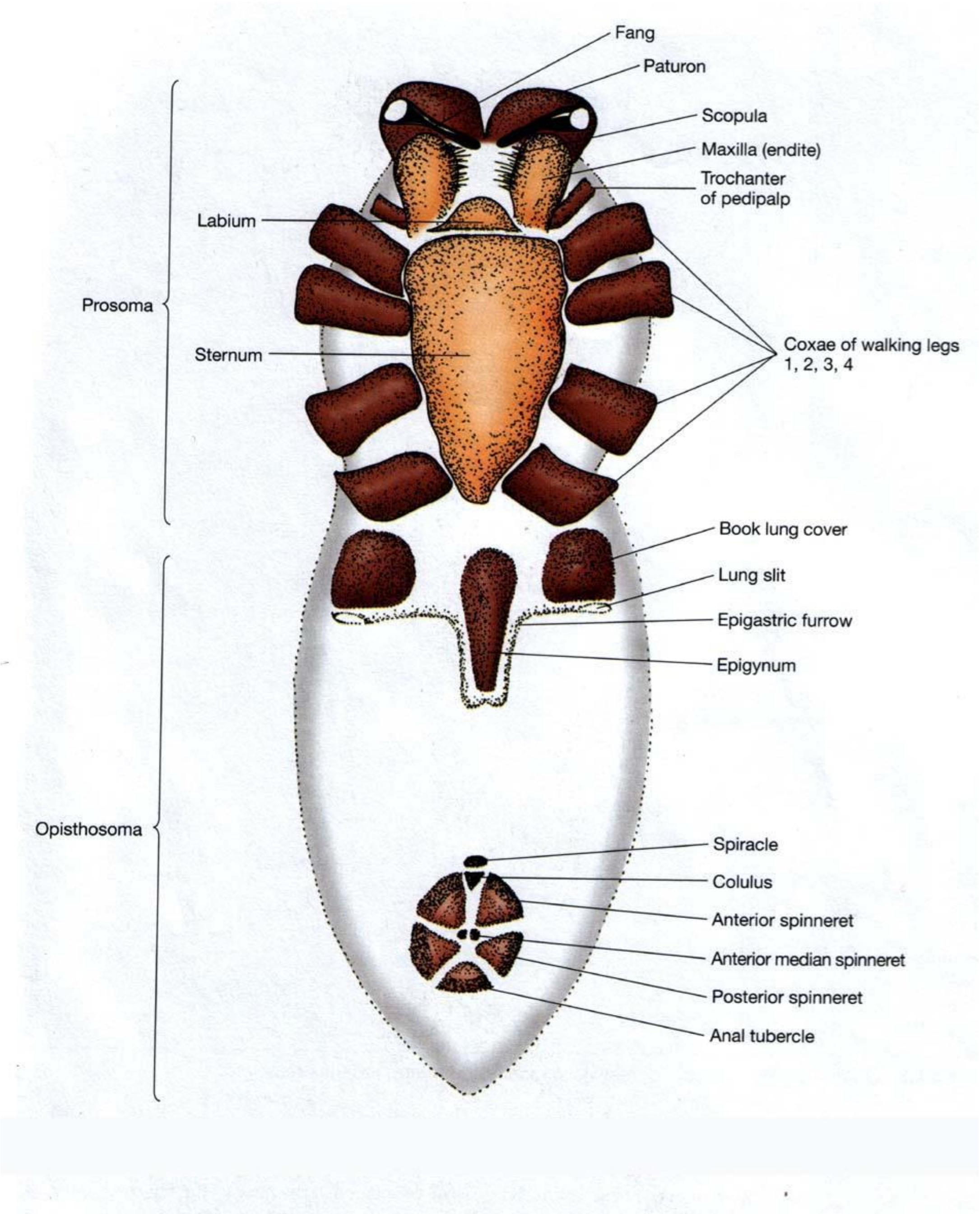


Fig. 18. Spider, internal anatomy

6. Nerve system: typical for arthropods

7. Sensory organ peculiarities: both compound and simple eyes

8.Reproduction: sexes are separated, fertilization if the interior

9. Development: Heterometabola (Dictyoptera, Isoptera, Dermaptera, Homoptera, Ephemeroptera, Odonata etc.) are the insects whose young stages, known as nymphs, closely resemble to adult in body form and type of mouth parts.

Holometabola (Coleoptera, Trichoptera, Lepidoptera, Diptera, Hymenoptera etc.) have yang stages known as larvae, which differ markedly from adult in body form and mouth parts; pupa is the intermediate stage.

PHYLUM CHORDATA

General unique features of chordates:

1. The chorda dorsalis, or notochord.

From this structure the phylum takes name. It occurs in embryo of most chordates as a long, flexible cord of specialized, vacuolated cells extending from head to tail along the dorsal midline. It lies between the alimentary canal and the dorsal cord of the central nervous system. In the higher Chordata, Craniata, in the few exceptions among lower forms, the notochord is replaced more or less completely in the adult by a segmented cartilaginous or bony axial structure, the vertebral column.

2. The branchial clefts.

The visceral clefts occur as a paired series of perforations leading from the pharynx, an anterior section of the alimentary canal, to the lateral surface of body. Within those clefts are the gills in many aquatic animals. In the creatures equipped by lungs, branchial clefts or branchial grooves are always found in embryo. In the adults of vertebrates, the branchial apparatus is sometimes converted to endocrine and other functions. In the more lowly members of the Chordata the branchial apparatus is used also as a feeding mechanism.

3. The central nervous system

The dorsal, tubular (Fig. 19), fluid-filled central nervous system, anteriorly differentiated into a brain in advanced forms, is another structure common to the most chordates in the larval or later stages of their development.

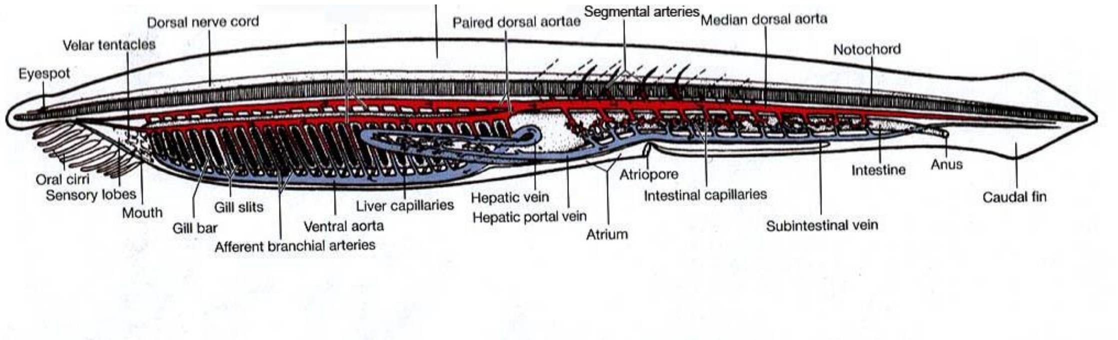


Fig. 19. Lancet, internal anatomy

Chordate features that are common for other phyla:

1. The Chordata are coelomate animals.
2. The Chordata has bilateral symmetry.
3. The Chordata has some organs that are metameric.
4. The Chordata are secondary-mouthed animals.

Sub-phylum Acrania

Branchiostoma lanceolatum

- No cranium
- Tubular nervous system is simple, not developed into the anterior (brain) and posterior (spinal) parts.
- Sensor organs are not developed
- Circulation system is closed, but no heart
- Skeleton exists as the notochord
- No paired limbs

Sub-phylum Tunicata

Class Appendicularia
Class Ascidia
Class Salpe

The chordate features take place in larval stage, in adult normally both notochord and nervous tube are absent.

Mostly sessile, mostly marine creatures.

Sub-phylum Vertebrata (Craniata)

Vertebrate animals with:

1. a skull (cranium)
2. a highly complex brain
3. a muscular heart of two, three or four chambers
4. red blood corpuscles (almost always)
5. Usually two pairs of limbs

Classification:

Anamnia

Respiratory organs are gills during the whole life or certain larval stage. No embryonic membranes appear in embryogenesis.

- Supra-class I. Agnatha
  - Class1. Cyclostomata
- Supra-class II. Pisces (fishes)
  - Class 2. Chondrichthyes (Fig. 20)
  - Class 3. Osteichthyes (Fig. 21)
- Supra-class III. Tetrapoda

Etymology

Until the 16th century,[sharks were known to mariners as "sea dogs". According to the OED the name "shark" first came into use after Sir John Hawkins' sailors exhibited one in London in 1569 and used the word to refer to the large sharks of the Caribbean Sea, and later as a general term for all sharks. It has also been suggested to be derived from the Yucatec Maya word for shark, *xok*, pronounced 'shok'.

Anatomy

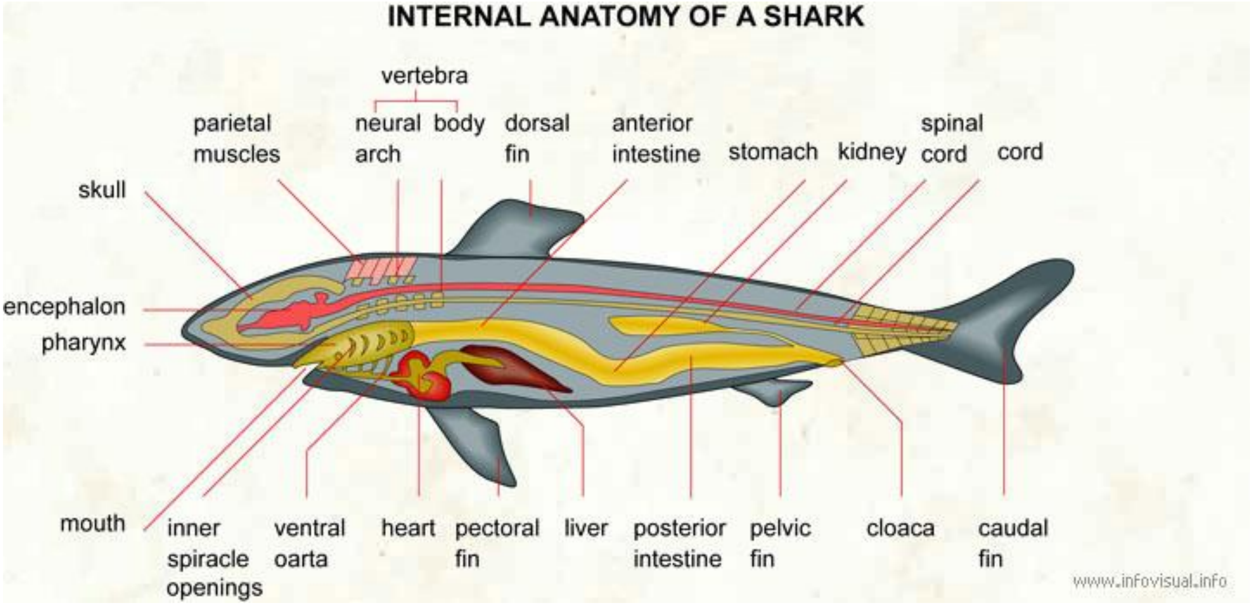


Fig. 20. Shark, internal anatomy

Internal anatomy of a shark: large, long and very powerful selachian fish. It is viviparous.

Parietal muscles: set of muscles of the side of the head.

Vertebra: each of the bones forming the spinal column.

Neural arch: arched part of a vertebra related to the nervous system.

Body: main part of a vertebra.

Dorsal fin: locomotive limb on the back of a shark.

Anterior intestine: part of the digestive tract just after the stomach.

Stomach: part of the digestive tract of a shark between the front and rear parts of the intestine.

Kidney: blood-purifying organ.

Spinal cord: part of the nervous system contained in the spinal column.

Cord: outlined part of the spinal column.

Caudal fin: locomotive limb at the end of a shark.

Cloaca: opening shared by the genital organs, the urinary and intestinal tracts.

Pelvic fin: locomotive limb situated beneath the pelvic girdle of a shark.

Posterior intestine: part of the digestive tract just after the stomach.

Liver: bile-producing digestive gland.

Pectoral fin: locomotive limb on the chest of a shark.

Heart: blood-pumping organ copyright bernard dery infovisual.info.

Ventral aorta: blood vessel in the abdomen that carries blood from the heart to other organs.

Inner spiracle openings: fissure containing the viscera.

Mouth: entrance to the digestive tract.

Pharynx: intersection of the respiratory and digestive tracts of a shark.

Encephalon: seat of the mental capacities of a shark.

Skull: bony case of the brain.

Teeth

The teeth of the tiger shark are oblique and serrated for sawing through flesh.

Main article: Shark teeth

Shark teeth are embedded in the gums rather than directly affixed to the jaw, and are constantly replaced throughout life. Multiple rows of replacement teeth grow in a groove on the inside of the jaw and steadily move forward as in a "conveyor belt"; some sharks lose 30,000 or more teeth in their lifetime. The rate of tooth replacement varies from once every 8–10 days to several months. In most species teeth are replaced one at a time, except in cookiecutter sharks the entire row of teeth is replaced simultaneously.

Tooth shape depends on diet: sharks that feed on mollusks and crustaceans have dense flattened teeth for crushing, those that feed on fish have needle-like teeth for gripping, and those that feed on larger prey such as mammals have pointed lower teeth for gripping and triangular upper teeth with serrated edges for cutting. The teeth of plankton-feeders such as the basking shark are smaller and non-functional.

Skeleton

Shark skeletons are very different from those of bony fish and terrestrial vertebrates. Sharks and other cartilaginous fish (skates and rays) have skeletons made of cartilage and connective tissue. Cartilage is flexible and durable, yet has about half the density of bone. This reduces the skeleton’s weight, saving energy. Sharks have no rib cage and therefore on land a shark's own weight can crush it.

Jaw

Like its relatives, rays and skates, the shark's jaw is not attached to the cranium. The jaw's surface, like the shark's vertebrae and gill arches, needs extra support due to its heavy exposure to physical stress and its need for strength. It has a layer of tiny hexagonal plates called "tesserae", which are crystal blocks of calcium salts arranged as a mosaic. This gives these areas much of the same strength found in the bony tissue found in other animals.

Generally sharks have only one layer of tesserae, but the jaws of large specimens, such as the bull shark, tiger shark, and the great white shark, have two to three layers or more, depending on body size. The jaws of a large great white shark may have up to five layers. In the rostrum (snout), the cartilage can be spongy and flexible to absorb the power of impacts.

Fins

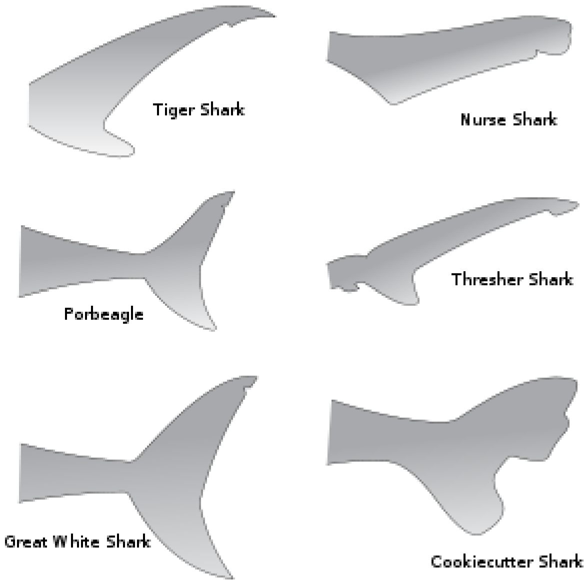
Fin skeletons are elongated and supported with soft and unsegmented rays named ceratotrichia, filaments of elastic protein resembling the horny keratin in hair and feathers. Sharks can only drift away from objects directly in front of them because their fins do not allow them to move in the tail-first direction.

Dermal denticles

Main article: Dermal denticle

Unlike bony fish, sharks have a complex dermal corset made of flexible collagenous fibers and arranged as a helical network surrounding their body. This works as an outer skeleton, providing attachment for their swimming muscles and thus saving energy. In the past, sharkskin has been used as sandpaper. Their dermal teeth give them hydrodynamic advantages as they reduce turbulence when swimming.

Tails



The range of shark tail shapes

Varying tail shapes have evolved in sharks adapted for different environments. Tail (caudal fins) vary considerably between species. The tail provides thrust, making speed and acceleration dependent on tail shape. Sharks possess a heterocercal caudal fin in which the dorsal portion is usually noticeably larger than the ventral portion. This is because the shark's vertebral column extends into that dorsal portion, providing a greater surface area for muscle attachment. This allows more efficient locomotion among these negatively buoyant cartilaginous fishes. By contrast, most bony fishes possess a homocercal caudal fin.

The tiger shark's tail has a large upper lobe which delivers maximum power for slow cruising or sudden bursts of speed. The tiger shark must be able to twist and turn in the water easily when hunting to support its varied diet, whereas the porbeagle, which hunts schooling fish such as mackerel and herring has a large lower lobe to help it keep pace with its fast-swimming prey. Some tail adaptations have other purposes. The thresher feeds on fish and squid, which it herds and stuns with its powerful and elongated upper lobe.

Physiology

Buoyancy

Unlike bony fish, sharks do not have gas-filled swim bladders for buoyancy. Instead, sharks rely on a large liver, filled with oil that contains squalene and the fact that cartilage is about half as dense as bone. The liver constitutes up to 30% of their body mass. The liver's effectiveness is limited, so sharks employ dynamic lift to maintain depth, sinking when they stop swimming. Sand tiger sharks store air in their stomachs, using it as a form of swim bladder. Most sharks need to constantly swim in order to breathe and cannot sleep very long, if at all, without sinking. However certain shark species, like the nurse shark, are capable of pumping water across their gills, allowing them to rest on the ocean bottom.

Some sharks, if inverted or stroked on the nose, enter a natural state of tonic immobility. Researchers use this condition to handle sharks safely.

Respiration

Like other fish, sharks extract oxygen from seawater as it passes over their gills. Unlike other fish, shark gill slits are not covered, but lie in a row behind the head. A modified slit called a spiracle lies just behind the eye; the spiracle assists water intake during respiration and plays a major role in bottom–dwelling sharks. Spiracles are reduced or missing in active pelagic sharks. While the shark is moving, water passes through the mouth and over the gills in a process known as "ram ventilation". While at rest, most sharks pump water over their gills to ensure a constant supply of oxygenated water. A small number of species have lost the ability to pump water through their gills and must swim without rest. These species are *obligate ram ventilators* and would presumably asphyxiate if unable to move. Obligate ram ventilation is also true of some pelagic bony fish species.

The respiration and circulation process begins when deoxygenated blood travels to the shark's two-chambered heart. Here the shark pumps blood to its gills via the ventral aorta artery where it branches into afferent brachial arteries. Reoxygenation takes place in the gills and the reoxygenated blood flows into the efferent brachial arteries, which come together to form the dorsal aorta. The blood flows from the dorsal aorta throughout the body. The deoxygenated blood from the body then flows through the posterior cardinal veins and enters the posterior cardinal sinuses. From there blood enters the heart ventricle and the cycle repeats.

Thermoregulation

Most sharks are "cold-blooded", or more precisely poikilothermic, meaning that their internal body temperature matches that of their ambient environment. Members of the family Lamnidae, such as the shortfin mako shark and the great white shark, are homeothermic and maintain a higher body temperature than the surrounding water. In these sharks, a strip of aerobic red muscle located near the center of the body generates the heat, which the body retains via a countercurrent exchange mechanism by a system of blood vessels called the rete mirabile ("miraculous net"). The common thresher shark has a similar mechanism for maintaining an elevated body temperature, which is thought to have evolved independently.

Osmoregulation

In contrast to bony fish, with the exception of the Coelacanth, the blood and other tissue of sharks and Chondrichthyes in general is isotonic to their marine environments because of the high concentration of urea and trimethylamine N-oxide (TMAO), allowing them to be in osmotic balance with the seawater. This adaptation prevents most sharks from surviving in fresh water, and they are therefore confined to marine environments. A few exceptions to this rule exist, such as the bull shark which has developed a way to change its kidney function to excrete large amounts of urea. When a shark dies the urea is broken down to ammonia by bacteria — because of this, the dead body will gradually start to smell strongly of ammonia.

Digestion

Digestion can take a long time. The food moves from the mouth to a 'J' shaped stomach, where it is stored and initial digestion occurs. Unwanted items may never get past the stomach, and instead the shark either vomits or turns its stomachs inside out and ejects unwanted items from its mouth.

One of the biggest differences between shark and mammalian digestion is sharks’ extremely short intestine. This short length is achieved by the spiral valve with multiple turns within a single short section instead of a long tube-like intestine. The valve provides a long surface area, requiring food to circulate inside the short gut until fully digested, when remaining waste products pass into the cloaca.

Senses

Smell

The shape of the hammerhead shark's head may enhance olfaction by spacing the nostrils further apart.

Sharks have keen olfactory senses, located in the short duct (which is not fused, unlike bony fish) between the anterior and posterior nasal openings, with some species able to detect as little as one part per million of blood in seawater. They are more attracted to the chemicals found in the guts of many species, and as a result often linger near or in sewage outfalls. Some species, such as nurse sharks, have external barbels that greatly increase their ability to sense prey.

Sight

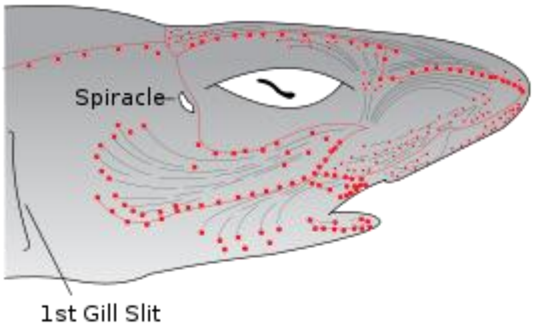
Shark eyes are similar to the eyes of other vertebrates, including similar lenses, corneas and retinas, though their eyesight is well adapted to the marine environment with the help of a tissue called tapetum lucidum. This means that sharks can contract and dilate their pupils, like humans, something no teleost fish can do. This tissue is behind the retina and reflects light back to it, thereby increasing visibility in the dark waters. The effectiveness of the tissue varies, with some sharks having stronger nocturnal adaptations. Sharks have eyelids, but they do not blink because the surrounding water cleans their eyes. To protect their eyes some species have nictitating membranes. This membrane covers the eyes while hunting and when the shark is being attacked. However, some species, including the great white shark (*Carcharodon carcharias*), do not have this membrane, but instead roll their eyes backwards to protect them when striking prey. The importance of sight in shark hunting behavior is debated. Some believe that electro- and chemoreception are more significant, while others point to the nictating membrane as evidence that sight is important. Presumably, the shark would not protect its eyes were they unimportant. The use of sight probably varies with species and water conditions. The shark's field of vision can swap between monocular and stereoscopic at any time.

Hearing

Although it is hard to test sharks' hearing, they may have a sharp sense of hearing and can possibly hear prey many miles away. A small opening on each side of their heads (not the spiracle) leads directly into the inner ear through a thin channel. The lateral line shows a similar arrangement, and is open to the environment via a series of openings called lateral line pores. This is a reminder of the common origin of these two vibration- and sound-detecting organs that are grouped together as the acoustico-lateralis system. In bony fish and tetrapods the external opening into the inner ear has been lost.

Electroreception

Main article: Electroreception



Electromagnetic field receptors (Ampullae of Lorenzini) and motion detecting canals in the head of a shark

The Ampullae of Lorenzini are the electroreceptor organs. They number in the hundreds to thousands. Sharks use the Ampullae of Lorenzini to detect the electromagnetic fields that all living things produce. This helps sharks (particularly the hammerhead shark) find prey. The shark has the greatest electrical sensitivity of any animal. Sharks find prey hidden in sand by detecting the electric fields they produce. Ocean currents moving in the magnetic field of the Earth also generate electric fields that sharks can use for orientation and possibly navigation.

Lateral line

Main article: Lateral line

This system is found in most fish, including sharks. It detects motion or vibrations in water. The shark can sense frequencies in the range of 25 to 50 Hz.

Life history

The claspers of male spotted wobbegong

Shark lifespans vary by species. Most live 20 to 30 years. The spiny dogfish has the longest lifespan at more than 100 years. Whale sharks (*Rhincodon typus*) may also live over 100 years.

Reproduction

Unlike most bony fishes, sharks are K-selected reproducers, meaning that they produce a small number of well-developed young as opposed to a large number of poorly developed young. Fecundity in sharks ranges from 2 to over 100 young per reproductive cycle. Sharks mature slowly relative to many other fish. For example, lemon sharks reach sexual maturity at around age 13–15.

Sexual

Sharks practice internal fertilization. The posterior part of a male shark's pelvic fins are modified into a pair of intromittent organs called claspers, analogous to a mammalian penis, of which one is used to deliver sperm into the female.

Mating has rarely been observed in sharks. The smaller catsharks often mate with the male curling around the female. In less flexible species the two sharks swim parallel to each other while the male inserts a clasper into the female's oviduct. Females in many of the larger species have bite marks that appear to be a result of a male grasping them to maintain position during mating. The bite marks may also come from courtship behavior: the male may bite the female to show his interest. In some species, females have evolved thicker skin to withstand these bites.

Asexual

There are two documented cases in which a female shark who has not been in contact with a male has conceived a pup on her own through parthenogenesis. The details of this process are not well understood, but genetic fingerprinting showed that the pups had no paternal genetic contribution, ruling out sperm storage. The extent of this behavior in the wild is unknown, as is whether other species have this capability. Mammals are now the only major vertebrate group in which asexual reproduction has not been observed.

Scientists assert that asexual reproduction in the wild is rare, and probably a last ditch effort to reproduce when a mate is not present. Asexual reproduction diminishes genetic diversity, which helps build defenses against threats to the species. Species that rely solely on it risk extinction. Asexual reproduction may have contributed to the blue shark's decline off the Irish coast.

Brooding

Sharks display three ways to bear their young, varying by species, oviparity, viviparity and ovoviviparity.

The spiral egg case of a Port Jackson shark

Ovoviviparity

Most sharks are ovoviviparous, meaning that the eggs hatch in the oviduct within the mother's body and that the egg's yolk and fluids secreted by glands in the walls of the oviduct nourishes the embryos. The young continue to be nourished by the remnants of the yolk and the oviduct's fluids. As in viviparity, the young are born alive and fully functional. Lamniforme sharks practice *oophagy*, where the first embryos to hatch eat the remaining eggs. Grey nurse shark pups intrauterine cannibalistically take this a step further and consume other developing embryos. The survival strategy for ovoviviparous species is to brood the young to a comparatively large size before birth. The whale shark is now classified as ovoviviparous rather than oviparous, because extrauterine eggs are now thought to have been aborted. Most ovoviviparous sharks give birth in sheltered areas, including bays, river mouths and shallow reefs. They choose such areas for protection from predators (mainly other sharks) and the abundance of food. Dogfish have the longest known gestation period of any shark, at 18 to 24 months. Basking sharks and frilled sharks appear to have even longer gestation periods, but accurate data are lacking.

Oviparity

Some species are oviparous like most other fish, laying their eggs in the water. In most oviparous shark species, an egg case with the consistency of leather protects the developing embryo(s). These cases may be corkscrewed into crevices for protection. Once empty, the egg case is known as the *mermaid's purse*, and can wash up on shore. Oviparous sharks include the horn shark, catshark, Port Jackson shark, and swellshark.

Viviparity

Finally some sharks maintain a *placental* link to the developing young, this method is called viviparity. This is more analogous to mammalian gestation than that of other fishes. The young are born alive and fully functional. Hammerheads, the requiem sharks (such as the bull and blue sharks), and smoothhounds are viviparous.

Behavior

The classic view describes a solitary hunter, ranging the oceans in search of food. However, this applies to only a few species. Most live far more sedentary, benthic lives. Even solitary sharks meet for breeding or at rich hunting grounds, which may lead them to cover thousands of miles in a year. Shark migration patterns may be even more complex than in birds, with many sharks covering entire ocean basins.

Sharks can be highly social, remaining in large schools. Sometimes more than 100 scalloped hammerheads congregate around seamounts and islands, e.g., in the Gulf of California. Cross-species social hierarchies exist. For example, oceanic whitetip sharks dominate silky sharks of comparable size during feeding.

When approached too closely some sharks perform a threat display. This usually consists of exaggerated swimming movements, and can vary in intensity according to the threat level.

Speed

In general, sharks swim ("cruise") at an average speed of 8 kilometres per hour (5.0 mph) but when feeding or attacking, the average shark can reach speeds upwards of 19 kilometres per hour (12 mph). The shortfin mako shark, the fastest shark and one of the fastest fish, can burst at speeds up to 50 kilometres per hour (31 mph). The great white shark is also capable of speed bursts. These exceptions may be due to the warm-blooded, or homeothermic, nature of these sharks' physiology.

Intelligence

Contrary to the common wisdom that sharks are instinct-driven "eating machines", recent studies have indicated that many species possess powerful problem-solving skills, social skills and curiosity. The brain- to body-mass ratios of sharks are similar to mammals and birds. In 1987, near Smitswinkle Bay, South Africa, a group of up to seven great white sharks worked together to move a partially beached dead whale to deeper waters to feed. Sharks can engage in playful activities. Porbeagle sharks have been seen repeatedly rolling in kelp and chasing an individual who trailed a piece of kelp behind it.

Sleep

Some sharks can lie on the bottom while actively pumping water over their gills, but their eyes remain open and actively follow divers. When a shark is resting, it does not use its nares, but rather its spiracles. If a shark tried to use its nares while resting on the ocean floor, it would "inhale" sand rather than water. Many scientists believe this is one of the reasons sharks have spiracles. The spiny dogfish's spinal cord, rather than its brain, coordinates swimming, so spiny dogfish can continue to swim while sleeping. It is also possible that sharks sleep in a manner similar to dolphins, one cerebral hemisphere at a time, thus maintaining some consciousness and cerebral activity at all times.

Ecology

Feeding

This section is about shark feeding. For the sport of shark feeding, see Shark baiting.

Like many sharks, the great white shark is an apex predator in its environment.

Most sharks are carnivorous. Some species, including tiger sharks, eat almost anything. The vast majority seek particular prey, and rarely vary their diet. Whale, basking and megamouth sharks filter feed. These three independently evolved plankton feeding using different strategies. Whale sharks use suction to take in plankton and small fishes. Basking sharks are ram-feeders, swimming through plankton blooms with their mouth wide open. Megamouth sharks make suction feeding more efficient, using luminescent tissue inside the mouth to attract prey in the deep ocean. This type of feeding requires gill rakers, long slender filaments that form a very efficient sieve, analogous to the baleen plates of the great whales. The shark traps the plankton in these filaments and swallows from time to time in huge mouthfuls. Teeth in these species are comparatively small because they are not needed for feeding.

Other highly specialized feeders include cookiecutter sharks, which feed on flesh sliced out of other larger fish and marine mammals. Cookiecutter teeth are enormous compared to the animal's size. The lower teeth are particularly sharp. Although they have never been observed feeding, they are believed to latch onto their prey and use their thick lips to make a seal, twisting their bodies to rip off flesh.

Some seabed–dwelling species are highly effective ambush predators. Angel sharks and wobbegongs use camouflage to lie in wait and suck prey into their mouths. Many benthic sharks feed solely on crustaceans which they crush with their flat molariform teeth.

Other sharks feed on squid or fish, which they swallow whole. The viper dogfish has teeth it can point outwards to strike and capture prey that it then swallows intact. The great white and other large predators either swallow small prey whole or take huge bites out of large animals. Thresher sharks use their long tails to stun shoaling fishes, and sawsharks either stir prey from the seabed or slash at swimming prey with their tooth-studded rostra.

Many sharks, including the whitetip reef shark are cooperative feeders and hunt in packs to herd and capture elusive prey. These social sharks are often migratory, traveling huge distances around ocean basins in large schools. These migrations may be partly necessary to find new food sources.

Range and habitat

Sharks are found in all seas. They generally do not live in freshwater, with a few exceptions such as the bull shark and the river shark which can swim both in seawater and freshwater. Sharks are common down to depths of 2,000 metres (7,000 ft), and some live even deeper, but they are almost entirely absent below 3,000 metres (10,000 ft). The deepest confirmed report of a shark is a Portuguese dogfish at 3,700 metres (12,100 ft)

The skeleton of fish,

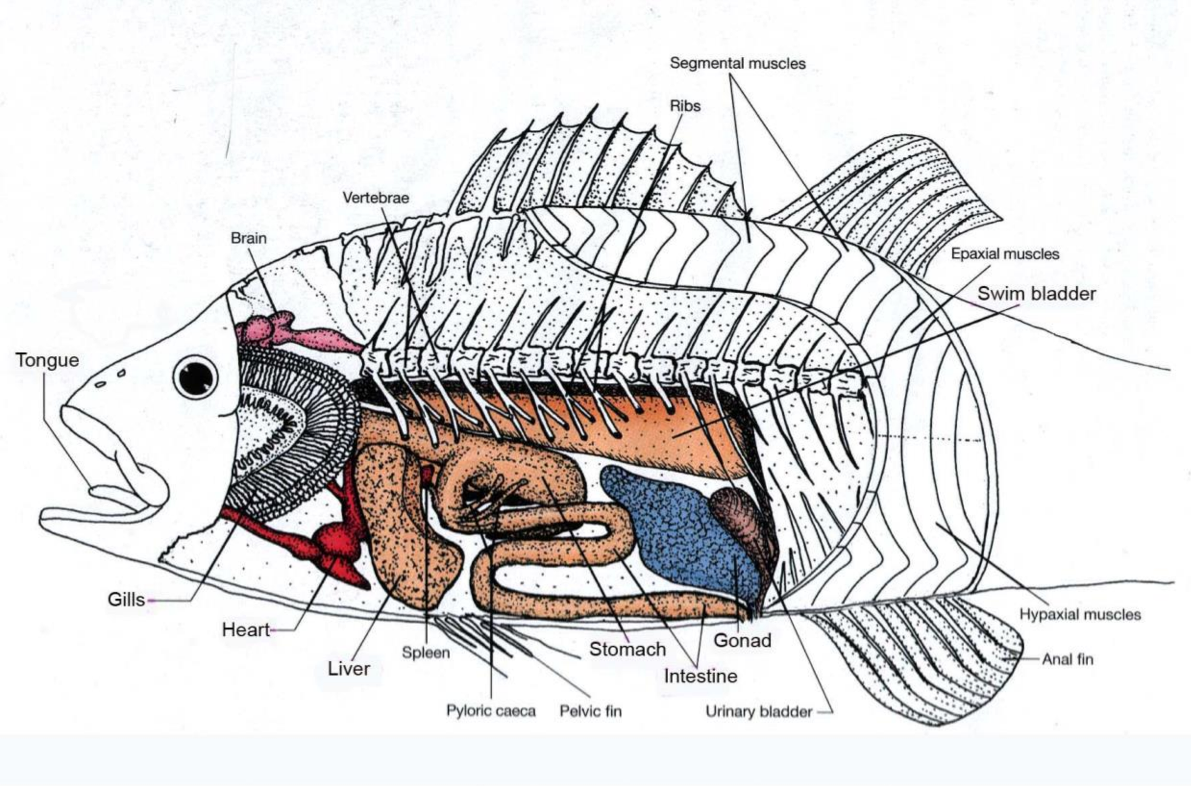


Fig. 21. Perch, internal anatomy

The skeletons of most fish consist mainly of (1) skull, (2) a backbone, (3) ribs, (4) fin rays, and (5) supports for fin rays or fins. The skeleton of a yellow perch is shown below. A fish's skeleton provides a framework for the head, trunk, tail, and fins. The central framework for the trunk and tail is the backbone. It consists of many separate segments of bone or cartilage called vertebrae. In bony fish, each vertebra has a spine at the top, and each tail vertebra also has a spine at the bottom. Ribs are attached to the vertebrae. The skull consists chiefly of the brain case and supports for the mouth and gills. The pectoral fins of most fish are attached to the back of the skull by a structure called a pectoral girdle. The pelvic fins are supported by a structure called a pelvic girdle, which is attached to the pectoral girdle or supported by muscular tissue in the abdomen. The dorsal fins are supported by structures of bone or cartilage, which are rooted in tissue above the backbone. The caudal fin is supported by the tail and the anal fin by structures of bone or cartilage below the backbone.

Like all vertebrates, fish have three kinds of muscles: (1) skeletal muscles, (2) smooth muscles, and (3) heart muscles. Fish use their skeletal muscles to move their bones and fins. A fish's flesh consists almost entirely of skeletal muscles. They are arranged one behind the other in broad vertical bands called myomeres. The myomeres can easily be seen in a skinned fish. Each myomere is controlled by a separate nerve. As a result, a fish can bend the front part of its body in one direction while bending its tail in the opposite direction. Most fish make such movements with their bodies to swim. A fish's smooth muscles and heart muscles work automatically. The smooth muscles are responsible for operating such internal organs as the stomach and intestines. Heart muscles form and operate the heart.

Systems of the body

The internal organs of fish, like those of other vertebrates, are grouped into various systems according to the function they serve. The major systems include the respiratory, digestive, circulatory, nervous, and reproductive systems. Some of these systems resemble those of other vertebrates, but others differ in many ways.

Respiratory system

Unlike land animals, almost all fish get their oxygen from water. Water contains a certain amount of dissolved oxygen. To get oxygen, fish gulp water through the mouth and pump it over the gills. Most fish have four pairs of gills enclosed in a gill chamber on each side of the head. Each gill consists of two rows of fleshy filaments attached to a gill arch.

Water passes into the gill chambers through gill slits. A flap of bone called a gill cover protects the gills of bony fish. Sharks and rays do not have gill covers. Their gill slits form visible openings on the outside of the body.

In a bony fish, the breathing process begins when the gill covers close and the mouth opens. At the same time, the walls of the mouth expand outward, drawing water into the mouth. The walls of the mouth then move inward, the mouth closes, and the gill covers open. This action forces the water from the mouth into the gill chambers. In each chamber, the water passes over the gill filaments. They absorb oxygen from the water and replace it with carbon dioxide formed during the breathing process. The water then passes out through the gill openings, and the process is repeated.

Digestive system

Digestive system, or digestive tract, changes food into materials that nourish the body cells. It eliminates materials that are not used. In fish, this system leads from the mouth to the anus, an opening in front of the anal fin. Most fish have a jawed mouth with a tongue and teeth. A fish cannot move its tongue. Most fish have their teeth rooted in the jaws. They use their teeth to seize prey or to tear off pieces of their victim's flesh. Some of them also have teeth on the roof of the mouth or on the tongue. Most fish also have teeth in the pharynx, a short tube behind the mouth. They use these teeth to crush or grind food.

In all fish, food passes through the pharynx on the way to the esophagus, another tubelike organ. A fish's esophagus expands easily, which allows the fish to swallow its food whole. From the esophagus, food passes into the stomach, where it is partly digested. Some fish have their esophagus or stomach enlarged into a gizzard. The gizzard grinds food into small pieces before it passes into the intestines. The digestive process is completed in the intestines. The digested food enters the blood stream. Waste products and undigested food pass out through the anus.

Circulatory system

Circulatory system distributes blood to all parts of the body. It includes the heart and blood vessels. A fish's heart consists of two main chambers - the atrium and the ventricle. The blood flows through veins to the atrium. It then passes to the ventricle. Muscles in the ventricle pump the blood through arteries to the gills, where the blood receives oxygen and gives off carbon dioxide. Arteries then carry the blood throughout the body. The blood carries food from the intestines and oxygen from the gills to the body cells. It also carries away waste products from the cells. A fish's kidneys remove the waste products from the blood, which returns to the heart through the veins.

Nervous system

Nervous system of fish, like that of other vertebrates, consists of a spinal cord, brain, and nerves. However, a fish's nervous system is not so complex as that of mammals and other higher vertebrates. The spinal cord, which consists of soft nerve tissue, runs from the brain through the backbone. The brain is an enlargement of the spinal cord and is enclosed in the skull. The nerves extend from the brain and spinal cord to every part of the body. Some nerves, called sensory nerves, carry messages from the sense organs to the spinal cord and brain. Other nerves, called motor nerves, carry messages from the brain and spinal cord to the muscles. A fish can consciously control its skeletal muscles. But it has no conscious control over the smooth muscles and heart muscles. These muscles work automatically.

Reproductive system

As in all vertebrates, the re-productive organs of fish are testes in males and ovaries in females. The testes produce male sex cells, or sperm. The sperm is contained in a fluid called milt The ovaries produce female sex cells, or eggs. Fish eggs are also called roe or spawn. Most fish release their sex cells into the water through an opening near the anus. The males of some species have special structures for transferring sperm directly into the females. Male sharks, for example, have such a structure, called a clasper, on each pelvic fin. The claspers are used to insert sperm into the female's body.

Special organs

Most bony fish have a swim bladder below the backbone. This baglike organ is also called an air bladder. In most fish, the swim bladder provides buoyancy, which enables the fish to remain at a particular depth in the water. In lungfish and a few other fish, the swim bladder serves as an air-breathing lung. Still other fish, including many catfish, use their swim bladders to produce sounds as well as to provide buoyancy. Some species communicate by means of such sounds. A fish would sink to the bottom if it did not have a way of keeping buoyant. Most fish gain buoyancy by inflating their swim bladder with gases produced by their blood. But water pressure increases with depth. As a fish swims deeper, the increased water pressure makes its swim bladder smaller and so reduces the fish's buoyancy. The amount of gas in the bladder must be in-creased so that the bladder remains large enough to maintain buoyancy. A fish's nervous system automatically regulates the amount of gas in the bladder so that it is kept properly filled. Sharks and rays do not have a swim bladder. To keep buoyant, these fish must swim constantly. When they rest, they stop swimming and so sink toward the bottom. Many bottom-dwelling bony fish also lack a swim bladder.

Many fish have organs that produce light or electricity. But these organs are simply adaptations of structures found in all or most fish. For example, many deep-sea fish have light-producing organs developed from parts of their skin or digestive tract. Some species use these organs to attract prey or possibly to communicate with others of their species. Various other fish have electricity-producing organs developed from muscles in their eyes, gills, or trunk. Some species use these organs to stun or kill enemies or prey.

Class 4. Amphibia

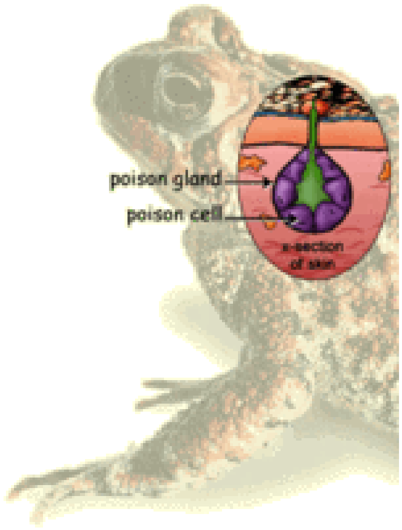
Skin

Grey tree frog (*Hyla versicolor).* (Photograph by Carla Zelmer)

An amphibian's very thin skin isn't covered by fur, feathers, or scales. This makes them vulnerable to dessication and abrupt temperature change, but also offers several advantages. Amphibians can breathe through the entire surface of their bodies. In the case of the lungless salamanders (Plethodontidae), gas exchange through the skin alone provides sufficient oxygen.

Water is also absorbed through an amphibian's skin making drinking unnecessary. Even in areas where open or running water is scarce, an amphibian's skin can absorb moisture from damp soil. Aquatic species would absorb too much water were it not constantly being expelled by their kidneys.

Amphibians display a startling variety of colour which results from different combinations of pigments within their skins. These patterns of colouration are usually designed to provide some form of defense frompredators.

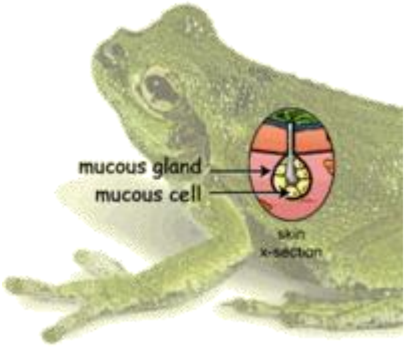


Amphibian granular gland. (Source: Canada's Aquatic Environment)

In the case of the grey tree frog (*Hyla versicolor*), colour is used to mimic the bark of lichen-covered trees, effectively hiding it from hungry eyes. By contrast, the poison dart frogs of South America use colour to attract attention and convey a message of warning: "eat me and die!" Similarly, the red eft of the red spotted newt (*Notophthalmus viridescens*) is named for its conspicuous colour which warns potential predators of the poison it can secrete from glands in its skin.

In the amphibian world, poison or "granular" glands are not the exception, but the rule. Nearly all amphibians can secrete toxins from their skins but most are only mildly poisonous. However, if you handle an American toad roughly, and then touch your lips, you may experience numbness for hours; eat the toad and you will feel thoroughly ill!

The mucous-producing glands in an amphibian's skin are what give this group their slimy reputation, but they also serve a very important purpose. The mucous moistens the skin, optimizing oxygen absorption and providing a thin layer of protection.



Amphibian mucous-gland. (Source: Canada's Aquatic Environment)

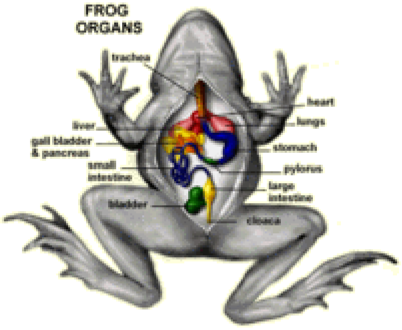
In some drier areas, a thin mucous layer isn't enough protection.

Phyllomedusa sauvagei is a large South American tree frog which spends much of its time in tree tops where the wind and heat can cause rapid water loss from evaporation. When *P. sauvagei* settles into a resting pose, special glands in its skin secrete a waxy substance which the frog then rubs all over its body. When dry, the waxy coat provides enough waterproofing to lower the frog's rate of water loss close to that of a desert iguana!

In addition to lubricating and protecting the skin, glands can function in communication. For example, "hedonic" glands produce pheromones used in courtship. The use of chemical signals is particularly important in the salamanders since they can't vocally announce their sexual readiness as the frogs do.

Internal Anatomy

Amphibian and Salamander skulls. (Source: Canada's Aquatic Environment)



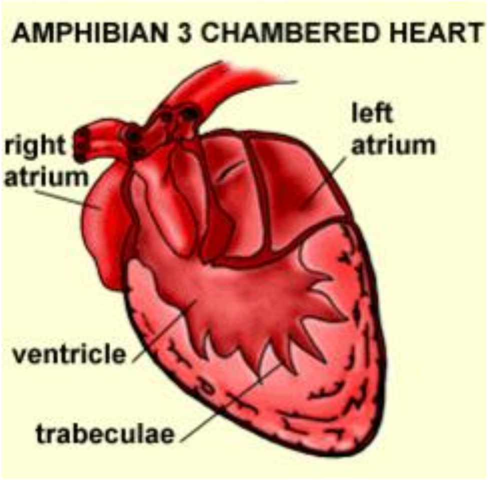
Frog Internal Anatomy. (Source: Canada's Aquatic Environment)

The skeleton of amphibians has both bony and cartilaginous components in different ratios, depending on the strength required for locomotion.

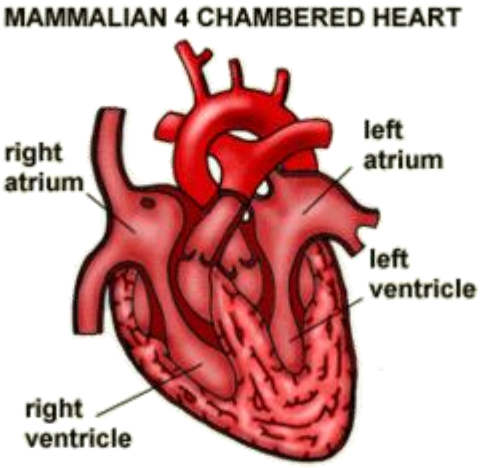
Salamanders have a largely cartilaginous skeleton, while that of frogs is more rigid and bony to withstand the impact of jumping and landing.Caecilians have dense, rigid skulls for burrowing through hard sediments, but they have lost all components of the appendicular skeleton.

Amphibian lungs are paired and they have a 3-chambered heart, unlike mammals, which have 4-chambered hearts.

Digestion occurs in the stomach and wastes are expelled through a cloaca which is also part of the reproductive system of females.



Amphibian 3-Chambered Heart. (Source: Canada's Aquatic Environment)



Mammalian 4-Chambered Heart. (Source: Canada's Aquatic Environment)

Senses

Amphibians are very susceptible to temperature and pressure change, and their highly permeable skins makes them particularly vulnerable to poisons in their environment. Their sensitive nervous and "lateral line" systems are designed to detect these threats.

Sight is of varied importance to amphibians depending on their habitat. In many species, sight is well developed for hunting. However, in others that live in almost complete darkness, like caecilians, eyes have been lost or have become greatly reduced.

Most amphibians are nocturnal and hunt in low light conditions. There are some general rules which relate pupil shape to vision type. For example, the "Kermit-like" vertical, slit-shaped pupil is an indication of excellent night vision, whereas rounder pupils tend to indicate better vision in daylight.

Amphibians have an ear structure which is similar to that of other vertebrates, but with a twist. Airborne sounds are heard in the same way, however a second unique pathway "hears" seismic vibrations through the amphibians front feet! As you rush to catch a frog, its jump to freedom may well be provoked by the rumbling vibrations of your footsteps.

Reproduction

Frogs mating. (Photograph by Rob McLaughlin)

Amphibians accomplish fertilization of their eggs in a variety of ways. External fertilization, employed by most frogs and toads, involves a male holding a female in a pose called amplexus. In amplexus, the male releases sperm over the female's eggs as they are laid. Less risky is the method employed by many salamanders whereby the male deposits a packet of sperm called a spermatophore onto the ground. The female then pulls it into her cloaca where fertilization occurs internally. By contrast, caecilians and tailed frogs use internal fertilization just like reptiles, birds and mammals. The male deposits sperm directly into the female's cloaca via an intromittent organ.

Most amphibians lay their eggs in water and then abandon them to their fates, but a few have developed strange ways to guard their eggs until they have hatched. The Surinam toad (*Pipa pipa*) of South America carries its eggs in pockets of skin on its back until the froglets hatch three months later. The gastric brooder (*Rheobatrachus silus*) of Australia no sooner lays its eggs than it swallows them! The eggs incubate in the frog's stomach where acid production ceases until the froglets hatch and crawl out through their mother's mouth.

In most cases, amphibian eggs hatch into free-living aquatic larvae which later metamorphose into juveniles in what may seem like a greatly accelerated re-enactment of amphibian evolution.

Frog and toad tadpoles are mostly herbivorous, having filter feeding mouthparts and long digestive tracts. They breathe through gills and have long swimming tails, but no limbs. During metamorphosis, their mouths widen, their guts shorten, and lungs form inside their growing chest cavities. Small legs appear on both sides of their diminished tails. Finally, forelimbs erupt from what had been the gill chambers and the froglets emerge onto land, sometimes in impressive numbers.

Amniota

No respiration with gills during the whole living cycle. Embryogenesis goes with the development of embryonic membranes (amnion and allantois).

The amniotes are a group of tetrapod vertebrates that include the Synapsida (mammals and mammal-like reptiles) and Sauropsida (reptiles and dinosaurs, including birds). Amniote embryos, whether laid as eggs or carried by the female, are protected and aided by several extensive membranes. In humans, these membranes include the amniotic sac that surrounds the fetus. These embryonic membranes, and the lack of a larval stage, distinguish amniotes from other tetrapods, the amphibians (Fig 23).

The first amniotes, which resembled small lizards, evolved 340 million years ago. Their eggs could survive out of the water, allowing amniotes to branch out into drier environments. The eggs could also "breathe" and cope with waste, allowing the eggs and the amniotes themselves to evolve into larger forms. The amniotes spread across the globe and are virtually the only land vertebrates.

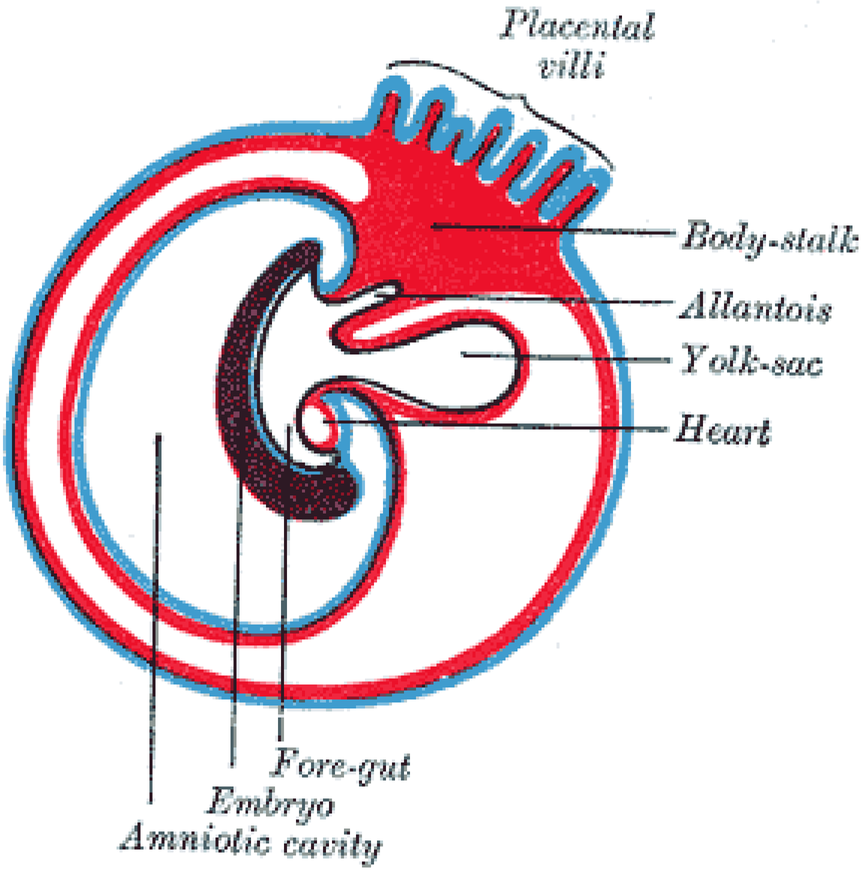


Fig. 23. Structure of amniotic embryo

Class 5. Reptilia (Fig. 24)

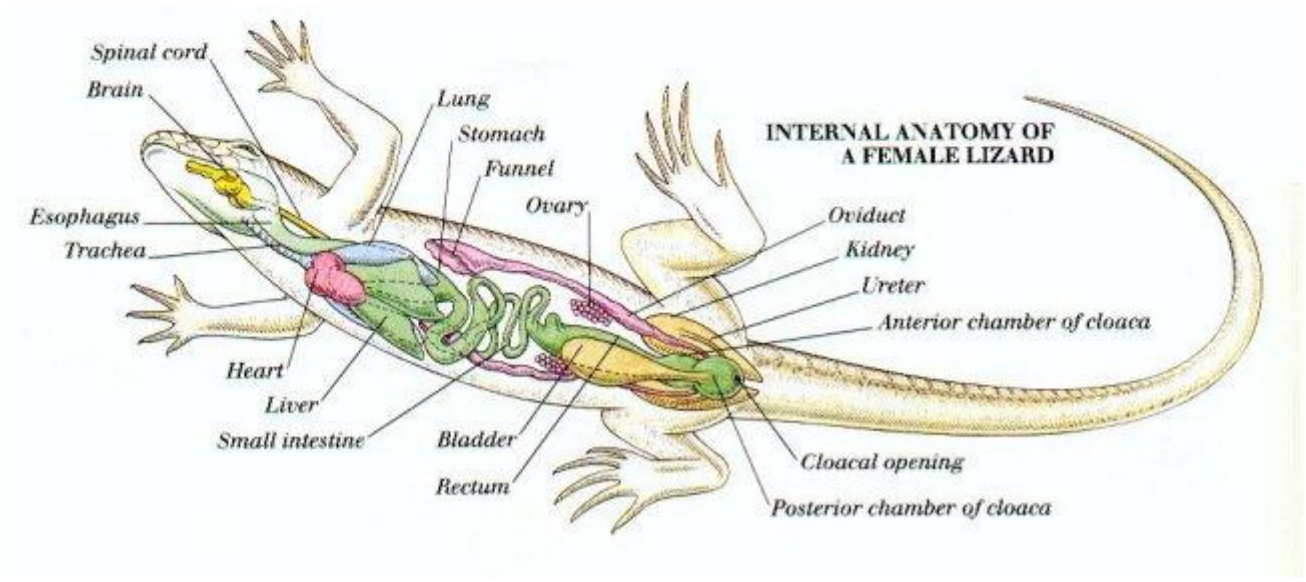


Fig. 24. Lizard, internal anatomy

Class 6. Aves (Fig 25).

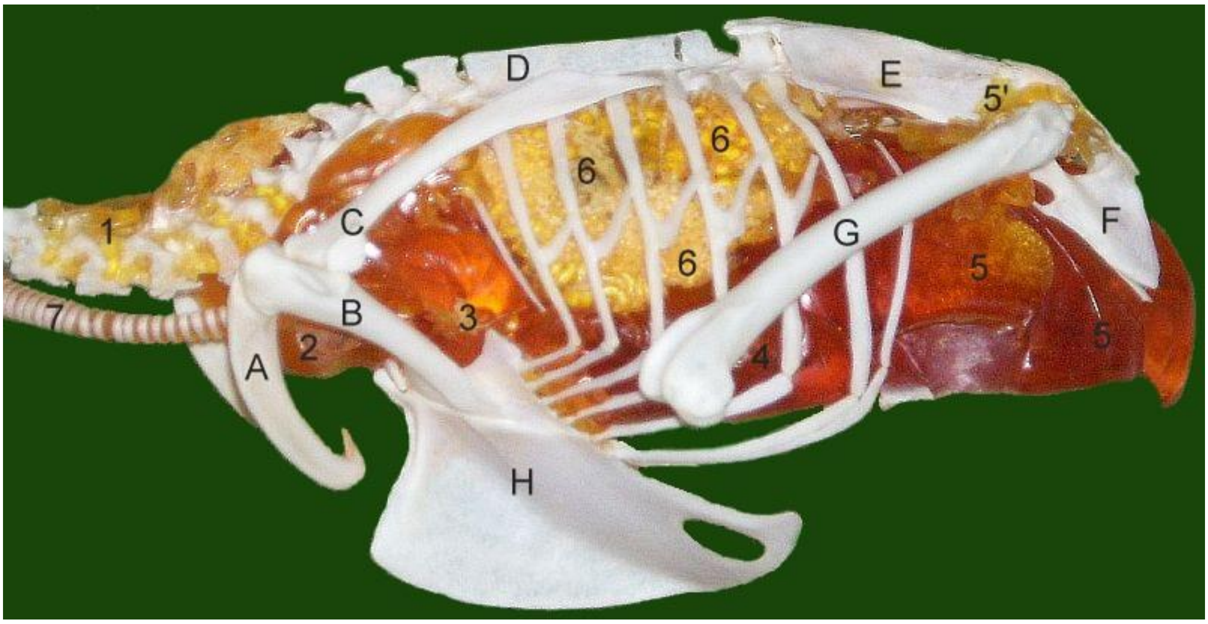


Fig. 25. Internal organs of bird

Air always flows from right (posterior) to left (anterior) through a bird's lungs during both inhalation and exhalation. Key to a Common Kestrel (Falco tinnunculus)'s circulatory lung system: 1 cervical air sac, 2 clavicular air sac, 3 cranial thoracal air sac, 4 caudal thoracal air sac, 5 abdominal air sac (5' diverticulus into pelvic girdle), 6 lung, 7 trachea

Class 7. Mammalia (Fig. 26)

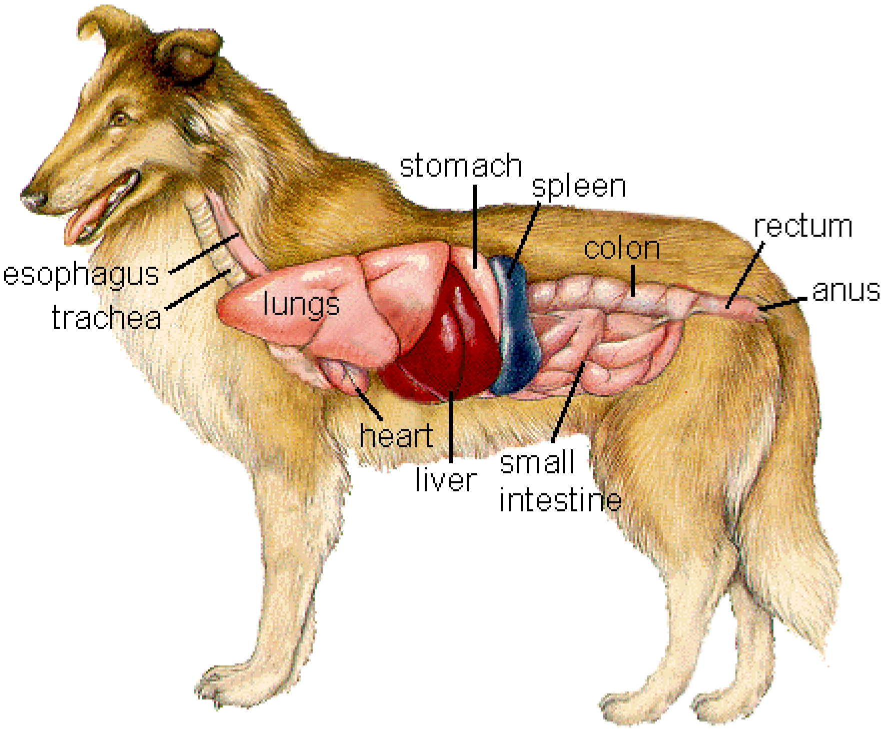


Fig. 26. Dog, internal anatomy

REFERENCES

C.P.Hickman, F.M.Hickman, L.Kats. Laboratory Studies in Integrated Principles of Zoology. Wm.C.Brown Publishers, Chicago, London, Sydney, Toronto, 1997. - 455 p.

J.Houseman. Digital Zoology, Version 2.0. CD-Rom and Students Workbook. , London, Sydney, Toronto, 2003. - 200 p. and CD.

C.F.Lytle. General Zoology. Laboratory Guide. Mc Graw Hill, Boston, Dubuque, Madison etc., 2000. – 371 p.

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