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В навчальному посібнику вивчаються тварини та їх взаємозв'язки з навколишнім середовищем, різноманітність світу тварин, систематика й класифікація тварин, будова їхнього тіла, закономірності індивідуального й історичного розвитку, зв'язки з середовищем.

Розраховано на студентів факультету ветеринарної медицини, а також усіх тих, хто цікавиться природничо-науковими дисциплінами англійською мовою.

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CONTENTS

1. 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 amoeba 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 environental 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.

1.1 PHYLUM SARCOMASTIGOPHORA

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

Class Sarcodina

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).

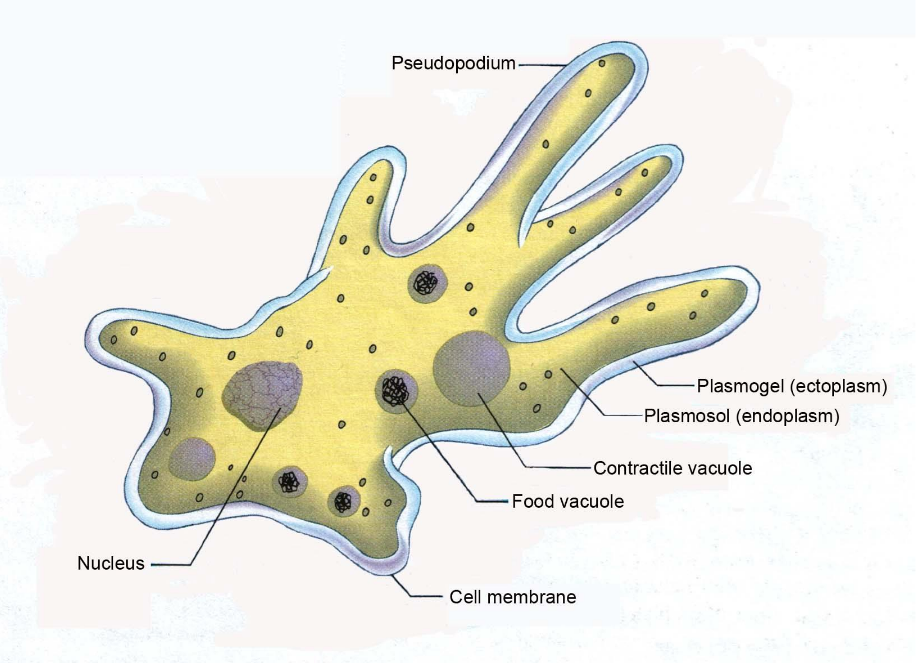

Fig. 1. *Amoeba proteus*

The Amoeba: General Structure. The protoplasm of an amoeba consist s of a thin external layer, the plasmalemma, which functions as a cell membrane; a non-granular region just within, the ectoplasm; and a granular inner region , the endoplasm, in which the nucleus lies. Features of cells like those of a vertebrate are thus apparent. The larger bodies distributed in the cell body, or cytosome, are granules of various sizes, food vacuoles in which digestion occurs, a single contractile vacuole, and other vacuoles containing watery fluid and comparable with those found in many other cells. Also present are crystals of definite forms, which may be distinctive for particular species of amoebas; oil globules; and many small inclusions ranging to the limits of microscopic visibility. The significance of these parts will be discussed as necessary in the accounts to follow.

Movements and Responsiveness. The manner in which an amoeba moves, by the flowing of its irregularly shaped body, has attracted attention ever since the animal was studied by the early microscopists, who called it the proteus animalcule, or "changing little animal"ю This amoeboid movement is simple in appearance, but it is surprisingly difficult to explain. Some of its features can be imitated by inanimate models, such as a drop of clove oil in a mixture of glycerin and alcohol; here changes in surface tension are responsible for he phenomena, and one theory assumed that similar forces were significant in amoeboid movement. However, it is now clear that the movements of inanimate models are not strictly comparable with those of an amoeba. Various accounts have been given of the changes to be observed in the formation of pseudopodia and in the locomotion of different species. Amoebas have been described as extending their pseudopodia like jets of water from a fountain, with a current flowing outward in the center of a pseudopod and backward on all sides. They have been described as rolling like a sac with elastic walls and fluid contents; and they have been said to "walk" upon stiff pseudopodia. Different kinds of amoebas thus move in different ways, but the formation of pseudopodia is probably fundamentally similar in all. The best and most generally applicable theory of amoeboid movement is based on the assumption that a relatively stiff, elastic layer, the plasmagel, surrounds the cell just beneath the plasmalemma and encloses the more fluid inner contents, or plasmasol. Localized changes cause a temporary liquefaction of the gelatinous outer layer at the point where a pseudopod is to arise; the elasticity of the remainder of the gelatinous sheath forces the fluid endoplasm against and through such a weakened area. Within the pseudopodia lobe thus formed, the fluid endoplasm flows peripherally and stiffens, addin to the plasmagel layer. This type of movement, therefore, involves one of the fundamental capacities of the endoplasm: that of changing its physical state from gel to sol, and the reversal of this process. An amoeba, we may say, moves as a tunnel might, if the mortar of its wall became fluid at the posterior end and flowed within the tunnel to its anterior end, carrying the bricks to be laid again anteriorly by a new setting of the mortar.

Feeding and Metabolism. Amoebas feed upon other organisms, both animal and plant, and may thus be described as holozoic in their nutrition. Such a species as Amoeba proteus is essentially a beast of prey, eating what ever it can capture, from small to relatively large protozoans and singlecelled plants.The most common food of this species consists of small flagellates and ciliates, which an amoeba consumes in large numbers. Ingestion involves the extension of pseudopodia about the prey, which is engulfed and transferred into the endoplasm. A food vacuole thus originates by the enclosure of a drop of water containing one or more food bodies. The feeding reactions are surprisingly complex and variable, considering the apparent simplicity of an amoeba. Forms such as motionless unicellular plants evoke responses different from those induced by active prey. A certain selectivity is exhibited by the amoeba: in the presence of two kinds of prey, equally abundant, the organism ingests the one kind which appears to be most easily digested, and rejects the other. Moreover, the responses are not fixed and mechanical but vary with the physiological state of the amoeba. In the adjustment of reaction to stimulus, and to the state of its physiology, an amoeba behaves in a manner resembling the behavior of multicellular organisms.

When a small flagellate, such as Chilomonas, is ingested by Amoeba proleus, the prey continues to move about for several minutes before it is killed by something within the vacuole. Meanwhile, the food vacuole, which at the outset contains a relatively large amount of water, shrinks by the diffusion of excess water into the cytoplasm. The fluid then remaining within the vacuole becomes alkaline, and in later stages it becomes acid. If the changes in individual vacuoles are followed, the Chilomonas will be seen to disintegrate gradually, until, some 12 or 24 hours later, there remain only certain granules that are apparently indigestible. Fat globules are liberated from the food mass and appear in the vacuolar fluid within 2 or 3 hours, after which they gradually decrease in size and disappear. Starch grains disintegrate into a pasty mass, which disappears as the vacuole slowly decreases in volume.

The disintegration of other particles and further shrinkage of the vacuole follow, until only a few granules remain. Even these remnants may pass into the endoplasm instead of being egested. Egestion occurs by the discharge of food in various stages of digestion, and of the indigestible residue of food, after all the digestible material has passed into the cytoplasm. Often several vacuoles in late stages coalesce, and the resulting mass comes into contact with the plasmalemma at or near the posterior end of the amoeba. The mass is egested by rupture of this membrane. From observations such as these, it is inferred that fats, carbohydrates, and proteins are digested in the food vacuoles, presumably by specific enzymes, as in the digestive tracts of manycelled animals.

Life Cycle and Reproduction. The life cycle, or life history, of a manycelled animal is the series of changes from egg to adult that occurs in each generation. Many protozoans, including some members of the Sarcodina, also exhibit serial changes of form which constitute their life cycles. In the common amoebas, however, the life history seems to involve nothing but an endless series of cell division by binary fission, although more complicated phenomena, such as encystment and sexual reproduction, have been described. Present indications are that Amoeba proteus, for example, reproduces only by binary fission, with subsequent growth of the daughter cells to full size, continuing in the active state with out syngamy or encystment. Amoebas may become smaller through starvation, or, as in some larger species, multinucleate forms may be produced by the failure of the cytosome to divide following nuclear division . The large fresh-water amoeba, Pelomyxa carolinensis, contains hundreds of nuclei produced in this way. At the time of cell division, the cytosome divides, distributing the nuclei between the resultant daughter individuals. In some of the other amoeboid forms, more complicated life cycles, with budding and encystment, have been discovered. Some of these cycles include flagellated stages, and in others, gametes and syngamy are known

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*).

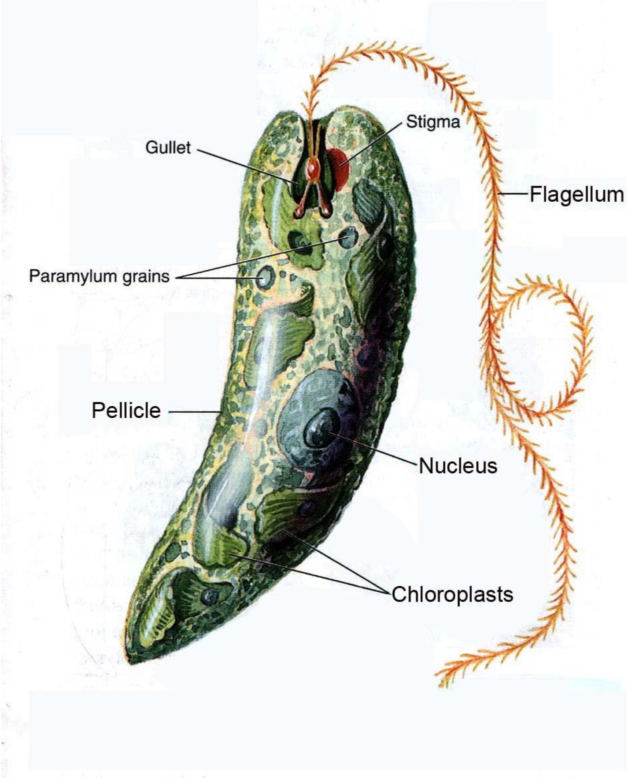

Fig. 2 *Euglena sp*.

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

The Euglena: General Structure. A typical euglena is covered by a thin pellicle, comparable with the cell wall in plant cells and often marked externally in a spiral pattern. The pellicle is stiff enough to preserve the contours of the organism as it swims through the water but flexible enough to allow the changes of shape called euglenoid movement. The anterior end of the organism bears a mouth-like notch, from which a flask-shaped cavity extends a short distance into the cell. The single flagellum protruding from this cavity arises from two branches, each of which originates in a granule, or blepharoplast. From one blepharoplast a fiber extends to the nuclear membrane. The flagellum it self consists of a central axial filament, formed by the union of the two branches, and a surrounding, spirally wound sheath.

In Euglena the cavity from which the flagellum extends does not function as a mouth and gullet, for in its nutrition the euglena is holophytic, like the green plants. In related flagellates which ingest and digest food, the anterior opening may more properly be called a mouth. In the euglena, in the anterior end of the cell, minute vacuoles periodically enlarge and coalesce to form a contractile vacuole, which discharges into the "gullet." As in the amoeba, such vacuole s arc believed to eliminate water from the cell, and only incidentally to serve for the expulsion of the soluble excreta which this water may contain.

A mass of red pigment at the anterior end of the organism is called stigma, or eyespot; it seems to be a light sensitive organelle. The nucleus lies near the center of the cell, surrounded by green chromatophores, the chloroplasts, which fill the cytoplasm. The chloroplast s contain chlorophyll and are responsible for the green color of the cell. Thi s chlorophyll is comparable with that in the green cells of plants. Between the chloroplasts the most conspicuous inclusions in the cytoplasm are bodies of characteristic shape, varying between different species, composed of par amylum. This is a complex carbohydrate related to starch, and the par amylum bodies are interpreted as stored food reserves. There is no flowing of the endoplasm as in the amoeba, although the plasticity of the cytosome is demonstrated when the euglenoid cell changes its shape.

Movements and Responsiveness. Characteristic expansions and contractions of the cell, occurring when the euglena is not in active locomotion, are called euglenoid movements. These are not interpreted as related to progressive locomotion, which is brought about by the action of the flagellum. The flagellum beats in such a way as to propel the organism in a spiral course, rotating upon its long axis.

By these movements of the cell body, and by spiral swimming, the organism reacts to a variety of stimuli. The behavior with respect to light, a necessary factor in the environment of these plant-like forms, has been studied especially. Observations have shown that a euglena which has been moving toward a source of light gradually changes its direction when the direction of the light is changed and so continues to orient positively toward the light. The adjustment involves a complex series of movements, including rotation of the cell upon its long axis; but once the orientation is accomplished, the animal continues its spiral progression in one direction. In general, the euglena responds positively to light of optimum intensity; if the light is very intense, a negative response will be exhibited. In these and other reactions the organism manifests the responsiveness characteristic of all cells.

Nutrition and Metabolism. Possessing chlorophyll, the euglena carries on holophytic nutrition like that of green plants. It is doubtful that ingestion of food ever occurs in Euglena, although such colorless flagellates as Peranema and others do ingest small organisms through the gullet and form food vacuoles. When kept in darkness, Euglena gracilis and other green flagellates lose their green color but continue to live and reproduce for long periods. This is true, however, only if certain organic compounds are present in the culture medium, to satisfy the energy requirements of the cells. Thus it has been established that the same species can maintain itself in the light by holophytic nutrition and in darkness by saprophytic or saprozoic nutrition. In the absence of light, the organism is unable to manufacture its energy-rich compounds by photosynthesis and must depend on external sources.

Life Cycle and Reproduction. As in man y other protozoans, the life cycle of some species of Euglena includes an active phase, during which the organism moves about, and an encysted phase, during which it is endosed within a cyst and is non-motile. It is questionable whether Euglena viridis ever undergoes encystment. In this species reproduction occurs by binary fission, which is typically a longitudinal division beginning at the anterior end of the cell. Jnother euglenas this division may proceed in either the active or the encysted phase. So far as is known, there is no sexual reproduction in flagellates like Euglena, although the production of gametes, and syngamy, are well known in other flagellates.

1.2 PHYLUM SPOROZOA

The class Sporozoa contains only parasitic species. In correlation with this mode of life, the locomotor and other structures necessary in free-livin animals are much reduced. The nam e Sporozoa ("seed animals") was iven because "seed -like" stages, or spores, are conspicuous in the life cycles of these protozoans. Representative examples are species of the genus Monocystis, which inhabit the seminal vesicles of earthworms. The full-grown individual is an elongated cell with a single nucleus. This organism is capable of a slow , gliding locomotion by local contractions and extensions of the cell, but there are no complex locomotor structures or behavior. Monocystis is first an intracellular parasite and later lies free in the fluid of the seminal vesicle. Presumably, food is absorbed through the cell membrane from the surrounding medium, and metabolic wastes are eliminated by diffusion. An abundant reserve of nutrients is stored in the cytoplasm and is utilized during encysted and gamete-forming stages. The life cycle, contains a stage in which rapid, successive divisions produce a large number of spores. This type of proliferative division, termed multiple fission, is a characteristic feature of the life cycles of all sporozoans.

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 reinfect 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).

Malaria and the Malaria Parasite. The agents of infection in this instance are Sporozoa, various species of the genus *Plasmodium*; *Plasmodium malariae*, for example, produces one form of malaria in man (Fig. 3). In the vertebrate host, the parasite lives intracellularly in the red blood cells and other cells, where asexual reproduction occurs by multiple fission or merogony.

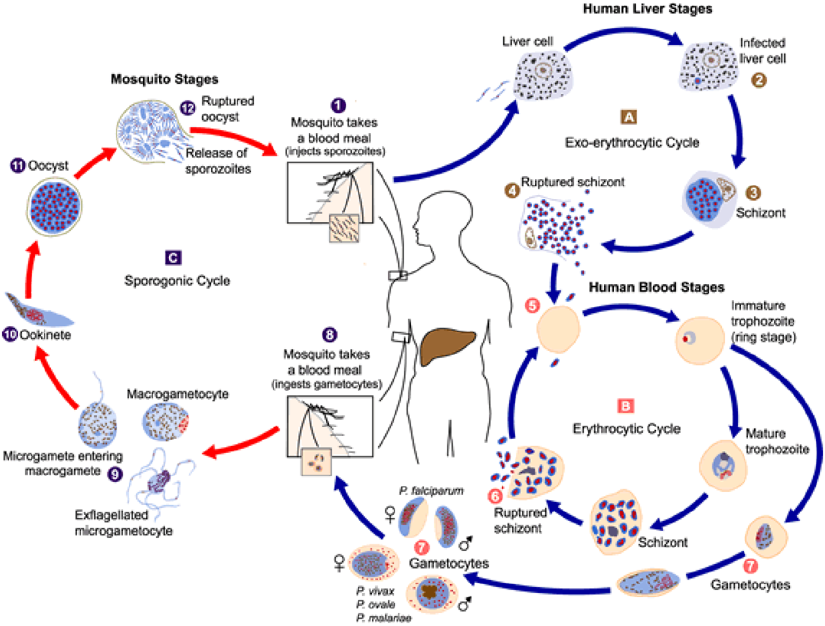

Fig. 3 Life cycle of *Plasmodium falciparum*

The resulting new generation of parasites (merozoites) are liberated with the destruction of the invaded erythrocytes, and in turn enter new cells in which the process is repeated. In this manner a very large number of erythrocytes may be destroyed and the population of the parasites greatly in creased. In the form of the disease produced by P. malariae, the patient suffers chills and fever which recur at intervals of about 72 hours. This periodicity coincides with the maturation and liberation of successive generations of merozoites in the red cells, and it is probable that the symptoms are precipitated by the toxins released by the disintegrating cells. After a considerable period of such asexual reproduction, the parasite forms macrogametocytes and microgametocytes, which remain in the red cells of the vertebrate host until the blood is ingested by a mosquito. In the stomach of this host the gametocytes differentiate into macrogametes and microgametes, and syngamy occurs. The resulting motile zygote passes through the epithelium of the gut and takes up a position on the outer surface of the mosquito’s digestive organs, where it becomes invested by a cyst wall. Within this cyst multiple fission again occurs, and eventually man y spindle-shaped cells, the sporozoites, are formed. The cyst wall finally bursts, and the sporozoites thus liberated into the mosquito's body cavity migrate into its salivary glands. Here they remain until ejected with saliva when the mosquito bites a human.

1.3 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

Class Ciliata includes the most generalized ciliates, such as *Paramecium* (Fig. 4) 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. The class Ciliata includes the protozoans in which the body is wholly or partially covered by cilia. Many of the ciliates are complex and highly specialized cells, whose structural complexitis far exceed those found at the cellular level in metazoans. A unique feature is the almost universal separation of the nuclear material into two parts, a larger macronucleus and at least one micronucleus, with important differences in function.

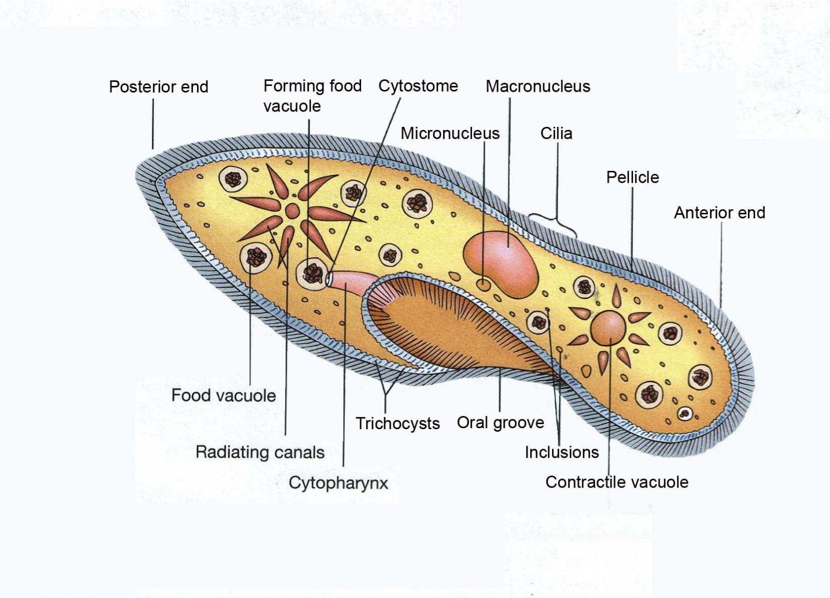

Fig. 4 *Paramecium caudatum*

The Paramecium: General Structure. If any forms can be called the omnipresent protozoans of fresh water, they are Paramecium aurelia and P. caudatum. No species of large size occur more commonly in cultures or under a wider range of conditions. Moreover, these species can be easily cultured in the laboratory and are favorable for study. The account to follow deals with P. caudatum, unless otherwise stated.

The size of the individuals seen in mixed cultures varies greatly. Like other kinds of animals which have been extensively studied, *P. caudatum* consists of many races which breed true among them selves but may differ widely when one race is compared with another. Reproduction, food, and environmental factors also influence body size. The cell is spindle-shaped, with the anterior end bluntly rounded and the posterior end more pointed. At one side, a depression, the oral groove, passes diagonally from the anterior end to about the middle of the body, where it ends in a gullet. The body is covered with cilia, which are of uniform length except for those at the posterior end and in the oral groove, which are slightly longer. Within the gullet the cilia are arranged in a special band-like undulating membrane. On the surface of the cell just posterior to the end of the oral groove lies the anal spot, where egestion occurs.

Movement and Responsiveness. Locomotion in Paramecium is effected by the action of the cilia, which by coordinated beating propel the animal in a spiral course. An understanding of this process involves two problems: first, that of explaining the operation of individual cilia; and second, that of accounting for the integration of the activities of the individual cilia in such a way as to provide for directed locomotion. It can be observed that the cilium is relatively stiff, and moves rapidly, during the effective or driving stroke, and that it becomes relatively limp and moves more slowly as it returns to its original position during the recovery phase. The factors governing these changes presumably result from the interaction of the basal granule, or kinetosome, of the cilium and the axial filament, which springs from the kinetosome and runs the length of the cilium. Experiments have shown that a single cilium exhibits spontaneous movements as long as its connection with the kinetosome remains intact. Without the kinetosome, the cilium is incapable of beating. This indicates that a capacity for initiating activity resides in the kinetosome. It seems reasonable to speculate that a common physicochemical mechanism may underlie all phenomena of protoplasmic contractility, including amoeboid movement and ciliary and flagellary action, as well as muscular contraction.

Feeding and Metabolism. In feeding, the cilia of *Parameciun* draw a current of water against the oral surface, so that particles like bacteria, smaller protozoans, algae, and organic debris enter the gullet. By means of the cilia, and by movements of the gullet, masses of this food included in a drop of water pass into the cytoplasm and are thus ingested. The food vacuoles so formed move along a definite course within the cytosome carried passively by currents in a process termed cyclosis. As in *Amoeba*, it is assumed that enzymes are secreted into the vacuoles and bring about digestion. The products of digestion are evidently transferred into the surrounding endoplasm, since the vacuole finally contains only material to be egested at the anal spot. The observations which can be made on *Paramecium* are similar to those described for *Amoeba*, and we reason similarly from them with the aid of knowledge concerning other animals. The products of digestion, passing out of the food vacuoles, are utilized during metabolism. Cellular respiration corresponds to the process in vertebrates; oxygen enters the cell directly from the surrounding fluid, and final breakdown of the cellular constituents occurs, with transformation of energy and formation of waste products. Excretion of the wastes of metabolism occurs chiefly by diffusion over the entire surface of the cell and to some extent by means of the contractile vacuoles. Under suitable conditions the storage of reserves such as glycogen and fat occurs in the cytoplasm. The nutrition of *Paramecium* is, therefore, holozoic; and its metabolism is fundamentally like that of higher animals.

Life Cycle and Reproduction. The life cycle of *Paramecium* consists of an active phase, which may continue indefinitely in a suitable medium. There is no encysted phase that may be commonly observed in the laboratory, although encystment has been described. Perhaps it occurs more frequently in nature, since it is difficult to understand how any protozoan can be so universally distributed in fresh water without undergoing occasional encystment to survive periods of drought. Paramecium, however, does not appear to encyst upon aquatic vegetation; it is rarely, if ever, obtained by placing such vegetation in sterile water. In the laboratory the life cycle is an endless active phase with frequent reproduction by transverse binary fission, which is an asexual process. Periodic phases of nuclear reorganization, termed endomixis, also occur. Reproduction by conjugation, or temporary union of individuals with exchange of nuclear material, may also be observed. Some strains of Paramecium, however, appear capable of maintaining themselves indefinitely, by fission and endomixis, without conjugation.

Class Suctoria

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.

The class Suctoria comprises a small group of Protozoa placed in the subphylum *Ciliophora* because cilia are present during the immature, motile phase of the life cycle. During the adult, attached phase of the cycle the cilia are replaced by structures called tentacles, used in feeding. Representative genera are *Ephelota*, *Podophrya*, and others. The mature animal is attached to the substratum by a stalk, and its tentacles radiate from the central cell body. Small organisms coming into contact with the knob-like ends of the tentacles are held fast. Appar ently the tentacles digest their way through the surface of the captive. The fluid contents of the prey may be seen later streaming down through the tentacles into the body of the suctorian, as the prey, if it is small enough to be destroyed in this manner, slowly shrivels until released as a crumpled mass. Frequently a suctorian attacks ciliates much larger than it self, such as *Paramecium*, which is sometimes seen swimming with a Podophrya attached. Reproduction in suctorians involves cell division of a peculiar type which is usually termed budding. In this process the nuclei divide, as in *Paramecium*, one set of daughter nuclei being pinched off with a bud of cytoplasm into a temporary cavity within the distal end of the adult body. Within this cavity the bud gradually enlarges and develops bands of cilia. When it is released, it swims about by means of these cilia for a short time, then settles to the substrate and develops the stalk and tentacles of an adult. A process of conjugation is also known for the *Suctoria*.

2. 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

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).

2.1 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 5).

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.

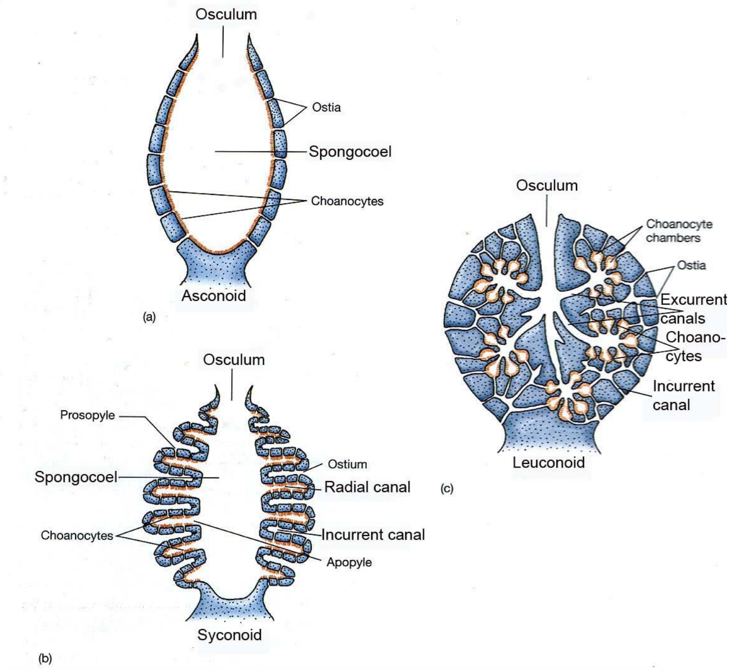

Fig. 5 Body types in *Sponges*

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.

2.2. 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. 6) 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.

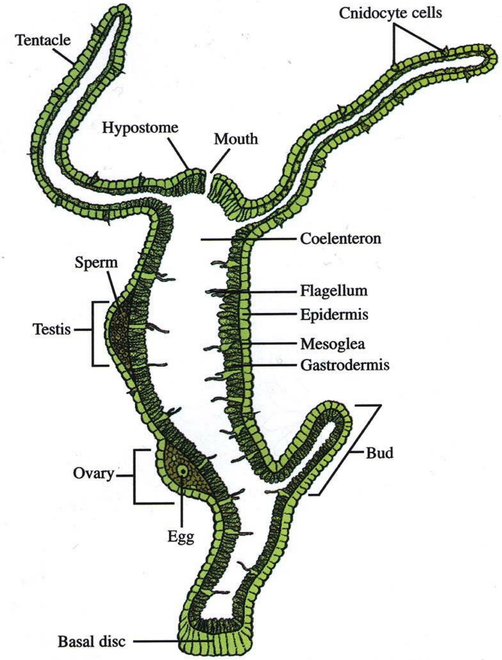

Fig. 6 *Hydra*, body construction

Classification

Class Hydrozoa

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

General Structure. The body of a hydra consists of a simple two-layered tube, the trunk, normally attached at one end, the base, and surmounted at the other by a circle of tentacles, varying in number. The tentacles enclose a conical region, the hypostome, which bears at its apex the mouth. The body wall surrounds a digestive cavity or coelenteron, which extends into the tentacles. The cell layers, an outer epidermis and an inner gastrodermis, are separated from each other by a non-cellular supporting lamella. This structure corresponds functionally to an elastic skeleton. It serves as a place of attachment for the cells and gives support and elasticity to the entire organism. In hydrozoan medusae, or jellyfish, this layer is represented by a thick, watery jelly without cells, termed the mesogloea ("middlejelly").

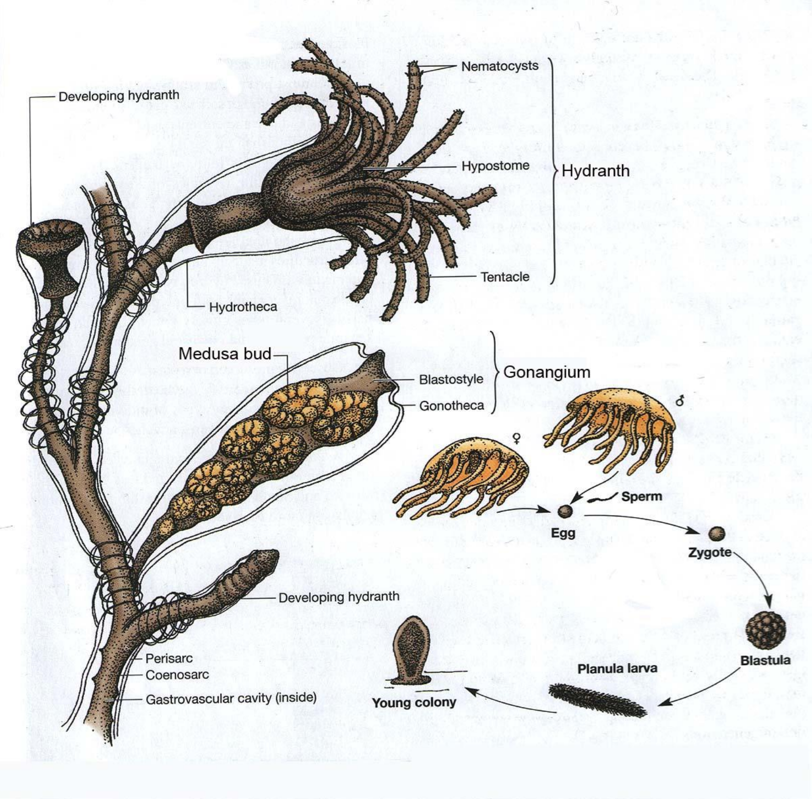

Fig. 7 *Orbelia* (Hydrozoa), life circle

Metabolism. The small animals serving as food for the hydra, after being paralyzed and held fast by the nematocysts, are brought to the mouth by the tentacles and are ingested by engulfing movements of the hypostome. The mouth is capable of a surprising degree of distension to accommodate large objects of food. Soon after its ingestion the food is shifted by peristaltic contractions of the body to a position in the distal half of the coelenteron, where the early stages of digestion occur. Although no structural differentiation exists other than the abundance of gland cells in the distal region, there is apparently a physiological division of the coelenteron into gastric and intestinal regions; the food mass is never found in the more proximal or basal part of the cavity.

The process of digestion in the hydra is twofold. Enzymes released from the gland cells bring about the disintegration of the softer parts of the food mass, liquefying it and hastening its breakdown into particles. The soluble products of this extracellular phase of digestion are absorbed directly by the gastrodermal cells. Finely divided particulate matter is ingested by pseudopodia formed by the large gastrodermal cells and comes to lie in food vacuoles within their cytoplasm. Here the intracellular phase of digestion occurs, which is presumably entirely comparable with the process as it occurs in an amoeba. The indigestible residues are cast off by the gastrodermal cells and, together with the resistant parts of the food mass in the coelenteron, are expelled through the mouth by a series of violent contractions of the body. The bottom of a culture dish near a vigorous and well-fed hydra may often be littered with the egested exoskeletons of the water fleas upon which the animal has been feeding.

Reproduction and Development. At certain seasons of the year, particularly in autumn, hydras reproduce by syngamy, the union of gametes. The testes are usually located on the distal half of the trunk, the ovaries near the middle. Testes may appear first and ovaries later on the same animal, or both may be present together. Animals in which the same individual possesses both ovaries and testes are said to be hermaphroditic or monoecious.

Monoeciou sness may be the usual condition in hydras, although species in which the individuals seem to be exclusively male or female, hence dioecious, have been reported. There are no secondary sexual characteristics in hydras; only by observing the testes or ovaries can the sex of an individual be determined. These gonads appear as swollen protuberances from the epidermis in the characteristic regions. Within them, ova or spermatozoa a rise from interstitial cells. Fully matured spermatozoa may be seen moving actively within the testis; they are discharged by the periodic opening of the apex of the testis, which thus liberates successive swarms. The spermatozoon then swims about until it dies, or until it comes into contact with an ovum which has been exposed by the rupture of its epidermal covering. The zygote formed by the union of these two gametes undergoes cleavage and secretes about it self a shell-like cyst, or theca. With in the theca, development proceeds until an outer layer of cells, the ectoderm, and an inner solid mass, the endoderm, have been formed. The embryo within its theca then becomes detached from the parent and drops to the bottom. Tentacles eventually develop; the embryo breaks from its cyst, becomes attached, develops a coelenteron, forms a mouth, and so becomes a miniature hydra. Zygotes developing in late autumn pass the winter with in the protective cyst.

Hydras frequently produce new individuals by budding, a process referred to as asexual reproduction. It is, essentially, reproduction by cell division. It differs, however, from the asexual reproduction of protozoans in that the mass of new cells produced is organized by some integrating influence into a multicellular individual with the characteristics of the parent. There is first an accumul at ion of nutrient material in the gastrodermal cells at some place toward the middle of the body, and cells in the epidermis of this region divide repeatedly to form a bud-like swelling. An extension of the coelenteron grows into the bud, which then appears as a blindly ending out growth of the two layers of the body wall. Tentacles appear as evaginations of epidermis and gastrodermis, and finally a mouth is formed. If food is abundant, the bud may remain attached to the parent for some time, and in exceptional cases it may rebud to form several generations in a branching system. Usually, however, the connection between parent and offspring becomes constricted, and the bud is detached as an independent individual as soon as the tentacles and mouth become functional

Class Scyphomedusae

Cnidaria with medusoid stage as the main stage in the life cycle. Most of the jellyfishes called hydromedusae are small, like Gonionemus, or smaller. The amount of solid or living material in such individuals would be small, however, because jellyfishes are composed chiefly of water. The bulk of their substance consists of the "jelly," which in these forms is a gelatinous mass conspicuously provided with cells resembling connective-tissue elements of higher animals. The jelly itself may thus be considered as intercellular material, comparable with the fibrous substance of connective tissue or the ground substance of cartilage. In scyphomedusans specialized organs of equilibration, termed statocysts, are located at intervals around the margin of the bell; these sense organs are important in the free-swimming locomotion of jelly fishes, and similar though simpler statocysts occur also in hydromedusae.

The genera *Cyanea* and *Aurellia* are representative *Scyphomedusae* found in North Atlantic waters. In typical cases the life cycle of a scyphomedusa consists of the following sequence: a planula larva develops from a zygote; this larva produces an attached polyp generation, the scyphistoma, from which free-swimming medusae arise in succession by transverse budding or strobilization. The young medusae released from the strobila are saucerlike individuals called ephyrae; they grow and transform into adult, sexually reproducing jellyfishes. Asexual reproduction of the polypoid generation, by budding to produce additional polyps, has also been reported.

Class Anthozoa

Cnidaria with only polyp stage represented in their life cycle. The Anthozoa are represented by the sea anemone, *Metridium dianthu*. As in anthozoans generally, the sea anemone is provided with a somewhat flattened oral disk surrounded by tentacles. The epidermis turns in at the mouth and hangs downward into the coelenteron to form a tubular pharynx or stomodaeum. This pharynx is attached to the lateral body wall by a series of radiating partitions or septa, which thus divide the upper part of the coelenteron into radial compartments, continuous with the undivided cavity below. The biradial symmetry characteristic of many Anthozoa is produced by the presence of one or more heavily ciliated grooves or gutters, called siphonoglyphs, traversing the pharynx longitudinally from its outer to its inner edge. These grooves presumably function to provide active currents of fresh, aerated water to the inner parts of the animal, and to flush away wastes.

Other representative anthozoans are the true corals, such as *Astrangia danae*, a northern coral, and the many species aboundin in tropical seas. The coral individual resembles a small sea anemone lying in a limy, cup-like skeleton secreted by its epidermal cells. The stony mass of a coral head or reef, covered completely by the living substance of its polyps, is contributed to by the secretory activites of large numbers of these individuals, producing skeletal material beneath them and forming new polyps by budding or subdivision as the size of the mass increases. The living individuals are found only at the surface, the underlying stony material is uninhabited, except as it may be invaded by a variety of worms, crustaceans, bivalves, and other animals of the reef. The part played by corals in the formation of coral islands and of the limestone in various deposits has given these coelenterates an important role in geologic history.

Class Ctenophora

The Ctenophora, commonly known as sea walnuts or comb jellies, are animals with biradial symmetry, epidermal and gastrodermal layers like those of coelenterates, definite muscular elements and a mesenchymal middle layer (collenchyme) that are both derived from mesoderm, and eight meridional rows of swimming plates or combs formed of fused cilia. Ctenophores are all small marine animals which float and swim near the surface, although a few aberrant species that have become adapted to a creeping existence upon the bottom are known. The free-swimming forms are sometimes present in such tremendous numbers that they constitute an important element in the floating life of the ocean. Their food consists of whatever small animals they may capture with the aid of the tentacles which some ctenophores possess, or with the parts related to the mouth. Abundant mucous secretions of the epidermis aid in trapping small animals which are then driven toward the mouth by ciliary currents. In contrast to the coelenterates, ctenophores lack nematocysts, but some possess adhesive cells on the tentacles which hold fast to the prey until it can be drawn into the mouth. The gastrovascular cavity is divided into pharynx, stomach, and branching diverticula which ramify extensively throughout the body. A small anus is present at the aboral end. The resemblances between coelenterates and ctenophores are thus rather superficial and are considered insufficient to warrant placing these groups in the same phylum.

The structure of a ctenophore is rather complicated for an animal whose basic organization is so simple. The eight rows of combs, responsible for the name Ctenophora ("comb bearers"), are a unique feature of the phylum. Each row consists of a series of comb-like plates composed of fused cilia; the combs are found in all members of the phylum except a few, where they are lost or modified in the course of development. Locomotion is effected by the beating of the combs, which has been much studied as an example of ciliary action controlled by a nervous system. In addition to a coelenterate-type nerve plexus throughout the body, nervous elements are concentrated beneath the ciliary rows.

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.

2.3 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*

Orde*r* 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 licneath 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 I'reservation in an irritant fluid such as acetic acid the body becomes covered wilh 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 l issues lost by injury.

Muscle. 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, .1 nd not a tube with a mouth and anus serving separately for the entry and exit i'I" 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 l lie *pharynx.* The pharynx itself may lie in a pit of the ventral body wall, called l lie *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 . i p pears 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 thickening 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 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.

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.

2.3.1 *Class 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.

Fresh-Water Planarians. **General Structure, and Activities.** The term planarian is sometimes applied to both polyclads and triclads but usually refers to the triclads alone. Triclads are common in fresh water. Like the hydras, the planarians have long been familiar objects of study to zoologists and are well suited to illustrate the structures and functions typical of the phylum to which they belong. they occur in ponds and streams, usually on the shaded sides of submerged objects. They avoid strong light and are probably nocturnal in many of their activities. In nature they feed on the bottom ooze with its microscopic plants and animals, on dead animals, and on living forms such as small mollusks and arthropods; these they capture by enfolding the prey with the margins of the body and then applying the extruded pharynx. When bits of meat are placed in a dish containing planarians not recently fed, the worms begin to move about and soon most of the individuals will be found with the pharynx attached to the food. Species of the genera Dendrocoelum and Procotyla have a special sucker-like organ at the anterior end, by means of which they seize active prey and hold it while the pharynx attaches for feeding.

Normal, gliding locomotion is brought about by the action of the ventral and lateral cilia, beating in a layer of mucus secreted as the animal moves. A more rapid and active locomotion is effected by a variety of muscular contractions of the body.

Structures and Functions Related to Metabolism. In feeding, the musclar, tube-like pharynx is extruded from the mouth and attached to the food, which may be partially digested by fluid from the pharynx before it is transferred to the digestive cavity. At rest the pharynx lies withdrawn into a sheath-like cavity; the mouth is actually the external opening into the pharynx sheath, and it is through this opening that the pharynx or proboscis is extended in feeding. Food is drawn in through the cavity within the pharynx itself and then passed into the enteron, with its three main branches and lesser subdivisions. Digestion occurs chiefly, if not entirely, within the gastrodermal cells lining the enteron; extracellular digestion is apparently limited to the preliminary softening or liquefaction of foods by the action of fluids from the pharynx. As in coelenterates, the planarian digestive cavity, extensively branched throughout the body, assumes in part the functions of a distributing system; no part of the body of the worm is far removed from a branch of the enteron. The products of digestion, as well as oxygen absorbed through the epidermis, are also distributed by way of the lymph-like fluid filling the interstices of the mesenchymal meshwork. The excretory system, as it is usually called, consists of minute tubules beginning as flame bulbs in all parts of the mesenchymal region and uniting to form larger tubes, which open to the exterior by a number of dorsolateral excretory pores. The flame bulbs, or flame cells, are so named because of the flickering tufts of cilia beating within their cavities.

These cavities are intracellular spaces and are continued as intracellular ducts within the cells making up the tubules. A system composed of these and other similar units is a distinctive feature of trematodes and cestodes, as well as of turbellarians; such systems also occur in animals belonging to other phyla. Flame bulbs are termed protonephridia, and any system of flame bulbs and ducts leading to external orifices is a protonephridial system. In ascribing an excretory function to protonephridia, it is supposed that the tufts of cilia in the flame bulbs, and other cilia lining the tubules, set up currents flowing toward the external openings. Fluids, containing metabolic wastes in solution, may presumably enter the system from the lymph by passing through the flame cells, and may be driven from the body through the excretory pores. It is probable, however, that the chief function of the protonephridia, as of protozoan contractile vacuoles, is in maintaining water balance, with excretion as an incidental process.

The Nervous System and Responsiveness. The nervous system is well developed in correlation with the complex musculature of planarians. A pair of eyes, consisting of cup-shaped groups of light-sensitive cells, is found in the dorsal surface of the head region. Beneath the eyes lies a concentration of nervous tissue, the brain or cerebral ganglia. Two nerve cords extend to the posterior end of the body, and there are transverse connections between these cords throughout their length. These elements altogether constitute what may be termed a central nervous system. From the brain and cords nerves extend to all parts of the body, particularly to the anterior end. Neurons are not easily recognizable in planarians, but they can be demonstrated in certain regions. It is assumed that the relationships of sensory, motor, and perhaps adjustor cells are comparable with those in other invertebrates that have central nervous systems. Planarians evidently have a well-organized nervous mechanism as the basis for their complex sensory and muscular reactions. At the surface of the body, in addition to the eyes, occur a variety of sensory receptor cells specialized for the reception of chemical and tactile stimuli. The structure of the eye in many planarians indicates that light from a definite direction may be an effective stimulus, as well as mere illumination; however, there seems to be no mechanism for image formation. Planarians respond to many different stimuli with a rather high degree of coordination.

The Reproductive System, Reproduction, and Development. The planarian reproductive system is complex and highly specialized. The worms are monoecious , each individual having both male and female systems. The male system includes numerous testes, arranged in paired longitu dinal rows . Each testis is connected by a ductus efferens to the longitudinal ductus deferens on its own side of the body. The two ductus deferentes enlarge posteriorly to form spermiducal vesicles in which spermatozoa are stored in advance of copulation. The spermiducal vesicles unite in the midline of the body, posterior to the pharynx sheath, and form the tubular cavity traversing the penis, or male copulatory organ. The penis lies in a cavity, the male antrum, which is just anterior to, and connects with, a second cavity, the genital atrium. The genital pore opens on the ventral side of the body, posterior to the mouth, and connects the genital atrium to the exterior. The relationship of the penis to its cavity, and to the genital atrium, is similar to that of the pharynx to its sheath. During copulation, the penis is thrust from the genital pore in the same manner as the pharynx is thru st from the mouth during feeding.

The female system consists of a pair of ovaries, from which the ova arise, located usually just behind the head region. A single oviduct leads posteriorly from each ovary, receiving in its course a series of smaller duct s from the numerous yolk glands which surround it throughout its length. The two oviducts may unite posteriorly at the midline to form a common chamber, the female antrum, lying just behind the genital atrium and connected to it. In other species the paired oviducts join the genital atrium directly. Most planarians possess also a bulbous, blindly ending chamber, the copulatory bursa, opening either from the genital atrium or from the female antrum and extending a short distance dorsally and anteriorly.

The functional aspects of this complex system may now be considered. Sexual reproduction in planarians usually involves copulation, in which the genital pores of two worms are brought together and the peni s of each worm is inserted through the genital opening and into the copulatory bursa of the other. Mutual exchange of spermatozoa from the spermiducal vesicles thus occurs, and copulation is completed by this insemination. After the partners have separated, the spermatozoa received in copulation are transferred, or move, from the copulatory bursa into the paired oviducts and finally come to rest in the anterior end of each oviduct. Here, adjacent to the ovary and separated from it by a membrane, is a seminal receptacle, in which spermatozoa are stored.

Eggs released by the ovary break through the membrane, are fertilized, and pass down the oviduct where they are surrounded by yolk cells. The zygotes and their accompanying supplies of yolk cells are gathered in the genital atrium, where numbers of them are enclosed in a shell or cocoon secreted by numerous gland cells in the wall of the atrium. A stalk, continuous with the cocoon, is secreted through the genital opening and fastened to the substratum; as the worm creeps away, the cocoon is drawn out of the atrium and left supported by its stalk. Within the cocoon the zygotes develop into embryos which engulf the yolk cells and use their substance as food during further development. After several days or a few weeks, depending on external conditions, the cocoon ruptures, and small juvenile worms emerge. Except for their smaller size and the absence of a reproductive system, which develops later, these juveniles resemble the adults in most respects.

Although complete male and female systems are thus present in each individual, conditions which are not well understood apparently prevent selffertilization in most cases. Only a few species of fresh-water planarians are known to produce fertile eggs without copulation; in some of these the eggs undoubtedly develop parthenogenetically, but the possibility remains that in others the eggs may be fertilized by spermatozoa from the same worm.

Regeneration. As may be demonstrated by a variety of experiments, many species of planarians have great powers of regeneration. The regenerative process , by which even a small piece of the animal may form a perfect individual, involves healing of the wound surfaces and formation of a small amount of new tissue at these regions, followed by the same processes encountered in the growth of a new individual after fission. Totipotent or formative cells are apparently instrumental in regeneration; these cells have been interpreted as undifferentiated cells of the mesenchyme which move into an injured area and by repeated divisions produce the tissues required for repair.

2.3.2 *Class 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.*

Order Heterocotylea (Monogenea.)

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 another 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 Trema-toda, 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.

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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 8,9) 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.

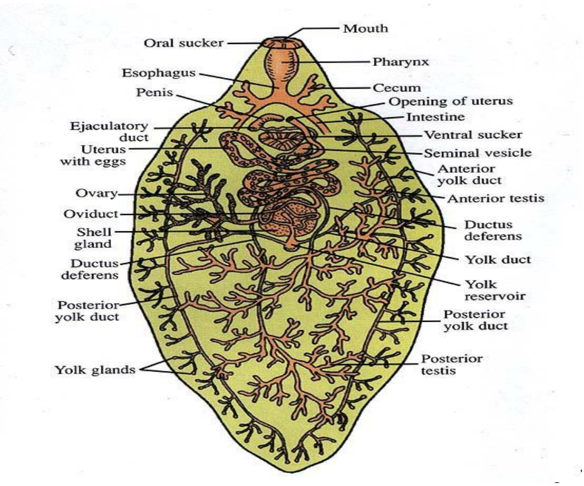


Fig. 8 *Fasciola*, whole mount

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, whilethe well-known Bucephalus larva of *Gasterostomum* is a cercaria with a forked tail.

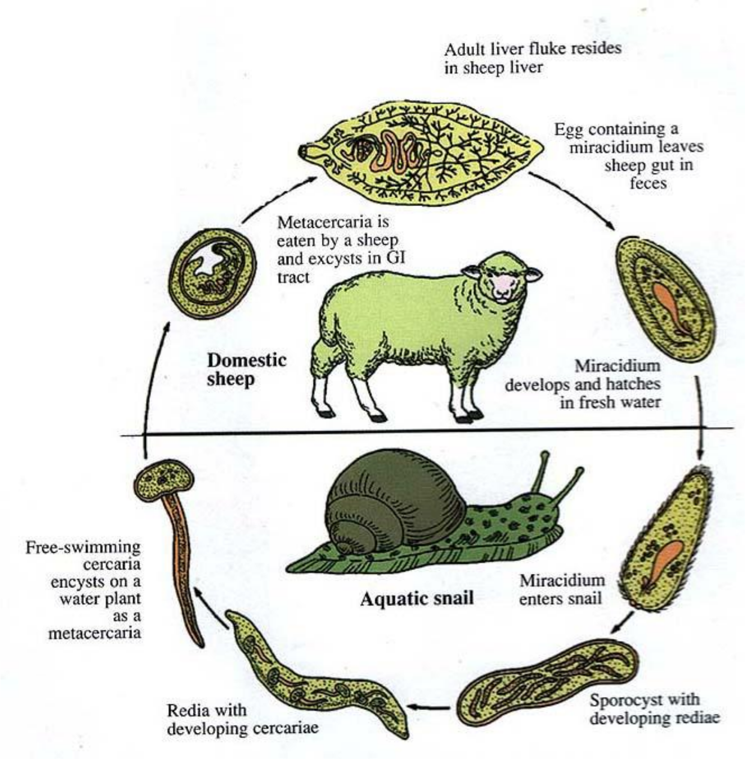


Fig. 9 *Fasciola*, sheep liver fluke, life circle

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.

2.3.3 *Class 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.

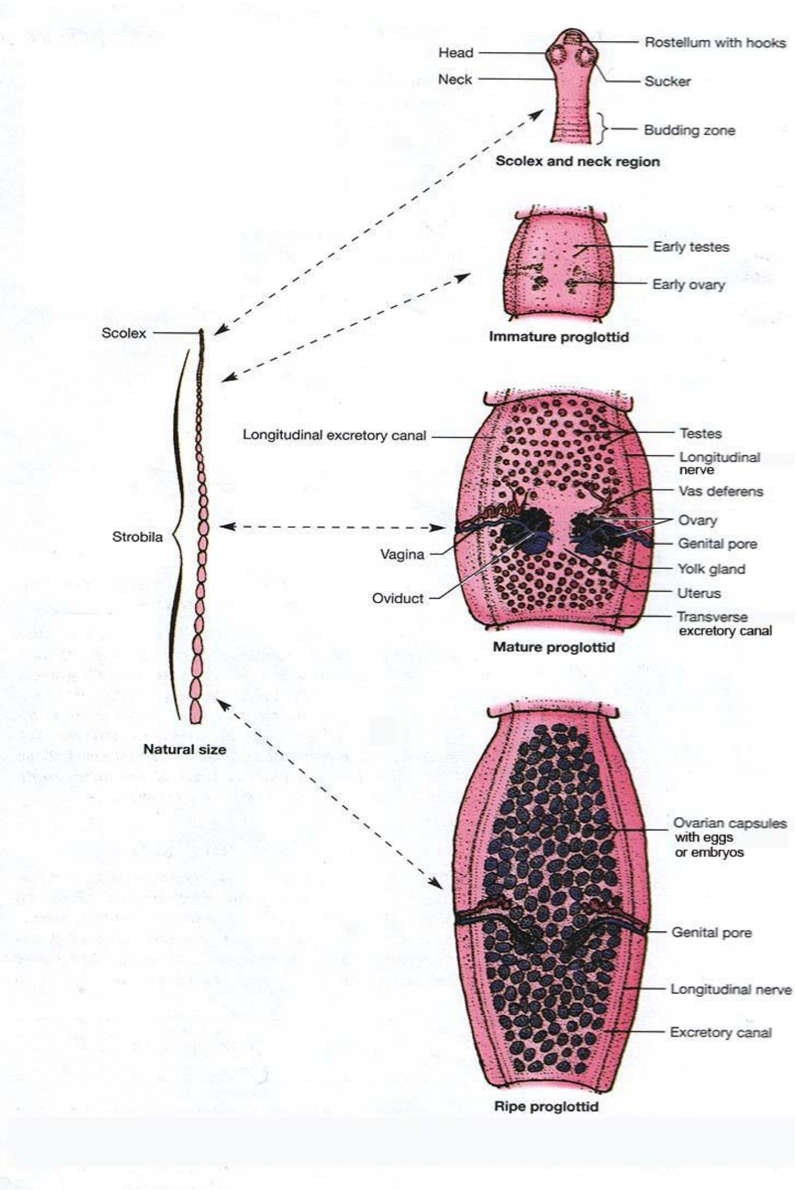


Fig. 10 *Dipylidium* (Cestoda), representative section of body

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.

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 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.

2.4 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 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. In these ganglia emerge a dorsal, ventral and several lateral nerves which length of the body. Cross connexions between these nerves occur along, he length of the body. Anteriorly from the nerve ring run six nerves to the mill.

Excretory systems. 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.

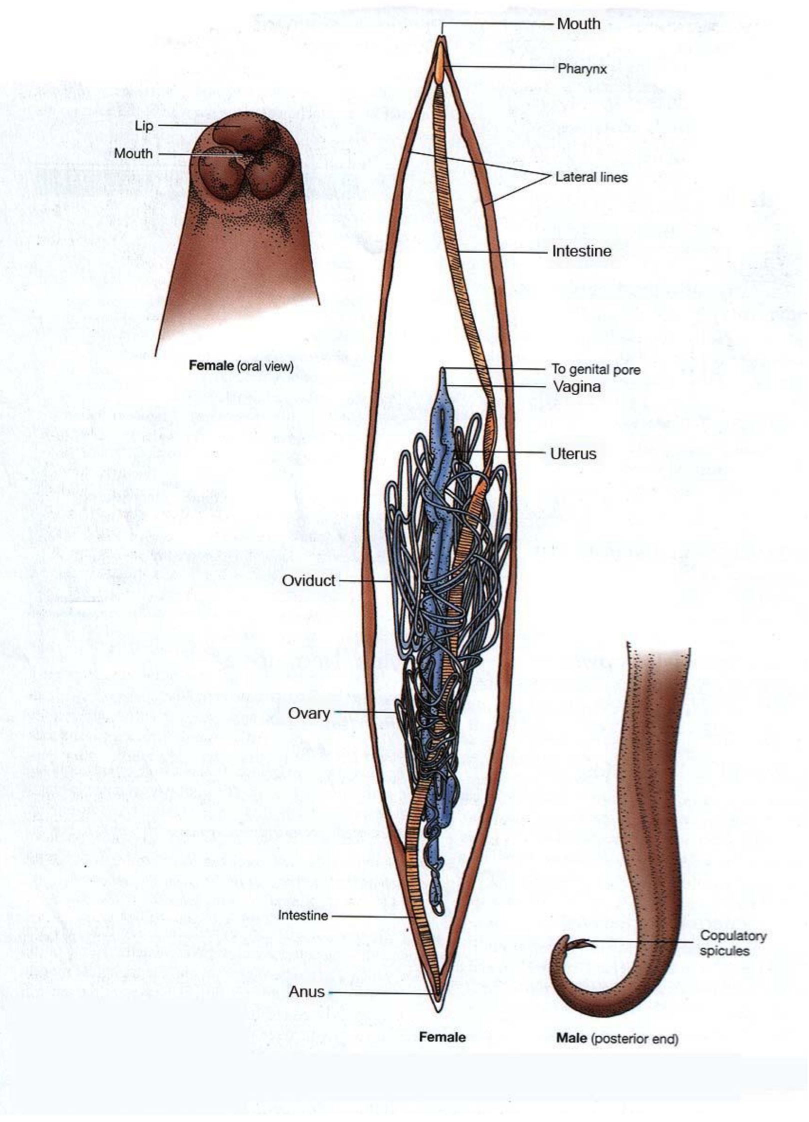


Fig. 11 *Ascaris sp*., internal anatomy

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.

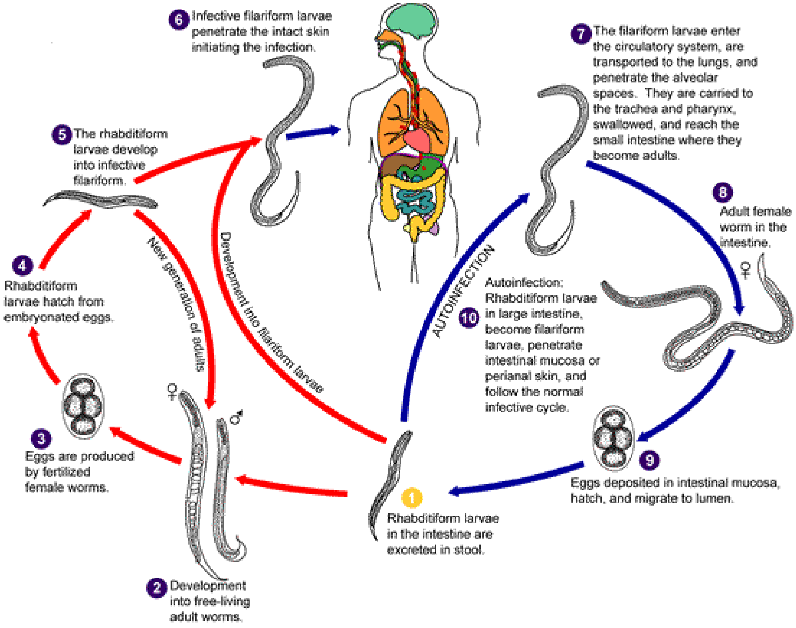


Fig.12 Life cycle *Ascaris lumbricoides*

(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.

2.5. 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 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 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 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 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 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.

2.5.1 *Class 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. 13) 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.

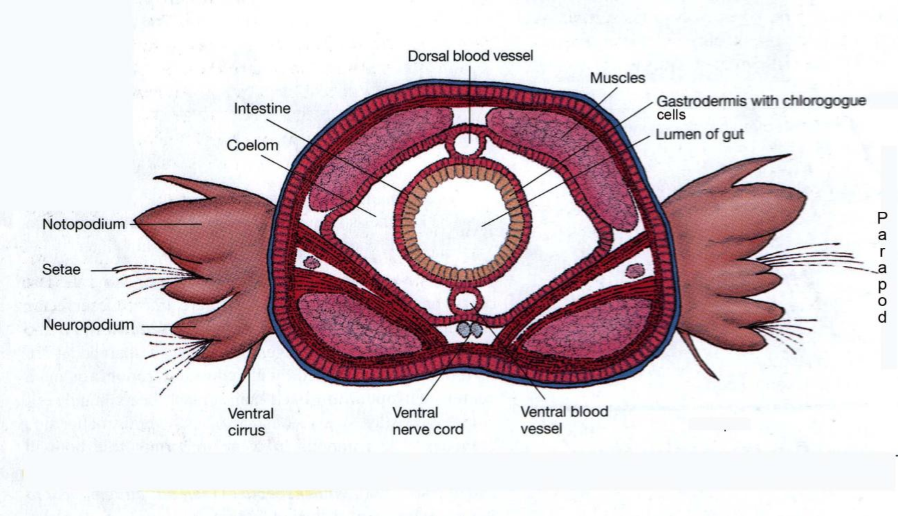


Fig. 13 Polychaeta, internal anatomy

Nervous system. The chief feature of the nervous system 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 system. 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.*

2.5.2 *Class 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.

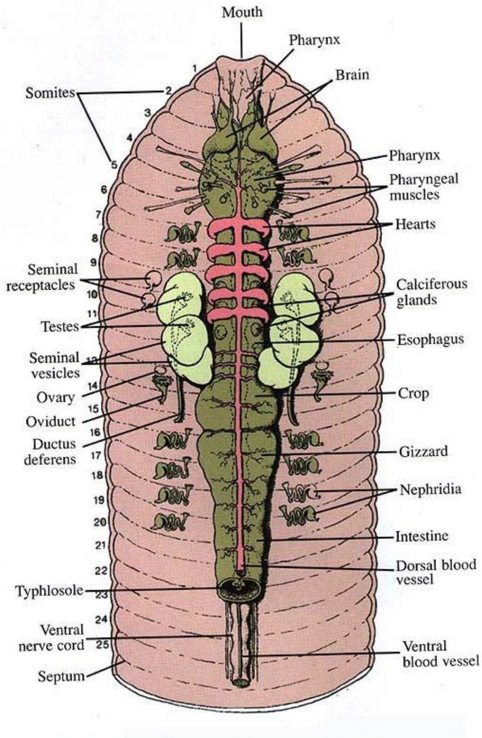
Certain main features of the reproductive system are the salient characters of the group. Its members are, without exception, hermaphrodite, and with a single possible exception cross-fertilization only is possible. The restriction of the gonads to a few segments occurs also in some sabellids umong the 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.

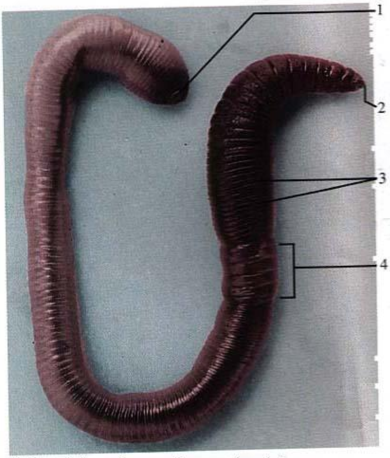
I 'or the purposes of the elementary student it is probably best to recognize that the Oligochaeta contain two well-marked ecological types, the 'earth-worm', a larger burrowing terrestrial form, and the aquatic oligochaete which In much smaller and simpler in structure. It is probable that the former 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. 14) 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.*



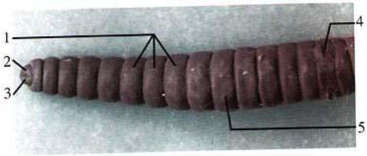
A diagram of the anterior end of the earthworm, *Lumbricus*



A dorsal view of an earthworm, *Lumbricus*

Lumbricus.

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



The anterior end of an earthworm, *Lumbricus*

Lumbricus.

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

Fig. 14 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.

2.5.3 *Class 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.

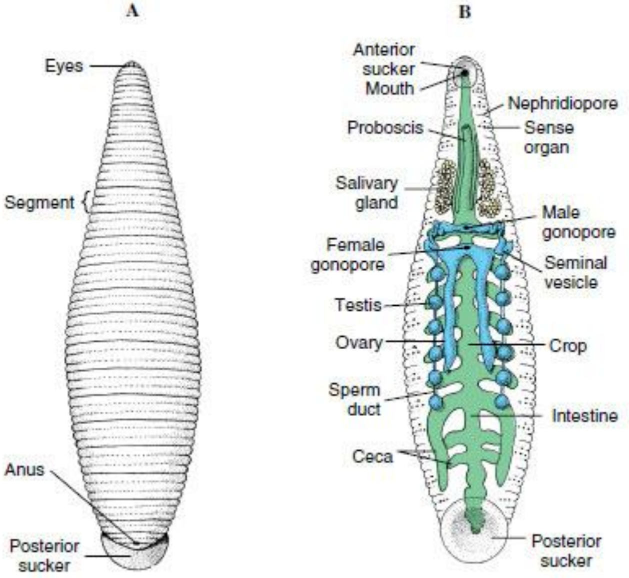


Fig.15 Structure of a leech, *Placobdella*. A, External appearance, dorsal view. B, Internal structure, ventral view.

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.

2.6 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 spirochaetes 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 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, 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 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 *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 13-18.

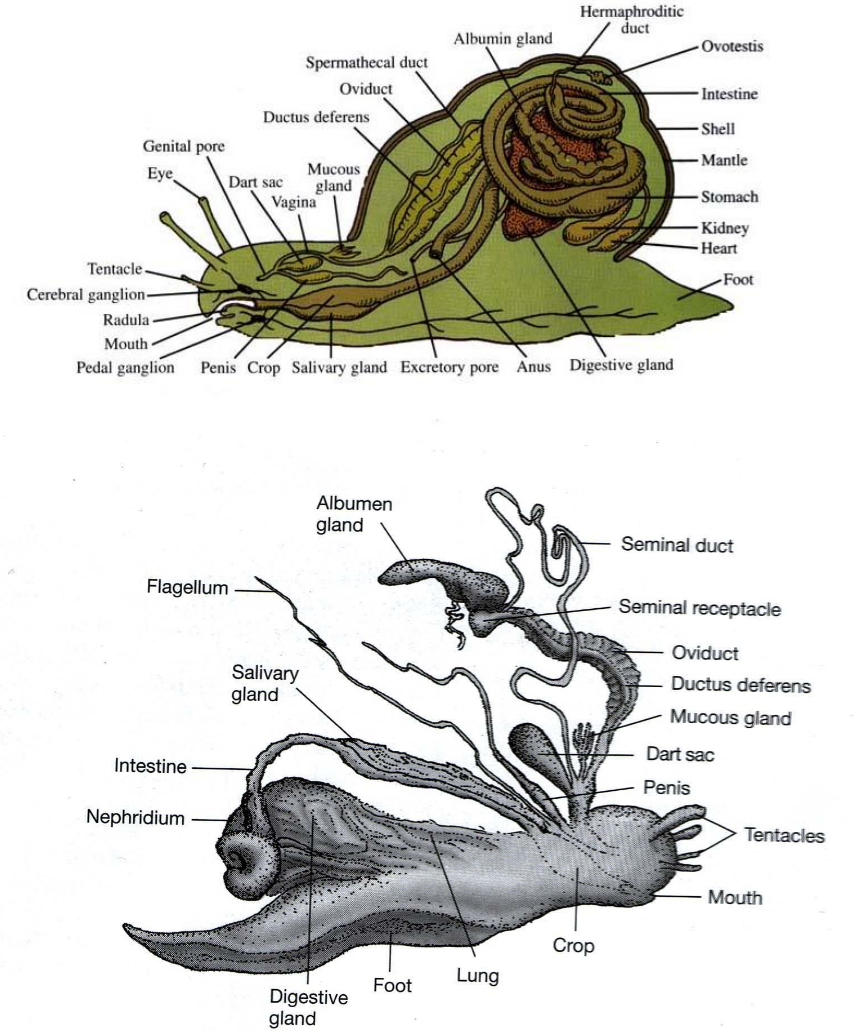


Fig. 16 *Helix* (the garden snail), internal organs

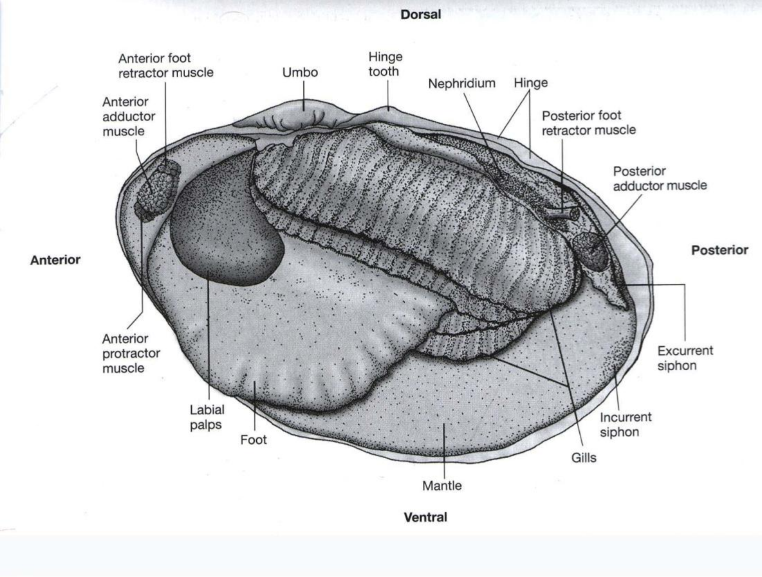


Fig. 17 Freshwater mussel, partly dissected, lateral view

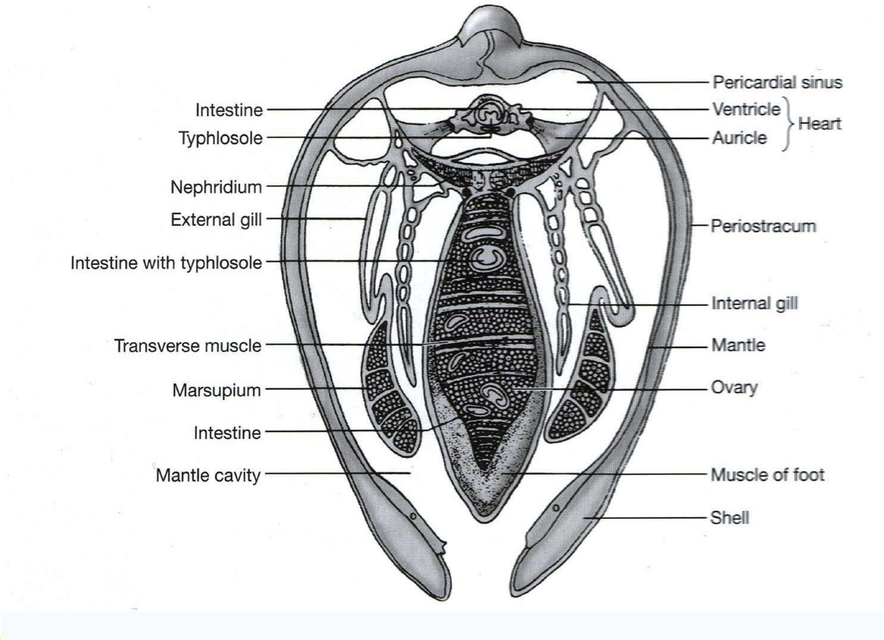


Fig. 18 Freshwater mussel, cross section trough heart region

2.7 PHYLUM ARTHROPODA

2.7.1 *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 much 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.* Moreover, 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.

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 Copepoda, 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 19.

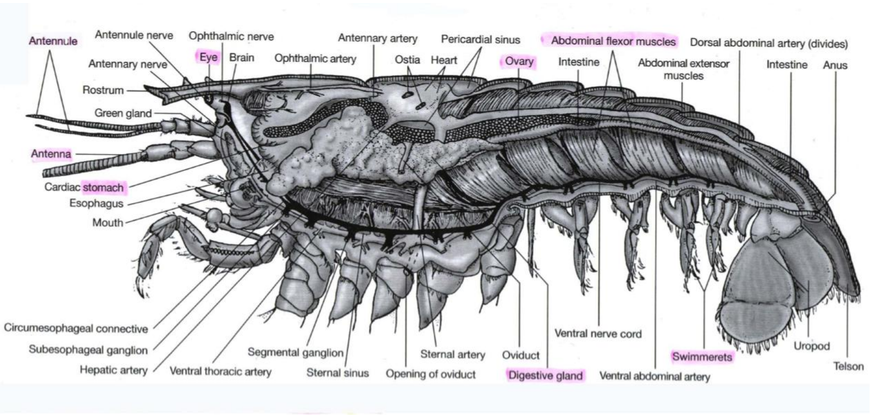


Fig. 19 Crayfish, internal anatomy, female

Class Chelicerata

Anatomy features of Chelicerata are presented at Fig. 18.

2.7.2 *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

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.

General Structure. The body is conspicuously divided into the three regions typical of insects: the head, the thorax, and the abdomen. The abdomen shows eight well-defined segments, with portions of at least three additional posterior somites. There are, as in other insects, three thoracic segments, the prothorax, mesothorax, and metathorax, each bearing a pair of legs. The number of segments in the head is problematical, but there is clearen vidence of at least four somites. The body is completely enclosed by the exoskeleton, which is firm in some regions but thinner and more flexible at the joints. Unlike the skeletons of many crustaceans, that of the locust is not hardened by depositions of calcium carbonate; it is composed of scleroproteins and chitin, covered at the surface by a thin waxy layer. As in other arthropods, an approaching molt is preceded by secretion of a new skeleton beneath the old one, through activities of the epidermal cells.

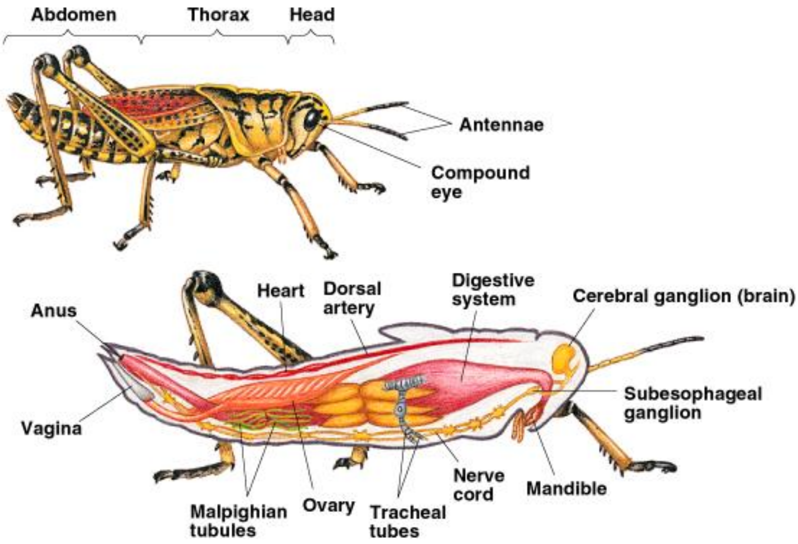


Fig.20 *Tettigonioidea* internal anatomy

The head bears a pair of large compound eyes and three small simple eyes, or ocelli. A single pair of antennae is present, bearing a great many sense organs. The antennae may be considered true segmental appendages that have been modified as sense organs, whereas the eyes and ocelli are primarily sensory structures and not appendages. The so-called "mouth parts" of the locust include segmental appendages as well as structures arising as median, unpaired outgrowths of the head. The true appendages are a pair of mandiblates, or chewing jaw; a pair of maxillae, jointed , leaf-like structures modified to aid in the manipulation of food; and a single lower lip, the labium, which is derived during development by the fusion of a pair of second maxillae. The mouth parts which are not segmental appendages are the labrum, or upper lip, formed as a down growth from the anterior surface of the head, and the hypopharynx, a median projection from the floor of the mouth which acts more or less as a tongue. Possessing mandibles and other mouth parts adapted for chewing, the locust is spoken of as a mandibulate in sect. As we shall see, in other insects the same fund a mental mouth parts may be modified for sucking, for piercing and sucking. and for lapping : however , the primitive insects are believed to have been mandibulate.

Each of the three thoracic segments bears a pair of jointed append ages, the legs. These are all similar in structure, but the posterior or metathoracic legs are highly developed and speciallized for leaping. At the distal end of each leg, a small pad and a pair of hooks provide grasping organs by which the insect obtains a firm hold upon vegetation. Two pairs of wings are at tached to the dorsolateral surface's of the mesothoracie and metathoracie segments, as in most other insects. In the locust the anterior wings are usually heavy and tough and function as protective covers for the delicate, membranous metathoracic wings. In the lubber locusts both pairs of wings are greatly reduced, with a corresponding decrease in the power of flight. The wings of insects are composed mainly of exoskeleton, with a very small amount of cellular material between the upper and lower skeletal layers. They are stiffened and supported by thickened structures, called "veins," between which the wing is thin and membranous. The veins also mark the pathways of channels through which blood circulates.

The abdomen lacks segmental appendages, and none appears in this region during development in the locust; in certain other insect s there are traces of vestigial abdominal appendages in the embryonic stages, and these persist to adulthood in some small, wingless, primitive insects. In the female locust a large ovipositor is present at the posterior end of the abdomen, surrounding the external opening of the female reproductive system. In the male an eversible penis marks the opening of the genital duct, just ventral to the anal opening at the tip of the abdomen.

External openings of the respiratory system appear as the paired spiracles; one lies on each side of every thoracic segment and each of the first eight abdominal segments. In life, the spiracles are opened and closed rhythmically with the breathing movements of the body. The so-called tympanic membranes, which are the external parts of the auditory organs, are conspicuous structures like eardrums on the dorsolateral portions of the first abdominal segment of the locust.

Structures and Functions Related to Metabolism. The internal anatomy is much the same in all species of locusts. The digestive system develops by specific modifications, extremely specialized in some insects, of an originally simple tube running from mouth to anus. Only the midregion of this tube, as in the crayfish, is lined by tissues derived from embryonic endoderm. The anterior and posterior regions arc lined by inward extensions of the epidermis and are covered by cuticle, which is shed as the animal molts. The buccal cavity, enclosed by the mouth parts described above, receives the ducts from the salivary glands lying in the thorax. From the buccal cavity a short esophagus leads dorsally, widening to produce a thinwalled crop which extends into the thorax. The crop tapers posteriorly and joins the stomach. The junction between crop and stomach is marked by six pairs of glandular outgrowths of the digestive tract known as gastric caeca; these caeca secrete a juice containing digestive enzymes. Posterior to the stomach lies the intestine, which has a narrow region, the "colon", followed by an expanded rectum leading to the anus. The division between stomach and intestine is marked by the zone of attachment of the Malpighian tubules, which are excretory organs.

In feeding, the animal bites off pieces of grass and other vegetation with its mandibles, using the labrum and labium as upper and lower lips, and the palps of the maxillae and labium as tactile and gustatory organs. The salivary secretion, emptied into the buccal cavity, serves as a lubricant in swallowing and as a digestive fluid acting upon food stored in the crop. Digestion may occur to some extent in the crop, but the cavity of the' stomach is the principal digestive region. Absorption of products of digestion into the circulating blood occurs in the stomach and the anterior part of the intestine, and assimilation follows the diffusion of these transported nutrients into the cells of the body.

As in the crayfish, the contribution of the embryonic coelom to the definitive body cavities of the locust is problematical. The spaces between muscles and surrounding the viscera are hemocoels and do not, on the whole, represent a modified coelom. In the adult locust this space is largely occupied by an irregular mass of storage tissue termed the fat body. Such fat bodies make up most of the body bulk in insect larvae storing up food reserves in advance of metamorphosis.

Leading from the spiracles on the thoracic and abdominal segments are the air tubes, or tracheae, which form the respiratory system. The tracheae unite and branch in a complex manner and expand into conspicuous reservoirs, or air sacs, in the abdominal region. The fine end branches of the tracheae, the tracheoles, ramify within all the tissues of the body and permit the direct delivery of atmospheric oxygen to the fluid s surrounding the cells. Air must first enter the body through the spiracles, a fact which makes it possible to kill insects by clogging these openings with dust or films of oil and soapsuds. Oxygen enters the cells of the insect from the intercellular fluid and is used, as in other animals, in cellular metabolism. The tracheal type of respiratory mechanism is found only among the higher arthropods and their relatives, the Onychophora. The fact that many insects are capable of rapid and sustained metabolic activities, as in prolonged periods of flight, is an indication that the tracheal system has been developed to a high point of efficiency.

Malpighian tubules are the chief excretory organs of insects, functioning to re move nitrogenous wastes of metabolism from the blood and eliminate them from the body. Each tubule, of which there may be dozens or hundreds, is composed of large cells surrounding a tubular lumen. The tubule is closed at its distal end, but the proximal end communicates with the lumen of the intestine.

It is generally spirally wound about by several strands of muscle fibers. The tubules lie in the hemocoel , bathed by blood, from which the cells extract wastes, chiefly in the form of salts of uric acid. These salts are passed through the wall of the tubule into the lumen and move downward, in solution, toward the intestine. Cells in the more proximal portions of the tubule extract water and certain inorganic constituents from this "urine," resulting in the precipitation of uric acid as crystals or concretions in the lumen of the tubule. By gentle muscular pulsations of the tubule, the precipitated mass, in the form of a paste, is emptied into the lumen of the hind-gut. Here more water is extracted, and the wastes are eliminated from the body with the feces. This excretory mechanism may be interpreted as an adaptation for the conservation of water, by eliminating wastes with the smallest possible loss of water.

The development of the tracheal system has relieved the blood of a function which in most other animals is of major importance, that of distributing respiratory gases. Consequently, it is not surprising to find that the circulatory system is not extensively developed, and that the flow of blood is relatively sluggish. The heart of the locust is a slender, pulsatile tube extending along the dorsal midline of the abdomen. In each segment throughout its length, the heart is provided with a pair of valved openings, or ostia. The heart is supported from the dorsolateral body wall on each side by fan-shaped groups of alary muscles and lies in a division of the hemocoel termed the pericardial sinus. This space is separated from the perivisceral hemocoel by a perforated membrane, the dorsal diaphragm. Blood enters the heart from the pericardial sinus through the ostia and is driven forward, into the thorax and head, through the aorta, which terminates near the brain. From the head, blood flows posteriorly through the hemocoelic spaces, bathing the tissues, until it again reaches the abdomen, passes through the dorsal diaphragm, and re-enters the pericardial sinus and the heart. There is a variety of colorless, amoeboid cells in the blood of insects, but nothing comparable to the erythrocytes of vertebrates; the blood contains no pigments involved in the transport of oxygen.

The Nervous System and Responsiveness. The nervous system of the locust is arranged according to the typical arthropod plan, as described for the crayfish. There is a compound ganglionic mass in the head, termed the "brain" or supraesophageal ganglion; a pair of circumesophageal connectives; a subesophageal ganglion; and a ventral chain of paired, segmental ganglia with their connectives and radiating nerves. The brain lies in the head between the compound eyes. Although it is obviously a compound structure produced by fusion of segmental ganglia, the exact number of such ganglia included cannot be determined. Large optic nerves pass into the brain from the compound eyes, smaller nerves from the ocelli , the antennae, and the labrum. Jn addition, small nerves extend ventrally to the frontal ganglion, from which the visceral or sympathetic nerve leads to the anterior part of the digestive tract. The circumesophageal connectives pass around the digestive tract and join the subesophageol ganglion. This also has a compound origin, apparently being formed during development by the coalescence of three pairs of segmental ganglia. From the subesophageal ganglion nerves radiate to the mandibles, the maxillae, and the labium. The thorax contains three paired ganglia, corresponding to the three thoracic somites. But the posterior ganglion is comparatively large, and its nerves are distributed in a way that indicates its formation by fusion of the third thoracic and first abdominal ganglia. There are five ganglionic masses in the abdomen, which again represent fusions, particularly at the posterior end of the nerve cord. The adult locust, therefore , has fewer ganglia than somites, but in the embryo there is a ganglion for each somite, as in the less highly specialized arthropods.

Like the majority of other insects, locusts are well equipped with sense organs . Small receptors for tactile stimuli are widely distributed over the surface of the body, and they are concentrated in especially sensitive areas, such as the antennae, the cerci at the tip of the abdomen, some of the mouth parts , and the distal segments of the legs. Olfactory stimuli also affect the basal parts of the antennae. Gustatory stimuli are perceived by taste organs on the mouth parts of the locust. The ocelli are sensitive to light but are probably incapable of forming images.

In the locust, the tympanic membranes are assumed to be auditory organs, more because of their structure than from any experimental evidence. Each consists of a membrane, against the inner side of which lie structures connected with nerves. Individual locusts react to, and so presumably "hear," the rattling sound produced by the wings of other locusts in flight. Comparable flight sounds are characteristic of many other insects; the buzz of a fly and the telltale whine of a mosquito are of this nature. The flight sounds of mosquitoes appear to be important in mating; recordings of the sounds emitted by females in flight have been shown to attract males in considerable numbers. The auditory organs of mosquitoes are located on the antennae.

The Reproductive System, Reproduction, and Development. In the account of external features the differences between male and female locusts have been described. Such differences in external characteristics are reflected in the internal details of the reproductive systems. In the male there are two testes, which lie as a saddle-shaped mass dorsal to the intestine. The tubules leading from the testes pass ventrolaterally and unite into right and left ductus deferentes (vasa deferentia), which join at the midline beneath the intestine to form a single ejaculatory duct traversing the penis. Accessory glands, which open into the anterior end of the ejaculatory duct , secrete a fluid apparently necessary to aid the transfer of spermatozoa from male to female at copulation. In the female there are two ovaries, lying in a position corresponding to that of the testes in the male. Each ovary is composed of large numbers of tubular ovarioles in which the ova are formed. The ovarioles have a common anterior origin in the ovarial ligament , and all the ovarioles of each side unite posteriorly to form an oviduct. Passing ventrally like the ductus deferentes of the male, the two oviducts join beneath the intestine into a median tube, the vagina, which opens externally between the valves of the ovipositor. A small, tubular appendage of the vagina, the seminal receptacle, receives and stores spermatozoa transferred by the male at copulation. At the time of oviposition, eggs pass singly down the oviducts and through the vagina; as they move past the opening of the seminal receptacle, they are penetrated by spermatozoa from the stored supply and so leave the vagina as zygotes. The female deposits these zygotes, called "eggs," in masses of several dozen , placing them in the soil in holes dug beneath the surface by thrusting movements of the abdomen and ovipositor. In temperate climates most species of locusts lay their eggs during late summer and autumn. The eggs undergo a period of dormancy, or diapause, and resume development only after they have been subjected to low temperature. Thus, the young do not normally hatch until the following spring. At hatching, the young locust , or nymph, resembles the adult, although the head is relatively larger and the wings are very small. The final size and normal adult proportions are reached through a series of molts.

Insect Life Cycles and Metamorphosis. The life cycles characteristic of different insects range from very simple to extremely complex. Insects that on other evidence are considered among the most primitive in existence show what is probably the ancestral type of development. Eggs hatch to produce young which are exactly like the adults, except that they are smaller and are incapable of sexual reproduction. Increase in size and development of sexual maturity occur during a series of successive molts. Such a simple life cycle, which does not include metamorphosis (change of form), is spoken of as ametabolous.

A different type of life cycle is characteristic of many insects such as locusts, which are not so primitive but are of rather generalized form. The young emerging from the eggshell is like a miniature adult in most respects, but its proportions are different, and the wings are relatively undeveloped. This immature individual is termed a nymph, which, like the young locust, gradually develops wings and attains adult proportions through a series of molts. This type of cycle, involving a gradual metamorphosis, is spoken of as paurometabolous.

Somewhat different from the paurometabolous forms arc those insects whose eggs are laid in water and develop into aquatic nymphs, or naiads. These immature forms are strikingly different from the adult and usually possess accessory structures, such as tracheal gills, related to their aquatic habitat. During its aquatic life the naiad increases in size by repeated molts; at maturity it crawls out of the water and in a final molt becomes the winged adult. This cycle includes a partial metamorphosis and is termed hemimetabolous.

The most highly evolved insects, belonging to what may be considered the most successful modern orders, have the most complex life cycles. The young emerge from the eggs as larvae, which are completely different from the adult in structure, in habitat relations, and very often in food habits and feeding mechanisms. The larva, primarily a feeding stage, stores up reserves of energy in its fat body and other tissues in the form of fats and glycogen. After passing through a defi'nite number of stages, each ending with a molt and an ; increase in size, the larva transforms into a resting stage, the pupa. At the conclusion of the molt marking the transition from larva to pupa, the general outlines of the adult body form are laid down and are often visible externally. The pupal stage may be brief, or it may last for several months. During this period the insect does not feed, and nothing enters or leaves the body except water vapor and respiratory gases. The pupa lives at the expense of reserves laid down during the larval stages, and after a longer or shorter period of quiescence, the organs of the adult begin to form. These structures are synthesized from stored reserves and from materials that become available as the special organs and tissues of the larva disintegrate. Eventually, the pupal skin splits, and the adult which has been formed within it emerges. This adult often has very small but perfect wings, which must immediately be inflated to full size and allowed to harden before they can be used. One of the first acts of the adult is the ejection from the anus of a mass of nitrogenous wastes, representing excreta which have accumulated during the period of pupal life. The life cycle just described, consisting of embryonic, larval, pupal, and adult stages and including complete metamorphosis, is of the holometabolous type.

2.7.3 *Class Arachnida.*

The great majority of chelicerates, some 60,000 species are members of the class Arachnida. In contrast to merostomes, arachnids are terrestrial. They are widely distributed, most living in vegetation, in leaf mold, and beneath bark, logs, and stones. Contributing to the great succes of arachnids as land animals has been the evolution of terrestrial gas exchange organs; a waxy epicuticle, which reduces evaporative water loss; and relatively insoluble nitrogenous waste products, which reduce excretory water loss.

The class is divided into 13 orders, 7 of which contain the most common and familiar species of temperate regions. Scorpions (order Scorpionida) are large arachnids with big chelate pedipalps and a long, segmented abdomen terminating in a sting. Paired eyes are mounted on tubercles in the middle of the carapace and two to five additional pairs of eyes may be present along the anterior lateral margins. Scorpions are secretive, largely nocturnal animals of the tropics and semitropics. In the United States thev are common only in the Gulf and southwestern states. Scorpions are ancient arachnids, known from the Silurian, and probably were among the first terrestrial arthropods.

Spiders (order Araneae) compose the largest of the achnid orders. About 32,000 species have been described, and they occur in far greater numbers than most people are aware of. An ungrazed meadow, for example, may support as many as 2,250,000 spiders per acre. The abdomen is unsegmented and connected to the cephalothorax by a narrow waist. The pedipalps are small and leglike. Usually eight eyes are arranged in two rows of four each across the front of the carapace.

Pseudoscorpions (order Pseudoscorpionida) are only a few millimeters in length and are common inhabitants of leaf mold in both tropical and temperate regions. These tiny arachnids have large pedipalps like scorpions, but the segmented abdomen is short and lacks a terminal sting.

Harvestmen (order Opiliones), also known as daddy longlegs, are distinguished from other arachnids by their very long legs and segmented abdomen broadly joined to the cephalothorax. A tubercle on the center of the carapace bears a single pair of eyes. The members of this order are common arachnids in both temperate and tropical regions.

The **mites** and **ticks** belong to three different orders and are sometimes collectively called the acari. The acari is the second largest and most diverse group of arachnids, and some acarologists believe that the 30,000 known species probably represent less than half of the total number in the orders. Most of the undescribed species will probably become extinct with the destruction of tropical rain forests and other habitats and will never be known.

Mites are found in all sorts of terrestrial microhabitats, and are especially abundant in leaf mold. They are the only arachnids that have reinvaded aquatic habitats, giving rise to species adapted for living in the sea and fresh water. Many species feed on human food products and on crop plants and are parasitic on humans and domesticated animals. As a consequence, mites are of great economic importance.

Mites are usually less than a millimeter in length, and their adaptive diversity may in part be attributed to their small size, which has enabled them to exploit many types of microhabitats. The abdomen of mites and ticks is unsegmented and broadly fused with the cephalothorax. The entire body is thus covered dorsally by a single skeletal piece . The pedipalps are small and usually leglike.

Of the seven orders of arachnids we have introduced, scorpions—with their long, segmented abdomen— exhibit the greatest degree of external metamerism; mites and ticks, the least. Silk is a fibroin protein in which a small number of certain repeating amino acids make up a major part of the protein polymer. Silk is produced by pseudoscorpions, spiders, certain mites, and some insects, such as the caterpillars of moths. However, of all these arthropods, spiders make the greatest use of silk.

Spider silk has about the same strength as nylon but can be stretched almost twice as much as nylon. The silk glands of spiders are located in the abdomen and open through conical spinnerets at the end of the abdomen each spinneret bearing numerous spigots. A particular species may possess from two to six afferent kinds of silk glands. The duct from each gland, of which there may be a large number belonging to any one type, opens at the end of one spigot. Silk hardens during the process of being drawn out, usually as a result of the spider moving away from the attached end of e line. The liquid silk changes from a water-soluble to a lid form as a result of changes in the molecular configuration and bonding.

Spiders utilize silk in many ways, but contrary to ropular notion, only some spiders use silk to construct webs for trapping prey. Silk is used to build nests, which ire used as retreats, for reproduction, or for overwintering; in all spiders the eggs are encased within a silken egg case.

Most spiders lay down a dragline behind them, anchoring it at intervals to the substratum. The dragline is demonstrated when a spider appears suspended in midair after being brushed off clothing or some other object. The dragline not only functions as a safety line for the spider but also is an important means of communication between members of the species. A spider may determine chemically from another dragline whether its owner is male or female and whether it is immature or adult.

Small spiders and newly hatched spiders use the silk as a means of dispersal. They climb to favorable take-oft points, tilt the abdomen upward, and release a strand of silk. When air currents produce sufficient pull, the spider lets go and sails out to whatever new habitat and fate the wind will take it. The wide distribution of many species of spiders is undoubtedly correlated with this ballooning phenomenon.

Aside from certain species of mites (spider mites), pseudoscorpions are the only other arachnids that make use of silk. The silk glands of pseudoscorpions open onto the chelicerae and are used in construction of nests or retreats.

Feeding. Most arachnids are predatory animals, and other arthropods are their usual prey. Arachnids detect prey by means of specialized sensory hairs, slit sense organs, and, in some species, eyes. Slit sense organs, many of which are located in the vicinity of joints, respond to stimuli, such as vibrations, which cause changes in the tension of the exoskeleton. As an aid to dispatching prey, certain arachnids have independently evolved poison glands. The poison glands of scorpions are located in the terminal sting at the end of the abdomen. Their prey is caught with the large pedipalps and then stabbed by the poison barb with a forward thrust of the abdomen. Although the sting of scorpions may be very painful, few species have a poison dangerous to human beings.

Pseudoscorpions catch prey with their large chelate pedipalps, which have a poison gland opening at the end of one or both fingers. Spiders have a poison gland associated with each chelicera, which consists of a terminal fang that folds down against a larger basal piece. The gland opens bv a duct through the end of the fang, and the poison is injected through a bite.

The poison of a very small number of spiders Is dangerous to humans. Few tarantulas have a toxic bite, despite popular mythology. The members of the cosmopolitan genus *Latrodectus*, which includes the black widows, are perhaps the most notorious of the poisonous species.

The method of prey catching can be a basis for dividing spiders into two adaptive groups: cursorial and web building spiders. Cursorial spiders include the tarantulas, crab spiders, wolf spiders, jumping spiders, and others. They spin silk draglines, nests, and cocoons, but they do not use silk to capture prey. Rather, the prey is stalked, pounced upon, and bitten. Cursorial spiders generally have heavier legs and more highly developed eyes than do web builders.

Web-building spiders construct various types of webs to trap prey, the web type—e.g., orb, horizontal sheet, funnel, irregular mesh—being characteristic of particular families. The first webs are believed to have been the irregular draglines laid down around the retreat of some primitive species.

Among living spiders, the orb web is perhaps the most familiar type and the one most commonly associated with spiders.

Web-building spiders are aerialists and have rather slender legs for climbing about the silken lines. Eyesight is poor, but web builders are able to detect and interpret the various vibrations of the web with great facility. Web vibrations inform an orb weaver, for example, about the size of the struggling prey and whether it is securely caught. The spider approaches the prey and gives it a fatal bite, sometimes swathing it in silk before or after the bite.

Arachnids are unusual in that most begin digestion of their prey outside their bodies. While the tissues are torn by the chelicerae, enzymes are secreted by the midgut, passed forward through the foregut, and poured out of the mouth into the prey. The partly digested tissues are then sucked in by the pumping action of a pan of the foregut. Digestion is completed and absorption occurs in the midgut, which may be greatly evaginated and ramify into various pans of the body.

There are some exceptions to the predatory feeding habit of most arachnids. Harvestmen are omnivores and feed upon vegetable material and dead animal remaias in addition to live invertebrates. The greatest diversity in feeding is displayed by mites. Some are predatory, others are herbivorous and have mouthparts adapted for piercing the cells of plants and sucking out the contents. Certain species of spider mites can be very destructive to plant Some mites feed on plant products, decomposing plant material, and fungi. Members of several groups of mites are scavengers, llair and feather mites spend their lives on the skin of mammals and birds, where they feed upon sloughed skin cells, gland secretions, and fragments of hair and feathers.

A number of groups of acari are parasitic for all or part of their life cycle. Ticks are bloodsucking ectoparasites of reptiles, birds, and mammals, and the chelicerae are adapted for penetrating and anchoring into the skin of the host. A tick feeds during each instar and usually prior tc egg laying. Some ticks stay on the same host, but many, including the common dog tick, drop off following feeding engorgement. They molt and then seek another host. Although there can be direct pathogenic responses in humans to the bite of ticks, transmission of diseases, such as Rocky Mountain spotted fever, tularemia, and Lyme disease, are usually more serious concerns.

Chiggers, or redbugs, are ectoparasites on terrestrial vertebrates during the posthatching instar. In feeding, the minute mite secretes enzymes that produce a deep well from which it sucks out the digested contents. The mite secretions produce an irritating reaction resembling a mosquito bite but lasting much longer. Following feeding the chigger falls off the host and is predaceous as an adult.

There are numerous species of mites that attack the skin of birds and mammals and can cause severe dermatitis in their hosts. For example, the itch mite Sarcoptes scabiei produces scabies in various mammals, including humans, The mites spend their entire lives on the host, and the female tunnels through the host's skin, depositing eggs in the burrows.

Gas Exchange. Large arachnids have book lungs for gas exchange; small arachnids have trachea. Thus scorpions have book lungs, four pairs with slitlike openings on the ventral surface of the anterior abdominal segments. Pseudoscorpions, harvestmen, and mites possess tracheae. Primitive spiders, such as the large tarantulas, have two pairs of book lungs, but most spiders have one pair of book lungs and one pair of tracheae. Some very small spiders have only tracheae. The openings of both types of gas exchange organs are located on the ventral side of the abdomen. Heart and blood vessels are best developed in those arachnids that possess book lungs.

Reproduction and Development. The paired gonads are located in the abdomen, and in both sexes a median gonopore opens onto die anterior ventral surface.

Indirect transfer of spermatophores appears to be a primitive condition in arachnids and perhaps represents the early arthropod solution to the problem of sperm transmission on land. Spermatophore transfer in scorpions is preceded by a "courtship" dance, during which tne large pedipalps of the male are locked with those of the female. In the course of the dance, the male Jeposits a spermatophore on the ground and then maneuvers the female so that it is taken up into her gonopore.

Pseudoscorpions also utilize spermatophores and exhibit a wide range of behavioral modifications that increase the likelihood of the female finding and picking up the spermatophore. Our knowledge of reproductive behavior in mites is still relatively poor. Some species transfer sperm indirectly by spermatophores; most transfer sperm directly, utilizing a penis. Sperm transfer is also direct in harvestmen.

The process of sperm transfer in spiders is remarkable and is paralleled in few other animals. The copulatory organs of the male are the ends of the pedipalps, which resemble a pair of boxing gloves. Prior to mating, the male spins a tiny web on which a droplet of semen is secreted. The two pedipalps are then dipped into the droplet until the semen is taken up within the reservoir of the palpal organ. The male now seeks a female.

The male is frequently smaller than the female, and the predatory nature of spiders makes it important for the male to ensure that the female does not mistake him for potential prey. Complex precopulatory behavior patterns have evolved utilizing visual, tactile, and chemical signals. Significantly, there is considerable difference in the preovulatory behavior of cursorial and web-building spiders, for the sensory cues that are important in prey catching are also the important ones in sex recognition and mating. Thus web vibrations are an important means by which the male signals a female in web-building spiders, and visual signals, such as posturing by the male, are important in many species of airsorial spiders.

Following various forms of precopulatory contact by the male, the palpal organ is locked onto the chitinous plate containing the female reproductive openings, and the ejaculatory process is inserted into the seminal receptacles. Sperm is transferred from one palp at a time. This unusual mode of sperm transfer in spiders probably had its origins in transfer by spermatophore. The male of some arachnid ancestral to the spiders may have used the palp to place a spermatophore into die female gonopore. In fact, there are certain living arachnids be longing to a small tropical and semitropical order in which the male uses his pedipalp to push the spermatophores into the gonopores of the female.

Harvestmen and free-living mites deposit their fertilized eggs in soil, in leaf mold, or beneath bark, but spiders place their eggs in silk cases, which are then usually left beneath stones, bark, or leaf mold or are attached to vegetation.

Brooding is common. Wolf spiders and fisher spiders carry their egg cases about with them. After hatching, wolf spiderlings are carried on the back of their mother. The eggs of scorpions develop within the body of the female. Following birth, the young are carried about on the female's back. Pseudoscorpions brood their eggs within a membranous sac overlying the gonopore.

Most arachnids have direct development, and theyoung at hatching or at birth resemble the adult form.

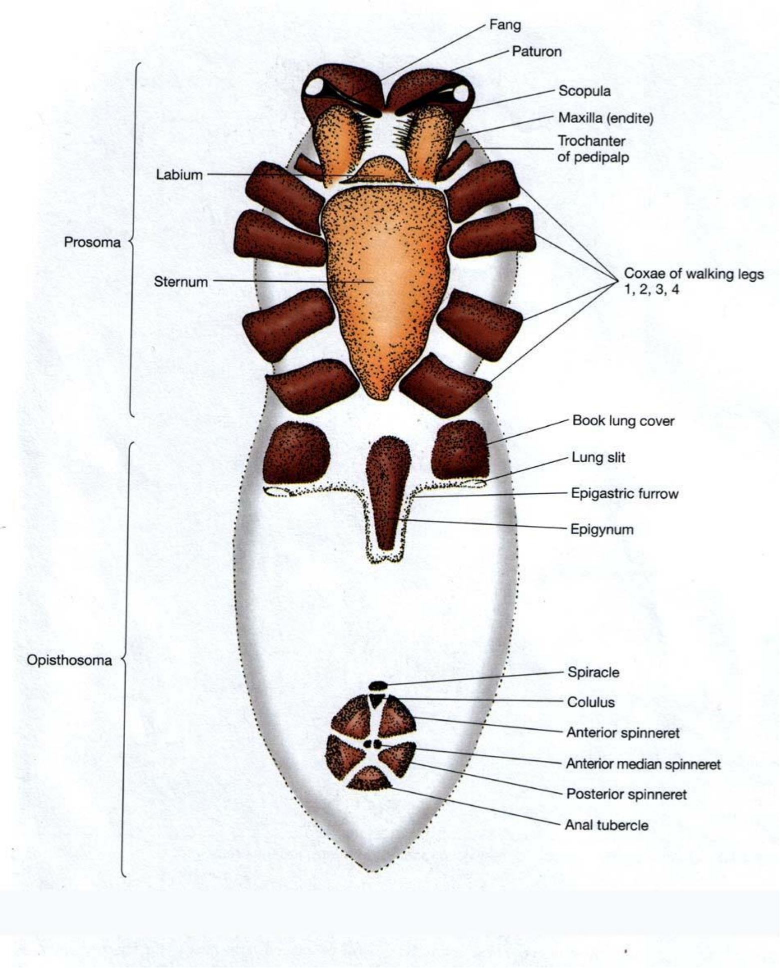


Fig. 21. Spider, internal anatomy

2.8. THE PHYLUM ECHINODERMATA

The Echinodermata are non-segmented, triploblastic forms showing a fivepart radial symmetry masking a fundamental bilaterality. Coelomic cavities are extensive , forming in the embryo as outpocketings of the primitive digestive tract. There is an endoskeleton composed of calcareous plates or spicules. A unique characteristic of echinoderms is the presence of a system of fluidfilled internal ducts, the so-called water-vascular system. In most echinoderms the blood-vascular system is so reduced as to be non-functional and very inconspicuous , and there are no traces of nephridial excretory organs.

The phylum may be divided into the subphylum Pelmatozoa, containing primitively stalked or attached forms, and the subphylum Eleutherozoa, including free-moving , unattached echinoderms. The Pelmatozoa, once very numerous , are now represented by only one modern class, the class Crinoidea, sea lilies and feather stars. Several other pelmatozoan classes, among them the Cystoidea and Blastoidea, contain extinct stalked forms known only as fossils. The Eleutherozoa contain the remaining four classes of echinoderms : the class Asteroidea, sea stars or starfishes; the class Ophiuroidea, brittle stars, serpent stars, and basket stars; the class Echinoidea, sea urchins and sand dollars; and the class Holothuroidea, sea cucumbers.

Echinoderms are typically slow-moving, bottom-dwelling animals. They are exclusively marine, and there is no evidence from the fossil record that members of the phylum have ever become established in fresh water. Because of their radial symmetry, the echinoderms were at one time classed with the coelenterates as "zoophytes." Further study, however, showed that echinoderms are animals with an extensive coelom , which coelenterates lack , and that even their radial symmetry differs markedly from th coelenterate type. A significant feature of the life cycle of echinoderms is the occurrence of a segmented , bilaterally symmetrical larva, which develops by a complicated metamorphosis into the non-metameric, radially symmetrical adult. The structure of the adult presents many puzzling characteristics when compa red with such familar types as mollusks, annelids, or chordates. If we interpret the evolut on of echinoderms from the events in the life cycle of a typical representative such as the starfish , however , their morphological peculiarities become intelligible. The indications are that the remote ancestors of echinoderm s were free-swimming, bilaterally symmetrical forms with segmentally arranged coelomic pouches. At some time long antedating the beginning of our fossil record , the ancestral forms apparently took up an attached way of life, and the secondary radial symmetry developed through some millions of years in connection with this fixed existence. The anatomical peculiarities of modern echinoderms, even of those that are no longer attached forms, are evidently related to these ancient adaptive changes. Embryo logical and serological evidence indicates that echinoderms are more closely related to the chordate evolutionary stem than to any other large group of animals.

From an economic standpoin , echinoderms are unimportant , except for starfishes, which sometimes destroy whole beds of shellfish. One of the few echinoderms used as food by man is a sea cucumber, gathered , dried , and sold as beche-de-mer, or trepang . Neither do echinoderms serve as food for many other animals; codfishes and related forms feed on starfishes, and the dugong , an aquatic mammal , eats sea cucumbers. On the whole, however, the spiny surfaces and the preponderance of skeletal material in the bodies of echinoderms have helped them avoid destruction by predatory enemies.

2.8.1 *The Class Asteroidea*

The body consists of a central disk and five radiating arms or rays. The upper or aboral surface is covered with short spines, which are skeletal structures; the surface between the spines bears thin-walled, finger like projections called papulae or dermal branchiae, functioning in respiratory exchange and in excretion. Clustered at the bases of the spines and among the papulae are minute , pincer-like structures, the pedicellariae, which function in keeping the surface free of foreign matter. In such a sluggish, slowmoving animal as the starfish, this is a very important function indeed. In addition to finely divided particles of silt and detritus, the ocean is full of minute larvae of such forms as sponges, coelenterates, encrusting ectoprocts, and barnacles, seeking surfaces on which to settle and produce their characteristic growths. Starfishes are never encumbered by such growths, probably because of the activities of pedicellariae in removing them and keeping the papulae free of obstructions.

At one side of the disk, between the bases of two of the arms, lies a porous plate, the madreporite or sieve plate; through its minute openings the internal water-vascular system communicates with the exterior. For convenience in reference , the two arms between which the madreporite lies are termed the bivium; the other three are the trivium. On the oral surface the mouth occupies the center of the disk, surrounded by an oral membrane or peristome. Radiating from the mouth along the arms are five ambulacral grooves, from which project numerous locomotor organs called tube feet. At the outer end of each ambulacral groove lies a small, reddish eye spot below a short sensory tentacle.

The starfish creeps slowly along the bottom by coordinated stepping movements of its tube feet. Although it seems inflexible, and its arms may be broken off by rough handling, the animal can bend and twist in a great variety of ways. For example, when a starfish is turned upside-down, it rights itself by twisting the arms until some of the tube feet become attached to the bottom. Using these attached points for traction and for reference , the animal slowly turns itself back to the normal position. Changes in shape and attitude are brought about by the action of muscles which interconnect the calcareous plates of the body wall. Normal locomotion, however, is effected primarily by the tube feet, which in Asterias terminate in suckers and can be firmly attached to a hard substrate. Under certain conditions these suckers seem to be necessary, as when the animal clings to a wharf pile or stone or walks up the glass wall of an aquarium. But the animal can walk perfectly well without attaching its suckers, over a loose, sandy bottom or upon a greased surface, and the tube feet of many species of starfishes lack suckers altogether. The mechanism by which the tube feet operate will be explained in connection with the ambulacral system of which they are a part.

There is nothing like a head or an anterior end in the starfish; the animal can travel in any direction, and no part appears to assume the lead more frequently than others. Once the animal has started in a particular direction, however , the tube feet of all the arms step in the direction taken by those of the leading arm. The starfish thus progresses steadily until it encounters something to change the course of locomotion. A comparable coordination is shown in the righting reaction, when all the arms and their tube feet move in an integrated fashion as soon as a firm hold has been secured by some of the tube feet of one of the arms.

Structures and Functions Related to Metabolism and Responsiveness. The food of the starfish consists principally of mollusks, such as clams, oysters, scallops, and snails. In feeding, the animal assumes a characteristic "humped" position over the prey; the more proximal tube feet are attached by their suckers to the outer surface of the shell , and the more distal ones commonly appear to secure a hold upon the substrate. In some manner still imperfectly understood, the starfish soon causes the valves of the mollusk to gape open. An older theory , without any demonstrable basis, held that the starfish secretes some noxious substance which finds its way between the valves, paralyzing the adductor muscles of the bivalve. Experimental work has shown that by powerful, sustained contraction of its muscles (probably those connecting the ambulacral ossicles), the starfish can exert enough force through its firmly attached tube feet to pull the valves apart, at least a few millimeters. It is clear that such a small gape can be produced , without damaging the adductor muscles of the clam, by the application of a degree of force which the starfish is capable of bringing to bear on the valves. When even a small opening has been produced, the stomach of the starfish is everted through the mouth and inserted into the mantle cavity of the bivalve. It has been established by experiment that the folds of the everted stomach can pass through a surprisingly small orifice. Having penetrated the outer defenses of the clam, the starfish releases into the mantle cavity digestive enzymes so powerful that they gradually bring about the complete disintegration of the soft parts of the mollusk. The products of this extracellular digestion are conducted by powerful Aagellary currents into the digestive cavity of the starfish. After completing its meal of the body of the mollusk, the starfish with draws its stomach, closes its mouth , and crawls away, leaving behind only the empty shell of its prey. By this peculiar method of feeding, Asterias forbesi and A. vulgaris destroy large numbers of shellfish. One investigator reported that during a 6-day period, a single starfish devoured 56 clams, some as long as an arm of the starfish itself. Starfishes also feed on dead or injured animals other than shellfish and even attack other starfishes and sea urchins. In the absence of food, a starfish can survive starvation for several months.

The central portion of the digestive system occupies the short oral-aboral axis of the starfish. The mouth opens into the cardiac stomach, the folded walls of which take up much of the cavity of the disk. Above the cardiac stomach, and communicating broadly with it, lies the small, flattened pyloric stomach, which leads upward into the short intestine. The intestine opens to the exterior at the anus, which is somewhat eccentrically placed on the aboral surface of the disk. The intestine bears a pair of branched, tubular organs, the rectal caeca, which lie between the roof of the pyloric stomach and the aboral body wall. These may be considered as homologous with the "water lungs" of holothurians, but their functions are unknown.

In addition to these central parts, the digestive tract also includes branched diverticula which extend into the cavities of the arms. These are the five pairs of pyloric caeca; one pair lies in each arm, and a single duct leads from each pair into the pyloric stomach. The pyloric caeca consist of series of sac-like evaginations, extending along a central, tube-like canal. The walls of the sacs contain numerous glandular cells which are the apparent source of powerful digestive enzymes. Interspersed among the glandular elements are other cells, which function in the absorption of products of digestion and in the storage of reserves. All these cells together constitute a single-layered epithelium, like the lining of the intestine in a vertebrate. In the pyloric caeca, however, the cells bear long flagella which maintain a steady circulation of fluids within the cavities of the organs. Specifically directed currents sweep digestive juices toward the cardiac stomach, where the enzymes are principally active, and carry the products of digestion into the caeca for absorption.

The coelomic fluid contained in the extensive coelomic body cavitie sperforms the functions of a circulatory system in the starfish. This colorless fluid contains many phagocytic, amoeboid cells and, very much like the hemocoelic blood of an arthropod , bathes the tissues of the body. In the starfish, however, there are no functional blood vessels, and there is no pulsatile heart. Circulation of the coelomic fluid is brought about by the action of flagella borne on the cells of the peritoneal lining. This singlelayered epithelium covers both the inner surface of the body wall and the outer surfaces of all the organs. It is composed of cuboidal or flattened cells, each of which bears a single long flagellum. These flagella together maintain specific currents which prevent stagnation of the fluid and facilitate exchange of materials between the fluid and the tissues. Nutrients are passed into the coelomic fluid by the cells of the pyloric caeca, for transport to all other parts of the body; oxygen diffuses into the fluid through the thin-walled, finger-like papulae of the body wall and is carried in simple physical solution. Carbon dioxide and soluble nitrogenous excreta are transferred to the external sea water through the papulae , which thus function also as excretory organs. In general , it is clear that the circulating coelomic fluid performs the major functions which in most other animals are subserved by the circulating blood. This is particularly interesting , in view of the fact that, aside from small amounts of proteins and nutrients dissolved in it, the coelom i c fluid is almost identical with sea water in its composition. In fact, certain organs of the starfish, notably isolated pyloric caeca, will survive for several days in cool, aerated sea water.

The nervous system of the starfish is basically organized on the radial plan typical of other parts of the body. Its chief components are a circumoral nerve ring, surrounding the peristomial membrane; a series of five radial nerve cords, one in each arm, extending from the nerve ring; and a generally distributed subepidermal nerve plexus with connections into the radial cords. In addition to the conspicuous eye spots and sensory tentacles at the tip of each arm, receptors are scattered throughout the epidermal layer. The nerve rin and radial cords, superficially located, consist of thickened and specialized areas of the epidermal layer. They contain many neurons, arranged in sensory, association, and motor tracts. Aside from the circular and radial nerve cords, there are no true nerves in the starfish; nerve cell bodies are not restricted to the cords, and nerve fibers pass out from the cords more or less individually. The receptors that occur in the epidermis send afferent branches into the plexus layer, from which motor fibers run directly to muscles of the papulae, pedicellariae, and spines. Localized reflex activities of these structures are thus possible without the intervention of the "central" nervous system. More generalized responses involve afferent fiber tracts from the plexus into the radial cords, and complex efferent or motor pathways involving series of neurons that course from the cords to specific muscles of the body wall and tube feet. At the central end of each radial cord, the nerve ring contains a "motor center," a large group of nerve cell bodies which appear to be responsible for coordinating the activities of the tube feet in all the arms. In locomotion, the assumption by one arm of the "lead" position seems to involve a temporary dominance by the motor center of the leading arm over all the other motor centers. This condition is transitory, however, and the "lead" passes to other arms and their centers in turn.

The wall of the digestive tract contains a conspicuous nerve plexus layer, which undoubtedly has connections with visceral receptors and also with the muscle layers of the gut wall. The functions of this part of the nervous system have never been analyzed. Although the nervous system of the starfish presents many peculiarities , both structural and functional , the operation of this sytem is apparently fundamentally comparable with that of the nervous systems of other metazoans .

A unique feature of the anatomy of all echinoderms is the water-vascular system, or ambulacral system. Through the projecting tube feet, the ambulacral system of the starfish functions chiefly in locomotion and in adherence to the substrate, although it may contribute significantly to the process of respiratory exchange also. The madreporite, lying on the aboral surface of the disk, contains many small openings into a tube , the stone canal, which passes orally and joins a circular ring canal around the mouth. From the ring canal a radial canal extends to the tip of each arm, passing just above the radial nerve cord. At frequent intervals the radial canal gives rise to short lateral canals, each of which terminates in a tube foot. At its inner end each tube foot bears a muscular bulb , the ampulla; the stalk of the tube foot projects through the body wall , passing between the closely set skeletal plates. The system as a whole contains a fluid which , like the coelomic fluid, is practically identical with sea water. Circulation through the system is maintained by the action of flagella on the lining epithelium. The arrangement is such that the fluid contents of the system may pass freely into each tube foot through the lateral canal , and within the tube foot may flow back and forth between the stalk and the ampulla. Backflow from the tube foot into the lateral canal is prevented by a valve-like structure . The wall of the stalk contains longitudinal muscle fibers, and the terminal disk or sucker is provided with muscle fibers whose contraction raises the central portion of the disk to provide a vacuum for attachment to the substrate . The longitudinal muscles are basally attached in a radial fashion to the adjacent skeletal plates of the body wall. These so-called "postural muscles" provide for the pointing of the tube foot in any direction and thus allow directed locomotion. The complex interactions of the musculature are reflexly coordinated: contraction of the muscles of the ampulla forces fluid into the stalk , causing it to extend in a direction determined by the state of the postural muscles; the sucker is then placed on the substrate and attached by contraction of its special muscles. As the body moves forward, the sucker is released , and contraction of the longitudinal muscles of the stalk forces fluid back into the ampulla and brings about retraction of the stalk. The cycle is then repeated through a new stepping sequence. The integration of all these activities involves the coordinating functions of the central nervous system.

The skeletal system is of mesodermal origin and lies beneath the epidermis of the body wall. It is thus an endoskeleton, showing similarities to the skeleton of a vertebrate, rather than a cuticular exoskeleton of the type more common among invertebrate animals. The plasticity of the body , as shown in righting and other activities, is accounted for by the fact that the skeleton of the starfish is composed of many small plates, bound together by connective tissue and muscle fibers.

The Reproductive System, Reproduction, and Development. Starfishes are dioecious. The reproductive system consists of five pairs of gonads, either ovaries or testes, one pair lying in the coelomic cavity of each arm, lateral to the pyloric caeca. Each gonad is continuous with a short stalk which forms its duct and attaches it to the body wall. The ducts open to the outside at genital pores located deep in the angles between the bases of adjacent arms. Gametes are discharged into the sea, where fertilization occurs. The eggs, and thus the zygotes, contain very little yolk , and cleavage is total and equal. Development proceeds rapidly through blastula and gastrula stages, the gastrul a soon transforming into a bilateral, ciliated larva , the bipinnaria. This larva has a complete digestive tract and feeds on unicellular algae as it swims about near the surface. Its free life may last for several weeks. Finally, the larva sinks to the bottom , becomes temporarily attached, and undergoes a radical metamorphosis into a tiny starfish. In the course of this metamorphosis, the organization of the larva changes completely. The left side of the larva becomes the oral surface of the adult ; the old openings of the digestive tract disappear, to be replaced by a new mouth and anus in shifted locations. The paired coclomic sacs of the larva are transformed into specific adult structures: one of the pouches establishes an external connection, the future madreporite, and develops into the watervascular system; other pouches give rise to various parts of the spacious perivisceral coelom of the adult. It is perhaps significant, in interpreting the evolution of echinoderms, that the change from bilaterality to radial symmetry in the starfish occurs during a temporarily attached phase of the life cycle.

Regeneration. Starfishes are often found in nature with one or more arms smaller than the rest. The small arms are in the process of regeneration. Under experimental conditions as many as four arms may be removed without causing the death of the animal, and all four can eventually be replaced by regeneration. When all five arms are removed, regeneration can still occur if the individual is fed after the formation of the new arms has begun. Although an isolated arm of Asterias can survive for several weeks , it will eventually die, since it cannot restore the disk and other arms. In some other starfishes, however, even a single isolated arm has the capacity to regenerate into a complete individual. Under rough or damaging treatment a starfish may shed an injured or restrained arm by a process termed autotomy. A break of this kind always occurs at the base of the arm, where the body cavity is restricted as it passes from disk to arm. The resultant opening in the side of the disk is immediately closed by the contraction of the adjacent body-wall musculature, and regenerative changes then begin.

2.8.2 *The Class Ophiuroidea*

Members of this class, the so-called serpent stars, brittle stars, and basket stars, arc recognizable by the relatively large and conspicuous disk and the slender, mobile arms. In basket stars the arms branch repeatedly and terminate in many small , flexible tendrils. In ophiuroids the organs of the digestive tract do not extend into the arms; the volume of the skeleton is relatively much greater than in the asteroids, and the arms are largely occupied by jointed skeletal units sometimes called "vertebrae." Brittle stars are so named because of the fragility of their arms, which lash about actively and break off very easily. In spite of their peculiarities, the ophiuroids are clearly echinoderms. The life cycle includes a bilateral, ciliated radial appendages of the digestive system as in the starfish. Aside from these special features, however, the internal organization is similar to that of the asteroids: the ambulacral and reproductive systems, as well as the nervous system, are generally comparable in arrangement to those of the starfish, although the circulatory system is better developed.

In Arbacia the sexes are separate; the five gonads are radially arranged, and each sheds its sexual products into the sea water through one of the pores located on the genital plates. Fertilization is thus external, and development proceeds rapidly to a bilateral, ciliated larval stage, the echinopluteus. This larva is comparable to the bipinnaria of the starfish, although in the presence of several pairs of long arms, each supported by an internal spine, it resembles even more closely the ophiopluteus of the ophiuroids. After several weeks of pelagic life, feeding on diatoms and microscopic algae, the pluteus sinks to the bottom and undergoes metamorphosis into a miniature sea urchin.

Other Echinoidea. In Arbacia the body is circular in its lateral outline, and the 20 rows of plates are arranged in a regular pattern. This regularity of skeletal arrangement has not always been characteristic of sea urchins, as shown by some fossil forms in which the plates are irregularly arranged. Among the modern echinoids the shape and symmetry of the body are highly variable. In Clypeaster the mouth is in the center of the oral surface, but the anus lies in an interambulacral area on the lateral margin of the somewhat flattened body; thus the animal is actually bilaterally symmetrical. In the sand dollar, Echinarachnius parma , the organization is like that of the clypeasters, although the flattening of the body is more extreme. In the type represented by Spatangus, the mouth has shifted peripherally , or in an "anterior" direction, along the ambulacral area opposite the anus. The fossil record and the life cycles of these bllateral urchins indicate that they have descended from ancestors which were circular and radial like Arbacia. The existence of fossil forms with irregularly arranged plates suggests, in turn, that the Arbacia type, with 20 rows regularly arranged, arose from ancestors without this skeletal regularity.

2.8.3 *The Class Holothuroidea*

The Sea Cucumber. Thyone briareus, a sea cucumber common along the Atlantic coast from Cape Cod southward, is an example of the holothurian type of echinoderm. Fundamentall y, it is radially symmetrical, but the characteristic elongation of the body between oral and aboral ends, and certain other specializations, give it a bilateral and often worm-like appearance. The texture of the body is very different from that found in the starfish and sea urchin: the expanded Thyone is soft, like a bladder partly distended with fluid, and there is no skeleton except minute calcareous spicules embedded in the body wall and a few larger plates in the oral region. At one end is the mouth, surrounded by ten branched tentacles, and at the other is the anus. The tube feet are not in distinct rows but lie scattered all over the body, although internally they are connected with five radial ambulacral canals as in other echinoderms. The animal usually lies on one side, and this "ventral" surface has larger and more numerous tube feet than the "dorsal" or uppermost side. In addition, the distance from mouth to anus is greater along the ventral midline than along the dorsal; and to this extent Thyone presents a bilateral appearance, with dorsoventral as well as anteroposterior differentiation.

Thyone lives partly embedded in the ooze of muddy bottoms just below low-tide level, with its anterior and posterior ends exposed. The anterior end is directed diagonally upward, and the tentacles are free to move over the surface of the surrounding mud. If the animal is disturbed, the tentacles are withdrawn by inversion of the entire oral end of the body; excess water is discharged from the anus, and the body becomes tense and turgid. In feeding, the tentacles are moved about until well covered with silt from the bottom and are then thrust, one at a time, deep within the mouth and relieved of their burden as they arc again withdrawn. The animal "breathes" sea water, pumping it in and out through the anus. In locomotion, the organism move s by extending its tube feet, attaching their terminal suckers, and dragging itself along. By this means it can even walk up the glass side of an aquarium.

The digestive system begins as a small, muscular pharynx, surrounded by the tough, ring-like structure to which the tentacles are attached, and which can be retracted by the contraction of five stout muscles running to the body wall. The pharynx is followed by a short esophagus, a small muscular stomach, and a long, looped intestine. The intestine traverses the length of the coelomic cavity three times, supported along part of its course by dorsal and ventral mesenteries containing blood vessels. At its posterior end, the intestine enlarges to form the cloaca, which opens to the exterior at the anus. The cloaca bears a pair of branching, tubular structures, the "water lungs," which are filled with water drawn through the anus and pumped into them by cloacal contractions. Through the walls of these tubules respiratory exchange occurs between the water and the coelomic fluid, and the water is periodically expelled by contraction of the body wall.

Thyone shows peculiarities in other organ systems. The ambulacral system consists of the same parts found in the starfish and the sea urchin, arranged somewhat differently. The ampullae of the tube feet are scattered over the internal surface of the body wall but connect with five radial ambulacral canals. The stone canal springs from the ring canal about the pharynx and ends in an internal madreporite, which hangs free in the coelomic cavity and has no external openings. A so-called haemal system, very rudimentary in other echinoderms, is well developed in holothurians. In Thyone it is particularly conspicuous in connection with the digestive tract, to which branches of the haemal system run in the mesenteries. Although there is no heart or other propulsive organ, the haemal system contains a fluid which probably circulates and serves some of the functions of a blood-vascular system. As in other echinoderms, however, the coelomic fluid is most important in this respect. The reproductive system in holothurians is peculiar in that there is only one gonad, the duct of which opens externally in the dorsal interambulacral area between two of the tentacles. The animals are dioecious; gametes are shed into the sea, fertilization is external, and as in other echinoderms there is a bilateral , ciliated larval stage, called in this instance the auricularia.

If its lack of a skeleton is disregarded, a sea cucumber is like a sea urchin with its body elongated in the axis of radial symmetry, which extends from mouth to anus. Correlated with this elongation are the anteroposterior and dorsoventral differentiations and the appearance of a superficial bilateral symmetry.

2.8.4 *The Class Crinoidea*

Members of the class Crinoidea have branched arms and are often attached to the bottom by a stalk, which joins the aboral surface of the disk. This gives the animal a flower-like appearance and is responsible for the common name, "sea lily." Even the type represented by Antedon, the so-called feather star, which has no stalk and is not permanently attached, bears a tuft of aboral filaments by which it commonly clings to the substrate. In all crinoids, the oral surface is uppermost; the mouth occupies the center of the oral surface of the disk, surrounded by five highly branched arms. The anus also lies on the oral surface, near the mouth, at the tip of an anal papilla. Ciliated ambulacral grooves radiate from the mouth, traversing the disk and continuin g along the oral surfaces of the arms and their branches. Currents maintained in these grooves converge upon the mouth and carry into it the microscopic particulate matter which constitutes the food of the crinoids. Tube feet are present , but they lack ampullae and terminal suckers; they have tactile functions and serve also in respiratory exchange. As in holothurians, the water-vascular system of the adult crinoid has no external madreporite; there are multiple "water tubes" or stone canals which furnish communications between the ambulacral ring canal and the coelomic cavity. The life cycle of the crinoids is best known for the feather star.

It includes a barrel-shaped, ciliated larva which, though simplified, is comparable with the larvae of other echinoderms. After a free-swimming period, this larva becomes attached and undergoes metamorphosis into a juvenile form with a jointed stalk like that of the sea lilies. Eventually, the connection between the stalk and the disk is broken, and the animal becomes free-moving. This stalked phase in the life cycle of Antedon indicates that feather stars have evolved from ancestors attached throughout their adult life. The fossil record shows that stalked crinoids have had an extremely long evolutionary history, dating from the end of the Cambrian period. Different crinoid groups have flourished during successive geological eras; most of them were stalked forms, and by far the majority have become extinct. The modern crinoid fauna is dominated by the free-moving feather star type.

2.8 PHYLUM HEMICHORDATA

The Balanoglossida: Saccoglossus. Species of this genus, and of such other genera as Balanoglossus, Glossobalanus, etc., are marine, worm-like animals that usually live in shallow water and are found burrowing in muddy or sandy bottoms. Externally, three body regions are apparent: the proboscis, the collar, and the trunk.

The mouth is located ventrally, just beneath the proboscis and within the anterior border of the collar; the anus lies at the posterior tip of the trunk. The gill slits form a dorsolateral row of perforations on each side in the anterior region of the trunk, extending posteriorly for some distance. These perforations are passages from the cavity of the pharynx to the exterior. Near the middle of the trunk region, transverse ridges are produced by paired, glandular caeca which arise from the digestive tract.

The digestive system includes a buccal region within the collar, a pharyngeal region marked by the gill slits, and an intestine which bears the caeca and leads to the anus. As the animal burrows through sand or mud, the proboscis is thrust forward, and the silt from which food is extracted enters the mouth and pharynx.

Excess water passes outward through the dorsolateral gill slits, aerating the blood in vessels lining their walls. The ingested silt, concentrated in a ciliated groove in the ventral region of the pharynx, is conducted posteriorly through the intestine, where usable food materials are digested and absorbed.

Coelomic spaces are found within proboscis, collar, and trunk, being derived from three pairs of primary embryonic coelomic pouches. The circulatory system consists of a median dorsal and a median ventral longitudinal vessel, interconnected by small lateral branches in the pharyngeal region and posteriorly.

A so-called "heart" lies in the proboscis, but the blood is probably propelled chiefly by peristaltic contractions of the longitudinal vessels. A glomerulus, which has been considered an excretory organ, is connected with blood vessels in the proboscis.

The nervous system is composed of two principal nerve trunks formed as ectodermal thickenings in the median dorsal and median ventral regions of the trunk. These cords appear to represent specialized areas of a generally distributed subepidermal nerve net, or plexus layer.

The cords are connected by a ring-like epidermal thickening in the collar, and the dorsal trunk proceeds anteriorly through the collar before dipping downward to enter the proboscis. The resemblance of this nervous system to the central nervous system of the typical chordate is not outstanding, although the nature of the dorsal nerve trunk in the collar region is somewhat suggestive of the chordate nerve cord.

A structure called the stomochord is present in the posterior part of the proboscis, arising as an anterior extension from the dorsal wall of the buccal cavity. This small supporting clement is probably homologous with the chordate notochord, but it is limited in its extent and of a very primitive nature.

The sexes are separate in the balanoglossids; the gonads are sac-like structures arranged serially on each side in the region of the genital ridges. When mature, each gonad establishes an individual, externally opening genital pore. The small eggs are fertilized externally, and development proceeds in the sea water. A pelagic, ciliated larva, the tornaria, occurs as a developmental stage in the life cycles of some species, but not in Saccoglossus.

The tornaria is so similar to the dipleurula-type larva of echinoderms that it was originally described as the larva of some unidentified echinoderm. This similarity may be interpreted as indicating an evolutionary relationship between echinoderms and hemichords, a relationship which is suggested also on the basis of certain biochemical similarities.

The Pterobranchia: Cephalodiscus and Rhabdopleura. These are small marine forms with the typical hemichord body regions of proboscis, collar, and trunk, the internal anatomy is comparable with that of the balanoglossids. In correlation with their generally sedentary mode of life, the gut is U-shaped, the anus opening near the mouth. The proboscis is modified into two or many arms, or tentacles, which in Rhabdopleura are retractable into the secreted testw ithin which the animal lives.

Reproduction is both sexual and asexual, in Rhabdopleura new individuals are produced by budding from a horizontal stolon growing along the substrate. Individuals thus formed constitute a colony of zooids comparable with those of colonial coelenterates.

The fossil remains of the extinct graptolites, long considered as either coelenterates or ectoprocts, have in the light of recent studies been interpreted as showing many similarities to the sessile and enclosed pterobranchs.

Relationships of the Hemichordata. In the phyla Echinodermata, Chaetognatha, Hemichordata, and Chordata, the embryonic origin of the coelom is by the enterocoelous method, as in no other animal groups except the anomalous Brachiopoda.

This common embryological feature is considered to indicate that these four groups are related by a common ancestry. Evidence from serological studies shows that the proteins of chordates resemble those of echinoderms and hemichords more closely than those of any other invertebrate group.

Further, biochemical studies on substances termed phosphagens, important in the functions of muscular tissues, also reveal significant similarities between these three groups.

The tornaria larva is suggestive of an evolutionary relationship between echinoderms and hemichords, and the presence in hemichords of visceral clefts, the stomochord, and rudiments of a dorsal nerve cord suggests affinities with the chordates. On the whole, the evidence may logically be interpreted as supporting the concept of a common evolutionary line of enterocoelous, deuterostomous organisms, possibly resembling the dipleurula or tornaria, from which by successive radiations the ancestors of the modern enterococlous groups arose.

The hemichords would seem to have evolved from this ancestral line after the divergence of the ancient echinoderms and chaetognaths but before the rise of the true chordates. These evolutionary changes must have antedated the beginning of our fossil record and undoubtedly involved small forms lacking hard parts.

2.9 PHYLUM CHORDATA

Classification:

DIVISION ACRANIATA. Without a skulI, or cranium, and without vertebrae or appendages.

Subphylum Urochordata or **Tunicata**. Adults hardly recognizable as chordates. Larvae, known as "tadpoles," with a notochord in the tail, with gill slits, and with a dorsal, tubular central nervous system. During metamorphosis the notochord is lost, the gill slits are modified into a pharyngeal basket, and the nerve cord is reduced to a ganglionic mass. Tunicates, or sea squirts, and many others.

Subphylum Cephalochordata. With some resemblances to the tadpoles of tunicates, and also to fishes; with persistent notochord and gill slits, with a persistent dorsal, tubular nervous system, but without a skul or vertebrae. The amphioxus or lancelet, Branchiostoma (Amphioxus), and others.

DIVISION CRANIATA. With a skull, or cranium, and usually with vertebrae and paired appendages.

Subphylum Vertebrata. Identical with Craniata: only subphylum in this division.

SUPERCLASS PISCES. With gills, and usually with appendages, commonly represented by two pairs of fins suited for locomotion in water. The various types of fishes.

Class Agnatha. Without true jaws and without limbs. Extinct forms, the ostracoderms, a large group of primitive fishes bearing large scales. Existing forms, the lampreys and hagfishes, without such scales.

Class Placodermi. Armored fishes of specialized type, extinct, and not closely related to any existing forms.

Class Chondrichthyes. Shark-like fishes, with exposed gill slits.

Extinct forms with bony skeletons, existing forms with cartilaginous skeletons. Sharks, rays, skates, etc.

Class Osteichthyes. With bony skeletons, and with gill slits covered externally by an operculum. Include the lobe-finned fishes (mostly extinct), the numerous existing ray-finned fishes, and the lungfishes. Common marine and fresh-water fishes.

SUPERCLASS TETRAPODA.

With lungs, and usually with appendages which are commonly represented by two pairs of limbs suited for locomotion on land. The air-breathin vertebrates.

Class Amphibia. Semiterrestrial and aquatic forms; cold-blooded; skin usually soft and moist; respiratory exchange usually by gills in larva and by lungs and skin in adult. Typically with eggs laid and developing in water. Salamanders, frogs, toads, etc.

Class Reptilia. Terrestrial or secondarily aquatic forms, covered with scales or horny plates. Cold-blooded; lung-breathing; typically oviparous, some ovoviviparous. Turtles, lizards. snakes, alligators, etc.

Class Aves. Terrestrial forms, usually adapted for flight, covered with feathers. Warm-blooded, lung-breathing , oviparous. Birds

Class Mammalia. Terrestrial or secondarily aquatic forms, at least partially covered with hair. Warm-blooded, lung-breathing, with mammary glands. Mostly viviparous. Mammals.

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.

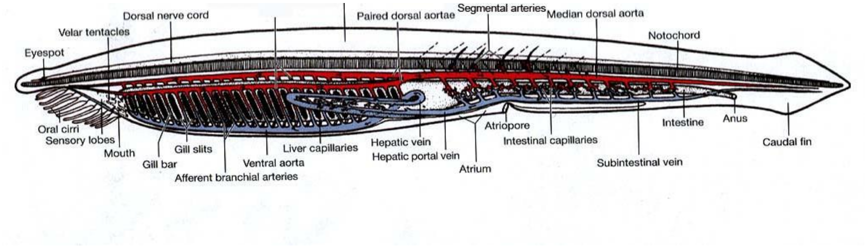


Fig. 22. Lancet, internal anatomy

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

2.10 SUBPHYLUM UROCHORDATA (TUNICATA)

These organisms constitute one of the three subphyla into which the phylum Chordata is divided. They are invertebrates, in that they lack vertebrae, but their characteristics are unmistakably those of the chordates. The subphylum Urochordata includes the classes Ascidiacea, Larvacea and Thaliacea, all of which are marine animals. Of these, the, Ascidiacea, or sea squirts, arc the best known; the Larvacea are an unusual type and the Thaliacca are the most highly specialized.

The Ascidiacea. The important features of the ascidians are the specializations of the adult for an attached mode of life and the apparent evolution of the group from free-moving ancestors. On the basis of superficial and functional characteristics, ascidians were long classified as mollusks; it was not until their life cycles became known, in 1866, that the chordate nature of the early developmental stages was recognized.

The sea squirt, Molgula manhattensis, is one of the species of tunicates most abundant along the Atlantic coast of North America. Molgula is found at tached to various submerged objects in shallow water, but it is most easily collected from the piling under wharves, where it is commonly associated with such other ascidians as Styela and Ciona. An expanded Molgula appears as a globular mass attached at one end and having two tubular processes, the siphons, extending from the other. If an undisturbed specimen is observed, a gentle current of water may be seen entering the longer of these siphons and flowing outward from the shorter one. As in pelecypod mollusks, the entire economy of the ascidian depends on these currents of water, which , again as in the mollusk, are maintained by internal ciliary activity. From the stream entering the incurrent siphon, the animal obtains its food by straining out minute organisms and particles of detritus; and the blood is aerated as the water passes through the modified gill slits. The feces and reproductive products are carried outward by the water as it flows through the atrium and the excurrent siphon.

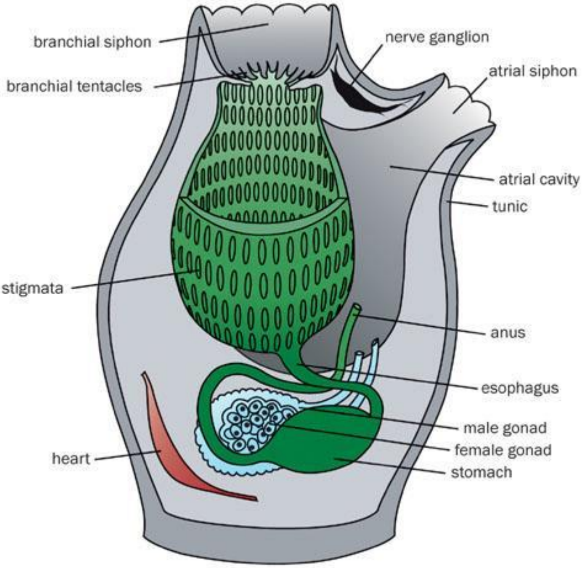


Fig.23 Ascidia internal anatomy

In any typical ascidian the entire body is covered by a membrane, thick in Molgula and Styela but thinner in Ciona, termed the test or tunic. This is firmly attached to the body only in the region of the siphons and can be removed without disturbing the internal parts of the animal. The tunic functions as a tough, elastic shell, although it contains the cells by which it is secreted, as well as blood spaces through which nutrients reach these cells. The principal constituent of the test is an organic compound which has been named tunicin;

this is very similar to cellulose, a compound common in plants but rarely produced by animal tissues. Removal of the test exposes the true outer surface of the body. Most of this surface is the socalled mantle, which encloses an extensive cavity, the atrium. The excurrent siphon is essentially a specialization of the mantle enclosing the median portion of the atrial cavity, from which lateral portions extend on each side beneath the mantle. Since the atrium is formed by the outgrowth of double flaps from the outer surface, it is lined by epidermal cells. The mantle consists of inner and outer epidermal layers, between which lie muscle fibers, connective tissue, and blood sinuses.

The opening of the incurrent siphon may be called the mouth, and the cavity within this siphon, the oral cavity. A circlet of tentacles marks the beginning of the pharynx, or branchial sac, which is relatively large and specialized for food collection and aeration of the blood. A digestive gland is also present, connected with the stomach by a duct. Water passes into the mouth, enters the branchialsac, and passes through the many small openings in its wall into the atrial cavity on either side, and thence to the excurrent siphon, from which it is discharged. The openings in the branchial sac hus function in the manner of the less numerous openings called gill slits in other chordates. As in hemichords, food is obtained by straining the nutrient material from water received through the mouth and discharged through lateral openings in the pharynx. In the tunicate the food particles are caught in mucus as the water leaves the pharynx and are conveyed by ciliary currents along a specialized path to the esophagus; at the same time the oxygen dissolved in this water diffuses into the blood within the vessels of the pharynx.

The circulatory system consists of a tubular heart, lying along the outercurvature of the stomach, with tubules extending from one end directly to the pharynx and mantle, and from the other end to the stomach and nearby organs and thence to the pharynx. There are no true blood vessels, the blood circulating through extensive tubular cavities which lack an endothelial lining. The blood contains several kinds of free cells, some of which contain pigments which function in the transport of oxygen. A unique feature of the circulatory system is the periodic reversal of the heart beat; after the peristaltic waves of contraction have swept across the heart in one direction for a time, they cease, shortly to be resumed in the reverse direction. This brings about a corresponding reversal in the flow of the blood.

The nervous system consists of a single elongated ganglion, embedded in the mantle between the two siphons, and of sensory and motor nerves extending from each end of the ganglion to the siphons and other parts of the body. A glandular mass beneath the ganglion has been compared to the hypophysis of vertebrates.

Most tunicates are monoecious. The reproductive system includes an ovary and a testis, lying against the intestine, with ducts opening into the atrial cavity near the anus. In most of the solitary ascidians, such as Molgula, the gametes are discharged into the atrium, and fertilization occurs in this cavity or in the external water, where development takes lace. The stages of cleavage and early differentiation are comparable with those of Branchiostoma. Embryonic development culminates in the appearance of a larva, the so-called tadpole, which possesses a dorsal, tubular nerve cord, a notochord, and gill slits. Later, this larva becomes attached by suckers at its anterior end and undergoes a complicated metamorphosis, during which its more conspicuous chordate characteristics are lost or modified.

The notochord is resorbed along with the tail; the nerve cord coalesces to form the ganglion of the adult. The gill slits of the larva are subdivided and modified to form the many openings of the adult pharynx. This mode of development is most reasonably explained by the assumption that the modern, sessile tunicates have descended from primitive chordate ancestors that were not attached, but free-swimming, like the tadpole. It is on this basis, and because of the presence of such unequivocal chordate characteristics in the larva, that tunicates are classified within the phylum Chordata.

The Cephalochordata. The subphylum Cephalochordata contains only the class Amphioxi, a small group of marine animals long regarded as closely related to the Vertebrata. The indications arc, however, that their affinities are with the tunicates, rather than with the vertebrates. It is suggested that the ancestors of the modern Amphioxi diverged from tunicate-like forms, giving up the at tached mode of life to become free-swimming animals, and giving rise in the long course of evolution to the group which we term the cephalochordates.

The Amphioxi: Branchiostoma lanceolatum. Among the few genera that compose the class Amphioxi, the best-known species is Branchiostoma (= Amphioxus) lanceolatum, which occurs in European waters. The common name for this species is "lancelet," but the former generic name "Amphioxus" has come to be the usual designation. The animals are found in shallow water, buried in the bottom with the anterior end exposed, at rest on the bottom, or swimming freely.

The body of the amphioxus is elongated and laterally compressed. A median dorsal fin, extending the length of the body, and a shorter ventral fin are specialized post eriorly to form a more conspicuous tail fin. Anterior to the ventral fin, two keel-like ridges extend a long the ventrolateral margins, marking the positions of the gonads. The mouth is located anteriorly within a hood-like structure, the edge of which forms a fringe of delicate processes called cirri. The anus is located on the left side, near the base of the tail fin. Another opening, the atriopore, lies just anterior to the ventral fin; it serves as the excurrent opening for water that has passed through the mouth and gill slits. The metameric arrangement of the musculature is conspicuous and may be seen through the thin epidermal covering of the body.

The digestive tract consists of a pharynx, or branchial sac, perforated by a series of paired gill slits, and an intestine leading posteriorly to the anus. A sac-like digestive gland, called the liver, is altached by a duct to the anterior end of the intestine. The pharynx is surrounded laterally and ventrally by a cavity, the atrium, which is enclosed by flaps of the body wall fused along the midventral line. The atrium communicates with the exterior through the atriopore. In the normal activities of the animal, sea water is drawn into the mouth and pharynx through the space enclosed by the hood and cirri. From the pharynx the water passes through the gill slits into the atrium and outward through the atriopore. Microscopic food particles are strained from the water in the pharynx and passed to the intestine, as in tunicates. The action of ciliated cells lining the gill slits and other parts is principally responsible for maintaining the now of water that brings in food materials and serves for gaseous exchange.

The circulatory system includes a ventral blood vessel, extending the length of the digestive tract, and a dorsal vessel, which is divided into right and left branches in the region of the pharynx. The dorsal and ventral vessels are interconnected, anteriorly by vessels in the walls of the pharynx and posteriorly by a network of vessels in the digestive tract and body wall. There is no heart, the circulation of the blood being brought about by peristaltic contractions of the longitudinal vessels. The course of the blood, anteriorly in the ventral vessel, upward in the vessels of the gill slits, and posteriorly in the dorsal vessel, resembles the course of circulation in vertebrate embryos and in fishes.

There is a conspicuous coelom in the region of the intestine, but anteriorly the coelom is reduced in the region of the pharynx. Numerous excretory organs, in the form of modified nephridia, open into the atrium; they occur in bilateral pairs and are segmentally arranged. It is a peculiar fact that solenocytic protonephridia also occur in the amphioxus. As seen in the intestinal region, the lateral parts of the body are largely occupied by the somatic musculature; anteriorly, the muscles fill only the dorsolateral quadrants. The notochord lies dorsal to the digestive tract, surrounded by the musculature; it is thus in a position completely comparable with that of the notochord in vertebrate embryos. The connective-tissue sheath surrounding the notochord extends dorsally as a sheath for the central nervous system, which is an axial, tubular cord resembling the spinal cord of a vertebrate. The cavity of this tube is slightly expanded at the anterior end, where there are a supposed olfactory organ and a median pigment spot. There is ho anterior differentiation of the nerve cord that can be fairly called a brain, although two pairs of nerves extending anteriorly have been termed cranial nerves. Posterior to these, a large number of bilaterally paired nerves pass from the nerve cord in a metameric arrangement corresponding with that of the muscle segments. The cord contains photoreceptors in the form of pigmented, cup-like bodies.

The reproductive organs consist of paired gonads, segmentally disposed and lying in the lateral walls of the atrium, into which they project. The sexes are separate, and the gametes are discharged into the atrium by rupture of the walls of the gonads.

The chordate features of Amphioxi are readily apparent from the foregoing description. The dorsal, tubular central nervous system is formed from the dorsal ectoderm. The notochord is obviously comparable with that of the vertebrates, both in its structure and in its anatomical relationships to the nerve cord and the gut. The gill slits, the arrangement of the blood vessels, and the course of the blood flow, along with other resemblances, mark these animals as chordates, although they are much simpler in their organization than the most primitive fishes.

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.

2.9.2. SUBPHYLUM 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:

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
    Class 3. Osteichthyes
Supra-class III. Tetrapoda

2.9.2.2 *Supra-class Pices (Fishes)*

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

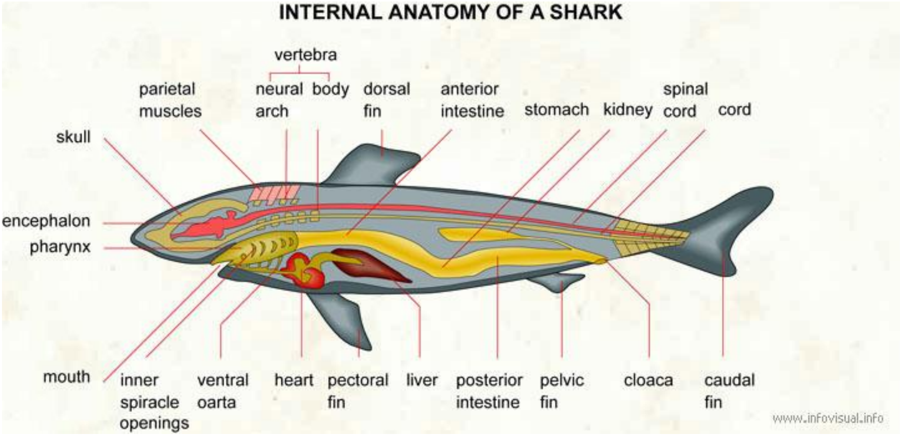


Fig. 24. Shark, internal anatomy

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

Fig. 25 Shark 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.

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

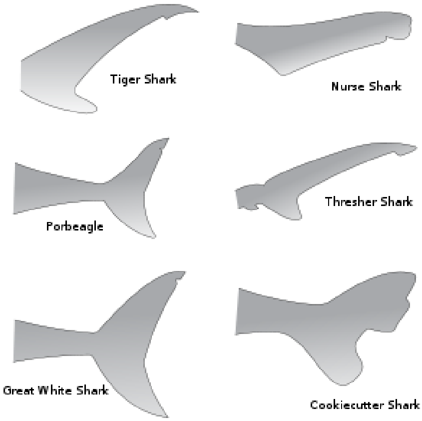


Fig. 26 The range of shark tail shapes

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.

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.

Fig. 27 The smooth hammerhead

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

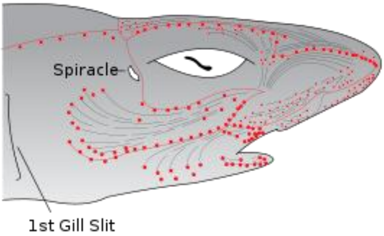


Fig. 28 Electroreception

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

Fig. 29 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.

Fig. 30 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

Fig. 31 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**

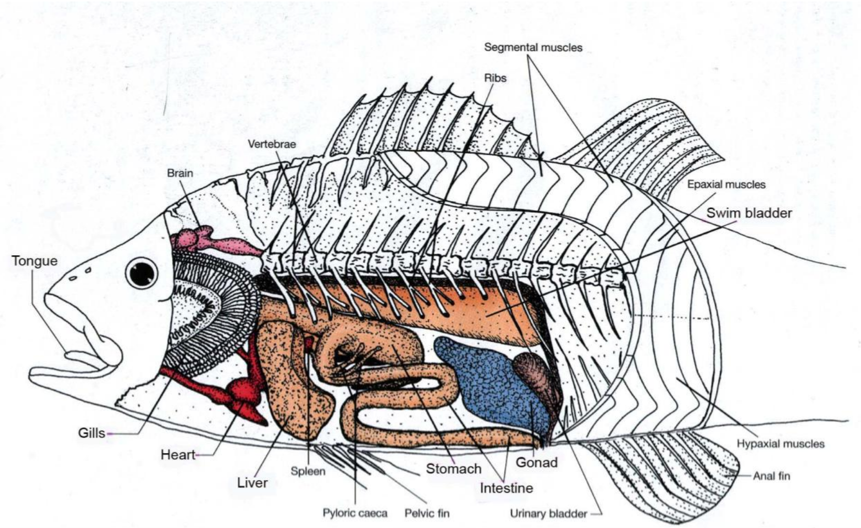


Fig. 32. Perch, internal anatomy

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 increased 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.

2.9.2.3 *Class Amphibia*

Class Amphibia (Gr. *amphi,* double + *bios,* life).

Subclass Labyrinthodontiaf (Gr. *labyrinthos,* labyrinth + *odontos,* tooth) Several orders of extinct and primitive amphibians collectively called labyrinthodonts; vertebral centra consisting of two or three arches of bone encasing the паю chord. *Ichthyostega.*

Subclass Lepospondylif (Gr. *lepos,* hi. *spondylos,* vertebra) Several orders of amphibia with spool-shaped verteb pierced by a longitudinal canal housing a persistent notochord.

Subclass Lissamphibia (Gr. *lisso,* smooth + amphibia) Modern amphibians, probably evolved from labyrinthodonts, having teeth with a fibrous segment between crown and root, an opercular bone, short ribs, never more than four toes on front foot.

Order Urodela (Gr. *oura,* tail + *delos*, visible) Salamanders. Tail well developed; legs usually present. The tiger salamander *(Ambystoma);* red-backed salamander *(Plethodon),* mud puppy *(Necturus).*

Summary

Order Anura (Gr. *a,* without + *oura,* tail) Modern frogs and toads. Short trunk; tail absent; caudal vertebrae form a urostyle; legs specialized for jumping. The leopard frog *(Rana),* American toad *(Bufo),* tree frog *(Hyla).*

Order Gymnophiona (Gr. *gymnos,* naked + *ophioneos,* snakelike) Caecilians. Wormlike trunk; limbs absent; tail very short; vestiges of dermal scales in the skin. Confined to the tropics.

Skin

Fig. 33 Grey tree frog (*Hyla versicolor)*

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.

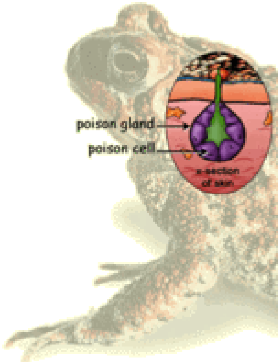


Fig. 34 Amphibian granular gland.

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.

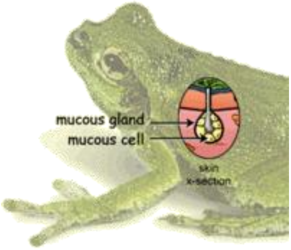


Fig 35. Amphibian mucous-gland

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

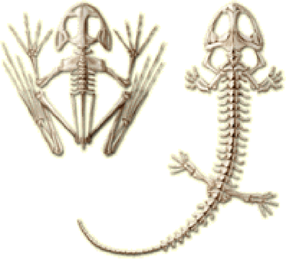


Fig. 36 Amphibian and Salamander skulls.

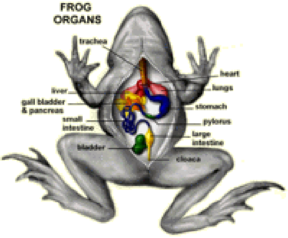


Fig. 37 Frog Internal Anatomy.

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.

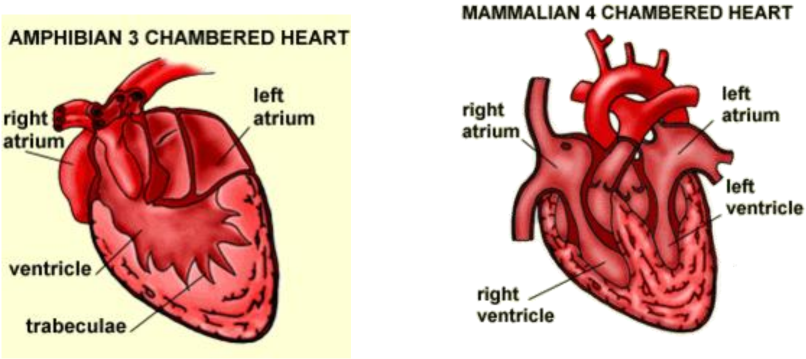


Fig. 38 Amphibian 3-Chambered Heart and Mammalian 4-Chambered Heart

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

Fig. 39 Frogs mating.

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.

Class Reptilia

Reptiles are animals in the (Linnaean) class Reptilia. They are characterized by breathing air, laying shelled eggs, and having skin covered in scales and/or scutes. Reptiles are classically viewed as having a "cold-blooded" metabolism. They are tetrapods (either having four limbs or being descended from four-limbed ancestors). Modern reptiles inhabit every continent with the exception of Antarctica, and four living orders are currently recognized:

- Crocodilia (crocodiles, gavials, caimans, and alligators): 23 species
- Sphenodontia (tuataras from New Zealand): 2 species
- Squamata (lizards, snakes, and worm lizards): approximately 7,900 species
- Testudines (turtles and tortoises): approximately 300 species

The majority of reptile species are oviparous (egg-laying), although certain species of squamates are capable of giving live birth. This is achieved by either ovoviviparity (egg retention) or viviparity (birth of offspring without the development of calcified eggs). Many of the viviparous species feed their fetuses through various forms of placentamanalogous to those ofmmammals, with some providing initial care for their hatchlings. Extant reptiles range in size from a tiny gecko, Sphaerodactylus ariasae, that grows to only 1.6 cm (0.6 in) to thesaltwater crocodile, *Crocodylus porosus*, that may reach 6 m in length and weigh over 1,000 kg. The science dealing with reptiles is calledherpetology.

Systems

Most reptiles have a three-chambered heart consisting of two atria, one variably partitioned ventricle, and two aortas that lead to the ystemic circulation. The degree of mixing of oxygenated and deoxygenated blood in the three-chambered heart varies depending on the species and physiological state. Under different conditions, deoxygenated blood can be shunted back to the body or oxygenated blood can be shunted back to the lungs. This variation in blood flow has been hypothesized to allow more effective thermoregulation and longer diving times for aquatic species, but has not been shown to be a fitness advantage.

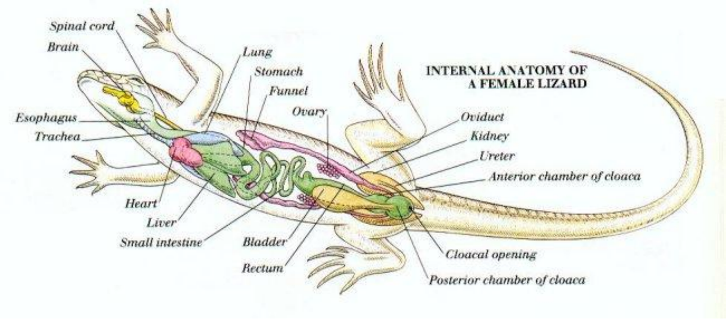


Fig. 40 Lizard Anatomy

There are some interesting exceptions to the general physiology. For instance, crocodilians have an anatomically four-chambered heart, but also have two systemic aortas and are therefore capable of bypassing only their pulmonary circulation. Also, some snake and lizard species (e.g., pythons and monitor lizards) have three-chambered hearts that become functionally four-chambered hearts during contraction. This is made possible by a muscular ridge that subdivides the ventricle during ventricular diastole and completely divides it during ventricular systole. Because of this ridge, some of these squamates are capable of producing ventricular pressure differentials that are equivalent to those seen in mammalian and avian hearts.

Metabolism

All reptiles exhibit some form of cold-bloodedness(i.e. some mix of poikilothermy, ectothermy, and bradymetabolism). This means that most reptiles have limited physiological means of keeping the body temperature constant, and often rely on external sources of heat. Due to a less stable core temperature than birds and mammals, reptilian biochemistry requires enzymes capable of maintaining efficiency over a greater range of temperatures than warm-blooded animals. The optimum body temperature range varies with species, but is typically below that of warm-blooded animals, in the 24°–35°C range for many lizards, while extreme heat adapted species like the American desert iguana *Dipsosaurus dorsalis* can have optimal physiological temperatures in the mammalian range, between 35 and 40°C. While the optimum temperature is often encountered when the animal is active, the low basal metabolism makes body temperature drop rapidly when the animal is inactive.

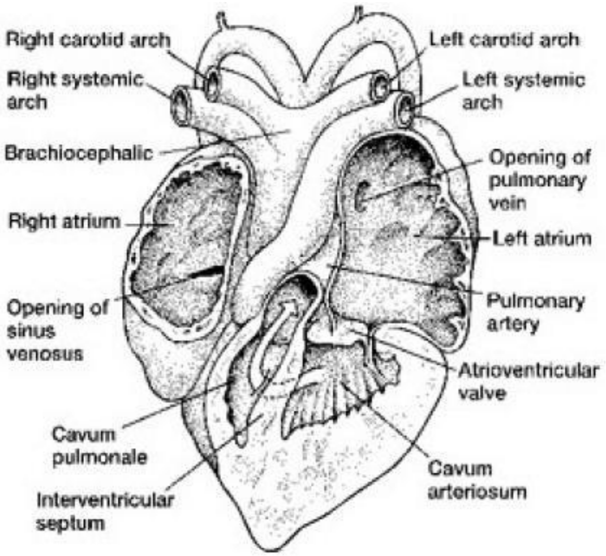


Fig. 41 Three-Chambered Heart

Like in all animals, reptilian muscle action produces heat. In large reptiles, like leatherback turtles, the low surface to volume ratio allows this metabolically produced heat to keep the animals warmer than their environment, despite not having a warm-blooded metabolism. This form of homeothermy is called gigantothermy, and has been suggested as having been common in large dinosaurs and other extinct large-bodied reptiles.

The benefits of a low resting metabolism is that it requires far less fuel to sustain bodily functions. By using temperature variations in their surroundings or by remaining cold when they do not need to move, reptiles can save considerable amounts of energy compared to endotherm animals of the same size. A crocodile need from a fifth to a tenth of the food necessary for a lion of the same weight, and can live half a year without eating. Lower food requirements and adaptive metabolisms allow reptiles to dominate the animal life in regions where net calorie production is too low to sustain large-bodied mammals and birds.

It is generally assumed that reptiles are unable to produce the sustained high energy output necessary for long distance chases or flying. Higher energetic capacity might have been responsible for the evolution of warm-bloodedness in birds and mammals. However, investigation of correlations between active capacity and thermophysiology show a weak relationship. Most extant reptiles are carnivores with a sit-and-wait feeding strategy, and whether reptiles are cold blooded due to their ecology, or if their metabolism is a result of their ecology is not clear. Energetic studies on some reptiles have shown active capacities equal to, or greater than similar sized warm-blooded animals.

Reptilian lungs

All reptiles breathe using lungs. Aquatic turtles have developed more permeable skin, and some species have modified their cloaca to increase the area for gas exchange. Even with these adaptations, breathing is never fully accomplished without lungs. Lung ventilation is accomplished differently in each main reptile group. In squamates, the lungs are ventilated almost exclusively by the axial musculature. This is also the same musculature that is used during locomotion. Because of this constraint, most squamates are forced to hold their breath during intense runs. Some, however, have found a way around it. Varanids, and a few other lizard species, employ buccal pumping as a complement to their normal "axial breathing." This allows the animals to completely fill their lungs during intense locomotion, and thus remain aerobically active for a long time. Tegu lizards are known to possess a proto-diaphragm, which separates the pulmonary cavity from the visceral cavity. While not actually capable of movement, it does allow for greater lung inflation, by taking the weight of the viscera off the lungs. Crocodilians actually have a muscular diaphragm that is analogous to the mammalian diaphragm. The difference is that the muscles for the crocodilian diaphragm pull the pubis (part of the pelvis, which is movable in crocodilians) back, which brings the liver down, thus freeing space for the lungs to expand. This type of diaphragmatic setup has been referred to as the "hepatic piston."

Turtles and tortoises

How turtles and tortoises breathe has been the subject of much study. To date, only a few species have been studied thoroughly enough to get an idea of how turtles do it. The results indicate that turtles and tortoises have found a variety of solutions to this problem.

The difficulty is that most turtle shells are rigid and do not allow for the type of expansion and contraction that other amniotes use to ventilate their lungs. Some turtles such as the Indian flapshell (*Lissemys punctata*) have a sheet of muscle that envelops the lungs. When it contracts, the turtle can exhale. When at rest, the turtle can retract the limbs into the body cavity and force air out of the lungs. When the turtle protracts its limbs, the pressure inside the lungs is reduced, and the turtle can suck air in. Turtle lungs are attached to the inside of the top of the shell (carapace), with the bottom of the lungs attached (via connective tissue) to the rest of the viscera. By using a series of special muscles (roughly equivalent to a diaphragm), turtles are capable of pushing their viscera up and down, resulting in effective respiration, since many of these muscles have attachment points in conjunction with their forelimbs (indeed, many of the muscles expand into the limb pockets during contraction).

Breathing during locomotion has been studied in three species, and they show different patterns. Adult female green sea turtles do not breathe as they crutch along their nesting beaches. They hold their breath during terrestrial locomotion and breathe in bouts as they rest. North American box turtles breathe continuously during locomotion, and the ventilation cycle is not coordinated with the limb movements. They are probably using their abdominal muscles to breathe during locomotion. The last species to have been studied is the red-eared slider, which also breathes during locomotion, but takes smaller breaths during locomotion than during small pauses between locomotor bouts, indicating that there may be mechanical interference between the limb movements and the breathing apparatus. Box turtles have also been observed to breathe while completely sealed up inside their shells.

Palate

Most reptiles lack a secondary palate, meaning that they must hold their breath while swallowing. Crocodilians have evolved a bony secondary palate that allows them to continue breathing while remaining submerged (and protect their brains against damage by struggling prey). Skinks (family Scincidae) also have evolved a bony secondary palate, to varying degrees. Snakes took a different approach and extended their trachea instead. Their tracheal extension sticks out like a fleshy straw, and allows these animals to swallow large prey without suffering from asphyxiation.

Skin

Reptilian skin is covered in a horny epidermis, making it watertight and enabling reptiles to live on dry land, in contrast to amphibians. Compared to mammalian skin, that of reptiles is rather thin and lacks the thick dermal layer that produces leather in mammals. Exposed parts of reptiles are protected by scales or scutes, sometimes with a bony base, forming armor. In lepidosaurians such as lizards and snakes, the whole skin is covered in overlapping epidermal scales. Such scales were once thought to be typical of the class Reptilia as a whole, but are now known to occur only in lepidosaurians. The scales found in turtles and crocodiles are of dermal, rather than epidermal, origin and are properly termed scutes. In turtles, the body is hidden inside a hard shell composed of fused scutes.

Lacking a thick dermis, reptilian leather is not as strong as mammalian leather. It is used in leather-wares for decorative purposes for shoes, belts and handbags, particularly crocodile skin. Due to reptiles lacking feathers or fur, reptiles are used as pets by people with allergies.

Excretory

Excretion is performed mainly by two small kidneys. In diapsids, uric acid is the main nitrogenous waste product; turtles, like mammals, excrete mainly urea. Unlike the kidneys of mammals and birds, reptile kidneys are unable to produce liquid urine more concentrated than their body fluid. This is because they lack a specialized structure called a loop of Henle, which is present in the nephrons of birds and mammals, because of this, many reptiles use the colon to aid in the reabsorption of water. Some are also able to take up water stored in the bladder. Excess salts are also excreted by nasal and lingualsalt glands in some reptiles.

Digestive

Most reptiles are carnivorous and have rather simple and comparatively short guts, meat being fairly simple to break down and digest. Digestion is slower than in mammals, reflecting their lower resting metabolism and their inability to divide and masticate their food. Theirpoikilotherm metabolism has very low energy requirements, allowing large reptiles like crocodiles and the large constrictors to live from a single large meal for months, digesting it slowly.

While modern reptiles are predominately carnivorous, during the early history of reptiles several groups produced a herbivorous megafauna: in the Paleozoic the pareiasaurs and the synapsid dicynodonts, and in the Mesozoic several lines of dinosaurs. Today the turtles are the only predominantly herbivorous reptile group, but several lines of agamas and iguanas have evolved to live wholly or partly on plants.

Herbivorous reptiles face the same problems of mastication as herbivorous mammals but, lacking the complex teeth of mammals, many species swallow rocks and pebbles (so called gastroliths) to aid in digestion: The rocks are washed around in the stomach, helping to grind up plant matter. Fossil gastroliths have been found associated with sauropods. Sea turtles, crocodiles, and marine iguanas also use gastroliths as ballast, helping them to dive.

Nervous

The reptilian nervous system contains the same basic part of the amphibian brain, but the reptile cerebrum and cerebellum are slightly larger. Most typical sense organs are well developed with certain exceptions, most notably the snake's lack of external ears (middle and inner ears are present). There are twelve pairs of cranial nerves. Due to their short cochlea, reptiles use electrical tuning to expand their range of audible frequencies.

Reptiles are generally considered less intelligent than mammals and birds. The size of their brain relative to their body is much less than that of mammals, the encephalization quotient being about one tenth of that of mammals. Crocodiles have relatively larger brains and show a fairly complex social structure. Larger lizards like the monitors are known to exhibit complex behavior, including cooperation. The Komodo dragon is known to engage in play.

Vision

Most reptiles are diurnal animals. The vision is typically adapted to daylight conditions, with color vision and more advanced visual depth perception than in amphibians and most mammals. In some species, such as blind snakes, vision is reduced. Some snakes have extra sets of visual organs (in the loosest sense of the word) in the form of pits sensitive to infrared radiation (heat). Such heat-sensitive pits are particularly well developed in the pit vipers, but are also found in boas and pythons. These pits allow the snakes to sense the body heat of birds and mammals, enabling pit vipers to hunt rodents in the dark.

Reproductive

Most reptiles reproduce sexually, though some are capable of asexual reproduction. All reproductive activity occurs through the cloaca, the single exit/entrance at the base of the tail where waste is also eliminated. Most reptiles have copulatory organs, which are usually retracted or inverted and stored inside the body. In turtles and crocodilians, the male has a single median penis, while squamates, including snakes and lizards, possess a pair of hemipenes. Tuataras, however, lack copulatory organs, and so the male and female simply press their cloacas together as the male excretes sperm.[52]

Most reptiles lay amniotic eggs covered with leathery or calcareous shells. An amnion, chorion, and allantois are present during embryonic life. There are no larval stages of development. Viviparity and ovoviviparity have evolved only in squamates, and many species, including all boas and most vipers, utilize this mode of reproduction. The degree of viviparity varies: some species simply retain the eggs until just before hatching, others provide maternal nourishment to supplement the yolk, and yet others lack any yolk and provide all nutrients via a structure similar to the mammalian placenta.

Asexual reproduction has been identified in squamates in six families of lizards and one snake. In some species of squamates, a population of females is able to produce a unisexual diploid clone of the mother. This form of asexual reproduction, called parthenogenesis, occurs in several species of gecko, and is particularly widespread in the teiids (especially *Aspidocelis*) and lacertids (Lacerta). In captivity, Komodo dragons (Varanidae) have reproduced by parthenogenesis.

Parthenogenetic species are suspected to occur among chameleons, agamids, xantusiids, and typhlopids.

Some reptiles exhibit temperature-dependent sex determination (TDSD), in which the incubation temperature determines whether a particular egg hatches as male or female. TDSD is most common in turtles and crocodiles, but also occurs in lizards and tuataras.To date, there has been no confirmation of whether TDSD occurs in snakes.

Defense mechanisms

Many small reptiles such as snakes and lizards which live on the ground or in the water are vulnerable to being preyed on by all kinds of carnivorous animals. Thus avoidance is the most common form of defense in reptiles. At the first sign of danger, most snakes and lizards crawl away into the undergrowth, and turtles and crocodiles will plunge into water and sink out of sight.

Reptiles may also avoid confrontation through camouflage. Using a variety of grays, greens, and browns, these animals can blend remarkably well into the background of their natural environment.

If the danger arises so suddenly that flight may be harmful, then crocodiles, turtles, some lizards, and some snakes hiss loudly when confronted by an enemy. Rattlesnakes rapidly vibrate the tip of the tail, which is composed of a series of nested, hollow beads.

If all this does not deter an enemy, different species will adopt different defensive tactics.

Snakes use a complicated set of behaviors when attacked. Some will first elevate their head and spread out the skin of their neck in an effort to look bigger and more threatening. Failure of this may lead to other measures practiced particularly by cobras, vipers, and closely related species, who use venom to attack. The venom is modified saliva, delivered through fangs.

When a crocodile is concerned about its safety, it will gape to expose the teeth and yellow tongue. If this doesn't work, the crocodile gets a little more agitated and typically begins to make hissing sounds. After this, the crocodile starts to get serious, changing its posture dramatically to make itself look more intimidating. The body is inflated to increase apparent size. If absolutely necessary it may decide to attack an enemy.

Some species try and bite, some will use their heads as sledgehammers and literally smash an opponent, some will rush or swim toward the threat from a distance, even chasing them onto land or galloping after them.

Geckos, skinks, and other lizards that are captured by the tail will shed part of the tail structure through a process called autotomy and thus be able to flee. The detached tail will continue to wiggle, creating a deceptive sense of continued struggle and distracting the predator's attention from the fleeing prey animal. The animal can partially regenerate its tail over a period of weeks. The new section will contain cartilage rather than bone, and the skin may be distinctly discolored compared to the rest of the body.

Class Aves

Birds may be exactly defined as **feathered animals;** no bird is without feathers, and no other animal possesses them. In addition, birds are warm-blooded vertebrates closely resembling reptiles, from which they have obviously arisen. Among the earliest reptiles one line, from which dinosaurs and pterosaurs originated, was ancestral also to crocodiles and to birds. Toward the end of the Paleozoic or the beginning of the Mesozoic, it is probable that small reptiles of this group, already specialized for locomotion with the hind limbs, were further modified for an arboreal habitat and for flight. The nature of the earliest adaptations for flight is uncertain. The earliest known birds, now assigned to the single genus *Archaeopteryx,* whose fossils were found in the Jurassic of Germany, had feathers and presumably were moderately good fliers. They retained, however, several reptilian characteristics which have since been lost, or much reduced, in the avian line. Among these primitive features were teeth , an elongate tail, and claws upon some of the digits of the fore limb. No other fossils of birds are known between the Jurassic and the Upper Cretaceous, when the toothed aquatic forms *Hesperornis* and *lchthyornis* flourished. These two genera represent lines that became highly specialized for aquatic life before they became extinct. It is assumed that birds were abundant in the Upper Cretaceous, because the birds of the early. Tertiary are diversified and essentially like those of today. In these modern forms the most important divergence is between the flightless birds, such as the existing emus, cassowaries, and ostriches, and the great majority of birds which are adapted for flight. The flying birds typically have a keeled sternum for attachment of the powerful wing muscles, whereas in the cursorialor running birds the wings and flight muscles are much reduced and the sternum is without a pronounced keel.

The poverty of the fossil record of birds seems explicable by the fact that a bird, with its light body, particularly its light bones, is much less likely to leave a record as a fossil than is a heavier animal. The usual habitats and habits of birds also make it less probable that these forms would fall to earth in places where fine sediments were being rapidly deposited. More fossils of birds may be discovered at any time, but it is unlikely that their record will ever approach that of animals more commonly buried in the mud of some shallow body of water and thus fossilized.

The class Aves is divided into the subclass Archaeornithes, containing the extinct forms with teeth and other conspicuous reptilian characteristics *(Archaeopteryx),* and the subclass Neornithes, including in four superorders the remaining known birds, extinct and existing. The Odontognathae are the extinct aquatic, toothed birds, *Hesperornis* and *lchthyornis;* the Palaeognathae are various flightless birds such as rheas , emus, cassowaries, ostriches, and others; the lmpennes are the penguins; and the Neognathae include the more common and familiar birds , forming the majority of existing species.

As we mentioned previously, a group of reptiles, the pterosaurs or pterodactyls, also evolved the power of flight, flourishing and then becoming extinct. These were contemporaneous with the primitive birds and sprang from the same reptilian line, although representing an independent offshoot. Characteristics of selective advantage, evolved by the ancestors of the birds, were their temperature-regulating ability, their nesting habit, the greater care given the young, and their feathers, which form a strong, light, and insulating covering for the body. The birds represent an advanced type of vertebrate animal which might have become dominant upon land instead of the mammals; they might even have evolved a level of intelligence comparable with that of man.

Instead, the integrative mechanisms of birds, like those of insects, evolved with emphasis on instinctive, inherited behavior patterns, apparent, for example, in their nesting habits, migratory flights, and other activities.

A review of existing birds is impossible within the limits of this chapter. Despite diversity in appearance and habits, they are a homogeneous group when compared with such classes as the reptiles, living and extinct, and the mammals. The flightless birds (Palaeognathae) seem to have originated from flying ancestors, rather than from ancestors in which the power of flight had never been developed. Loss of flight in these birds may have been related to their isolation in such regions as Australia, New Zealand, and Madagascar, where there were few if any carnivorous enemies. Apparently the ability to fly has been lost in a number of independent lines of birds during the evolution of the class. Many recent birds have become modified in relation to aquatic life, although none so completely as the penguins (Impennes). Most characteristic of existing bird life are the small perching birds familiar as our common songsters.

Birds, class Aves. contain more species (about 8800) than any other terrestrial vertebrate class. Birds adapted to flight early in their evolution, and most species are excellent fliers. Even the few species that have reverted to a completely terrestrial life show anatomical and physiological features that reflect their evolution from flying ancestors. Adaptation for flight has imposed a certain uniformity in bird structure and physiology; thus birds show less anatomical diversity than do species in other vertebrate classes. In addition to feathers and wings, or vestiges of wings in certain terrestrial species, flight requires a high expenditure of energy. All birds are endothermic and have developed ways of achieving high metabolic rates in a body of light weight. Endothermy and the powers of flight have enabled birds to have a wide distribution from the polar regions to the equator; they live in mountains, deserts, forests, and jungles. Some species spend most of their lives on the ocean, returning to land only to nest.

Bird flight. Since flight has played such a key role in the evolution and adaptations of birds, we begin by examining the ways birds fly. The movement of air across the surface of a bird's wing generates lift and drag forces, as it does in all wings. Wing shape allows a smooth flow of air across the surface and minimizes lift-reducing eddies, but some of the air flow does roll up as a vortex, which is shed from the trailing margin and tips of the wings as a pair of vortex lines. Vortex lines often can be seen in high-flying aircrafts appearing as a pair of vapor trails as the air within them condenses.

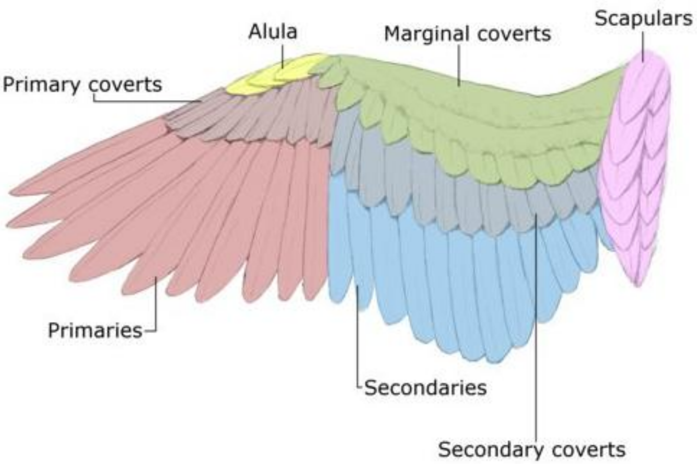


Fig. 42 Wing anatomy

Many features of the wing affect lift. Lift increases in direct proportion to the surface area of the wing. Wing area differs among different species of birds. Individual birds can also control their wing area by altering the degree to which the wing is stretched out or unfolded. Lift also increases greatly as the speed of airflow across the wing increases, for lift is proportional to the square of the speed. Fast flying birds, such as the swift, have relatively smaller wings than slower flying species. Additional lift is generated during take off and landing, when air speed is low by increasing the wing's angle of attack. Compensation for the lift-reducing turbulence that is also produced is accomplished by separating certain feathers to produce slots through which the air moves very rapidly. A small group of feathers, the alula (L. diminutive oiala, wing), can produce a slot at the front of the wing. Additional slots are often formed along the trailing margin of the wing and at the wing tip. The latter slots reduce the turbulence known as tip vortex.

General Structure. The flight of birds requires a very high energetic output, and they have evolved true endothermy. Their level of metabolism is many times that of reptiles. Heat is produced internally, and its loss is controlled at the body surface. Insulation is provided by subcutaneous fat and by feathers. Feathers evolved from the horny scales of reptiles, but scales are retained on parts of their legs, on their feet and, in modified form, as a covering for their beaks. Water, a very good conductor of heat, is prevented from penetrating the feathers by an oily secretion produced by the uropygeal gland (Gr. oura, tail + puge, rump) located on the back near the tail base. When a bird preens, or draws the feathers through its bill, it spreads an oily secretion from this gland over the feathers. Water fowl have very large uropygeal glands.

Heat loss at the feet is reduced in many birds by a vascular countercurrent mechanism. Arteries earning blood down the legs break up into a network of small vessels that are entwined with veins returning from the feet. Heat flowing peripherally in the arterial blood of this network, or rete mirabile (L. wonderful nets), is transferred to the cooler venous blood returning to the body, and body heat is conserved. Thus birds' feet are not kept very warm. At an air temperature of 18° C, the temperature of a pheasant's feet is 27° C, but body temperature remains Close to 40° C.

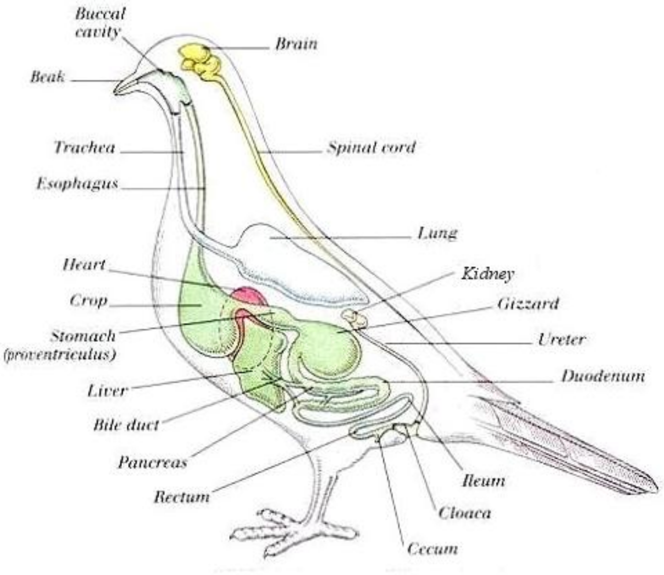


Fig. 43 Internal anatomy of a Bird

Control of body temperature involves several interacting mechanisms. When temperatures fall, the feathers are fluffed out; this increases the thickness of the insulating layer of air trapped between them. At very low temperatures, the bird must produce more heat by raising its metabolic level, as mammals do. When excess heat is to be lost, the feathers are held closer to the body, more blood is directed through the skin (and especially to uninsulated areas, such as the legs), and panting starts. Birds have no sweat glands that would allow evaporative loss of heat. Sweat glands would be of little use in a body densely covered with feathers. These mechanisms enable birds to maintain their body temperature constant and at relatively high levels, 40° to' 43° C.

The contour feathers that cover the body and provide the flying surface consist of a stiff central shaft, whose base, the calamus (Gr. kalamos, quill), is embedded in a follicle in the skin. The distal part of the shaft, the rachis (Gr. rhakhis, spine), bears a vane composed of numerous side branches, the barbs (L. barba, beard). Each barb bears minute hooked branches, barbules, along its side that interlock with the barbules of adjacent barbs. If the barbs separate, the bird can preen the feather with its bill until the barbules hook together again; thus, the vane is a strong, light, and easily repaired surface ideal for both insulation and flight. In birds that have lost the power of flight, such as the ostrich, hooks are not present upon the barbules and the feather is very fluffy, functioning only in insulation. A small aftershaft, which is often reduced to a tuft, may arise from the distal end of the calamus.

The contour feathers on the posterior border of the arm, hand, and tail form the flying surfaces and are called the flight feathers. In birds that are good fliers, the rachis of a wing feather is close to the leading edge, thus thickening this pan and giving the feather properties of an airfoil.

Down is a type of feather that covers young birds and is found under the contour feathers in the adults of certain species, particularly aquatic ones. It is unusually good insulation, for it has a reduced shaft and long fluffy barbs arising directly from the distal end of the calamus.

A filopiume consists of a slender, whiplike rachis bearing a few barbs at its tip. Filoplumes are interspersed among the flight feathers, and their follicles are richly supplied with nerve endings, which suggests that they may serve as sense organs that help regulate the movements of the flight feathers.

Bristles are stiff, vaneless feathers often found around the eyes and nose where they help keep out dirt. Some insect-catching birds, such as nighthawks, have long, slender bristles around their mouths that act as insect nets.

Since feathers are nonliving structures that fray and break, most birds shed them at least once a year during a molt that usually occurs after the breeding season, when birds are not under stress. Species with special breeding plumages also molt before the breeding season. Feathers are lost and replaced in a sequence characteristic for each species. The process is gradual in most species, and the birds can move about normally during molting. Many water birds, including ducks, geese, and loons, have diffi-culty flying when only a few flight feathers are missing. Their adaptive strategy is to complete the molt as quickly as possible. They shed the large flight feathers on their wings so rapidly that they are unable to fly for a while. Prior to the molt, they retreat to sheltered bodies of water where food is plentiful and where they can escape enemies by swimming.

Skeleton. Many adaptations for flight are apparent in the skeleton of birds. Among the most important is reduction of weight in the skeleton, thus reducing the effort needed to sustain flight. Bird bones are thin, hollow, and very light. Extensions from the lungs enter many bones, and these bones are described as pneumatic (Gr pneiima, air). The skeleton of a frigate bird having a wingspan of over 2 m weighs only 115 g, which is less than the weight of its feathers! The skeletons of all birds weigh less in relation to their body weight than do the skeletons of mammals. Many bird bones are strengthened by internal struts of bone arranged in a manner similar to the trusses inside the wing of an airplane.

The skull is notable for the large size of the cranial region, the large orbits, and the toothless beak. A toothless beak reduces weight in comparison with toothed and heavy jaws. The neck region is very long, and the cervical vertebrae are articulated in such a way that the head and neck are very mobile. Since the birds bill is used for feeding, preening, nest building, and defense, freedom of movement of the head is very important. The trunk region, in contrast, is shortened, and the trunk vertebrae are firmly united to form a strong fulcrum for the action of the wings and a strong point of attachment for the pelvic girdle and hind legs. In the pigeon, 13 of the posterior trunk, sacrai and caudal vertebrae are fused together to form a synsacrum, with which the pelvic girdle is fused. Several free caudal vertebrae, which permit movement of the tail follow the synsacrum. The terminal caudal vertebrae are fused together as a pygostyle (Gr. puge, rump + L. stylus - writing instrument) that supports the large tail feathers.

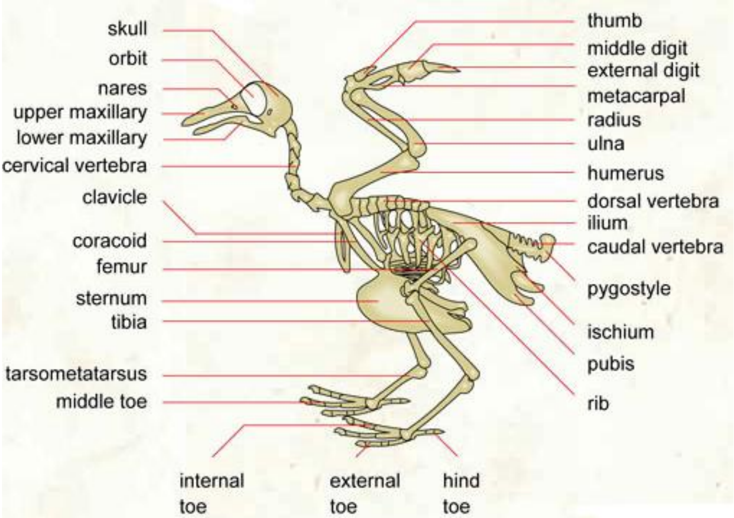


Fig.44 Skeleton of a Bird

The last two cervical venebrae of the pigeon and the thoracic vertebrae bear distinct ribs. The thoracic basket is firm yet flexible. Extra firmness is provided by the ossification of the ventral portions of the thoracic ribs and by posteriorly projecting uncinate processes (L. uncinus, a hook) on the dorsal portions of the ribs, which overlap the next posterior ribs. Flexibility, needed in respiratory movements, is made possible by the joints between the dorsal and ventral portions of the ribs. The sternum, or breastbone, is greatly expanded and, in all but the flightless birds, has a large midventral keel that increases the area available for the attachment of the flight muscles.

The bones of the wing are homologous to those of the pectoral appendage of other tetrapods, but those distal to the wrist have been greatly modified. Three short fingers arise from a fused carpometacarpus. The most anterior of these supports the alula. The pectoral girdle, which supports the wing, consists of a narrow dorsal scapula, a stout coracoid extending as a prop from the shoulder joint to the sternum, and a delicate clavicle which unites distally with its mate of the opposite side to form what is commonly called the wishbone.

Muscles. The strong and intricate movements of the wings and the support of the body by a single pair of legs entail numerous modifications of the avian muscular system. The flight muscles include the pectoralis, which originates on the ventral surface of the humerus. It is responsible for the powerful downstroke of the wings. One might expect that dorsally placed muscles would be responsible for the recovery stroke, but instead another ventral muscle, the supracoracoideus, is responsible for the upstroke. The origin of the supracoracoideus is on the sternum dorsal to the pectoralis. Its tendon passes through a pulley-like canal in the pectoral girdle near the shoulder joint and inserts on the dorsal surface of the humerus. These two muscles are exceptionally large and together make up as much as 25 to 35% of body weight in birds that are powerful fliers. In ducks and other birds that fly a great deal, the flight muscles consist mostly of aerobic slow phasic fibers, which are rich in muscle hemoglobin (myoglobin) and dark in color. In chickens and other birds that beat their wings rapidly but intermittently, the flight muscles are primarily fast phasic or glycolytic fibers and are whitish in color.

Muscle strength is roughly proportional to muscle mass. This imposes an upper limit on the weight of flying species because, as birds become larger, muscle mass increases at a faster rate than wing surface area. Large birds have compensated for this by evolving relatively larger wings than have small species, but a point is reached, at a weight of about 15 kg (33 lb), when the mass of the muscles needed to move increasingly large wings is simply more than can be sustained. The great bustards, swans, and condors all approach this upper limit, as did die large extinct pterosaurs.

Sense Organs and Nervous System. In animals that spend much of their life off the ground, the sense of smell is less important than many other senses, and the olfactory organ and olfactory parts of the brain are reduced in most species of birds. Nevertheless, carrion feeders and ground-dwelling species have a well-developed sense of smell. The nocturnal kiwi of New

Zealand has nostrils at the tip of a long bill and finds earthworms by smelling them as it probes the ground.

Sight is very important to flying animals, thus the eyes of birds are relatively large, constituting 15% or more of the weight of the head. (They are only 1% of head weight in humans.) Color vision is well developed. Rods and cones are packed more closely in the bird retina than in the mammalian retina, making the visual acuity of birds—the ability to distinguish objects as they become smaller and closer together—several times greater than that of hu¬mans. The fovea, where cones are particularly abundant, is the area of greatest acuity. Hawks and some other predaceous species have an extra laterally placed fovea in addition to the central one. The avian eye resem¬bles that of reptiles in containing a peculiar vascular fold, the pecten, that probably has a nutritive function.

Birds can also accommodate or change focus very rapidly, since they must change quickly from distant to near vision as they maneuver among the branches of a tree or swoop to the ground from a considerable height. To focus on a near object, the ciliary body contracts and squeezes upon an annular pad around the periphery of the lens. Lens thickness increases. Owls, hawks, and some other species also focus with small muscles that extend from a ring of peripheral sclerotic bones to the lens and pull it forward, and with other muscles that can change the curvature of the cornea.

The placement of the eyes on the head correlates with the birds' mode of life. Ducks, for example, have laterally placed eyes and can see behind themselves as well as forward. The eyes of hawks and owls are directed forward, and those of bitterns, a species that searches for food in marshes, are directed downward.

The sense of hearing, too, is highly developed in most birds, as one would expect from the importance of songs in the behavior of many species. Although the cochlea of their ear is not as long as it is in mammals, experiments have shown that birds detect as wide a range of frequencies as humans do, and their ability to detect rapid change in frequency is greater.

Birds have large brains in which the cerebrum, opticlobes, and cerebellum are particularly well developed. The large cerebrum results from the enlargement of a deeply situated mass of gray matter rather than from an enlarged cortex, which makes up much of the brain of mammals. The cerebral cortex of birds is thin and removal of it has little effect on behavior. On the other hand, removal of parts of the gray matter withir the cerebrum seriously affects eating, locomotion, and reproductive behavior.

Digestion. Birds eat a variety of high-caloric foods, primarily insects and other arthropods, small vertebrates, fruits, and seeds rich in digestible organic foods. They seldom eat bulky low-caloric foods such as leaves and grass, which contain in high proportion of cellulose and other materials that are difficult to digest. The structure of the bills of birds is highly specialized for the type of food they eat.

The compact and efficient avian digestive system reduces weight and allows for the processing of the large volume of food needed to sustain a high metabolic rate. Pigeons, finches, game birds, and similar seed- and grain eating species have a crop that has developed from the lower end of the esophagus. Seeds are temporarily stored here and softened by the uptake of water. Food is mixed with peptic enzymes in the proventriculus (Gr. pro, in front of + L. ventriculus stomach), which is homologous to the proximal part of the stomach into which the esophagus leads in other vertebrates, and then passes into the gizzard (Old Fr. gezier, cooked entrails), the highly modified distal part of the stomach charac terized by thick muscular walls and modified glands that secrete a horny lining. Many species swallow small stones or grit that lodge in the gizzard and aid in grinding the food to a pulp and mixing it with the gastric juices. The gizzard is not as large in owls and other carnivorous species as it is in seed-eating species. It acts as a trap in many carnivorous species, preventing sharp bones, hair, and similar indigestible material from entering the intestine. This material is then regurgitated as pellets. Digestion continues in the intestine, which is relatively shorter and not as clearly differentiated into small and large intestines as in mammals. Villi are present on the lining of the small intestine. A pair of small ceca are present in some species at the junction of small and large intestines. The intestine enters the cloaca.

Gas Exchange. The lungs of birds are comparatively much smaller than those of mammals, but they are more efficient because air flows through them in one direction rather than back and forth. One-way air flow through the lungs functions to maintain a much greater concentration of oxygen at the epithelial exchange surfaces than in other terrestrial vertebrates that ventilate their lungs bidirectionally. A unidirectional flow is made possible by a unique pattern of airways through the lungs that connects with a system of anterior and posterior air sacs. The air sacs act as bellows and extend into many pans of the body, some entering the bones through small openings. Each main bronchus extends through the lungs to the posterior air sacs. A branch of the main bronchus also leads to groups of small, parallel passages, the parabronchi, that make up much of the lung. Minute branching and anastomosing air capillaries extend from the parabronchi. Distances are very short, and gases diffuse easily between the parabronchi and air capillaries. The air capillaries are surrounded by blood capillaries, and it is here that gas exchange with the blood occurs. Another bronchial branch leads from the parabronchi to the anterior air sacs and back to the main bronchus.

Two cycles of inspiration and expiration are required for a unit of air to move through the system. During the first inspiration the sternum is lowered and the air sacs expand, drawing air directly through the main bronchus to the posterior sacs. During the first expiration the sternum is raised and the posterior air sacs are com-pressed, forcing air into the parabronchi from whence it diffuses into the air capillaries. On the second inspiration the air in the parabronchi is pulled into the expanding anterior sacs. On the second expiration the air in the anterior sacs is expelled to the outside. Notice that during inspiration both sets of air sacs expand, but they receive different types of air: the posterior sacs receive oxygen rich air from the outside; the anterior sacs, oxygen depleted air from the lungs. During expiration both sets of sacs are compressed but send air to different places: the posterior sacs, to the parabronchi; the anterior sacs, to the outside. Thus with each expiration and inspiration air is drawn anteriorly through the parabronchi, maintaining a high oxygen concentration at the respirator}' surface between the air capillaries and blood.

Because air flows through the lungs in only one direction, the air at the gas exchange surfaces has a higher oxygen content than is the case in the blind alveoli of a mammal's lung. Birds can obtain adequate oxygen even when flying at high altitudes, where the partial pressure of oxygen is low. In an experiment simulating an altitude of 20,000 feet, a sparrow was able to fly but a similar-sized mouse was barely able to crawl owing to die great reduc-tion in available oxygen.

The air sacs also have other advantages. To the extent that they enter the bones and replace marrow, they lighten the bird. They also provide a large surface area through which water evaporates, making them important in the evaporative dissipation of body heat.

A mechanism for the production of sounds is associ ated with the air passages. Membranes are set vibrating b the movement of air in a syrinx (Gr., shepherd's pipe) at the posterior end of the trachea. Muscle associated with the syrinx vary the pitch of the notes.

Circulaytion. The circulatory system of birds is also very efficient. As in mammals, the heart is relatively large and completely divided into left and right sides, keeping oxygen-depleted and oxygen-rich blood from mixing. Most birds are small and their heart beats very rapidly, up to 400 to 500 times per minute in a sparrow. This is comparable to the heart beat of a mammal of similar size. Blood vessels supplying the flight muscles are very large.

Excretion and Water Balance. Birds, in common with other amniotes, have metanephric kidneys, but the urinary bladder found in reptiles has been lost in birds, possibly as one adaptation that reduces body weight. The high rate of metabolism of birds requires a large number of kidney tubules of birds have loops of Henle that enable water to be reabsorbet from the tubules, as it is in mammals. However, birds cannot produce as cincertrated a urine in this way as mammals can. Birds conserve most of their body water by excreting 75 to 90% of their nitrogenous wastes as uric acid. Since most of the uric acid is secreted into the tubules rather than en tering by filtration, a great deal of water need not be filtered by the renal corpuscles. The renal corpuscles of birds are small. Water needed to carry off uric acid and other waste products is reabsorbed in the cloaca, and the uric acid is discharged as a white, crystalline material mixed with the feces. The excess salts that sea birds gain are eliminated by salt-excreting glands that are located above the eyes and discharge into the nasal cavities.

Reprodution and Development. All birds are oviparous, have cleidoic eggs, and they are the largest group of externally brooding animals. Fertilization is internal. A few male birds, including the ostriches, ducks, and geese, have a copulatory organ for the transfer of sperm, but sperm is transferred in most species by the two sexes briefly bringing their cloacas together. Possibly as an adaptation for weight reduction in a flying animal, birds lose the right ovary and oviduct during development. The remaining ovary is small, except during the reproductive season, when it enlarges greatly as the eggs accumulate their store of yolk. The absence of a pelvic symphysis facilitates laying large, fragile eggs.

As is the case in many other animals, a great deal of the activity of birds is focused on reproduction and rearing young. Prior to the breeding season, the males of most species establish a mating and nesting territory, an area that the male will defend aggressively against the incursions of other males of the same species. The brilliant plumage and colorful songs of many males serve both to warn other males to stay away from their territories and to attract potential mates. Territorial behavior spaces the birds and prevents the disadvantages of overcrowding.

After a territory has been established and a female has taken up residence, the birds engage in species-specific courtship behavior. Some of these courtship displays are very elaborate. Courtship establishes that the two birds are in fact members of the same species, leads to the establishment of a strong pair bond between them, and prepares the partners physiologically for effective copulation. Ancestral birds may have buried their eggs as crocodiles do and depended upon environmental temperature to incubate them. The Egyptian plover still does this today, and many species cover their eggs with vegetation when they leave them to forage for food. However, most species build nests that may be as simple as a depression on the ground used by whippoorwills or as elaborate as the woven nests of African weaver birds. After eggs have been laid, adults brood and incubate them. Many bird species lose some feathers on the underside of their abdomen at this time and form brood patches that facilitate heat transfer from the parents' bare skin to the eggs. In gulls and many other sea and aquatic birds, the two parents share equally in brooding, but in most songbirds the female generally is the chief or sole brooder. The male brings her food.

Near the end of the embryonic period, the chick develops powerful dorsal neck muscles and a horny thickening, or egg tooth, on the end of its bill that it uses to break through the shell at hatching. Ducks, shore birds, chickens, and quail are examples of species in which the young are well developed at hatching, that is, they are precocial (L.praecox, ripening before its time). Their eyes are open and the birds are covered with down at hatching. Such chicks are able to locomote and follow their parents right away, and the parents help them to find food and may- feed them for a short time. In contrast, other birds are altricial (L. altrLx, nourisher). Their eyes are closed, and they are featherless at hatching. The parents must continue to brood and feed them until they are ready to leave the nest. The nestlings' first attempts at flight are often rudimentary, and they alight on the ground. The parents remain close to the young and try to scare off or distract potential predators.

Raising a brood of young is a very time- and energy-consuming activity for most birds. Some cuckoos, cowbirds, and a few other species avoid the energy-consuming activity of brood raising by practicing brood parasitism. These species lay their eggs in the nests of other birds. The foster parents usually are tricked into accepting the eggs and treat them as their own, allowing the parasitic species to avoid the major metabolic costs and dangers associated with nesting and raising young. The European cuckoo helps to ensure this by laying eggs that resemble those of the host species. In a further adaptation for parasitism, the young cuckoo hatches before the host's own eggs and then rolls the unhatched eggs out of the nest, thereby insuring that it will receive the exclusive care of the host parent that does not recognize the cuckoo as an intruder.

Class Mammalia

A mammal might be loosely defined as a reptile further specialized for terrestrial life. Mammals can be defined technically as vertebrates with hair and mammary glands, without specifying the less obvious characteristics by which they may be further distinguished. In intelligence they are the highest class of vertebrates, and we think of them as most advanced in complexity of structure, although birds and mammals represent comparable climaxes in vertebrate specialization. The characteristics by which mammals are better qualified than reptiles for terrestrial life are their temperature regulation, their manner of reproduction, their mechanisms of locomotion , and, by no means least, their brains. To a lesser extent their eyes, ears, and teeth seem more efficient than those of reptiles. The comparison presents the mammal as an animal more capable of going into action, maintaining action, and reproducing its kind than any of its reptilian ancestors or contemporaries.

The class **Mammalia** is subdivided into three subclasses, on the basis of clear-cut differences in reproductive habits. The subclass Prototheria includes the oviparous, or egg-laying, mammals: *Ornithorhynchus*, the platypus, and *Echidna*, the spiny anteater. The subclass Metatheria, or Marsupialia, contains the marsupial or pouched mammals: bandicoots, opossums, wombats, phalangers, and kangaroos. The subclass Eutheria, or Placentalia, includes the viviparous mammals, represented by all the more advanced and familiar forms. These are distributed among sixteen orders, of which the following are representative:

Order Insectivore: moles, shrews, and hedgehogs.

Order Chiroptera: bats.

Order Primates: lemurs, monkeys, apes, and man.

Order Carnivora: cats, lions, dogs, wolves, foxes, bears, raccoons, seals, sea lions, walruses, and many others.

Order Perissodactyla: even-toed hoofed mammals, such as horses, zebras, tapirs, and rhinoceroses.

Order Artiodactyla: even-toed hoofed mammals, such as swine, hippopotami, camels, llamas, deer, cattle, and many others.

Order Cetacea: whales, dolphins, and porpoises.

Order Proboscidea: elephants.

Order Rodentia: rodents, such as squirrels, rats, mice, beavers, porcupines, and many others.

Order Edentata: sloths, armadillos, and anteaters

General Structure. Mammals are endothermic vertebrates. Hair and subcutaneous fat form an insulating layer. Cutaneous glands are abundant, secreting sweat, oil, and pheromones. The limbs of most mammals are carried in a position to a lesser or larger extent beneath the body. The skull is of the synapsid type and has a relatively large braincase. The jaw joint lies between the dentary bone of the lower jaw and the squamosal (temporal) bone of the skull. There are three auditory ossicles in the middle ear and a spiral cochlea in the inner ear. The cerebrum is large and has a gray cortex. Large cerebellar hemispheres are present. Teeth are heterodont and have a precise occlusion, and their replacement is limited. The small intestine has numerous multicellular intestinal glands and microscopic villi. Most species lack a cloaca. Respiratory and digestive passages are nearly completely separated in the oral and pharyngeal regions by a secondary palate. Numerous lung alveoli greatly increase respiratory surface area. A muscular rib cage and diaphragm play major roles in lung ventilation. Oxvgen-depleted and oxygen-rich blood are completely separated as they move through the heart. Nitrogenous wastes are eliminated primarily as urea by metanephric kidneys. Long loops of Henle in the renal tubules make possible the production of a urine hyperosmotic to the blood. The testes of most mammals either lie permanently within a scrotum or descend into the scrotum during die reproductive season. Males have a penis, and fertilization is internal. Except for primitive egg-laving mammals, the ovaries arc small and produce few eggs; little yolk is deposited in the eggs. The oviducts have differentiated into vaginal, uterine, and uterine tube regions. Monotremes are oviparous; other mammals are viviparous. The uterine lining and certain extraembryonic membranes unite to form a placenta. Mammary glands are always present in females.

Of all the vertebrate groups, mammals (class Mammalia), are of particular interest to us because we are mammals, as are most of our domestic animals, which help us in our labors and provide us with wool, leather, and much of our food. Although mammals are not a large class (There are only about 4500 species), their evolution has not been constrained, as has that of birds, by adaptation to a particular mode of life. Mammals are a very diverse group. Most are terrestrial, but some, such as the whales, are highly adapted for an aquatic life, and others, the bats, have evolved flapping flight. Mammals range in size from a small species of bat that weighs only 1 5 g to the giant whales that exceed 100 tons. The class includes the egg-laying duckbilled platypus and spiny anteater (monotremes) of the Australian region; the opossum, kangaroo, and other pouched marsupials; and a wide variety of true placental mammals. They all produce few young but invest consider¬able time and energy in caring for them. All are endother- mic, and most can maintain their body temperature at nearly constant levels irrespective of changes in the external environment. This ability- has allowed mammals to occupy a wide range of habitats including the polar seas, high mountain ranges, deserts, and tropical jungles. Endothermy and greater care of the young have been the touchstones of mammalian evolution, and most of their characteristics are related to these attributes.

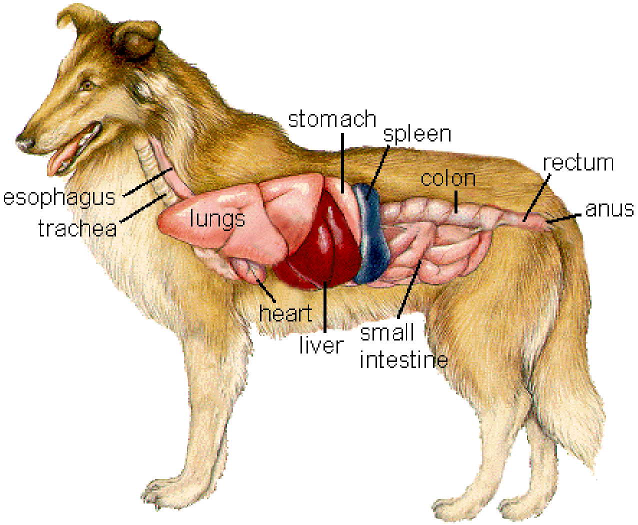


Fig. 45 Dog, internal anatomy

Endothermy and Temperature Regulation. Endothermy in mammals probably evolved gradually, and ancestral mammals likely had a lower metabolic rate and a simpler set of thermoregulatory controls than contempo¬rary species. We can make some inferences as to how endothermy evolved by reconstructing the mtxle of life of ancestral mammals. The earliest mammals of the late Triassic and early Jurassic periods were small, mouse-sized creatures whose dentition was adapted for feeding on insects. Their skull showsagreat elaboration of the cochlear region of the ear and of the olfactory organ. These conditions suggest that early mammals were nocturnal insect eaters because well-developed senses of smell and hearing would be essential for this mode of life.

It would not have been difficult for small mammals to be active at night at ambient temperatures of 25° to 30° C. provided they had insulating layers of subcutaneous fat and fur that would reduce the loss of body heat produced by a modest metabolic level. Ancestral mammals probably did not maintain a body temperature much higher than that of their nocturnal surroundings, and they probably- retreated to cool shelters during the daytime. The European hedgehog and the tenrecs of Africa and Madagascar are contemporary nocturnal insectivores of this type that probably have occupied this niche throughout their evolutionary history. They maintain their body tem-perature only a few degrees above the nocturnal ambient temperature and can do so with no more oxygen consumption than a reptile of similar size and activity at the same temperature.

When diurnal ecological niches became available to mammals as a result of the late Cretaceous extinction of the dinosaurs, some early mammals evolved the ability to become active during the daytime, when ambient temperatures would be much higher. To maintain a body temperature as low as that of their nocturnal ancestors, i.e., 25° to 30° C, would require considerable evaporative cooling and loss of precious body water. They evolved a higher body temperature of approximately 35° to 40° C. Hut for a small animal to maintain this temperature at cooler times of the day required a greater energy expenditure than that of reptiles. Their energetics presumably changed in this context, and their metabolic rate became three to five times higher than that of reptiles of similar size and under similar conditions.

Contemporary mammals maintain their body temperature by regulating the rate of heat loss at the body surface and the rate of heat production. Each mammalian species has a characteristic thermal neutral zone, a range of ambient temperature at which body temperature can be maintained with little change in metabolic rate. Substantially more energy needs to be ex- expended to maintain body temperatures when ambient temperatures fall below or go above the thermal neutral zone. Most mammals do maintain their body temperature, even when the thermal neutral zone is exceeded, but some species permit body temperature to rise or fall over a limited range.

Mammals that live in areas where the environment may become very cold have evolved adaptations that supplement thermal regulation. Many mammals with a thick coat of hair (the pelage) molt mice a year. In early fall, they gradually lose their thin summer pelage and develop a much thicker undercoat for the winter. A second molt to a summer pelage occurs in the spring. In addition to an undercoat, the pelage of many mammals includes long, coarse guard hairs that protect the undercoat. A thicker fur for winter extends the thermal neutral zone to a lower temperature and decreases the steepness of the slope of the ambient temperature-metabolic rate curve. Less energy need be expended to maintain body temperature than would be the case if a thicker pelage did not develop.

As in birds, the appendages cannot be insulated as well as the rest of the body. Their temperature is permitted to fall below that of the body core. Arteries carrying blood to the limbs are sometimes closely intermeshed with the veins returning blood so that a countercurrent exchange mechanism is established in which much body heat moves from the arteries to the veins and is not lost. Enough heat must be permitted to enter the appendages, however, to keep them from freezing. Nerves and other organs in the distal part of the limbs are adapted to function at lower temperatures.

Some arctic and temperate mammals, notably many insectivores, bats, and rodents, adjust to winter weather by going into a period of dormancy known as hibernation. During this period, the thermostat in the hypothalamus is turned down, in some species as much as 20° C below the normal body temperature. Unlike amphibian and reptilian hibernators, in which body temperature falls to ambient levels, mammalian hibernators maintain body temperature, but at a low thermostat set point. Energy is conserved because metabolism is very low during hibernation yet high enough to sustain life and to keep the body from freezing. There are certain advantages to hibernation for a small endotherm. In many regions, insects and certain types of plant food are not available in sufficient quantity during the winter, making it difficult for the animal to get enough food to sustain the necessary metabolic rate. By permitting its body temperature and metabolic rate to drop, the animal can get by on food reserves stored within its body.

Some other mammals avoid the problem of cold temperatures by retreating to more sheltered or warmer climates. Many small rodents remain active all winter beneath the snow cover, where the temperature seldom falls far below 0 °C. Occasionally they venture forth on the snow surface. A few of the larger mammals undergo extensive seasonal migrations. For example, the caribou of Alaska and Canada spend the summer on the arctic tundra, but retreat south to the more sheltered forests in the winter.

Mammals living in very hot climates also have special adaptations that help keep them cool without an excessive loss of body water due to evaporative cooling. Water often is in short supply. Small desert rodents avoid overheating by being nocturnal. During the day they burrow so they are sheltered in a cool and moist microhabitat.

Camels and some gazelles have thick fur coats that reduce heat loss in cold periods and heat gain in warm periods. Elephants, on the other hand, have very little body hair. Their large body size provides thermal stability, and their large ears function as efficient radiators.

Some mammals can allow their body temperature to rise and avoid the necessity of evaporative cooling. Camels can tolerate a body temperature as high as 41° C in the daytime. Their body cools down at night, when ambient temperatures fall. Permitting body temperature to rise is possible in many large mammals living in hot, open habitats because they can keep the critical brain temperature lower by a countercurrent exchange mechanism. Arteries supplying the brain first break up into minute passages that are entwined with veins returning cool venous blood from the nasal passages. Considerable heat passes from the warm arterial blood to the cooler venous blood before the arterial blood reaches the brain.

Locomotion and Coordination. Changes in all of the mammalian organ systems are closely correlated with the increased activity made possible by endothermv. Greater activity and agility are reflected in the skeletal system of even the earliest mammals of theTriassic period. The arched back, the posterior inclination of the vertebral spines of the thoracic vertebrae, and the anterior inclination of the spines of the lumbar vertebrae are typical of quadruped mammals and are correlated with the abandoning of lateral trunk undulations in locomotion. The elbow and knee have moved in close to the trunk, with the elbow pointing posteriorly and the knee anteriorly, so that the legs extend down to the ground more or less under the body. This position provides better mechanical support and the potential for a longer swing of the appendage, increased stride length, and greater speed. Primitively, the feet were placed flat upon the ground, a posture called plantigrade. Most mam¬mals have a sacrum formed by the fusion of three sacral vertebrae that forms a strong articulation between the pelvic girdle and vertebral column. Many species use the tail for balancing, as do cats, and it plays a major role in the propulsion of whales, but in most mammals the tail has lost its primitive locomotor function and is frequently reduced in size or is absent.

More complex patterns of locomotion, and probably the increased exploratory behavior and agility of mammals, require more complex muscular, sensory, and nervous systems. The senses of smell and hearing are very-acute in primitive mammals. The eyes are well developed in most species, but are reduced in burrowing species and some nocturnal species. The brain is extraordinarily well developed. The cerebrum is greatly enlarged, with a gray cortex containing centers associated with sensory input and important motor centers. The cerebellum also enlarges as motor coordination becomes more intricate.

Digestion. To sustain their high level of metabolism, mammals must obtain large supplies of food The lower temporal opening of the skull (svnapsid fenestra) is enlarged and houses powerful jaw muscles. Mammals cut and crush their food within their mouths, and the teeth are firmly rooted in sockets in the jaws. The teeth of mammals also have differentiated into types that perform different functions during food processing. Such teeth are described as heterodont (Gr. heteros, other + odous, tooth) in contrast to the uniform homodont (Gr. homos, same) dentition of most other vertebrates in which all of the teeth are very similar, usuall simple cones of different sizes, that are used primarily to seize and hold the food. Chisel-shaped incisors at the firont of each jaw are used for nipping and cropping. Next is a single canine tooth, which is primitively a long sharp tooth with a piercing and tearing action. A series of premolars and molars follows the canine. These cheek teeth may have a sheering action (carnivores) or a grinding action (herbivores). In primitive living mammals, each molar tooth bears three small cones, called cusps, that are arranged in a triangle. The triangle of cusps is called a trigon in an upper molar and a trigonid in a lower molar. Trigon and trigonid are mirror images of each other, so good shearing action occurs as parts of the trigon and trigonid slide past each other. Crushing of food occurs when the primary cusp of the trigon falls upon a Iow heel, or talonid. located on the posterior surface of the trigonid. Additional shearing action occurs as the premolars slide past each other.

In order to perform these functions, upper and lower teeth must come together, or occlude, in a very precise manner. Young mammals are suckled and are born without teeth. A first set of incisors, canines, and premolars develops as the young begin to feed for themselves. As the jaw grows in size, good occlusion is maintained as these socalled milk teeth are gradually replaced by larger permanent teeth. The molar teeth appear sequentially as a mammal matures and the jaw enlarges further. They are not replaced. Reptiles, in contrast, frequently lose teeth, and gaps are present in the tooth row where replacement teeth are growing in. Tooth replacement in reptiles is continuous throughout life.

As mammals chew their food, they mix it with saliva that lubricates the food and often contains amylase, an enzyme that begins the digestion of starches. Digestion continues in the stomach and intestine. Numerous microscopic villi line the small intestine and increase the surface area available for digestion and absorption.

Respiration. The greater exchange of oxygen and carbon dioxide required to maintain a high level of metabolism is made possible by the evolution of pulmonary alveoli that greatly increase the respiratory surface of the lungs and by the evolution of a diaphragm that increases the efficiency ventilation. The palate of mammals is a horizontal partitior of bone and flesh that separates the air and food passage- in the mouth cavity and pharynx. The palate permits nearly continuous breathing. Mammals can manipulate food in their mouths while still breathing, for food and air passages cross only in the laryngeal part of the phatynx. The mammalian palate is quite different from that of other terrestrial vertebrates in which the nasal cavities open into the front of the mouth cavity. The mammalian palate is technically a secondary palate, a new shelf of bone and flesh that divided the primitive mouth cavity and anterior pan of the pharynx into passages for gas transport and food processing.

Circulation. Mammals, like birds, have evolved a heart that is completely divided internally so there is no mixing of oxygen-depleted blood with oxygen-rich blood. The complete separation of blood streams going to the lungs and body allows the musculature of the left ventricle to become more massive and powerful than that in the right ventricle. Systemic blood pressure is much higher than it is in reptiles, and blood is circulated rapidly throughout the body.

Excretion and Water Balance. The high metabolic rate of mammals results in the formation of a larger amount of nitrogenous wastes than in ectothermic vertebrates. As in amphibians (and unlike reptiles and birds), most of the nitrogenous waste is urea, which, being toxic, requires a considerable volume of water to carry it off. Mammals have many kidney tubules and a high filtration rate because the glomeruli are large and blood pressure is high. Large amounts of water leave the blood along with urea, but little water is lost because the loops of Henle make it possible for approximately 99% of the water that starts down the kidney tubules to be reabsorbed. Mammals produce a very concentrated urine that is hyperosmotic to the blood.

Reproduction and Care of the Young. Upon hatching from its egg, or upon birth, a young reptile must feed and fend for itself. Some are successful, many are not. Mammals have evolved a different reproductive strategy. Fewer young are produced, but considerable maternal energy and care are invested in the few that are conceived and raised. The embryos of endothermic mammals must themselves develop in a warm and closely-controlled environment. The platypus and spiny anteater resemble most reptiles in being oviparous, but the eggs are carefully brooded, and die newborn are fed milk secreted by the mammary glands or breasts. Mammary glands are unique to mammals, and the class name, Mammalia, is derived from their presence (L. mamma, breast). They probably evolved from either sweat or sebaceous glands that occur in mammalian skin.

All other mammals are viviparous and retain their embryos in a uterus. All of the extraembryonic membranes characteristic of amniotes are present. The yolk sac contains little or no yolk, and a placental relationship develops between the mother and embryo(s) allowing the transfer of maternal nutrients to the embryo and embryonic wastes to die mother. The placenta is transitory in the opossum and other marsupials; die young are born at a very small size and complete their development attached to the mother's nipples, which are usually located in an external pouch. The placental relationship with the mother lasts for a longer time in other mammals and the young are born at a more advanced stage of development.

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