M.Sc. Previous Year
Zoology, Paper II

STRUCTURE AND FUNCTION IN INVERTEBRATES

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SYLLABI-BOOK MAPPING TABLE

Structure and Function in Invertebrates

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UNIT-1 **Organization of Coelom:** (a) Acoelomates (b) Pseudocoelomates, (c) Coelomates: Protostomia and Deuterostomia. **Locomotion:** (a) Flagella and Ciliary movement in Protozoa (b) Hydrostatic movement in Coelenterata, Annelida & Echinodermata.	**Unit-1:** Organization of Coelom and Locomotion in Invertebrates **(Pages 3-27)**
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INTRODUCTION

NOTES

Invertebrates are animals that neither possess nor develop a vertebral column, commonly known as a backbone or spine, derived from the notochord. This simple definition hides the tremendous diversity found within this group which includes protozoa, corals, sponges, sea urchins, starfish, sand dollars, worms, snails, clams, spiders, crabs, and insects. In fact, more than 98 percent of the nearly two million described species are invertebrates. They range in size from less than one millimeter to several meters long. Invertebrates display a fascinating diversity of body forms, means of locomotion, and feeding habits.

Invertebrates are ectotherms, they warm their bodies by absorbing heat from their surroundings. Most invertebrates live in water or spend at least some part of their life in water. The external layers of aquatic invertebrates are generally thin and permeable to water. This structure allows the ready exchange of gases needed to keep the animal alive. Some aquatic vertebrates do have specialized respiratory structures on their body surface. Aquatic invertebrates feed by ingesting their prey directly, by filter feeding, or by actively capturing prey.

Some groups of invertebrates live on land. Common examples include the earthworms, insects, and spiders. These invertebrates need to have special structures to deal with life on land. For example, earthworms have strong muscles for crawling and burrowing and, since drying out on land is a problem for them, they secrete mucous to keep their bodies moist. Insects and spiders move by means of several pairs of legs and are waterproof. Like vertebrates, most invertebrates reproduce at least partly through sexual reproduction. They produce specialized reproductive cells that undergo meiosis to produce smaller, motile spermatozoa or larger, non-motile ova. These fuse to form zygotes, which develop into new individuals. Others are capable of asexual reproduction, or sometimes, both methods of reproduction.

Social behaviour is widespread in invertebrates, including cockroaches, termites, aphids, thrips, ants, bees, passalidae, acari, spiders, and more.

This book is divided into four units that attempt to give the students a in depth knowledge of organization of coelom and locomotion in invertebrates, nutrition, digestion and respiration, excretion and nervous system in invertebrates, and general characters of invertebrate larvae and minor phyla of invertebrates. The book is divided into four units that follow the Self-Instruction Mode (SIM) with each unit beginning with an Introduction to the unit, followed by an outline of the Objectives. The detailed content is then presented in a simple but structured manner interspersed with Check Your Progress to test the student's understanding of the topic. A Summary along with a list of Key Terms and a set of Self-Assessment Questions and Exercises is also provided at the end of each unit for understanding, revision and recapitulation.

UNIT 1 ORGANIZATION OF COELOM AND LOCOMOTION IN INVERTEBRATES

NOTES

Structure

1.0 INTRODUCTION

Invertebrates are the most diverse and numerous group of animals on Earth. An invertebrate is a cold-blooded animal with no backbone. Invertebrates can live on land-like insects, spiders, and worms-or in water. Marine invertebrates include crustaceans (such as crabs and lobsters), mollusks (such as squids and clams), and coral.

In invertebrates, the coelom is the main body cavity and is positioned inside the body to surround and contain the digestive tract and other organs. In some animals, it is lined with mesothelium. In other animals, such as molluscs, it remains undifferentiated. The term coelom derives from the ancient Greek word κοιλία (koilía), which means 'hollow cavity'.

Coelom refers to the fluid-filled cavity bounded on all the sides by mesoderm and is positioned in between the alimentary canal and the body wall. The peritoneal cavity in our abdomen is a part of our coelom. Basically, there are four types of coeloms, such as:

- Acoelom
- Pseudocoelom
- Coelom or Eucoelom
- Haemocoelom

Locomotion is any of a variety of movements among animals that results in progression from one place to another. To locomote, all animals require both propulsive and control mechanisms like hydrostatic movements.

Hydrostatic skeletons are typically arranged in cylindrical pattern and possess two mechanical units; the muscle layer and the body wall. The contraction of longitudinal, circular, radial, or transverse muscles increases the fluid pressure within thhe cylinder resulting in changes in length.

In general, coelomic organisms, i.e., animals possessing a coelomic cavity have hydrostatic movements, however, more advanced organisms are referred to as hydrostatic when they possess hydrostatic organ instead of a hydrostatic skeleton.

1.1 OBJECTIVES

After going through this unit, you will be able to:

- Understand the concept and importance of coelom in invertebrates
- Differentiate between various types of coeloms
- Explain the various modes of coelom formation
- Understand the various theories regarding the coelom formation
- Conceptualize the process of locomotion in invertebrates
- Explain the structure and advantages of hydrostatic skeleton in invertebrates
- Describe various types of hydrostatic movements in various organisms
- Explain the water vascular system and its functions

1.2 ORGANIZATION OF COELOM

Coelom (Greek: *coel* = hollow cavity) refers to the fluid-filled cavity bounded on all sides by mesoderm and is positioned in between the alimentary canal and the body wall. The peritoneal cavity in our abdomen is part of our coelom and there are similar spaces around our heart and lungs. However, the type of coelom differs among group of animals both in structure and mode of development.

There are three structural types of body plans related to the coelom.

Special features of coelom can be mentioned as:

- Developmentally, coelom arises as a split in mesoderm which bifurcates into two layers, a somatic layer next to the epidermis and a splanchnic layer around the endoderm.
- Coelom becomes bounded by coelomic epithelium which secretes coelomic fluid.
- Greater part of the coelom forms the perivisceral cavity or the splanchnocoel.
- It is a fluid-filled space inside which viscera is lodged.
- Because of this packing, viscera remains independent of the movement of muscles of the body wall.
- In some higher animals, part of the perivisceral cavity is separate to form restricted cavities whose coelomic nature can only be realised if their developmental history is followed.

- The ancestral coelomate animals are thought to have had segmentally arranged mesodermal pouches.
- From the mesodermal pouches, gametes were formed by the process of proliferation of epithelial lining.
- Later, these pouches became modified into specialized structure and performing different functions.
- Evolution of these pouches is evident in the present-day coelomates.

Types of Coelom

There are four types of coelom (Refer Figure 1.1), which are as follows:

- Acoelom
- Pseudocoelom
- Coelom or Eucoelom
- Haemocoelom

(i) **Acoelom:** It means without a coelom or fluid-filled cavity. The space between the gut and body wall is filled by densely packed connective tissue derived from both ectoderm and endomesoderm (entomesoderm), called parenchyme. Examples **-** Gnathostomulida, Platyhelminthes and Nemertea, Gastrotricha, Kinorhyncha, etc.

(ii) **Pseudocoelom:** Pseudocoelom means false cavity, formed by persistence of embryonic blastocoel. The term 'pseudocoelom' usually refers to the space which is not developed from embryonic mesoderm and is not lined by coelomic epithelium derived from the mesoderm. The body cavity is bounded externally by the fibrous processes of the longitudinal muscle cells (mesoderm) and internally by the intestine (endoderm). The pseudocoelomic fluid acts as a hydrostatic skeleton and maintaing body shape and circulate the nutrients. Animals containing a pseudocoel are called pseudo- coelomates or pseudocoelomate animals. Pseudocoelomates are also referred as haemocoelomate or blastocoelomate (Brusca and Brusca, 2003). Examples: *Rotifera, Nematoda, Nematomorpha, and Loricifera*. In rotifers, a huge fluid-filled pseudocoel occurs beneath the body wall and surrounds the gut and other internal organs.

(iii) **Coelom or Eucoelom:** It is the true coelom lying between the gut and outer body wall musculature and is lined by coelomic epithelium derived from the embryonic mesoderm. It is of mesodermal origin and opens to the exterior through the coelomoducts, for example the oviducts and the excretory ducts. The coelomic fluid contains amoeboid cells or amoebocytes. The animals containing such a body cavity or coelom are known as coelomates. Examples: Sipuncula, Echiura, Priapulida, Mollusca, Annelida, Arthropoda, Onychophora, Phoronida, Brachiopoda, Bryozoa, Echinodermata, Chaetognatha, Hemichordata, and Chordata.

(iv) **Haemocoelom:** In this the true coleomic cavity is greatly reduced and filled with blood. Example: Arthropoda and Mollusca.

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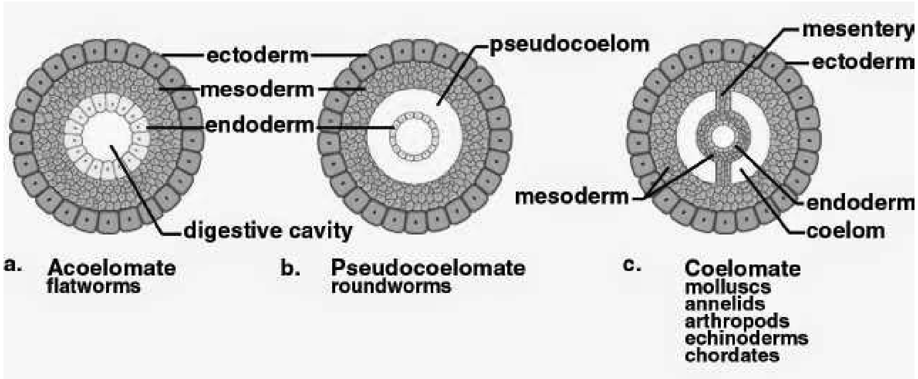

Fig. 1.1 *Different Types of Coelom*

Mode of Coelom Formation

There are three types which are noted in protostomes and deuterostomes:

- **Schizocoely:** The process in which coelom arises by splitting of the mesodermal bands during embryonic development. For example Protostomia, Mollusca, Echiura, Priapulida, Annelida, Arthropoda and Onychophora.
- **Enterocoely:** The process though which coelom is formed by the evagination from the embryonic archenteron, pouch-like structures detach from the archenteron and gradually occupy the whole body by enlargement. Examples: Deuterostomia, Echinochordata, Hemichordata and Chordata.
- **Myocoel:** This type of coelom originates in Phoronida. In such cases, the mesenchyme rearranges to enclose a place called coelom (Marshall and Williams, 1972). It is an unusual method of coelom formation. It is neither entero-coelomous nor schizocoelous.

Coelom in Different Groups

- In Sipuncula, there are two coelomic cavities, one is a ring-like tentacular coelom situated at the base of the tentacles and extending three branches in each tentacle. Trunk coelom is spacious and occupies the trunk region separated from the tentacular coelom.
- The coelomic fluid within the coelom is in constant circulation by movement of the cilia of peritoneal cells and by the contractions of the muscular body. The coelomic fluid contains wandering leucocytes, disc-like haemerythrin, reproductive cells, and excretory cells.
- In Priapulida, it is not clear if the body cavity is a pseudocoelom or a coelom. The body cavity fluid contains amoebocytes and erythrocytes.
- In Onychophora, the main body cavity is haemocoel, not a true coelom. This type of body cavity is known as mixocoel. True coelom is restricted to the gonadal cavities and excretory organs. Blood-filled cavity is called haemocoel. In Mollusca, the coelom comprises a pericardial coelom around the heart, a gonadal coelom, and paired coelomic ducts serve as excretory

organs. In Arthropods, the coelom is represented by cavity of gonads and excretory organs in some species.

- In annelids there is a pair of sacs—the right and left coelomic vesicles lying between each segment of the gut and the corresponding segment of the body wall. The cavities of the coelomic vesicles contain a fluid and corpuscles and are lined by peritoneum derived from mesodermic epithelium. Each segment of annelida has a dorsal mesentery, ventral mesentery, and a transverse septum.
- Two sheets of peritoneum meeting in the mid-line above and below the gut form the dorsal mesentery and ventral mesentery respectively. The septum is a screen between two successive segments and is formed by meeting of the two peritoneal sheets at boundary between the segments.
- The mesentery is made up of double-fold of peritoneum of coelomic epithelium. In rare exceptions, the septa and mesenteries form a complete series of transverse or longitudinal partitions throughout the entire length of the body of the animal. In most cases the septa are perforated, and the mesenteries are incomplete so that there exists a close communication between coelomic vesicle and coelom.
- In Echinodermata, the coelom in the adult echinoderms is represented as several distinct spaces. It develops as pair of lateral pouches and later become separated from the embryonic enteron.
- These pouches represent future coelomic cavities and the cells which comprise the pouch walls represent the mesoderm. The two original pouches, one on each side, give rise by subdivisions to coelomic vesicles, arranged one behind the other and are called the axocoel, the hydrocoel, and the somatocoel respectively.
- These coelomic vesicles complement to the protocoel, mesocoel, and metacoel of the hemichordates. The water vascular system arises from the hydrocoel. The two somatocoels convert into gut mesenteries and the axocoel transforms into the hydropore.

Theories Regarding the Coelom Formation

Regarding the origin of coelom, there are four basic theories given by Clark (1964).

- **Enterocoel Theory:** First proposed by Lankester, supported by Lang, Sedgwick. This theory states that coelom may have originated by evagination as a pouch-structure in the wall of embryonic archenteron. This type of coelom formation occurs in many existing enterocoelous animals. This concept was proposed by Lankester (1877). Sedgwick, 1884 suggested that the gastric pouches of anthozoans (Cnidaria) separate from the main gastric cavity (gastrovascular cavity) and transform into coelomic pouches (Refer Figure 1.2).

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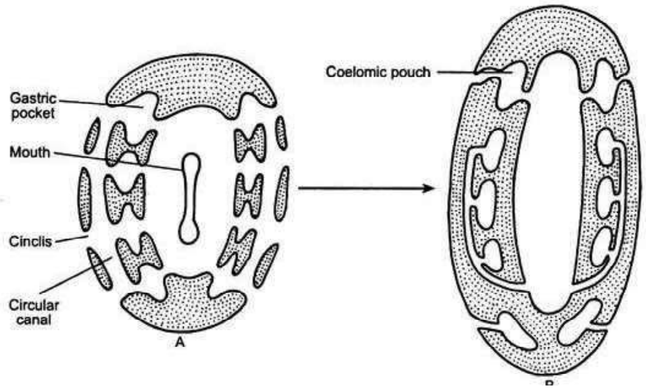

Fig. 1.2 Diagrams showing the enterocoel theory of coelom formation. A-Diagram illustrating the gastric pockets of an anthozoan animal. B-Showing the coelomic pouches after transformation of the gastric pockets of anthozoans.

- **Gonocoel Theory (HatSchek, 1877, 1878), Bergh (1885), Meyer (1890), Goodrich (1946):** Gonocoel theory states that first coelomic cavity arose from the mesodermally derived expanded gonadal cavity and the cavity persisted after the release of gametes. For example, the gonads of tricladid flatworms are arranged in a linear order and segmental coelom of annelida may have developed from this tricladid (Refer Figure 1.3).

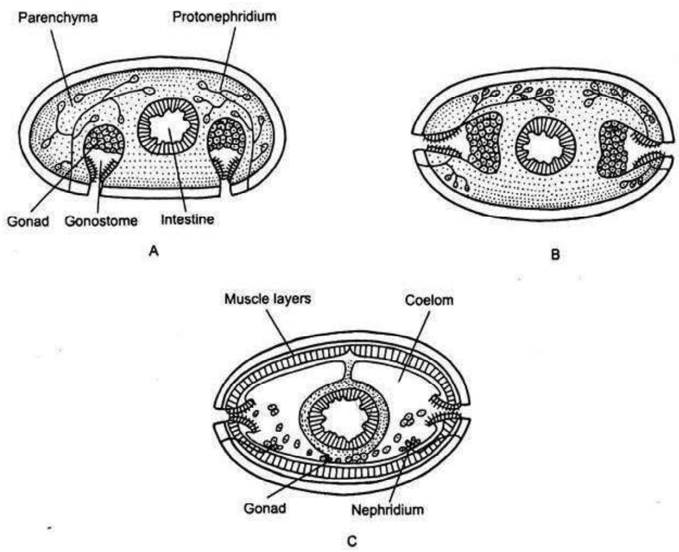

Fig. 1.3 Gonocoel Theory of Coelom Formation

- **Nephrocoel Theory (Lankester, 1874, Snodgrass, 1938):** The theory states that the coelom originated from expanded nephridia of flatworms. The chief objection of this theory is that the protonephridia was not recorded in all coelomates, even the echinoderms do not have excretory organs.

Schizocoel Theory (Clark, 1964): The theory states that the coelom could have evolved by splitting of mesodermal plates.

Significance of Coelom

The coelom plays a great role in life of the animals. Some important reasons are:

- The coelomic fluid contents facilitate smooth transportation of particles or materials in solution.

- Coelom provides flexibility to the body and enhances room for the movement of the gut which remains suspended.
- Gonads which develop from coelomic epithelium are housed in cavity of the coelom. So are the nephridial tubules, which connect the coelom to the exterior and in some cases also allow the passage of eggs and sperms.
- Coelom filled with incompressible coelomic fluid acts as a hydrostatic skeleton and helps majorly in locomotion.

1.2.1 Acoelomates

Acoelomate are the animals that does not possess a body cavity. Unlike coelomates (eucoelomates), animals with a true body cavity, acoelomates lack a fluid-filled cavity between the body wall and digestive tract. Acoelomates have a triploblastic body plan, meaning that their tissues and organs develop from three primary embryonic cell (germ cell) layers.

Acoelomates lack a fluid-filled body cavity between the body wall and digestive tract. This can cause some serious disadvantages. Fluid compression is negligible, while the tissue surrounding the organs of these animals will compress. Therefore, acoelomate organs are not protected from crushing forces applied to the animal's outer surface.

In addition to not having a body cavity, acoelomates have simple forms and lack highly developed organ systems. For example, acoelomates lack a cardiovascular system and respiratory system and must rely on diffusion across their flat, thin bodies for gas exchange. Acoelomates commonly possess a simple digestive tract, nervous system, and excretory system.

They have sense organs for detecting light and food sources, as well as specialized cells and tubules for eliminating waste. Acoelomates commonly have a single orifice that serves as both an inlet for food and an exit point for undigested waste. They have a defined head region and display bilateral symmetry that means they can be divided into two equal left and right halves.

Examples of acoelomates are found in the kingdom animalia and the phylum platyhelminthes. Commonly known as flatworms, these invertebrate animals are unsegmented worms with bilateral symmetry. Some flatworms are free-living and commonly found in freshwater habitats.

In short, the key features of acoelomates can be listed as:

- The body is usually dorsa-ventrally compressed.
- There is no proboscis dorsal to the gut.
- The gut, when present, has a single aperture (the mouth) and tends to be complex, ramifying throughout the body.
- There is no blood vascular system.
- The excretory system consists of a series of scattered flame cells which occur throughout the body.
- They are usually hermaphrodite.
- The reproductive organs are very complex. The female gonad is usually divided into an ovarium and a vitellarium.

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- The genital ducts are complex and permanent. They may be free-living, epizoic, or ecto- or endoparasites.

1.2.2 Pseudocoelomates

An organism with a body cavity that is not derived from the mesoderm, as in a true coelom, or body cavity is known as pseudocoelomate. The body cavity of a pseudocoelomate is derived from the blastocoel, or cavity within the embryo and therefore it is also known as a blastocoelomate. A true coelom is lined with a peritoneum which separates the fluid from the body cavity. The fluid present in the cavity gives oxygen and nutrients to the organs in a pseudocoelomate. They have a body cavity but it is not lined with mesodermal cells. It exists between the mesoderm and the endoderm that makes up the walls of the gut.

The pseudocoelomates include the nematodes, rotifers, gastrotrichs and introverts. They derive their body cavity partly from endoderm tissue and partly from mesoderm.

1.2.3 Coelomates: Protostomia and Deuterostomia

On the basis of their origin and embryonic development, metazoans are divided into protostomes and deuterostomes. Protostomes are the primitive invertebrates, while deuterostomes include chordates and echinoderms. The main difference between protostomes and deuterostomes is that the blastopore in protostomes are developed into a mouth while the blastopore in deuterostomes is developed into an anal opening.

An outline of classification of animal kingdom on the basis of level of organisation is given below.

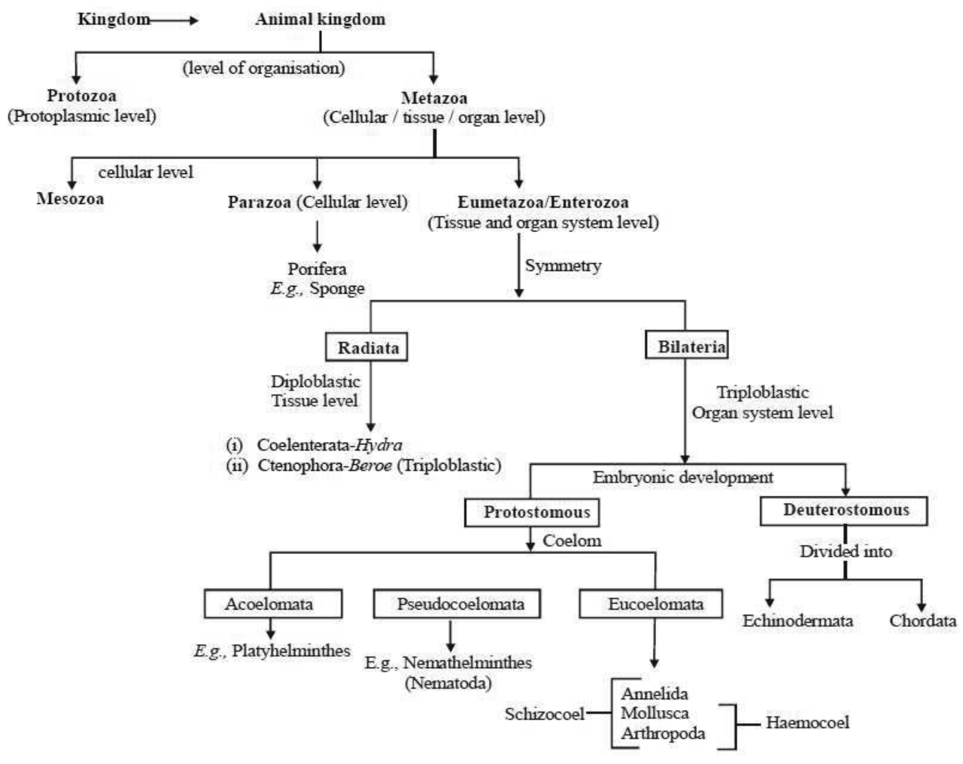

Fig. 1.4 *An outline of classification of animal kingdom*

Protostomia: Protostomia is the class of animals that were once thought to be characterized by the formation of the organism's mouth before its anus during embryonic development. This nature has since been discovered to be extremely variable among the protostomia's members, although, the reverse is typically true of its sister class, deuterostomia. Some examples of protostomes are nematodes, arthropods, flatworms, annelids and molluscs.

In animals like earthworms, the first phase in gut development involves the embryo forming a dent on one side (the blastopore) which deepens to become its digestive tube (the archenteron). In the sister-clade, the deuterostomes, the original dent becomes the anus while the gut eventually tunnels through to make another opening, which forms the mouth. The protostomes were so named because it was once believed that in all cases the embryological dent formed the mouth while the anus was formed later, at the opening made by the other end of the gut. It is now known that the fate of the blastopore among protostomes is extremely variable; while the evolutionary distinction between deuterostomes and protostomes remains valid, the descriptive accuracy of the name protostome is disputable.

Deuterostomia: Deutrostomia are the animals typically characterized by their anus forming before their mouth during embryonic development. Protostomia are the animals whose digestive tract's development is more varied. Some examples of deuterostomes include sea stars, and crinoids.

In deuterostomy, the developing embryo's first opening (the blastopore) becomes the anus, while the mouth is formed at a different site later on. This was initially the group's distinguishing characteristic, but deuterostomy has since been discovered among protostomes as well. This group is also known as enterocoelomates, because their coelom develops through enterocoely.

The three major clades of deuterostomes are chordata (e.g., vertebrates), echinodermata (e.g., starfish), and hemichordata (e.g., acorn worms). Together with protostomia and their out-group xenacoelomorpha, these compose the bilateria, animals with bilateral symmetry and three germ layers.

Initially, deuterostomia included the phyla brachiopoda, bryozoa, chaetognatha, and phoronida based on morphological and embryological characteristics. However, superphylum deuterostomia was redefined in 1995 based on DNA molecular sequence analyses when the lophophorates were removed from it and combined with other protostome animals to form superphylum lophotrochozoa. The phylum chaetognatha (arrow worms) may belong here, but molecular studies have placed them in the protostomes more often.

Protostome and deuterostome embryos differ in several other ways. Many protostomes (the Spiralia clade) undergo spiral cleavage during cell division instead of radial cleavage. Spiral cleavage happens because the cells' division planes are angled to the polar major axis, instead of being parallel or perpendicular to it. Another difference is that secondary body cavities (coeloms) generally form by schizocoely, where the coelom forms out of a solid mass of embryonic tissue splitting away from the rest, instead of by enterocoelic pouching, where the coelom would otherwise form out of in-folded gut walls.

While protostomes as a monophyletic group has strong support, research have shown that deuterostomes may be paraphyletic, and what was once considered traits of deuterostomes could instead be traits of the last common bilaterian ancestor. This suggests the deuterostome branch is very short or non-existent. The xenambulacraria's sister group could be both the chordates and the protostomes, or be equally distantly related to them both.

The common ancestor of protostomes and deuterostomes was evidently a worm-like aquatic animal. The two clades diverged about 600 million years ago. Protostomes evolved into over a million species alive today, compared to about 60,000 deuterostome species.

Check Your Progress

1. Define coelom.
2. Define acoelomates.
3. What is the main role of coelom?
4. What do you understand by pseudocoelom?
5. Define haemocoelom.

1.3 LOCOMOTION

Let us study the various kinds of movements, such as flagella and ciliary movement and hydrostatic movement.

1.3.1 Flagella and Ciliary Movement in Protozoa

Protozoans are located in most habitats; free-living species inhabit freshwater and marine environments, whereas terrestrial species inhabit decaying organic matter. A few species of protozoans are parasitic in nature. They are unicellular or acellular eukaryotic organisms. The body comprises mass of protoplasm; hence they are called acellular animals. A single cell performs all the vital metabolic functions of the body. They are notable for their ability to move independently, a characteristic found in the majority of species. Protozoans vary substantially in size and shape. Smaller species are of the size of fungal cells; larger species may be visible to the unaided eye. Protozoan cells lack cell walls and therefore can take an infinite variety of shapes. Body of the organisms is either naked or covered with a structure known as pellicle. Most protozoan species are aerobic, but some anaerobic species have also been found in the human intestine and animal rumen. No specialized respiratory structures. It occurs through the general body surface. Protozoans are heterotrophic microorganisms, and most species obtain large food particles by phagocytosis. The food particles are ingested into a food vacuole and lysosomal enzymes then digest the nutrients in the particle, and the products of digestion are distributed throughout the cell. Some species have specialized structures known as cytostomes, through which particles passes inside. Many protozoans alternate between a free-living vegetative form known as trophozoite and a resting form called a cyst. Many protozoan parasites are taken into the body in their cyst form.

The protozoan cyst is somewhat analogous to the bacterial spore, since it resists harsh environmental conditions. Protozoans need to move in search of food, to avoid predators, to get into or out of sunlight, to move towards chemicals they need, or away from chemicals that poison them. With all the diversity of microscopic life, single-celled eukaryotes basically all move around in three or maybe four different ways. Most protozoal species move independently by one of three types of locomotor organelles: flagella, cilia, and pseudopodia. Flagella and cilia are structurally similar, having a "9-plus-2" system of microtubules, the same type of structure found in the tail of animal sperm cells and certain cells of unicellular algae. How a protozoan move is an important consideration in assigning it to a group. Protozoans are loosely classified by their style of movement. In this section, we shall discuss the ciliary and flagellar mode of locomotion in protozoans.

1. Locomotion by Flagella

Flagella are extremely fine, delicate and highly vibratile thread like extension of protoplasm. They are used for a variety of purpose like: generating food currents, anchorage as well as a sensory organelle. Flagella are thread-like cylindrical or flattened band like structure typically consisting of central stiff elastic axoneme. Axoneme is surrounded by a contractile outer sheath. Axoneme may be spirally coiled or straight. In a few flagellates, the outer sheath bears laterally frayed fibrils like structure known as mastigonemes. They are also known as flimmer.

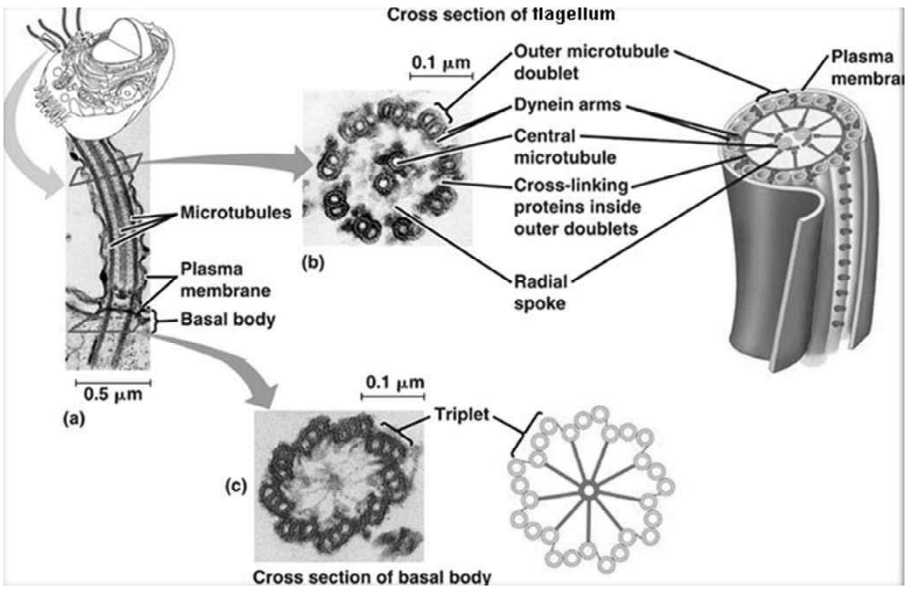

Fig 1.5 *Cross-Section of a Flagellum*

On the basis of presence and arrangement of mastigonemes, flagella are classified as follows:

(a) **Stichonematic Flagella-** Stichonematic flagella bears only a single row of lateral mastigonemes. For instance, as seen in *Euglena*.

(b) **Pantonematic Flagella-** Pantonematic flagella bears lateral mastigonemes on both sides. For instance, as seen in *Peranema*.

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(c) **Acronematic Flagella-** Acronematic flagella bears a single or terminal mastigoneme or filament. This type of flagella is also known as whip flagellum. For instance, as seen in *Cerconomas.*

(d) **Pentachronematic Flagella-** Pentachronematic flagella bears mastigonemes on one or both lateral sides as well as at the tip of flagella.

(e) **Simple Flagella-** Simple flagella bears neither terminal filament nor the the mastigoneme. For instance: as seen in *Trypanosoma*.

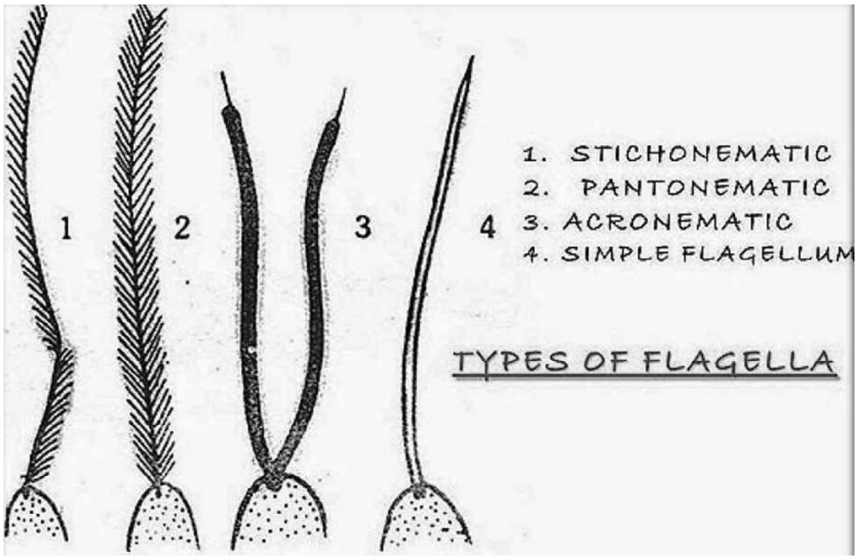


Fig 1.6 *Different Types of Flagella on the Basis of Presence and Arrangement of Mastigonemes*

Flagella begins from the anterior body end either directly or via a grove known as pit or cytopharynx. The axoneme arises from a basal granule referred to as kinetosome or blepharoplast. Basal granule is usually connected to the nucleus via fibrils referred to as rhizoplast which might associate it with a parabasal body.

The number of flagella present in an organism varies from species to species. Generally, one or rarely two flagella are seen in an organism. However, numerous flagella are observed in parasitic forms such as *Giardia*. The flagella which is directed in forward direction is referred to as tractellum whereas the other which is directed in backword direction is the chief organ of propulsion of organism and is known as trailing flagellum. Rarely, a flagellum, might be inserted at the posterior end of the body is known as choanoflagellate.

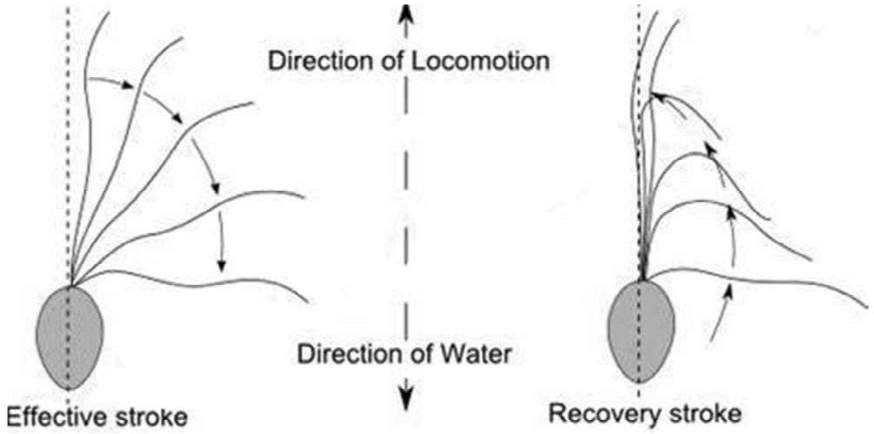
Mastigonemes (protozoans that possess flagella as the chief locomotory organ) exhibits flagellar movement. Flagellar movement are of following types:

A. Simple conical gyration

This refers to a series of lateral movements which drives the organism in forward direction. This type of movement was first described in Butschli's screw theory. This theory postulates about spiral turning like a screw. This screw-like motion leads to the pulling of the animal in the forward direction with spiral rotation as well as gyration. Even though, the exact mechanism for this type of flagellar movement is not known, it is supposed that axonemal fibres are involved in this process. Further, sliding tubules theory postulates that doublet slide past each other, which is the major cause of movement in flagella. The energy for this type of movement comes from mitochondrial ATP.

B. Paddle stroke

For the first time, this type of flagellar movement is described by Ulehla and Krijsman in the year 1925. Paddle stroke kind of flagellar movement consist of an effective stroke or down-stroke in the opposite direction of movement and relaxed recovery stroke in the direction of water's movement. During recovery stroke, flagellum is brought again in the forward direction, for next effective stroke. As flagella give effective stroke in water in backward direction then water propels organism in the forward direction.



Sidewise Lash Movement of Flagellum

Fig 1.7 *Paddle Stroke Movement of Flagellated Animals*

C. Undulating motion

Undulating movement involves wave-like undulation which happens from base to tip or from tip to base. If these wave-like undulation takes place from tip to base, the animal is pulled in the forward direction, and if wave-like undulation takes place from base to tip animal is pulled in the backward direction. And when undulations are spiral the animal starts rotating.

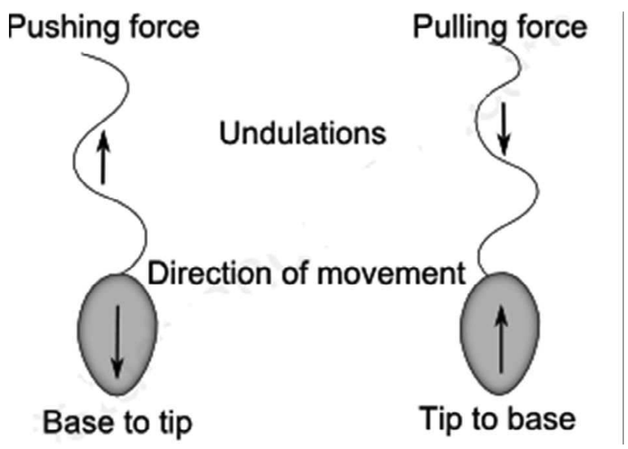


Fig 1.8 *Undulating Movement of Flagellum*

2. Locomotion by Cilia

Cilia are short, fine, hair like structure majorly composed of ectoplasm. Cilia aid in food capturing, serve as tactile organelles in several organisms and also are locomotory in function. Cilia may be arranged longitudinally, diagonally or spirally on the body surface of a protozoa. They may be present throughout the body of a ciliary organism or may be restricted to particular zones known as ciliary zones or fields. They may be uniform in length or slightly longer in certain parts of an organism body surface. For instance, in vorticella, the cilia are restricted only in a concentric circle at the distal end of the body. Cilia are usually ar-ranged in definite rows. A cilium has practi-cally the same histology as that of a flagel-lum. The Paramecium moves forward in a ro-tating fashion by the beating movement of the cilia. The cilia act as small oars and the backward strokes are swift, which push the animal forward.

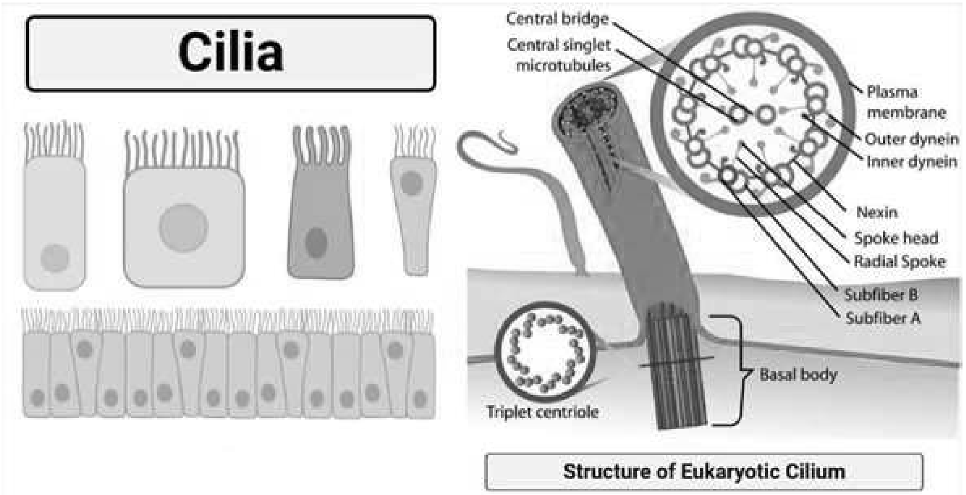


Fig 1.9 *Structure of a Eukaryotic Cilium*

Cilia fuses together to form compound ciliary organelles namely:

A. Undulating membrane

Undulating membranes are thin, transparent flat sheet like structure which comprises one to numerous rows of longitudinal cilia. Undulating membrane aid in food capturing as they can be protruded out to act as scoop for capturing food.

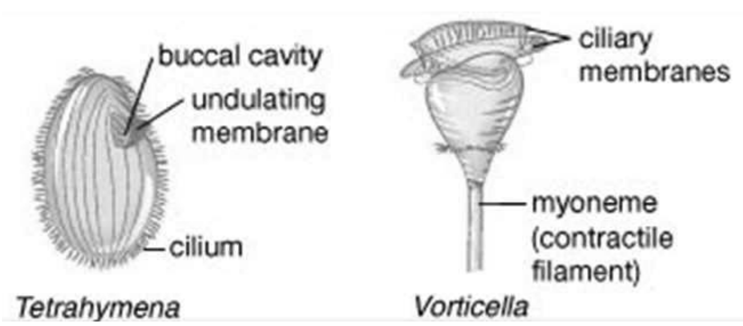


Fig 1.10 *Structure of Undulating Membrane and Ciliary Membranelles in Ciliated Organism*

B. Membranelles

Membranelles are triangular flap like structure formed by the fusion of one to numerous transverse rows of cilia. However, these fused cilia remain free at their edges. Membranelles aid in locomotion or to bring the food particle to cytostome.

C. Cirri

Cirri can occur on frontal, ventral, caudal, or anal surface of an organism. They are composed of a tuft of cilia arranged in two or three rows fused entirely. As cirri are highly movable structures, they can be used like legs for performing crawling like motion.

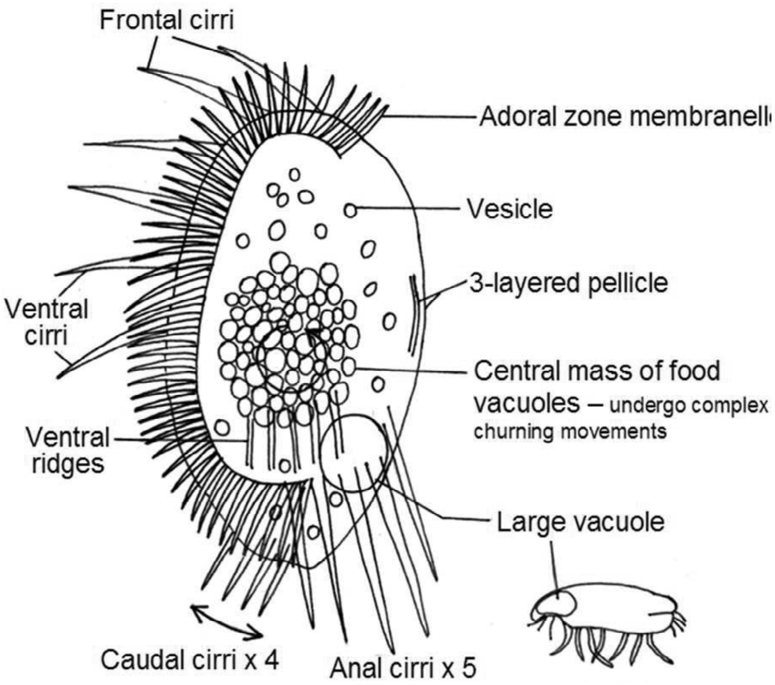


Fig 1.11 *Cirri in a Ciliated Organism*

Ciliary movement involves the oscillation of cilia in a pendulum-like fashion. At each oscillation, there is a fast effective stroke which is followed by the recovery stroke, just like mentioned above for flagellar movement. During the effective stroke, cilia expel the water in the backward direction like an oar of the boat, and in response to this effective stroke water propels the animal in the forward direction. During recovery stroke, cilia come in forward direction ready for next effective stroke. Cilia neither beat simultaneously nor independently. Cilia beat progressively in a characterized wave-like manner.

Due to ciliary movement, animal does not move in the straight path, on the contrary, it rotates spirally like a bullet of rifle in left-handed helix manner. This happens as cilia do not beat directly straight, beating is somehow obliquely toward the right and might be cilia at oral groove beat more obliquely and vigorously away from the mouth. This combined effect causes swimming movement in the ciliated animal.

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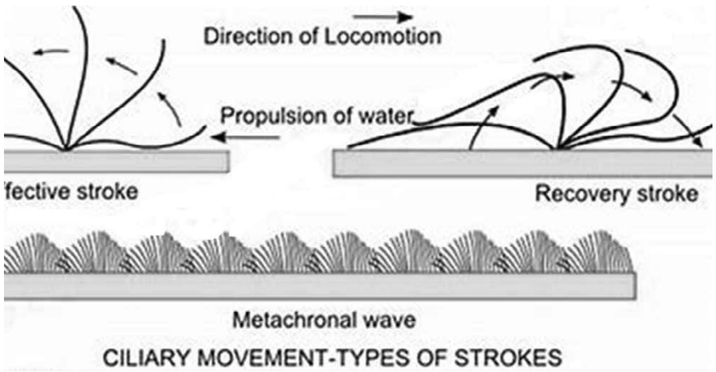

Fig 1.12 *Ciliary Movement in a Ciliated Organism*

Let us study the difference between flagella and cilia.

Table 1.1 *Differences between Flagella and Cilia*

Flagella	Cilia
• Flagella are large in size.	• Cilia are small in size.
• They are commonly present at one end of the organism or rarely at both ends	• They are present throughout the body.
• Flagella beat in a whip-like motion.	• Cilia beat in an oar-like motion.
• Flagella mostly helps in locomotion. feeding	• Cilia helps in locomotion, aeration, as well as circulation.
• Only a few flagella are present in an organism.	• Numerous cilia are present on the surface of organism.

1.3.2 Hydrostatic Movement in Coelenterata, Annelida and Echinodermata

First, let us study the hydroskeleton in detail.

Hydroskeleton

Hydrostatic skeleton refers to a flexible skeleton supported by fluid pressure. As the name suggests, hydro means 'water' and being hydrostatic means that the skeleton or organ is filled with fluid. In general, coelomic organism, i.e., animals having a coelomic cavity or marine animals possess hydrostatic skeletons which are is generally seen in coelomic animals like earthworm or aquatic animals like jelly fish, starfish and sea anemones. Earthworms possess rings of muscles filled with fluid, making their entire body hydrostatic. On the contrary, sea anemone has a hydrostatic head with arms radiating out around the oral structure (mouth) which helps in feeding and locomotion. However, more advanced organisms are referred to as hydrostatic when they possess hydrostatic organ instead of a hydrostatic skeleton.

Structure of Hydrostatic Skeleton

Hydrostatic skeletons are typically arranged in cylindrical pattern and possess two mechanical units: the muscle layers and the body wall. The contraction of longitudinal and circular muscles helps to shorten and lengthen the organism body respectively. Further, due to uniform distribution of the fluid throughout the body, the force generated spread through whole organism.

- Contractions of the circular muscles lengthen the organism's body, while contractions of the longitudinal muscles shorten the organism's body. These muscle fibres are arranged either in continuous sheets or as isolated bundles.
- The diameter is controlled by three different types of muscles, namely circular, radial, and transverse. Circular muscles wrap around the circumference of the cylinder and its contractions helps to lengthen the organism body; radial muscles extend from the central portion of the cylinder towards the surface whereas transverse muscles are arranged in a parallel and perpendicular fashion traversing the diameter of the cylinder.

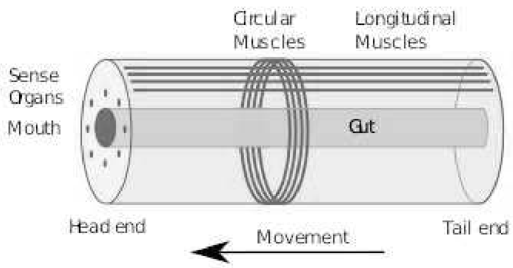

Fig. 1.13 *Structure of Hydrostatic Skeleton Showing Arrangement of Circular and Longitudinal Muscles*

Hydrostatic skeletons are filled with fluid which is most often water. This fluid is highly resistant to changes in volume. The contraction of longitudinal, circular, radial or transverse muscles increases the fluid pressure within the cylinder resulting in changes in length.

Changes in shape are limited by connective tissue fibres which are arranged in a helical shape within the wall of the hydrostatic skeleton and are often collagenous in nature. The helical shape formed by these fibres allow for lengthening and shortening of the skeleton while remaining rigid to prevent torsion. The pitch of the helix will change with the shape of the cylinder. The angle relative to the longitudinal axis will decrease during elongation and increase during shortening of the cylinder.

Advantages of Hydrostatic Skeleton

Most of the invertebrate animals are soft bodied and the presence of a hydrostatic skeleton provides them with much flexibility to move through with very little muscle mass.

- It helps the animals to move around easily and rapidly while swimming and burrowing.
- They can move easily through passages of variable shape and size helping them to escape predators.
- They can heal their wound faster than those possessing hard skeletons.
- The fluid filled system helps provides effective protection to internal organs.

Disadvantages of Hydrostatic Skeleton

- These are simpler organisms with limited ability for attachment of limbs and hence fail to grab on to things.
- Organisms with hydrostatic skeletons continuously require being in an environment that allows them to acquire their fluid that is essential for their survival. Hence, hydrostatic skeleton is common in marine animals.

Let us study hydrostatic movement in different phyla.

(a) In Coelenterates

Aurelia is a genus of scyphozoan jellyfish, commonly called moon jellies which can be considered to study the hydrostatic movements in coelenterates.

The well-developed musculature of the Aurelia is mainly confined to its subumbrellar region. The muscle processes are formed of epithelio-muscle cells of epidermis. The types of muscle found in Aurelia are:

- **Coronal Muscle:** It is broad, circular and peripheral muscle band which extends along the periphery of sub-umbrella.
- **Longitudinal Muscle:** They are present in tentacles, manubrium and oral arms.
- **Radial Muscle:** They extend from manubrium to coronal muscle.

The highly developed musculature helps in performing the locomotion during which the exumbrellar surface of the Aurelia is kept upwards. The water is forced out of the subumbrellar cavity by rhythmic contractions of the circular muscles. As a result, body propels in upward and forward direction. This type of jet propulsion is referred to as hydropropulsion. However, the body gradually sinks to the bottom as the contractions stop. On the other hand, horizontal movements are passive depending upon water currents and the wave action. The gel-like mesoglea provides buoyancy whereas tentaculocytes maintain equilibrium in case the body of the animal gets tilted while swimming.

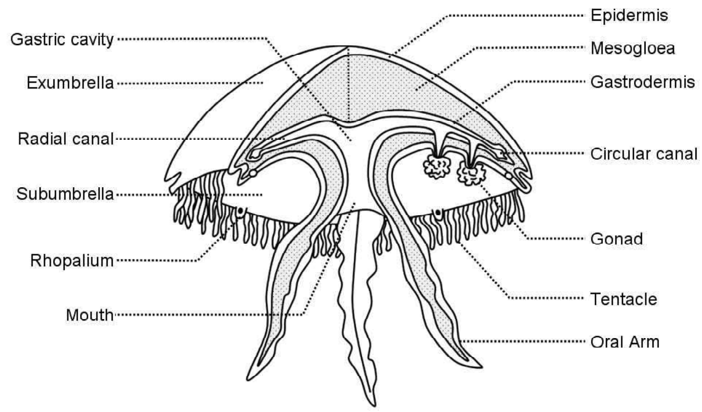

Fig 1.14 *Medusa Stage of Aurelia*

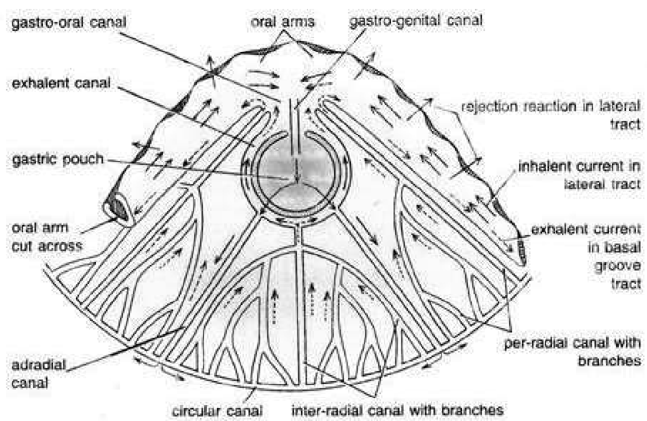

Fig 1.15 *Circulation of Water in Aurelia*

(b) In Annelida

Annelids are aquatic (either marine or fresh water) or terrestrial; free-living or parasitic organism having organ-system level of body organization and bilateral symmetry. They are triploblastic i.e., possess three germ layers namely ectoderm, mesoderm and endoderm. They are coelomate animals with metameric segmentation. The body surface is noticeably marked out into segments called as metameres and hence, the phylum is known as Annelida. They possess longitudinal and circular muscles fibres which help in locomotion. *Pheretima,* commonly known as earthworm, is the best example of terrestrial annelids. It is a burrower i.e. it prefers to live in burrows.

It is nocturnal (active at night) in habit and chooses to stay in its burrows during day time. It feeds on dead and decaying organic matter present in the soil. It is vermiform, elongated, cylindrical animal with pointed front. It measures about 150 mm in length and 3 to 5 mm in width. It is of clay to brown colour which is due to the pigment porphyrin present in the body wall. The dorsal surface of the animal is darker than the ventral surface. The soft body of the animal is divided into 100 to 120 segments called as metameres or somites. The segments are separated from each other by ring like grooves. The external segmentation is in accordance with the internal segmentation.

A distinct head as well as sense organs like cirri, eyes are absent in earthworm. A girdle-like thick glandular tissue permanently surrounding the segment 14-16 is known as clitellum. The primary function of the clitellum is to secrete mucus, albumen or cocoon for eggs. Due to clitellum, the body of the earthworm is divided into three regions namely peri-clitellar, clitellar and post-clitellar. At the middle of each segment, a ring of tiny bristles called setae are present which are composed of horny nitrogenous substance known as chitin.

Approximately, 80 to 100 setae are present on each segment, however, they are absent on clitellum, peristomium and pygidium. *Pheretima* contains a lot of apertures:- Mouth- a crescentic anterior aperture; Anus- a slit like aperture at posterior end; Female genital pore- aperture of oviduct located on ventral surface of 14^{th} segment; Male genital pore- opening of prostatic and spermatic ducts on ventral surface of 18^{th} segment; Nephridiopores- minute openings of integumentary nephridia; Dorsal pores- minute apertures of coelomic chambers; Genital papillae- Two pairs of rounded elevations, one pair each on 17^{th} and 19^{th} segment are located on ventral surface.

Hydrostatic Skeleton in Annelida

Body cavity of earthworm is true coelom. True coelom lies between the gut and outer body wall musculature and lined by coelomic epithelium derived from the embry-onic mesoderm. The coelom in earthworm is partitioned by a series of transverse intersegmental septa. The septa are of two types i.e., perforated and non-perforated. Septa are absent in the first four segments where the coelom is continuous. There are transverse and oblique septa anterior to clitellum while in the posterior region all septa are porous. Contraction of these septa increases the pressure on coelomic fluid, hence making the anterior segments elongated during locomotion or burrowing. The coelom of *Pheretima* is filled with alkaline, colourless or milky coelomic fluid containing salts, proteins and water. Coelom consist of four different types of corpuscles like phagocytes, mucocytes, circular nucleated cells and chloragogen cells which are excretory in function and helps in removing excretory waste products from coelomic fluid. Coelomic fluid performs a variety of function like:-

- It helps in performing locomotion.
- It helps in distribution of digested food.
- It keeps the body moist and help in performing cutaneous respiration.
- It forms a protective, shock proof jacket around the internal organs.
- Chloragogen cells of coelomic fluid helps in removing the excretory products out of the body.
- It also destroys harmful bacteria and parasites in soil.

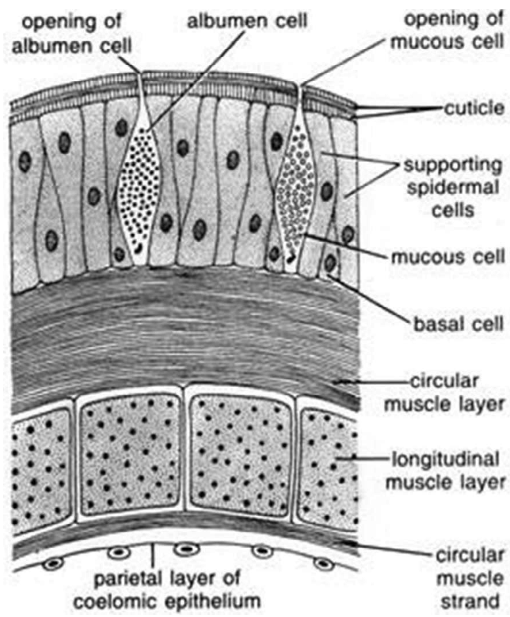

Fig 1.16 *T.S of Body Wall of Pheretima*

A proper skeleton composed of bone or cartilage is absent in earthworm. Instead, earthworm has hydrostatic skeleton. Hydrostatic skeleton refers to a flexible skeleton supported by fluid pressure. As the name suggests, hydro means "water" and being hydrostatic means that the skeleton or organ is filled with fluid. In general, coelomic organism i.e., animals having a coelomic cavity or marine animals possess hydrostatic skeleton. It is generally seen in coelomic animals like earthworm or aquatic animals like jelly fish, starfish and sea anemones. Earthworms possess rings of muscles filled with fluid, making their entire body hydrostatic. On the contrary, sea anemone has a hydrostatic head with arms radiating out around the oral structure (mouth) which helps in feeding and locomotion. However, more advance organisms are referred to as hydrostatic when they possess hydrostatic organ instead of a hydrostatic skeleton.

During burrowing, the posterior muscles of the earthworm contracts, forcing the coelomic fluid towards the anterior end. The hydraulic force of the coelomic fluid transforms transverse septa into oblique and oblique septa into transverse type. This makes the anterior four segments very hard for burrowing into the soil.

Locomotion in earthworm is brought about by musculature of body wall and setae. During locomotion, contraction of circular muscles commences at the anterior end and this wave travels backwards, leading the anterior region to extent in the forward direction. The anterior end of the animal grips the substratum whereas setae act as anchors. Further, the circular muscles relax and longitudinal muscles of the anterior segments start contracting. This wave of contraction shortens the anterior end and causes the posterior part of body to pull forward. Alternate contractions of circular and longitudinal muscles cause wave of thickening to pass backward. During the process of locomotion, coelomic fluid serves as hydraulic skeleton whereas setae cause the body to anchor firmly.

(c) In Echinodermata

Water Vascular System: The water vascular system is present in all Echinoderms and develops from the left hydrocoel. This hydraulic system is enterocoelic in origin. The water vascular system is positioned just above the haemal system. This hydraulic system is primarily locomotory in function but also sub-serves the function of excretion, tactile and respiratory organs in some Echinoderms. The histology of the water vascular system discloses that the canals comprise an inner lining of flat ciliated epithelium, a layer of longitudinal muscles, a connective tissue layer and an outermost layer of flat ciliated cells.

Check Your Progress

6. Define undulating membranes.
7. What do understand by cilia?
8. Define membranelles.
9. What do you understand by clitellum?
10. Define hydrostatic skeleton.

1.4 ANSWERS TO 'CHECK YOUR PROGRESS'

1. Coelom refers to the fluid-filled cavity bounded on all sides by mesoderm and is positioned in between the alimentary canal and the body wall.
2. Aceolomates means without a coelom or fluid-filled cavity. The space between the gut and body wall is filled by densely packed connective tissue derived from both ectoderm and endomesoderm (entomesoderm), called parenchyme.
3. Coelom provides flexibility to the body and enhances room for the movement of the gut which remains suspended.
4. Pseudocoelom means false cavity, formed by persistence of embryonic blastocoel. The term 'pseudocoelom' usually refers to the space which is not develop from embryonic mesoderm and is not lined by coelomic epithelium derived from the mesoderm.

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5. Coelom in which the true coleomic cavity is greatly reduced and filed with boold. Example: arthropoda and mollusca.
6. Undulating membranes are thin, transparent flat sheet like structure which comprises of one to numerous rows of longitudinal cilia.
7. Cilia are short, fine, hair like structure majorly composed of ectoplasm. Cilia aid in food capturing, serve as tactile organelles in several organisms and also are locomotory in function.
8. Membranelles are triangular flap-like structure formed by the fusion of one to numerous transverse rows of cilia. However, these fused cilia remain free at their edges.
9. A girdle-like thick glandular tissue permanently present in earthworm, surrounding the segment 14-16 is known as clitellum.
10. Hydrostatic skeleton refers to a flexible skeleton supported by fluid pressure. As the name suggests, hydro means "water" and being hydrostatic means that the skeleton or organ is filled with fluid.

1.5 SUMMARY

- Coelom (Greek: coel = hollow cavity) refers to the fluid-filled cavity bounded on all sides by mesoderm and is positioned in between the alimentary canal and the body wall.
- Developmentally, coelom arises as a split in mesoderm which bifurcates into two layers, a somatic layer next to the epidermis and a splanchnic layer around the endoderm.
- Acoelomate are the animals that does not possess a body cavity. Unlike coelomates (eucoelomates), animals with a true body cavity, acoelomates lack a fluid-filled cavity between the body wall and digestive tract.
- Acoelomates lack a fluid-filled body cavity between the body wall and digestive tract. This can cause some serious disadvantages.
- The ancestral coelomate animals are thought to have had segmentally arranged mesodermal pouches.
- From the mesodermal pouches, gametes were formed, by the process of proliferation of epithelial lining.
- The coelomic fluid within the coelom is in constant circulation by movement of the cilia of peritoneal cells and by the contractions of the muscular body. The coelomic fluid contains wandering leucocytes, disc-like haemerythrin, reproductive cells and excretory cells.
- In Echinodermata, the coelom in the adult echinoderms is represented as several distinct spaces. It develops as pair of lateral pouches and later become separated from the embryonic enteron.

- The coelomic fluid contents facilitate smooth transportation of particles or materials in solution.
- Coelom provides flexibility to the body and enhances room for the movement of the gut which remains suspended.
- Gonads which develop from coelomic epithelium are housed in cavity of the coelom. So are the nephridial tubules, which connect the coelom to the exterior and in some cases also allow the passage of eggs and sperms.
- Coelom filled with incompressible coelomic fluid acts as a hydrostatic skeleton and helps majorly in locomotion.
- Hydrostatic skeleton refers to a flexible skeleton supported by fluid pressure. As the name suggests, hydro means 'water' and being hydrostatic means that the skeleton or organ is filled with fluid.
- Hydrostatic skeletons are typically arranged in cylindrical pattern and possess two mechanical units: the muscle layers and the body wall. The contraction of longitudinal and circular muscles helps to shorten and lengthen the organism body, respectively.
- Most of the invertebrate animals are soft bodied and the presence of a hydrostatic skeleton provides them with much flexibility to move through with very little muscle mass.
- The water vascular system is present in all echinoderms and develops from the left hydrocoel. This hydraulic system is enterocoelic in origin.
- The canals of the hydraulic system contain a fluid of albuminous nature having sea water and leucocytes.
- Protozoans are located in most habitats; free-living species inhabit freshwater and marine environments, whereas terrestrial species inhabit decaying organic matter.
- Most protozoan species are aerobic, but some anaerobic species have also been found in the human intestine and animal rumen.
- Most protozoal species move independently by one of three types of locomotor organelles: flagella, cilia, and pseudopodia.
- Flagella and cilia are structurally similar, having a “9-plus-2” system of microtubules, the same type of structure found in the tail of animal sperm cells and certain cells of unicellular algae.
- Undulating movement involves wave-like undulation which happens from base to tip or from tip to base. If these wave-like undulation takes place from tip to base, the animal is pulled in the forward direction, and if wave-like undulation takes place from base to tip animal is pulled in the backward direction.
- Cilia are short, fine, hair like structure majorly composed of ectoplasm. Cilia aid in food capturing, serve as tactile organelles in several organisms and also are locomotory in function.

1.6 KEY TERMS

- **Coelom:** It refers to the fluid-filled cavity bounded on all sides by mesoderm and is positioned in between the alimentary canal and the body wall.
- **Acoelom:** It means without a coelom or fluid-filled cavity. The space between the gut and body wall is filled by densely packed connective tissue derived from both ectoderm and endomesoderm (entomesoderm), called parenchyme.
- **Pseudocoelom:** Pseudocoelom means false cavity, formed by persistence of embryonic blastocoel. The term 'pseudocoelom' usually refers to the space which is not develop from embryonic mesoderm and is not lined by coelomic epithelium derived from the mesoderm.
- **Haemocoelom:** In this the true coleomic cavity is greatly reduced and filed with boold. Example: Arthropoda and Mollusca.
- **Schizocoely:** The process in which coelom arises by splitting of the mesodermal bands during embryonic development.
- **Enterocoely:** The process through which coelom is formed by the evagination from the embryonic archenteron, pouch-like structures detach from the archenteron and gradually occupy the whole body by enlargement.
- **Myocoel:** This type of coelom originates in Phoronida. In such cases the mesenchyme rearranges to enclose a place called coelom (Marshall and Williams, 1972). It is an unusual method of coelom formation. It is neither entero-coeloms nor schizocoelous.
- **Stone Canal:** Stone canal is also known as the madreporite canal. It is an S-shaped tube whose inner walls are lined by calcareous rings and hence known by the name of stone canal.
- **Ring Canal:** It is a wide pentagonal canal which forms a ring around the oesophagus.
- **Polian Vesicles:** These are pear shaped structure which serves as contractile bladder.
- **Flagella:** Flagella are extremely fine, delicate and highly vibratile thread like extension of protoplasm. They are used for a variety of purpose like: generating food currents, anchorage as well as a sensory organelle.
- **Undulating Membranes**: Undulating membranes are thin, transparent flat sheet like structure which comprises one to numerous rows of longitudinal cilia.
- **Membranelles:** Membranelles are triangular flap like structure formed by the fusion of one to numerous transverse rows of cilia. However, these fused cilia remain free at their edges.

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1.7 SELF-ASSESSMENT QUESTIONS AND EXERCISES

Short-Answer Questions

1. What is the main body cavity in onycophora?
2. Who proposed the enterocoel theory? Give the statement of this theory.
3. Who proposed the gonocoel theory?
4. What is the main role of coelom in invertebrates?
5. What do you understand by hydrostatic movements?

Long-Answer Questions

1. Describe the organization of coelom in invertebrates in detail.
2. Explain the various types of coeloms found in invertebrates.
3. Describe the various theories regarding the coelom formation in detail.
4. Explain the structure of hydrostatic skeleton.
5. Describe the hydrostatic movements in echinodermata in detail.

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NOTES

UNIT 2 NUTRITION, DIGESTION AND RESPIRATION IN INVERTEBRATES

Structure

2.0 INTRODUCTION

Invertebrates are animals that neither possess nor develop a vertebral column (commonly known as a backbone or spine), derived from the notochord. This includes all animals apart from the chordate subphylum Vertebrata. Familiar examples of invertebrates include arthropods (insects, arachnids, crustaceans, and myriapods), mollusks (chitons, snail, bivalves, squids, and octopuses), annelid (earthworms and leeches), and cnidarians (hydras, jellyfishes, sea anemones, and corals).

The majority of animal species are invertebrates; one estimate puts the figure at 97%. Many invertebrate taxa have a greater number and variety of species than the entire subphylum of Vertebrata. Invertebrates vary widely in size, from 50 ?m (0.002 in) rotifers to the 9-10 m (30-33 ft) colossal squid.

The word 'digestion' comes from two Latin words meaning "to carry" (gerere) and "apart" or "asunder" (dis). In all the members of the animal kingdom, the food are made up of organic materials, e.g., carbohydrate, protein, fats, etc. These compounds have a very large molecular configuration.

The large molecules of food are first broken down into simpler units, like monosaccharide's, amino acids, fatty acids and glycerol from polysaccharides, proteins and fats, respectively These are then absorbed and either incorporated into the body or metabolized to provide energy.

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Filter feeding is a form of food procurement in which food particles or small organisms are randomly strained from water. Filter feeding is found primarily among the small- to medium-sized invertebrates but occurs in a few large vertebrates as well.

The respiratory system (also respiratory apparatus, ventilatory system) is a biological system consisting of specific organs and structures used for gas exchange in organisms. Other animals, such as insects, have respiratory systems with very simple anatomical features.

Most insects breath passively through their spiracles (special openings in the exoskeleton) and the air reaches every part of the body by means of a series of smaller and smaller tubes called 'trachaea' when their diameters are relatively large, and 'tracheoles' when their diameters are very small.

The number of spiracles an insect has is variable between species, however, they always come in pairs, one on each side of the body, and usually one pair per segment. The tracheoles make contact with individual cells throughout the body.

Molluscs generally possess gills that allow gas exchange between the aqueous environment and their circulatory systems. These animals also possess a heart that pumps blood containing hemocyanin as its oxygen-capturing molecule.

2.1 OBJECTIVES

After going through this unit, you will be able to:

- Understand various physiological processes in invertebrates
- Describe the histology of alimentary canal in invertebrates
- Explain the process of filter feeding
- Describe the process of nutrition and digestion in invertebrates
- Explain the mechanism of respiration in invertebrates
- Understand the process of respiration in various insects, aquatic, and terrestrial organisms

2.2 NUTRITION AND DIGESTION

Polychaetes is known to be the largest class of phylum Annelida comprising of 1600 genera and more than 5000 species. Ecologically, they are divided in to two groups:

- **Errantia:** This group comprises free swimming, pelagic, crawling, actively burrowing and partially tubicolous forms.
- **Sedentaria:** This group comprises permanent burrowers or tube dwellers.

Polychaete exhibits different types of nutrition mechanism like carnivores or raptorial feeders, direct deposit feeders, indirect deposit feeders and filter feeders. Filter feeder polychaetes are generally sedentary and tubicolous, for example sabella, serpula, etc.

Structure of Alimentary Canal

- It is a straight tube, opening at both the ends- the anterior opening is mouth and posterior opening is anus.
- It is divisible into 3 parts:
  - o **Stomodaeum**: Also termed as foregut, comprises buccal cavity and pharynx
  - o **Mesentron**: Known as midgut, comprises the oesophagus and stomach-intestine
  - o **Proctodaeum**: Also called hindgut, comprises rectum
- Foregut and hingut are lined with ectodermal epithelium, whereas, midgut is lined with the endodermal epithelium.

Histology of the Alimentary Canal

The gut wall is made up of:

- Visceral Peritoneum (outermost layer)
- Longitudinal Muscle Layer
- Circular muscle Layer
- Enteric Epithelium: ectodermal in midgut and ectodermal for foregut and midgut.
- Cuticle layer : Absent in midgut

Filter Feeding in Chaetopterus

- Chaetopterus lives in a U-shaped parchment tube and strains food from water by a unique method.
- The beating of the fans [notopodia of segment 14 -16 are modified to form fan like structure] generates a water current that enters inside the tube via its anterior end and flows out via opposite end.
- Notopodia located at the 10th segment is long wing like structures. The ciliated glandular epithelium of the 10th segment secretes mucous which traps the food particles.
- This mucous bag with entrapped food particles terminates in a ciliated food cup where the food is rolled up into a ball like structure.
- The food ball is pushed along a mid-dorsal ciliary groove to the mouth (Refer Figure 2.1).

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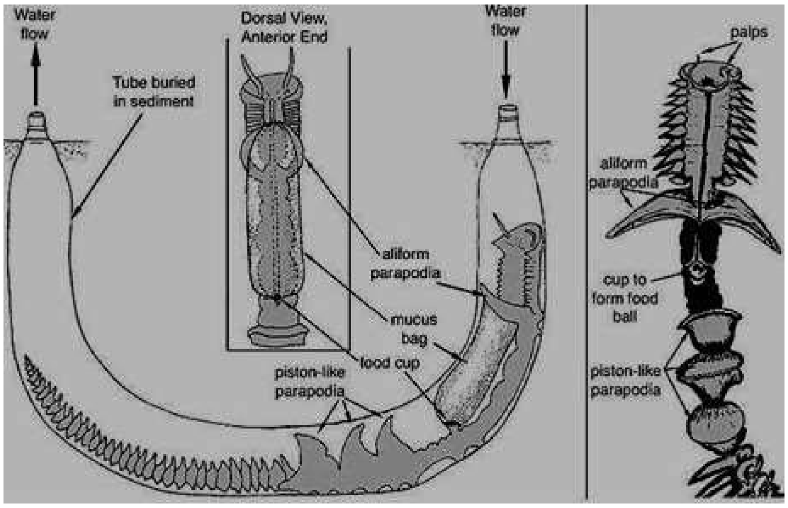

Fig. 2.1 *Filter Feeding Mechanism in Chaetopterus*

The parapodia pumps the water through the tube from anterior to posterior side. A mucus laden bag located between the parapodia and attached to the food cup serves as filter for the water.

Filter Feeding in Arenicola

Arenicola were earlier thought to be direct deposit feeders. In 1959, Kriiger, suggested that they are filter feeders.

- **Arenicola** (lungworms) dig out a L- shaped burrow and ingest sand regularly with its proboscis, which results in the formation of a funnel –shaped depression at the surface.
- When water percolates down the funnel, food particles are filtered by sand.
- This food rich sand is ingested by the animal.
- Defeacation of waste occurs by organism arrival back to the surface, leaving characteristic castings (Refer Figure 2. 2).

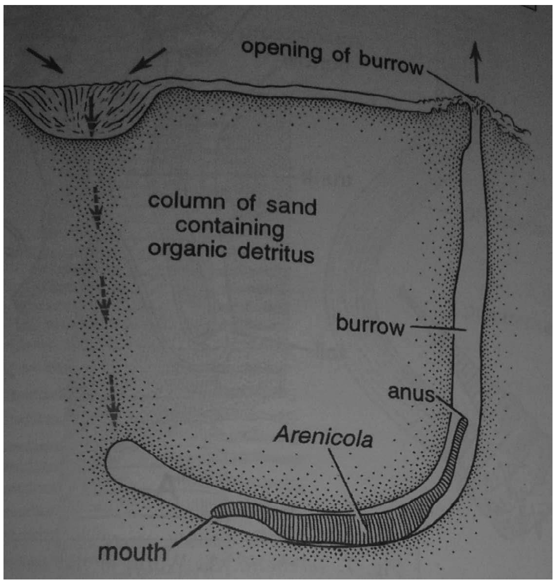

Fig. 2.2 *Food Water Currents in Arenicola*

Filter Feeding in *Nereis diversicolor*

Nereis is a carnivorous and raptorial feeder. However, *Nereis diversicolor* frequently exhibits the mechanism of filter feeding.

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- It secretes a mucous cone at one end of the burrow.
- A constant water current is generated by the dorso-ventarl undulations of its body.
- Water enters inside the burrow from the mucous laden end, whereas, it exits through the other end.
- Mucous serves as a strainer for collecting the food particles coming along with incurrent water current.
- The food laden mucous is finally ingested by the animal.

Components of Digestive System

The major components of digestive system are:

A. Alimentary Canal: It is a long-coiled tube which allows passage of food from mouth to the anus (Refer Figure 2.3).

(a) Mouth

- It appears as a transverse slit located postero-ventrally to the anterior adductor muscles.
- It is bounded by two flattened fleshy flaps called labial palps.
- The upper lip is formed by the fusion of outer palps above the mouth, whereas inner palps fuse below the mouth to form lower lip.
- Both the lips enclose a ciliated oral groove, leading into the mouth.
- The jaws and radula are absent.

(b) Oesophagus

- The mouth terminates into a short and narrow tube called oesophagus.
- It comprises a ciliated inner wall.

(c) Stomach

- The oesophagus opens into a sac-like structure known as the stomach. It is surrounded by large digestive gland which is equivalent to liver. The stomach is divisible into two regions:

Ventral Region

- Ventral tubular style sac consisting of a gelatinous rod called the crystalline style forms this region.
- The rod comprises concentric layers of mucoprotein secreted by ciliated epithelium of the style sac.

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- The rod contains a lot digestive enzymes, amylase and glycogenase.
- Cilia of the style sac cause the rod to rotate and move forward such that its head hits the opposite wall of the stomach (also known as gastric shield). This rotation results in breaking of small fragments containing enzymes from gastric shield and eventually they get mixed with the food particles.
- The entire crystalline style structure slowly dissolves in absence of feeding or when the animal is moved away from water.

Dorsal Region

- The oesophagus and digestive glands opens into this region.
- This portion is folded over the opening of the ducts of the digestive system and helps in sorting mechanism.
- It helps in conduction of partially digested food into digestive duct, dumps the waste material returning from duct into intestine without remixing in the food.

d) Intestine

- The posterior end of the stomach leads into intestine.
- It runs ventrally into the foot coiling through the visceral mass in a characteristic pattern, i.e., ascending limb runs parallel to the descending limb and continues into rectum.

e) Rectum

- The post terminal part of the rectum.
- Its wall appears as a longitudinal, mid-ventral fold called typhlosole.
- It runs posteriorly through the pericardial cavity and eventually opens through the anus into posterior part of cloaca.

B. Digestive Gland

- It is also termed as digestive diverticulum or liver.
- It is a paired structure, dark green or brown in colour that surrounds the stomach.
- It opens into dorsal portion of the stomach through several ducts.
- In Unio, the duct system has two tracts- inhalant and exhalent.
- The inhalant tract is non-ciliated and conducts the food particles into the gland.
- The exhalent tract is ciliated and conducts the waste back into stomach region.

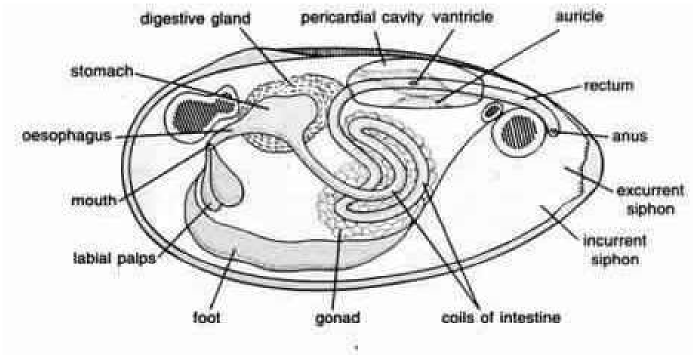

Fig. 2.3 *Alimentary Canal and Digestive Gland of Unio*

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C. Food and Feeding Process

- Unio is a planktonic feeder and feeds on diatoms, microorganism, and organic detritus.
- Filter feeding is shown by bivalves in mollusca, for example, unio.
- The process involves extracting food by straining large amount of water.

Structures Involved in the Process of Filter Feeding

- The paired gills are present in the mantle cavity on either side of the foot.
- Each gill is folded to form two laminae each comprising of two lamellae.
- The gills are plate like structures, formed by the fusion of successive gill filaments, which themselves are perforated with minute pores and surfaced with cilia.
- The water enters into infra- branchial chamber via incurrent siphon and after passing over supra –branchial chamber exits via excurrent siphon.

Process of Filter Feeding

- The process starts with the beating of the lateral cilia of gill filaments against the water, which is then guided by incurrent siphon to the infra-branchial chamber of the mantle cavity.
- The water enters the gills through ostia, passes over supra branchial chamber of the mantle cavity and then exit via excurrent siphon.
- The incurrent water current brings inside a lot of microorganism.
- The beating of latero-frontal cilia of the gill filaments towards the outer surface of lamellae pushes fine food particles on the lamaller surfaces whereas, the heavier sand particles are carried from the gill surface to the edge of the laminae which touches the mantle. These heavier sand particles are dumped in the bottom of mantle cavity.
- The mucous sheet secreted by lameller surfaces entraps the food particles. The downward movement of the frontal cilia of gill filaments pushes the mucous sheet downwards.

- The mucous from both the sides of each gill lamina starts to move into the food groove. Therefore, ciliary beating pushes the food towards the mouth.
- While moving further towards mouth, another sorting mechanism occurs by a series of overlapping folds on the inner surface of labial palps.
- In the gutters between these folds, a set of ciliary tract beat outsides causing the heavier sand particles to move out of mucous into these gutters.
- Another set of ciliary tracts allows the fine food particles to reach the mouth, from where it is passed into stomach via oesophagus.

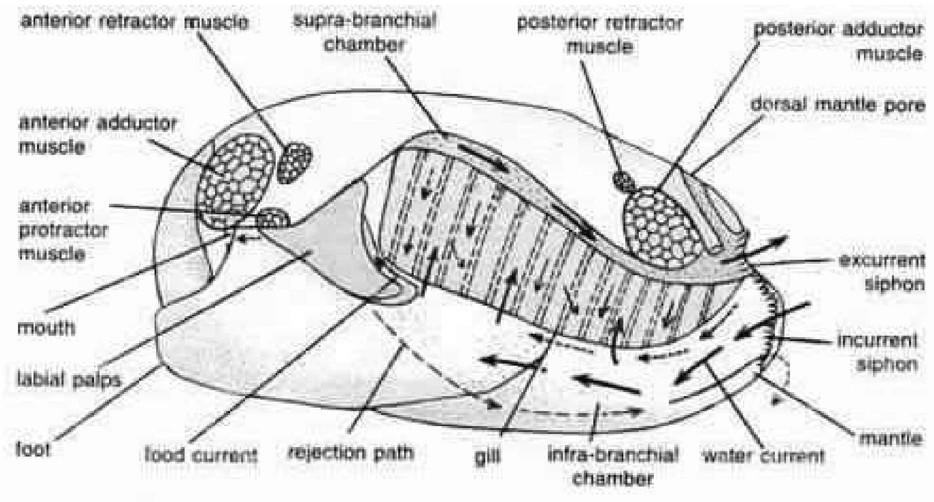

Fig. 2.4 *Water and Food Currents in Unio*

Absorption and Egestion

- Within the stomach, food particles are subjected to sorting, maceration, enzymatic digestion and absorption.
- The crystalline style acts as a stirring rod and its rotation is facilitated by the style sac cilia.
- The rotation led to removal of food particles from mucous sheet entering the stomach.
- The style releases its amylase enzyme into the stomach fluid where it keeps on hydrolysing the carbohydrates extracellularly.
- The dorsal region of stomach guides the fine food particles towards the openings of digestive glands ducts.
- The food is directed to digestive glands by the openings of its ducts wherein it is engulfed by the phagocytotic cells of the epithelial lining.
- Complete intracellular digestion then takes place with the help of carbohydrate, protein, and fat digesting enzymes.
- The undigested food is sent back to stomach from where it is transported to the intestine and packaged as faecal pellets to be ejected from cloaca with the outgoing water current.

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2.2.1 Patterns of Feeding and Digestion in Lower Metazoa

Life commenced on the planet Earth about 3.7 billion years ago. However, first cell to appear was a prokaryote cell without a defined nucleus. Much later, the eukaryotic cell developed having a well-organized nucleus bounded by nuclear membrane. The earlier unicellular organisms were neither plant nor animal in nature instead Ernst Haeckel (1866) called them protista, i.e., small size organisms consisting of a nuclear apparatus in a cytoplasmic body which is not divided into cells. However, multicellularity developed in both plants and animals known as metaphyta and metazoa respectively with an increase in complexity of life. To date, no direct evidence about the ancestors of metazoans have been provided. Though, zoologists agree that the metazoans must have evolved from some primitive unicellular or acellular organisms, such as Protozoans. However, the origin of metazoans from single celled protozoan still possessed several difficult question as earliest metazoan were soft bodied individual with no fossil record. Metazoans are the multicellular organism which develops from embryo. They are heterotrophic and motile eukaryotic organisms having a polarized body along an anterior-posterior locomotory axis. Metazoans body is composed of functional specialized cells, each type of which is dedicate to one or a few functions. Metazoan hierarchy is based on the basis of important features like symmetry, coelom and metamerism. For instance: on the basis of asymmetry animal phyla can be arranged as follows: asymmetrical (most porifera), radially symmetrical (coelentrata) and bilaterally symmetrical (platyhelminthes, nemathelminths, Annelida, Arthropoda, Mollusca, Echinodermata). Similarly, on the basis of germ layers, animal phyla can be arranged as diploblastic (porifera and coelentrata) and triploblastic (platyhelminthes, nematohelminthes, annelida, arthropoda, mollusca, echinodermata). Further, on the basis of presence or absence of coelom animal phyla can be categorized as acoelomate (porifera to platyhelminthes), pseudocoelomate (aschelminthes) and coelomate (annelida, arthropoda, mollusca, echinodermata). Metazoans can be divided as lower metazoa and higher metazoan. Lower metazoans encompass a diverse grouping of animal phyla traditionally considered primitive by most biologists in the nineteenth and twentieth centuries. Despite claims about their primitive appearance (e.g., simple anatomy, small size), the lower metazoa collectively displays some of the greatest morphological and developmental diversity within the kingdom animalia. Lower Metazoans includes members of phylum: porifera, coelenterata, ctenophora, platyhelminthes, aschelminthes, entoprocta and acanthocephala. Lower metazoans are unsegmented, radially or bilaterally symmetrical, diploblastic or triploblastic and acoelomate/pseudocoelomate animals. On the contrary, higher metazoans include the members of remaining phyla namely mollusca, annelida, arthropoda, echinodermata and chordata. Higher metazoans are triploblastic and truly coelomate animals. The requirement of food by animals can be assigned on two major aspects:

i. It provides fuel in terms of energy in order to keep the organism alive as well as to maintain body processes, muscle contractions and other metabolic & physiological functions of the body.

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ii. Food provides the basic raw materials for building and maintaining cellular and metabolic machinery, and also for growth and reproduction.

Plants synthesize their own food via the process of photosynthesis in the presence of sunlight. They are capable of converting inorganic raw material carbon dioxide and water to organic matter. All animals use chemical compounds to get energy as well as for their building materials. The chemical compounds or energy that animals need is derived from plants and therefore, indirectly from sunlight. The process of acquisition and ingestion of food by the animals is referred to as feeding. The food taken by animals, whether of plant or animal origin, are composed of highly complex compounds. These organic compounds cannot be utilized in their native forms as body fuels. Hence, they need to be broken down into simpler units. The phenomenon of breaking down complex food molecules into simpler molecules is known as digestion.

Yonge (1928), divided invertebrate feeding mechanisms into three major groups in accordance with the size as well as type of food utilized:

i. Microphagy:

Microphagy is the phenomenon of dealing with small food particles or it refers to the feeding on items that are very much smaller than the organism consuming them. In this process pseudopodia, cilia, tentacles, mucus, setae and muscles are used for capturing food.

ii. Macrophagy:

Macrophagy is the phenomenon of dealing with large food particles or masses or it refers to feeding on large particulate matter. Macrophagy involves steps in the order: swallowing of inactive food, scraping, boring, and seizing the prey. After seizing the prey, the animals chew, swallow and digest the food externally.

iii. Fluid or Soft Tissue Feeding:

Fluid or Soft Tissue Feeding refers to sucking fluid food. Some organism pierce and then suck the body fluid of the prey whereas, a few organism simply absorb the liquid food from the substrate via body surface.

Morton (1967), divided the animals into different categories depending upon the food habits.

(a) **Herbivores:** They feed on plants and plant-based products.

(b) **Carnivores:** They feed on other animals or meat-based products.

(c) **Omnivores:** They feed on both plant and meat-based products, i.e., these animals have digestive system meant for plant as well as animal food digestion.

(d) **Deposit Feeders:** Deposit feeders ingest particles associated with sediments or, in many cases, they ingest the sediment particles themselves and strip off nutrition in the form of detritus associated with the sediment grains and also associated microbes. (From: Encyclopedia of Biodiversity, Second Edition, 2013) Deposit feeders obtain food particles by sifting through soil, vaguely analogous to the way that filter feeders get food by filtering water.

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e. **Filter Feeders:** Filter feeders are the organism that feeds upon suspended food particles. It is an adaptation that allows the organism to feed on the food particles that are strained from water, typically by passing the water over a specialized filtering structure.

f. **Fluid Feeders:** Fluid feeding is defined as getting your nutrients by consuming the fluids of another organism.

g. **Bulk Feeders:** Bulk feeding is one of five feeding strategies used by animals to obtain food. Bulk feeding is exhibited by animals that eat pieces of other organisms or swallow them whole.

h. **Phagocytosis:** Phagocytosis is the phenomenon used by cells to engulf and then ingest particles of nutrients or bacteria. This phenomenon is very essential part of cell function, allowing cells to obtain vital nutrients as well as allowing the body to protect itself from harmful bacteria. A cell that specializes in this process is known as a phagocyte.

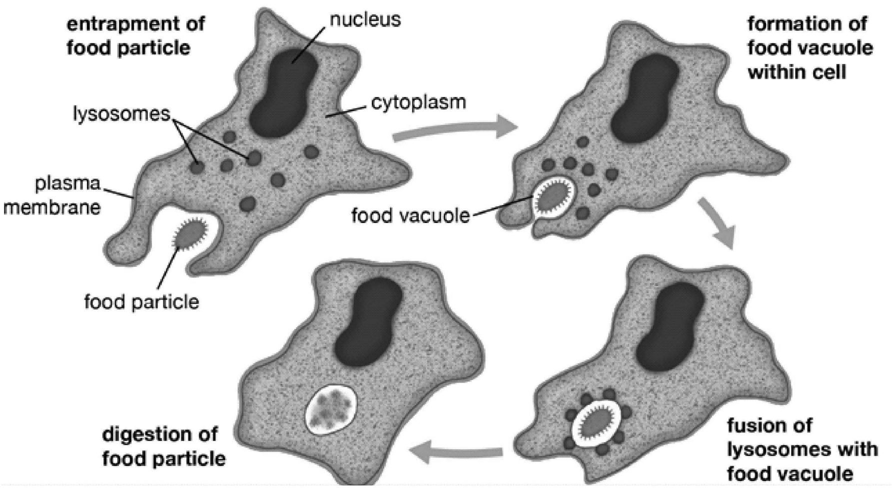

Fig. 2.5 *Process of Phagocytosis in Amoeba*

During the process of digestion, the large complex molecules of food are first broken down into simpler units, like monosaccharide's, amino acids, fatty acids and glycerol from polysaccharides, proteins and fats, respectively These smaller units are then absorbed and either incorporated into the body or metabolized to provide energy. All the ingested food molecules/particles irrespective of their size gets digested once taken inside the body. The entire process of digestion in organism is divided into two stages:

(i) Mechanical Digestion: Mechanical digestion is the breaking down of food into smaller particles so that it can more easily be processed by the digestive system. Mechanical digestion involves different components of the mouth parts as well as different specialised parts of the digestive tracts.

(ii) Chemical Digestion: Chemical digestion refers to the breaking down of complex food into simpler substances by the action of digestive enzymes. Chemical digestion involves the secretions of enzymes throughout your digestive tract. These enzymes break the chemical bonds that hold food

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particles together. This allows food to be broken down into small, digestible parts.

Further, in accordance with the site of enzymatic action, chemical digestion is of two types:

1. Intracellular Digestion

Intracellular digestion refers to a form of digestion where the breakdown of materials into small components takes place inside the cell. The hydrolytic enzymes stored in the lysosomes are responsible for the chemical digestion of the food particle. Intracellular digestion mainly occurs in unicellular organisms such as protozoans or poriferans.

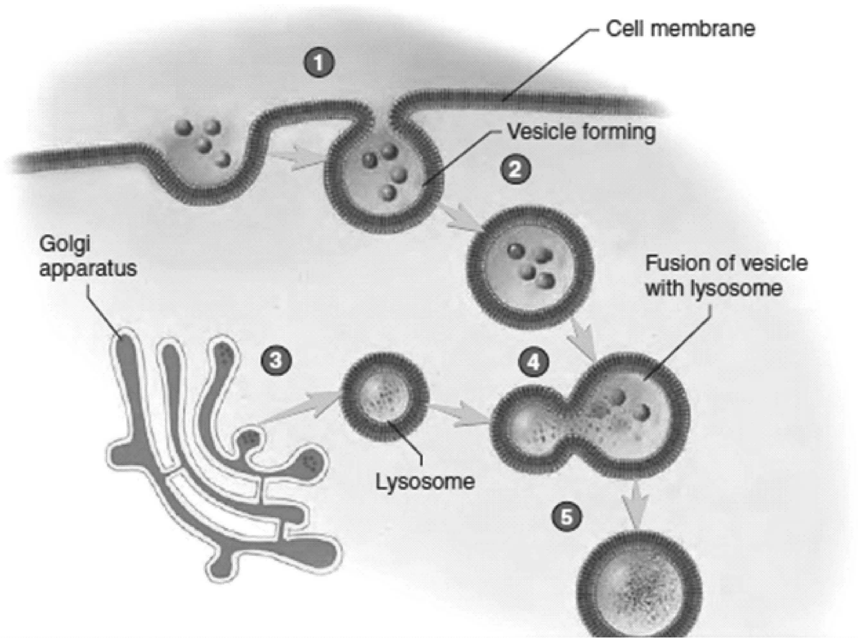

Fig. 2.6 *Process of Intracellular Digestion. 1: A Vesicle is Formed Around the Food Material; 2: Vesicles Gets Separated from the Main Cell Membrane; 3: A Lysosome is Pinched Off from the Main Golgi Apparatus; 4: Vesicle Containing Food Material Fuses with Lysosomes; 5: Food within the Vesicles is Digested by the Action of Lysozyme Enzymes*

1. Extracellular Digestion

Extracellular digestion refers to a form of digestion where the breakdown of materials into smaller components takes place outside the cell. Thus, the hydrolytic enzymes are secreted on the food materials via the cell membrane. In animals, extracellular digestion occurs inside the lumen of the alimentary canal.

The process of digestion is entirely intracellular in Protozoans as well as Poriferans. However, in other phyla extra-cellular digestion either supplements the intracellular digestion or completely replaces it. In the following section, we shall describe the process of feeding and digestion in lower metazoans.

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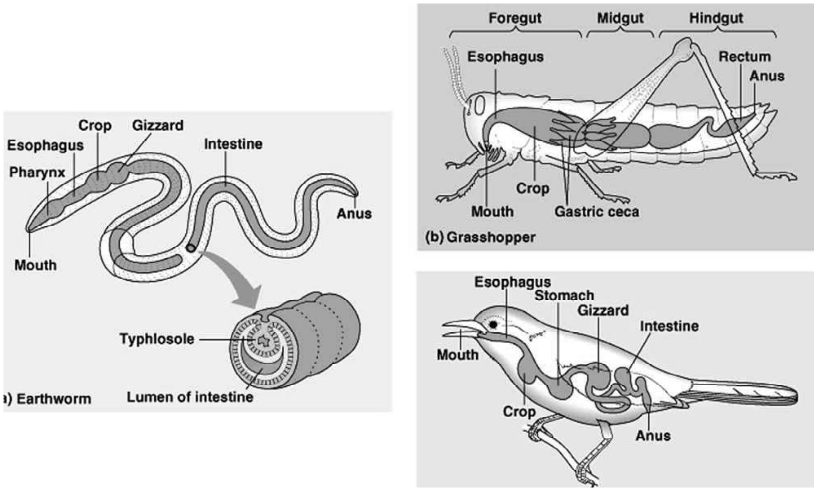

Fig. 2.7 *Process of Extracellular Digestion in Earthworm, Grasshopper and Birds Respectively*

Pattern of Feeding and Digestion in Porifera

Sycon (Porifera) is a marine sponge and is widely distributed but is primarily seen in North Atlantic shores. Scypha can be solitary of form colonies also by asexual reproduction i.e. budding. Sycon is vase-shaped animal measuring 3 cm in height and 5 to 6 mm in diameter. The base remains attached to the substratum. Near the attachment are found small tubular projections called as buds. A large number of minute holes can be seen all over the body called as ostia which leads into the central spongocoel via numerous channels. At the top, there is a single large opening referred to as osculum. The osculum is surrounded by osculate fringe which is composed of monoaxon spicules. The body surface is lined with skeletal spicules which gives a bristly appearance to the animal. Sycon type of canal system is present in *Scypha or Sycon*. The components of sycon canal system are as follows:

1) **Ostia or Dermal Pores:** The body is perforated by numerous small pores called as ostia. These ostia serve as entry gate for outside sea water. Ostia is surrounded by contractile cells known as myocytes which regulate the amount of water entering inside the canal system.
2) **Incurrent Canal:** Ostia directs the water inside the incurrent canal or inhalent canals which is infolding of the body wall of animal. This canal communicates with the outside sea water via ostia but ends blindly towards spongocoel. The incurrent canals are lined by pinacocytes.
3) **Prosopyle:** Prosopyle are tube like structures which directs the movement of water from incurrent canals to radial canals.
4) **Radial Canals:** A radial canal or flagellated canal communicates with incurrent canals via prosopyle and with spongocoel via apopyle; however, they ends blindly towards outside sea water. These canals are parallel and alternate to the radial canal. These canals are lined with specialized flagellated cells known as choanocytes.
5) **Apopyle:** These are the openings of radial canals into the spongocoel. Apopyle are surrounded by contractile cells known as myocytes which regulates the movement of water.

6) **Spongocoel:** Spongocoel is a large central cavity which communicates with the radial canals via apopyle. In Ascon type ofcanal system, the whole of the spongocoel is lined with flagellated cells whereas in sycon canal system only the radial canals arelined with flagellated cells. The spongocoel in sycon canal system is lined with pinacocytes.

7) **Osculum:** It is a large opening present at the top of the animal surrounded by specialized contractile pinacocytes known as myocytes.

8) **Current of Water:**

The flow of water is as follows:

Sea water from outside ⟶ Ostia ⟶ Incurrent canal ⟶ Prosopyle ⟶ Radial canal ⟶ Excurrent canal ⟶ Spongocoel ⟶ Osculum ⟶ Outside

The rate of flow of water in sponges is about 0.01 mm/sec.

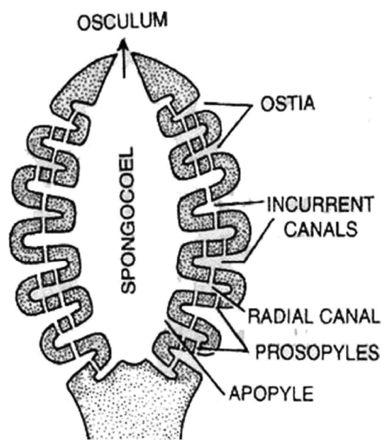

Fig. 2.8 Flow of Water Carrying Food Particle in Sycon

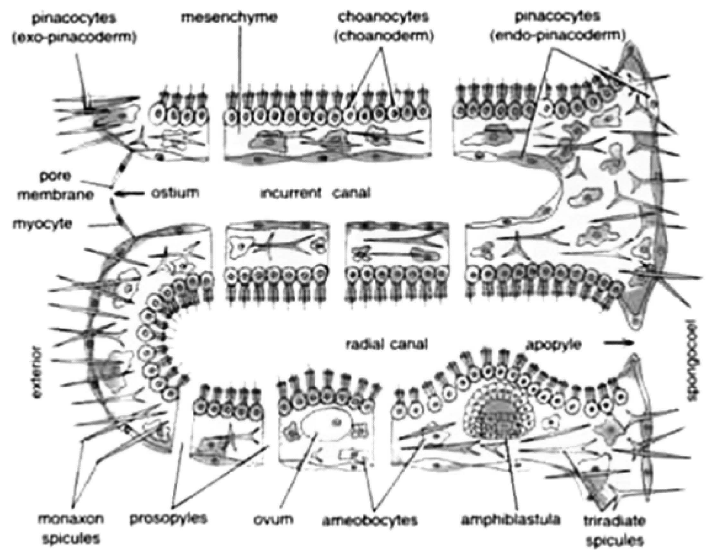

Fig. 2.9 Flow of Water Carrying Food Particles in Sycon

The two types of cellular layers which are present in Sycon are Pinacoderm and Choanoderm with an intermediate mesenchyme.

(A) Pinacoderm: Pinacoderm comprises flat polygonal cells known as pinacocytes. A pinacocyte is a flat cell with a central bulge containing the nucleus. The adjacent pinacocytes cements with each other forming the pinacoderm. Pinacoderm is of two type:

1. **Exopinacoderm:** It covers the entire body surface except dermal ostia and osculum.
2. **Endopinacoderm:** It covers the surface of incurrent canal as well as spongocoel.

   Pinacocytes cells are highly contractile in nature due to which it can hugely increase or decrease the surface area of the animal.

(B) Choanoderm: Choanoderm comprises flagellated collar cells known as choanocytes. A choanocyte consists of a collar, central nucleus, contractile vacoules, a few droplets of reserve food, a single basal granule from where originate a long whip like flagella.

(C) Mesenchyme: Mesenchyme is a gelatinous matrix is present in between the pinacoderm and choanoderm. The mesenchyme consist of several cells called as amoebocytes which are secreted by pinacoderm into mesenchyme. A few types of amoebocytes which are present in the mesenchyme are:

- **(i) Archaeocytes:** These are undifferentiated totipotent cells which can differentiate to form other types of cells present in the mesenchyme.
- **(ii) Chromocytes:** These are pigmented cells with pseudopodia.
- **(iii) Thesocytes:** These are storage cells.
- **(iv) Myocytes:** These are specialized contractile cells.
- **(v) Scleroblast:** These are spicules producing cells and accordingly can be calcoblast producing calcareous spicules; silicoblast producing siliceous spicules or spongioblast forming sponging fibres.
- **(vi) Gland cells:** They secrete plenty of mucus or slime.
- **(vii) Germ cells:** Amoebocytes differentiate to form gems cells, i.e., ova and sperm.

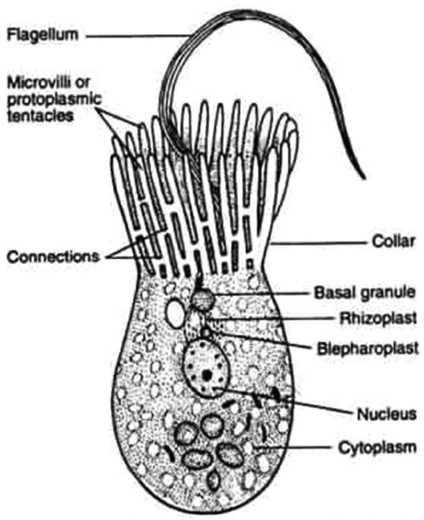

Fig. 2.10 *Structure of a Choanocyte Cell which Aids in the Process of Digestion*

The canal system is the most significant system of animal which brings in the food, gases and takes away the waste material as well as the reproductive bodies. Sycon feeds on small organic particles. The movement of food particle is shown below:

Food in the sea water → food enters into animal's body via ostia → food enters in to radial canals → food taken inside the choanocyte cells → food taken inside food vacuoles

The first phase inside food vacuoles is acidic and then basic. The food undergoes partial digestion inside food vacuoles and this partially digested food is passed on to amoebocytes in mesenchyme. The complete digestion happens inside the amoebocytes. The digested food is distributed to all cells of the body. A few cells like thesocytes store the food particles. The indigestible food particles are eliminated from the animal's body along with outgoing water current.

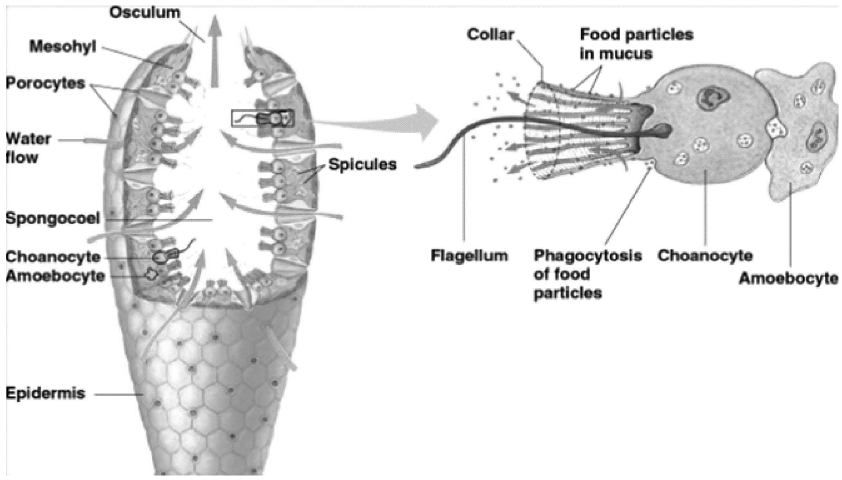

Fig. 2.11 *Food Movement and Digestion in Porifera*

Pattern of Feeding and Digestion in Coelenterates

Obelia is a sedentary, marine and colonial trimorphic hydrozoan having three zooids namely polyp, medusa and blastostyle stages in its life cycle. It is abundant in both Atlantic and Pacific coastal waters and present upto depth of 80 meters. Obelia forms a small branched hydroid colony which is primarily remains attached to stones, shells of animals, rocks, or on large seaweeds. The colony appears like a delicate whitish or light brownish fur-like growth. The sexual form of the colony is a bell-like medusa which possesses gonads and performs the function of sexual reproduction. Obelia colony is trimorphic consisting of two polyp zooids attached to the sedentary colony and a free swimming medusoid zooid. Obelia colony consists of a horizontally branching structure known as hydrorhiza from which come out several vertical branching stems called hydrocaulus. Branches emerging from the stem terminate either to functional nutritive zooids, called the polyps or hydranths or in reproductive zooids called blastostyles or gonangia, which produce free swimming medusa. The obelia colony is made of an inner, tubular and living tissue, the coenosarc, which encloses a canal known as the gastrovascular cavity. The gastrovascular cavity consist of an outer epidermis and an inner gasrodermis with a gelatinous mesogloea in between. The living coenosarc is surrounded externally by a yellowish or brownish, non-living chitinous layer, called perisarc. The function of the perisarc is to protect the colony and also serves as an exoskeleton. The folds on perisarc called as annuli permits limited swaying movements and bending of the zooids.

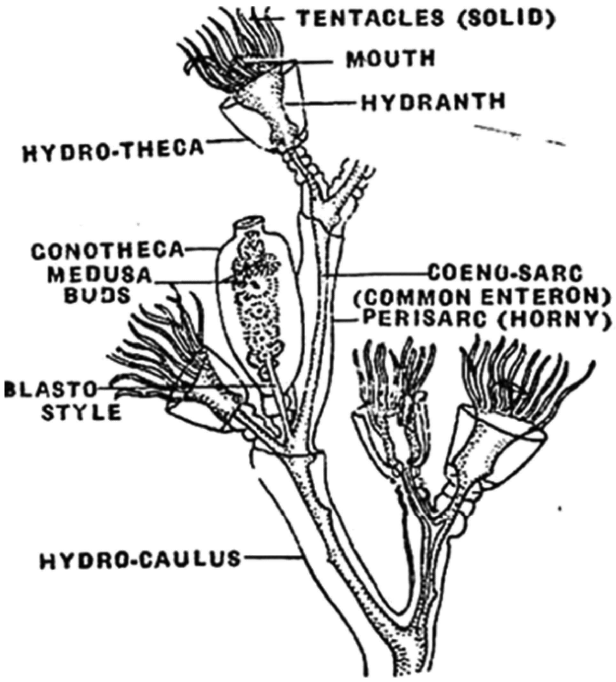

Fig. 2.12 *Structure of Obelia*

Obelia colony is diploblastic, i.e., comprises of two layers, the outer epidermis and inner gastrodermis with a thin, transparent, non-cellular gelatinous layer called mesogloea sandwiched between them. Epidermis carries nematocysts (stinging cells) which are the main weapon of offence and defence. These cells are abundantly present on the tentacles forming batteries. Gastrodermis consists of large nutritive-muscle cells and narrower gland cells that secrete digestive enzymes and aid in the process of digestion. There are three types of zooids in obelia colony as follows:

(a) Polyp or Hydranth or Gastrozooid

The nutritive zooid of the colony is referred to as gastrozooid or trophozooid. The distal end of this zooid forms a projection referred to as manubrium or hypostome. In the centre of the manubrium is located the mouth surrounded by a circlet of tentacles arising from the base of hypostome. The tentacles are loaded with nematocyst which serves as the cells of offence and defence. Perisarc around the hydranth dilates to form a loose cup-like, transparent protective sheath, the hydrotheca into which the polyp withdraws when in danger.

(b) Blastostyle or Gonangium

On attaining its complete development, colony forms special club shaped bodies called as blastostyles or blastozooids or gonozooids. When the colony has reached full development, it produces special club-shaped bodies called blastostyles or blastozooids or gonozooids. The outer perisarc covering the blastostyle forms a loose, transparent, vase-like capsule called the gonotheca. Blastostyle by asexual reproduction (budding) produces produces sexual medusa or gonophores. When medusae becomes fully developed it escapes out of blastostyle via an aperture called as gonopore. Gonotheca, along with blastostyle and medusae is called as gonangium.

(c) Medusa or Nectophore

Medusa is an umbrella shaped zooid measuring 1 or 2 mm in diameter. The subumbrellar surface of the medusa has four radial canals and a circular canal on the margin. A mature male or female medusa bears four gonads, one in the middle of each radial canal. A projection referred to as manubrium bearing mouth hangs down from the centre of the sub-umbrellar surface. The outer edge of umbrella is folded inwards to form velum devoid of any canal. The margin of the umbrella bears numerous short tentacles loaded with nematocysts. Medusa with manubrium hanging downward and tentacles swaying freely floats freely in water along with water currents. It can also swims actively by aid of powerful muscular contractions and also of velum. Medusa is carnivorous in nature and feeds on small planktons. It has sense organs in the form of eight marginal statocysts, situated at the bases of tentacles on the subumbrellar surface. These statocysts help the animal in orientation as well in maintaining equilibrium while swimming. The nervous system of medusa is a diffused network of neurons.

The major function of the medusa zooid is sexual reproduction as well as dispersal of colony. Medusa are dioecious, i.e., male and female are separate individuals having testes and ovaries respectively. The sex cells in the gonads migrate from the epidermis of blastostyle. The process of spermatogenesis and oogenesis takes place inside the blastostyle and the resulting sex cells, i.e., sperms and ova migrate and fill the gonads of the medusa.

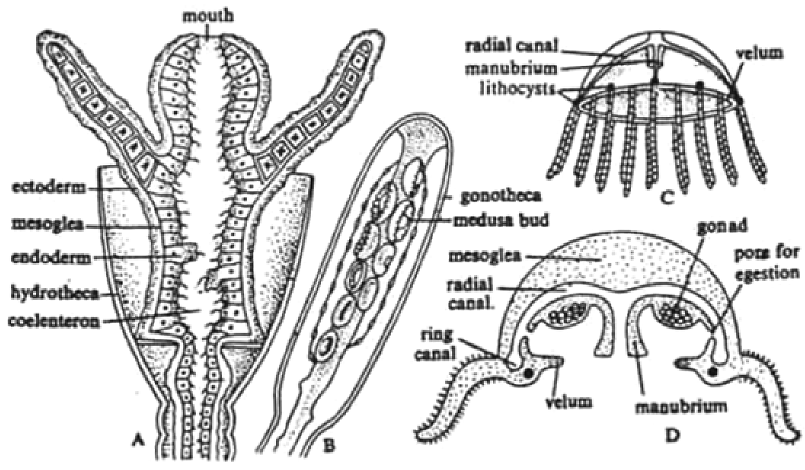

Fig. 2.13 *Mouth/Anus View of Zooids of Obelia Colony. A) Gastrozooid B) Blastostyle C) Medusa D) Sectional View of Medusa*

Gastro-zooid or nutritive zooids are the feeding zooids of the obelia colony. Nutritive zooid and medusa are carnivorous in habit. They feed upon small aquatic crustaceans, nematodes and other worms. Tentacles are armed with nematocysts which can paralyze and capture the prey. The captured prey is conveyed to the mouth. Digestive juices are secreted by gland cells which act upon the food particles. This causes partial extra-cellular digestion in the gastro-vascular cavity. The partially digested food is circulated to the entire colony via beating of flagella of endoderm. Endodermal cells with their pseudopodia processes engulf small pieces of this food and further digest them intracellularly. Finally, the undigested food is then egested through the single opening, i.e., mouth.

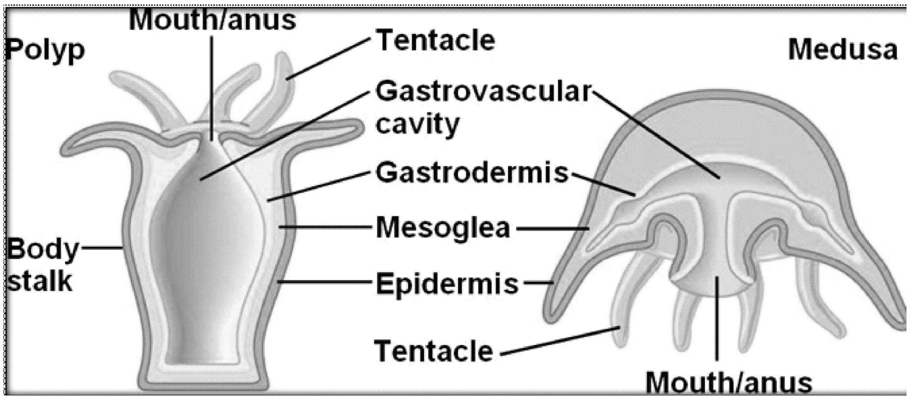

Fig. 2.14 *Position of Mouth/Anus in Polyp and Medusa Form of Coelenterates*

Pattern of Feeding and Diegestion in Ctenophora

The term ctenophora was coined by Eschscholtz in 1829 for a group of marine planktonic animals commonly known as "*Sea walnuts*" or "*Comb jellies*" due to the presence of locomotory comb-like plates on the body (Ctenos – comb, phoroa – bearing). To date, 80 species have been described under the phylum ctenophora. The spherical body can be divided into two hemispheres with mouth at oral pole and sense organ at the aboral end. It also comprises a unique set of combplates and tentacles. Eight equally spaced rows of paddle plates or comb plates are arranged on the sides of the body. These comb rows bears a series of short but strong ctenes or ciliary plates which propel the animal slowly through the water. There are two tentacles located at the aboral end on opposite sides of the body. These long-solid tentacles with short lateral branches or pinnae emerge from deep ciliated epidermal blind pouch or tentacular sheath. They lack nematocysts but possess peculiar adhesive cells called colloblasts or lasso cells which help in capturing food.

The mouth is a slit-like structure situated in the centre of the lower end and leads into a long tubular pharynx lined with epidermis. The pharynx opens into a small wide stomach which gives out a system of five gastrovascular canals extending throughout jelly in a specific arrangement. The stomach and gastrovascular canals are lined with gastrodermis. Further, two anal canals open to the outside each via an anal pore near the aboral sense organ.

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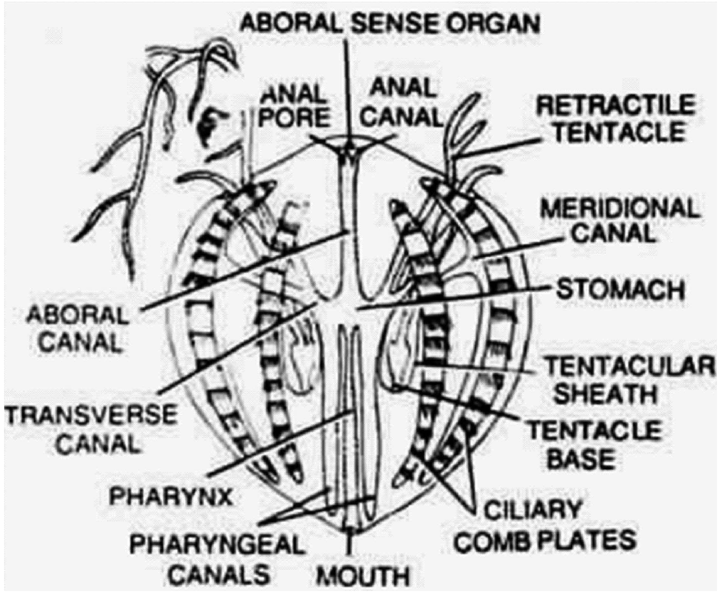

Fig. 2.15 *Digestive System of Pleurobrachia (Ctenophora)*

Ctenophores are voracious feeders and feed on small planktonic organisms. Food is captured by colloblast cells located on the tentacles. Digestion is extracellular in pharynx and intracellular in gastrovascular canals.

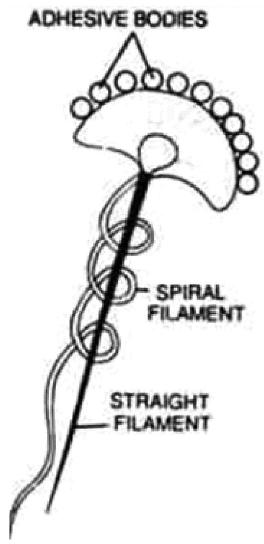

Fig. 2.16 *Colloblast Cell which Aids in Food Capturing*

Pattern of Feeding and Digestion in Platyhelminthes

Fasciola hepatica commonly known as fluke is found in the liver and bile ducts of sheep, pig, rabbit, cattle, goat, dog etc. Infection by F. hepatica causes severe damage to the liver tissues producing liver rot. The life cycle of *F. hepatica* is completed in two hosts i.e. a vertebrate host sheep and an invertebrate host, i.e., snail or genera like limnaea, planorbis, and bulinus. *Fasciola hepatica* is a soft, oval, leaf like, dorso-ventrally flattened helmith. It is bilaterally symmetrical and measures around 1.8 to 3 cm in length & 0.4 to 1.5 cm in width. The body of the animal ends in a conical projection at the anterior end whereas the posterior end is bluntly pointed. *Fasciola hepatica* is a pinkish helmith. The anterior end of the body is drawn into a conical projection known as head lobe or oral cone. At the tip of oral cone, there is present a triangular aperture i.e. mouth. There are two suckers located at the anterior and ventral surface respectively. A cup-shaped oral sucker is located at the anterior end. Oral sucker act as a suctorial organ as well as perform the function of adhesive organ. Another sucker, known as ventral sucker or acetabulum is located mid-ventrally and acts as adhesive organ. Apart from mouth, there are two more permanent aperture on helminth's body namely gonopore located mid-ventrally in front of acetabulum and a excretory pore lying at the posterior end towards the ventral surface. Another opening, i.e., Laurer's canal appears on dorsal surface, a little anterior to middle of body. Body of F. hepatica is covered with tegument from which projects numerous backwardly directed scales or spicules. The spicules serve as an anchor to host.

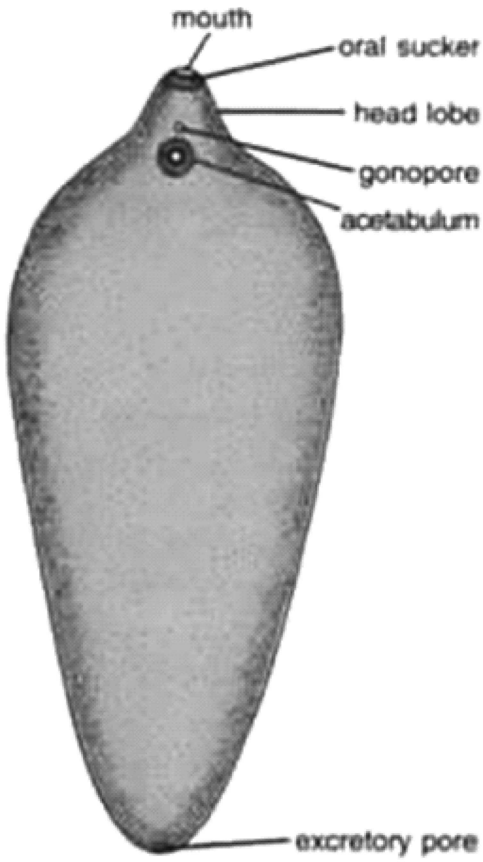

Fig. 2.17 *Mouth and Anus of F. hepatica*

The body of *F. hepatica* is covered with a tough resistant cuticle or tegument which is made of scleroprotein. The primary function of this tegument is to protect the fluke body from abrasive action of host's digestive juices. The skin also bears small backwardly directed spinules or scales which anchor the fluke's body to host. The lowest layer of the cuticle forms a delicate basement membrane. The integumentary muscles are smooth and consist of an outer layer of circular muscles and an inner layer of longitudinal as well as oblique or diagonal muscles. Mesoderm constitutes uninucleate and binucleate cells with syncytial network filled with cytoplasm. The major function of the skin is to provide protection and also acts as

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the site of gaseous exchange. It also helps in diffusing out various nitrogenous wastes from the body. It also helps in the absorption of pre-digested nutrients from the host's body.

Fasciola hepatica has a blind sac alimentary canal, i.e., it has only one opening as mouth which is situated in the middle of anterior sucker. Mouth leads into bulb-like pharynx which is highly muscular and suctorial in nature. The intestine is bifurcated into two caeca and gives off numerous branches or diverticula which help in distributing the food to all parts of the body. Digestion is extracellular. Reserve food in the form of glycogen and fats is stored in the parenchyma.

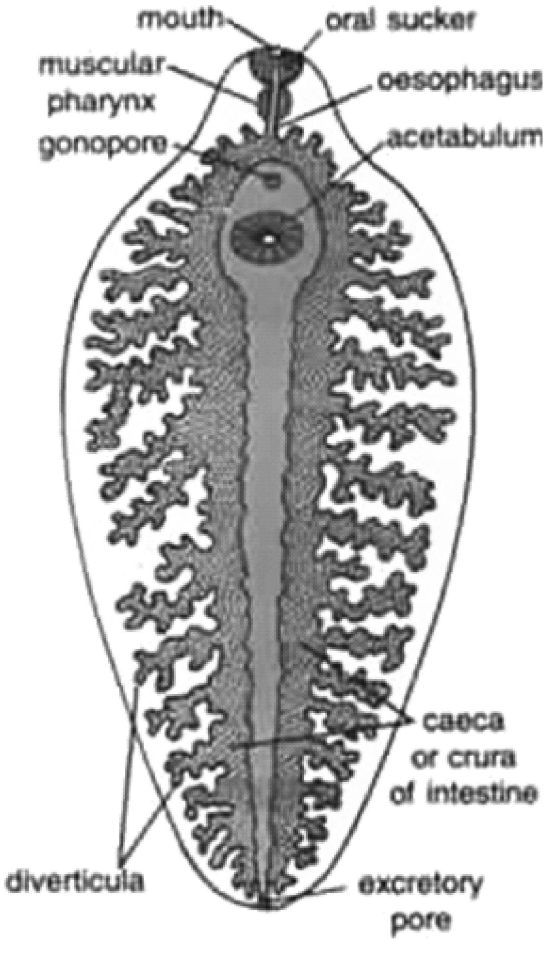

Fig. 2.18 *Digestive System of F. hepatica*

Pattern of Feeding and Digestion in Nemertinea

A definite head is absent. The mouth is located at the anterior end on the ventral side. A long hollow muscular organ known as proboscis protrudes out via a small opening present near the mouth. The digestive tract is complete. It is a simple ciliated tube which runs throughout the length of the body from the mouth to the anus. The anterior part of the digestive tube is generally a simple tube-oesophagus (stomodaeum), however, it may be more complex in some species and is divided into various regions, occasionally with paired diverticula. Posteriorly, it opens into the intestine. The intestine may be a simple un-constricted tube in some species while in others it might be slightly constricted at intervals by the paired gonads. In

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most species, the constrictions corresponding to the gonads are very deep so that the intestine comes to be provided with two rows of lateral diverticula or caeca which may be branched. The lateral diverticula or caeca are separated from each other via incomplete transverse septa composed of dorsoventral muscular fibres. This arrangement of the caeca and septa along with the alternately arranged gonads brings about an appearance of imperfect metamerism as observed in flatworms or Platyhelminthes. The intestine finally opens to the exterior via anal aperture at the posterior end of the body. The nemertines usually feed at night on living or dead animals mostly annelids, molluscs, crustaceans and fishes, etc.

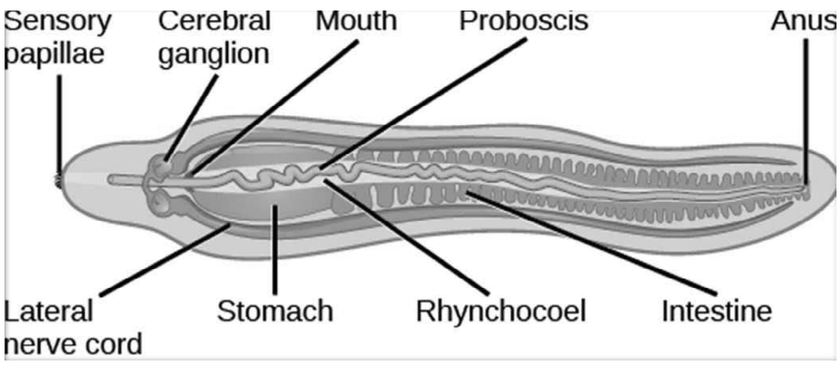

Fig. 2.19 *General Anatomy of a Nemertea*

Pattern of Feeding and Digestion in Acanthocephalia

Acanthocephalans lacks digestive system; however, they selectively absorb nutrients from the host's intestine across their tegument. A few studies are conducted on feeding and digestion in acanthocephalans till date. Based on that, it is concluded that the major substrate for acanthocephalan metabolism is carbohydrate, with ethanol being the main end product. Uptake of monosaccharides appears to involve active transport mechanisms (active transport mechanism involves expenditure of energy). A few Acanthocephalans are known to store glucose in the proboscis receptacle muscle as well as in the cytoplasmic core of the hollow muscles. However, it is yet not known whether the hollow muscles acts as a storage site or helps in distributing nutrients throughout the body. The plasma membrane present at the surface of the tegument exhibits hydrolytic activity and tegumental surface crypts within which various enzymatic activities have been localized. The primary function of the crypt is to increase the absorptive surface area and are considered to be extra-cytoplasmic digestive organelles. A lot of amino acids are also known to be absorbed via tegument, however, their function in metabolism is not known. The main channels of absorption keep on varying with amino acid. Lipids are absorbed and then stored for future use in the lemnisci, however, it is still not clear whether the primary site of lipid absorption is the body wall or the neck/proboscis region. Even though, a large amount of lipids may be deposited in acanthocephalans, they are not thought to be used in metabolism.

Pattern of Feeding and Digestion in Entoprocta

This group represent a cluster of tiny, sedentary and marine animals which are either solitary or colonial forms. Superficially, these animals resemble the phylum hydroidea and bryozoa. In the past, this group was placed under bryozoa

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(ectoprocta), however, recently they have excluded them from bryozoa and included them under the phylum entoprocta. Almost all the forms are marine excepting the fresh-water form, urnatella. The stalked cup-like body of the animal is called calyx which bears a crown of tentacles at its free edge. The hollow or cavity of this cup is called atrium or vesti-bule and it include both mouth as well as anus. The digestive tube is curved to form a U-shaped structure. They are acoelomate as the empty space between the body wall and the digestive tube is filled up with parenchyma. In the solitary form (loxosoma), the body is divided into a calyx and a stalk which possesses foot-gland at the base whereas in the colonial forms (pedicellina and urnatella) the body of each zooid is separated from the stalk by a diaphragm. Asexual reproduction takes place by the process of budding from any part of the body and the buds stay attached to the parental body forming colony. Development is indirect and the cleavage is of 'spiral' type forming a free-swimming ciliated larvae. It is a trochophore type larva which feeds on planktonic organism. Subsequent to a brief swimming phase, the larva fastens itself to the free surface of some other animal with the assistance of an attachment organ located at the postero-ventral position and then transforms into the zooid form. On the basis of development, it is presumed that they are linked to those groups that have trochophore larva during their development and most likely have evolved from a common ancestor, shared with the coelomate bryozoans.

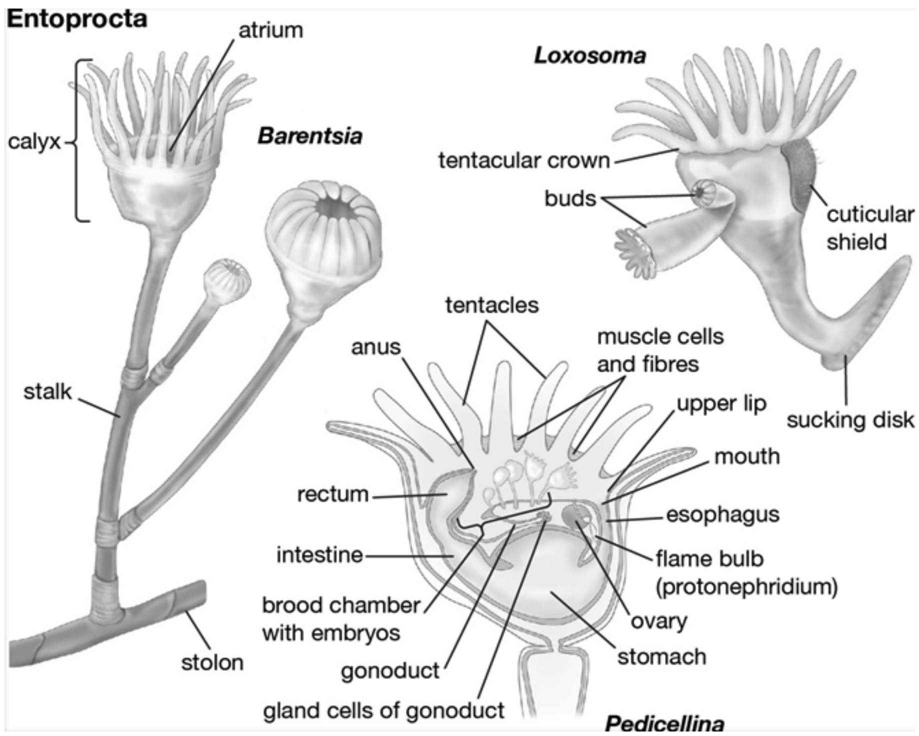

Fig. 2.20 *Parts of Digestive System in Entoprocta*

A band of cells, each with multiple cilia, runs along the sides of the tentacles, connecting each tentacle to its neighbours, except that there is a gap in the band nearest the anus. A separate band of cilia runs along a groove that runs close to the inner side of the base of the "crown", with a narrow extension up the inner surface of each tentacle. The cilia on the sides of the tentacles create a current that flows

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into the "crown" at the bases of the tentacles and exits above the center of the "crown". These cilia pass food particles to the cilia on the inner surface of the tentacles, and the inner cillia produce a downward current that drives particles into and round the groove, and then to the mouth. Entoprocts generally use one or both of: ciliary sieving, in which one band of cilia creates the feeding current and another traps food particles (the seive); and downstream collecting, in which food articles are trapped as they are about to exit past them. In entoprocts, downstream collecting is done by the same bands of cilia that generate the current; trochozoan larvae also use downstream collecting, but use a separate set of cilia to trap food particles. In addition glands in the tentacles secrete sticky threads that capture large particles. A non-colonial species reported from around the Antarctic Peninsula in 1993 has cells that superficially resemble the cnidocytes of cnidaria, and fire sticky threads. These unusual cells lie around the mouth, and may provide an additional means of capturing prey. The stomach and intestine are lined with microvilli, which are thought to absorb nutrients. The anus, which opens inside the "crown", ejects solid wastes into the outgoing current after the tentacles have filtered food out of the water; in some families it is raised on a cone above the level of the groove that conducts food to the mouth. Most species have a pair of protonephridia which extract soluble wastes from the internal fluids and eliminate them through pores near the mouth. However, the freshwater species *Urnatella gracilis* has multiple nephridia in the calyx and stalk. The zooids absorb oxygen and emit carbon dioxide by diffusion, which works well for small animals.

Pattern of Feeding and Digestion in Rotifera

The rotifers, most common inhabitants of freshwaters also live in brackish water and a few in the ocean or on land in damp sites. Various lifestyles include creeping, swimming, pelagic and sessile types, as well as carnivores and bacteria feeders. Rotifers are generally solitary. Some of the sessile species form spherical swimming colonies in which the individuals have no organic continuity. Rotifers are also called wheel animalcules. They are minute animals ranging from 0.04 to 2 mm in length. The rotifer body is divisible into the broad or narrowed or lobed anterior end usually having a ciliary apparatus, an elongated trunk, and the tail or foot. The body is covered with yellowish cuticle ringed throughout or in certain regions. The cuticle may be thickened on the trunk to form the lorica, a hard encasement, of one to several plates that may be variously ornamented. The anterior end is typically broad and truncate or slightly convex and bears the mouth corona, a ciliated zone and an un-ciliated region, the apical field, encircled by the corona. The mouth is located in the corona in the mid-ventral line of the head. The head has a pair of prominent lateral ciliated projections, called auricles. Eyes (pigment spot ocelli) appear as red streaks, occur singly or paired in the brain, as lateral paired eyes in or near the corona and as paired frontal eyes on the apical field or on the rostrum. Coronal protrusion serves as lower lip. The trunk may be cylindrical or variously flattened and broadened and is enclosed in a lorica which is often ornamented or spiny. Characteristic trunk structures are the dorsal and lateral antennae or palps. The dorsal antenna is situated in the mid-dorsal line of the anterior end of the trunk and is a finger-like projection tipped with sensory hairs. The anus is in the mid-dorsal line at or near the boundary of trunk and foot. The body tapers gradually into the foot or the foot may be sharply set off from the stout trunk as a cylindrical tail-like region. Its cuticle is commonly ringed into a few joints that serve for clinging to objects in creeping types or acts as a rudder in swimming types. In sessile forms, the foot is modified to a long stalk. The foot is reduced or absent in wholly pelagic life. The foot is provided at or near its end with one to four movable projections known as toes, used in holding the substratum while creeping. They may be short and conical or slender and spine- like. The pedal glands commonly open at the tips of the toes. The rotifers are dioecious.

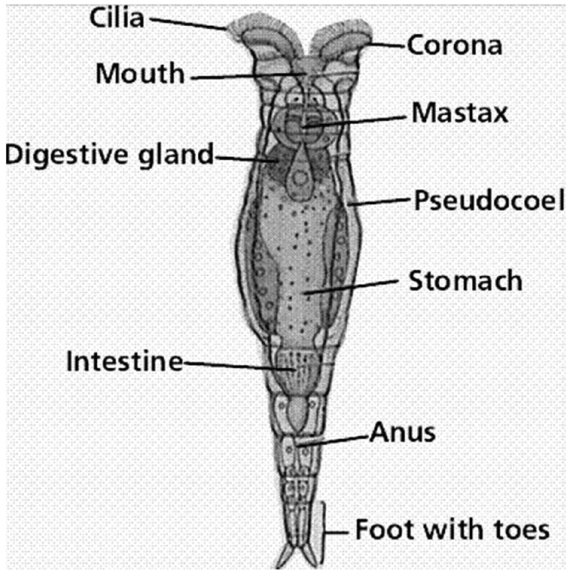

Fig. 2.21 *Parts of Digetive System in Rotifera*

The ground plan of the corona or "wheel organ" comprises a large oval ventral field, the buccal field evenly ciliated with short cilia and surrounding the mouth, and a circum apical band extending from this to encircle the margin of the head, alters mostly in the direction of enlargement of its marginal cilia with loss of the interior cilia. In some groups of rotifers, the enlargement of the cilia along both margins of the apical band, results in two circles of cilia or membranelles that is trochus, an inner or anterior circlet and cingulum, an outer or posterior one. The reduced buccal field becomes incorporated into these circlets and, hence, the corona consists essentially of two circlets, with the mouth between them ventrally. The adult females of the genera atrochus, cupelopagis and acyclus have no corona but it is present in normal form in the males and young females of these genera. The corona of male rotifers is usually less modified than that of females of the same species. The body wall consists of cuticle, epidermis and sub-epidermal muscles. The non-chitinous cuticle, secreted by the epidermis consists of scleroproteins. It is frequently segmented and lends flexibility permitting a variety of body movements. In many rotifers the trunk cuticle is thickened and hardened into a lorica that, however, is slightly flexible.

The lorica may consist of several pieces or two dorsal or two ventral plates or two dorsal and one ventral or of single dorsal and ventral plates or of one piece with or without a longitudinal suture. Loricates are dorso-ventrally or laterally flattened; the margins of the lorica project as teeth or spines. A groove like structure known as head shield marked off the part of lorica covering the neck region from the general trunk lorica. The syncytial epidermis contains scattered nuclei which are arranged in a bilateral manner and are constant in position and number for each species. The cytoplasm is heaped up into an elevation projecting into the pseudocoel around each nucleus or group of nuclei. The retro-cerebral organ, situated above and behind the brain and the pedal glands are the principal glands attached to the epidermis. The retro-cerebral organ consist of a median retro-cerebral sac whose duct forks along with the outlets of a pair of lateral sub-cerebral glands and open on the apical field, often on a single or paired papilla. Sac and gland are different in relative and absolute size in different rotifers. There may be a single sub-cerebral gland or the sac may occur without glands or the glands without the sac. Sac and glands consist of a syncytium and secrete droplets giving them a vacuolated appearance. The sac and glands contain strongly diffractive granules**.** The function of the retro-cerebral organ is uncertain. The pedal glands can be unicellular glands or multinucleate syncytia located in the foot and secrete an adhesive material used for permanent attachment or in creeping and also in the construction of tubes and cases. They may be numerous or reduced to a single pair and often rudimentary or absent in the sessile adults. They open by ducts on the tips of toes or at sides or base of the toes or on the spurs or at the foot end.

In rotifers, the sub-epidermal muscles are circular and longitudinal muscles and found in different parts of the body. In addition to these body wall muscles there are cutaneovisceral muscles that extend to the viscera, especially the digestive tract, from the body wall, and visceral muscles in the walls of the viscera themselves. The circular musculature of the body wall consists of a single muscle band, mostly three to seven, widely spaced running close to the underside of the epidermis in a circular direction forming complete rings often very incomplete ventrally so that they may consist chiefly of short lateral arcs. They occur in neck and trunk, generally absent from the foot and reduced in loricates. The circular bands are enucleate, hence, is part of the epidermal syncytium. The contraction of the circular muscles serves to extend the body. The coronal sphincter is composed of one to several broad bands in the head directly behind the corona. It serves to close the neck over the retracted corona. A similar pedal sphincter is present at the junction of trunk and foot. Bands running the body length directly under the circular bands are the longitudinal body wall muscles attached at frequent intervals to the epidermis. Loss of these insertions cause the longitudinal bands to run more directly through the pseudocoel and to act primarily on head and foot as retractors.

The 4 principal head retractors are the central, dorsal, lateral and ventral pairs. The lateral is commonly subdivided into three bands, superior, median and inferior. The longitudinal retractors have one or more nuclei.

The mouth is ventral, rounded, slit-like or triangular. The cingulum forms a definite lower tip beneath the mouth. In forms with a large buccal field, the posterior end of the field may project as the chin. The mouth may open directly or by ciliated buccal tube into the pharynx. The pharynx or mastax is a highly muscular, rounded, trilobed or elongated organ whose inner wall bears the masticatory apparatus composed of hard cuticularised pieces, the trophy that are of different types for different modes of life like malleate type, virgate type, cardate type,

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forcipate type, incudate type, ramate type, uncinate type, fulcrate type. The trophi consist of 7 main pieces, the unpaired fulcrum and the paired rami, unci and manubria. The salivary glands are 2 to 7 in number, occur in the mastax wall in many rotifers as uninucleate or syncytial masses with granular or vacuolated cytoplasm. The function of the salivary glands is presumably concerned with ingestion or digestion. The mastax is followed by the oesophagus lined with cuticle or ciliated throughout or at the posterior end only. The oesophagus is devoid of glands. The oesophagus is followed by the stomach. It is an enlarged thick-walled sac or tube. The stomach has a muscular layer consisting of muscle cells. At the junction of oesophagus and stomach occurs a pair of syncytial gastric glands having a constant number of nuclei and opening into the stomach by a simple pore on each side. The secretion comprises droplets or granules aggregated around the pore and are presumably enzymatic. The stomach is followed by the intestine. In one case the intestine is tubular and in other bladder-like. The stomach and intestine are attached to the body wall by the usual cutaneo-visceral muscles.

Pattern of Feeding and Digestion in Aschelminthes

In cross-section, the body of worms of aschelminthes is circular and hence the name as round worms. They are very abundant and can be found almost everywhere i.e., they may be terrestrial, aquatic, free-living or parasitic. They are either larger or smaller, some microscopic. Nematodes are characterized by the presence of an external (outer) layer of cuticle, a strong and flexible noncellular layer that is secreted by the hypodermis below it. The Nematodes lacks coelom, instead, they have a pseudocoel formed directly from the cavity of the blastula. The pseudocoel cavity aids in the circulation. Further, an excretory tube eliminates body wastes from the pseudocoelomic body cavity through the excretory pore. The nervous system is basically anterior nervous tissue that covers the pharynx which forms dorsal and ventral nerve chords from one end to the other. Nematodes represent the first phylum having a complete digestive system with a well-developed muscular pharynx. ascaris (round worm), ancylostoma (hookworm), wuchereria (filaria worm) are the best examples of nematodes.

The digestive system in nematodes is complete and is divided into three separate regions namely: the stomodaeum (fore-gut), the mesenteron (mid-gut) and the proctodaeum (hind-gut). Stomodaeum and proctodaeum are internally lined with cuticle.

I. Stomodaeum

- Stomodaeum begins at the oral aperture or the mouth which is located terminally and is bounded by 6 lips. (2 sub-dorsal, 2 sub-ventral and 2 lateral in position).
- The oral aperture leads internally into a cavity which is known as stoma or buccal cavity.
- Oesophagus/pharynx is next part of stomodaeum. It acts as a pumping organ which sucks in as well as pushes the ingested food material into the intestine.
- Each of these three parts are used a lot in taxonomy and classification of nematodes, as well as giving as indication of feeding habit or trophic group.

II. Mesenteron

- Mesenteron comprises a simple straight tube i.e., the intestine running most of the length of the body.
- The intestine is composed of a single layer of endodermal epithelial cells.
- Internally, these cells bear a layer of finger-like projections (microvilli), which are absorptive and secretory in function.

III. Proctodaeum

- Proctodaeum consists of a short flat tube known as rectum which is lined internally by cuticle.
- Rectum opens to the outside ventrally via anus in females.

  However, in males, the reproductive system joins the rectum to form a common tube referred to as cloaca. Cloaca opens to the outside via cloacal aperture on the ventral side.

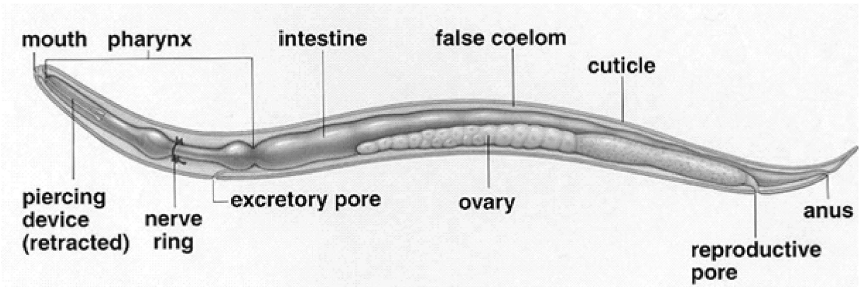

Fig. 2.22 *Digestive System in Nematodes*

Ascaris is a genus of parasitic nematode worms known as the giant intestinal roundworms. A few species of the ascaris worm infect pigs, while others, and affects human populations. They are dominant in the sub-tropical as well as tropical areas with poor health conditions that allow for ascaris worms to infect human beings. Ascaris has a mouth structure for the ingestion of food that is connected to a tube, which passes via the body of the worm and terminates at an anus, where undigested food material/waste products are excreted. The digestive tract of the Ascaris includes one muscular structure to ensure that food moves easily via the tract in the proper direction. Finally, Ascaris includes an intestinal region where absorption of small molecules like glucose, amino acids etc. takes place. Thus, the overall function of the digestive tract of Ascaris is to ingest food, breaks macromolecules into their subunits, and allows for the absorption of glucose and amino acids. The detailed digestive system tract as well as mode of digestion in ascaris is as follows:

(a) Mouth- The mouth of ascaris is tripartite structure situated at the anterior tip surrounded bounded by three lips or labia.

(b) Alimentary Canal- Alimentary canal consists of mouth, a short pharynx region or oesophagus forming the foregut; a long tubular intestine or the midgut and a short rectum or hindgut.

(c) Pharynx

The terminally located mouth leads into a cylindrical thick-walled pharynx or oesophagus which has a posterior swelling known as end bulb provided with valves. The pharynx is composed of muscular walls having radial muscle fibres which dilate the lumen. Internally, the pharynx is lined by cuticle which, at the margin of mouth, is continued with the cuticle of the body wall. The pharynx has three large branching gland cells which open via cuticular ducts into the lumen. These glands are commonly known as pharyngeal or oesophageal glands. The cavity of the pharynx composed of three deep longitudinal grooves lined by cuticle, and when observed in a transverse section the lumen appears triradiate. The connective tissue fibres arise from each of the three internal grooves and go to the cuticle covering the pharynx region. They help in maintaining the triradiate shape of the lumen. The above-mentioned region constitutes the stomodaeum or foregut of *Ascaris lumbricoides*.

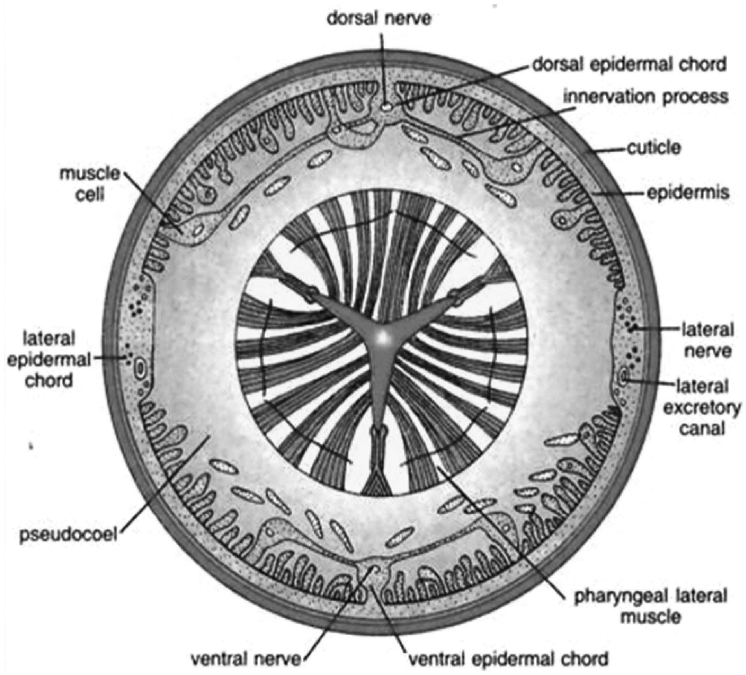

Fig. 2.23 *Transverse Section (T.S) of Ascaris lumbricoides via Pharynx Region*

(d) Intestine

The pharynx opens posteriorly into a thin-walled dorsoventrally flattened intestine or midgut which extends almost through entire length of the nematode. Intestine is composed of single layer of columnar epithelial cells lined externally by a thin layer of cuticle. The free inner margin of each intestinal cell is produced into several finger-like projections, the microvilli (Kessel et al., 1961). These microvilli increase the absorptive surface area of the intestine. Microvilli form a sort of tightly packed brush border which increases the surface area. The intestine lacks muscle layer.

(e) Rectum

Intestine region is followed by the, hindgut or rectum which is also dorsoventrally flattened. The wall of the rectum/hindgut comprises tall columnar cells and lined

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internally by cuticle and externally by few muscle fibres. In male, the rectum opens out via cloaca as it receives the ejaculatory duct, however, in females, the rectum opens out via a transverse slit-like aperture referred as the anus. The anal aperture is closely bounded by anterior and posterior lips and is associated with a few special dilator muscles known as depressor anal muscles runs from the rectum to the body wall. The contraction of the dilator muscles every now and then causes the faecal matters to be discharged out. The rectum is also composed of large unicellular rectal glands. In females, there are three rectal glands whereas six rectal glands are present in case of males.

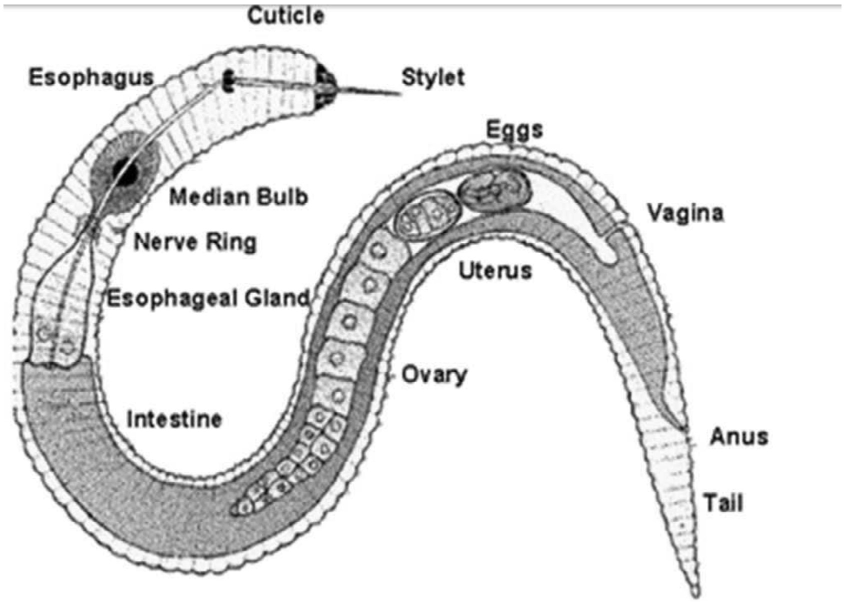

Fig. 2.24 *Generalized Digestive Tube Structure of a Nematode*

Ascaris lumbricoides is a parasite and its food is composed of blood, tissue exudes as well as partly or fully digested food of the host. Food is sucked inside the body of organism by the suctorial action of the pharynx. Digestion is extracellular in nature i.e., it takes place in a separate digestive tube and not within the cells. Here, in *Ascaris lumbricoides* the process of digestion happens inside the intestinal lumen. Several enzymes like proteases, amylase and lipase secreted by the gland cells of the pharynx assist in the chemical digestion of food. The digested nutrients are finally absorbed in the intestinal wall and distributed via the pseudocoelomic fluid. Excess food absorbed is generally stored as reserve glycogen as well as fat in the intestinal wall, muscles and syncytial epidermis. Though, extracellular digestion occurs predominantly, intracellular digestion has also been observed to occur in the cells of intestinal wall as they engulf solid particles to digest intracellularly. The undigested wastes, if any, are defecated out by the contraction of special muscles of rectum through anus or cloaca.

Similarly, the hookworm is a parasitic nematode that lives in the small intestine of its host, which may be in a mammal such as a dog, cat, or human. Hookworms are comparatively smaller than the larger roundworm, such as; ascaris. The hookworms feed voraciously on human blood and damage cells within the body. Like other nematodes, hookworms also have a complete digestive

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system, with a separate zone for food indigestion as well as excretion of waste products from the body. The pseudocoelom body cavity of the hookworm lacks the muscles of coelomate animals that force food down the digestive tract, so hookworms depend on internal/external pressures as well as body movement to move food through their digestive tracts to survive.

2.2.2 Filter Feeding in Polychaeta, Mollusca and Echinodermata

Filter feeding is a way to procure food particles from water. It is found in primarily among small-to medium-sized invertebrates. Let us study filter feeding in different phyla in detail.

Filter Feeding in Polychaetes

- Many tubicolous and sedentary polychaetes like Sabella, Serpula, etc., are filter feeders.
- These animals lack a proboscis
- The head region is often provided with a long tentacle known as radides, with a ciliated groove running along their oral surface.
- The function of these tentacles is to gather food particles from water.

Filter Feeding Mechanism in Mollusca

Filter feeders are the organism that feeds upon suspended food particles. It is an adaptation that allows the organism to feed on the food particles that are strained from water, typically by passing the water over a specialized filtering structure. Most bivalve mollusc, for example, mussels, unio, etc., are filter feeders.

Filter feeders are a sub-group of suspension feeding animals that feed by straining suspended matter, food particles or small microscopic organisms like bacteria, algae, diatoms from water, typically by passing the water over a specialized filtering structure. Filter feeding is mostly found in small to medium-sized invertebrates, although it is also observed in a few large vertebrates. Filter feeders also play a vital role in water clarification and are hence classified as ecosystem engineers.

There are two types of filter feeders:

1. Internal Filter Feeders – Animals having an internal filter feeder possess a basket-like filter inside a body cavity with two syphons that open to the outside. The water current is brought in by one hole which is known as the incurrent syphon, pumped through the filter to remove minute food particles, and then the rest of the water is discharged via another opening known as the excurrent siphon. Food particles are moved from the filter to the animal's mouth via mechanisms.

2. External Filter Feeders - All crustaceans, both acorn and goose, polychaete worms, adopt this method of filter feeding. Instead of pushing water over the filter, external feeders uses a grabbing motion, where they extend their feet upwards into the water in a rhythmic manner and then quickly bringing them back within the shell, along with any collected food.

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Echinoderms are exclusively marine animals. They use a variety of feeding methods to obtain their food for sustaining. For instance; feather stars (crinoids) and brittle stars use passive filter feeding to capture food particles that float in the water while sea stars are hunters that pursue and capture their prey, bending their arms to push the food into their mouths. Further, Sea urchins are grazers that scrape algae off rocks and other surfaces whereas sea cucumbers are known as deposit feeders as they eat small food particles that settle down on the ocean floor.

Filter Feeding in Echinodermata

Most of the adult sea stars possess pentamerous radial symmetry even though the larval stages possess bilateral symmetry. Adult body possess a central disc from which five elongated arms or rays radiates out. However, in several genera the number of arms varies, e.g., in solaster, there are around 7-14 arms. The average size of the adult sea star varies from 10cm-20cm in diameter. Although, there are genera present in nature having size less or greater than specified above. The colour of the adult sea star varies from shades of orange, brown, yellow, pink or purple. The body of the sea star is divided into two surfaces i.e. oral and aboral.

1. Oral Surface

The lower surface of the body which is directed towards substratum is called as the oral surface or ventral surface. The central disc on the oral surface bears a centrally positioned pentagonal structure known as mouth or actinostome. The surface of the mouth is encircled by soft and delicate perioral membrane. It is further protected by five groups of mouth papillae or oral spines. From, each side of mouth (remember mouth is pentagonal) runs a ambulacral groove which extends through the ventral surface of its corresponding arm. The groove is protected on all sides by two or three rows of movable adambulacral spines. External to movable spines are three more rows of immovable spines and beyond them occur a series of marginal spines separating the oral and aboral surfaces. The ambulacral groove comprised of two double rows of short tubular projections called as podia or tube feet. At the tip of each arm, there is present a hollow non-retractile projection which serves as olfactory and tactile organ. At its base, there occurs red spot composed of several ocelli. This red spot is photosensitive in nature.

2. Aboral Surface

The upper convex side of the body is called as dorsal surface or aboral surface. The aboral surface bears numerous immovable, calcareous spines called as tubercles. Surrounding and in between these spines are present tiny structures called as pedicellariae. These tiny structures are also present on the oral surface. The primary function of these pedicellariae is cleaning or guarding the body surface. Minute finger like projections called as dermal branchiae appears both on oral and aboral surface and serve for carrying out respiration as well as eliminating excretory products from the body. On the aboral surface of central disc is present an aperture which serves as anus. Another, circular area known as madreporite is present in an interradius between the two arms. Madreporite serves as sieve to filter the water before it enters into the water vascular system. These two arms (between which the madreporite is located) are called as bivium whereas the rest of three arms are known as trivium.

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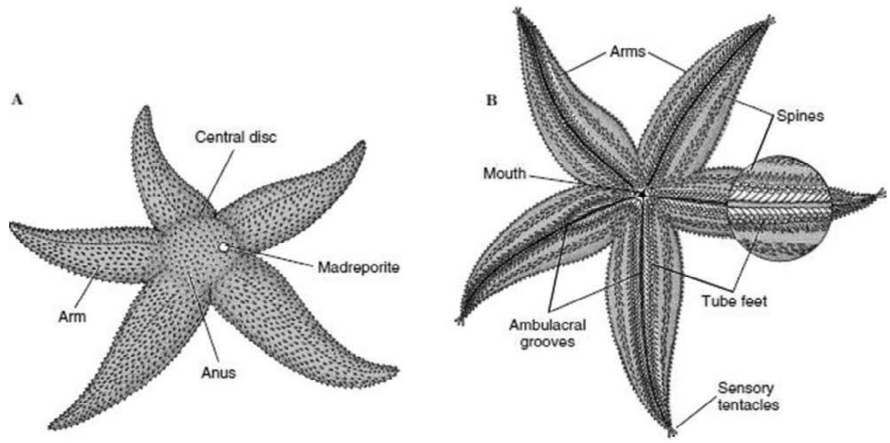

Fig. 2.25 *Parts of Digestive Tract in Sea-Star (A Filter Feeder). A- Aboral View; B- Oral View*

In star fish, water vascular system serves as the main system for carrying out the process of filter feeding. Water vascular system is a characteristic feature of echinoderms and is not observed in any other group. The water vascular system is present in all Echinoderms and develops from left hydrocoel. This hydraulic system is enterocoelic in origin. The water vascular system is positioned just above the haemal system. This hydraulic system is primarily locomotory in function but also sub-serves the function of excretion, tactile and respiratory organs in some Echinoderms. The histology of the water vascular system discloses that the canals comprise an inner lining of flat ciliated epithelium, a layer of longitudinal muscles, a connective tissue layer and an outermost layer of flat ciliated cells. The canals of the hydraulic system contain a fluid of albuminous nature having sea water and leucocytes. However, presence of red corpuscles is reported in an ophiuroid named *Ophiactis virens*. In 1964, Binyon, reported the level of potassium in the canal's fluid to the extent of 60% above the sea water value. In 1966, Boolootian, has predicted up to 14 different types of amoebocytes in this fluid. The general plan of water vascular system is similar in different classes of Echinodermata. It comprises a few canals and appendages attached to these canals. The characteristic arrangement of the hydraulic system is exhibited by Asterias (Common name: Star fish; Class: Asteroidea). The major components of canal system are:

(A) Madreporite: Madreporite is situated on the aboral surface of the central disc. It is rounded, thick sieve like calcareous plate whose surface is permeated by as many as 250 minute pores. Each individual pore leads into a short pore canal. Pore canals combine together to form collecting canal which further unite to form a sac-like ampulla. Ampulla continues into stone canal.

(B) Stone Canal: Stone canal is also known as madreporite canal. It is a S-shaped tube whose inner walls are lined by calcareous rings and hence known by the name of stone canal. The inner wall comprises tall cells having cilia or flagella. Stone canal opens on the oral side into a ring canal surrounding the mouth.

(C) Ring Canal: It is a wide pentagonal canal which forms a ring around the oesophagus.

(D) Tiedemann's Bodies: Tiedmann's bodies are also known as the racemose glands. The inner side of the ring canal is lined by tiedmann's bodies which are small, rounded, yellowish glandular sacs. There is a total of nine tiedmann's body lining the inner of ring canal. There is no tiedmann body at the position where stone canal enters the ring canal. The exact function of the tiedmann's bosy is not known. However, some scientist believes that they serve as filter devices while other suggests them as enzyme-forming bodies or lymphatic glands manufacturing amoebocytes which are ultimately released into water vascular system.

(E) Pollian Vesicles: These are pear shaped structure which serves as contractile bladder. Their number varies from one to four. The exact function of pollian vesicle is not known however scientists believe that they store water and hence helps in regulating the pressure in the water vascular system.

(F) Radial Canals: The ring canal gives out radial canal which lies below the ambulacral ossicles and terminates as lumen of the terminal tentacle.

(G) Lateral Canal: Each radial canal gives rise to short narrow lateral or podial canals along its entire length on both the sides. Each lateral canal opens up into tube feet. The opening is guarded by a valve which prevents the backflow of water into the radial canal.

(H) Tube Feet: Each tube foot is closed thin-walled structure. The walls of the tube feet possess strong longitudinal and circular muscles. It is divided into three regions namely:

(I) Ampulla: A rounded sac-like structure projecting into the coelom

(II) Podium: It is the middle tubular portion of the tube feet.

(III) Sucker: It is located at the terminal end of tube-like podium.

Water vascular system sets up a hydraulic pressure which helps the animal to perform locomotion. Hydrostatic skeleton refers to a flexible skeleton supported by fluid pressure. As the name suggests, hydro means "water" and being hydrostatic means that the skeleton or organ is filled with fluid. In general, coelomic organism i.e animals having a coelomic cavity or marine animals possess hydrostatic skeleton. It is generally seen in coelomic animals like earthworm or aquatic animals like jelly fish, starfish and sea anemones. Earthworms possess rings of muscles filled with fluid, making their entire body hydrostatic. On the contrary, sea anemone has a hydrostatic head with arms radiating out around the oral structure (mouth) which helps in feeding and locomotion. By the action of cilia lining the ambulacral canals, sea water enters via madreporite and enters into all canals up to tube feet in following order:

Madreporite $\rightarrow$ Stone Canal $\rightarrow$ Ring canal $\rightarrow$ Radial Canal $\rightarrow$ Lateral canal $\rightarrow$ Ampulla of tube feet $\rightarrow$ Podia of tube feet

Tube feet alternately adhere and release off from the substratum which aides in locomotion. One or two arms, are raised from the substrata in the direction of motion. Consequently, the circular muscles of ampullae of these tube feet contract.

This elevates the hydraulic pressure within the tube feet which then elongate, expand forward and firmly attach to the ground with the help of their suckers. Then, by muscular contraction tube feet drags the whole body in the direction of motion. These elongated tube feet then shorten down by the contraction of the longitudinal muscles thus forcing out water back to the ampullae in the process. As a result, the grip of the suckers also gets loosen on the surface. Generally, one or two arms guide the direction of motion pushing along the entire body in a coordinated manner at a speed of about 15cm per minute.

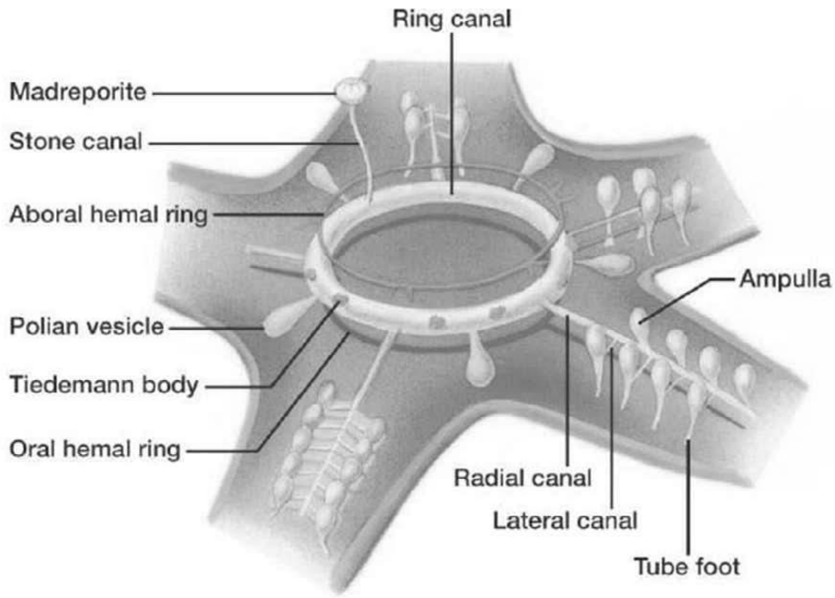

Fig. 2.26 *Components of a Water Vascular System in Echinoderm*

Sea star have several arms may be up to 20 can be seen in some species. These long arms are covered in spines, which themselves are covered with small snapping jaws known as pedicellariae. By attaching their centre to a surface and waving these long arms in the water, these starfish filter feed, snagging small zooplankton and other critters as they drift by. The entire process can be explained as follows:

1. Spines come off the lateral sides. They project off the tube foot furrow. In few species, spines are even present on the surface of the body. All the spines are arranged in a familiar "cruciform" arrangement that are generally seen in suspension/filter feeders.
2. Spines are covered by a "sock" of pedicellariae. These spines are covered by a sheath of tissue, like a sock. Pedicellariae are little jaw-like structures that cover the surface.
3. The pedicellariae essentially "go off" when food hits them. Food particles like some small shrimp, krill or other tasty bit of organic are caught by the spine/pedicellariae. Prey are held fast by the pedicellariae similar to velcro.
4. Once the food is captured, it is then moved via the tube feet to the mouth and devoured.

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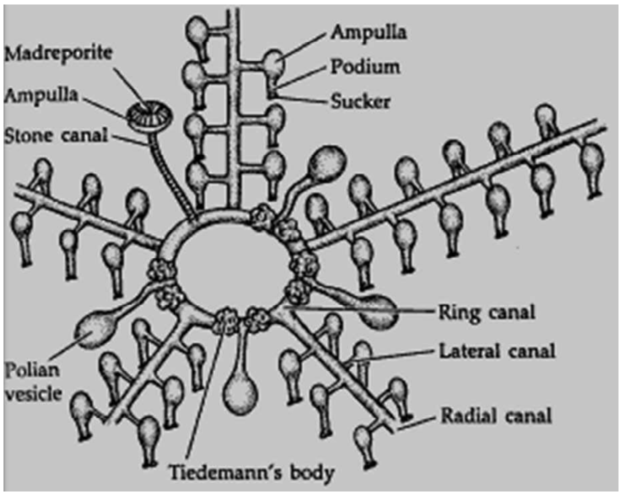

Fig. 2.27 *Portion of the Water Vascular System Used for Capturing the Prey in Echinoderms*

The physical make-up of a sea star's digestion system is as follows: The mouth of the sea star is found on the underside of the sea star creature. Food enters the mouth and then into the primary/first stomach. Then, it is passed onto the secondary stomach and then into the many digestive glands that are located within each of the arms of the sea star. These digestive glands secrete enzymes and absorb the much-needed nutrients from the food obtained from the water current. Further, a small intestine runs from the secondary stomach to the external port (where the sea star disposes waste) which is located in the central upper part of the body. A few species of Sea Stars eat their prey and begin digesting it before sending it to the digestive glands in the Sea Star's arms. However, other species of Sea Star are able to put their stomach outside their bodies, where it can eat food and begin the digestion process. It passes this food to its secondary stomach, which always stays inside the Sea Star. Further digestion occurs at the Sea Star's intestine. Finally, waste is excreted through the Sea Star's anus on its aboral side of the body.

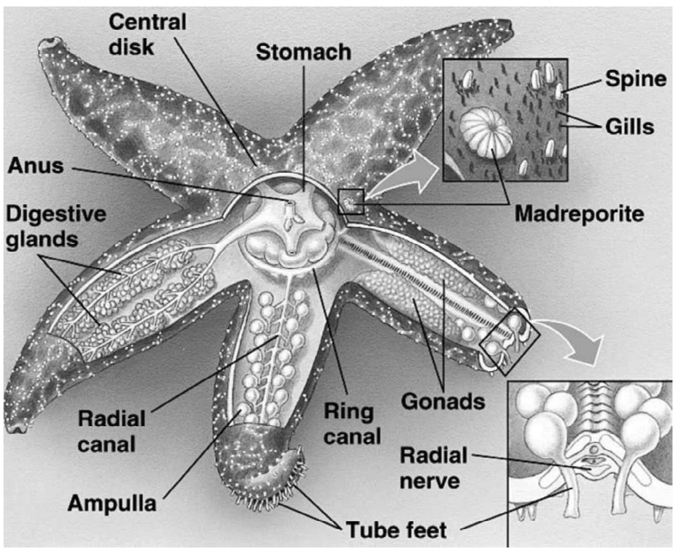

Fig. 2.28 *Digestive System in Sea-Star*

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Check Your Progress

1. Define polychaetes.
2. What do you understand by alimentary canal?
3. What do you understand by digestion?
4. Define stomach.

2.3 RESPIRATION

The process of respiration involves various organs in invertebrates. Let us study the process of respiration in detail.

2.3.1 Organs of Respiration: Gills Longs and Trachea

In invertebrates, the organs associated with conveying oxygen and carbon dioxide between the external respiratory surfaces and the metabolizing tissues are called as respiratory organs.

- **Branchiostegal Lung:** A branchiostegal lung is a respiratory organ which is used by some air- breathing arthropods. It is one of the most significant adaptations of some crabs and hermit crabs like, coconut crab to their terrestrial habitats.

  The branchiostegal (gill) tissue is supported by folds in order to increase the surface area for carrying out respiration. These folds are of a similar tissue to that are normally found in gills. In this case, the lung more suitable for the absorption of oxygen from air, rather than water.

  A few terrestrial hermit crabs like *Coenobita* and *Birgus*, possess numerous gills and small lungs alongside several gas diffusion methods supporting the transition from aquatic to terrestrial habitat.

  The developmental shift from 'gills' to 'lungs' can be associated with the requirement for reduced rates of water loss in air.

- **Pneumostome:** The pneumostome serves as the respiratory opening present on the right side of the mantle of an air-breathing land slug or land snail. It is a component of the respiratory system of gastropods. This wide respiratory opening is clearly visible, when open. However, it is difficult to view it when this opening is completely closed. It opens and then closes in a cyclical manner. Air enters through the pneumostome into the animal's single lung (a highly vascularized area of tissue that functions as a lung inside the mantle cavity) which is an air-filled mantle cavity. In fully hydrated slugs and snails, the frequency of pneumostome closing and opening is typically less than 0.5 closures per minute. The more dehydrated the slug is more is the rate of closures per minute.

- **Ctenidium:** A ctenidium (Greek *ktenidion* which means 'little comb') is a respiratory organ or gill found in many molluscs. This structure is present in bivalves, cephalopods, and aquatic gastropods, i.e., in some freshwater snails, sea snails, and also in some sea slugs. Some aquatic gastropods enclose one ctenidium, others possess a pair of ctenidia.

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A ctenidium is a comb or a feather like structure with a central portion from which arises numerous filaments or plate-like structures, lined up in a row. It is suspended into the mantle cavity and augments the surface area that is available for gas exchange.

- **Siphon:** A siphon is a breathing tube like respiratory organ seen in some insects which generally spend most of their time underwater. The larval form of several insects, including mosquitoes, tabanid flies, and belostomatidae live in water and respire with the help of a siphon.

  Some adult insects like adult water scorpions which spend substantial time underwater possess an abdominal breathing tube. They possess the caudal process which carries a pair of half-tubes capable of being locked together to form a siphon tube via which air is conducted to the tracheae at the apex of the abdomen when the tip of the tube is thrust above the surface of the water. However, in immature forms the siphon is not fully developed and breathing takes place via six pairs of abdominal appendages.

  All animals require a constant supply of oxygen into the cells to obtain energy for carrying out the physical and metabolic activities. Further, carbon dioxide produced during metabolic activities needs to be transferred out from the body. In small animals, physical forces of diffusion alone are enough to carry out these exchanges. However, larger animals due to their high rate of respiration and impermeable protective body surfaces requires specialized respiratory structures for the exchange of oxygen and carbon-dioxide between the external environment and the internal environment.

  The processes that are involved in inhaling and utilizing oxygen lie under the general category of respiration which has broadly two different aspects namely external respiration and internal respiration.

  - Firstly, there is an exchange of oxygen and carbon dioxide between the organism and the external environment called as the external respiration.
  - Secondly, there is the complex reaction that takes place inside the cell resulting in the release of energy in the form of ATP by the oxidation of energy rich molecules derived from the food. The process is known as internal respiration.

    Then there is a transport mechanism that links both by conveying the oxygen and carbon dioxide between the external respiratory surfaces and the metabolizing tissues. Organs associated with these functions make up the respiratory system.

- **Gills:** The respiratory organ of aquatic animals is gills. It may be external for example as in echinoderms, polychaetes, some larval and adult amphibians and fishes, or internal for example as in crustaceans, molluscs and teleost fishes. The class crustacea displays a wide variety of gills that are bathed thoroughly to bring water close to the circulating blood. The gills of the mollusc are present inside the mantle cavity.

- **Lungs:** Air creates additional hazards for terrestrial life because it is a richer resource of oxygen. The evolution of terrestrial animals has been dependent

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on the innovation of special air sacs and air tubes. The lung is nothing but a vascularized air sac. Lungs are therefore found in several of the terrestrial invertebrate groups such as the pulmonate snails, scorpions, some spiders, chilopods, decapods, etc. Basically, in all of them, diffusion-lungs are present which lack good ventilating system. Ventilation lungs are characteristics of terrestrial vertebrates where a rhythmic exchange of air is created by coordinated muscle movements. The tracheal systems of terrestrial arthropods serve both the functions: bringing air into the body and distributing it to the cells.

The system of air tube is often compared with a lung in which the alveoli have extended throughout the intercellular space as a rami-form network of tubes. Whereas, in actual the air capillaries or the tracheoles do not enter the cell but only sink into the plasma membrane of cells with high oxygen demand. In this way tracheoles are functionally intracellular and help in bringing oxygen very close to the mitochondria. This arrangement is highly efficient as it permits high rates of metabolism and activity as seen in the flying insects.

- **Trachea:** The invertebrate trachea refers to the open respiratory system of terrestrial arthropods. It consists of spiracles, tracheae, and tracheoles that take metabolic gases to and from tissues. The distribution of spiracles varies, but in general each segment of the body has only one pair of spiracles, each of which connects to an atrium and has a relatively large tracheal tube behind it.

  The smallest tubes, tracheoles, penetrate cells and diffuse water, oxygen, and carbon dioxide. Gas may be moved actively or by passive diffusion. Unlike vertebrates, insects do not generally carry oxygen in their haemolymph. This is one of the factors that may limit their size.

  A tracheal tube may contain ridge-like circumferential rings of taenidia in various geometries such as loops or helices. In the head, thorax, or abdomen, tracheae may also be connected to air sacs. Many insects, such as grasshoppers and bees, which actively pump the air sacs in their abdomen, are able to control the flow of air through their body. In some aquatic insects, the tracheae exchange gas through the body wall directly, in the form of a gill, or function as normal, via a plastron.

  It is a tube that transports air, moistens and warms it as it passes through the lungs, and shields the respiratory surface from foreign particles. A moist mucous-membrane layer lining the trachea is made up of cells with tiny hair-like projections called cilia.

2.3.2 Respiratory Pigments in Invertebrates

Most animals have developed respiratory pigments to facilitate the transport of oxygen to different parts of the body. Respiratory pigments are of profound physiological importance, especially in large sized animals, because the uniform distribution of oxygen to all parts of the body by way of simple diffusion would be a very difficult process.

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In general, respiratory pigments are coloured proteins that consist of a metallic element in their constitution and have the property of forming loose combination with oxygen and seldom with carbon dioxide.

The following four different (biochemically) respiratory pigments:

- Haemoglobin
- Hemocyanin
- Chlorocruorin
- Hemerythrin

The same phylum may have several distinct pigments, and more than one distribution of four pigments in the animal pigment may exist in the same animal. For details of the distribution of different respiratory pigments in animal kingdom (Refer Figure 2.29 and Table 2.1)

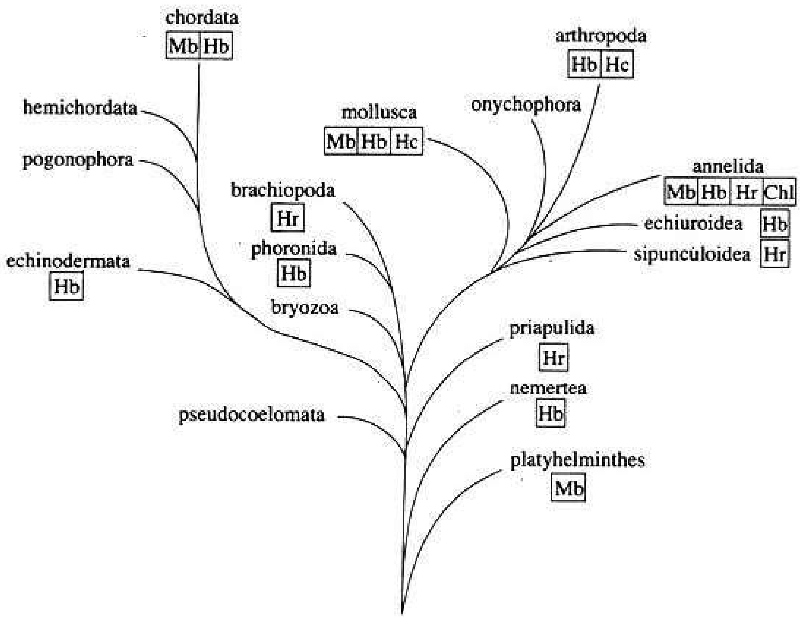

Fig. 2.29 *Distribution of Different Respiratory Pigments in Animal Kingdom. Chl-chlorocruorin; Hb-Haemoglobin; Hc-haemocyanin, Hr- Haemerythrin; Mb- Myoglobin.*

Table 2.1 *Table Depicting Distribution of Respiratory Pigments in the Kingdom Animalia*

Pigment	Colour	Site	Animal
Haemoglobin	Red	Corpuscles	Mammals
			Birds
			Reptiles
			Amphibians
			Fishes (gnathostome)
			Cyclostomes
		Plasma	Annelids
			Molluscs
Haemocyanin	Blue	Plasma	Molluscs
			Gastropods (*Helix*)
			Cephalopods
			Crustaceans
Chlorocruorin	Green	Plasma	Annelids
Haemerythrin	Red	Corpuscles	Annelids

- **Haemoglobin**: Haemoglobin is the most efficient respiratory pigment. It is widely distributed in the animal kingdom: from some protozoa, such as, paramecium to almost all vertebrates except eel larvae and few Antarctic fish. Some invertebrate phyla viz., Porifera, Cnidaria and Ctenophora completely lack it though.

  It is also found in the plant world. In vertebrates, it is always housed inside the erythrocytes of blood. In invertebrates, it may be dissolved in blood plasma, (for example, Oligochaetes, Hirudinea, Arenicola, Nereis, etc.) or may be present inside erythroid coelomocytes (for example, Holothurians, some polychaetes like Capitella, Glycera, etc.).

  The molecular weight of vertebrate haemoglobins varies between 64,000-68,000 Daltons. The intracellular haemoglobin of invertebrates is generally of low molecular weight that ranges between 15,000-17,000 Daltons. But extracellular haemoglobin in invertebrates is of higher molecular weight varying between 1 to 3 million Daltons.

  Haemoglobin consists of an iron porphyrin compound, haeme, that is associated with a protein, globin. Haeme is made up of four pyrrole rings linked by methenyl-bridges (—CH=) to form a super-ring with an atom of ferrous iron situated in the centre attached to the pyrrole nitrogen (Refer Figure 2.30).

  The haeme component is a constant structural feature of all haemoglobins. It is the globin portion that varies in different species. In addition, varying numbers of haemoglobin units get united to form polymers of several sizes.

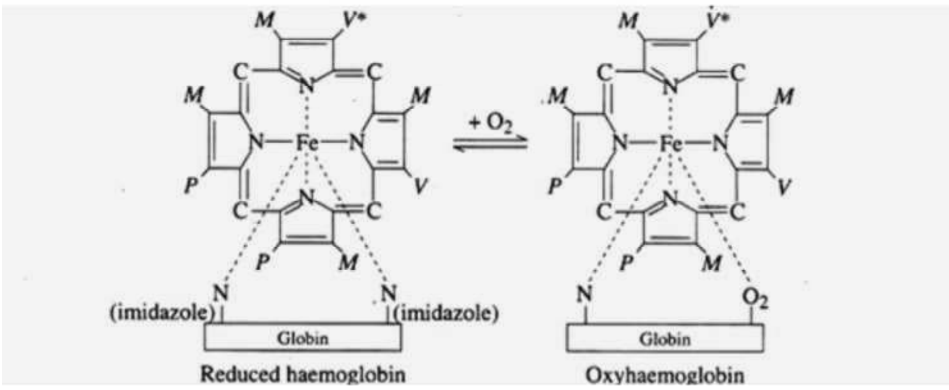

Fig. 2.30 *Structure of Heme Molecule, with the Attachment of Highly Variable Globin Part of the Molecule.M, Methyl group- CH_3, V, vinyl group –CH=CH_2, P, propionic group— CH_2-CH_2-COOH. In Chlorocruorin, Position 2 is Filled by the Formylgroup O=CH.*

For example, myoglobin or muscle haemoglobin of all vertebrates and oxyhaemoglobin of cyclostomes consist of just one unit, whereas, two units unite in some haemoglobins of the polychaete worm glycera. Haemoglobin of several forms are regularly found within the same animal for example: A man has four peptide chains in the globin of vascular haemoglobins.

In the adult human, 90% haemoglobin is composed of two β-chains combined with two α-chains to make up a single tetrameric molecule known as

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Haemoglobin A. There are 141 amino acids present in an α-Peptide Chain whereas each β-Chain consists of 146 amino acids. Adult blood too has small amount of Haemoglobin A_2 in which the α-Chain is replaced by 6-Chains.

These molecular changes give different transport properties which are adopted to the then changes in respiratory requirements. In the tetramer, a molecule of heme is bonded to one of the histidine residues of each chain; the four chains are folded together into an intricate molecule which has been mapped in detail by X-ray analysis [Refer Figure 2.31(a)].

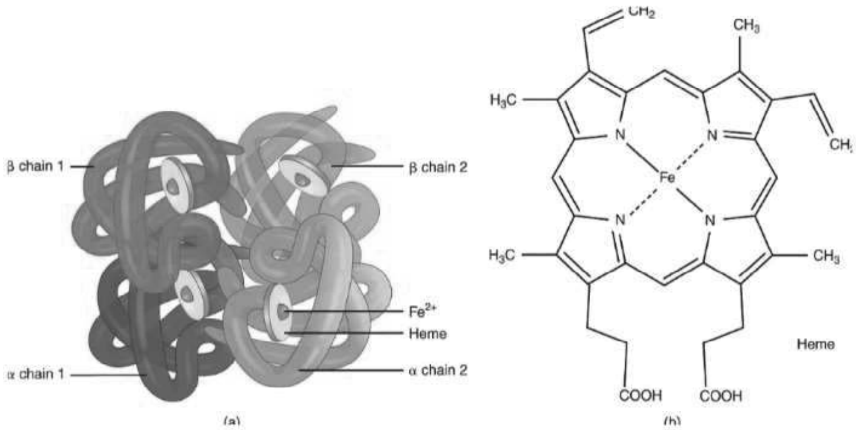

Fig. 2.31 (a) *Human Haemoglobin Molecule*
(b) *Chemical Bonding in a Human haemoglobin Molecule*

Changes in amino acids of the peptide chain greatly alter its physiology. The main difference between the invertebrate and vertebrate haemoglobins is that the invertebrate ones have less histidine and lysine, and more arginine and cysteine, though these may also differ among themselves.

In all cases, one thing is common, and that is the atoms of ferrous ion which remain associated (non-enzymatically) with one molecule of oxygen to form oxyhaemoglobin. The reaction is readily reversible and the non-oxygenated compound is known as reduced haemoglobin. Haemoglobin is red in colour in oxygenated as well as non-oxygenated states.

The association of haemoglobin with oxygen depends on the availability of oxygen as well as on the pH and ionic content of the solution. The partial pressure of oxygen at which haemoglobin is half saturated with oxygen (P_{50}) ranges between 10-20 mm of mercury (Hg) in fishes, 20-40 mm Hg in land vertebrates, 40-60 mm Hg in birds and in invertebrates the value is generally below 10 mm Hg.

- **Hemocyanin**: Among all the copper-proteins occurring in nature, only hemocyanin can reversibly combine with oxygen and therefore it serves the purpose of a transport pigment. It is present in chitons, some gastropods and cephalopods amongst the molluscs and in crustaceans and limulus amongst the arthropods. It is always dissolved in the plasma.

The molecular weight is very high, ranging from 4,00,000 Daltons in some crustaceans to 13,00,00,000 Daltons in some gastropods. The numbers of subunits also vary from a few to many in hemocyanin.

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Generally, molluscan hemocyanins consist of a greater number of subunits as well as are larger than the arthropodan pigment. Porphyrin is absent in hemocyanin. In this metalloprotein, the metallic part is made by copper (Cu^{++}), which is directly linked to the protein part.

The molecules of hemocyanin are build-up of units composed of one copper atom that is associated with a peptide chain of just over 200 amino acids. During oxygenation, two atoms of copper get reversibly oxidized to the cupric form. In de-oxyhemocyanin, the copper is present in the cuprous form. Hemocyanin is colourless in deoxygenated state but it is bluish in oxygenated form. Hemocyanin gets saturated with oxygen at different concentrations in different species. The partial pressure of oxygen ranges between 15-35 mm Hg in molluscs and 50-20 mm Hg in arthropods. The oxygen transporting capacity of hemocyanin is lower than that of haemoglobin.

Besides these two principal respiratory pigments, several other pigments also occur in some animals such as:

- **Chlorocruorin**: This green coloured metalloprotein is present in the plasma of some polychaete families, viz., Sabellidae, Serpulidae, etc. It is a metalloprotein which consists of a metal, *i.e.,* iron (Fe^{++}); the metalloporphyrin that is similar to heme of haemoglobin except that one vinyl ($CH = CH_2$) group gets replaced by formyl (0=CH) group in chlorocruorin. The porphyrin is known as the chlorocruoheme.
- **Hemerythrin**: It is a violet coloured pigment and is found inside the corpuscles of animals which belong to the phyla Sipunculidea, Priapulida and Brachiopoda, and also in the polychaete worm Magelona. It is also an iron containing metalloprotein, but porphyrin is absent.
- **Pinna Globin**: It is a brown coloured, manganese containing pigment and is found in the plasma of the Lamellibranch and Pinna.

2.3.3 Mechanism of Respiration in Invertebrates

Let us study the mechanism of respiration in arthropods and molluscs in detail.

Aquatic Respiration in Arthropods

Arthropods are invertebrate animals characterised by presence of exoskeleton, paired jointed appendages, and segmented bodies. They can be terrestrial as well as aquatic, where the respiration is quite different in aquatic forms (crustaceans and chelicerata) than those of the terresterial forms (insects and arachnids).

These are the organs responsible for aquatic respiration in arthropods:

- Gills or Branchiae
- Tracheal Gills
- Blood Gills
- Rectal Gills
- Book Gills
- Branchiostegite or Gill Cover

- Epipodite
- Branchial Basket

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I. Gills or Branchiae

Origin of Gills in Crustacean: Gills develop as out-pushings of the body wall. In amphipoda, the gills are outgrowth of thoracic limbs whereas endopodites of second and fifth pleapods are transformed as gills in isopods.

Occurrence: Gills are the chief respiratory organs of aquatic arthropods. These are very well developed in crustaceans.

Location: Gills are positioned within the gill chambers. The gill chamber is situated on each side of cephalothorax and covered by gill cover also called branchiostegite.

Structure of Gills in Crustacea: Typical gill of a crustacean is crescent- shaped (Refer Figure 2.32). It is characterized by the presence of a central axis or rod with blade like filaments arranged on both sides. These filaments are known as lamellae. One end of the lamella stays attached to the central axis while the other end remains free. An afferent and an efferent branchial channel runs through the central axis or the rod of each gill.

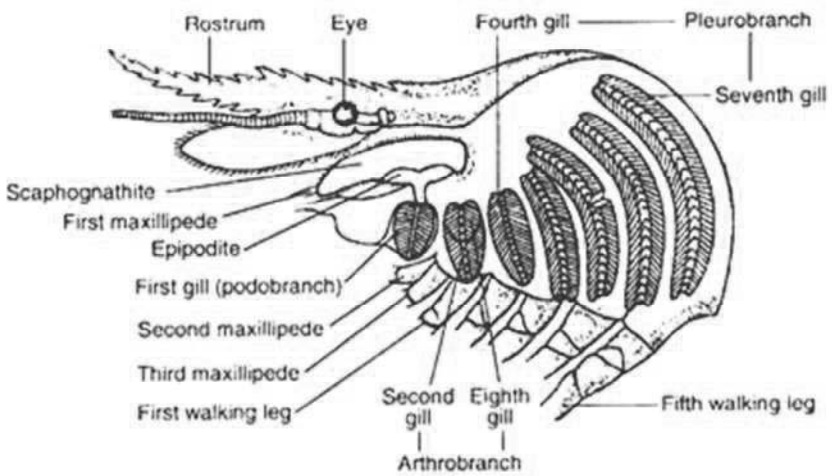

Fig. 2.32 *Respiratory Organs (Gills) of Palaemon*

Note that the branchiostegite of one side has been removed to expose the gill-chamber.

Types of Gills Found in Crustaceans

i. Based on the shape of the lamellae or gill filament, the gills are of the following types:

- **Phyllobranchiate Gill:** Gill lamellae are seen as flat, broad leaf-like structures arranged in two rows [Refer Figure 2.33 (A), (B)]. It can be seen in crabs and prawns (Palaemon).
- **Trichobranchiate Gill:** The gill filaments are tubular-shaped. It can be seen in crayfish (for example, Astacus) and rock lobsters. It consists of central axis with numerous gill filaments, developed as an outgrowth of skin of the legs or from side of the body [Refer Figure 2.33 (C), (D)].

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- **Dendrobranchiate Gill:** Leaf like lamellae of the gills is divided into fine branched filaments [Refer Figure 2.33 (E), (F)]. It is seen in Penaeus.

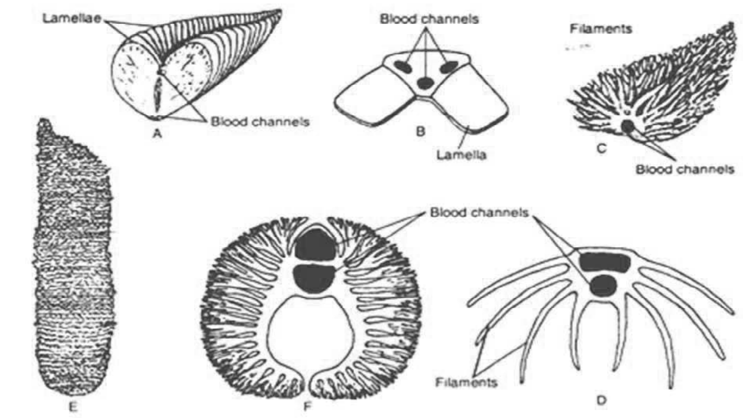

Fig. 2.33 *Types of Gills in Decapod Crustacea*

The above Figure 2.33 shows gills types where A. lateral view of a phyllobranchiate gill with flat lamellae, B. Transverse section of a phyllobranchiate gill, C. An entire view of a trichobranchiate gill, D. Transverse section of a trichobranchiate gill, E. An entire view of a dendrobranchiate gill, F. Transverse section of dendrobranchiate gill (from various sources)

ii. Based on the mode of attachment, the gills may be of three types:

- **Podobranch:** Podobranch are small pair of gills attached to the coxopodite of thoracic segment. In macrobrachium (Palaemon), penaeus the podobranchs are one pair and stay attached to the second maxillipedes.
- **Arthrobranch:** Arthrobranch gills are attached to the arthroidal membrane that connects the appendages of the thorax. In Palaemon, these are two arthrobranch, attached to the arthroidal membrane of third maxillipede. In Penaeus, arthrobranchs are eleven pairs in number, beginning from second maxilliped to third walking leg, two found in each appendage and fourth walking legs contains single arthrobranch.
- **Pleurobranch:** Pleurobranch gills are attached to the lateral walls of the thorax. Five pleurobranchs attached to the lateral side of the thorax are found in Palaemon. Moreover, there are six pairs of pleurobranchs attached to the last six pairs of thoracic appendages in penaeus.

Number of Gills in Crustacea

Number of gills varies with groups. Decapods containing all the types of gills show extreme variation. In the shrimp-lucifer, gills are absent; peacrab has 6 gills; penaeid shrimp has 24; homarus has 20. There are 8 pairs of gills in palaemon and the magnitude of the gills increases from anterior gills to the posterior.

Modification of Gills in Arthropoda

The gills are modified in various ways in crustaceans and other arthropods. Broad epipodites of the thoracic appendages work as gills in the phyllocarida. Similar type of gills is seen in cumacea. Plate like gills are seen in amphipoda and flattened in a decapod, palinurus. The tufted podobranch is not covered by carapace in euphausiacea. The gills seem as a row of small branchial lamellae on each side of cyprididae. In the Phyllopods, the leaf-like pleopods function as gills. Among the crustaceans, abdominal gills are only present in isopods and stomatopods.

II. Tracheal Gills

Tracheal gills are so called as they are highly supplied with trachea. These are present in aquatic larvae of many insects. It comprises a series of simple and divided external processes that are attached to the abdominal segments of the body and help in carrying out respiration [Refer Figure. 2.34 (A)].

III. Blood Gills

In aquatic larval forms of some insects (chironomidae), branching tubular outgrowths containing blood vessels replaces trachea and hence they are known to be blood gills.

IV. Rectal Gills

In the nymphs of several insects, inner surface of the rectum contains gills known as rectal gills.

V. Book Gills

In Xiphosurids, abdominal appendages exhibit specialised plate like outgrowths known as the book gills. These are formed by the evagination of posterior margins of ninth to thirteenth segments of opisthosoma. Each gill possesses nearly 150 lamellae arranged like leaves of book [Refer Figure. 2.34 (E)].

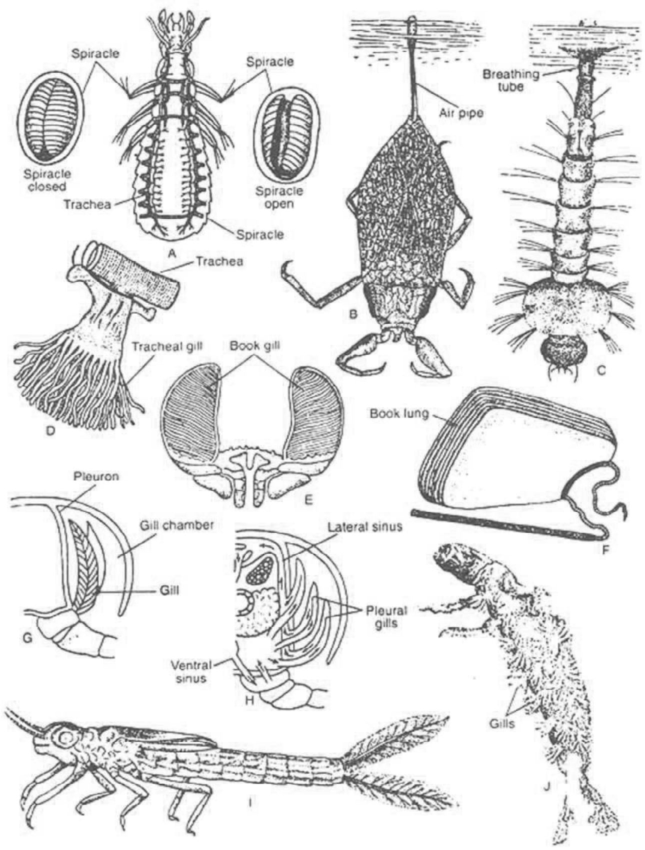

Fig. 2.34 Respiratory Structures of a Few Arthropods

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The above figure 3.6 show respiratory A. Tracheal system of a typical insect, B. Air pipe of water scorpion, C. Breathing tubes of a mosquito larva, D. Tracheal gill of an insect, E. Book gill of *Limulus*. F. Book-lung of spider. G. Podobranchial gill of crustacea. I. Leaf-like gill of a damsel-fly nymph. J. Mesh of gills in a caddisfly larva.

Mechanism of Gill Respiration

Most crustaceans do not possess a gill cover, or the gills are exposed to the outside but in decapods the carapace extends from sides to house the gills in a specialized chamber thus providing protection to these delicate organs.

In these forms with chamber, the gills are bathed in water coming inside from one end and moves out from other direction. In xiphosurids and crustaceans, the exchange of gas takes place in the gills between blood and water, which is different from those of insects where after exchange of gas the oxygen passes to tracheal tubes.

Branchial Formula: Branchial formula gives the number and arrangement of gills on each side. Branchial formula of one freshwater prawn (for example, Macrobrachium sp. = Palaemon sp.) is given below in Table 2.2.

Table 2.2 *Showing the Branchial Formula of a Prawn,*
Macrobrachium *sp. (= Palaemon sp.)*

Appendages	Podobranchs	Arthrobranchs	Pleurobranchs	Epipodites	Total
I Maxilliped	—	—	—	1	1
II Maxilliped	1	—	—	1	2
III Maxilliped	—	2	—	1	3
I Walking leg	—	—	1	—	1
II Walking leg	—	—	1	--	1
III Walking leg	—	—	1	—	1
IV Walking leg	—	—	1	—	1
V Walking leg	—	—	1	—	1
Total	1	2	5	3	11

VI. Branchiostegites

Gill cover or branchiostegite are lateral extension of the carapace for covering gill chamber. The branchiostegite are found in crustaceans. The inner lining of gill cover is thin, membranous, and highly supplied with blood. Due to its direct contact with water current, gaseous exchange takes place here between the water and the blood.

VII. Epipodites

The integument of outer side of coxa of mixillipeds gets high vascularization forming leaf-like outgrowth in the first three thoracic segment. These are present at the anterior part of gill chamber and are responsible for carrying out respiratory functions (for example, crustacea).

VIII. Branchial Basket

In immature odonates (insects), rectum is modified into a branchial basket having contractile wall richly supplied with the branches of tracheae. This type of respiration is referred as anal respiration.

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Aerial Respiration

This is the mode of respiration for terrestrial arthropods (i.e., living on land).

The organs for respiration are the following:

- Trachea
- Lungs
- Book-lungs
- Pseudotracheae or Air Tubes
- Anal Respiration
- Miscellaneous Devices

1. Trachea

This is the most significant organ for respiration in terrestrial arthropods, such as; centipedes, insects, and many arachnids. It is characterized by chitin-lined tubes found on the lateral side of the thoracic and abdominal segments of the body with openings.

Types of Tracheae Found

- **Ventilation trachea**—oval and collapses after exhaling air
- **Diffused Trachea**—rigid, does not collapse after exhaling air

Origin

The tracheae have developed by invagination of body walls.

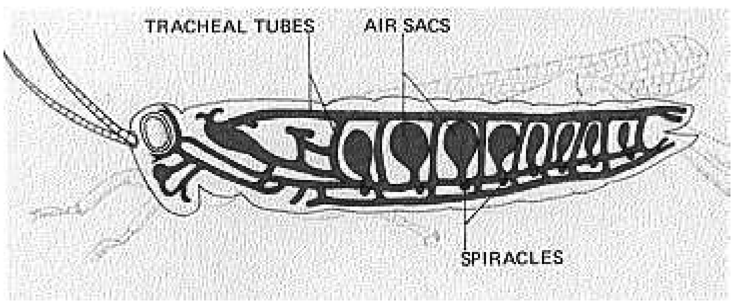

Fig. 2. 35 *Tracheal System in Insects*

Structures of Trachea and Associated Parts

- Trachea is a tube where the walls are formed of polygonal cells.
- Wall of trachea is formed of three layers—namely internal layer called as intima; middle layer of epithelium, and an outer layer of basement membrane.
- The intima is surrounded by spiral cuticular ridges, called taenidea for preventing collapse of tracheae.
- The tracheal cuticle has the same layers as that of the surface cuticle except the wax layer and cement layer.
- The opening of tracheae to external environment is called stigmata or spiracles.
- These are located along the lateral sides of the body.

- Each spiracle opens up into a chamber, called as atrium and the penetrene is a plate like structure on which the spiracle rests.
- Each spiracle possesses two lids, one for opening and the other for closing.
- A filtering apparatus is present in the chamber for removing foreign particles, which contains either special bundles of setae or sieve-like membrane.
- Some tracheal parts dilate to form air sacs which serves as air reservoirs
- The tracheae branch internally to form tracheoles which lack inner taenidial ridges. A tracheole can measure 1 μ in diameter and reaches every cell of the body.
- The end of a tracheole is immersed into fluid through which gaseous exchange takes place.

Classification of Tracheae

- The adult insects have tracheal system of one kind.
- The primitive conditions had 12 pairs of spiracles, now 2 thoracic and 8 abdominal pairs of spiracles are found in adult insects.
- Some forms may lack spiracles, but they appear during early stages of development. For example, metathoracic spiracles of hymenoptera, lepidoptera, coleopteran and few others is absent, the queen termite possesses only 6 pairs of spiracles.
- Millipedes possess a pair of thoracic spiracles and two pairs of abdominal spiracles.
- Spiracles develop in variety of ways in different insects during development.

Classification of Spiracles

Based on number of functional spiracles, the tracheal system in larvae may be classified as:

A. Polypneustic

Tracheal system which opens up to the outside via 8 pairs or more than 8 pairs of functional spiracles.

Polypneustic may again be subdivided into the following:

- **Holopneustic:** A total of 10 pairs of functional spiracles present, 2 thoracic and 8 abdominal pairs.
- **Peripneustic:** The abdominal spiracles are present on all the abdominal segments. A total of one thoracic and eight abdominal spiracles are present on each side of the body.
- **Hemipneustic:** A respiratory system having 1 thoracic and 7 abdominal spiracles located on each side of the body. This term is used if one or more pairs of spiracles are nonfunctional.

B. Oligopneustic

In this respiratory system, only one or two pairs of spiracles are functional.

It includes divisions like:

- **Amphipneustic:** This is the condition seen in the larva of common house fly when one pair of thoracic and one pair of post-abdominal spiracles are present.
- **Metapneustic:** This is seen in larva of mosquitoes when only one pair of post-abdominal spiracles is functional.
- **Propneustic:** This is present in some dipteran pupae where only one pair of thoracic spiracles is functional.

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C. Apneustic

In this respiratory system, functional spiracles are absent. This is present in aquatic larva of some insects where the gaseous exchange takes place via integument.

Mechanism of Tracheal Respiration

The trachea branches into several fine networks called tracheoles that end into tissues where gaseous exchange takes place by the mechanism of diffusion. Air is drawn in and out through the spiracles by alternate contraction and relaxation of the body. Mostly, the spiracles remain closed and the gaseous exchange is done through ventilation and diffusion.

Recent studies have indicated that spiracles open very little but not always to prevent loss in haemocoelomic pressure. Spiracles are closed by valves which check water loss and its opening is regulated by CO_2 concentration. Gaseous exchange primarily takes place by diffusion through the tracheae and the tracheoles are fluid filled which facilitate O_2 transport to the tissues.

It is also found that tracheal movement is marked by the alternate contraction and relaxation of the body. In bed bugs, rigid sternum does not contribute in respiratory movement, which is done only by elastic tergum. In cockroaches, intersegmental membrane separates the tergum and sternum of segments which bulges out while respiration.

Modifications of the Tracheae

The tracheae are absent in most collembola and the respiration is mostly cutaneous. Segmental tracheae originate from spiracles in *Machiles* but do not bear trunks. The larva of Musca is provided with one pair of anterior and one pair of posterior apertures on its dorsal longitudinal trunk.

Mosquito larvae have a single spiracle connected to its dorsal trunk. In myriapods, spiracles open within air chamber from where large number of tracheae arise. Other peculiarities are that tracheae are branched in diplopoda and two tracheae are present on the head in symphylan.

Other Modes for Aerial Respiration

- **Lungs:** In the Crustacea, Birgus, aerial respiration is achieved by vascular tufts within the upper part of the gill chamber separated from the rest and forms a closed chamber.
- **Book-lungs:** The book-lungs are well developed in scorpions and spiders they are also regarded as modified abdominal appendages. These are blind sacs like structure formed by evagination of opisthosoma.

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The inner lining of the sacs is raised into numerous folds like book leaves, which are highly vascularised and therefore respiration in scorpions is dependent on circulation. Each book lung interacts to the outside via stigma.

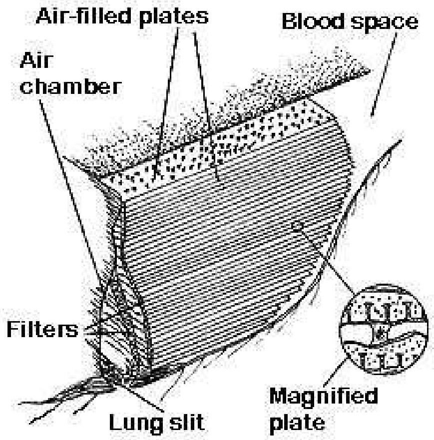

Fig. 2.36 *Book Lungs In spider*

- **Pseudotracheae or Air Tubes:** The only land-dwelling crustacea, oniscus (wood lice) possesses abundant minute tube-like projections in the abdominal appendages called *Pseudotracheae* that help it in respiration.
- **Anal Respiration:** This type of respiration is common in lower crustaceans such as cyclops where the contraction and relaxation of intestine facilitate respiration by taking in and expelling out water.
- **Miscellaneous Devices:** A combination of tracheae and book lungs can be seen in spiders. Mosquito larvae uses a long tube called siphon to draw air from water surface. Aquatic members of hemiptera and coleoptera carry respiratory tubes attached to the posterior end of the body, formed by two cerci.

Respiration in Molluscs

Respiratory organs in molluscs are as follows:

- Mantle and skin
- Molluscan gills or Branchiae Or Ctenidia
- Lungs or Pulmonary Sac

The skin and mantle usually act as accessory respiratory organs.

1. Skin and Mantle — as Respiratory Organs

Skin is the simplest type of respiratory structure found in molluscs. It works as a respiratory organ in certain forms without any respiratory device. Such type of respiratory structure is present in limapontid, cenia, parasitic entoconcha, etc.

Most of the members belonging to aeolididae have papillae on the dorsal surface of the body. The papillae are of different size and communicate with the heart via veins. Most of the Nudibranchia respire via skin while in some forms like chaetoderma, dentalium, neomenia, aplysia, etc. the mantle is used for the same.

2. Ctenidium — as the Respiratory Organ

Aquatic molluscs carry out respiration using ctenidia which are the comb-like outgrowths from mantle, located within the mantle cavity.

Structure of Ctenidium: Each ctenidium or molluscan gill has a long flattened axis hanging from anterior wall of mantle cavity. It contains afferent and efferent blood vessels, muscles as well as nerves. A row of flattened, triangular gill filaments or lamellae is associated with each side of long ctenidial axis. The surface of ctenidia is usually covered with cilia.

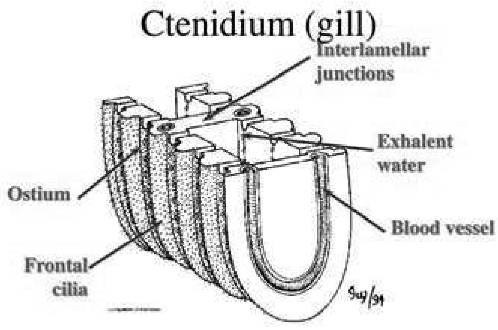

***Fig 2.37** Ctenidium*

Aquatic Respiration

Mechanism of Aquatic Respiration: The movement of water happens through the mantle cavity by the repeated beating of cilia. The ctenidium receives deoxygenated blood from the body through the afferent blood vessel and after oxygenation through gill filaments it is sent to the heart via efferent blood vessel.

Number of Gills: In polyplacophora, the number of gills varies between 6-80 pairs. In Monoplacophora, it varies between 3-6 pairs. In primitive gastropods, either two bipectinate gills or single bipectinate gill may be present. Mesogastropods (for example, Viviparus, Pila, Lambis, Cypraea, etc.) and Neogastropods (for example, Murex, Xancus, Conus, etc.), contain single monopectinate gill. In bivalves, one pair platelike gills are present however in cephalopods, 4 platelike gills are observed in nautilus and 2 in coleoidea (for example, Sepia, Loligo and Octopus).

Based on topography, the ctenidia present in molluscs can be divided into following categories:

- Holobranchiate Type
- Merobranchiate Type
- Plicate Type
- Monopectinate Type
- Bipectinate Type (either be equal or unequal)
- Feathered Type

1. Holobranchiate Type

This type of ctenedial arrangement is seen in polyplacophora. In holobranchiate type, ctenidia extend all over surface of the body. The number of ctenidia varies

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between 14-70 pairs; however, in some cases it may be about eighty pairs as seen in acanthopleura.

In patella (Gastropoda), a circle of gill lamellae extends entirely around the margin of mantle. It bears superficial resemblance with that of chiton.

The true nature of ctenidia differs highly. In chiton, the ctenidia exist along the margin of the body except the head and anus, but in patella the ctenidia are present throughout the body.

2. Merobranchiate Type

When the ctenidia are confined to a particular area of the body, it is the merobranchiate type. This type of ctenidia can be subdivided into the following depending on the leaflet arrangement.

3. Plicate Type

This type of gill has flat transversely folded and projecting integumentary laminae. In neomenia, a bunch of filaments arises from the cloacal wall.

4. Monopectinate Type

This type has flattened gill filaments arranged only on a single side of the ctenidial axis as seen in pila, triton.

5. Bipectinate Type

This type of ctenidium contains flattened gill filaments arranged in two rows.

They may be of two types:

- **Unequal:** Gill filaments are present on both the sides but the right one is smaller as observed in fissurella, haliotis.
- **Equal:** On both the sides, the gill filaments are equal in size as seen in bivalves. Among bivalves, they get variously modified like in nucula it contains short flat leaflets while in some forms long filamentous leaflets are present. These filaments may be free [Refer Figure 2.38 (B), (C)] or joined by ciliary connectives [Refer Figure 2.38 (D)]. In unio, [Refer Figure 2.38 (E)] ciliary junctions get replaced by membranes. In poromya, [Refer Figure 2.35 (F)] ctenidium gets reduced and is represented by a transverse partition.

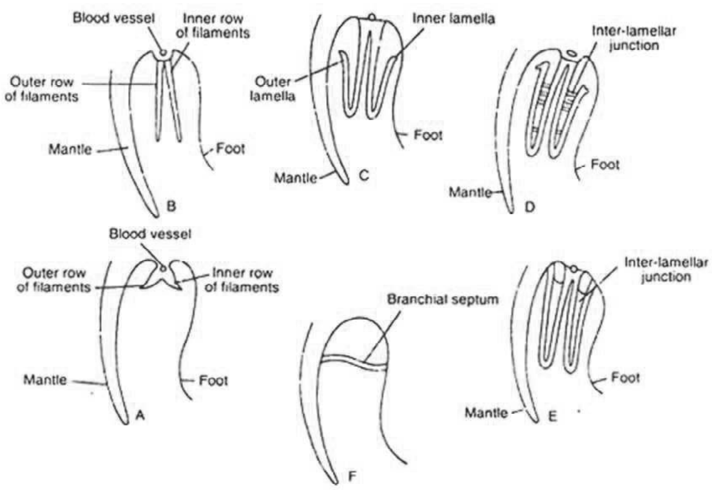

Fig. 2.38 *Transverse Sections Showing the Arrangement of Gills in Bivalves A: Nucula,B. Amusium, C Arca, D. Mytilus, E. Unio, F. Poromya*

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6. Feathered Type

The ctenidia are of feather shape. This type of ctenidia is a characteristic of the cephalopods.

Modifications of Ctenidia

Differen types of modifications in ctenidial are given as under:

Anal Gills

In doris, delicate leaflets form a rosette around the anus and are referred to as anal gills. In Pterotrachea, mantle fold is absent, and the filamentous branchial leaflets are freely projected and remain exposed. In several cases, the mantle may function as respiratory organ.

In solenogastres, cloacal gills occur. Gradual degradation is observed in the cloacal gills. In chaetoderma, two gills are present and are symmetrically positioned one on each side of cloaca. Single gill is observed in neomenia while in proneomenia, the gills appeared as folds on the cloacal wall.

Cerata

In aeolis, highly vascular secondary gills (Cerata) are present on dorsal surface of body [Refer Figure 2.39 (C)] providing surface area for gaseous exchange.

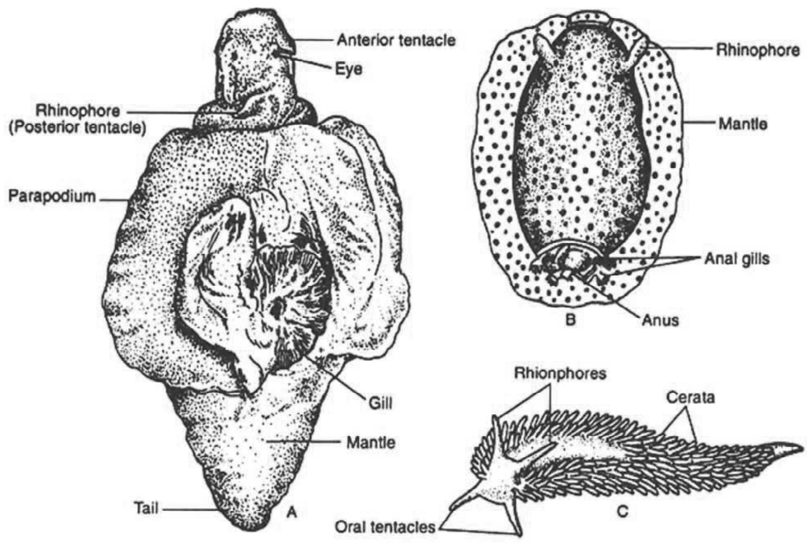

Fig. 2.39 *External Features of: A. Aplysia B. Doris C. Aeolis*

Relationship between Heart and Gills

The heart and the gills are closely related because the main function of the gills is to pass oxygenated blood to heart. The number of gills is directly proportional to that of the auricles (Refer Figure 2.40). For example, in octopus and ooligo, both gills and auricles are two in number, while, in chiton are present, two auricles correspond to two sets of multiple gills. In nautilus, there are four gills and four auricles. Interestingly, when the gill is unpaired, only one auricle is present in heart as seen in opisthobranchs, mesogastropods, neogastropods, etc.

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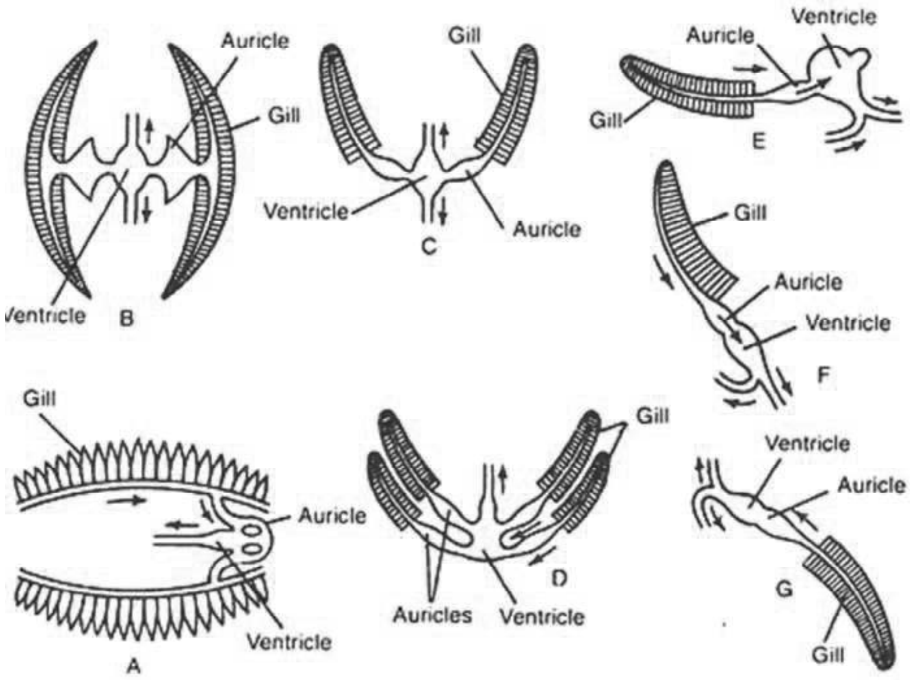

Fig. 2.40 *Figures showing Relationship Between Gills and Heart in Different Molluscs A.chitons, B. Bivalves C. Dibranchiate cephalopod D. tetrabranchiate cephalopod E. Prosobranchia(diatocardia) F. Prosobranchia(monotocardia) G. Opisthobranchia*

Respiratory Organs for Terrestrial Life

Terrestrial habit leads to a complete loss of gills and an array of respiratory organs develop to suit the requirements of the environment.

The respiratory organs for terrestrial mode of living are as follows:

- **Pulmonary Sac:** In most pulmonata, the mantle cavity forms a pulmonary chamber with a highly vascularised inner surface wall.
- **Trachea:** In some pulmonata, the pulmonary chamber forms breathing air-tubes referred to as trachea.
- **Nuchal Lobe:** In monotocardia (Mesogastropoda), the left nuchal lobe is very well developed and forms a long respiratory siphon.
- **Amphibious Forms:** These forms are seen in pila. It possesses both ctenidium and pulmonary sac. The genus siphonaria contains a lung- cavity and a ctenidium. The presence of both the forms corresponds to the transitional stage between aquatic and land life.
- **Circulatory System:** The circulatory system of molluscs is quite well-developed and almost all members of this phylum (except scaphopoda that lacks a distinct heart) possess distinct heart that receives oxygenated blood supply from respiratory organs and pass it to the entire body.
- **Blood:** In molluscs, the blood is colourless. The respiratory pigment of molluscs is known as haemocyanin. It contains both iron and copper. However, in some rare case like planorbis, haemoglobin may also be present.

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- **Heart:** The heart has a muscular ventricle and thin-walled auricle. The auricle gives origin to the aorta that in turn divides into arteries to supply blood to the different parts of the body.

  Deoxygenated blood from different parts of the body returns to respiratory organs for oxygenation. The ventricle is usually single but the number of auricles may vary from one to four.

  As discussed above also, the number of auricles corresponds to that of ctenidia present. Majority of the molluscs have one auricle. Double auricles are seen in dibranchiate, chitons, bivalves, cephalopods whereas tetrabranchiate cephalopods contain four auricles. The number of aortae originating from ventricle fluctuates from one to two. Single aorta is seen in chitons, solenogastres, prosobranchia, etc. In some forms, two aortae lead out of the two ends of the ventricle. However, in majority of the gastropods, single aorta bifurcates into an anterior cephalic aorta and a posterior visceral aorta. The heart is positioned within the pericardium. In bilaterally symmetrical molluscs, heart rests on the median line of the body while in asymmetrical forms the heart usually shifts to the right side.

Course of Circulation

In molluscs, oxygenated blood from the ventricle passes through aorta into the arteries. The arteries in turn supply blood to different parts of body. After moving through different organ systems, the blood finally gets collected into irregular spaces – called lacunae which in turn open into sinuses.

Capillary system exists in dibranchiate, cephalopods and in some bivalves. The relationship between foot-pore and circulatory system in some molluscs has not yet been fully identified. According to many workers, these foot-pores assist the inward movement of water into circulatory system.

Check Your Progress

5. Define haemoglobin.
6. Define hemocyanin.
7. What do you understand by blood gills?
8. Define pulmonary sac.

2.4 ANSWERS TO 'CHECK YOUR PROGRESS'

1. Polychaetes are known to be the largest class of phylum annelida comprising of 1600 genera and more than 5000 species.
2. Alimentary canal is a straight tube, opening at both the ends- the anterior opening is mouth and posterior opening is anus.
3. Digestion is the process of breaking down of the large molecules of food into the simpler units which are then absorbed and either incorporated into the body or metabolized to provide energy.

NOTES

4. The oesophagus opens into a sac-like structure known as the stomach. It is surrounded by large digestive gland which is equivalent to liver.
5. Haemoglobin is the most efficient respiratory pigment. It is widely distributed in the animal kingdom: from some protozoa such as paramecium to almost all vertebrates except eel larvae and few antarctic fish.
6. Hemocyanin is a respiratory pigment found in invertebrates that reversibly combines with oxygen and serves as a purpose of transport pigment.
7. In aquatic larval forms of some insects (chironomidae), branching tubular outgrowths containing blood vessels replaces trachea and hence they are known to be blood gills.
8. In most pulmonata, the mantle cavity forms a pulmonary chamber with a highly vascularized inner surface wall, which is called pulmonary sac.

2.5 SUMMARY

- Invertebrates are animals that neither possess nor develop a vertebral column (commonly known as a backbone or spine), derived from the notochord.
- Digestion is the process of breaking down of the large molecules of food into the simpler units which are then absorbed and either incorporated into the body or metabolized to provide energy.
- Filter feeding is a form of food procurement in which food particles or small organisms are randomly strained from water.
- Filter feeding is found primarily among the small to medium sized invertebrates but occurs in a few large vertebrates as well.
- Polychaetes is known to be the largest class of phylum annelida comprising of 1600 genera and more than 5000 species.
- Polychaete exhibits different type of nutrition mechanism like carnivores or raptorial feeders, direct deposit feeders, indirect deposit feeders and filter feeders.
- Filter feeders are the organism that feeds upon suspended food particles. It is an adaptation that allows the organism to feed on the food particles that are strained from water, typically by passing the water over a specialized filtering structure.
- The process of filter feeding starts with the beating of the lateral cilia of gill filaments against the water, which is then guided by incurrent siphon to the infra-branchial chamber of the mantle cavity.
- The respiratory system is a biological system consisting of specific organs and structures used for gas exchange in organisms.
- Most insects breath passively through their spiracles (special openings in the exoskeleton) and the air reaches every part of the body by means of a series of smaller and smaller tubes called 'trachaea' when their diameters are relatively large, and 'tracheoles' when their diameters are very small.

- Molluscs generally possess gills that allow gas exchange between the aqueous environment and their circulatory systems. These animals also possess a heart that pumps blood containing hemocyanin as its oxygen-capturing molecule.
- A branchiostegal lung is a respiratory organ which is used by some air-breathing arthropods. It is one of the most significant adaptations of some crabs and hermit crabs like coconut crab to their terrestrial habitats.
- A few terrestrial hermit crabs like Coenobita and Birgus, possess numerous gills and small lungs alongside several gas diffusion methods supporting the transition from aquatic to terrestrial habitat.
- The pneumostome serves as the respiratory opening present on the right side of the mantle of an air-breathing land slug or land snail. It is a component of the respiratory system of gastropods.
- All animals require a constant supply of oxygen into the cells to obtain energy for carrying out the physical and metabolic activities. Further, carbon dioxide produced during metabolic activities needs to be transferred out from the body.
- The processes that are involved in inhaling and utilizing oxygen lie under the general category of respiration which has broadly two different aspects namely external respiration and internal respiration.
- Most animals have developed respiratory pigments to facilitate the transport of oxygen to different parts of the body.
- Respiratory pigments are of profound physiological importance, especially in large sized animals, because the uniform distribution of oxygen to all parts of the body by way of simple diffusion would be a very difficult process.
- Respiratory pigments are coloured proteins that consist of a metallic element in their constitution and have the property of forming loose combination with oxygen and seldom with carbon dioxide.
- Haemoglobin is the most efficient respiratory pigment. It is widely distributed in the animal kingdom: from some protozoa such as Paramecium to almost all vertebrates except eel larvae and few Antarctic fish.
- Among all the copper-proteins occurring in nature, only hemocyanin can reversibly combine with oxygen and therefore it serves the purpose of a transport pigment.
- The partial pressure of oxygen ranges between 15-35 mm Hg in Mollusca and 50-20 mm Hg in arthropods. The oxygen transporting capacity of hemocyanin is lower than that of haemoglobin.
- In de-oxyhemocyanin, the copper is present in the cuprous form. Hemocyanin is colourless in deoxygenated state but it is bluish in oxygenated form.
- Most crustaceans do not possess a gill cover, or the gills are exposed to the outside but in Decapods the carapace extends from sides to house the gills in a specialized chamber thus providing protection to these delicate organs.

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- Trachea is the most significant organ for respiration in terrestrial arthropods, such as centipedes, insects and many arachnids. It is characterized by chitin-lined tubes found on the lateral side of the thoracic and abdominal segments of the body with openings.
- The trachea branches into several fine networks called tracheoles that end into tissues where gaseous exchange takes place by the mechanism of diffusion.
- Aquatic molluscs carry out respiration using ctenidia which are the comb-like outgrowths from mantle, located within the mantle cavity.
- Terrestrial habit leads to a complete loss of gills and an array of respiratory organs develop to suit the requirements of the environment.
- The heart and the gills are closely related because the main function of the gills is to pass oxygenated blood to heart.
- In molluscs, oxygenated blood from the ventricle passes through aorta into the arteries. The arteries in turn supply blood to different parts of body.

2.6 KEY TERMS

- **Invertebrates:** Invertebrates are animals that neither possess nor develop a vertebral column (commonly known as a backbone or spine), derived from the notochord.
- **Digestion:** Process of breaking down of the large molecules of food into the simpler units which are then absorbed and either incorporated into the body or metabolized to provide energy.
- **Filter Feeding:** A form of food procurement in which food particles or small organisms are randomly strained from water. Filter feeding is found primarily among the small to medium sized invertebrates but occurs in a few large vertebrates as well.
- **Polychaetes:** Polychaetes are known to be the largest class of phylum Annelida comprising of 1600 genera and more than 5000 species.
- **Respiratory System:** The respiratory system is a biological system consisting of specific organs and structures used for gas exchange in organisms.
- **Branchiostegal Lung:** It is a respiratory organ which is used by some air-breathing arthropods. It is one of the most significant adaptations of some crabs and hermit crabs like coconut crab to their terrestrial habitats.
- **Pneumostome:** The pneumostome serves as the respiratory opening present on the right side of the mantle of an air-breathing land slug or land snail. It is a component of the respiratory system of gastropods.
- **Respiratory Pigments:** Respiratory pigments are coloured proteins that consist of a metallic element in their constitution and have the property of forming loose combination with oxygen and seldom with carbon dioxide.

NOTES

- **Haemoglobin:** It is the most efficient respiratory pigment. It is widely distributed in the animal kingdom: from some protozoa such as Paramecium to almost all vertebrates except eel larvae and few Antarctic fish.
- **Trachea:** It is the most significant organ for respiration in terrestrial arthropods, such as centipedes, insects and many arachnids. It is characterized by chitin-lined tubes found on the lateral side of the thoracic and abdominal segments of the body with openings.

2.7 SELF-ASSESSMENT QUESTIONS AND EXERCISES

Short-Answer Questions

1. Define invertebrates.
2. What do you understand by respiration?
3. What do you understand by filter feeding?
4. Define chlorocruorin.
5. What do you understand by branchiostegal lung?

Long-Answer Questions

1. Describe the structure and histology of alimentary canal in invertebrates.
2. Explain the process of filter feeding in chaetopterus.
3. Explain the components of digestive system in invertebrates in detail.
4. Explain the filter feeding in echinodermata.
5. Explain the respiratory organs in invertebrates.
6. Describe the various types of respiratory pigments in invertebrates.

2.8 FURTHER READING

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NOTES

UNIT 3 EXCRETION AND NERVOUS SYSTEM IN INVERTEBRATES

Structure

3.0 INTRODUCTION

In unicellular organisms, the process of excretion occurs through diffusion. Simple diffusion occurs when a substance moves from a region of higher concentration to a region of lower concentration. In some invertebrates, contractile vacuoles help in the process of excretion. In some coelenterates like the hydra, and certain sponges, waste material diffuse into the surrounding environment through the epidermal cells. Organisms like the flatworm possess defined excretory structures called the protonephridia, which help, waste disposal.

In annelids like earthworms, leeches, lugworms, and bristleworms, waste is excreted through structures called metanephridia. They are highly coiled tubes that have openings at both their ends. The internal opening (nephrostome) lies in the body cavity and the external opening (nephridiopore) opens outside on the skin. Insects on the other hand, have Malpighian tubules also known as renal corpuscles that aid in collecting metabolic wastes from the hemolymph and draining them out of the system as nitrogenous compounds. In some arthropods, the excretory function is taken over by the maxillary gland. Molluscs possess nephridia that collect waste from the coelom and blood.

In echinoderms, excretion is performed by amoebocytes, which are mobile cells moving around in the body of certain invertebrates. Animals like sea anemones have a single opening that acts both as a mouth for food to go in, and an anus for waste to go out.

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The cellular components of an invertebrate nervous system include: sensory neurons, which convert physical variables (e.g., light level or muscle force) into electrical signals; motor neurons, which make synapses with muscles or other effector organs (e.g., light-producing organs, glands); interneurons, which transmit information between other neurons; and glia, which are electrically inexcitable cells that influence the ionic environment surrounding neurons and the transmission of signals between them.

In invertebrates, unlike vertebrates, the somata of motor neurons and interneurons are not important sites of synaptic input. Instead they give rise to a single primary neurite that enters the core of the ganglion and divides into dendritic and axonal regions.

3.1 OBJECTIVES

After going through this unit, you will be able to:

- Understand the physiology of invertebrates
- Explain the mode and mechanism of excretion in invertebrates
- Mention the excretory organs in invertebrates
- Define the various physiological activities in invertebrates
- Describe the nervous system of invertebrates
- Compare between the primitive and advanced nervous system in invertebrates

3.2 EXCRETION

A contractile vacuole (CV) is a sub-cellular structure or organelle which is primarily involved in the process of osmoregulation. It is observed chiefly in protists and unicellular algae. It was previously known as pulsatile or pulsating vacuole (PV). The salient features of the contractile vacuole are mentioned below.

1. Shape, Size and Occurrence

The contractile vacuoles are found in majority of freshwater protozoans (flagellata, sarcodina and ciliata) and some marine ciliates. They are not found in parasitic protozoans. They are usually large, colorless, and fluid filled pulsating organelles.

The simplest form of contractile vacuoles is found in sarcodina like amoeba. These are usually spherical vesicles (Refer Figure 3.1). Sometimes they may be irregular and bounded by a limiting membrane. They are surrounded by a circlet of mitochondria to provide energy for pulsations.

More complicated vacuole is found in flagellates like euglena. This complicated vacuole is surrounded by large number of accessory contractile vacuoles (Refer Figure 3.2). In Ciliata, like Paramecium, the contractile vacuoles are surrounded by 5 to 12 radiating canals (feeding canals) used to collect water from various parts of the body (Refer Figure 3.3).

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However, the numeral values of vacuoles differ in ciliates. The radiating canals serve as feeders as they discharge their contents into the contractile vacuole.

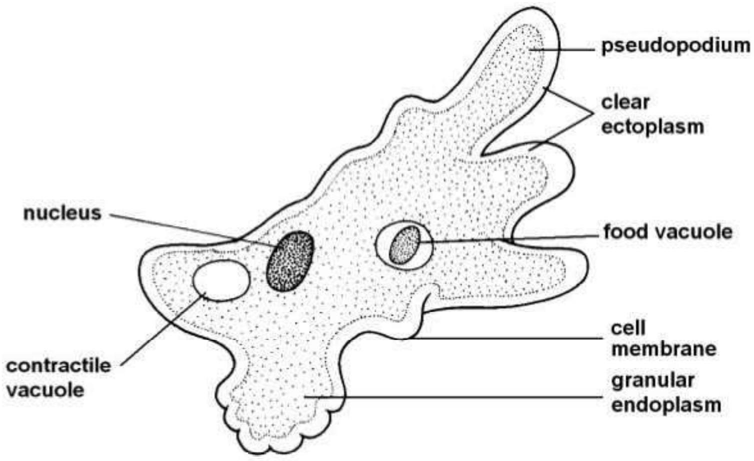

Fig. 3.1 *Contractile Vacuole in Amoeba*

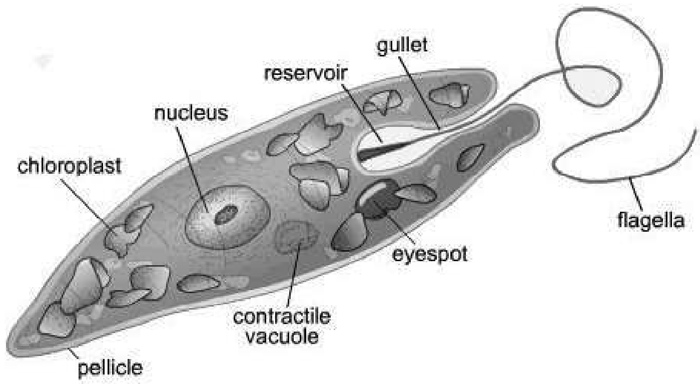

Fig. 3.2 *Contractile Vacuole in Euglena*

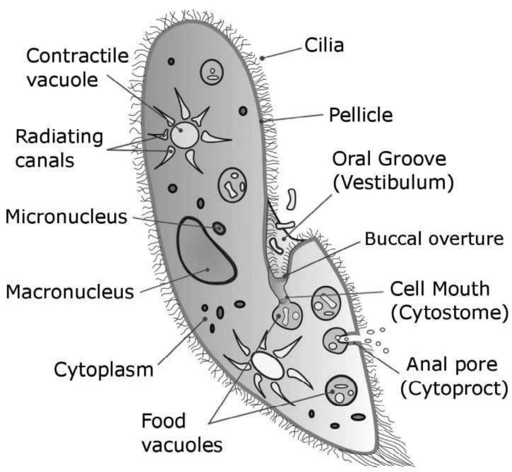

Fig. 3.3 *Contractile Vacuole in Paramecium*

2. Situation and Number

In sarcodina, the position of contractile value could be anywhere in the endoplasm. However, it is found near the anterior end at the side of reservoir. They are two in number in paramecium, each on the either end of the body.

Different group of protozoans have different number of vacuoles, but same species have same number of vacuoles. It is single in amoeba and euglena, two in paramecium (Refer Figure 3.3) and many in radiolaria and heliozoa.

3. Structure

It is a clear space filled with fluid and bounded by a limiting membrane made up of lipoprotein like that of plasma membrane.

4. Mode of Working

Contractile vacuole works in two steps:

- **Diastole**: It is the phase when contractile vacuole enlarges to maximum size.
- **Systole**: It is the phase when the vacuole contracts to expel its contents. In sarcodina, the systole occurs by sudden burst but in others, the vacuole empties into a reservoir.

A contractile vacuole is formed when a large numbers of tiny droplets fuse in the area where the contractile vacuole is to be formed as in amoeba or around the mitochondria contractile vacuole as in euglena. The energy required for the functioning of contractile vacuole is provided by the mitochondria surrounding the vacuole. (Refer Figure 3.4 and Figure 3.5).

Although the mechanism of working of contractile vacuole is not clear, the following theories try to explain it:

- **Osmotic Theory:** This theory suggests that the water in contractile vacuole enters through the cytoplasm via osmosis.
- **Filtration Theory:** This theory states that water from the cytoplasm is forced into the vacuole through its membrane because of the hydrostatic pressure inside the vacuole. However, this theory was contradicted by Kitching.
- **Secretion Theory:** This is not a widely accepted theory. It states that water is actively secreted into the vacuole through its wall during diastole.

5. Function and Significance

Contractile vacuoles osmoregulate by removing excess water from the body. It's also believed to be excretory in function.

In freshwater forms, the body fluid is hypertonic to the surrounding medium. Being surrounded by water dominant media, water continuously enters the body of freshwater protozoans increasing the internal hydrostatic pressure. This inhibits normal functioning and after a threshold the body may burst. Thus, by removing excess water, contractile vacuole maintains the internal hydrostatic pressure.

However, in marine and parasitic protozoans, the media surrounding them is isotonic such that no water enters the body. Thus, these forms don't require a contractile vacuole.

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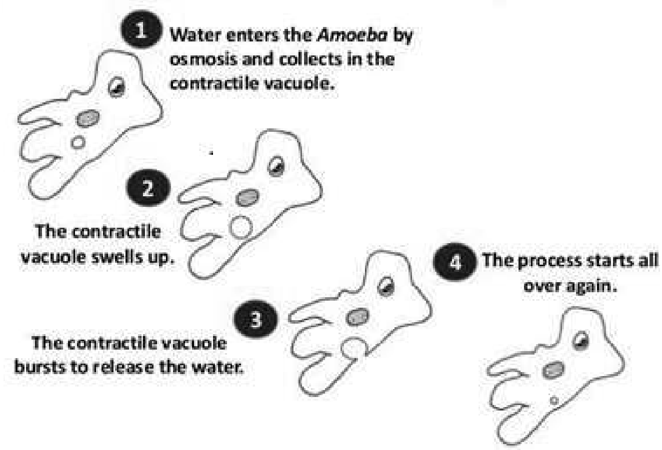


Fig. 3.4 *Picture Depicting Osmoregulation in Amoeba*

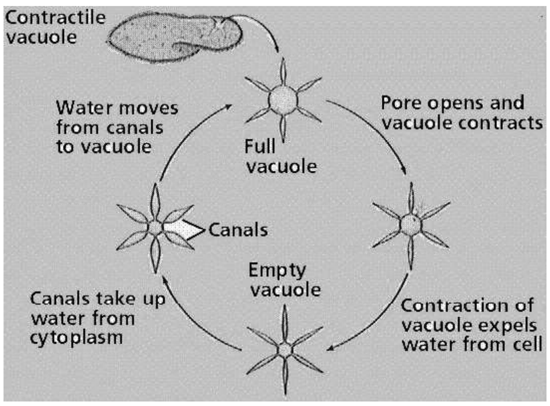


Fig. 3.5 *Figure Depicting Osmoregulation in Paramecium*

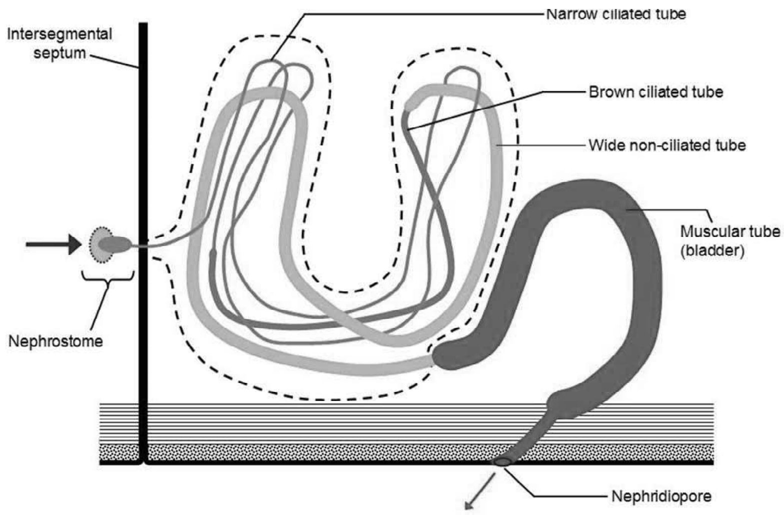
3.2.1 Organs of Excretion: Coelom, Coelomducts, Nephridia and Malpighian Tubules

Excretory system is a vital system in invertebrates as well as vertebrates that aids in eliminating nitrogenous waste from the body. In invertebrates, the excretory organs are classified into three type namely contractile vacuoles in protozoa, nephridia (flame cell system) in most invertebrate animals and malpighian tubules (arthropod kidney) in insects. While, in vertebrates, the primary excretory organ used for eliminating nitrogenous waste is kidney. Overall, excretory organs serve to eliminate nitrogenous waste as well as helps in maintaining the ionic balance of the organism.

Role of coelom as excretory organ

The fluid inside the coelom is referred to as coelomic fluid. This is circulated by mesothelial cilia or by contraction of muscles in the body wall. The coelomic fluid serves several functions: it serves as a hydroskeleton; it allows free movement and growth of internal organs; it serves for transport of gases, nutrients and waste products around the body; it allows storage of sperm and eggs during maturation; and it acts as a reservoir for waste. For instance, in annelids, excretory tubule (nephridium) opens to the outside through the nephridiopore and the inner end of the tubule is blind (associated with terminal cells or solenocytes) in the protonephridium or opens in the coelom via the ciliated funnel or called nephrostome in metanephridium. A typical nephridium is mainly made up of a nephrostome or a ciliated funnel which remains suspended into the coelom and leads to the nephridial duct. The nephridial duct or body of the nephridium can be short, long, convolute or variously modified. The duct is ciliated on its internal side, located transversely and followed by blood vessels. The nephridial duct communicates to the outside via an opening called nephridiopore.

In all annelids, the excretory system utilizes a two-stage filtration process. During this two-stage filtration process, excretory waste materials as well as fluids are extracted and then filtered again to consume left over re-usable substances while deposing of toxic and drained materials as urine. Species belonging to phylum annelida are capable of using one of two different ways to remove soluble waste products. The excretory system in the organisms included in this phylum with blood vessels relies on metanephridia, while the organisms without blood vessels carry out the excretory system using protonephridia.



The nephridium of Lumbricus terrestris; coelomic fluid is drawn in (blue arrow) through the nephrostome and urine emerges (red arrow) through the nephridiopore.

Fig. 3.6 *Flow of Waste Material from Coelomic Fluid to Outside in Annelids*

The illustrations below depict the nephridium of the night-crawler earthworm *Lumbricus terrestris*. In *Lumbricus terrestris*, there is one pair of these nephridia (literally 'little kidneys') are present in each segment. The head region or nephrostome of each nephridium passes via the intersegmental septum to project into the coelom of the preceding segment. The nephrostome is an open funnel like structure which uses tiny beating hair-like cilia to draw coelomic fluid inside it.

This coelomic fluid is then pumped via a coiled tube, by means of cilia that line the tube. As the coelomic fluid travels through via coiled nephridial tube it gets modified and transformed into urine. This urine is stored for a short period of time in a muscular bladder prior to its release to the outside via a small nephridiopore in the worm's under-surface. All the illustration below depicts how the coelomic fluid containing excretory and nitrogenous wastes is eliminated out of the body in annelids.

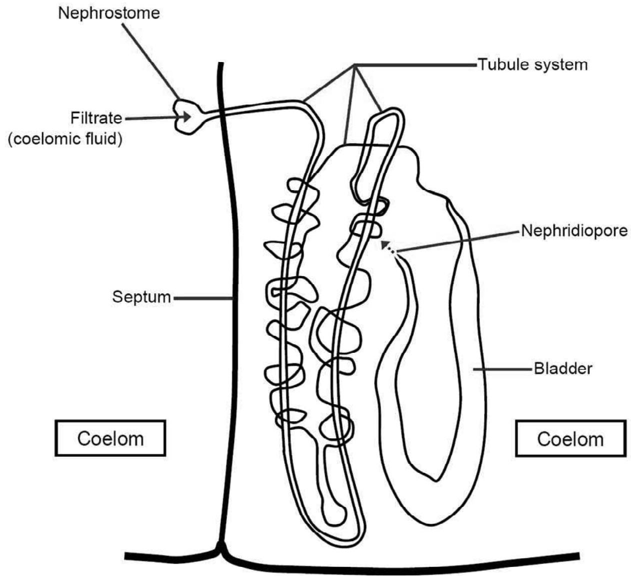


Fig. 3.7 *Metanephridium in situ in Lumbricus*

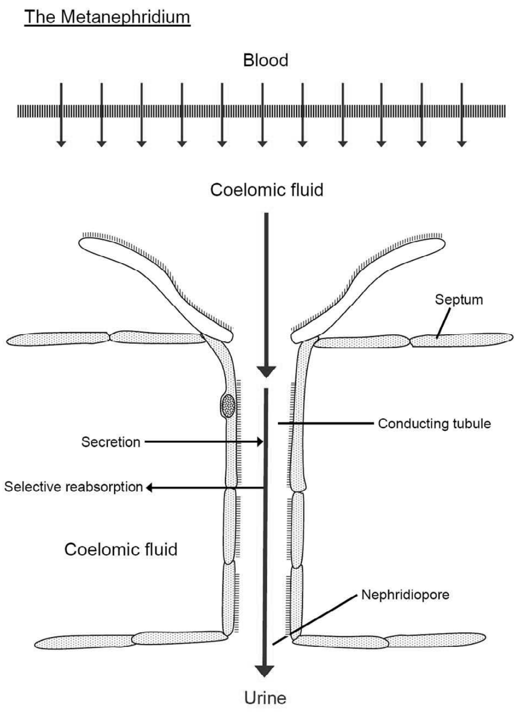


Fig. 3.8 *The Metanephridium*

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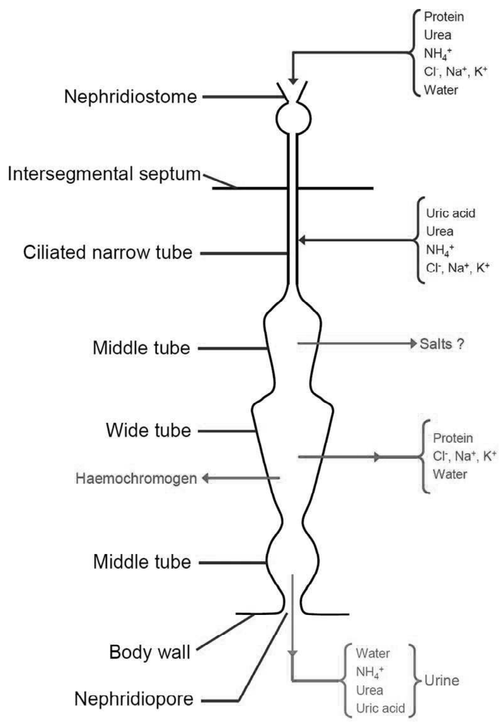

Fig. 3.9 *Excretory Process in Earthworm*

Coelomoducts

In ancestral coelomates, each mesodermal pouch was provided with a pair of ducts, called coelomoducts or gonoducts that serves as a passage for the exit of gametes while a single nephridial tubule primarily removes nitrogenous wastes from the body. Such primitive nephridia are made up of ectodermal tubules projecting into the coelom and ending in specialised cells called solenocytes.

Nephromixia are complex structures which are formed by the partial or complete fusion between mesodermal coelomoduct (gonoduct) and ectodermal nephridium. Nephromixia serve as passageway for both excretory products as well as gametes.

The combinations between the coelomoduct and the nephridium are of the following types:

(a) Protonephromyxium:

- In this case, the coelomoduct unites to form protonephridium.
- Both reproductive and excretory products are passed to the exterior by it.
- Protonephromyxia condition often occurs in Phyllodoce.

(b) Metanephromyxium:

- In this case, the coelomoduct becomes united to a metanephridium.
- It is seen Hesione.

(c) Mixonephridium:

- In this case, complete fusion between the coelomoduct and the nephridium leads to the formation of a simple funnel-like organ.
- This condition is often present in Arenicola.

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(D) Coelomoduct:

- In ancestral coelomates, each mesodermal pouch was provided with a pair of ducts, known as coelomoducts (gonoducts).
- These gonoducts/coelomoducts acts as passage for the exit of gametes and a single nephridial tubule, for the removal of nitrogenous wastes.
- These primitive kind of nephridia resembled the flame cells (excretory structures) of Platyhelminthes.
- Hence, they comprise ectodermal tubules projecting into the coelom and ending in specialised cells, referred to as solenocytes.

(E) Nephromyxia:

- In several polychaetes, the association between the coelomoduct (gonoduct) and nephridium makes for an interesting study.
- Instead of remaining as separate structure, the coelomoduct and nephridium undergoes partial or complete fusion to form a dual segmental organ, known as nephromyxia.
- As the nephridium is ectodermal in origin whereas the coelomoduct is mesodermal in origin, it leads to the formation of a nephromixium.
- The nephromixium performs two functions.
- Firstly, it serves the function of excretion and secondly, it also acts as a passage for the exit of gametes.
- In few cases, they share the same external opening but when the association between them becomes very close they often share the same duct.

(F) Ciliated Organs:

- In this case, coelomoducts become very much reduced and give rise to ciliated organs which do not open to outside.
- Such ciliated organs are found in Nereis and they remain attached to the dorsolateral longitudinal muscles.

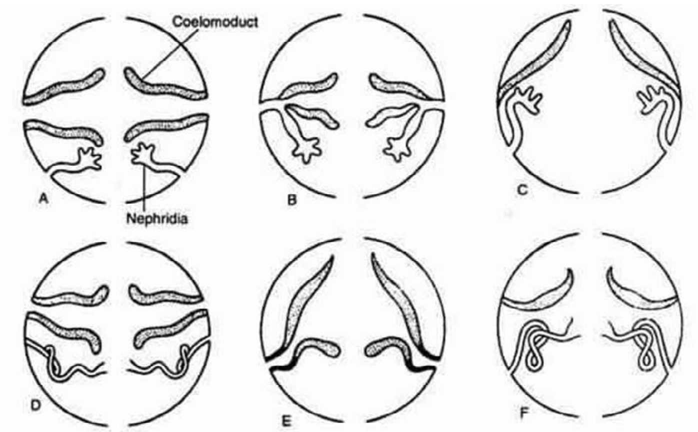

Fig. 3.10 *Relationship between Coelomoducts and Nephridia in Polychaetes. (A) Closed Nephridia with Separated Coelomoducts; (B) Closed Nephridia United with Coelomoduct; (C) Coelomoduct Reduced as Ciliated Organ; (D) Nephridia with Nephrostome and Separated Coelomoducts; (E) Nephridia with Nephrostomes and United Coelmoducts; (F) Nephridia with Nephrostome and Separated Coleomoducts which are Reduced as Ciliated Organs*

NOTES

Excretion in Annelida

Nephridium

An excretory tubule which opens to the outside through the nephridiopore and the inner end of the tubule is blind (associated with terminal cells or solenocytes) in the protonephridium or opens in the coelom through the ciliated funnel are called nephrostome in metanephridium.

Structure of a Typical Nephridium

- A typical nephridium is mainly made up of a nephrostome or a ciliated funnel which remains suspended into the coelom and leads to the nephridial duct.
- The nephridial duct or body of the nephridium can be short, long, convolute or variously modified.
- The duct is ciliated on its internal side, located transversely and followed by blood vessels.
- The nephridial duct communicates to the outside via an opening called nephridiopore.

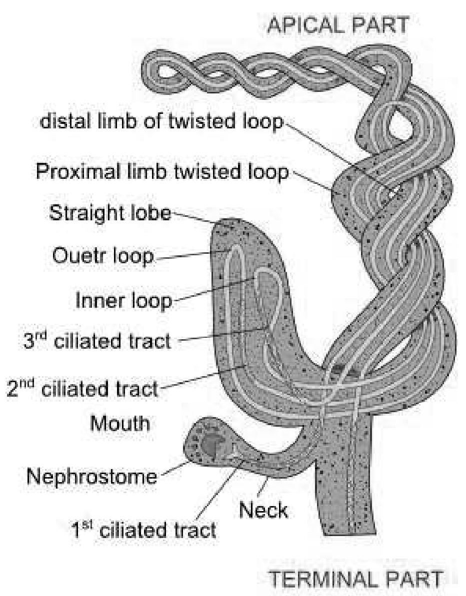

Fig. 3.11 *Typical Septal Metanephridium of Pheretima*

In general, the excretory system is made up of paired lobes, called nephridia, which are metamerically segmented and the inner aperture of the nephridium is present in the coelom, and the outer aperture lies in the integument.

Origin of Nephridium

Each nephridium formed from a single cell, called nephroblast. The nephridia are mainly ectodermal in origin.

Classification of Nephridium

Prof. K. N. Bahl classified nephridia which is the most accepted classification all over the world (Refer Figure 3.12).

There are two types of nephridial systems which are mainly encountered:

- Provisional or embryonic nephridia are found in the embryonic or developmental stages of annelids.
- Permanent nephridia are seen in adult annelids.

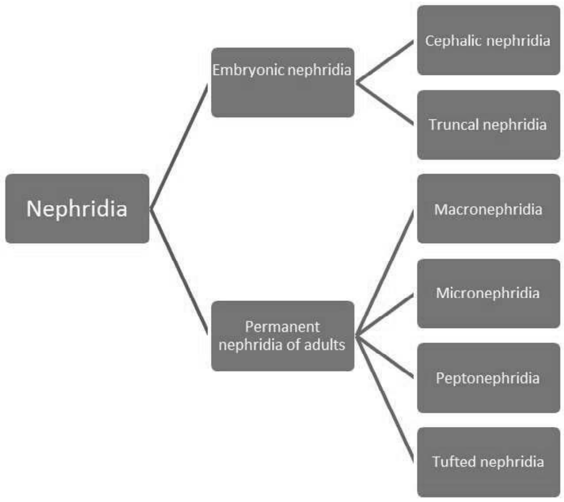

Fig. 3.12 *Figure Depicting Classification of Nephridia*

Stages of Nephridium in Annelida

Two types of nephridial systems are observed during developmental stages of nephridium in Annelida

1. Provisional or Embryonic Nephridia

Embryonic nephridia are temporary structures which start to disappear as soon as permanent nephridia start developing. Embryonic nephridia are further divided as:

a. Embryonic Head Nephridia

- They are found mainly in polychaetes and oligochaetes and are often branched as seen in echiurus, polygordius.
- Found in paired conditions in both larva as well as embryos.
- End portion lie in the embryonic head cavity.
- Solenocytes occur at the end of the tube.

b. Embryonic Trunk Nephridia

- Segmentally arranged
- Only one pair in each segment
- Funnel opens into trunk region.

The embryonic trunk nephridia are present only in those forms whose permanent nephridia do not develop at all. For example: *Nereis* has five such pairs of nephridia. Most of the oligochaetes and several other polychaetes and hirudinea lack permanent nephridia in the anterior segments. On the basis of structure, embryonic nephridium is almost same as those of permanent nephridium.

2. Permanent Nephridia

The characteristics are the same as that of typical nephridium:

- The ciliated nephrostome opens into the coelom.
- The long internally coiled duct opens to the exterior by the nephridiopore.
- Nephrostome and nephridiopore may occur in the same segment or nephrostome can be present a segment forward.

Types of Nephridia Based on Segment Size and Numbers

Following are the types of nephridia based on size and number present in a segment:

- Meganephridia or Holonephridia
- Micronephridia or Meronephridia
- Peptonephridia
- Tufted nephridia

Meganephridia or Holonephridia

- Large in size
- Only one pair occurs in each segment.

Micronephridia or Meronephridia

- Small in size
- Several micronephridia occur in each segment.
- Zoologists believe that the micro-nephridia are broken or disintegrated form of meganephridia.

Peptonephridia

- These are formed by the modification of salivary glands.
- These are found in buccal and pharyngeal region in clusters.
- These are seen in oligochaets.

Tufted Nephridia

- These are formed from micro or macro-nephridia.
- They are incompletely branched and grouped together.
- These are usually found in one or many of pre-clitellar segments of several earthworms.
- Bahl (1942) states that tufted nephridia represent an intermediate stage between holonephridium and a cluster of completely separated meronephridia.

Types of Nephridia Based on Nephrostome

Further, nephridia can be closed or open types according to the presence of nephrostome:

- **Open Type:** When the nephridium is having a funnel, i.e., nephrostome
- **Closed Type:** Absence of a funnel in the nephridium

Types of Nephridia Based on Openings to the Exterior

Based on their opening to the exterior, nephridia may be exonephric or enteronephric type:

- **Exo Nephric Type:** Exterior opening is present, for example, Integumentary nephridia.
- **Enteronephric Type:** They open into the enteric canal, for example, septal nephridia and pharyngeal nephridia.

  Micronephric type of nephridia is present in Pheretima posthuma whereas, the nephridia of lumbricus, chaetogaster and nereis are of meganephric type. In megascolecidae, same segment possesses both micronephridia as well as meganephridia. In serpula, anterior segments have meganephridia while the micronephridia occur in the posterior segments. Some polychaetes have Protonephridia in which the inner end of each nephridium terminates in flame cells and often the second types of nephridia called as metanephridia in which the inner end of the nephridium possess an open funnel or nephrostome.

Types of Permanent Nephridia in Different Classes of Annelida

Polychaetes

Usually, the metanephridia are present in the polychaetes.

Outline of a Typical Metanephridium

- An inner ciliated aperture known as nephrostome opening into the body cavity or coelom.
- A coiled tube is mainly connected to the nephrostome. The tube is dilated internally with glandular wall.
- Nephridia usually terminate in a laterally placed aperture called nephridiopore.
- In errantia, each segment is having a pair of nephridia.
- Arenicola is having six pairs of nephridia.
- In capitellidae, permanent nephridia may vary from 1 to 6 pairs in each of the trunk segments.
- In terebellidae, only one to three pairs of nephridia are present in the thorax region.
- In both, sabellidae and serpulidae just one pair of nephridia is present in the thorax region. However, in all of these families, numerous nephridia occur in the posterior segments.
- In many polychaetes like phyllgdoce segmentally arranged ciliated funnels, called coelomoducts are present.
- Coelomoducts rarely open to the outside and frequently fuse partly or entirely with the nephridia to serve the passage of both excretory and reproductive product.

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- In some families like phyllodocidae and glyceridae, protonephridia are present in place of metanephridia.
- In protonephridia, the ciliated coelomic aperture called as nephrostome is absent.
- The tubes open blindly in the coelom and are either separated or cluster of cells called as solenocytes remain attached to the blind end of the tubes.
- Each solenocyte is a round cell with a slender tubular projection which harbor on the blind tube.
- Electron micrograph reveals that long tube of protonephridium consists of an unusually long flagellum to propel the internal accumulated fluid.

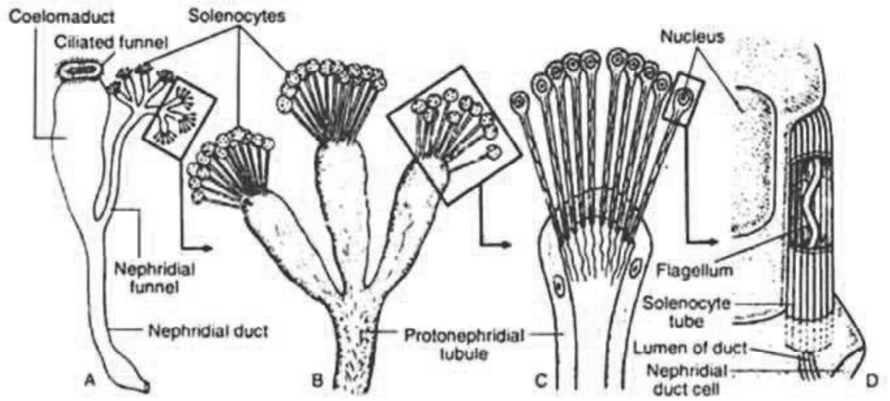

Fig. 3.13 *Structure of Protonephridium and Coelomoduct in* Phyllodice*.*
(A) Protonephridium and coelomoduct; (B) Branched end protonephridium;
(C) Solenocytes of a protonephridial branch; (D) Detailed structure of a solenocyte

Oligochaetes

- In oligochaetes, metanephridia are primarily present in all segments except a few anterior ones.
- Generally, there is one pair of nephridia in each of the segment but in brachidrilus, there are present two pairs, in trinephros, there are three pairs whereas four pairs found in acanthoarilus.
- In tropical megascolecidae, nephridia are often called diffused or plectonephric nephridia as the nephridial primordia in each segment splits up and as a result various nephridia occur in each segment.
- In the tropical *Phretima posthuma*, numerous nephridia open into the pharynx (Peptonephric) a well as in the alimentary canal (Enteronephric).

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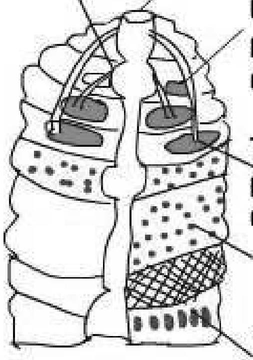

Fig. 3.14 *Excretory System in Pheretima*

Hirudinaria

- In hirudinaria the excretory system includes 17 pairs of Nephridia. They are arranged in 6th to 22nd segments, one pair in each segment. In these 17 pairs the first six pairs do not show contact with testis. They are called pre-testicular nephridia.
- Metanephridium are made up of a ciliated funnel or nephrostome that guides into an ampulla embedded with amoebocytes and closed off against a nephridial duct.
- Besides the nephrostome, rest of the nephridium parts is formed by a close set of gland cell traversed by intracellular ducts or spaces.
- The nephrostome begins from the coelomic space, from ventral median channel (a seen in glossiphonia), from contractile spherical enlargement or ampullae (a seen in haemopis) or from blood sinuses in which the testes lie (as seen in hirudo).
- In pontobdella, distinct nephridium is not seen and its place is taken up by a complex network located on the ventral side of the body.
- The anal tubes in echiuroidea are considered as excretory structures.
- Nephridia serves as osmoregulatory organs especially in the freshwater forms.

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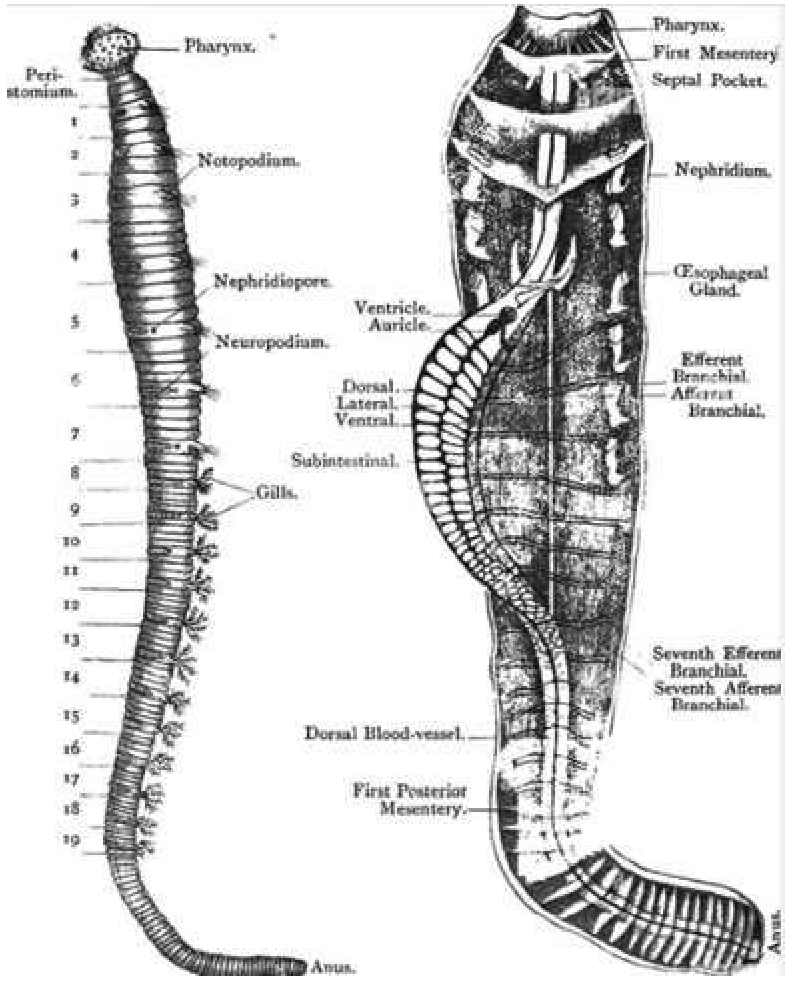

Fig. 3.15 *Nephridium in Hirudinaria*

Physiology of Nephridium

In most annelids, both blood vascular system and coelom (if present) are deliberately involved in the excretion of waste products from the body. Protonephridia are present in the polychaetes in which the blood-vascular system is absent or reduced. The remaining groups of polychaetes and others possess both blood-vascular system and metanephridia for removal of nitrogenous waste products from the body as well as for performing other crucial functions.

In annelids possessing protonephridia, the ultrafiltration of the coelomic fluid takes place with the help of solenocytes present at its terminal end and the filtrate fluid thus obtained passes down through the protonephridial tubule. Along the protonephridial tubule some essential salts and amino acids are usually reabsorbed and only the primary excretory product, i.e., ammonia is excreted out of the body through the nephridiopore.

However, metanephridium contains nephrostome (open ciliated funnel) via which coelomic fluid is drawn out by the ciliary action of funnel. A few essential substances like salts, aminoacids are reabsorbed while passing through the metanephridium tubule whereas other nitrogenous waste products like ammonia and urea are excreted.

Functions of Nephridium

- It removes the liquid nitrogenous waste products from the body to the outside.
- It removes the basic and non-volatile acid radicals from the body.
- It sustains the water-ionic balance of the body.
- It maintains the osmotic relation between the blood and tissue.
- In some annelids, they convey the reproductive units and act as gonoducts or coelomoducts.

Malpighian Tubules

In insects, myriapods, arachnids, and tardigrades, the Malpighian tubule system is a form of excretory and osmoregulatory system. The major purpose of malpighian tubules is to aid in the excretion process. This system helps in the absorption of water, solutes, and waste from the fluid present in vertebrates, i.e., haemolymph. These wastes are discharged into the environment as calcium oxalate and nitrogenous compounds. Malpighian tubules do not exist in humans. Instead of malpighian tubules, we have kidneys, which assist us in filtering waste from our bodies.

Mechanism of Excretion by Malpighian Tubes

The Malpighian tubule system is a type of excretory and osmoregulatory system found in some insects, myriapods, arachnids and tardigrades.

The system consists of branching tubules extending from the alimentary canal that absorbs solutes, water, and wastes from the surrounding hemolymph. The wastes then are released from the organism in the form of solid nitrogenous compounds and calcium oxalate.

Malpighian tubules are slender tubes normally present in the posterior regions of arthropod alimentary canals. Each tubule have a single layer of cells that is closed off at the distal end with the proximal end joining the alimentary canal at the junction between the midgut and hindgut. Most tubules are normally highly convoluted. The number of tubules varies between species although most occur in multiples of two. Tubules are usually bathed in hemolymph and are in proximity to fat body tissue. They contain actin for structural support and microvilli for propulsion of substances along the tubules. Malpighian tubules in most insects also contain accessory musculature associated with the tubules which may function to mix the contents of the tubules or expose the tubules to more hemolymph. The insect orders, Dermaptera and Thysanoptera do not possess these muscles and Collembola and Hemiptera:Aphididae completely lack a Malpighian tubule system.

Pre-urine is formed in the tubules, when nitrogenous waste and electrolytes are transported through the tubule walls. Wastes such as urea and amino acids are thought to diffuse through the walls, while ions such as sodium and potassium are transported by active pump mechanisms. Water follows thereafter. The pre-urine, along with digested food, merge in the hindgut. At this time, uric acid precipitates out, and sodium and potassium ions are actively absorbed by the rectum, along with water via osmosis. Uric acid is left to mix with feces, which are then excreted.

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The primary urine from the malpighian tubules has to pass through the rectum before it leaves the insect's body, and in the rectum its composition is markedly changed. The insect excretory system therefore comprises the malpighian tubules and the rectum acting together.

The primary urine is formed by a process of secretion in the following way: Potassium ions are actively transported from the blood into the cavity of the tubule and are necessarily followed by negatively charged ions so as to maintain electroneutrality. In turn, water follows the ions, probably by osmosis, and various other substances—sugars, amino acids, and urate ions—also enter the primary urine by diffusion from the blood.

The primary urine, together with soluble products of digestion and insoluble indigestible matter from the midgut, then passes to the rectum. There (or in some insects at an earlier stage) the urine is acidified and the soluble urate is thereby converted to insoluble uric acid, which comes out of solution. Water is then reabsorbed together with the soluble products of digestion and other useful substances, including the bulk of the ions that entered the primary urine. In insects that live in dry surroundings the rectum has remarkable powers of reabsorption, its contents finally being voided as hard, dry pellets containing solid uric acid.

Complex cycling systems of Malpighian tubules are also found in some insect orders. Hemipteran insects use tubules that allow movement of solutes into the distal portion of the tubules while reabsorption of water and essential ions directly to the hemolymph occurs in the proximal portion and the rectum. Both Coleoptera and Lepidoptera use a cryptonephridial arrangement where the distal end of the tubules are embedded in fat tissue surrounding the rectum. Such an arrangement may serve to increase the efficiency of solute processing in the Malpighian tubules.

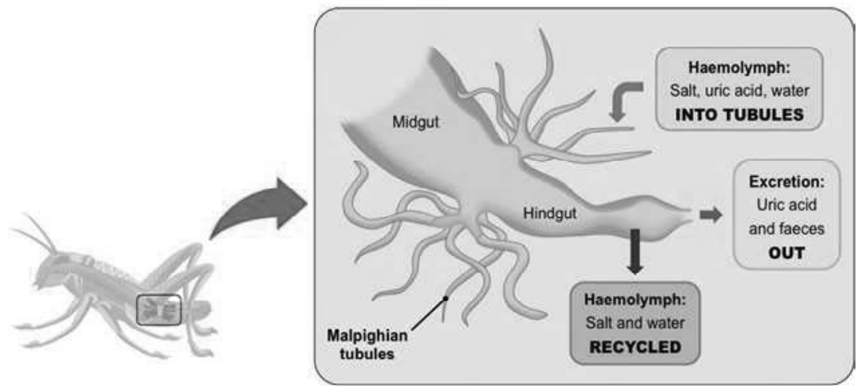

Fig. 3.16 *Excretion by Malpighian Tube*

Other Excretory Organ in Arthropod

The coxal gland is a gland found in some arthropods, for collecting and excreting urine. They are found in all arachnids (with the exception of some Acari), and in other chelicerates, such as horseshoe crabs. The coxal gland is thought to be homologous with the antennal gland of crustaceans. The gland consists of an end sac (saccule), a long duct (labyrinth) and a terminal bladder (reservoir). There is generally only one pair (two in some spiders), and they open on the coxae of the walking legs. The coxal secretion of adult female ticks of Ornithodoros erraticus contains a sex pheromone.

Excretory organs of prawn are known as green glands or antennary glands. These are paired white organs which remain within the coxa of each second antenna.

Antennal or green glands: A pair of enteric glands are found in the coxa (Grap) of each antenna. They are green in color, hence the name "green gland." The antennal gland consists of four regions:

End sac: This is the smallest part which is bean-shaped. It is located between the bladder and the labrum.

Labyrinth: The labyrinth is highly coiled and is made up of branched excretory tubules. Blood vessels are found in the connective tissue mass. These ducts have a large excretory system are covered by a single layer of cells. The labyrinth is involved with the movement of ions and reabsorption of proteins.

Bladder: This is the inner side of the last cell and is the largest part. It is made up of a single layer of excretory epithelium. Its inner wall emerges to form a small ureter or ureter. The ureter is enclosed outside by a round renal aperture, which is located on the inner surface of the coxa of the antennae on top of a papilla. The bladder stores urine. A ureter connects the bladder to the nephropore (excretory pore) under the base of the second antennae.

Lateral ducts: A narrow lateral duct emerges from the bladder of each hyaline gland at the back. The lateral vessels on either side are joined by a transverse connective in front of the brain. After this, moving backward along both the esophagus opens into the renal sac.

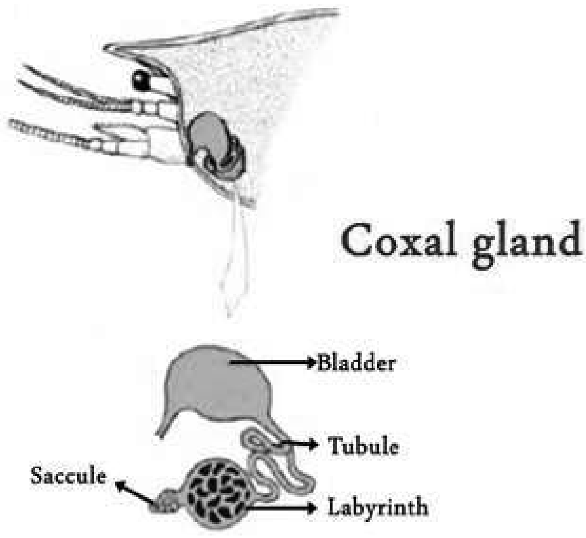

Fig. 3.17 *Coxal Glands*

3.2.2 Mechanism of Excretion

In invertebrates, the excretory system, follows the same rules as other species when it comes to detoxication mechanisms: aquatic forms get rid of ammonia by

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diffusion through the body surface, while terrestrial forms transform ammonia to uric acid. This indicates that in aquatic forms, the excretory organ is of the principal importance for their body fluid composition. The excretory organs of other invertebrates are of diverse evolutionary origin. Each invertebrate phylum has evolved its own particular type of excretory organ; rather, there appear to be five main types of invertebrate excretory organ: contractile vacuole, nephridium, renal gland, coxal gland, and malpighian tubule. In this section, we shall discuss the mechanism of excretion in different groups of invertebrates:

1) Mechanism of Excretion in Protozoa

Excretion of metabolic wastes is dope almost exclusively by diffusion. All protozoans are ammonotelic, i.e., the end product of their nitrogen metabolism is ammonia, which is readily diffused in the surrounding medium. In few Protozoans, contractile vacuoles are also believed to be excretory in nature.

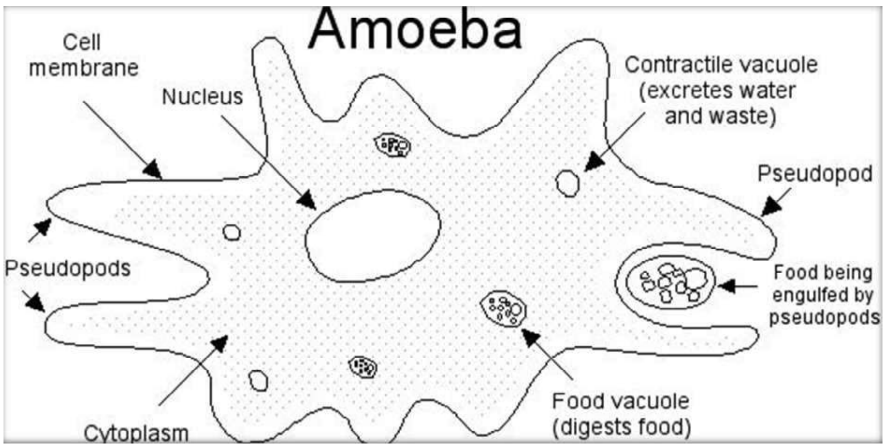

Fig. 3.18 *Amoeba*

2) Mechanism of Excretion in Sponges

Sponges are ammonotelic, i.e., they excrete nitrogenous waste in the form of ammonia. Ammonia moves out of the body of animal along with out going water current. Sycon type of canal system is present in scypha or sycon. The components of sycon canal system are as follows:

1) **Ostia or dermal pores:** The body is perforated by numerous small pores called as ostia. These ostia serve as entry gate for outside sea water. Ostia is surrounded by contractile cells known as myocytes which regulate the amount of water entering inside the canal system.
2) **Incurrent canal:** Ostia directs the water inside the incurrent canal or inhalent canals which is infolding of the body wall of animal. This canal communicates with the outside sea water via ostia but ends blindly towards spongocoel. The incurrent canals are lined by pinacocytes.
3) **Prosopyle:** Prosopyle are tube-like structures which directs the movement of water from incurrent canals to radial canals.

4) **Radial canals:** A radial canal or flagellated canal communicates with incurrent canals via prosopyle and with spongocoel via apopyle; however, they ends blindly towards outside sea water. These canals are parallel and alternate to the radial canal. These canals are lined with specialized flagellated cells known as choanocytes.
5) **Apopyle:** These are the openings of radial canals into the spongocoel. Apopyle are surrounded by contractile cells known as myocytes which regulates the movement of water.
6) **Spongocoel:** Spongocoel is a large central cavity which communicates with the radial canals via apopyle. In Ascon type ofcanal system, the whole of the spongocoel is lined with flagellated cells whereas in sycon canal system only the radial canals arelined with flagellated cells. The spongocoel in sycon canal system is lined with pinacocytes.
7) **Osculum:** It is a large opening present at the top of the animal surrounded by specialized contractile pinacocytes known as myocytes.

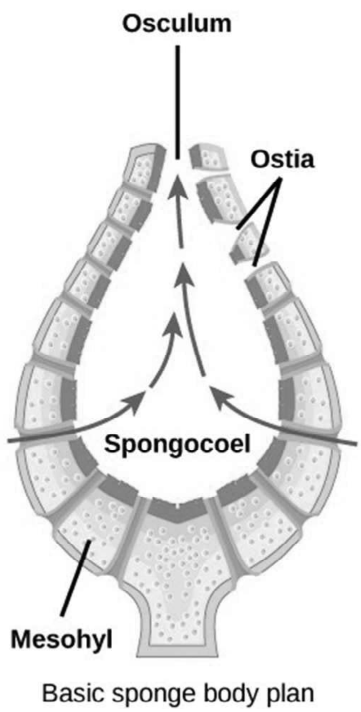

Fig. 3.19 *Excretory Route in a Sponge*

3) Mechanism of Excretion in Coelenterates

There are no specific respiratory, circulatory and excretory organs in obelia. Oxygen diffuses form surrounding water into the cells. Carbon dioxide and other nitrogenous excretory products diffuse out of the cells into the environment.

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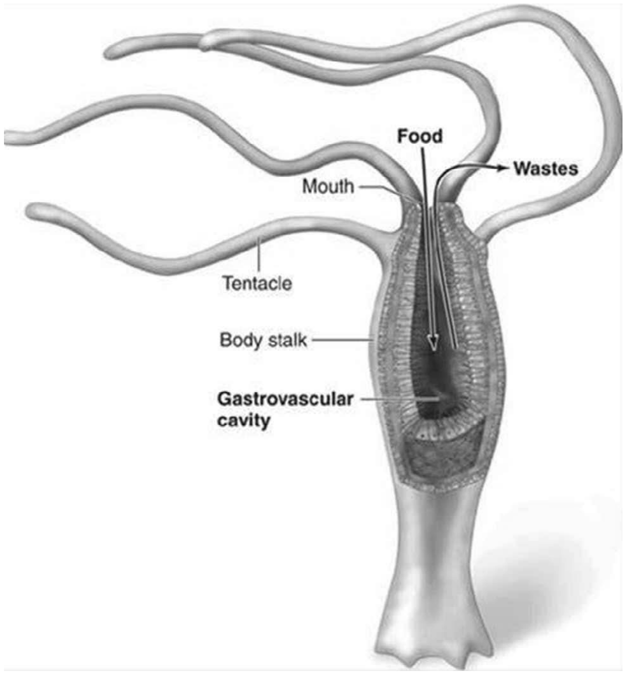

Fig 3.20 *Movement of Water in Coelenterate*

4) Mechanism of Excretion in Ctenophora

No definite excretory organs are present. However, there are present some specific cells like 'Cell rosettes' which might be excretory or osmoregulatory in nature. They consist of a double circlet of ciliated gastrodermal cells surrounding openings leading from the gastrovascular canals to the mesogloea.

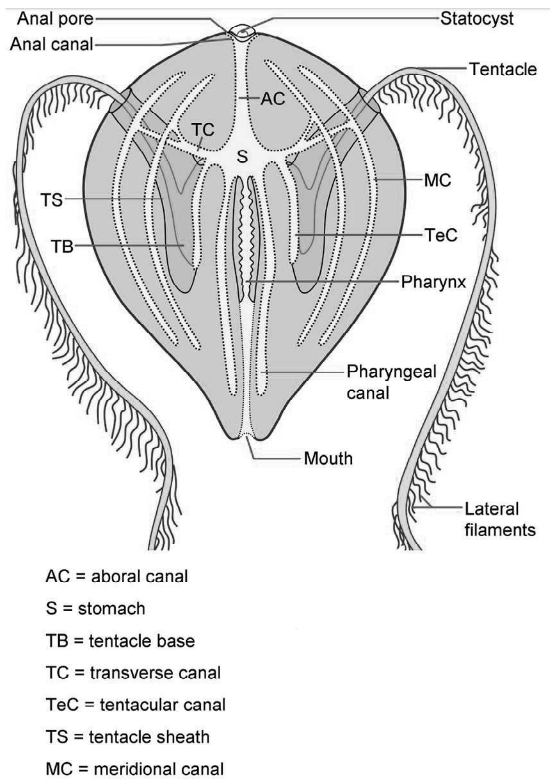

Fig. 3.21 *Excretory Route in Ctenophore*

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5) Mechanism of Excretion in Nemertine

The excretory system of nemertine comprises of a pair of longitudinal vessels which sends off branches. Each longitudinal vessel opens to the exterior via nephridiopore on each side. The fine terminal branches of the excretory system are associated with ciliary flames.

6) Mechanism of Excretion in Acanthocephalans

Excretory organs of most Acanthocephalans comprise a pair of small bodies, protonephridia, situated at the posterior end near the genital aperture. Each protonephridium is comprised of a branching mass of flame bulbs attached to a common stem. The total number of flame bulbs in each protonephridium varies from varies from 250 to 700. The flame bulbs are lined by a row of cilia. In genera like *Oligacanthorhynchus* and *Nephridiorhynchus*, the flame bulbs open directly into a sac from which the nephridial canal leads (Meyer, 1931).

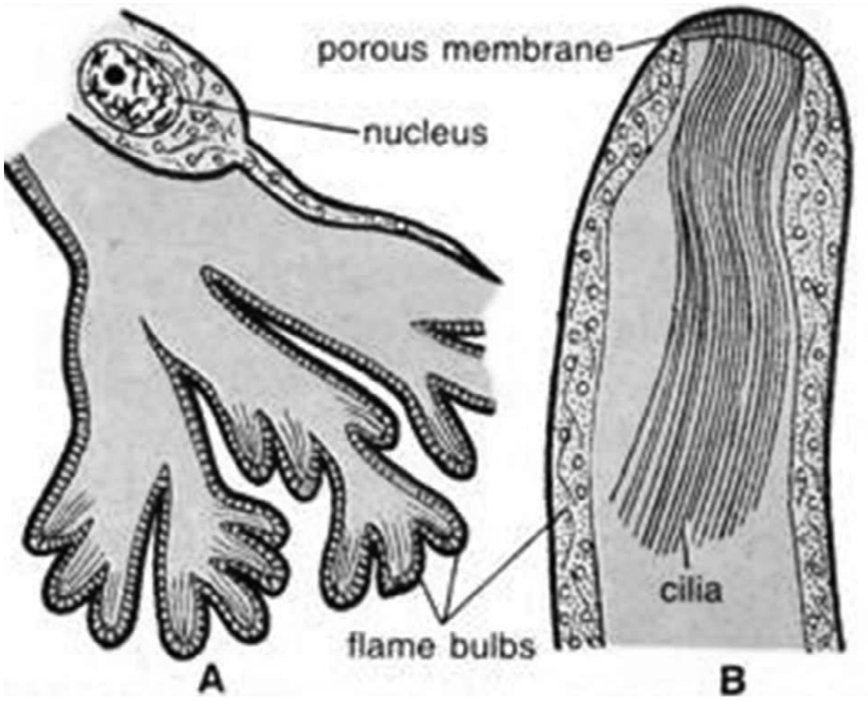

Fig. 3.22 *Excretory Structures in Acanthocephala. A- L.S via Terminal Twigs of a Protonephridium; B- L.S of a Flame Cell*

7) Mechanism of Excretion in Entoprocta

The excretory system consists of a pair of ciliated intracellular tubes which represent protonephridial type of excretory organs. Each excretory tube begins with a flame cell. The two excretory ciliated intracellular tubes might open individually or may fuse to form a common duct opening into the cloaca.

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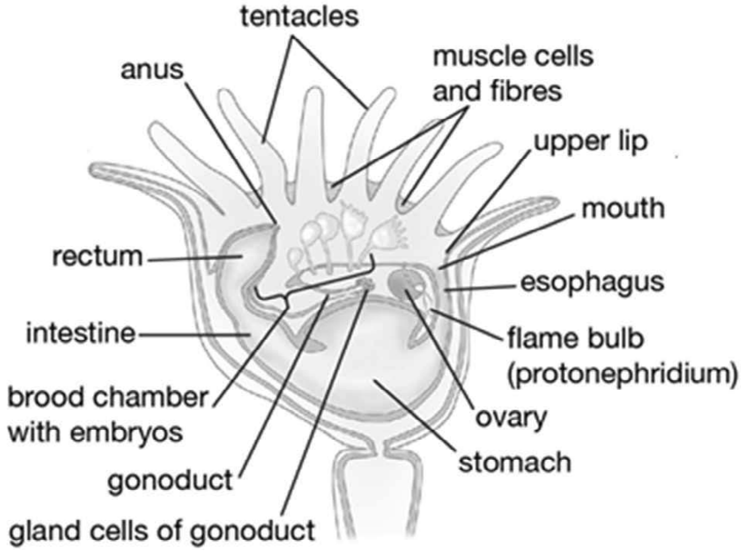

Fig 3.23 *Excretion in Entoprocta*

8) Mechanism of Excretion in Rotifers

The excretory system consists of a pair of protonephridia and tubules provided with flame-bulbs which open posteriorly into a common urinary bladder. The main tubules fork into an anterior and a posterior branch and extend lengthwise the animal, one on each side. The flame bulbs are two to eight in number on each side and open into a ciliated capillary that enters the end of the main tubule or its branches and may run alongside the main tubule for some distance. Huxley's anastomosis, a similar capillary run transversely between the anterior terminations of the main tubules and receive additional flame bulbs. The flame bulbs vary in shape from a tubular to a flattened triangular form and contain a slender to triangular membrane kept in constant motion. The thickened cap-like end frequently bears one to several protoplasmic filaments. These filaments anchor the bulb mostly to the body wall. The flame bulbs are not cells and are enucleated but are part of the general nephridial syncytium. Posteriorly the tubules open separately into a urinary bladder situated ventral to the cloaca or they unite to a common stem that enters the ventral wall of the cloaca.

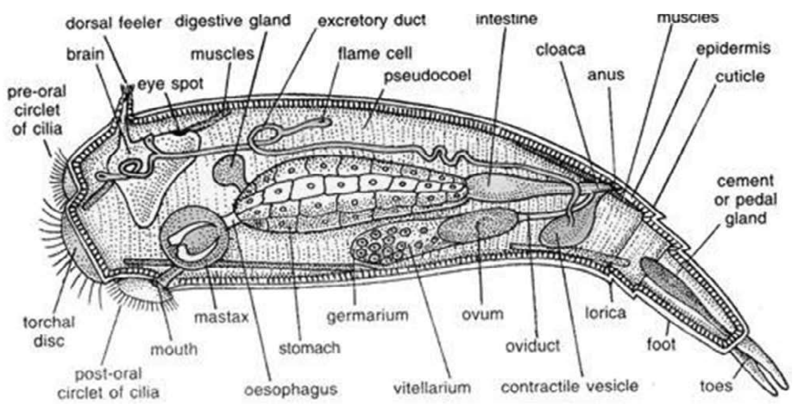

Fig. 3.24 *Excretory structure in a Rotifer*

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9) Mechanism of Excretion in Platyhelminthes

Excretory system of Platyhelminthes consists of *Flame cells* which are modified mesenchyme cells of irregular shape. Flame cells send out pseudopodial processes into the surrounding tissue. Excretory products such as fatty acid and ammonia diffuse from the surrounding mesenchyme into the flame cells from where they are collected by capillaries that join into the intracellular cavity of flame cells. The capillaries anastomose and open into the excretory ducts which eventually join the median longitudinal excretory canal. The longitudinal excrtory canal is non-ciliated whereas capillaries and ducts are ciliated. The cilia maintain the flow of excretory wastes from cavities into the excretory ducts from where it moves into the main excretory canal and finally leaves the body of host via excretory pore.

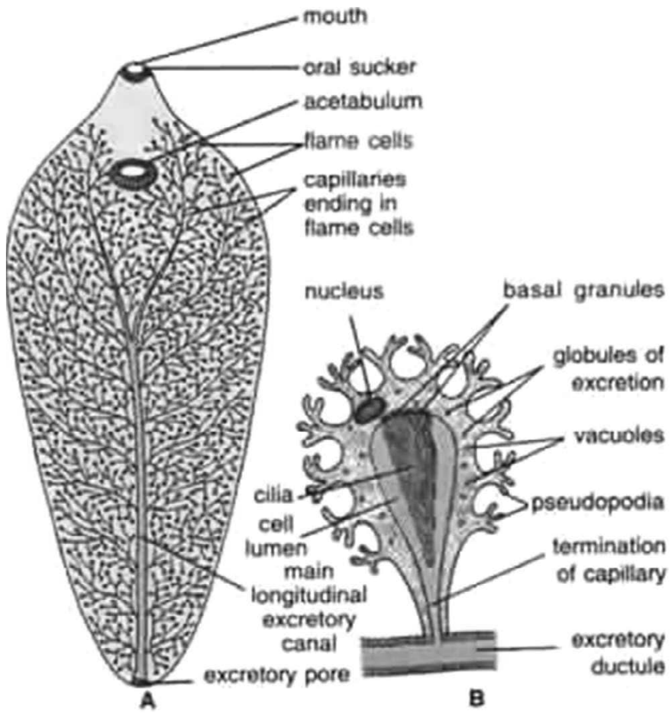

Fig. 3.25 *Excretory system of F. hepatica. A- Excretory system, B- Flame cell*

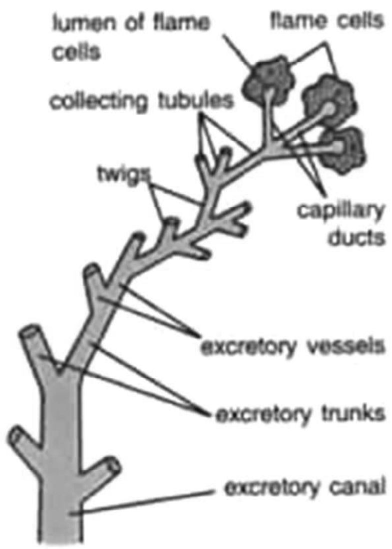

Fig. 3.26 *Arrangement of Flame Cells and Excretory Ducts*

10) Mechanism of Excretion in Nematohelminthes

The excretory system helps in the removal of nitrogenous waste in the form of ammonia through the body wall. Substances like amino acids, peptides, amines, carbon dioxide, fatty acids, as well as urea are also excreted by the nematodes. The cells that make up the excretory system of nematodes are: one pore cell, one canal cell, one duct cell, and a fused pair of gland cells.

- The excretory cell helps in maintaining the osmotic/ionic regulation as well as the elimination of waste products.
- The excretory cell collects fluids and then empties via the excretory duct as well as the excretory pore.
- Materials are also secreted from large membrane-bound vesicles.
- The secretion from the excretory canal as well as gland cells pass via a cuticle lined duct located under the pharynx region, in the excretory duct cell.
- The excretory cell, the gland cell, as well as the duct cell joins with each other at specialized intercellular junction known as secretory-excretory junction. The secretion from the glands and excretion pass via the duct to the outside of the body.

3.2.3 Excretion and Osmoregulation

Excretion is defined as the elimination of the metabolic wastes from the body, usually in aqueous solution. Metabolism produces a number of by-products. These by-products needs to be eliminated from the body with the help of specialised excretory organs. The excretory organs perform a variety of function. All these functions aim to maintain a constant internal environment of the organism. The functions of excretory system can be listed as follows:

(i) Maintenance of ionic content of the body fluids, i.e., proper concentrations of individual ions (Na^+, K^+, Cl^-, Ca^{++}, H^+, etc.)

(ii) Maintenance of fluid/water level in the body, i.e., proper body volume

(iii) Maintenance of osmotic concentration

(iv) Removal of nitrogenous waste, i.e., metabolic end products from the body

(v) Removal of foreign substances and/or their metabolic products

Thus, excretion refers to the removal process of harmful and unnecessary substances from the body. It is done by specialized structures known as excretory organs. Whereas, osmoregulation is another way of maintaining homeostasis of the body. It is the process of maintaining the water balance of the body. Organisms regulate the osmotic pressure of their body fluids to maintain the water balance in order to prevent body fluids becoming too diluted or too concentrated. Thus, the major difference between the process of excretion and osmoregulation is that excretion is the removal of metabolic waste, toxic substances and non-useful material from the body while osmoregulation is the homeostatic regulation of osmotic pressure in the body in order to maintain constant water content. We have already studied about excretory organs and mechanism of excretion in previous section. Here, we will study about the process of osmoregulation in invertebrates.

Osmoregulation and Osmoconformers

The active regulation of the osmotic pressure of an organism's body fluids is called Osmoregulation, It is detected by osmoreceptors, to maintain the homeostasis of the organism's water content. It maintains the fluid balance and the concentration of electrolytes to keep the required concentration of the body fluids. Osmotic pressure is a measure of the tendency of water to move into one solution from another by osmosis. If the osmotic pressure of a solution id higher, more water tends to move into it.

There are two major types of osmoregulation, they are osmoconformers and osmoregulators. Osmoconformers match their body osmolarity to their environment actively or passively. Most marine invertebrates are osmoconformers, although their ionic composition may be different from that of seawater. In a strictly osmoregulating animal, the amounts of internal salt and water are held relatively constant in the face of environmental changes. It requires that intake and outflow of water and salts be equal over an extended period of time.

Organisms that maintain an internal osmolarity different from the medium in which they are stay are called osmoregulators. They regulate their body osmolarity, maintaining constant internal conditions. They are more common in the animal kingdom. Osmoregulators actively control salt concentrations accordingly to the salt concentrations in their surroundings. An example is freshwater fish. The gills actively uptake salt from the environment by the use of mitochondria-rich cells. Water diffuse into the fish, so it excretes a very hypotonic (dilute) urine to expel all the excess water. A marine fish has an internal osmotic concentration lower than that of the surrounding seawater, so it tends to lose water and gain salt. It actively excretes salt out from the gills.

Some marine organisms maintain an internal environment which is isotonic to their external environment these are known as osmoconformers. In these organism the osmotic pressure of the organism's cells is equal to the osmotic pressure of their surrounding environment. By reducing the osmotic gradient, they reduce the net influx and efflux of water inside and outside of cells.

An advantage of osmoconformation is that these organisms need to invest lesser energy as compared to osmoregulators, in order to regulate ion gradients. A disadvantage to osmoconformation is that the organisms are subject to changes in the osmolarity of their environment.

Similarities between Excretion and Osmoregulation

- Excretion as well as osmoregulation help in maintaining the homeostasis of the body.
- Excretion as well as osmoregulation are essential life processes of living organisms.
- Excretion as well as osmoregulation helps in removal of excess water from the body.

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Table 3.1 *Difference between Excretion and Osmoregulation*

	Excretion	Osmoregulation
Definition	Excretion is the process of removing waste products and toxic substances from the body.	Osmoregulation refers to the process of maintaining constant osmotic pressure within the body fluids by keeping the water balance.
Type of Process	Excretion is a type of elimination.	Osmoregulation is a type of balancing the uptake and loss of water.
Main Occurrences	Excretion events are exhalation, defecation, and urination mainly.	Exosmosis and endosmosis are the main events of osmoregulation.

Osmoregulation in Some Other Invertebrates

When marine invertebrates penetrates dilute sea water they are more likely to survive as they have adjusted their body fluid concentrations as per the dilution and maintained a new and lower ionic concentrations in body fluids. Oysters, starfish and other osmoconformers from those in diluted medium but same osmotic concentration as the diluted sea water. On the contrary, the osmoregulator remain hyperosmotic and successfully resist the dilution.

Carcinus (a crustacean arthropod), the Eastern shore crab, is an example of active osmoregulator. On long runs, the fluctuations in the medium is better resisted by the active regulators in comparison to passive osmoconformers which can cope with substantial dilutions such as oysters which keeps its shells closed in an estuary in order to resist the effects of periodic water dilutions. In principle, the brackish water osmoregulators are osmotically mimicked by the fresh-water animals but with considerable differences in the concentrations at which they maintain their body fluids.

Osmoregulation is an ecologically important function in nemerteans, as in all freshwater invertebrates with permeable body walls. It is controlled by the cerebral organs and involves several organs and enzymatic systems associated with blood vessels. Well-developed nephridia may play a role in osmoregulation as well as in the removal of nitrogenous wastes (but the latter has not yet been demonstrated)

Osmoregulation in Fish

Freshwater fish and marine fish osmoregulate in different ways. The environments in which they live have different levels of salinity, so the process of osmoregulation is different.

Osmoregulation in Freshwater Fish: Freshwater fishes are hypertonic to their surrounding environment, i.e., the salt concentration is higher in their blood than their surrounding water. They absorb a controlled amount of water through the mouth and the gill membranes. Due to this intake of water, they produce large quantities of urine through which a lot of salt is lost. The salt is replaced with the

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help of mitochondria-rich cells in the gills. These cells absorb salt into the blood from the surrounding water.

Osmoregulation in Marine Fish: In comparison with freshwater fish, marine fish face the opposite problem. They have a higher concentration of water in their blood than their surrounding environment. Consequently, it results in the tendency to lose water and absorb the salt. To avoid this, marine fish drink more water and restrict urination. Another additional energy expenditure also arises as these organisms actively need to expel salt from the body (through the gills).

Check Your Progress

1. Define excretion.
2. What do you understand by excretory system?
3. What is contractile vacuole?
4. What is diastole?
5. Define systole.
6. What do you understand by nephridium?

3.3 NERVOUS SYSTEM

Invertebrates are often referred to as 'simple animals' with small nervous systems comprising of fewer nerve cells as compared to the tiniest vertebrates. Regardless of the above fact, these animals can live in highly organized colonies, can resolve the basic survival issues, and can receive and comprehend complex messages.

A nervous system is as an organized collection of neurons that interact at points of contact known as synapses. Synapses are functional junction where the membranes of two or more neurons come very close together. Neurons are electrically excitable cells whose membranes can generate and transmit signals in the form of changes in voltage. These small changes in voltage can be graded together or are all-or-none events of fixed amplitude known as action potentials. At electrical synapse, signals are passed directly to other cells whereas at chemical synapse, signals are converted into chemical signals that diffuse across a small synaptic gap present between the membranes of two interacting neurons.

An invertebrate's nervous system is composed of sensory neurons, which receive physical signals from the environment (for example, light level or muscle force) and convert them into electrical signals; motor neurons, which transmit signals from central processing system to muscles or other effector organs (for example. light-producing organs, glands); interneurons, which transmit information between sensory and motor neurons; and glia, which are electrically inexcitable cells that influence the transmission of signals between neurons by altering the ionic environment surrounding them. Thus, the ability of neurons to generate and transmit electrical signals, and for these signals to pass between different cells, be summed, multiplied and transformed by different types of cells and synapses, facilitate nervous systems to process huge information without much effort.

Changes in the environmental conditions are detected by sensory structures, encoded in the activity of neurons, evaluated for significance against the background of earlier experience, transmitted via nervous system, and then used to drive suitable actions. The actions may be compensatory (for example, postural) or active (for example, producing a sound or generating locomotion). Some of these actions are concluded within fractions of a second, the only limitation being the speed of neuronal activity; whereas others may conclude over hours, days or even the lifetime of the animal. How are all these functions carried out in different invertebrates is matter of investigation.

3.3.1 Primitive Nervous System: Coelenterata and Echinodermata

The nervous system helps the body to respond to external stimuli or in other words is essential to our interaction with the outside world, and its development made it possible to integrate senses and movements in a precise and faster way. The nervous system utilizes both electrical as well as chemical means to send and receive messages. The large distribution of nerve cells in the animal kingdom implies that possessing a nervous system must have been a huge evolutionary advantage.

Species belonging to Phylum Porifera lack a proper nervous system. Perhaps, this is the only phylum in the kingdom Animalia which lacks a defined nervous system. Porifera has a cellular level of organisation and thus, they do not have any organ or organ system. Whereas, in Coelenterates, nerve cells are present, however, it is not organised into a nervous system, this type of unorganised diffused nervous system is referred to as primitive nervous system.

Here, nerve cells are distributed below the outer epidermis throughout the body of the organism. Ctenophores, Echinoderms as well as Balanoglossus (Phylum- Hemichordata) also possesses a primitive kind of nervous system having a diffuse network of nerves & neurons. On the other hand, a centralized nervous system is a more advanced form of the nervous system, which occurs in animals with bilateral symmetry. It contains concentrated nerve cells in the central part of the body such as the brain and the spinal cord. For instance, Annelids also have a nervous system made up of two ventral cords and a single large nervous cell acting as a brain.

1) Nervous System in Coelenterata

Cnidarians possess a primitive diffused kind of nervous system. The nervous system is a primitive nerve net. Nervous system of cnidarians comprises one or more networks or nerve-cells and neurites located in the ectoderm as well as endoderm. Nervous system is in the form of typical nerve net without a concentrated Central Nervous System (CNS), i.e., no concentrated grouping of nerve cells forming a central nervous system is observed in cnidarians. Central Nervous System does not provide advantage for radially symmetrical animals where stimuli approach from all sides. The nervous system is diffuse, as in the polyp, but in some medusae it becomes concentrated to form a nerve ring and in connection with this well-defined sense organs are formed. Medusa with manubrium hanging downward and tentacles swaying freely floats freely in water along with water currents. It can also swim actively by aid of powerful muscular contractions and also of velum.

Medusa is carnivorous in nature and feeds on small planktons. It has sense organs in the form of eight marginal statocysts, situated at the bases of tentacles on the subumbrellar surface. These statocysts help the animal in orientation as well in maintaining equilibrium while swimming i.e., presence of sense organs at the base of tentacles is highly advantageous to its free-swimming habit. The nervous system of medusa is a diffused network of neurons. Nervous system is better developed in medusa form owing to its free-swimming habit.

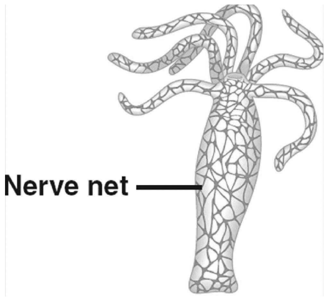

Fig. 3.27 *Diffused Primitive Kind of Nervous System in Cnidarians*

Coelenterates do possess some sensory structures. Obelia colony is diploblastic, i.e., comprises two layers, the outer epidermis and inner *gastrodermis* with a thin, transparent, non-cellular gelatinous layer called mesogloea sandwiched between them. Epidermis carries nematocysts (Cnidoblast/stinging cells) which are the main weapon of offence and defence. These cells are abundantly present on the tentacles forming batteries. The sensory structure of cnidoblast is cnidocil. Apart from cnidoblast, epidermis also consist of epitheliomuscular cells, interstitial cells, nerve cells, sensory cells. Gastrodermis consists of large nutritive-muscle cells and narrower gland cells that secrete digestive enzymes and aid in the process of digestion. Apart from this, Gastrodermis also comprises of epitheliomuscular nutritive cells, gland cells, interstitial cells, nerve cells and sensory cells.

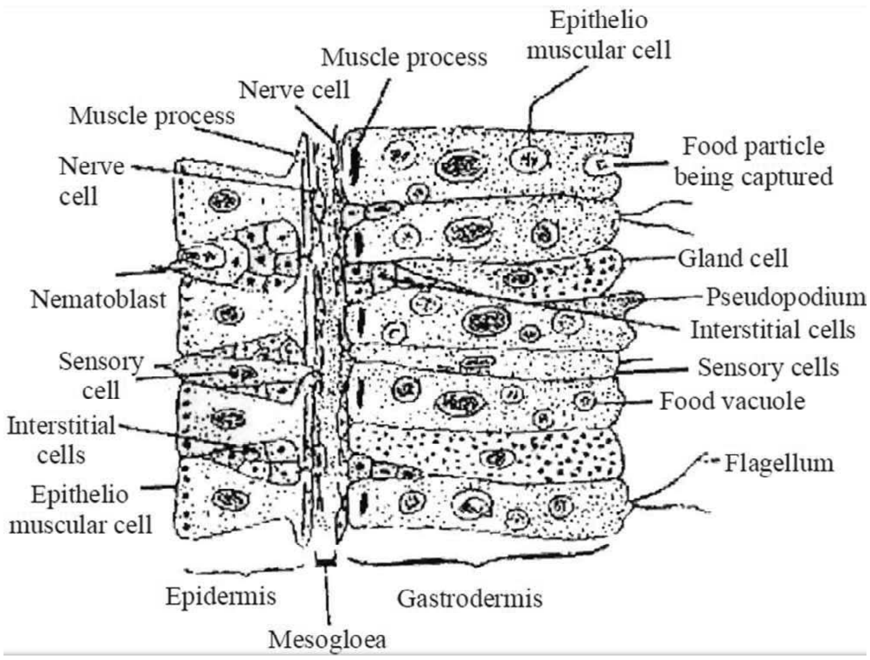

Fig. 3.28 *Sensory Structures in Body Wall of Coelenterates*

Nematocysts are modified epidermal interstitial cells. A Cnidoblast is an oval or rounded cell with a conspicuous nucleus lying on basal side. Inside the cnidoblast, an oval or pyriform sac or bladder is present which is filled with a toxin known as *hypnotoxin*. Hypnotoxin is a mixture of proteins and phenols. The outer end of the capsule is invaginated to form a long, hollow and tubular filament or thread tube. This thread is coiled like a watch-spring inside the sac itself. The base of the thread tube is swollen to form another structure known as *butt*. The butt comprises three large spines known as *barbs* or *stylets* and alos three spiral rows of minute spines. A lid or operculum covers the bladder on the top. Near the lid or operculum, is present a hair-like process, *called as Cnidocil*. Cnidocil acts like a trigger for the discharge of the thread tube. Contractile muscle fibrils and a restraining thread at the base, called *lasso*, are present in the cytoplasm of cnidoblast. The primary function of the Lasso is to prevent the nematocyst from being thrown out of cell. The other cell organelles present inside the cytoplasm are same as that of other normal cell.

The discharge of nematocyst depends upon the mechanical or chemical stimuli received by the cnidocil. At resting phase, the capsule wall is not at all permeable to water,. This leads to very high osmotic pressure as the hypnotoxin inside is hypertonic to external water. As the cnidocil is triggered due to mechanical or chemical stimuli, the permeability of the capsule wall increases causing water to rush inside the capsule, leading to an increased hydrostatic pressure. Due to increased hydrostatic pressure, the opercular lid opens up and the thread tube inverts inside out with great strength and penetrates deep in the tissue of the victim injecting toxic *hypnotoxin*. Once discharged, the thread tube cannot be withdrawn back. The discharged nematoblasts are replaced by the new one.

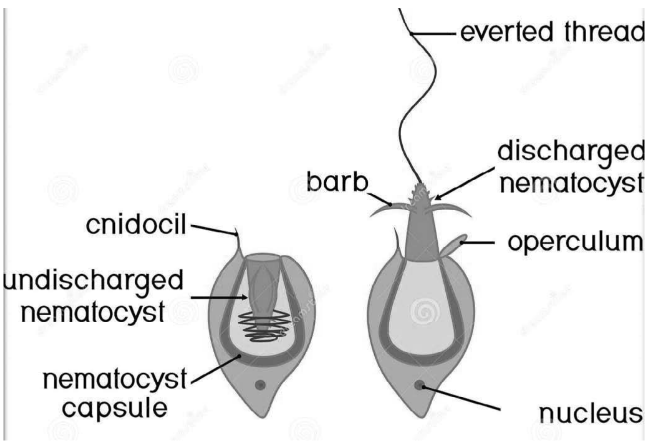

Fig. 3.29 *Structure of a Cnidoblast*

2) Nervous System in Echinodermata

The nervous system of Echinoderms is of primitive kind just like that of Coelenterates and Ctenophores. However, it is little bit complex when compared to both Coelenterates and Ctenophores. All group of Echinoderms possess a network of nerves referred to as nerve plexus. These nerves run intertwined (entangled to each other) under the surface of an Echinoderm's skin. In addition to this, the oesophagus is surrounded by one to several nerve rings, from which run radial nerves often in parallel with branches of the water-vascular system. Ring and radial nerves coordinate righting activity.

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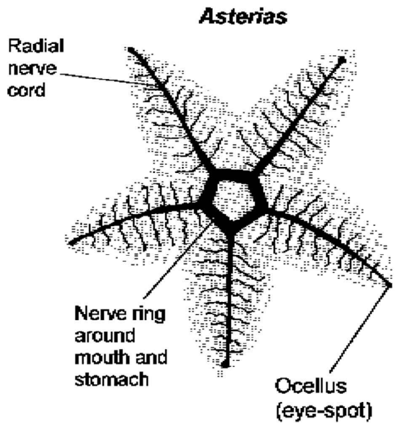

Fig. 3.30 *Nervous System of Echinoderms*

Although, echinoderms are not known to have well developed sensory inputs, they are sensitive to stimuli like touch, light, temperature, orientation as well as the status of water around them. The tube feet, spines, pedicellariae, and skin respond to touch, and light-sensitive organs have been found in echinoids, holothurians, and asteroids.

a) **Tube Feet:** The ambulacral groove comprised of two double rows of short tubular projections called as podia or tube feet. At the tip of each arm, there is present a hollow non-retractile projection which serves as olfactory and tactile organ. At its base, there occurs red spot composed of several ocelli. This red spot is photosensitive in nature. Each tube foot is closed thin walled structure. It is divide into three regions namely:

   I) Ampulla: It is a rounded sac-like structure projecting into the coelom.

   II) Podium: It is the middle tubular portion of the tube feet.

   III) Sucker: It is located at the terminal end of tube like podium.

   The walls of the tube possess strong longitudinal and circular muscles. The tube-feet are sensory in function in ophiuroidea and holothuridea, whereas, in echinoidea, the tube-feet of the aboral side lack terminal disc and are sensory in function (Hyman, 1955).

b) **Ocelli:** The eye spots of echinoderms comprise of a mass of ocelli. These ocelli consist of pigmented epithelial cells that respond to light intensity, and are lined with sensory cells in between them. Further, each ocellus is covered by a cuticle that serves the dual function, i.e., it protects them through it thickness as well as serve as a lens with its transparency.

c) **Pedicellariae:** The upper convex side of the body is called as dorsal surface or aboral surface. The aboral surface bears numerous immovable, calcareous spines called as tubercles. Surrounding and in between these spines are preset tiny structures called as pedicellariae. These tiny structures are also present on the oral surface. The primary function of these pedicellariae is cleaning or guarding the body surface. However, they are also sensory in nature.

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d) **Spines:** The lower surface of the body which is directed towards substratum is called as the oral surface or ventral surface. The central disc on the oral surface bears a centrally positioned pentagonal structure known as mouth or actinostome. The surface of the mouth is encircled by soft and delicate perioral membrane. It is further protected by five groups of mouth papillae or oral spines. From, each side of mouth (remember mouth is pentagonal) runs an ambulacral groove which extends through the ventral surface of its corresponding arm. The groove is protected on all sides by two or three rows of movable adambulacral spines. External to movable spines are three more rows of immovable spines and beyond them occur a series of marginal spines separating the oral and aboral surfaces. These spines are sensory in nature. Further, the otocysts of Holothuroidea and Sphaeridea (modified spines) of Echinoidea are the or gans of special sense.

e) **Skin:** The shining spots on the skin of an Echinoid, Diadema, are also allocated to be visual in function.

Besides all the above-mentioned sensory structures, several neurosensory cells are scattered all over the body of echinoderms which are either serve as tactile organs or chemoreceptors.

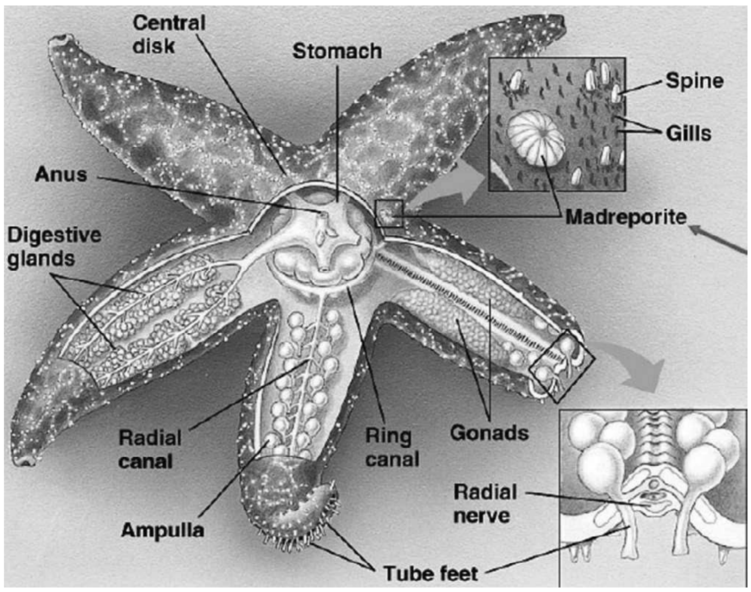

Fig. 3.31 *Different Sense Organs of Echinoderms*

This nervous system of echinoderms primarily consists of:

(1) Ventral nervous system

(2) Deep oral nervous system

(3) Apical nervous system

The nervous system of echinoderms is placed superficially. It comprises diffused sub-epithelial nerve plexus which becomes concentrated in the different parts of the body. It is highly sensory in nature and supplies nerves to different parts of the body like the integument, tube-feet and gut.

The ectodermal region of the nerve plexus is referred to as ectoneural and the endodermal part is referred to as endoneural. The ectoneural nerve plexus

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gets concentrated around the mouth mouth region as the circumoral nerve ring which in turn gives radial nerves along the radii. In the classes- echinoidea, ophiuroidea and holothuroidea of phylum Echinodermata, the circumoral nerve ring and radial nerves are placed in the wall of the epineural canal.

The ectoneural plexus extends into sensory structures like the tube-feet, spines as well as the pedicellariae. The endoneural plexus is well formed in class Asteroidea and forms perioesophageal nerve ring around the mouth opening. The deep oral nervous system comprises two nerve cords known as the Lange's cords in each radius. These two nerve cords are present in the ectoneural system and are differentiated from the radial nerve via connective tissue layer.

The apical nervous system comprises a cord located in the mid-dorsal line of the body. It develops from the dorsal peritoneum. Apical nervous system is best developed in class Crinoidea. on the other side, it is entirely absent in class Holothuroidea. Apical nervous system is solely motor in nature and mesodermal in origin.

a) Nervous System in *Pisaster ochraceus* (Star Fish)

The star fish is considered as having a central core situated around its mouth/anus with several arms radiating out of it. The number of arms varies from usual 5 to the rare 50. For instance: *Pisaster ochraceus* of the asteroidea class also known as the purple sea star or ochre sea star has 5 limbs.

In a starfish, a central nerve ring lines the oesophagus and it sends off radial nerves into each of the arms. These radial nerves run parallel with the branches of the water vascular system. The ring nerves as well as the radial nerves coordinate the sea star's balance and directional systems. The tube feet, spines, and pedicellariae present on sea stars are sensitive to several stimuli like touch, light etc. The number of eye spots varies from 80 to 200 on each end of a star fish's arm. Further, tube feet at the tip of the rays are sensitive to chemicals. Apart from eye spots, numerous starfish also possess individual photo receptor cells throughout their body allowing them to sense light even when their eye spots are incapable of proper function.

The nervous system of a star fish plays a huge role in its capability to regenerate even from a single limb. Initial loss of limbs which may be caused due to autotomy, in which connective tissues in limbs grasped by predators quickly deteriorate and detach. This is due to sensory signals sent out from the nervous system.

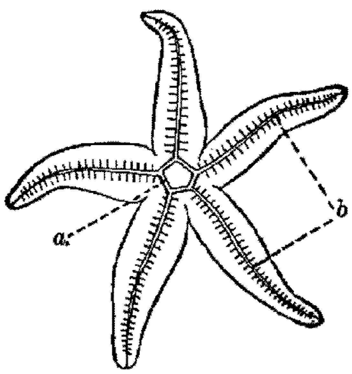

Fig. 3.32 *Nervous system of a Star Fish.*
a) Central Nerve Ring; b) Peripheral Nerves of the Arms. (Loeb)

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b) Nervous System of *Echinus melo (Sea Urchin)*

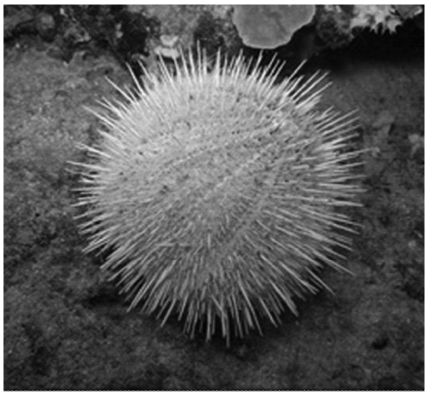

Fig. 3.33 *Echinus melo (Sea Urchin)*

Sea urchins are mainly divided into two classes namely: echinoida and cidaroida. They are characterized by their globular shape as well as presence of their defensive array of spines radiating out from its endoskeleton, only leaving the mouth measurably vulnerable.

A sea urchin like *Echinus melo* possess a simple nervous system. The nerve system, radiates from a central nerve ring situated around the lantern of the sea urchin. Five nerves branch out of the central nerve ring and radiate underneath the radial canals of the water vascular system. These nerves further branches into small nerve points ending in the sensory structures like tube feet, spines, and pedicellariae of the sea urchin.

Sea urchins are highly sensitive to stimulus like touch, light as well as chemicals. Instead of eye spots, sea urchin possess a compound eye. Stacocysts known as *spheridia* are present in sea urchins which detect the position of sea urchins with respect to their surface. These sensory structures sends off neurons warning/informing the sea urchin of its exposure, making it to take appropriate action and to re-align its body in upright position.

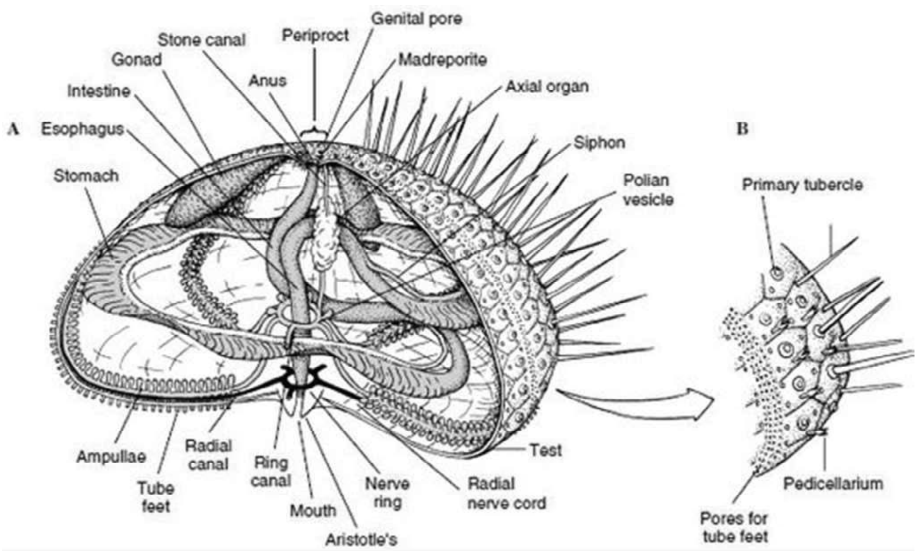

Fig. 3.34 *Nervous System of Sea-Urchin*

c) Nervous System of *Parastichopus californicus* (Sea Cucumber)

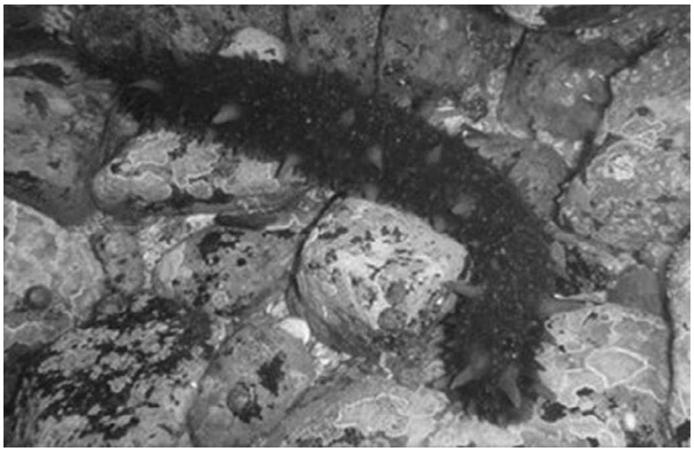

Fig. 3.35 *Parastichopus Californicus (Sea Cucumber)*

Parastichopus californicus, also referred to as the Red Sea Cucumber, is part of the class *Holothuroidea*, or simply known as sea cucumbers.

The sea cucumber lacks a central functional brain and relays on five nerves radiating out from a centrally located nerve ring around the pharynx. These nerves transmit nerve impulses/signal throughout the body of sea cucumber. However, sea cucumber lacks any additional sensory structures.

The order Apodida of sea cucumbers does however have species with statocysts.

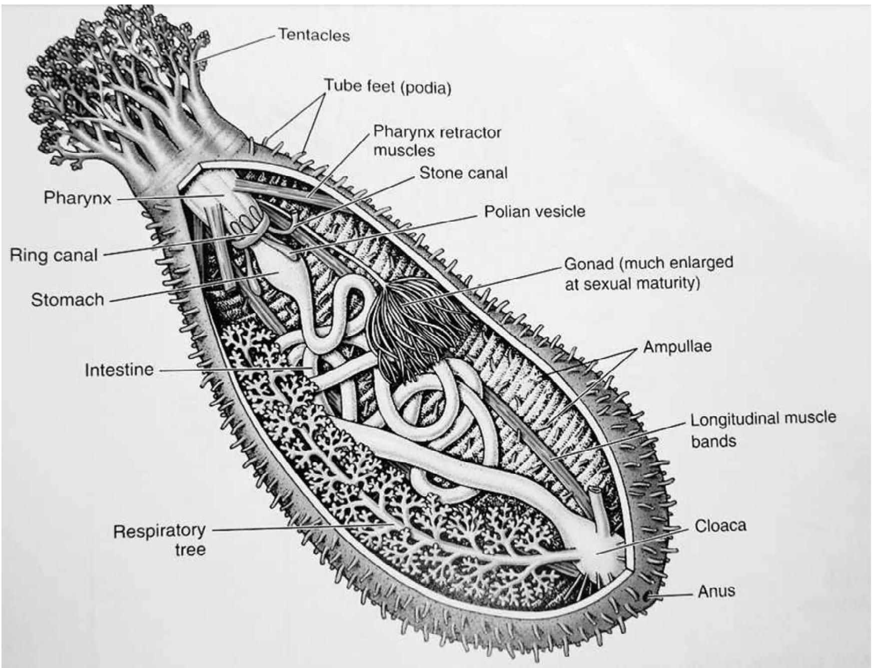

Fig. 3.36 *Nervous System of Sea-Cucumber*

3.3.2 Advanced Nervous System: Annelida, Arthropoda (Crustacea and Insecta) and Mollusca (Cephalopoda)

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Let us study the advanced nervous system in detail.

I. Nervous Sysmtem of Annelida

The body surface of the annelids is noticeably marked out into segments called as metameres and hence, the phylum is called as Annelida. They may be *aquatic* either marine or fresh water; or terrestrial; free-living or parasitic. They are coelomate animals having organ-system level of body organization. Annelids exhibit bilateral symmetry and are triploblastic, i.e., they possess three germ layers namely ectoderm, mesoderm and endoderm. The typical nervous system of annelids consists of three parts:

1) Central nervous system
2) Peripheral nervous system
3) Sympathetic nervous system

(1) Central Nervous System

It is present within the ventral haemocoelomic channel and comprises:

I. Anterior nerve ring
II. Ventral nerve cord
III. Terminal ganglionic mass

(I) Anterior Nerve Ring

- It lies dorsally above the anterior part of pharynx.
- It includes small dorsal brain made up of a pair of fused cerebral or supra pharyngeal ganglia.
- It is connected by a pair of short lateral peripharyngeal connectives present on either side of pharynx, with a ventral sub-pharyngeal ganglionic mass situated beneath pharynx in 5^{th} segment.
- Triangular shaped sub-pharyngeal ganglionic mass is a complex structure formed of 4 pairs of fused embryonic ganglia.
- Cerebral ganglia and sub -pharyngeal ganglionic mass represent ganglia of first 5 segments.

(II) Ventral Nerve Cord

- It arises from posterior end of sub -pharyngeal ganglionic mass and runs towards the back along mid ventral line, from $6\text{-}26^{th}$ segment.
- Though it appears as a single structure, in reality, it is double as seen in earthworm.
- It carries 21 well-formed ganglia located in the first annulus of its own segment.

- The ventral nerve cord is made up of nerve cells and nerve fibres.
- Nerve cells are restricted to ganglia, where they encircle nerve fibres.
- The entire ventral nerve cord is covered with neurilemma.

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(III) Terminal Ganglionic Mass

- The ventral nerve cord terminates as ovoid ganglionic mass, situated within the posterior sucker.
- It is produced by the fusion of 7 pairs of embryonic ganglia of last 7 segments that comprises the posterior sucker.

(2) Peripheral Nervous System

- It consists of paired nerve beginning from ganglia of central nervous system.
- Paired optic nerves begins anteriorly from brain or cerebral ganglia and runs forward to supply 1st pair of eyes ,prostomium and roof of buccal chamber
- 4 pairs of optic nerves begin laterally from sub-pharyngeal ganglionic mass and supply 2^{nd}, 3^{rd}, 4^{th} and 5^{th} pairs of eyes respectively.
- A few nerves also arises ventrally from the ganglionic mass and supply the floor of buccal cavity, musculature of body wall and segmented receptor organ of five anterior segments.
- Each ganglia of ventral nerve cord gives off two pairs of nerves:

  (A) Anterior laterals

  (B) Posterior laterals
- Arises anteriorly from ganglion
- These solid nerves branches to supply nephridium vesicle, vas deferens, muscle of body wall as well as segmental receptor organs of five anterior segments.

Posterior Laterals

- Arises from posterior part of ganglion
- These solid nerves branches to supply dorsal body wall, rest of dorsal receptor, viscera and testis sac of their own side.
- Terminal ganglionic mass sends off numerous nerves supplying the receptor organs and other structures present in the posterior sucker.

(3) Sympathetic or Autonomic Nervous System

- It comprises a widespread nerve plexus lying beneath epidermis, within muscles and on gut wall.
- On one side, it connects with certain cells on both sides of peripharyngeal connectives while on the other side with multipolar ganglion cells which are on-uniformly scattered over the entire plexus of gut wall.

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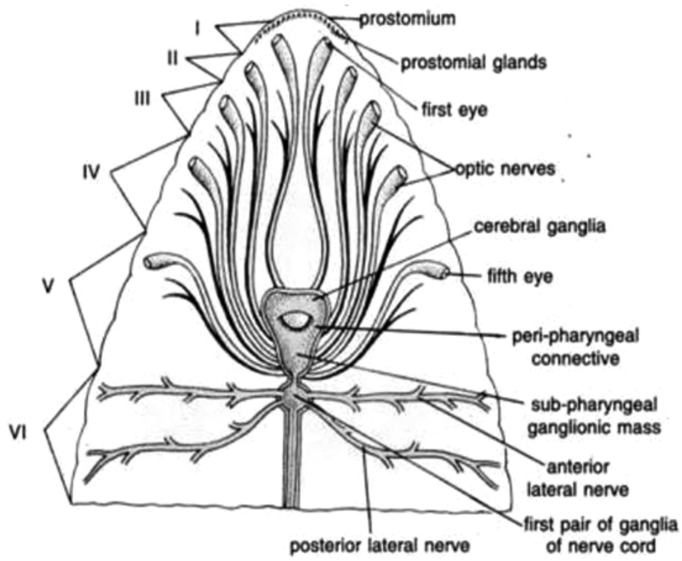

Fig. 3.37 *Nervous System in the Anterior End of Annelid Body*

The nervous system of earthworm is composed of a pair of cerebral ganglia positioned in the third segment above the pharynx. Circum- pharyngeal connectives encircle the pharynx and meet with a pair of sub-pharyngeal ganglia below the pharynx. The ventral nerve cord runs in the middle on the ventral side from the subpharyngeal ganglia to the last segment of the body. In each body segment of earthworm, there is one fused paired ganglion called segmental ganglion from which arise other three pairs of peripheral nerves.

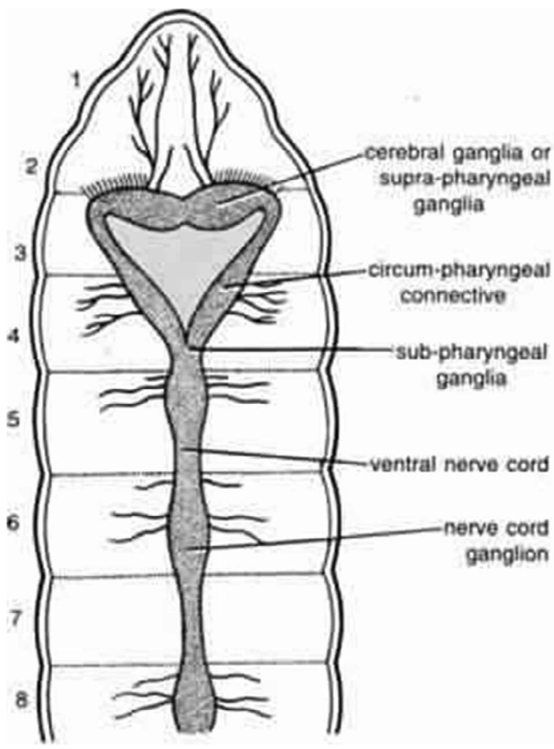

Fig. 3.38 *Nervous System in Pheretima*

NOTES

The sense organs or receptors of earthworm are as follows:

- **Epidermal Receptors:** These receptors are long sensory tactile cells which are further surrounded by supporting cells. They are scattered all over the epidermis making the skin highly sensitive to touch.
- **Buccal Receptors:** They are also group of sensory cells located in the buccal cavity. These cells perceive chemical stimuli as well as help in smelling and tasting the food.
- **Photo Receptors:** They are solitary cells (embedded in the epidermis) containing a crystalline structure in the cytoplasm and a nerve connection at the base. They are located on the anterior side of body.

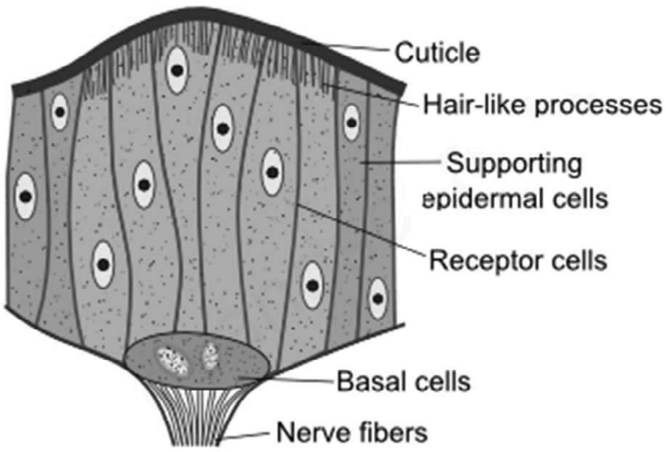

Fig. 3.39 *Epidermal Receptor of Pheretima*

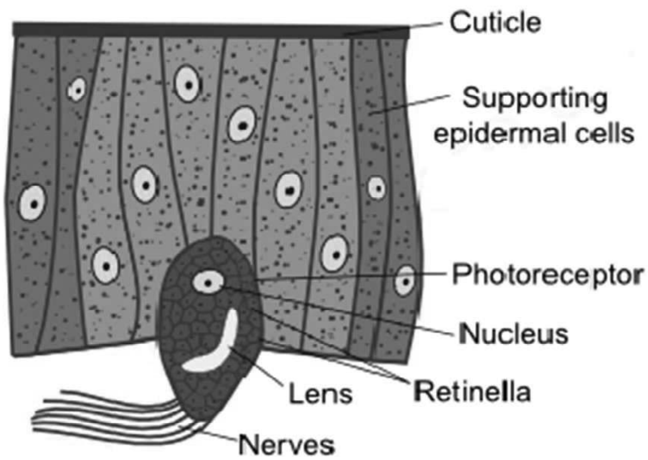

Fig. 3.40 *Photo Receptor in Pheretima*

NOTES

II. Nervous System of Arthropoda

A. Crustacea

Nervous System of Crustaceans

The nervous system of crustaceans is divided into following parts:

(1) Central Nervous System: It runs from anterior to posterior end and contains following structures.

a) **Brain or Supra-Oesophageal Ganglia**: The brain is made up of a pair of supra-oesophageal ganglia which are placed dorsally near the base of the rostrum. It innervates the anterior end of the cephalothorax.

b) **Circum-Oesophageal Commissures**: Supra-oesophageal ganglion gives off paired nerves known as circum-oesophageal commissures. They run posteriorly along the ventro-lateral wall of the cephalothoracic cavity. A small ganglion is located on each commissure to supply nerve to the mandibles. Both the cords are coupled via transverse loop, which is present immediately after the oesophagus. Eventually, the two connectives connect at the floor of the thoracic cavity with a large ganglion known as the thoracic ganglionic mass.

c) **Ventral Thoracic Ganglionic Mass:** A large ventral thoracic ganglionic mass is formed by the fusion of eleven pairs of ganglia. It sends eleven pairs of peripheral nerves.

d) **Ventral Nerve Cord:** A ventral nerve cord formed by the fusion of two separate cords originates from the posterior end of the thoracic ganglionic mass. It runs up to the posterior-most segment. The ventral nerve cord along its course bears a ganglion in each segment. Out of them, 6th ganglion is the largest of all and is referred to as stellate ganglion.

(2) Peripheral Nervous System

Central nervous system sends off nerves to all parts of the body. These nerves constitute the peripheral nervous system. A peripheral nerves constitute of two different types of fibres namely—motor and sensory fibres. All motor fibres carries message from central nervous system to different parts of body whereas sensory fibres sends messages from body to central nervous system. The peripheral nervous system consists of the following parts-

a) **Optic nerve:** It innervates the retinal layer of eye.

b) **Antennular nerve:** It inervates the statocyst and structures present in the first antenna.

c) **Antennary nerve:** It innervates various parts within second antenna including green gland.

d) **Cephalothoracic nerves:** They originate from thoracic ganglionic mass to supply different muscles and appendages in that region.

e) **Abdominal nerves:** It innervates muscles and appendages. Additionally, stellate ganglion sends nerves to telson, rectum and other adjoining structures.

(3) Autonomic Nervous System

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It comprises a few minute ganglia and slender nerves which are positioned over the cardiac stomach to supply involuntary parts of the body.

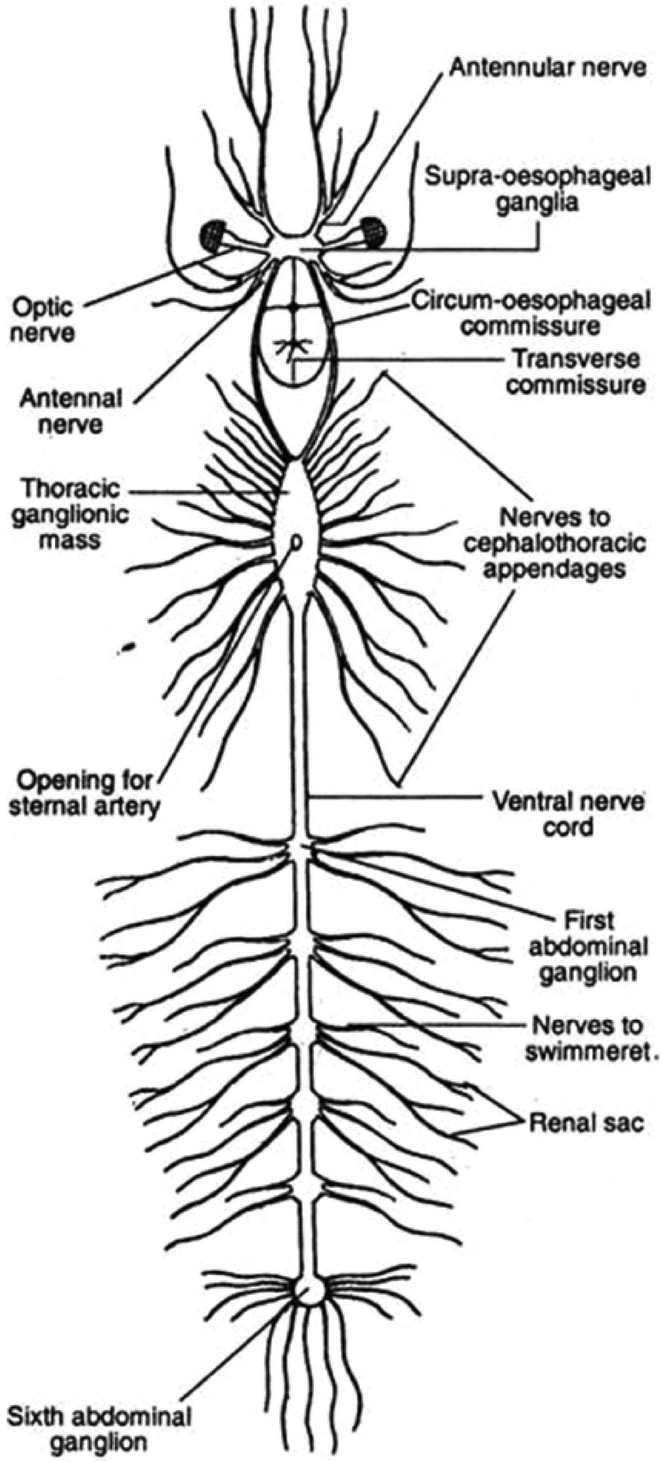

Fig. 3.41 *Nervous system of Palaemon*

NOTES

Crustaceans form a large, diverse arthropod taxon which includes such animals as crabs, lobsters, crayfish, shrimps, prawns, krill, woodlice, and barnacles. Generally, prawn habitats fresh-water areas such as ponds, rivers, streams and lakes. It is nocturnal, bottom-dweller and lives within underwater crevices or aquatic vegetation. It is omnivorous, i.e., feeds on all kinds of food specially dead and decaying leaves. It may attain a length up to 90 cm. Prawn is an elongated, hemispherical animal, tapering slightly at the posterior end. The fresh specimen is somewhat bluish in colour due to the presence of respiratory segment haemocyanin in blood plasma. The entire external surface of the animal's body is covered by hard exoskeleton. The body is broadly divided into two regions namely—cephalothorax and abdomen. Both cephalothorax and abdomen bear paired appendages on their ventral surface. These appendages are biramous, i.e., two branched and are specialized for performing different functions. The two regions of the body, i.e., cephalothorax and abdomen bear several sensory structures as described below.

Sense Organs of Crustacea

Cephalothorax is the broad, un-segmented and cylindrical anterior part of prawn which is formed by the fusion of head and thorax and carries the stalked eye. It is covered by an exoskeletal covering known as carapace which hangs freely on both the ventro-lateral sides and acts as gill cover for the gill chambers. During the developmental process of prawn, one pre-segmental region and first fourteen segments fuse together to form cephalothorax. The following sensory structures are present on cephalothoracic region:

(1) Rostrum (Defensive Structures)

The carapace is drawn into a long serrated projection towards the anterior end known as the rostrum. Rostrum is defensive in function.

(2) Eye (Photosensitive Structures)

At the base of the rostrum, a pair of stalked, compound eye is placed on each side of the carapace. The eyes are black in color, hemispherical in shape and made up of several visual elements called as ommatidia. The Prawn can move its eye considerably and has nearly 360° vision. Each eye is composed of numerous small visual units known as ommatidium or ocelli.

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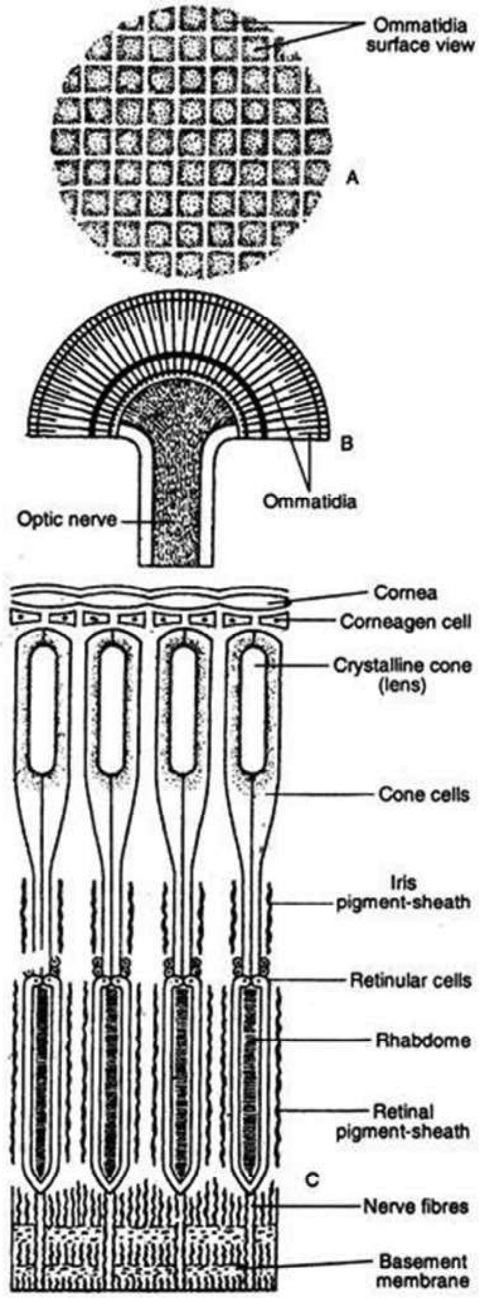

Fig. 3.42 *(A) Compound Eye of Palaemon (B) L.S of Compound Eye of Palaemon (C) L.S of Four Ommatidia*

(a) Structure of an Ommatidium

Each ommatidium is divided into two parts; outer dioptrical region comprising of cornea, corneagen cells, crystalline cone and cone cells and inner retinal region including rhabdome, retinular cells & pigment sheath. The outer dioptrical part is used for focussing the light rays falling from the object whereas inner retinal part receives light stimuli and aid in image formation.

- **(i) Cornea:** It is the outermost transparent cuticular layer and acts as lens.
- **(ii) Corneagen Cells:** Corneagen cells are present below the cornea and are responsible to replace the cornea in case of wear and tear.

NOTES

(iii) Crystalline Cone: Crystalline cone is present be neath the corneagen cells and works as a second lens.

(iv) Cone cells or Vitrellae: They are four in number and encircle the cone or lens to provide nourishment.

(v) Rhabdome: These are elongated transversely striated body which is placed beneath the cone cells.

(vi) Retinular Cells: These are elongated sickle-shaped cells; seven in number and secrete the rhabdome. They encircle the rhabdome and provide nutrition to it.

(vii) Pigment Sheath: Two separate sheaths containing chromatophores separates one ommatidium from the other. The pigment sheath which is present around cone and cone cells is called iris sheath whereas the pigment sheath present around rhabdome and retinular cells is known as retinal sheath. Pigment sheaths are able to contract and expand depending upon the intensity of light.

(b) Mechanism of Image Formation

The complete image which is produced by the compound eye is made up several pieces of small images as each ommatidia produces a separate image of a part of the object. Hence, the vision produced by the compound eye is known as mosaic vision.

During bright light, both pigment sheaths expand completely, separating ommatidia from each other. This results in the formation of a separate image of a part of the object by each ommatidum. These images formed in bright light are sharp images, known as apposition images. This kind of vision is known as mosaic vision.

During dim light, both pigment sheaths contracts, ommatidia coordinate together to form a single blurred image, known as superposition image. This kind of vision is known as superposition image.

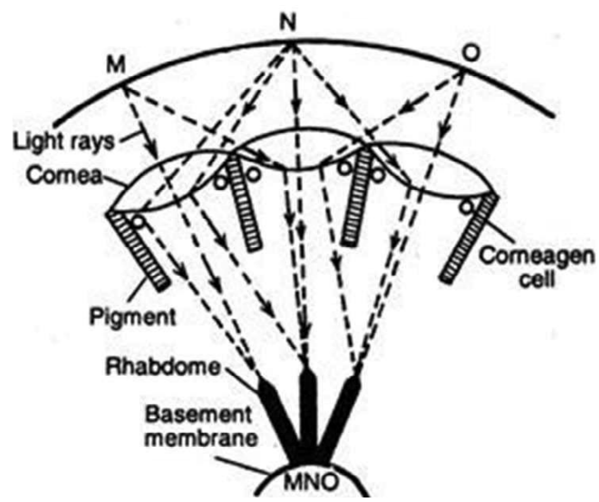

Fig. 3.43 *Superposition Image by Compound Eye of Palaemon*

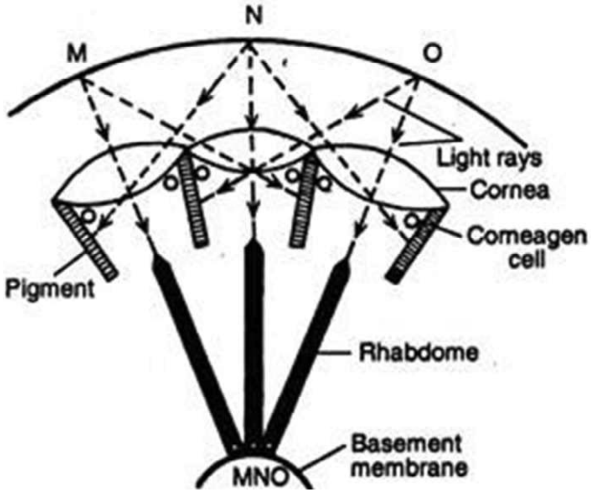

Fig. 3.44 *Apposition Image by Compound Eye of Palaemon*

(3) Spines

On each lateral side of the carapace, there are small pointed structures known as spines are present in paired condition. The anterior pair of spines is known as antennal spines whereas the short posterior pair is known as the hepatic spines.

(4) Appendages

Thirteen pairs of appendages are present on the ventral side of prawn. The appendages are of two types namely cephalic and thoracic appendages. Cephalic appendages constitute first five pairs of appendages, i.e., first antenna or antennule, second antenna, mandible, first maxilla or maxillula and second maxilla whereas thoracic appendages constitute remaining eight pairs of appendages, i.e., three pairs of Maxillipeds and five pairs of walking legs.

Cephalic Appendages

(a) First Antenna (Presence of Statocyst and Olfactory Setae)

It is also known as antennules and is located near the base of the eye stalk. Its protopodite carries an extra segment, i.e., a spiny precoxa. Coxa is smaller than basis and carries numerous sensory hairs. The precoxa carries the balancing organ known as statocyst. The statocyst is present as a small, white and spherical cuticular sac. They help the animal to maintain equilibrium. Also, both exo and endopodites are modified as feelers or flagella. The outer feeler has long and short branches and the smaller branch hold olfactory setae for determining smell. They are located on the small inner branch of the outer feeler of the first antenna. These are responsible for detecting smell.

(b) Second Antenna (Presence of Balancer)

Second antenna is positioned just after the first antenna. The coxa contains a specialised organ known as antennal gland or green gland which serves as excretory organ. The exopodite is modified as a scale or squama where scale functions as balancer during swimming. The exopodite bears numerous setae along its inner margin. The endopodite turns out to be a long structure which carries numerous tactile setae.

NOTES

(c) Mandible (Sensory Setae)

Mandibles are located on the outer surface of the mouth and are accountable for crushing the food matter. The coxa of the mandible is modified as spoon-shaped proximal apophysis and a solid distal part known as head. The head region contains teeths. The basis portion of protopodite and the endopodite form a three- jointed mandibular palp which carries sensory setae.

(d) First Maxilla or Maxillula (Sensory Setae)

Maxillula is a crown-shaped appendage located posterior to the mouth and aid in pushing the food inside mouth. It consists of three small leaf-like plates carrying sensory setae along their margins. The plates formed by coxa and basis are directed inwards and known as jaws. The remaining plate, i.e., endopodite is directed outwards.

(e) Second Maxilla

Second maxilla is a fan-shaped structure and is located after the first maxilla. The coxa is short and the basis is bifurcated inwardly to form jaws. The exopodite is large, fan-shaped structure known as scaphognathite whereas endopodite is small located between the basis and exopodite. The second maxilla performs dual function where jaws aid in procuring food and scaphognathite helps in generating continuous water current within gill chambers.

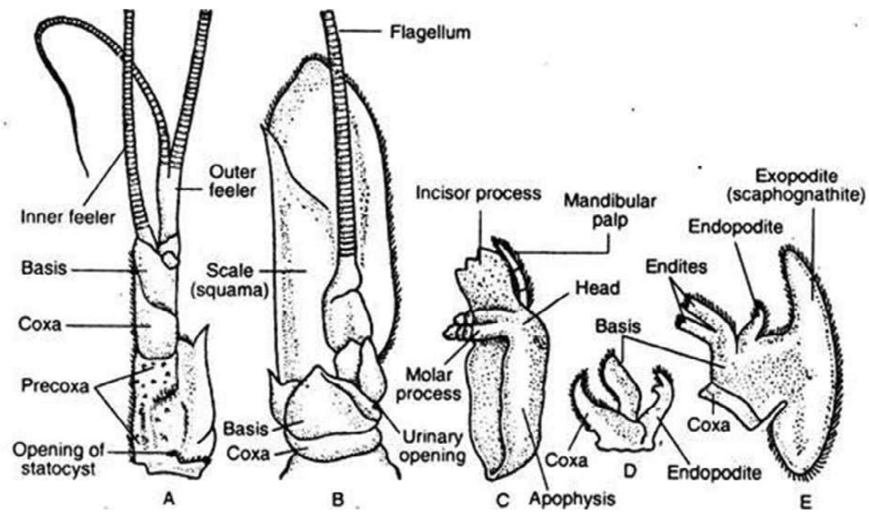

Fig. 3.45 *Cephalic appendages of Palaemon. A) Antennule of First Antenna B) Second Antenna C) Mandible D) Maxillula or First Maxilla E) Second Maxilla*

Thoracic Appendages

(a) First Maxillipede

The coxa and basis of the protopodite get flattened to develop into jaws and bear numerous stiff setae on its internal margins. The coxa bears a bilobed epipodite along with a short endopodite and long exopodite. The exo, endopodite parts of coxa along with basis aid to push the food inside.

(b) Second Maxillipede

The short coxa, on its outer surface carries a small epipodite and a gill. The exopodite is long structure with numerous setae while endopodite is made up of five segments namely ischium, merus, carpus, propodus and dactylus. The last two segments are bent back-wards and inwards and possess cutting margins.

(c) Third Maxillipede

This thoracic appendage is leg-like and its coxa carries a thin epipodite on the outer surface. The exopodite is thin and un-jointed but the endopodite bear three segments i.e. proximal, middle and distal segments.

(d) Walking Legs

In total, there are five pairs of walking legs used for crawling. Each walking leg constitutes a short protopodite with coxa, basis and a distinct five segmented endopodite. The first and second legs possess pincers and are known as chelate legs, whereas the remaining legs lack pincers and are known as non-chelate legs.

(5) Apertures (Statocyst Openings)

(a) Mouth: It is a slit like opening on the ventral side of the cephalothorax and is situated in between 3rd and 4th segments.

(b) Renal Apertures: It is located at the base of each second antenna and removes the nitrogenous waste of the body.

(c) Gonopores: In males, gonopores are located on inner sides of the coxae of fifth walking legs whereas in females they are located on inner sides of the coxae of third walking legs.

(d) Statocyst Openings: Two statocyst are located at the base of each first antenna. They are the organs of equilibrium and communicated to outside via minute pores.

Abdomen: Abdomen comprises six different segments and a posterior-most triangular structure called as telson. Each abdominal segment is bounded by a ring-like exoskeletal piece, known as the sclerite. The sclerite comprises a ventral plate-like sternum and a dorsal arch-shaped tergum. Each abdominal segment carries a pair of appendages on its ventral surface. The appendages present on abdominal segments are as follows:

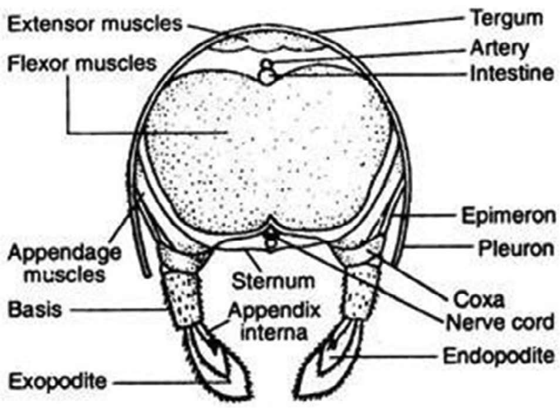

Fig. 3.46 *T.S through Abdominal Region of Palaemon*

(a) Pleopods or Swimmerets: (Tactile Setae)

They are present in paired condition on first five abdominal segments. The primary function of pleopod is to perform swimming. A typical pleopod consists of a coxa and cylindrical basis. The cylindrical basis bears a small flattened structure known as endopodite and a large exopodite. Outer surface of basis and margins of both endopodite and exopodite bears numerous tactile setae.

Tactile setae are present along the margin of antenna and other appendages. A tactile seta is composed of a swollen base and a pointed plumose with barbs on both sides. These setae are accountable for sensation of touch.

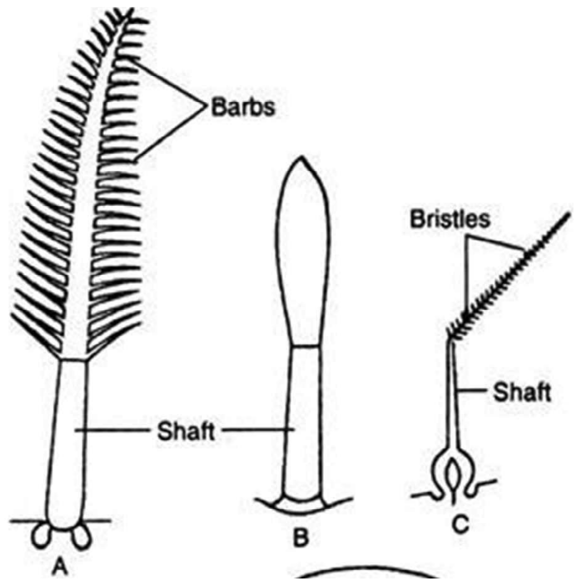

Fig. 3.47 *Sensory Setae of Palaemon. (A) Tactile Seta (B) Olfactory Setae (C) Statocystic Seta*

Additionally, a hook-like process known as the appendix interna is present on the inner surface of endopodites of 2nd, 3rd, 4th and 5th pleopods. In females, these hook like unite to form a egg carrying basket. In males, the 2nd pleopods consist of an added rod-like process bearing setae known as appendix masculina.

(b) Uropod: (Tactile Setae)

The 6th pair of abdominal appendage one on each side of the telson is known as uropod. Both the exo- and endopodites are large and fan-shaped with numerous tactile setae arranged around the margin. The exopodite is divided by a fine suture but the endopodite is not sutured. The primary function of the uropods is for changing the direction and also for leaping backwards.

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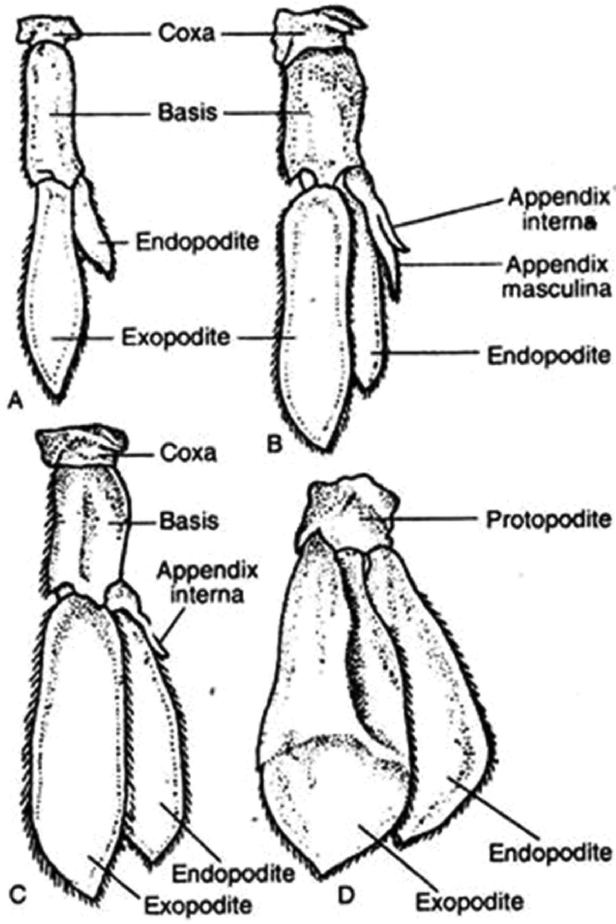

Fig. 3.48 *(A) First Swimmeret of Palaemon (B) Second Swimmeret of Palaemon (C) Third Swimmeret of Palaemon (D) Uropod of Palaemon*

B. Insects

Class insecta contains all insects and belong to the phylum Arthropoda. It is the most diverse group of organisms on earth. Insects are found on land, in the air, and in the sea and the diversity is astonishing. Insects belong to the phylum arthropoda, which means literally "jointed legs". The body is divided into three distinct regions: head, thorax and abdomen. Head comprises one pair of antennae: - the antennae are usually used as tactile organs (= organs pertaining to the sense of touch). They can also be used as olfactory organs (= organs of smell). Most insects possess one pair of compound eyes and sometimes some simple eyes called "ocelli". There is a big variety in types of mouthparts; biting, sucking, stinging, licking, etc. Thorax: Thoracic region contains three pairs of legs. The thorax is divided into three regions namely pro-thorax, meso-thorax and meta-thorax. Each segment has one pair of legs. The different parts of the leg are called coxa, trochanter, femur, tibia, and tarsus. The wings are borne by the second and/ or third of the thoracic segments.

Note: Some insects are wingless.

Abdomen: The gonopore (genital opening) is at the posterior end of the abdomen. No appendages used for moving on the abdomen of adults (except in a few primitive insects). Sometimes there are some appendages at the end of the abdomen.

NOTES

Nervous system of an insect is a network of specialized cells known as neurons. These neurons serve as an "information highway" within the body of insect as well as that of higher vertebrates. Neurons generate high electrical impulses commonly known as action potential. This action potential travel as waves of depolarization along the cell's membrane. Every neuron comprises a nerve cell body containing the nucleus; and filament-like processes like dendrites, axons and collaterals. Dendrites receives the electrical impulse or action potential whereas axon helps in the propagation of nerve impulse. The propagation of nerve impulse is unidirectional i.e., signal moves toward the nerve cell body along a dendrite or a collateral and away from the nerve cell body along an axon. On the basis of their function within the nervous system, neurons can be divided into three categories:

a) **Afferent (Sensory) Neurons**: These neurons caries the signal towards the central nervous system. They can be bipolar, i.e., having one axonic and one dendritic process or they can be multipolar having several dendrites that are associated with sense organs or receptors.

b) Efferent (Motor) Neurons: These neurons carry the signal away from the central nervous system and stimulate the responses in muscles and glands.

c) Inter Neurons: These neurons connect sensory and motor neuron. These neurons conduct signals within the central nervous system.

Individual nerve cells connect with one another through special functional junctions, known as gap junction or synapses. As soon as electrical impulse reaches the gap junction it releases a chemical messenger referred to as neurotransmitter. This neurotransmitter diffuses across the synapse and sets up a new impulse in the dendrite of next neuron. Acetylcholine, 5-hydroxytryptamine, dopamine, and noradrenaline are examples of neurotransmitters found in both vertebrate as well as invertebrate nervous systems.

Nerve cells are typically found grouped in bundles. A nerve is simply a bundle of dendrites or axons that serve the same part of the body. A ganglion is a dense cluster of interconnected neurons that process sensory information or control motor outputs.

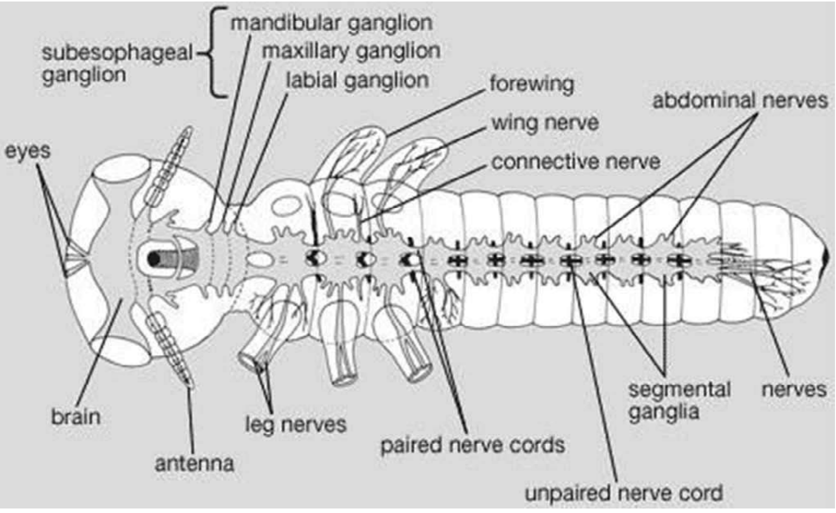

Fig. 3.49 *An Insect's Brain*

The Central Nervous System

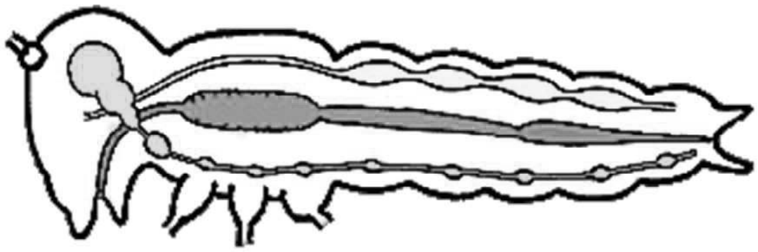

Fig. 3.50 Relative Position of Circulatory (Yellow), Digestive (Green), and Nervous (Blue) Systems in an Insect

NOTES

Like most other arthropods, insects possess a relatively Simple Central Nervous system (CNS). CNS comprises a dorsal brain linked to a ventral nerve cord. Ventral nerve cord is comprised of paired segmental ganglia running along the ventral midline of the thorax and abdomen. Within each segment, ganglia are connected via commissure. Further, they are joined by intersegmental connectives to ganglia in adjacent body segments. Thus, in general, the central nervous system appears ladder-like. Commissures acts as the rungs of the ladder whereas intersegmental connectives serve as the rails. In more "advanced" insect orders, there is a tendency for individual ganglia to combine (both laterally and longitudinally) into larger ganglia that serve multiple body segments.

An insect's brain is a complex structure comprising of six fused ganglia (three pairs) located dorsally within the head capsule. Each part of the brain controls a limited range of activities in the insect's body:

- **Protocerebrum**: Protocerebrum represents the first pair of ganglia. They are largely concerned with vision. Protocerebrum innervate the compound eyes as well as ocelli, i.e., the photoreceptors of insect.
- **Deutocerebrum**: Deutocerebrum represents the second pair of ganglia. They are majorly concerned with processing of sensory information collected by the antennae.
- **Tritocerebrum**: Tritocerebrum represents the third pair of ganglia. It innervate the labrum as well as integrate sensory inputs from both proto- and deutocerebrums. Further, they connect the brain with the rest of the ventral nerve cord as well as the stomodaeal nervous system. Stomodaeal nervous system is associated with controlling the internal organs. The commissure for the tritocerebrum loops around the digestive system, suggesting that these ganglia were originally located behind the mouth and migrated forward (around the esophagus) during evolution.

Subesophageal Ganglia- Sub-esophageal ganglia are located ventrally in the head capsule just below the brain and esophagus. The subesophageal ganglion innervates mandibles, maxillae, labium, hypopharynx, salivary glands as well as neck muscles. A pair of circumesophageal connectives loop around the digestive system to link the brain and subesophageal complex together.

Thoracic ganglia: Thoracic Ganglia (three pairs) are located in the thoracic region. They control the locomotion by innervating the legs as well as wings. Both thoracic muscles as well as sensory receptors are associated with these ganglia.

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Abdominal Ganglia: Abdominal ganglion control movements of abdominal muscles. Spiracles (concerned with respiration in insects) located in both the thoracic and abdominal region are controlled via a pair of lateral nerves that arise from each segmental ganglion (or by a median ventral nerve that branches to each side).

Caudal Ganglion: Abdominal ganglia located at the terminal end fuses together to form a large caudal ganglion. Caudal ganglion innervate the anus, internal and external genitalia, and sensory receptors (such as cerci) located on the insect's back end.

The Stomodaeal Nervous System

Stomodaeal nervous system also referred to as the stomatogastric nervous system, control the insect's internal organs. A pair of frontal nerves rising close to the base of the tritocerebrum connect the brain with a frontal ganglion (unpaired) located on the anterior wall of the esophagus. Frontal ganglion innervates the pharynx as well as muscles associated with swallowing. A recurrent nerve present along the anterio-dorsal surface of the foregut connects the frontal ganglion with a hypocerebral ganglion. Hypocerebral ganglion innervates the heart, corpora cardiaca as well as the portions of the foregut. Gastric nerves arises from the hypocerebral ganglion. Gastric nerves run posteriorly to ingluvial ganglia (paired structures) in the abdomen.

The different types of sense organs present in insects are as follows:

1. Mechano Receptors
2. Auditory Receptors
3. Chemo Receptors
4. Thermo Receptors
5. Photo Receptors

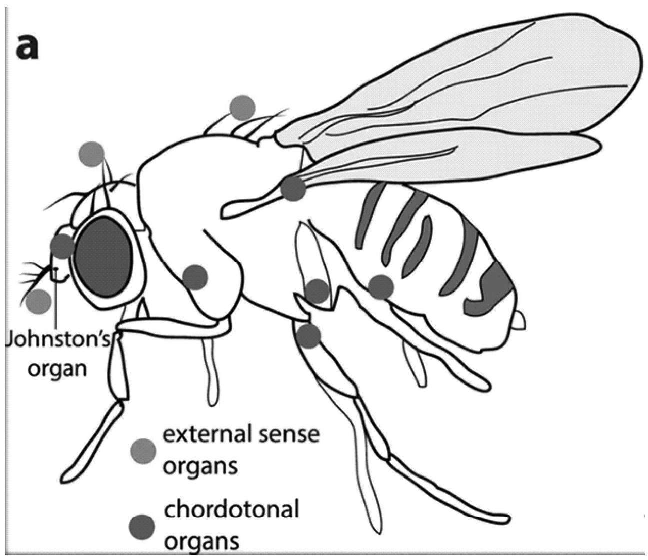

Fig. 3.51 *Sense Organs in Insect*

Source: *http://www.nature.com/article-assets/npg/srep/2015/150728/srep12492/images_hires/w926/srep12492-f1.jpg*

NOTES

1. Mechano Receptors: They detect mechanical forces.

i. **Trichoid sensilla**: These are hair-like little sense organ. Trichoid sensilla are associated with spur as well as seta. Trichoid sensilla are sensitive to touch and are located in antenna as well as mouth parts of the insect.

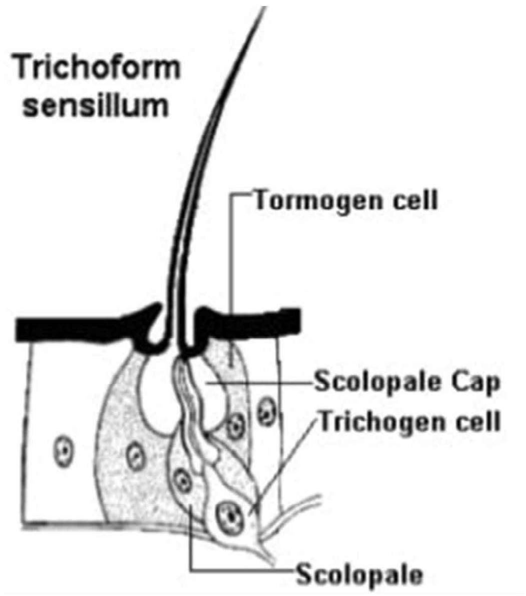

Fig. 3.52 *Trichoid Sensilla*

ii. **Campaniform sensilla** (**Dome sensilla**): Terminal end of campaniform sensilla are rod like structure and inserted into dome shaped cuticula. These sensilla are highly sensitive to pressure and located in leg joints as well as bese of wings.

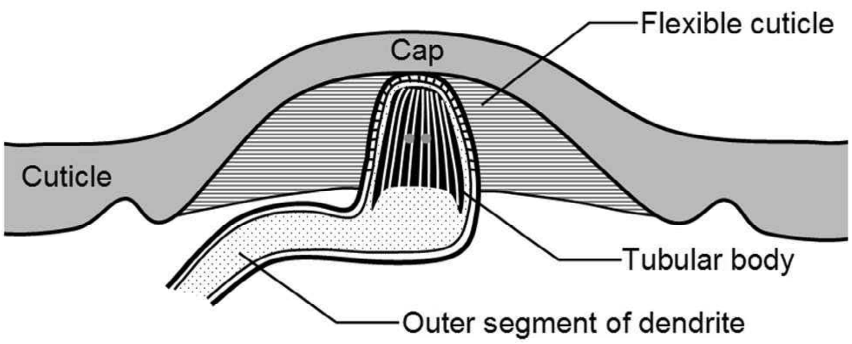

Fig. 3.53 *Section through Campaniform Organ*

iii. **Chordotonal organ**: Chordotonal organ are specialized subcuticular mechano receptors (sensory structures) that receive vibrations. A chordotonal organ consists of one to several scolopidia. Each scolopidia consist of cap cell, scolopale cell and dendrite. These organs are interoceptors attached to both ends of body wall.

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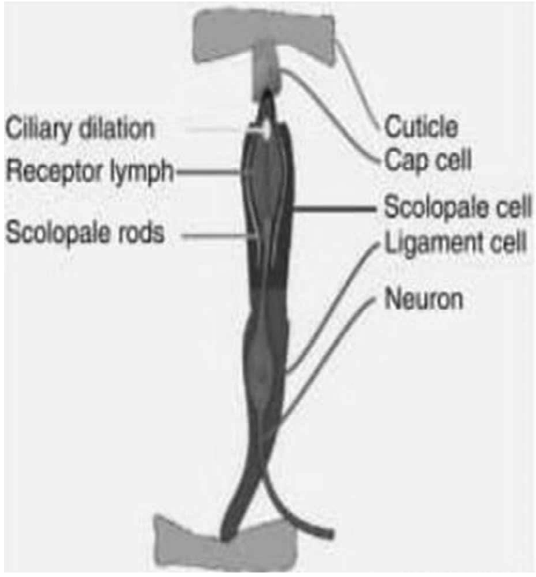

Fig. 3.54 *Chordotonal Organ in Insect*

Mechanoreceptors perform different functions in the body:-

- **Proprioception**- They help in positioning the body with respect to gravity.
- Mechanoreceptors are highly sensitive to sound waves, vibration of substratum as well as pressure changes.
- **Johnston's organ**: All adult insects as well as several larval forms possess a specialized chordotonal organ referred to as Johnston's organ. Johnston's organ lies within the second antennal segment (Pedicel). Johnston's organ sense movements of antennal flagellum. Apart from this, in few insects like midges and male mosquitoes, it aids in hearing.
- **Subgenual organ**: These are also another type of chordotonal organ located in the proximal tibia of each leg. They help in detecting substrate vibration. These organs are present in almost all the insects, the only exception being- coleoptera and diptera.

2. Auditory Receptors: They detect sound waves or vibrations.

i. **Delicate Tactile Hair**: Delicate tactile hairs are present in plumose antenna of male mosquito.

ii. **Tympanum**: Tympanum is a membrane stretched across tympanic cavity and responds to sounds produced at some distance. Tympanal membranes are linked to chordotonal organs that enhance sound reception. Tympanal organs are usually located between:

- the metathoracic legs of mantids.
- the metathorax of many nectuid moths.
- the prothoracic legs of many orthopterans.
- the abdomen of short horned grasshopper, cicada.
- the wings of certain moths and lacewings.

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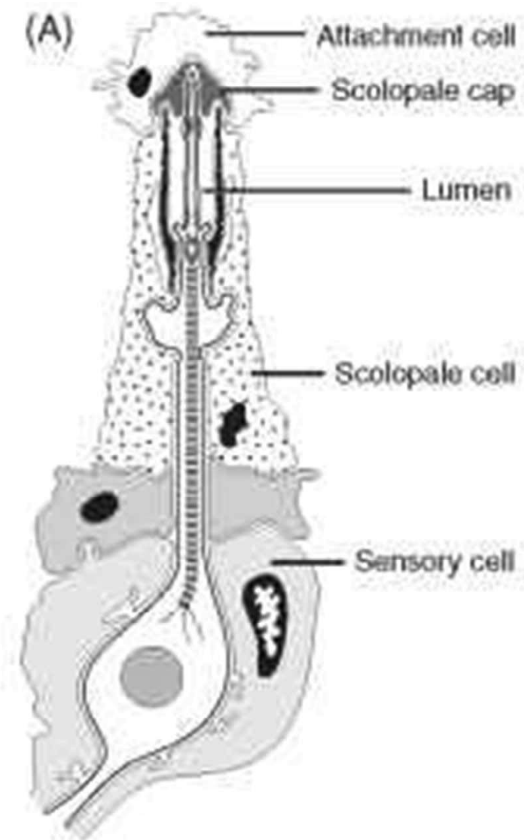

Fig. 3.55 *Auditory Receptor in Insect*

3. Chemoreceptors (Detect Smell and Taste): Chemoreceptors helps in detecting the chemical present in the surrounding environment.

Insect chemoreceptors can be uniporous or multiporous. Uniporous chemoreceptors possess one pore whereas multiporous have many more pores. Uniporous chemorceptors mostly detect chemicals of solid as well as liquid form by direct contact. They are commonly known as gustatory receptor. Many sensor neurons located in antenna are of this type.

On the contrary, multiporous chemoreceptors detect chemicals in vapour form. They need not be in direct contact with the stimulus and can detect chemicals from a distance. They are commonly known as olfactory receptor. Few sensory neurons located in trophi and tarsi are of multiporous or olfactory types of receptor. Each pore forms a chamber known as pore kettle with numerous pore tubules that run inwards to meet multibranched dendrites.

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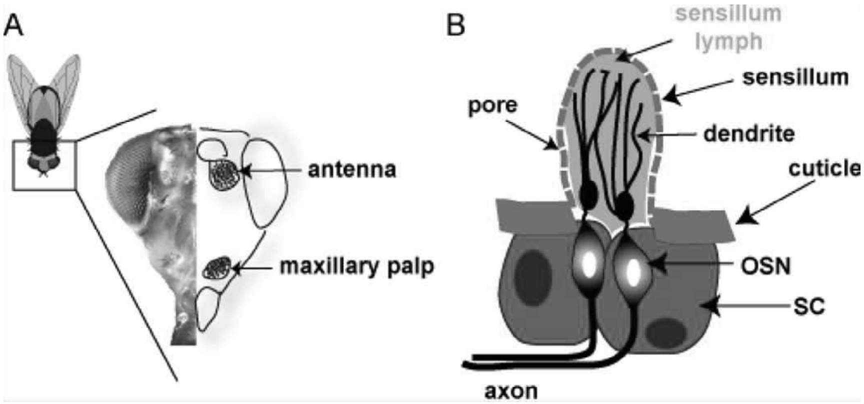

Fig. 3.56 *Olfactory Receptor of an Insect*

Source of Figure: Sensors | Free Full-Text | First Contact to Odors: Our Current Knowledge about Odorant Receptor | HTML (mdpi.com)

4. Thermoreceptors- They detect heat energy.

Thermoreceptors are present in poikilothermic insects. Thermoreceptors are highly sensitive to temperature changes. In bed bug, it is useful to locate the host utilizing the temperature gradient of the host.

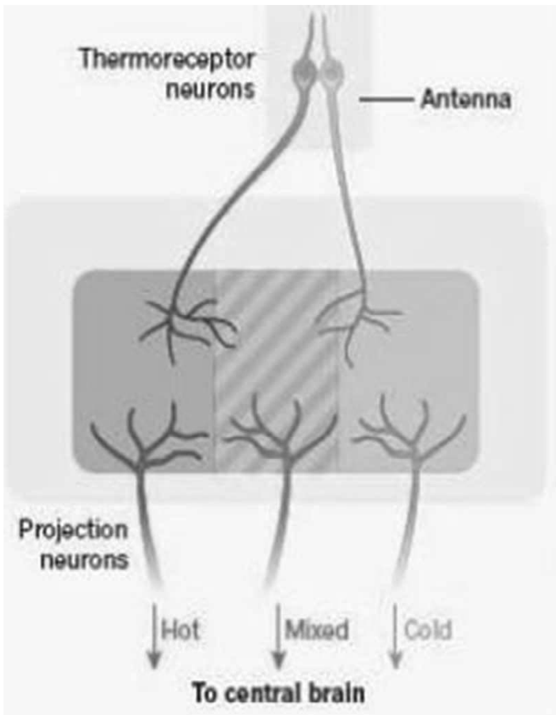

Fig. 3.57 *Thermoreceptor in Insect*

5. Photoreceptors: They detect light energy**.** Insect possess both simple ocelli as well as compound eye.

a) Compound Eye

A pair of compound eye is present on stalk. The Prawn can move its eye considerably and has nearly 360° vision. Each eye is composed of numerous

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small visual units known as ommatidium or ocelli. Each ommatidium is divided into two parts—outer dioptrical region comprising of cornea, corneagen cells, crystalline cone & cone cells and inner retinal region including rhabdome, retinular cells & pigment sheath. The outer dioptrical part is used for focussing the light rays falling from the object whereas inner retinal part receives light stimuli and aid in image formation. Cornea represents the outermost transparent cuticular layer and acts as lens. Corneagen cells are present below the cornea and are responsible to replace the cornea in case of wear and tear. Crystalline cone is present beneath the corneagen cells and works as a second lens. Cone cells or Vitrellae are four in number and encircle the cone or lens to provide nourishment. Rhabdome are elongated transversely striated body which is placed beneath the cone cells. Retinular cells:are elongated sickle-shaped cells; seven in number and secrete the rhabdome. They encircle the rhabdome and provide nutrition to it. Two separate pigment sheaths containing chromatophores separates one ommatidium from the other. The pigment sheath which is present around cone and cone cells is called iris sheath whereas the pigment sheath present around rhabdome and retinular cells is known as retinal sheath. Pigment sheaths are able to contract and expand depending upon the intensity of light.

The complete image which is produced by the compound eye is made up several pieces of small images as each ommatidia produces a separate image of a part of the object. Hence, the vision produced by the compound eye is known as mosaic vision. During bright light, both pigment sheaths expand completely, separating ommatidia from each other. This results in the formation of a separate image of a part of the object by each ommatidum. These images formed in bright light are sharp images, known as apposition images. This kind of vision is known as mosaic vision. During dim light, both pigment sheaths contracts, ommatidia coordinate together to form a single blurred image, known as superposition image. This kind of vision is known as superposition image.

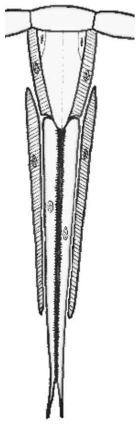

Fig. 3.58 *Ommatidium of Insect*

b) Ocelli: Simple Eyes

Two types of "simple eyes" are seen in the class Insecta: dorsal ocelli and lateral ocelli (=stemmata). Although, both types of ocelli are similar in structure, they are believed to have separate phylogenetic and embryological origins.

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1) Dorsal Ocelli

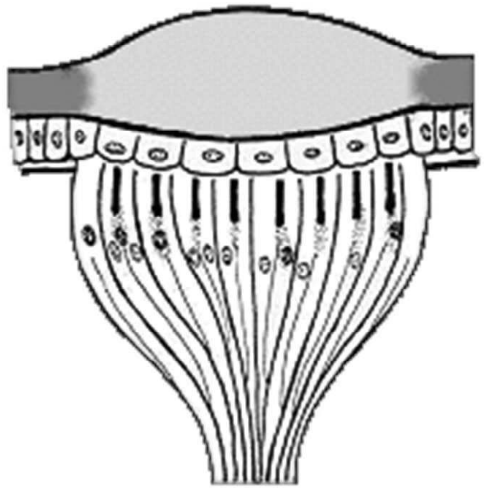

Fig. 3.59 *Dorsal Ocellus*

Dorsal ocelli are usually observed in adults as well as in the immature stages (nymphs) of many hemimetabolous insect species. Dorsal ocelli are not independent visual organs. They never occur in insect species that lack complex compound eyes. Dorsal ocelli appear as two or three small, convex swellings on the dorsal or facial regions of the head. Dorsal ocellus contains only a single corneal lens covering an array of numerous rhabdom-like sensory rods. These ocelli do not participate in image formation, however, they are sensitive to a wide range of wavelengths, react to the polarization of light, as well as respond quickly to changes in the intensity of light.

2) Lateral Ocelli

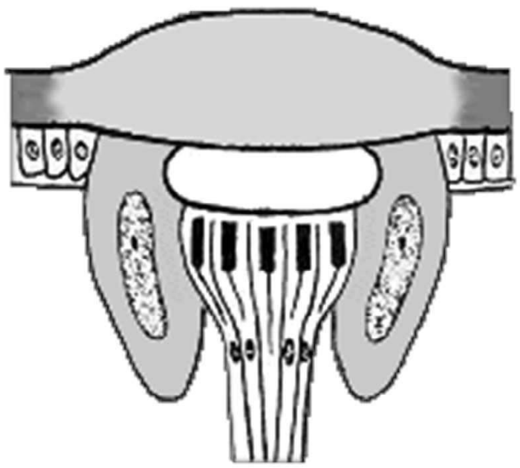

Fig. 3.60 *Lateral Ocellus*

Lateral ocelli (=stemmata) are the only visual organs present in holometabolous larvae as well as certain adults belonging to the order- Collembola, Zygentoma, Siphonaptera, and Strepsiptera. They are present laterally on the head, and their number vary from one to six on each side. Structurally, lateral ocelli resembles dorsal ocelli, however, they have a crystalline cone located under the cornea and fewer sensory rods. Larval stages use these simple eyes to detect the intensity of light and also to detect outlines of objects located nearby. These ocelli can even track the movements of predators or prey.

III. In Mollusca (Cephalopoda)

The nervous system of molluscs is present at the ventral side and in ancient molluscs, remains of a metamerous (segmented) division of the nervous system can be recognised. The mollusc nervous system is commonly called as tetraneural nervous system, due to the presence of four main neural strands: Two pairs of connectives link the cerebral ganglia to the pedal ganglia on the ventral side; another to the visceral ganglia and parietal ganglia passing the pleural ganglia on the dorsal side. The nervous system is asymmetrical due to torsion of visceral mass. The components of nervous system are as follows:

1. **Ganglia:** These are aggregations of nerve cells.
   - **a) Cerebral Ganglia**: They are triangular in shape and are located on the dorsal-lateral side of buccal mass.
   - **b) Buccal Ganglia**: A pair of triangular shaped buccal ganglia are located in the floor of the buccal cavity
   - **c) Pleuro-Pedal Ganglia**: A pair of large ganglionic masses located on ventro-lateral sides of the buccal mass
   - **d) Supra-Intestinal Ganglion**: An unpaired ganglion, lying in a sinus behind the left Pleuro-pedal ganglia
   - **e) Visceral Ganglia**: A single ganglionic mass which lies in the posterior part of the visceral mass
2. **Commissures**: These are the nerves which connect two similar ganglia.
   - **a) Cerebral Commissure:** They connect two cerebral ganglia.
   - **b) Buccal Commissure:** They connect two buccal ganglia.
   - **c) Pedal Commissure:** They connect two pleuro-pedal ganglia.
3. **Connectives:** These are the nerves that connects two different ganglia. In *Pila*, following connectives are present:
   - a) Two cerebro-buccal connective
   - b) Two cerebro-pleural connective
   - c) Two cerebro-pedal connective
   - d) Pleuro-infra intestinal connective
   - e) Infra-intestinal visceral connective
   - f) Supra-intestinal visceral connective
   - g) Supra-intestinal-pleural connective
   - h) Zygoneury: It is present between the pleural part of the left pleuropedal ganglionic mass and supra-intestinal ganglion.
4. **Nerves to Different Part of Body**
   - **a) Cerebral Ganglion:** Sends nerves to snout, skin, tentacle, buccal mass, eye and statocyst

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b) **Buccal Ganglia:** Sends nerves to buccal mass, salivary glands, radular sac, oesophagus

c) **Pedal Ganglia:** Sends nerves to foot and statocyst

d) **Left pleural Ganglia:** Sends nerves to parietal wall, mantle, osphradium, left nuchal lobe, columella

e) **Right pleural Ganglia:** Sends nerves to copulatory organs, right nuchal lobe.

f) **Supra-Intestinal Ganglia:** Sends nerves to mantle, anterior part of the ctenidium

g) **Visceral Ganglia:** Sends nerves to renal organs, genital organs, stomach, intestine, pericardium and digestive gland

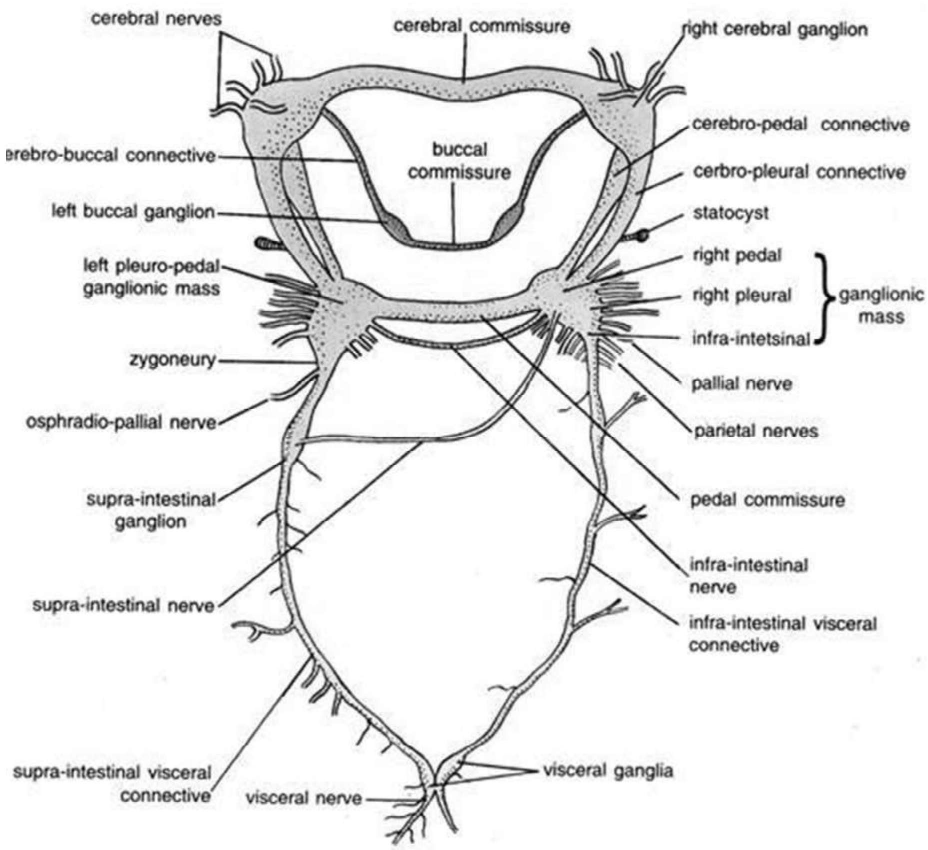

Fig. 3.61 *Nervous System in Pila (Mollusc)*

Further, the sense organs present in *Pila* are listed below:

A) Eye- Snail's head carries a pair of fleshy stalk or ommatophores, one on either side, behind the second pair of tentacles. Each ommatophore bear a pair of small, black and circular eye. The outer cornea of the eye is made of epidermis of the skin whereas inner cornea is made of the epithelium of the optic capsule. The lens of the eye is surrounded by sensory retinal cells and pigmented cells.

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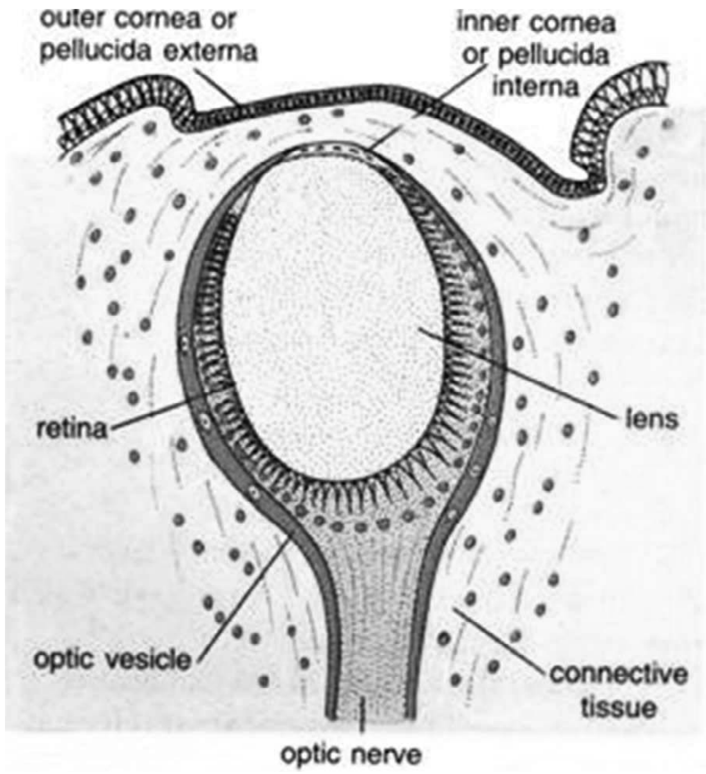

Fig. 3.62 *Section of the Eye of Pila*

B) Statocyst- It is a pair of small organs located one on either side attached to the pedal ganglion via band of connective tissues. Statocyst functions as organ of equilibrium.

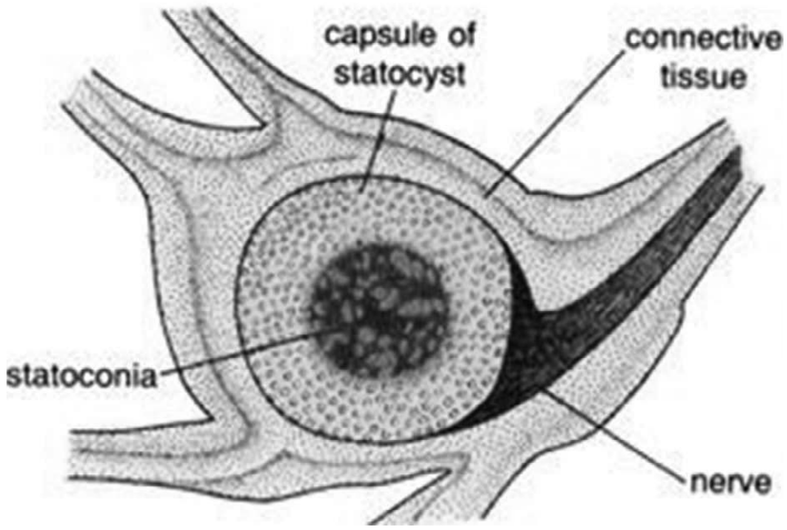

Fig. 3.63 *Statocyst of Pila*

C) Osphradium- It is a small, elongated, oval chemosensory structure located on the left side of the animal suspended from the roof of the mantle cavity close to the entrance through left nuchal lobe. It helps in detecting the chemical nature of water.

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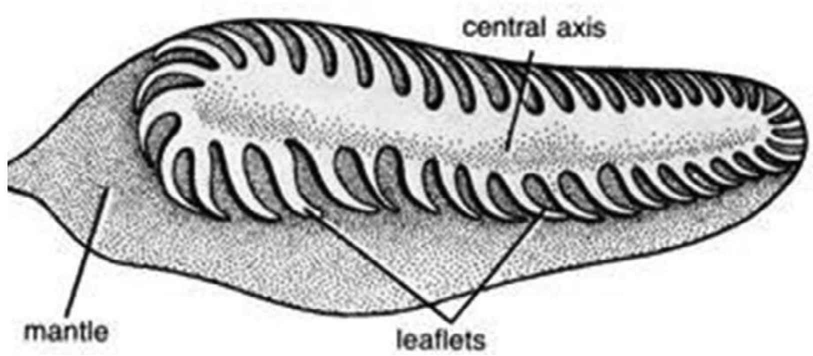

Fig. 3.64 *Osphradium in Pila*

D) **Tentacles-** Two pair of short, contractile tentacle are present anteriorly bordering the mouth. The first pair of tentacles are known as labial palps. Behind labial palps, a pair of long filamentous, highly contractile whip like second pair of tentacles are present.

E) **Mantle** – Mantle is also tactile in nature.

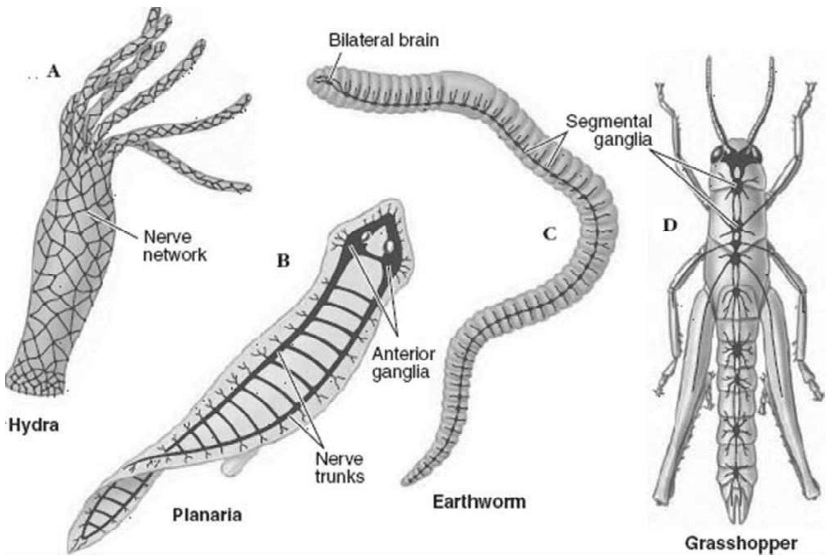

Fig. 3.65 *Figure Depicting the Invertebrate Nervous System. A) Nerve-Net Kind of Nervous System of Cnidaria; B) Linear Type Nervous System of Flatworm; C- Annelid Nervous System, Organized into a Bilobed Brain and Ventral Cord with Segmental Ganglia; D- Arthropod Nervous System with Large Ganglia and more Elaborate Sense Organs*

3.3.3 Trends in Neural Evolution

Invertebrates are often referred to as 'simple animals' with a small nervous systems comprising of fewer nerve cells as compared to the tiniest vertebrates. Regardless of the above fact, these animals can live in highly organized colonies, can resolve the basic survival issues, and can receive and comprehend complex messages. A nervous system is as an organized collection of neurons that interact at points of contact known as synapses. Synapses are functional junction where the membranes of two or more neurons come very close together. Neurons are electrically excitable cells whose membranes can generate and transmit signals in the form of changes in voltage. These small changes in voltage can be graded together or are all-or-none events of fixed amplitude known as action potentials.

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At electrical synapse, signals are passed directly to other cells whereas at chemical synapse, signals are converted into chemical signals that diffuse across a small synaptic gap present between the membranes of two interacting neurons. An invertebrate nervous system composed of: sensory neurons, which receives physical signals from the environment(e.g. light level or muscle force) and convert them into electrical signals; motor neurons, which transmit signals from central processing system to muscles or other effector organs (e.g. light-producing organs, glands); interneurons, which transmit information between sensory and motor neurons; and glia, which are electrically unexcitable cells that influence the transmission of signals between the neurons by altering the ionic environment surrounding them.

Thus, the ability of neurons to generate and transmit electrical signals, and for these signals to pass between different cells, be summed, multiplied and transformed by different types of cells and synapses, facilitate nervous systems to process huge information without much effort. Changes in the environmental conditions are detected by sensory structures, encoded in the activity of neurons, evaluated for significance against the background of earlier experience, transmitted via nervous system, and then used to drive suitable actions. The actions may be compensatory (e.g. postural) or active (e.g. producing a sound or generating locomotion). Some of these actions are concluded within fractions of a second, the only limitation being the speed of neuronal activity; whereas others may conclude over hours, days or even the lifetime of the animal. How are all these functions carried out in different invertebrates is matter of investigation. Before, we discuss the trends in neural evolution. Let us begin with discussing the major evolutionary trends in invertebrates. The major evolutionary trends in invertebrates is on the basis of features like:-

(a) **Cellular Organization**: It involves change from being diploblastic i.e., having two germ layers (ectoderm and endoderm) to triploblastic having three embryonic germ layers namely ectoderm, mesoderm and endoderm. It also involves the increase in organization and specialization of cells, i.e., from cellular level $\rightarrow$ tissues level $\rightarrow$ organs level $\rightarrow$ organ systems level of organization. Further, the symmetry of animals changes from radial to bilateral.

(b) **Cephalization:** In bilaterally symmetrical animals, all the sense organs as well as the feeding organs gets concentrated in the anterior end of the animals leading to the formation of a definite head. It also shows the evolution of concentrations of nerve cell $\rightarrow$ ganglia $\rightarrow$ brain, and increasing complexity of neural processing

(c) **Evolution of the Coelom**: It also involves the development of coelom (space between digestive tract and body wall, lined with mesoderm for better placement of internal organs). It evolves from acoelomate—pseudocoelomate—coelomate.

(d) **Evolution of Segmentation:** This is a division of the body into multiple segments. This trait increases flexibility. It permits a wider range of motion. All annelids and arthropods are segmented. Arthropods also evolved

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jointed appendages. Segmentation permits specialization of different segments

(e) **Evolution of the Exoskeleton:** The exoskeleton provides protection to the animal and is shed between developmental stages via a unique evolutionarily conserved process known as molting/ecdysis. Molting is triggered by steroid hormones, the ecdysteroids, and the regulation of their biosynthesis has long been proposed as a contributor to the success of arthropods during evolution.

Sponges lack a proper nervous system. Perhaps, this is the only phylum in the kingdom Animalia which lacks a defined nervous system. In the absence of nervous system, there is no coordinated movement of the while body. However, individual cells do respond to stimuli. For example, myocytes surrounding the osculum are contractile in nature, and regulate the water movement to outside. Only animals with at least tissue level of organization have true nervous system. In diploblastic and triploblastic invertebrates (other sponges), five general evolutionary trends in nervous system development are seen. The next section deals with these five trends in detail.

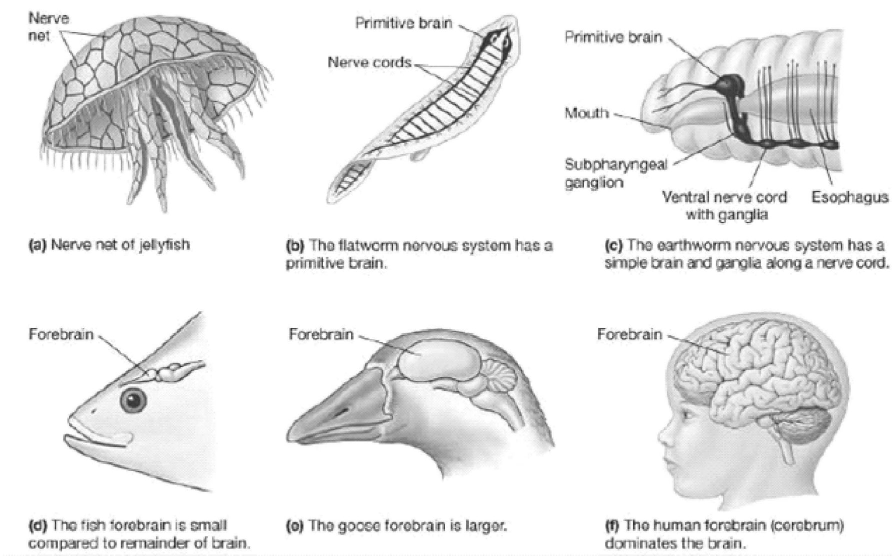

Fig. 3.66 *Evolution of Nervous System from Simple to Complex*

1. First Trend- Firstly, there is a nerve net with a bidirectional nerve impulse flow usually seen in simple radially/biradially (Symmetrical arrangement of body parts around a single main or central axis such that the organism can be divided into similar halves by any plane passing through the central axis) symmetrical animals, such as cnidarians as well as in phylum Ctenophora or a slightly complex nerve net with some degree of central coordination (sea star) as in seen in echinoderms, conduct nerve impulses from one area to other.

A) Nervous System of Cnidaria

Cnidarians are mostly marine animals lacking coelom, having radial symmetry, tissue level of organization and diploblastic body wall with outer ectoderm and inner endoderm. Cnidarians exist in two forms namely polyp (sessile form) and medusa (free-swimming form). Nervous system comprises one or more networks or nerve-cells and neurites are located both in the ectoderm as well as endoderm, however, a concentrated central nervous system is absent. Cnidarians possess a diffuse kind of nervous system as seen in polyp forms but in medusa nervous system is better developed owing to its free-swimming habit. In medusa form, nervous system gets concentrated to form a nerve ring and in connection with this well-defined sense organs are also formed. Medusa with manubrium hanging downward and tentacles swaying freely floats freely in water along with water currents. It can also swim actively by aid of powerful muscular contractions and also of velum. Medusa is carnivorous in nature and feeds on small planktons. It has sense organs in the form of eight marginal statocysts, situated at the bases of tentacles on the subumbrellar surface. These statocysts help the animal in orientation as well in maintaining equilibrium while swimming, i.e., presence of sense organs at the base of tentacles is highly advantageous to its free-swimming habit. The details of the nervous system in Coelenterates have already been provided in previous section.

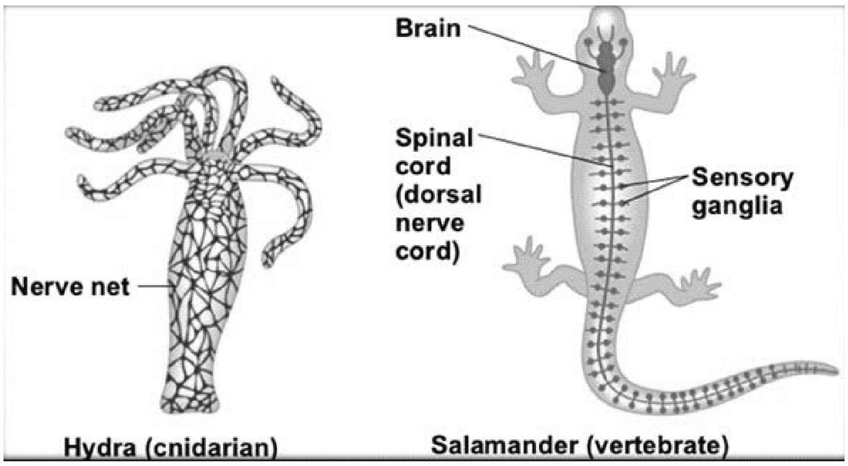

Fig. 3.67 *Comparison between Nervous System of Cnidaria and a Salamander*

B) Nervous System of Ctenophora

Ctenophores, commonly known as *comb jellies* or *sea walnuts* are exclusively marine animals lacking coelom, having biradial symmetry, tissue level of organization and diploblastic body wall with outer ectoderm and inner endoderm. The spherical body can be divided into two hemispheres with mouth at oral pole and sense organ at the aboral end. It also comprises a unique set of combplates and tentacles.

Eight equally spaced rows of paddle plates or comb plates are arranged on the sides of the body. These comb rows bear a series of short but strong ctenes or ciliary plates which propel the animal slowly through the water. Further, there are two tentacles located at the aboral end on opposite sides of the body. These long-solid tentacles with short lateral branches or pinnae emerge from deep ciliated epidermal blind pouch or tentacular sheath. They lack Nematocysts but possess peculiar adhesive cells called colloblasts or lasso cells which help in capturing food.

In Ctenophores, there is no localized nervous control centre as such. The epidermal nerve plexus is concentrated in a ring like fashion around the mouth and at the base of the comb rows where it forms the radial nerves. These nerves are not true nerves but the condensation of the nerve net. The nervous system organization controls muscular actions as well as determines the activity of cilia on the comb-rows. Further, the statocyst located at the aboral end serves as balancing organ useful in maintaining normal orientation of the animal in water. Although, being an aquatic phylum, Ctenophora consist of a lot of sense organs.

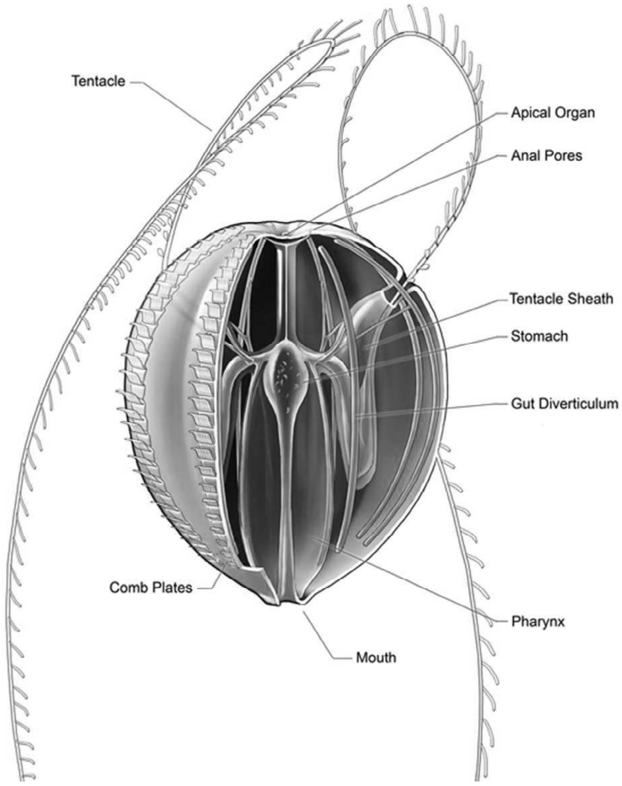

Fig. 3.68 *Sense Organs in a Ctenophore*

Aboral pole bears deep seated statocyst which is lined by tall, ciliated epithelial cells. Statocyst comprised of statolith (a tiny grain of calcium carbonate) supported on four bundles of cilia, referred to as balancers. It is protected by a roof like a dome or bell formed of fused cilia. The sensory organ serves as an organ of equilibrium.

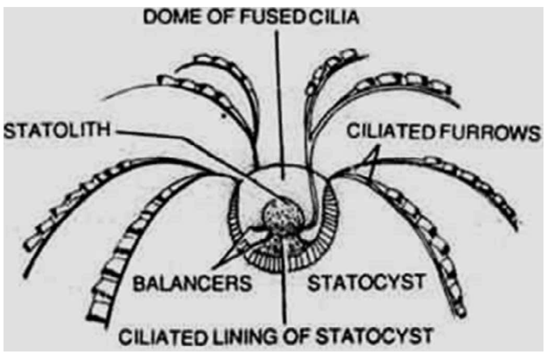

Fig. 3.69 *Aboral Sense Organs Seen in 'Pleurobrachia' (Ctenophora)*

Further, the animal is diploblastic with an outer epidermis and an inner gastrodermis separated by an intermediate thick layer of gelatinous mesogloea. The epidermis is syncytial and contains a lot of sensory cells, gland cells and pigment granules whereas Mesogloea contains amoebocytes, muscle fibres, connective tissue fibres and a few nerve cells.

C) Nervous System of Echinodermata

Echinoderms are exclusively marine animals with adults having radial symmetry but larval forms are bilateral symmetrical. Echinoderms are coelomate animals having organ-system level of organization and three germ layers namely-ectoderm, mesoderm and endoderm. The nervous system of Echinoderms is also primitive types like Cnidarians; however, it is slightly complex. Echinoderms lack a concentrated central brain like cnidarians but possesses a network of nerves called nerve plexus running intertwined under the surface of an Echinoderm's skin. In addition to this, the oesophagus is surrounded by one to several nerve rings, from which run radial nerves often in parallel with branches of the water-vascular system. Ring and radial nerves coordinate righting activity. Although, echinoderms are not known to have well developed sensory inputs, they are sensitive to stimuli like touch, light, temperature, orientation as well as the status of water around them. The tube feet, spines, pedicellariae, and skin respond to touch, and light-sensitive organs have been found in echinoids, holothurians, and asteroids.

D) Nervous System in Balanoglossus

Balanoglossus is vermiform, soft, cylindrical and bilaterally symmetrical animal. It measures around 10 to 50 cm in length. Body is uniformly covered with cilia and lack any exoskeleton. The colour of the animal varies from bright or drab with tint of orange or red. Balanoglossus is marine, tubicolous animal inhabiting shallow coastal as well as deeper water. Animal lives inside a U-shape burrow or tube with two vertical limbs. The burrow is 50-75 cm deep with two openings 10-30 cm apart. The body is divided into three major parts namely; Proboscis, Collar and Trunk. Balanoglossus coelom is enterocoelous in origin and is separated into three coelomic cavities namely: Proboscis coelom, collar coelom and trunk coelom. Adult coelom is represented five separate coelomic cavities: one coelomic cavity in proboscis, two in collar and other two in trunk region. The nervous system of Balanoglossus is of a very primitive type resembling that of coelenterates and echinoderms. Nervous system is of primitive types like that of non-chordates. Nervous system composed of two main nerve cords: mid-dorsal and mid-ventral which runs throughout the length of the trunk region. Circumcentric ring connects the ventral and dorsal nerve cord at the collar-trunk septum. Dorsal cord extends up to the base of proboscis region where it is connected to other circular strand called anterior nerve ring.

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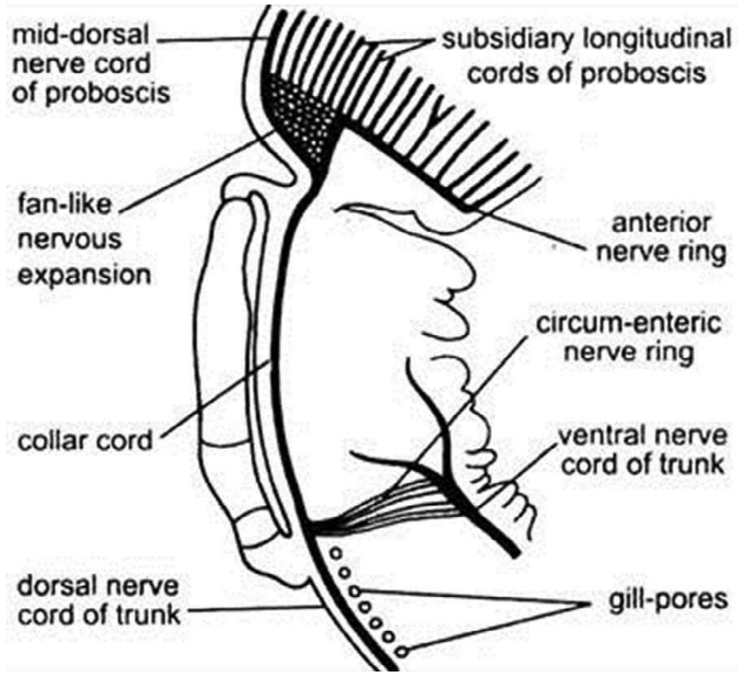

Fig. 3.70 Nerve Cords in the Anterior Region of the Body of Balanoglossus

Sense organs of balanoglossus are composed of:

a) **Neuro-Sensory Cells**: These cells are present in the proboscis as well as anterior region of collar and are highly responsive to stimuli such as touch and light.

b) **Preoral Ciliary Organ**: It is a chemoreceptor which is situated ventrally at the base of proboscis.

c) **Epidermis**: Epidermal layer of the body wall is composed of tall, ciliated and columnar cells. Three different kinds of gland cells secreting mucus are present namely: goblet gland cells, reticulate gland cells and granular gland cells. Epidermis also composed of neuro-sensory cells along the proboscis and anterior collar region.

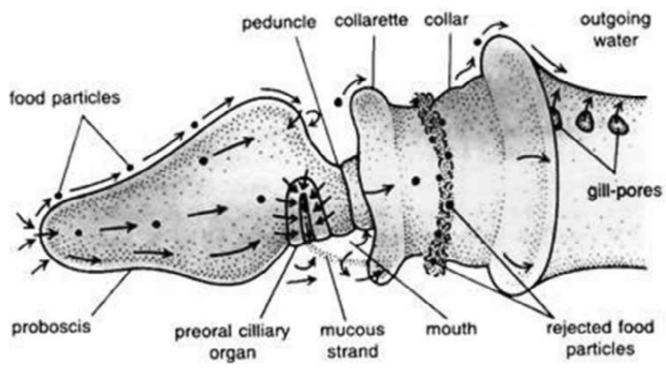

Fig. 3.71 Pre-Oral Sensory Structure in Balanoglossus

2. Second Trend- Secondly, in bilateral animals that move in a forward direction, there is tendency towards centralization i.e., concentration of all the receptors, sense organs and nervous tissue in the animal's anterior end, known as ganglia "brain" as seen in flatworms (Platyhelminthes)and roundworms (Nematodes).

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(Bilateral animals' moves in forward direction, hence, their sense organs are concentrated in the anterior body region that first encounters the new environmental stimuli).

a) Nervous System in Flatworms (Platyhelminthes)

Platyhelminthes are commonly known as flatworms due to their *dorso-ventrally* flattened body. Terrestrial, Fresh-water and marine-water can be the habitat of Platyhelminthes which are mostly endoparasites of animals and human beings. Platyhelminthes are acoelomate (lacking a body cavity) having bilateral symmetry, Organ level of organization and three germ layers namely-ectoderm, mesoderm and endoderm. Nervous system consists of a pair of cerebral ganglia situated on either side of oesophagus. The ganglia are connected via a cerebral ring around the oesophagus. From the nerve ganglia, nerves are given off to the head lobe as well as to the posterior part of the body. Three pairs of longitudinal nerve cords, i.e., dorsal, ventral and lateral extend to the posterior side and give out numerous fine peripheral branches to various organs. Sense organs are poorly developed in adult fluke due to its parasitic nature. However, sensory eye spots are present in larval stages as they lead a free-swimming life.

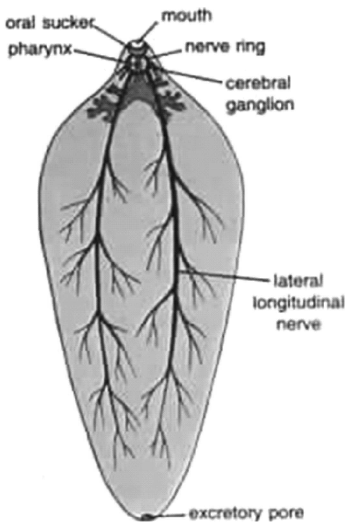

Fig. 3.72 *Nervous System of Fasciola hepatica*

b) Nervous System in Nematodes (Nematohelminthes)

In a cross-section, the body of aschelminths is circular and hence they are named as round worms. They may be terrestrial, aquatic, free-living or parasitic. Round worms are pseudocoelomate (false body cavity) having organ-system level of organization. They are bilaterally symmetrical. They are triploblastic animals having three germ layers namely ectoderm, mesoderm and endoderm. Nervous system of nematodes is made up of a nerve ring, which is made up of four ganglia, and nerve cords. Further, the ganglia connect to four peripheral nerves which run along the length of the body on the dorsal, ventral as well as the lateral surfaces. Longitudinal nerve trunks connect nerves in the oesophageal region to nerves in the anus region. The nerves lie within a cord of connective tissue, which lie under the cuticle and between muscle cells. The ventral nerve is the largest one, and has a double structure forward of the excretory pore. The dorsal nerve is accountable for motor control, whereas the lateral nerves are sensory in nature, and the ventral

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combines both functions. The nervous system of nematodes is ciliated, i.e., it contains cilia, which are all nonmotile and with a sensory function.

At the anterior end of the nematode, the nerves branch out from a dense, circular nerve ring present around the pharynx, and serving as the brain of animal. Smaller nerves run in forward direction from the ring to supply the sensory organs of the head region. Further, the body of animal (nematode) is covered with several sensory bristles as well as papillae that together provide a sense of touch. Behind the sensory bristles, on the head region lie two small pits known as amphids. Amphids are well supplied with nerve cells and are chemoreceptive in nature i.e., they probably act as chemoreception organs. Further, pigmented eye spots are often seen in few aquatic nematodes, even though their sensory nature is still uncertain.

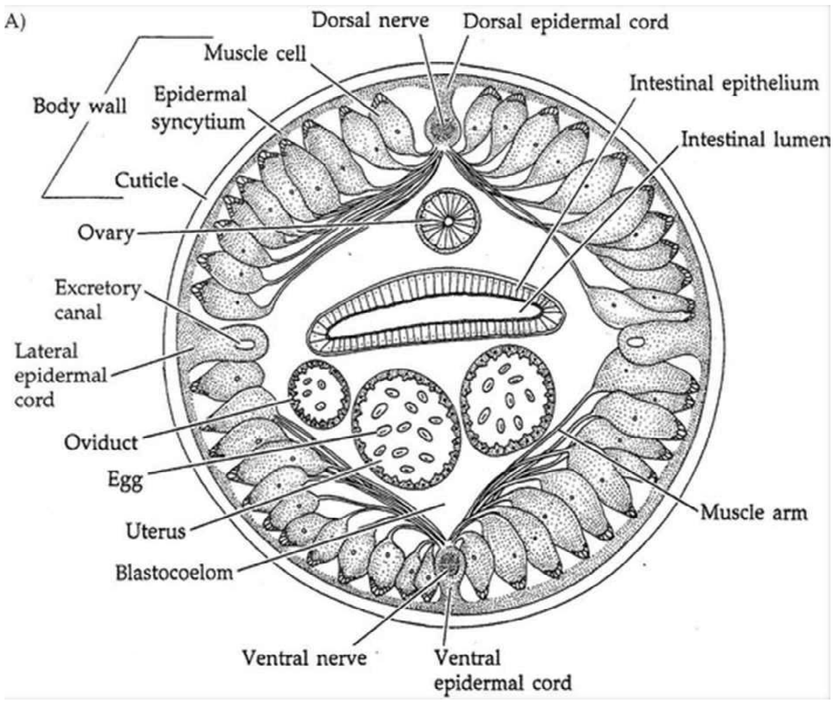

Fig. 3.73 *Cross-Section of Intestinal Region of a Nematode*

c) Nervous System in Rotifera

The rotifers, most common inhabitants of freshwaters also live-in brackish water and a few in the ocean or on land in damp sites. Various lifestyles include creeping, swimming, pelagic and sessile types, as well as carnivores and bacteria feeders. Rotifers are generally solitary. Some of the sessile species form spherical swimming colonies in which the individuals have no organic continuity. Rotifers are also called wheel animalcules. They are minute animals ranging from 0.04 to 2 mm in length. The rotifer body is divisible into the broad or narrowed or lobed anterior end usually having a ciliary apparatus, an elongated trunk, and the tail or foot.The body is covered with yellowish cuticle ringed throughout or in certain regions. The cuticle may be thickened on the trunk to form the lorica, a hard encasement, of one to several plates that may be variously ornamented.

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The nervous system consists of a bilobed rounded, triangular or quadrangular brain or cerebral ganglia lying dorsal to the mastax, some sensory and motor nerves, some additional ganglionic masses and 2 main ventral nerve cords. From the various sense organs of the head, the eyes, the sensory bristles and pits on apical field, the rostrum and the dorsal antenna, a number of paired sensory nerves extend to the brain which sends motor nerves to the anterior parts of the various muscles, as the dorsal, lateral and central retractors and to the salivary glands. The ganglionated cords that is main ventral nerves, spring from the sides of the brain and proceed backward in latero-ventral position into the foot. They bear an anterior ganglion near the brain and a geniculate ganglion farther posteriorly. The ventral cords terminate posteriorly in ganglia serving the urinary bladder and foot. These ganglia may be fused in one mass, the cardiovascular ganglion.

In rotifers, sensory cells and sense organs occur abundantly on the anterior end in the form of sensory membranelles, styles, ciliated pits, sensory papillae, etc. The sensory membranelles or styles are single stiff bristles situated near the inner edge of the circumapical band and named from their position as dorsolateral, lateral and ventrolateral styles. Similar apical styles occur on the apical field. Oral styles may be present near the mouth. These styles seem to be tactile organs and each is underlined by one or two sensory nerve cells from which fibres go to brain. Paired ciliated pits are chemo-receptors occurring on the apical field. Conical or finger-like palps tipped with sensory hairs or without hairs are present on the apical field. Ocelli, seen as red pigment spots, are of common occurrence. A single, less often paired, cerebral eye is embedded in the dorsal and ventral surface of the brain. Cerebral and apical or cerebral and lateral eyes may be present simultaneously. The dorsal antenna or tentacle is a movable papillae or finger-like projection provided at its tip with one or more tufts of sensory hairs.

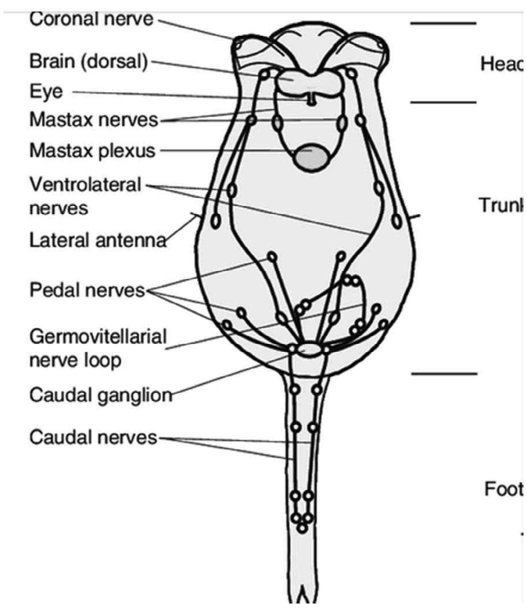

Fig. 3.74 *Nervous System of Rotifer*

3. Third Trend- The third trend in the evolution of nervous system in invertebrates overlaps with the evolution of bilateral symmetry (Symmetrical arrangement of body parts along a central axis such that the organism can be divided into two equal halves.). There is development of paired neurons, paired sensory structure, muscles, and brain centres, which enables synchronized ambulatory movements, such as climbing, crawling, flying and walking.

4. Fourth Trend- The fourth evolutionary trend is seen in metamerically segmented worms (annelids), arthropods (crustaceans, arthropods) in which axons join into nerve cords, and in addition to a small, centralized brain, smaller peripheral ganglia help coordinate outlying regions of the animal's body. The more complex an animal, the more interneurons it has. Interneurons in ganglia integrate impulses (to effectors), so the more interneurons in an animal, more are the behaviour patterns.

a) Nervous System of Annelids

The formation of nervous system begins with the flatworms. Flatworms possess a rudimentary brain composed of a cluster of nerve cell bodies concentrated in the head, or cephalic region. Two large nerves known as nerve cords radiates out from the primitive brain and form a nerve network that innervates distal regions of the flatworm body. On the contrary, in advance non-chordates, like segmented annelids clusters of cell bodies are not limited to the cephalic region, but also occur in fused pairs, called ganglia (singular ganglion) along a nerve cord. As each segment of the annelids, comprises a ganglion, simple reflexes can be integrated within a segment without any input from the cephalic region. Such reflexes that do not require any input from the cephalic/brain region also occur in higher animals and are referred to as spinal reflexes in humans as well as other vertebrates.

Annelids and higher invertebrates have complex reflexes controlled through neural networks. These nerve cell bodies clustered as ganglions into brains continue through the more advanced phyla and become more complicated. Cephalization is defined as the evolutionary trend toward nervous system centralization and the development of a head and brain.

Cephalized organisms display bilateral symmetry. Sense organs or tissues are concentrated on or near the head, which is at the front of the animal as it moves forward and it is the part of the body that first contacts the environment as the animal moves. As the brain evolved, sense organs like eyes for vision and chemoreceptors for smell and taste got concentrated on or near the head region. In the higher arthropods, like insects, specific regions of the brain are associated with particular functions.

More complex regions of the brain are associated with complex behaviours, like the ability of social insects (ants and bees) to organize themselves into colonies, divide labour, or to communicate with one another. The octopus (a cephalopod mollusc) has the most sophisticated brain development among the invertebrates, as well as the most sophisticated behaviour seen in the forebrain region.

b) Nervous System in Crustacens

Crustaceans possess an advanced nervous system. The nervous system of crustaceans is divided into three parts name central nervous system, peripheral nervous system and autonomous nervous system. Central nervous system runs from anterior to posterior end and contains brain or supra-oesophageal ganglia, circum-oesophageal commissures, Ventral thoracic ganglionic mass, and ventral nerve cord. Central nervous system sends off nerves to all parts of the body. These nerves constitute the peripheral nervous system.

A peripheral nerves constitute of two different types of fibres namely—motor and sensory fibres. All motor fibres carries message from central nervous system to different parts of body, whereas, sensory fibres sends messages from body to central nervous system. The peripheral nervous system consist of Optic nerve: innervating the retinal layer of eye; Antennular nerve: innervating the statocyst and structures present in the first antenna; antennary nerve: innervating various parts within second antenna including green gland; cephalothoracic nerves: originate from thoracic ganglionic mass to supply different muscles and appendages in that region; abdominal nerves: innervating muscles and appendages.

Additionally, stellate ganglion sends nerves to telson, rectum and other adjoining structures. Autonomic nervous system comprises a few minute ganglia and slender nerves which are positioned over the cardiac stomach to supply involuntary parts of the body. Apart from this, crustaceans possess a lot of sense organs like compound eye, statocyst, tactile setae etc.

c) Nervous System in Insects

Like most other arthropods, insects possess a relatively simple central nervous system (CNS). CNS comprises a dorsal brain linked to a ventral nerve cord. Ventral nerve cord is comprised of paired segmental ganglia running along the ventral midline of the thorax and abdomen. Within each segment, ganglia are connected via commissure. Further, they are joined by intersegmental connectives to ganglia in adjacent body segments. Thus, in general, the central nervous system appears ladder-like. Commissures acts as the rungs of the ladder whereas intersegmental connectives serve as the rails. In more "advanced" insect orders, there is a tendency for individual ganglia to combine (both laterally and longitudinally) into larger ganglia that serve multiple body segments. An insect's brain is a complex structure comprising six fused ganglia (three pairs) located dorsally within the head capsule.

Protocerebrum: Protocerebrum represents the first pair of ganglia. They are largely concerned with vision. Deutocerebrum: Deutocerebrum represents the second pair of ganglia. They are majorly concerned with processing of sensory information collected by the antennae. Tritocerebrum: Tritocerebrum represents the third pair of ganglia. It innervate the labrum as well as integrate sensory inputs from both proto- and deutocerebrums. Further, they connect the brain with the rest of the ventral nerve cord as well as the stomodaeal nervous system. Stomodaeal nervous system is associated with controlling the internal organs. The commissure for the tritocerebrum loops around the digestive system, suggesting that these ganglia were originally located behind the mouth and migrated forward (around the esophagus) during evolution. Further, the insect nervous system comprises several sense organs namely mechanoreceptors, auditory receptors, chemoreceptors, thermoreceptors and photoreceptors.

d) Nervous System in Mollusca

The nervous system of molluscs, is fundamentally different from vertebrate nervous systems. Molluscs, with the exception of the most highly developed cephalopods, have no brain in the strict sense of the word. However, the cell bodies (pericarya) of nerve cells are concentrated in nerve knots (ganglia) in important parts of the body. Mollusc nerve cells lack myelin sheath. Hence, saltatory conduction is absent. In its place, in the highly developed cephalopods, like squids, giant axons have developed, whose large diameters make a faster transport of impulses possible. Fundamentally, the nervous system of molluscs can be derived from a rope-ladder like nervous system of metamerically segmented worms (*Annelida*). This points out that molluscs and annelids at least had a common ancestor.

5. Fifth Trend- The fifth trend is a consequence of the increasing number of interneurons. The brain contains the largest number of neurons, and the more complex the animal, and the more complicated its behaviour, the more neurons are concentrated in the brain and the bilaterally organized ganglia. Vertebrate brains are an excellent example of this trend.

Nervous System in Vertebrates

The major function of the nervous system is control and coordination i.e. this part of an animal's body coordinates its behaviour and transmits signals between different body areas. In vertebrates, nervous system is divided as follows.

a) CNS- (Central Nervous System): The CNS contains the brain and spinal cord.

b) PNS- (Peripheral Nervous System): The PNS consists mostly of nerves, which are elongated fibres that connect the CNS to every other part of the animal's body. It also includes other components like peripheral ganglia, sympathetic and parasympathetic ganglia, and the enteric nervous system, a semi-independent part of the nervous system whose major function is to control the gastrointestinal system.

Neuron is the structural and functional unit of the nervous system i.e. at the cellular level, the nervous system is defined by the presence of a special type of cell, known as the neuron, also called as a "nerve cell". Neurons helps in transmitting signals rapidly and precisely to other cells in the form of electrochemical waves traveling along thin fibers known as axons, which ultimately cause chemicals known as neurotransmitters to be released at junctions to other neurons. These functional junction present between the two neurons are called as synapses. The cell that receives a synaptic signal from a neuron (a postsynaptic neuron) may get excited, inhibited, or otherwise modulated depending upon the kind of neurotransmitter/ chemical released at the synapse. The connections between neurons form neural circuits that can generate very complex patterns of dynamical activity. The nervous system is also composed of other specialized cells called as glial cells (or simply glia), which provide structural and metabolic support to the neurons.

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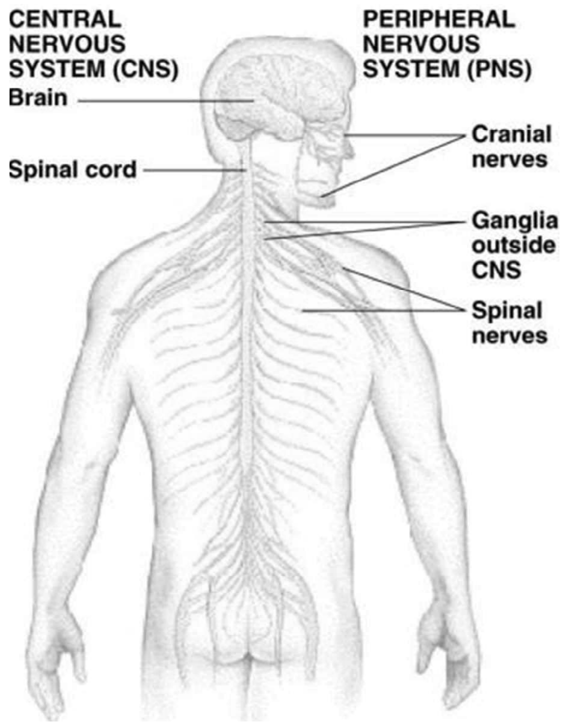

Fig. 3.75 *CNS and PNS of a Vertebrate (Human Being)*

Thus, to conclude, various metazoan phyla reveal a progressive increase in complexity of nervous systems that probably reflects in a general way the stages in evolution of nervous systems.

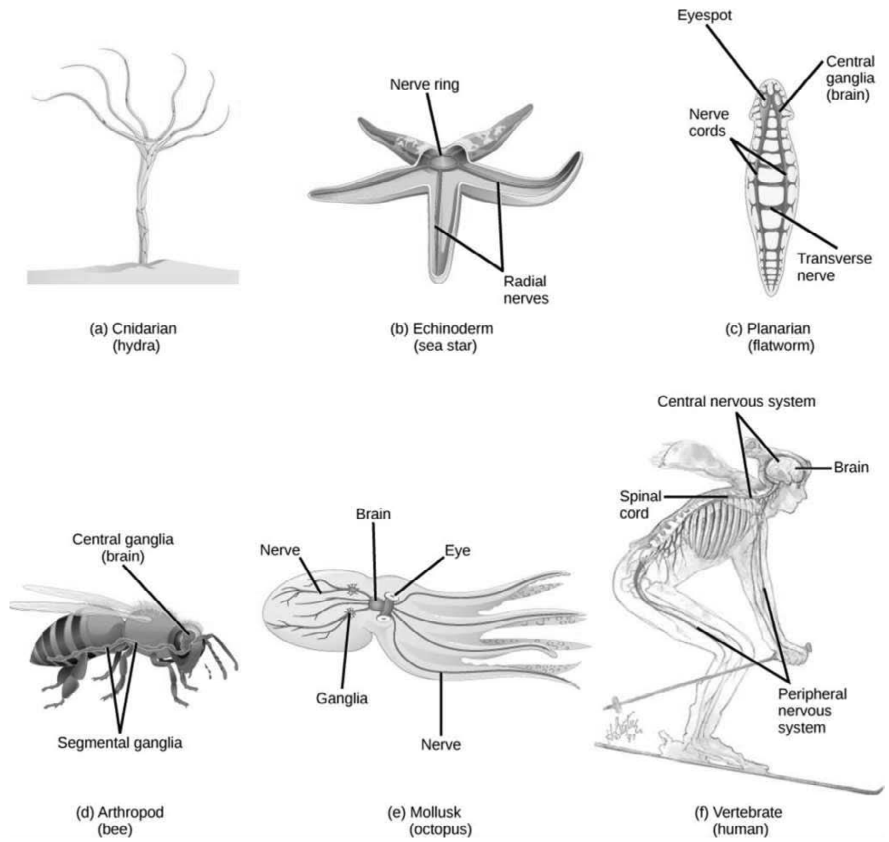

Fig. 3.76 *Complexity of Nervous System across Different Phyla*

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Check Your Progress

7. What do you understand by nervous system?
8. Define protoneurous condition.
9. What do you mean by neurons?
10. Define synapses.

3.4 ANSWERS TO 'CHECK YOUR PROGRESS'

1. Excretion is defined as the elimination of the metabolic wastes from the body, usually in aqueous solution. Metabolism produces a number of by-products.
2. Excretory system is a vital system in invertebrates as well as vertebrates that aids in eliminating nitrogenous waste from the body.
3. A contractile vacuole (CV) previously known as pulsatile or pulsating vacuole (PV) is a sub-cellular structure or organelle which is primarily involved in the process of osmoregulation.
4. Diastole is the phase when contractile vacuole enlarges to maximum size.
5. Systole is the phase when the vacuole contracts to expel its contents. In sarcodina, the systole occurs by sudden burst but in others, the vacuole empties into a reservoir.
6. An excretory tubule which opens to the outside through the nephridiopore and the inner end of the tubule is blind in the protonephridium or opens in the coelom through the ciliated funnel or called nephrostome in metanephridium is called nephridium.
7. A nervous system is as an organized collection of neurons that interact at points of contact known as synapses.
8. Protoneurous condition is the simplest modified form and more or less like the hypothetical nervous system.
9. Neurons are electrically excitable cells whose membranes can generate and transmit signals in the form of changes in voltage.
10. Synapses are the functional junction where the membranes of two or more neurons come very close together.

3.5 SUMMARY

- Invertebrates are often referred to as 'simple animals' with small nervous systems comprising of fewer nerve cells as compared to the tiniest vertebrates.
- In unicellular organisms the process of excretion occurs through diffusion. Simple diffusion occurs when a substance moves from a region of higher concentration to a region of lower concentration.

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- In some invertebrates, contractile vacuoles help in the process of excretion. In some coelenterates like the hydra, and certain sponges, waste material diffuse into the surrounding environment through the epidermal cells.
- A contractile vacuole (CV) previously known as pulsatile or pulsating vacuole (PV) is a sub-cellular structure or organelle which is primarily involved in the process of osmoregulation.
- The contractile vacuoles are found in majority of freshwater protozoans (Flagellata, Sarcodina and Ciliata) and some marine ciliates.
- The simplest form of contractile vacuoles is found in sarcodina like amoeba.
- In sarcodina, the position of contractile value could be anywhere in the endoplasm. However, it is found near the anterior end at the side of reservoir. They are two in number in paramecium, each on the either end of the body.
- Different group of protozoans have different number of vacuoles, but same species have same number of vacuoles.
- Contractile vacuoles osmoregulate by removing excess water from the body. It's also believed to be excretory in function.
- Excretory system is a vital system in invertebrates as well as vertebrates that aids in eliminating nitrogenous waste from the body.
- In general, the excretory system is made up of paired lobes, called nephridia, which are metamerically segmented and the inner aperture of the nephridium is present in the coelom.
- In vertebrates, the primary excretory organ used for eliminating nitrogenous waste is kidney.
- Embryonic nephridia are temporary structures which start to disappear as soon as permanent nephridia start developing.
- The Embryonic Trunk Nephridia (ETN) are present only in those forms whose permanent nephridia do not develop at all.
- Micronephric type of nephridia is present in pheretima whereas the nephridia of lumbricus, chaetogaster and nereis are of meganephric type.
- In most annelids, both blood vascular system and coelom (if present) are deliberately involved in the excretion of waste products from the body.
- In annelids possessing protonephridia, the ultrafiltration of the coelomic fluid takes place with the help of solenocytes present at its terminal end and the filtrate fluid thus obtained passes down through the protonephridial tubule.
- A nervous system is as an organized collection of neurons that interact at points of contact known as synapses.
- An invertebrate's nervous system is composed of sensory neurons, which receive physical signals from the environment.
- Changes in the environmental conditions are detected by sensory structures, encoded in the activity of neurons, evaluated for significance against the background of earlier experience, transmitted via nervous system, and then used to drive suitable actions.

- The nervous system helps the body to respond to external stimuli or in other words is essential to our interaction with the outside world, and its development made it possible to integrate senses and movements in a precise and faster way.
- Cnidarians possess a primitive diffused kind of nervous system. The nervous system is a primitive nerve net.

3.6 KEY TERMS

- **Excretion:** Excretion is defined as the elimination of the metabolic wastes from the body, usually in aqueous solution. Metabolism produces a number of by-products.
- **Contractile Vacuole:** A contractile vacuole (CV) previously known as pulsatile or pulsating vacuole (PV) is a sub-cellular structure or organelle which is primarily involved in the process of osmoregulation.
- **Excretory System:** Excretory system is a vital system in invertebrates as well as vertebrates that aids in eliminating nitrogenous waste from the body.
- **Embryonic Nephridia:** Embryonic nephridia are temporary structures which start to disappear as soon as permanent nephridia start developing.
- **Diastole:** It is the phase when contractile vacuole enlarges to maximum size.
- **Systole:** It is the phase when the vacuole contracts to expel its contents. In sarcodina, the systole occurs by sudden burst but in others, the vacuole empties into a reservoir.
- **Nephridium:** An excretory tubule which opens to the outside through the nephridiopore and the inner end of the tubule is blind in the protonephridium or opens in the coelom through the ciliated funnel or called nephrostome in metanephridium.
- **Nervous System:** A nervous system is as an organized collection of neurons that interact at points of contact known as synapses.
- **Protoneurous Condition:** Protoneurous condition is the simplest modified form and more or less like the hypothetical nervous system.
- **Neurons:** Neurons are electrically excitable cells whose membranes can generate and transmit signals in the form of changes in voltage.
- **Synapses**: Synapses are the functional junction where the membranes of two or more neurons come very close together.

3.7 SELF-ASSESSMENT QUESTIONS AND EXERCISES

Short-Answer Questions

1. How is contractile vacuole formed?

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2. Define the filtration theory of osmoregulations.
3. Where are Embryonic Trunk Nephridia found?
4. What do you understand by permanent nephridia?
5. Mention the types of nephridia.
6. Define nephromyxia.
7. What do you understand by ciliated organs?
8. What is the ventral nerve cord.
9. What do you understand by terminal ganglionic mass?
10. Define the peripheral nervous system.

Long-Answer Questions

1. Explain the process of osmoregulation in protozoans in detail.
2. Describe the process of excretion in annelida.
3. Differentiate between coelomoduct and nephromyxia.
4. Explain the physiology of nephridium.
5. Describe the various components of the nervous system in annelids.
6. Explain the comparatives of nervous system in molluscs.
7. Describe the nervous system of cephalopoda.

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NOTES

UNIT 4 INVERTEBRATE LARVAE AND MINOR PHYLA GENERAL CHARACTERS

Structure

4.0 INTRODUCTION

The invertebrates comprise about 90 percent of the total number of animals inhabiting the surface of earth. The invertebrates are so vast and heterogeneous that every group has certain structural and functional peculiarities and a distinct classification system.

However, the life of invertebrates is as complex, appealing and informative as that of the vertebrates. Without thorough information regarding invertebrates, it is impossible to know the intricacies of life on earth. Currently, there are 30 known invertebrate phyla which are defined by a unity of basic structural pattern, i.e., though the members in each phylum may differ in external features; the anatomical characteristics have developed similarly in several respects.

A larva is a distinct juvenile form many animals undergo before metamorphosis into adults. Animals with indirect development such as insects, amphibians, or cnidarians typically have a larval phase of their life cycle. In some species the larva is free-living and the adult is an attached or nonmobile form; in others the larva is aquatic and the adult lives on land. In forms with nonmobile adults, the mobile larva increases the geographic distribution of the species.

Larvae appear in a variety of forms. Many invertebrates (e.g., cnidarians) have a simple ciliated larva called a planula. Flukes have several larval stages, and annelids, mollusks, and crustaceans have various larval forms. The larval forms of the various insects are called caterpillars, grubs, maggots, and nymphs. Echinoderms (e.g., starfish) also have larval forms.

4.1 OBJECTIVES

After going through this unit, you will be able to:

- Understand the larval forms of invertebrates
- Explain various strategies and significance of larval form of invertebrate larvae
- Differentiate between the larval forms of free living invertebrates and parasites
- Understand the concept and significance of minor phyla
- Explain the differences between coelomates and non-coelomates

4.2 LARVAL FORMS OF FREE LIVING INVERTEBRATES

Parasitic invertebrates are much less advanced or complex when compared to free –living organism. However, over a period of time they have adapted well to fit a lifestyle where they do not have to get their own food or look for their habitat. Instead, they rely completely on a host to provide them with the necessary nutrients as well as safe & secure habitat. Thus, a parasite and a free-living organism are quite different from each other when it comes to successful survival. A parasitic organism lives inside the body of its host, and hence does not require the complex structures and organs of a free-living organism like sense organs, elaborate digestive or nervous system etc.

A free-living organism can be carnivorous or a scavenger, feeding on tiny aquatic organisms and decomposing matter and organisms. Thus, for free-living organism, these complex structures are essential to survive in the outside world as compared to parasites. On the other hand, parasites stay safely inside their host and feed off of their host, meaning they primarily consume blood, tissue fluids, pieces of cells and pre-digested food from the host, hence, they do not require structures like eyes or statocysts as there is no need for detecting light to search for food or look for direction.

Free-living worms ingest their food through their pharynx (a tube-like structure that extends from the middle of their body on the ventral side) and the food is digested in the gastrovascular cavity. For parasitic organism, they don't even have elaborate or complete digestive systems as they absorb the pre-digested food or nutrients via their skin. A few parasitic organisms have a pharynx as well but the food is pumped into a dead-end digestive tract and the waste is excreted through cellular diffusion. For free-living organisms, these structures are a lot more significant as they are independent creatures and need to look for the food in their surroundings. Further, they require sense organs to detect the changes happening in their surroundings. The table below list the major difference between parasite and free-living organism:

Table 4.1 *Major Difference between Parasite and Free Living Organism*

	Parasite	Free-living organism
Body structure	Long tube-shaped body having suckers and hooks at the anterior end that helps the parasite for attaching to host's body.	Short, flattened body with sensory organs concentrated at the anterior end
Eyes	Usually lacks eyes as there is no need for detecting light to search for food or look for direction	Has well developed eyes or eye spots as they are independent creatures and need to look for the food in their surroundings. They also need to navigate their way
Nervous system	Lacks nervous system as they need not to respond to external stimuli or surroundings. They stay in safe and secure habitat.	Nervous system is highly developed. Sense organs are concentrated at the anterior end. Cephalization is also seen prominently.
Digestive system	Parasites stay safely inside their host and feed off of their host, meaning they primarily consume blood, tissue fluids, pieces of cells and pre-digested food from the host. For parasitic organism, they don't even have elaborate or complete digestive systems as they absorb the pre-digested food or nutrients via their skin.	Free-living worms ingest their food through their pharynx (a tube-like structure that extends from the middle of their body on the ventral side) and the food is digested in the gastrovascular cavity.

In the following section, we shall discuss the larval forms of free-living invertebrates.

1) Larval Forms of Porifera

Members are commonly known as sponges. They are mostly marine; few are freshwater forms. Mostly are asymmetrical animals, i.e., having no definite shape of the body. These are primitive multicellular animals with cellular grade of organization. Adult sponges are sessile as they require a substratum to fasten themselves to a surface. Sponges are filter feeders. Digestion is intracellular. Body of sponges is supported by a skeleton made of calcareous spicules, siliceous spicules or spongin fibres. They are hermaphrodites where eggs and sperms are produced by the same individual. Poriferans can reproduce both asexually as well as sexually. Asexual reproduction occurs via fragmentation. The process of asexual reproduction occurs via budding. A cylindrical bud arises at the base of the animal and develops the osculum at the free end. Fully grown bud may remain attached to the parent body or can get detached to form a new Poriferan by attaching to the substratum. Sexual reproduction occurs via formation of gametes. Fertilization is internal. Development is indirect having a larval stage which is morphologically distinct from the adult. In the following discussion, we shall discuss about the larval forms of two poriferans, i.e, sycon and leucosolenia.

A. Larval Forms of Sycon

Sycon is monoecious, however animal shows cross fertilization due to protgyny (a condition where female reproductive parts matures faster as compared to male reproductive parts). Archeocytes differentiate to form two different types of sex cells, i.e., sperm and ova found in mesenchyme.

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B. Larval Forms of Leucosolenia

Leucosolenia reproduces both asexually and sexually. Leucosolenia reproduces asexually by the method of budding. In budding, leucosolenia gives out new horizontal buds/branches which grow over rocks or other substrata. These newly formed buds or branches give rise to erect vase-shaped individuals later on. When the upright branches attain sufficient size their tops break through as oscula. Sexual reproduction in leucosolenia takes place by the formation of gametes, i.e., ova and sperms. Leucosolenia is hermaphrodite, as both the gametes are formed inside the body of same individual, even though the primary gonads are altogether absent. Thus, the gametes are formed by the differentiation of amoebocyte cells. Cross-fertilisation is usually observed and is internal. The sperms are drawn in the body of *Leucosolenia* with the water current which fertilize the ova.

Zygote formed by the fusion of ova & sperm undergoes equal and holoblastic cleavage to form an oval hollow blastula, known as coeloblastula. The coeloblastula is composed of narrow flagellated cells except at the posterior pole, where a group of rounded non-flagellated cells are present. These cells together with adjacent flagellated cells (which lose their flagella later on) moves into the interior and fill it with a mass of cells. The resulting larva is, known, as stereogastrula or parenchymula.

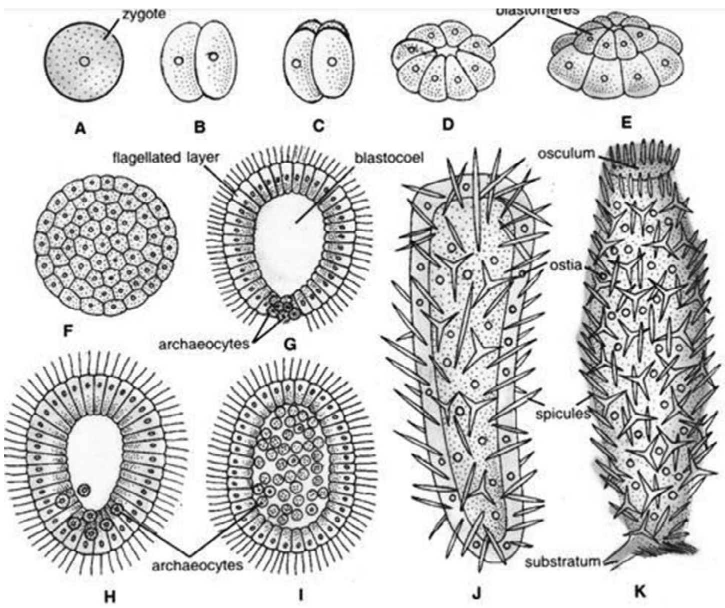

Fig. 4.1 *Stages of Development in Leucosolenia. A- Zygote; B to E- Cleaving Stages; F- Early Blastula; G and H- Coeloblastula; I- Parenchymula; J- Young Sponge; K- Adult Sponge*

The parenchymula larval stage of leucosolenia swims freely for few hours. Subsequently, it attaches to the substratum via its anterior pole and then develops into a flat plate with an irregular outline. The amoeboid cells (interior cells) migrate to the external surface and form the epidermis (pinacoderm) and mesenchyme.

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The enclosed flagellated cells become the choanocytes. A central spongocoel appears, an osculum breaks through, and spicules are secreted. Consequently, after few days, the larva is converted into the adult sponge.

2) Larval Forms of Coelenterates

They are mostly marine animals. They are sessile or free-swimming. They exhibit tissue level of organization. Body wall is diploblastic having outer ectoderm and inner endoderm. They are radially symmetrical. They have a central gastro-vascular cavity with a single opening known as hypostome surrounded by numerous tentacles, single opening serves as both the mouth and anus for animal. Cnidarians exhibit two basic body forms called as *polyp* and *medusa*. Polyp is a sessile form which is cylindrical in shape like the Hydra, Adamsia etc. Medusae form is free-swimming, umbrella shaped form like Aurelia or jelly-fish. Cnidarian's exhibit metagenesis or alteration of generation where Polyps produce medusae asexually and medusae form the polyps sexually. Life History of Obelia comprises both asexual (sedentary hydroid colonies) and sexual generations (medusa phase) that regularly alternate with each other to complete the life cycle. Sedentary hydroid colony reproduces by asexual budding to produce hydranths and blastostyles. Male and female medusae are also produced by budding from blastostyle. They are free swimming sexual forms carrying gonads which release both spems and ova in water. Sperm and ova liberated by male and female medusa respectively in sea water fuses together to form zygote. Parents medusa generally dies off soon after liberating the gametes. Zygote undergoes equal holoblastic cleavage to form a solid ball of cells known as morula. Morula undergoes further cleavage to form a hollow ball of cells known as blastula which encloses a cavity, i.e., blastocoel. Further, cells of blastula (blastomeres) undergoes morphogenetic movements to form a solid gastrula, i.e., stereogastrula. The outer layer of stereogastrula is known as ectoderm whereas the inner layer as endoderm.

A) **Planula Larva:** The ectodermal cells of the elongated gastrula acquire cilia resulting in a fee swimming ciliated planula larva. The endoderm splits to form a cavity referred to as enteron. Thus, bilayered planula larva has a ciliated ectoderm and an inner non-ciliated endoderm.

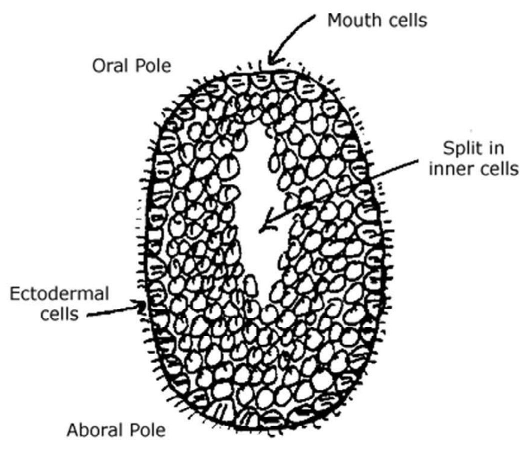

Fig. 4.2 *Planula Larva of Obelia*

B) Hydrula: After briefly swimming, planula larva settles down, and attaches to the substratum via its broader anterior end to undergo metamorphosis. The proximal end of the larva forms a basal disc for attachment whereas its distal end develops the manubrium with mouth surrounded by tentacles. The newly transformed larva resembles a polyp and is now referred to as hydrula. Hydrula undergoes asexual reproduction to form branched obelia colony.

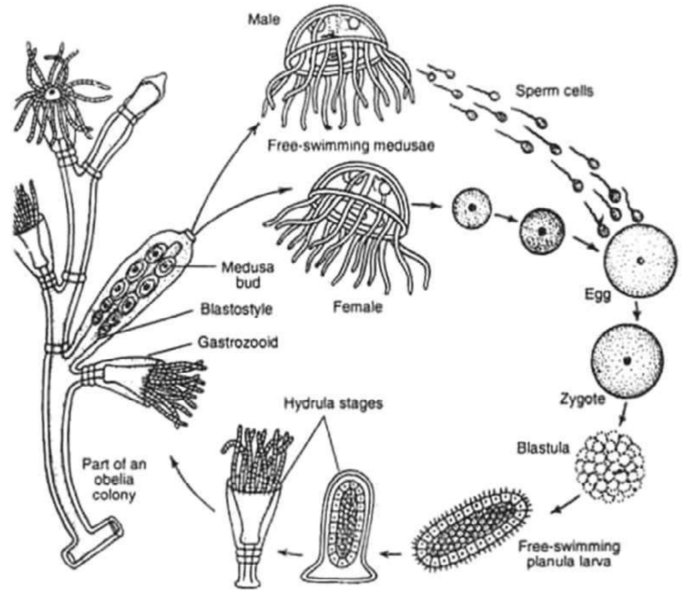

Fig. 4.3 *Larval Stages of Obelia*

Alternation of generation refers to the phenomenon where asexual diploid phase alternates with sexual haploid phase in the life history of organism. This condition is mostly seen in plants like ferns and mosses. In Cnidarians, alternation of asexual polypoid phase with sexual medusoid phase has given rise to the idea of alternation of generation, also called as metagenesis in them. This kind of alternation is not considered as true alternation of generation due to following reason:

(a) Sexual medusiod phase is derived from blastostyle (diploid) by asexual reproduction (budding). Hence, both male and female medusae which represent the sexual phase are diploid.

(b) Gametes do not originate in medusa but they migrate into the gonads from epidermis of blastostyle.

The above-mentioned facts show that medusa phase does not represent true sexual generation of the cnidarians. It represents a free-swimming form which helps in the dispersal of colonies.

C) Ephyra Larva: Ephyra are the larval forms of jellyfish that can inhabit the planktonic range. Ephyra break off of the scyphistoma (a stalk fixed to a hard substrate that produces larval jellyfish through budding) and become free-swimming organisms that eventually grow into adult jellyfish. The ephyra are part of the life cycle of the class Scyphozoa which are characterized by the general cup-shape of their bell, 4 part symmetry, lack a defined pharynx, and lack a tissue self (velum or velarium). Scyphozoa live in marine habitats as free-swimming organisms and feed on food particles to fish or other jellyfish depending on the size of the scyphozoan. They have no digestive tract so food and waste passes through the same opening. Food is caught on the tentacles and oral arms by stinging cells called nematocysts. Some species of cyphozoan are solitary in their life while others travel as large groups known as a smack.

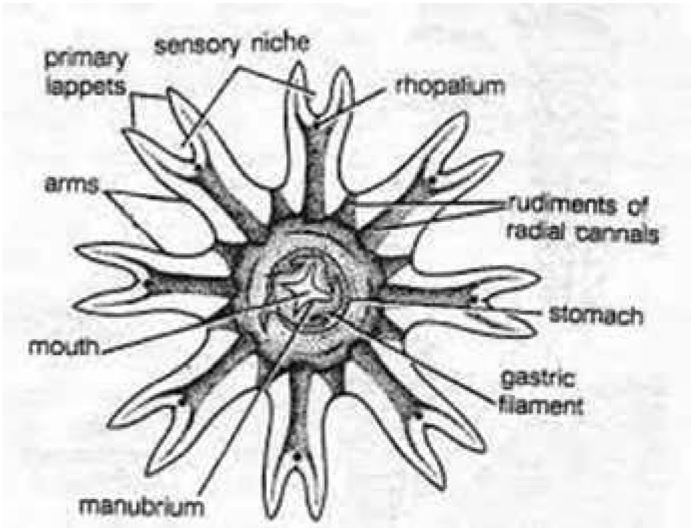

Fig. 4.4 *Ephyra Larva*

3) Larval Forms of Ctenophora

The term "Ctenophora" was coined by Eschscholtz in 1829 for a group of marine planktonic animals commonly known as "Sea walnuts" or "Comb jellies" due to the presence of locomotory comb-like plates on the body (Ctenos – comb, phoroa – bearing). To date, 80 species have been described under the phylum Ctenophora. There is no fixed shape and it varies greatly among different members of Ctenophores like Pleurobrachia is somewhat spherical in shape. The size ranges from few millimeters to 20 cms. The genera belonging to the Phylum ctenophore are usually transparent with tentacles and combplates are tinged with orange, white or purple. The animals are Biradially symmetrical and the structures are arranged tetramerously in a radial fashion around the oral-aboral axis. The spherical body can be divided into two hemispheres with mouth at oral pole and sense organ at the abora l end. It also comprises a unique set of combplates and tentacles. Eight equally spaced rows of paddle plates or comb plates are arranged on the sides of the body. These comb rows bear a series of short but strong ctenes or ciliary plates which propel the animal slowly through the water. There are two tentacles located at the aboral end on opposite sides of the body. These long-solid tentacles with short lateral branches or pinnae emerge from deep ciliated epidermal blind pouch or tentacular sheath. They lack Nematocysts but possess peculiar adhesive cells called colloblasts or lasso cells which help in capturing food.

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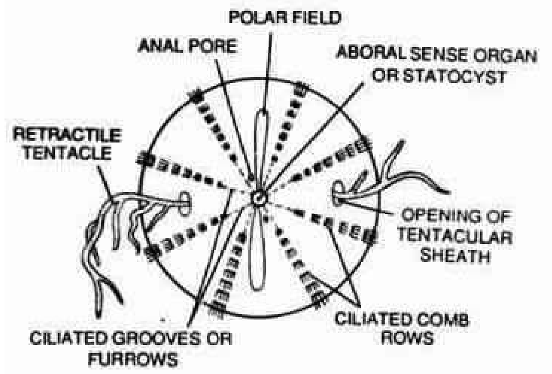

Fig. 4.5 *Aboral View of Pleurobrachia*

Almost, all the species belonging to Phylum 'Ctenophora' are hermaphrodites. Gonads develop from endoderm in the form of bands in the meridional canals of the gastrovascular system. Generally fertilization is external. During the early embryonic development cleavage is total, determinate and unique in ctenophores. Usually free-swimming characteristic 'cydippid larva' occurs which undergoes gradual metamorphosis. Cydippid larva is ovoid or spherical in shape with a pair of retractable tentacles. They are free swimming larvae, which swim with the help of cilia. Some ctenophores exhibit a strange phenomenon called '*dissogeny*' in which both the larva and adult reproduce sexually. There is no alternation of generation seen in ctenophores.

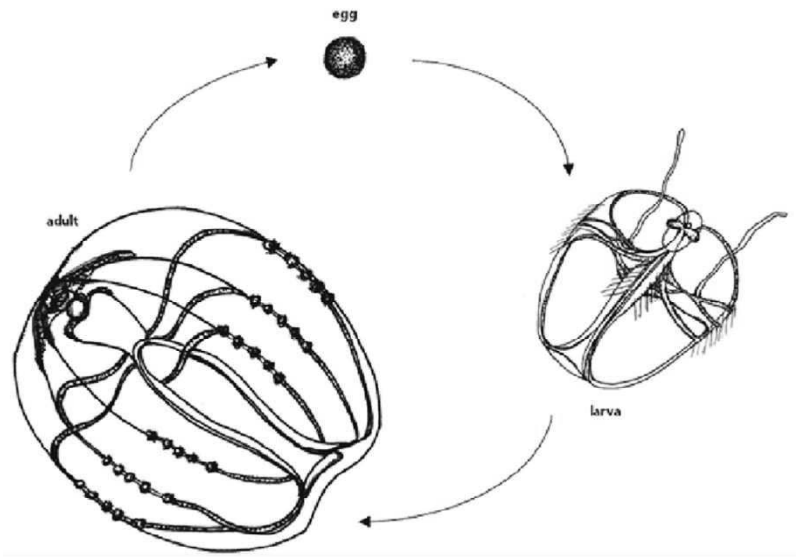

Fig. 4.6 *Life cycle of a Ctenophore. Egg— Free Swimming Larval Stage—Adult*

4) Larval Forms of Mollusca

Molluscs represents the second largest phylum. Molluscs can be terrestrial or inhabit freshwater or marine water. They exhibit organ-system level of organization and are bilaterally symmetrical. They are triploblastic i.e., having three germ layers namely-ectoderm, mesoderm and endoderm. The body cavity is a true coelom. The body is protected by a calcareous shell and lacks segmentation. The body is divided into- a distinct head, muscular foot and visceral hump. Mouth of the molluscs encloses a tongue-like organ called radula having several rows of teeth and helps in scraping food. A fold of soft and spongy layer of skin surrounding the body organs is known as mantle. The space between the hump and the mantle is referred to as the *mantle cavity*. Feather like gills which perform respiratory and excretory functions are present inside the mantle cavity. Anterior head region has sensory tentacles. The life history of several organism passes through different larval stages which are morphologically and ecologically distinct from the adult. Larvae of any animal serves two functional purposes:

a) To look for new sites or location to settle down, this helps the progeny to propagate

b) To look for new sources of nutritious rich food

Earlier molluscan larva is a trocophore larva having tuft of cilia at the anterior end followed by a ciliary band in the middle. Loven, a Swedish naturalist, was the first man who discovered trochophore larva in 1840. The larva was earlier known as Loven's larva. In 1859, Semper used the name Trochosphaera whereas it was Ray Lankester who gave the name 'Trochophore' to this larval form in 1877. In 1879, Hatschek also supported this name for the larval form. Hyman (1957) and Barnes (1980) tried to reveal evolutionary significance of the larva by establishing relationship of trochophore with other groups of animals. The Generalized structure of the Trochophore Larva is as follows:

- Trochophore is a marine, planktonic (as it feeds on planktons and other small microscopic organism) and lecithotrophic (a larval form which derives nutrition from yolky eggs and does not take any external nutrition) larval form.
- Larva exhibits bilateral symmetry.
- The anterior end of the larva is much broader than its posterior end.
- Larva has a mouth, gut and anus. Mouth leads into sac like stomach followed by a narrow alimentary canal. The whole of the digestive tube from mouth to anus is lined cilia.
- Two significant ciliary bands are present. A third band might be present or absent in certain forms of trochophore.
- Prototroch (pre-oral ciliary band) encircle the body around mouth and it lies above mouth. Prototroch arises from a set of specialized cells known as trochoblast.
- Metatroch (ciliary transverse ring) lies behind the mouth.
- Telotroch, another ciliary band is present around the anal region.
- In some forms, neurotroch, is present along the mid-ventral part of the body.
- The major function of the ciliary bands is to perform locomotion and feeding.
- Metamerism is absent in the larval form.
- Larva has a pair of protonephridia which are made up of hollow cells, certain amount of mesenchyme and larval muscles.
- Apical end bears numerous long cilia which emerge from the apical plate and is called apical tuft of cilia.

- Sense organs like sensory eye spots (ocelli) are present below the apical plate.
- Trochophore larva is divided into three regions namely- pretrochal region which includes region above the prototroch, posterior region which includes telotroch and anal area and middle region (growth zone) between the mouth and telotroch.

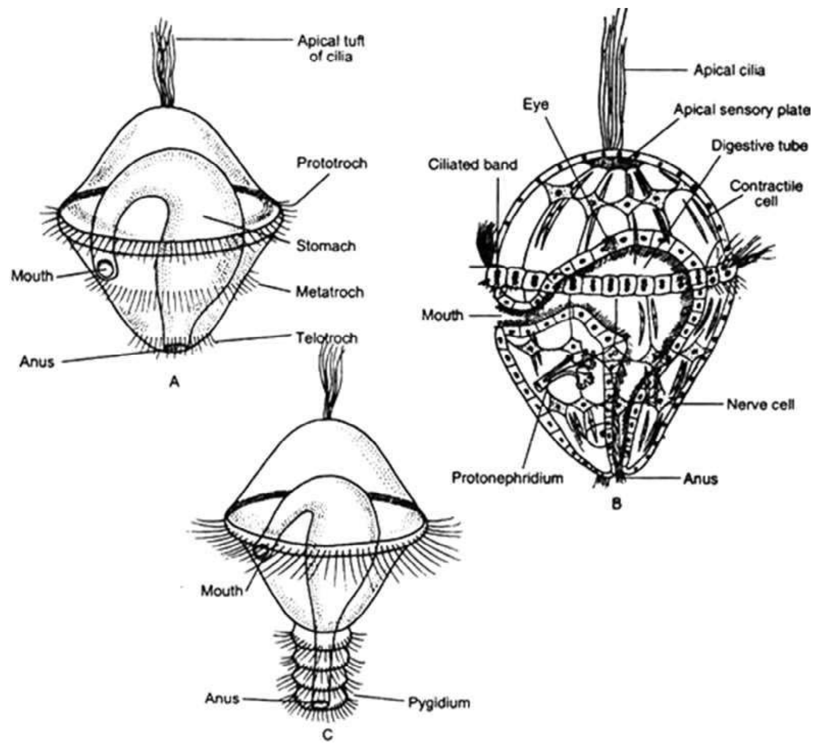

Fig. 4.7 *Trocophore Larva*

- The ciliary band gives rise to the girdle of larval tentacles. The cilia that borders the pre-oral lobe of Actinotrocha rep-resents the metatroch and prototroch of Trochophore respectively. Both have a similar dispo-sition of the telotroch.
- The apical plate of Trochophore (sometimes bearing eyes) is represented be a thickening of the ectoderm of the preoral lobe in Actinotrocha.
- Presence of a pair of solenocytic nephridia in both
- The alimentary canal is similarly placed and has similar divisions in both the larval forms.

The evolutionary significance of the Trochophore larva is further strengthened by the affinity it shows with different invertebrate groups as discussed above. Due to this, embryologists like Hatscheck suggested a theory popularly known as trochophore theory in 1878. This theory states that animal groups have descended from a common hypothetical ancestor called trochozoon having trochophore-like features. Trochophore larva theory primarily accounts for a common ancestor of the coelomate prostomia, however, some biologists believe that this resemblance is purely coincidental as a result of adaptive radiation and not due to any evolutionary significance. At the same time, this theory does not hold any significant ground for acoelomate groups.

There are three different types of molluscan larva on the basis of pelagic phase and amount of food consumed:

a) Planktotrophic Larva with Long Larval Life

These larvae are found in tropical, sub-tropical areas and have a shelf life of two to three months as seen in lamillibranchs and prosobranchs. Such larvae are ciliary feeders and the large velar cilia collects food particles present on to a tract at the base of velum leading to mouth.

b) Planktotrophic Larva with Short Swimming Life

These larvae have an average shelf life of a week as seen in nudibranch larva, *Gibbula cineraria, Hydrobia ulva, Turitella communis* and *Bela trevelyana*. Due to their short life span, these larvae do not feed and hence the primary function is dispersal. Further, such larvae are highly adaptable to unfavourable environmental conditions.

c) Yolk Larvae

Such larvae don't require any food as they hatch from yolky eggs, thus forming yolky larvae. They swim for a short period and are then carried passively in the plankton. Such larvae are normally observed in amphineura, scaphopoda and lamellibranchia. In chiton, yolk larvae are modified trocophore with a broad ciliary ring. These larvae spend 6 hours to few days in the plankton. In yoldia, yolk larva form a large barrel shaped ciliated test which is thrown off as the larvae settles down.

5) Larval Forms of Crustacea

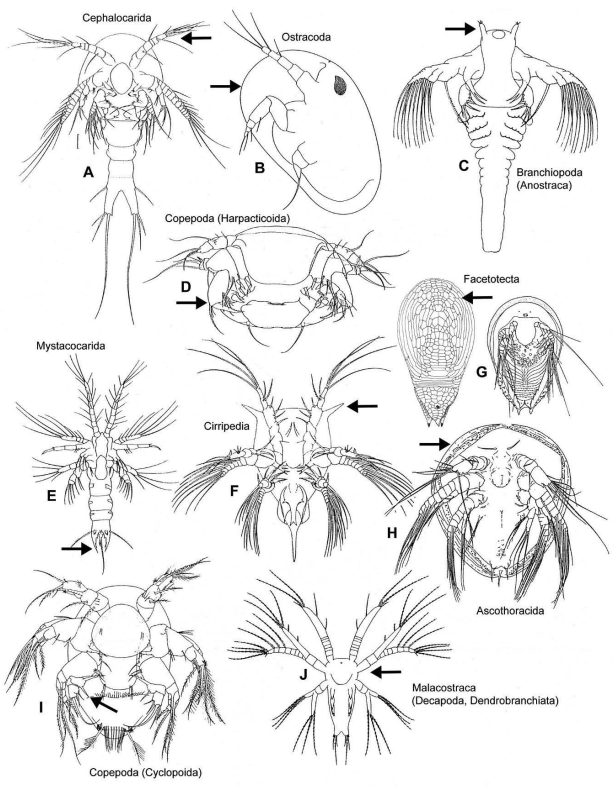

Fig. 4. 8 *Various Crustacean Larvae*

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Crustaceans are Arthropods whose body is protected with a chitinous exoskeleton covering. This exoskeleton is hard and in order to grow into adult while passing through different larval stages, crustaceans undergo moulting or ecdysis. Every moult result in larval form which is entirely different from the previous one. Hence, Crustaceans go through various stages of larvae before becoming an adult. The different larval stages are as follows:

a) Nauplius Larva

This larva is the first fundamental stage in all the crustaceans and was discovered by Muller in the 18^{th} century. This larval stage may passes inside the egg or it may hatch from the egg as seen in branchiopoda and copepoda. The larva has an unsegmented oval body with a large cephalothorax and a rudimentary abdomen. It possesses three pairs of appendages namely: antennules, antenna and mandibles. Antenna and mandibles are biramous and are used for swimming in water. A single median eye is present. They digestive system is well developed for feeding and digesting planktons.

b) Metanauplius Larva

The nauplius larva transforms into metanauplius in some Branchiopods like Apus. It is slightly larger than the nauplius and possesses cephalothorax, abdomen and a caudal furca. It retains the median eye. Antenna is large, biramous and used for locomotion while antennule is uniramous. Reduced mandibles are used for chewing. Apart from this, it also has two pairs of maxillae and maxillipedes each which serve for feeding purpose.

c) Protozoea Larva

This larva hatches from the eggs of marine prawns and lobsters. It has a large cephalothorax and an elongated unsegmented abdomen with a caudal fork and a pair of small uropods. Antenna is biramous whereas antenuule is uniramous. Single median eye is present. Mandibles are small and functions as masticator. Two pairs of maxillipedes are present which helps in gathering food. Three pairs of thoracic limbs occur as buds. Cephalothorax is present and is covered by a carapace.

d) Zoea Larva

It is the most common larva found in decapods hence it has a lot of variants in different species. it possess large cephalothorax which is protected by helmet-shaped carapace. The carapace also sports spines and it protruded into a rostrum in front. One pair of compound eyes is present. Short antennule and antenna are sensory in function. First and second maxillipedes are large and biramous. These are used for swimming. Non-functional thoracic appendages are present in the form of buds. Abdomen has six segments with a caudal furca at the tip along with a telson. Appendages are not present on the abdomen. In some Malacostraca, zoea transforms to metazoea which develop abdominal appendages for performing swimming action.

e) Mysis Larva

Zoea transforms into mysis larva in shrimps and some lobsters. It resembles mysis and has a cylindrical, elongated body with a cephalothorax and an abdomen with 6 segments. Carapace is protruded into a pointed rostrum in the front. Antennule and antenna are sensory in nature. Six pairs of biramous thoracic appendages are present which are used for locomotion. In addition to this, six pairs of abdominal appendages are present for swimming, out of these; the last one is modified as uropod. A pointed telson is present at the tip of the abdomen.

f) Schizopoda Larva

This larva is found in some crustacean decapods, such as homarus, nephrops. It is similar to megalopa and mysis larva in general features. It has a cylindrical body. Pleopods are present on the abdomen. These are biramous and are used for swimming. Cephalothorax also possesses biramous appendages.

g) Phyllosoma Larva

In spiny lobsters, egg hatches to form phyllosoma larva. The body of the larva is divided into head, thorax and abdomen. It has a pair of compound eyes present on a stalk. Apart from this, a pair of antennules and a pair of antenna act as sensory organs. The body is transparent and flattened dorsoventrally. There are 3 maxillipedes. First one is rudimentary, second is uniramous and the third one is large, biramous and is used for swimming. The small abdomen is segmented and lack appendages. Three long paired thoracic appendages are used for swimming as their tips are oar like (flattened).

h) Megalopa Larva

In crabs, zoea is transformed into megalopa larva. It has a large cephalothorax and small abdomen with small pleopods. An extremely small telson is also present. A pair of stalked eyes is present along with antennule and antenna which are small and sensory in function. The first pair of thoracic legs are similar to that of adult i.e. large and chelate. The other four pairs of thoracic legs are long, thin and helps in crawling movements. Glaucothea is the other name of megalopa larva of hermit crab as it is slightly different. Abdomen has pleopods. Hook like telson is present at the end of the abdomen.

i) Alima Larva

The zoea larva of some lobsters such as in squilla is called Alima larva because of its slightly different appearance. It has a large cephalothorax covered with carapace. Abdomen is segmented and bears paired pleopods and a telson. The carapace has spines and rostrum in the front. Reduced thoracic limbs are present. The antennules and antenna are uniramous and are sensory in nature. The second maxillipedes are prehensile and helps in capturing food. Though, the larva is pelagic in nature but it has transparent body which makes it invisible to the predators.

j) Cypris Larva

Nauplius larva transforms into cypris larva in subclasses Ostracoda and Cirripedia. A bivalve shell secured by an adductor muscle covers the body of the larva. One pair of compound eyes is observed. The large antennule is modified to attach to substratum with cement gland. No second antenna is seen. 6 pairs of biramous thoracic appendages are present and help in swimming. A caudal furca is present at the tip of the abdomen.

k) Kentrogen Larva

In sacculina, kentrogen larva is formed when cypris larva attaches to the host crab via its antennule and shed its bivalve shell and appendages. Body is elongated, sac-like with mass of undifferentiated cells and a chitinous tube like dart inside the body. Appendages are absent.

l) Erichthus and Erichthoidina Larvae

They are found in stomatopods of malacostraca such as squilla. They have elongated cylindrical body. Abdomen is segmented. Cephalothorax is covered with large carapace which points into a rostrum. 2 uniramous antennae are present and both are sensory in nature. Compound eyes are present on a stalk. In both the larvae, the anterior three thoracic limbs are rudimentary while the posterior limbs are well adapted for swimming. Pleopods are tiny and hardly functional. Maxillipedes are prehensile in erichthus and are used to capture food.

m) Calyptopsis Larva

It is the larval stage seen in euphasia. It resembles erichthoidina in general appearance but does not sport a rostrum on the anterior end of the carapace. Abdomen is limbless and segmented. Antennae are well developed, the first one being uniramous and the second one being biramous. 4-5 pairs of biramous thoracic legs are present for swimming. The carapace is highly prominent.

n) Epicardian Larva

This larva is found in parasitic isopods like bopyrus. The larva has an oval shaped body which has 6 pairs of hook like thoracic limbs to attach to the host. 6 pairs of biramous pleopods helps in swimming. First thoracic pair of appendage is prehensile. 2 uniramous antennae are present which are sensory in function. One pair of mandibles is modified to become sharp and pierce through the host. The larva is found in gill chambers of fishes and prawns.

o) Cryptoniscus Larva

This is second stage larva of bopyrus that is found in the gill chambers of prawns and lobsters. Body is oval and elongated. 6 pairs of thoracic appendages are modified to cling to the host. Single pair of pleopods is present for swimming. First pair of antenna is not found whereas the second is long and uniramous. Piercing and sucking type of mouth parts are present.

According the biogenetic law proposed by Haeckel, ontogeny recapitulates phylogeny. In other words, it means that, the successive stages of individual development correspond with successive ancestors in the line of evolutionary descent. Nauplius larva comes about in the development of all the crustaceans either inside the egg or as the first larval stage and so it was considered as the ancestral form of crustaceans. The old idea of recapitulations stands significantly modified now-a-days and the crustacean larval forms are now considered to be the larval reversions of simpler crustacean ancestors.

The larval forms are helpful for looking out homologies and the affinities among diverse groups. The animals which pass through similar stages are closely related. Larvae are helpful in extensive distribution of species and also in maintaining the food reserves of eggs to a minimum.

6) Larval Forms of Echinodermata

Echinoderms are exclusively marine. The endoskeleton of echinoderms comprises calcareous ossicles, and hence the name Echinodermata (spiny bodied). Echinoderms are Triploblastic, i.e., having three germ layers namely-ectoderm, mesoderm and endoderm. They are coelomate animals having organ-system level of organization. Adults of phylum Echinodermata are radially symmetrical, but the larvae are bilaterally symmetrical. Digestive system is complete with a mouth on the ventral side and anus on the dorsal side. The most characteristic feature is the presence of water vascular system which helps in locomotion, capturing food, transportation of food and respiration. Excretory system is absent. Echinoderms are dioecious, i.e., sexes are separate. Reproduction is by sexual means. Echinoderms show external fertilization, releasing the gametes in water that result in the formation of zygote. The zygote shows radial, holoblastic and intermediate cleavage. When the larvae hatch, they are bilaterally symmetrical but they grow through various stages or metamorphosis and become radially symmetrical adults. Different types of larvae can be observed in various classes of echinoderms.

I) Larvae of Asteroidea

The three larval stages of asteroidea are as follows:

a) **Early-bipinnaria** - The larva has an oval body and does not have any arms. Thus, it looks like hypothetical dipleurula larvae. It also possesses ciliary bands that helps in locomotion. A well-developed alimentary canal helps in feeding and then the larva grows into bipinnaria larva.

b) **Bipinnaria** - This larva looks like auricularia larva of holothuroidea. It has 5 pair of arms without skeletal support. The arms possess cilia and are used for swimming. It also possesses preoral and postoral ciliary bands. Bipinnaria larvae feeds on planktons.

c) **Brachiolaria** - This larva comes into shape after 6-7 weeks of fertilization and becomes sedentary. It remains attached to the hard substratum with the help of three brachiolarian arms with tips possessing adhesive discs. Ciliary arms have no function in this larva as they get reduced, becomes thin and functionless. Digestive system is complete with a well-developed mouth, gut and anus. It also has hydocoel, axocoel and stomatocoel that further develops into the water vascular system of adult.

II) Larvae of Holothuroidea

This class has 2 larval stages:

a) **Auricularia**: It has 4-5 paired, ciliated arms thus resembling bipinnaria of asteroidea. These arms help in swimming. Mouth, gut and anus are well developed.

b) **Doliolaria**: It possesses 5 ciliated bands around its barrel like body. Mouth is located ventrally. The anterior side has a neural sensory plate and an apical ciliary tuft which helps to balance while swimming. This larva leads into an adult but some species might not even have doliolaria stage.

III) Larva of Echinoidea

Echinopluteus is the only larval stage in echinoidea. It has an oval body and is bilaterally symmetrical. It possesses long paired arms with cilia and calcareous skeletal rods for support. Posterolateral arm is not present but it has preoral arm. Anterolateral, postoral and posterodorsal arms are the other three arms which are present. It also has well developed mouth, anus and gut. It grows into an adult.

IV) Larva of Ophiuroidea

This class shows only one larval stage and that is ophiopluteus that resembles echinopluteus larva. It has very long posterolateral arms but preoral arm are absent. It also possesses anterolateral, postoral and posterodorsal arms. All the arms are supported by calcareous skeletal rods. This larva leads into adult brittle star.

V) Larvae of Crinoidea

The basic larval stage is pentactula but it passes inside the egg. Sea lillies show only one or two larval stages. Some sea lillies have doliolaria larva (a.k.a. vitellaria larva). It is like the doliolaria larva of holothuroids but additionally on the ventral side, it has adhesive pit helping it to attach to the substratum. The resemblance in the two larvae indicates evolutionary relationship between crinoidea and holothuroidea.

Pentacrinoid is a sedentary larva having an attachment plate to adhere to the substratum. A stalk supports the body. There are 10 tentacles with cilia to capture food. Mouth and anus are present on the same side of the disc. An adult emerges from pentacrinoid.

The larval forms of all classes in Echinodermata will demonstrate general resemblance. However, the crinoidea larva diverge from this pattern. In general, all the larvae exhibit that they might have arrived from same ancestor. Hence, the common ancestor is a coelomate, free swimming and bilaterally symmetrical animal.

These larvae also show resemblance with toronaria larvae of balanoglossus. Thus, the study of Echinoderm larva has a phylogenetic significance.

7) Larval forms of Balanoglossus

Balanoglossus is commonly known as acorn worm or tongue worm. Genetic term balanoglossus is composed of two words, i.e., Balano: means acorn and glossus means tongue. Acorn refers to the proboscis part projecting from the collar portion of the worm giving it the appearance of acorn (oak fruit); hence the name acorn worm. Term glossus refers to the collective shape of proboscis, collar and trunk; giving it the appearance of an ox tongue; hence, naming it as tongue worms. Balanoglossus exhibits both asexual as well sexual reproduction.

1) **Asexual reproduction:** It is rarely observed in class enteropneusta. However, in *Balanoglossus capensis*, the body is divided into several parts from tail end during the summer period. During winter, each part undergoes regeneration to form complete sexually active individual.

2) **Sexual reproduction:** Balanoglossus is dioecious. It is hard to distinguish male from females externally except for the difference in the coloration of ripe glands of living specimens. Testes and ovaries are sac like bodies arranged in longitudinal rows in the genital wings, on each side of the digestive tube. Each gonad communicates to the outside via gonopore.

Development of Larva

1) **Fertilization:** Sperm and ova are released from their burrow by the male and female respectively in open water where they get united to form zygote.

2) **Pre-Larval Development:** Zygote undergoes equal and holoblastic type of cleavage to form a sphere of blastomeres known as morula. Morula, undergoes reorganization to form a spherical, single-layered hollow embryo known as coeloblastula. Coeloblastula forms 6-15 hrs after fertilization with a central cavity known as blastocoel. Blastula undergoes invagination to form an archenteron that communicates to outside via blastopore. Blastopore closes up and the structure is now called as gastrula which lengthens in anterior-posterior direction. The tip of the archenteron pinch off to form protocoel whereas the remaining portion forms the future gut. One side of the triangular shaped protocoel gets attached to the underside of apical thickening whereas its other side communicates to outside via hydropore. Protcoel and hydropore forms the future proboscis coelom and proboscis pore. Collar and trunk arises as solid evagination of the hindgut.

3) **Larval Development:** As soon as the protocoel is formed, the inner end of the gut moves towards ventral surface and opens to outside via mouth. Gut is now divided into different regions: oesophagus, stomach and intestine which open via anus (formed by blastopore). The uniformly ciliated larva escapes out from the egg membranes into open water to lead a free swimming life. The newly hatched larva is called as tornaria larva, called so due to its habit of rotating in circles.

   Tornaria larva is an oval shaped transparent larva up to 3mm in size. Tornaria larva has a ventral mouth, posterior anus and a well differentiated gut. There are two ciliary bands located on the body: Anterior ciliary band also called as circumoral band serves to collect food whereas posterior ciliary band or telotroch serves as locomotor organ. The anterior end of the larva is somewhat thickened to form an apical plate (composed of epidermal cells) bearing ocelli or eye spots and a tuft of sensory cilia called ciliary organ or apical tuft. Proboscis coelom or protocoel communicates to outside via proboscis pore or hydrocoel to the right side of which is present a pulsating heart.

4) **Metamorphosis:** After swimming freely and feeding on planktonic microorganism, larva undergoes metamorphosis to form an adult worm. The ciliary bands are lost and body becomes differentiated into three regions namely: proboscis, collar and trunk. The adult worm finally settles down at the bottom to lead a benthonic life.

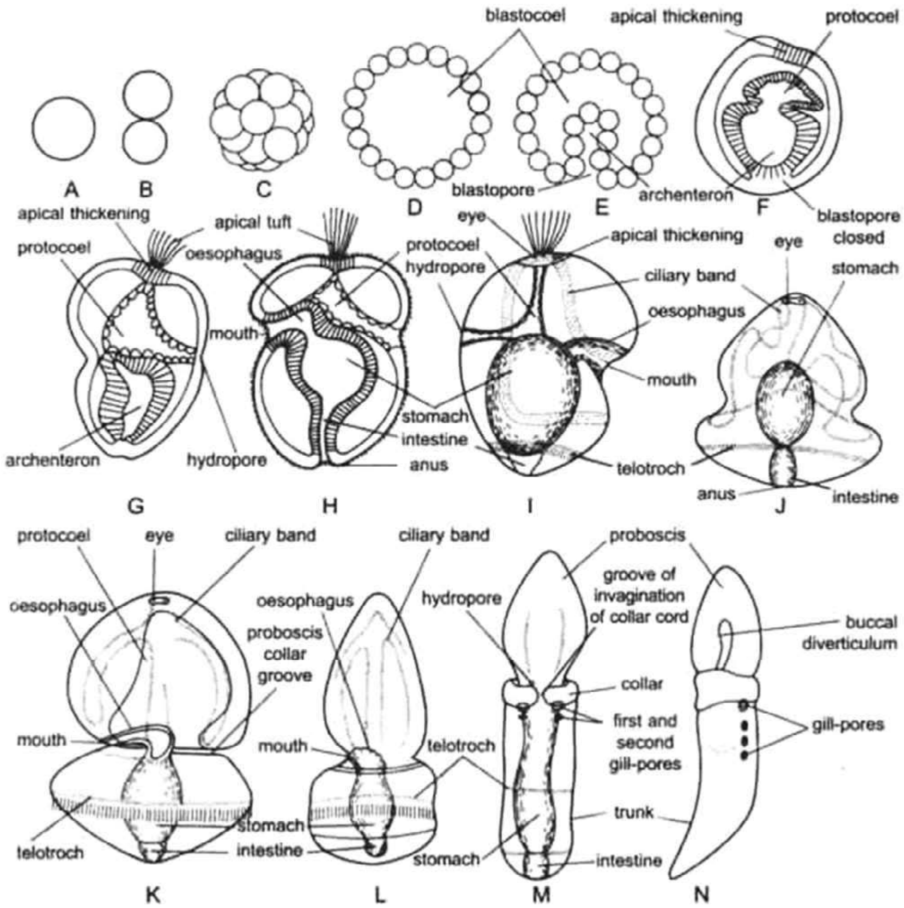

Fig. 4.9 *Stages of Development in Balanoglossus.* ***A-*** *Zygote,* ***B-*** *2-Cell Stage,* ***C-*** *Morula,* ***D-*** *Coeloblastula,* ***E-*** *Gastrulation,* ***F-*** *Gastrula,* ***G-*** *Early Tornaria,* ***H-*** *A Section of Young Tornaria Larva* ***I-*** *Young Tornaria,* ***J-*** *Fully Formed Tornaria Larva* ***K to N-*** *Metamorphosis of Tornaria to Young Balanoglossus.*

4.2.1 Larval Forms of Parasites

A parasite is those organisms which lives at the expense of other organism, and in return it causes injury or harm to the host. Such an association in which one organism, the parasite, is benefited while another one, the host, is harmed is called parasitism. Helminthes are a group of invertebrate organisms which include animals belonging to two important phyla namely, platyhelminthes and nemathelminthes. Several species of the group helminthes have adapted themselves to the parasitic mode of life.

Larval form of Trematodes

Trematodes are parasitic flatworms of the class Trematoda, specifically parasitic flukes with two suckers: one ventral and the other oral. Trematodes are covered by a tegument, that protects the organism from the environment by providing secretory and absorptive functions. The life cycle of a typical trematode begins with an egg. Some trematode eggs hatch directly in the environment (water), while others are eaten and hatched within a host, typically a mollusc. The hatchling is called a miracidium, a free-swimming, ciliated larva. Miracidia will then grow and develop within the intermediate host into a sac-like structure known as a sporocyst or into rediae, either of which may give rise to free-swimming, motile cercariae larvae. The cercariae then could either infect a vertebrate host or a second intermediate host. Adult metacercariae or mesocercariae, depending on the individual trematode's life cycle, will then infect the vertebrate host or be rejected and excreted through the rejected host's faeces or urine. Larvae hatch from eggs, either inside or outside the host, depending on the type of organism. For eggs in moist soil at optimal temperature and oxygen levels, the embryo develops into an infective larva after 2 to 4 weeks, named "second-stage larva". Once ingested by a host, this larva has the ability to get out of the egg, hatch in the small intestine and migrate to different organs. These infective larvae (or "infective eggs") may remain viable in soil for two years or longer. The process of larval maturation in the host can take from about two weeks up to four months, depending on the species.

The Miracidium larva: The Miracidium is the second stage in the life cycle of trematodes. When trematode eggs are laid and come into contact with fresh water, they hatch and release miracidium. In this phase, miracidia are ciliated and free-swimming. This stage is completed upon coming in contact with, and entering into, a suitable intermediate host for the purposes of asexual reproduction. There are many species of trematoda exist, expressing some variation in the physiology and appearance of the miracidia. The various trematode species implement similar strategies to increase their chances of locating and colonizing a new host. The trematode *Hirundinella ventricosa* releases eggs in strings. Each egg contains a single miracidium, while the string contains living spermatozoa. Miracidia have cilia that are only present in the upper portion of the body near an apical gland with 12 hook-like spines in the opening.

The miracidia are oval-shaped and their body is almost entirely covered in cilia except for the most anterior portions, taken up by "apical papilla". The miracidia have four papillae on each side, which contain sensory hairs. They each have an apical gland that leads to the apical papilla. They have four rows of epidermal plates, with row two made up of eight plates, while the other three rows each have six. Their eyespots are dark brown and shaped like an inverted capital letter L, located between the first and second row of plates. A single "large cephalic ganglion" along with several smaller nuclei, make up the nervous system.

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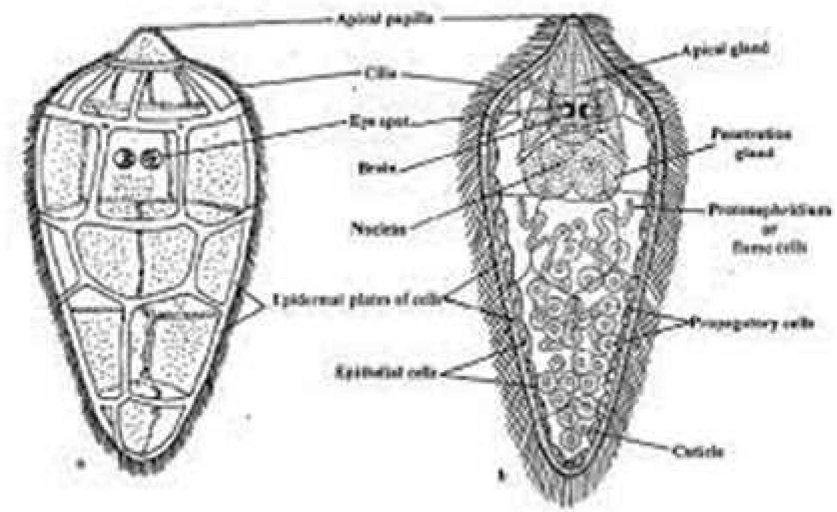

Fig. 4.10 *Miracidium larva*

Sporocyst Larva: Sporocyst a saclike larval stage of many trematodes which produces rediae by asexual development from germinal cells. Sporocysts are elongated sacs that produce either more sporocysts or rediae. This is where larvae can develop. Sporocyst is an elongated sac-like structure, covered with cuticle. Body wall of the sporocyst consists of sub epithelial cells, mesenchyme and muscle layers. Body sac contains germ cells and flame cells. It is a non-feeding stage. Germ cells within the sporocyst give rise to the next larval stage known as redia larva which develop within it. One sporocyst may give rise to 5-6 redia. Mother Sporocyst have loose plates (cilia) and migrate to gonads and daughter sporocyst are an asexual production of cercariae; they absorb nutrients while having no mouth. It is the second larval stage in the life cycle of F. hepatica. It develops from the miracidium larva within the pulmonary chamber of its snail host. It shows extreme degree of parasitism. As a result alimentary canal and locomotry organs are absent.

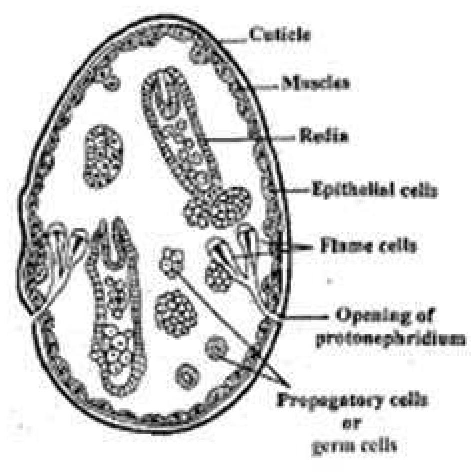

Fig. 4.11 *Sporocyst Larva*

Redia: After the sporocyst form the larva. The first development from it forms the redia. They have a mouth which allows them to have an advantage to their

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competitors because they can just consume them and will either produce more rediae or start to form cercariae. Rediae consume host tissue, including gonadal tissue, as the infection progresses, usurping host nutrients and space for parasitic growth. Each redia is elongate and normally possesses two or four bud-like, antero- and posterolateral projections, the ambulatory buds (or procruscula). As their name implies, the ambulatory buds facilitate movement of the larva through the tissues of the molluskan host. Unlike the sporocyst, the redia possesses a digestive tract with an anterior mouth, a muscular pharynx, and an unbranched cecum. As the redia moves through the host's tissues, it actively ingests host cells.

Co-infections of different parasite species within the same host could occur and cause competition between the rediae and sporocysts. Not all trematode species have a redia stage; some may just have a sporocyst stage depending on the life cycle. The rediae are dominant over sporocysts because they have mouths and are able to either eat their competitors' food or their competitors.

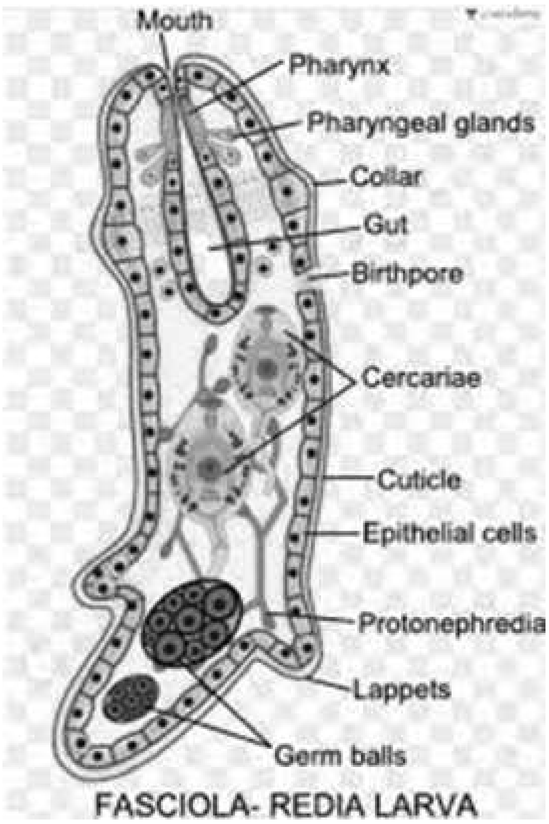

Fig. 4.12 *Redia Larva*

Cercaria: It is the larval form of the parasite develops within the germinal cells of the sporocyst or redia. A cercaria has a tapering head with large penetration glands. It may or may not have a long swimming "tail", depending on the species. The motile cercaria finds and settles in a host where it will become either an adult, or a mesocercaria, or a metacercaria, according to species.

Mesocercaria are involved in an encysted stage either on vegetation or in a host tissue on the second intermediate host. They have a hard shell and are also involved in the trophic transmission. This is where the parasite is able to infect the definitive host because it consumes the second intermediate host that has metacercariae on/in it. Metacercaria are encysted and resting stage, they are only involved when there are 3 intermediate host life cycles.

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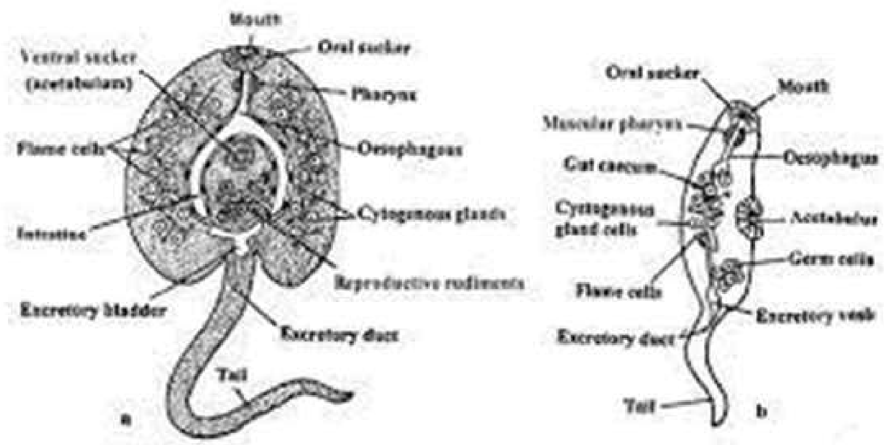

Fig. 4.13 *Cercaria Larva*

Larval form of Cestoda

Cestoda is a class of parasitic worms in the flatworm phylum (Platyhelminthes). They are known as tapeworms because of their ribbon-like adult worms. Their bodies consist of many similar units known as roglottids essentially packages of eggs which are regularly shed into the environment to infect other organisms. They are are mainly fish infecting parasites species.

In the aquatic medium they develop into a hair like larva and are eaten by tiny crustaceans, which, in turn, are eaten by a fish. In the fish, the tapeworm larva encysts in muscle tissue. When the fish is eaten by a mammal, the larva attaches to the mammalian intestine and develops into a mature adult. Cestodes produce large numbers of eggs, but each one has a low probability of finding a host. To increase their chances, different species have adopted various strategies of egg release. One on them is to have very long-lived larvae; as in Echinococcus, the hydatid larvae can survive for ten years or more in humans and other vertebrate hosts, giving the tapeworm an exceptionally long time window in which to find another host.

Normally tapeworms have a two-phase lifecycle with two host. The adult *Taenia saginata* lives in the gut of a primate such as a human, its definitive host. The parasite completes its lifecycle when the intermediate host passes on the parasite to the definitive host.

Diphyllobothrium exhibits complex, three-phase lifecycle. If the eggs are laid in water, they develop into free-swimming oncosphere larvae. An oncosphere is the larval form of a tapeworm once it has been ingested by an intermediate host animal. The intermediate host must ingest the tapeworm's eggs either in food or water, the eggs than hatch and develop into oncospheres, which embedded into the gut wall of the intermediate host to access the organs or tissues of that host where they continue the next stage of their development as cysticerci or bladderworms. After ingestion by a suitable freshwater crustacean such as a copepod, the first intermediate host, they develop into procercoid larvae. When the copepod is eaten by a suitable second intermediate host, typically a minnow or other small freshwater fish, the procercoid larvae migrate into the fish's flesh where they develop into plerocercoid larvae. Procercoid is the first larval stage of some tapeworms, which usually develops inside the body cavity of copepods. Flatworm in this stage is not enclosed in a protective cyst, but is infectious. Procercoids resemble their adult forms in pathways of energy metabolism.

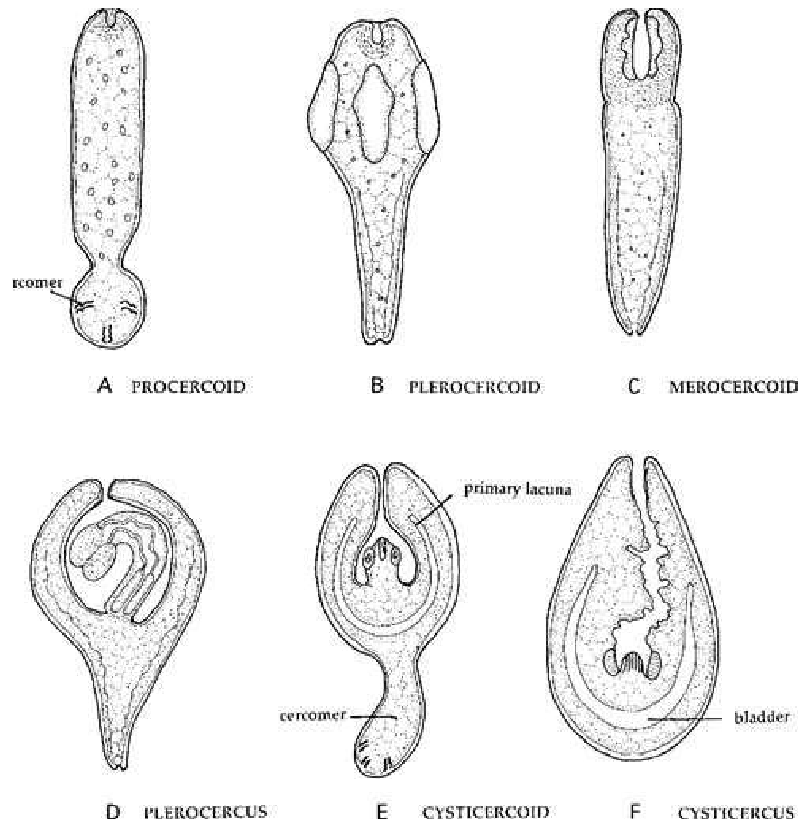

Fig. 4.14 *Larval form of Cestoda*

4.2.2 Strategies and Significance of Larval Forms

According the biogenetic law proposed by Haeckel, "*ontogeny recapitulates phylogeny*". In other words, it means that, the successive stages of individual development correspond with successive ancestors in the line of evolutionary descent. Nauplius larva comes about in the development of all the crustaceans either inside the egg or as the first larval stage and so it was considered as the ancestral form of crustaceans. The old idea of recapitulations stands significantly modified nowadays and the crustacean larval forms are now considered to be the larval reversions of simpler crustacean ancestors.

The larval forms are helpful for seeking out homologies and the affinities among diverse groups. The animals which pass through similar stages are closely related. Larvae are helpful in extensive distribution of species and also in maintaining the food reserves of eggs to a minimum.

Echinoderms show external fertilization, releasing the gametes in water that result in the formation of zygote. The zygote shows radial, holoblastic, and intermediate cleavage. When the larvae hatch, they are bilaterally symmetrical, but they grow through various stages or metamorphosis and become radially symmetrical adults.

Check Your Progress

1. Define crustaceans.
2. What do you understand by nauplius larva?
3. What do you understand by metanauplius larva?
4. Define protozoea larva.
5. Which is the only larval stage in echinoidea?

4.3 MINOR PHYLA

The invertebrates comprise about 90 percent of the total number of animals inhabiting the surface of earth. The invertebrates are so vast and heterogeneous that every group has certain structural and functional peculiarities and a distinct classification system.

However, the life of invertebrates is as complex, appealing, and informative as that of the vertebrates. Without thorough information regarding invertebrates, it is impossible to know the intricacies of life on earth. Currently, there are 30 known invertebrate phyla which are defined by a unity of basic structural pattern, i.e., though the members in each phylum may differ in external features; the anatomical characteristics have developed similarly in several respects.

Another significant feature, by which the members of the individual phylum are associated with one another, is the common shared ancestry.

Evolutionary studies have established that all the individuals of a phylum have been derived directly or indirectly from a common primitive ancestor. Thus, 30 phyla display 30 patterns, with each marking a characteristic, anatomical and functional integrity and common ancestry.

Major and Minor Invertebrate Phyla

The invertebrate phyla are broadly divided into two, i.e., major and minor phyla. The concept of major and minor phyla is based on two factors:

- Total number of species and individuals belonging to that phylum; and
- Contribution of the phylum in ecological communities or ecological significance of the phylum.

According to first factor, 11 phyla namely: Protozoa, Porifera, Coelenterata, platyhelminthes, rotifera, nematoda, annelida, arthropoda, mollusca, ectoprocta and echinodermata appear to be major phyla.

However, based on participation of the phyla in ecological communities, rotifera and ectoprocta cannot be considered as major phyla. Thus, keeping in view the above two factors, biologist regard only nine phyla as major and the rest as minor phyla.

The following table lists the 30 invertebrate phyla with approximate number of species in each phylum:

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Table 4.2 *Invertebrate Phyla with the Approximate Number of species Each of these*

S. No.	Phylum	Number of Species
1	Protozoa	50,000
2	Mesozoa	50
3	Porifera	10,000
4	Coelenterata	11,000
5	Platyhelminthes	90
6	Ctenophora	15,000
7	Nemertinea	750
8	Acanthocephala	300
9	Entoprocta	60
10	Rotifera	1500
11	Gastrotricha	175
12	Kinorhyncha	100
13	Nematoda	10,000
14	Nematomorpha	250
15	Priapulida	8
16	Sipuncullida	275
17	Mollusca	80,000
18	Echiurida	60
19	Annelida	7,000
20	Tardigrada	180
21	Onychophora	65
22	Pentastomida	70
23	Arthropoda	900,000
24	Phoronida	15
25	Ectoprocta (Bryozoa)	4,000
26	Brachiopoda	260
27	Echinodermata	6,000
28	Chaetognatha	50
29	Pogonophora	80
30	Hemichordata	80

4.3.1 Concept and Significance

The characteristics used to understand how these animals are related to each other and to other invertebrate phyla include the formation of the body cavity as well as the nature of their larval forms. These animals are displayed in the table below on the basis of their way of life as well as to show that how different phyla evolved to meet the different demands of parasitism, of living between grains of sand, mud or soil, of a sessile or burrowing existence.

- Phyla comprising free-living and parasitic members or only parasitic members**:**
  - o **Protozoa**

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- o **Parasitic worms:** Platyhelminthes, Nematoda, Nematomorpha, Acanthocephala, Pentastomida
- Phyla with only free-living members:
  - o **Meiofauna**- The term "*Meiofauna*" is related to microscopically small benthic invertebrates that live in both marine as well as fresh water environments. Meiofauna was earlier defined as a group of organisms by their size, larger than microfauna however smaller than macrofauna. In practice, these are metazoan (however some zoologist include protozoan as well) animals that can easily pass via a 0.5 – 1 mm mesh but will be retained by a 30 ìm mesh. However, the exact size varies from researcher to researcher. Currently, the term meiofauna is used interchangeably with the term meiobenthos. Meiofauna is mostly seen in and on soft sediments, but also on underwater algae as well as on higher plants and other hard substrates. The heterogeneity of meiofaunal habitats is so large and meiobenthic taxa so diverse. In practice, most of the classes of Metazoa are represented in the meiofauna of sandy beaches, while the Protozoa are represented by their largest forms, e.g., Foraminifera and Ciliata. The smaller protozoans are generally considered as microfauna. Most common metazoan phyla represented in the benthic meiofauna:
- **Cnidaria**: Hydroida, Scyphozoa, Anthozoa
- **Platyhelminthes**: Turbellaria
- **Gnathifera**: Gnathostomulida, Rotifera, Rotatoria
- **Nemertinea**
- **Nemathelminthes**: Nematoda, Kinorhyncha, Priapulida, Loricifera, Gastrotricha
- **Tardigrada**
- **Crustacea**: Cephalocarida, Ostracoda, Mystacocarida, Copepoda (e.g. Harpacticoida, Cyclopoida), Malacostraca (e. g. Tanaidacea, Isopoda, Amphipoda)
- **Chelicerata**: Acari
- **Annelida:** Polychaeta, Oligochaeta
- **Sipuncula**
- **Mollusca**: Aplacophora, Gastropoda
- **Tentaculata**: Bryozoa
- **Echinodermata**: Holothuroidea
- **Chaetognatha**
- **Tunicata:** Ascidiacea
  - o **Free-living marine worms**: Chaetognatha, Pogonophora, Sipuncula, Echiura, Nemertea
  - o **Lophophorate coelomates:** Bryozoa, Entoprocta, Phoronida, Brachiopoda.

Further, a conventional tree-of-life based on the nature of the body cavity or *coelom* exhibits that how some of these animals are thought to be related not only to each other but to other invertebrate groups too. Similarities as well as differences in larval forms may indicate the closeness of relationships between different phyla and have helped to place invertebrates, including members of the minor phyla, on the tree of life.

Different kinds of minor taxa are essential to this discussion. Some groups like mesozoans as well as placozoans have been taken as the representative's forms of the stem line- age leading to triploblastic animals. Whereas, other minor phyla groups exhibit uncertain affinities as they appear to have simple body plans, and are usually very small in size. On the basis of presence of a pseudocoelom, several minor phyla (For instance minor phyla like rotifera, acan- thocephala, nematoda, nematomorpha, priapulida, kinorhyncha, gastrotricha) historically have been grouped together into the "Aschelminthes". Other minor phyla appear to be sister taxa to larger as well as more well defined groups. For inatnce, echiurans, sipunculids, pogonophorans and vestimentiferans have long been considered to be protostomes (organism in which mouth originates from the first opening, i.e., blastopore), perhaps associated with annelids or molluscs. Then, there are the lophophorates (phyla that possess a crown of tentacles known as lophophore. This helps in filter feeding), a group of three minor phyla (Phoronida, brachiopoda, bryozoa) that have been placed either intermediate between protostomes and deuterostomes (Willmer, 1990), as deuterostomes (Brusca and Brusca, 1990) or have been proposed to be polyphyletic with some being protostomes whereas others being deuterostomes (Nielsen, 1995). Generally, Entoprocts have been associated with molluscs (Bartolomaeus, 1993), with aschelminths (Brusca and Brusca, 1990), or with ectoprocts (Nielsen, 1995). Onychophorans are generally associated with annelids or arthropods, while tardigrades have been associated to both "aschelminths" (Ruppert and Barnes, 1994) as well as arthropods (Brusca and Brusca, 1990) at various times.

4.3.2 Organization and General Characters of Non-Coelomate and Coelomate

Different phyla how their own characteristic features. They are broadly classified into two categories non-coelomate and coelomate.

A. Non-Coelomate: Rotifera, Acanthocephala, Nemertins and Endoprocta/ Entoprocta

Let us study them in detail.

(1) Rotifera

Habit and Habitat

The rotifers are the most common inhabitants of freshwaters, that are also found in small numbers in brackish water bodies such as the ocean and on land in damp sites. They are found to exhibit various lifestyles include creeping, swimming, pelagic, and sessile types, as well as carnivores and bacteria feeders. Rotifers are generally solitary. Some of the sessile species form spherical swimming colonies in which the individuals have no organic continuity.

External Characters

Rotifers are also called wheel animalcules, which are minute animals ranging from 0.04 to 2 mm in length. The rotifer body is divisible into the broad or narrowed or lobed anterior end usually having a ciliary apparatus, an elongated trunk, and the tail or foot.

The body of rotifers is covered with yellowish cuticle which is ringed throughout or in certain regions. The cuticle may be thickened on the trunk to form the lorica, a hard encasement, of one to several plates that may be variously ornamented.

The anterior end is typically broad and truncate or slightly convex and bears the mouth corona, a ciliated zone and an un-ciliated region, the apical field, encircled by the corona. The mouth is in the corona in the mid-ventral line of the head.

The head has a pair of prominent lateral ciliated projections, called auricles. Eyes (pigment spot ocelli) appear as red streaks, occur singly, or paired in the brain, as lateral paired eyes in or near the corona and as paired frontal eyes on the apical field or on the rostrum. Coronal protrusion serves as lower lip.

The trunk may be cylindrical or variously flattened and broadened and is enclosed in a lorica which is often ornamented or spiny. Characteristic trunk structures are the dorsal and lateral antennae or palps. The dorsal antenna is situated in the mid-dorsal line of the anterior end of the trunk and is a finger-like projection tipped with sensory hairs. The anus is in the mid-dorsal line at or near the boundary of trunk and foot.

The body tapers gradually into the foot or the foot may be sharply set off from the stout trunk as a cylindrical tail-like region. Its cuticle is ringed into a few joints that serve for clinging to objects in creeping types or acts as a rudder in swimming types. In sessile forms, the foot is modified to a long stalk. The foot is reduced or absent in wholly pelagic life. The foot is provided at or near its end with one to four movable projections known as toes, used in holding the substratum while creeping. They may be short and conical or slender and spine- like. The pedal glands commonly open at the tips of the toes. Though the rotifers are dioecious, the males are smaller in size and morphology.

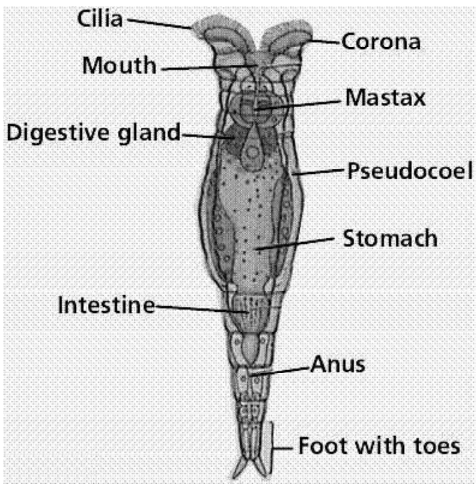

Fig. 4.15 *Depiction of a Rotifer*

Corona of Rotifera

The ground plan of the corona or wheel organ comprises a large oval ventral field, the buccal field evenly ciliated with short cilia and surrounding the mouth, and a circum apical band extending from this to encircle the margin of the head, alters mostly in the direction of enlargement of its marginal cilia with loss of the interior cilia.

In some groups of rotifers, the enlargement of the cilia along both margins of the apical band, results in two circles of cilia or membranelles that is trochus, an inner or anterior circlet and cingulum, an outer or posterior one.

The reduced buccal field becomes incorporated into these circlets and, hence, the corona consists essentially of two circlets, with the mouth between them ventrally.

The adult females of the genera atrochus, cupelopagis and acyclus have no corona but it is present in normal form in the males and young females of these genera. The corona of male rotifers is usually less modified than that of females of the same species.

Body Wall and Associated Glands

The body wall of rotifers consists of cuticle, epidermis and sub-epidermal muscles. The non-chitinous cuticle, secreted by the epidermis consists of scleroproteins. It is frequently segmented and lends flexibility permitting a variety of body movements. In many rotifers the trunk cuticle is thickened and hardened into a lorica that, however, is slightly flexible.

The lorica may consist of several pieces or two dorsal or two ventral plates or two dorsal and one ventral or of single dorsal and ventral plates or of one piece with or without a longitudinal suture.

Loricates are dorsoventrally or laterally flattened; the margins of the lorica project as teeth or spines. A groove like structure known as head shield marked off the part of lorica covering the neck region from the general trunk lorica.

The syncytial epidermis contains scattered nuclei which are arranged in a bilateral manner and are constant in position and number for each species. The cytoplasm is heaped up into an elevation projecting into the pseudocoel around each nucleus or group of nuclei. The retro-cerebral organ, situated above and behind the brain and the pedal glands are the principal glands attached to the epidermis. The retro-cerebral organ consists of a median retro-cerebral sac whose duct forks along with the outlets of a pair of lateral sub-cerebral glands and open on the apical field, often on a single or paired papilla. Sac and gland are different in relative and absolute size in different rotifers. There may be a single sub-cerebral gland or the sac may occur without glands or the glands without the sac. Sac and glands consist of a syncytium and secrete droplets giving them a vacuolated appearance. The sac and glands contain strongly diffractive granules**.** The function of the retro-cerebral organ is uncertain.

The pedal glands in rotifers can be unicellular glands or multinucleate syncytia located in the foot and secrete an adhesive material used for permanent attachment or in creeping and in the construction of tubes and cases. They may be numerous or reduced to a single pair and often rudimentary or absent in the sessile adults. They open by ducts on the tips of toes or at sides or base of the toes or on the spurs or at the foot end.

Muscular System of Rotifers

In Rotifers, the sub-epidermal muscles are circular and longitudinal muscles and found in different parts of the body. In addition to these body wall muscles there are cutaneovisceral muscles that extend to the viscera, especially the digestive tract, from the body wall, and visceral muscles in the walls of the viscera themselves.

The circular musculature of the body wall consists of a single muscle band, mostly three to seven, widely spaced running close to the underside of the epidermis in a circular direction forming complete rings often very incomplete ventrally so that they may consist chiefly of short lateral arcs.

They occur in neck and trunk, generally absent from the foot and reduced in loricates. The circular bands are enucleate, hence, is part of the epidermal syncytium.

The contraction of the circular muscles serves to extend the body. The coronal sphincter is composed of one to several broad bands in the head directly behind the corona. It serves to close the neck over the retracted corona. A similar pedal sphincter is present at the junction of trunk and foot.

Bands running the body length directly under the circular bands are the longitudinal body wall muscles attached at frequent intervals to the epidermis. Loss of these insertions cause the longitudinal bands to run more directly through the pseudocoel and to act primarily on head and foot as retractors.

The 4 principal head retractors are the central, dorsal, lateral, and ventral pairs. The lateral is commonly subdivided into three bands, superior, median, and inferior. The longitudinal retractors have one or more nuclei.

Digestive System of Rotifers

The mouth is ventral, rounded, slit-like or triangular. The cingulum forms a definite lower tip beneath the mouth. In forms with a large buccal field, the posterior end of the field may project as the chin. The mouth may open directly or by ciliated buccal tube into the pharynx.

The pharynx or mastax is a highly muscular, rounded, trilobed or elongated organ whose inner wall bears the masticatory apparatus composed of hard cuticularised pieces, the trophy that are of different types for different modes of life like malleate type, virgate type, cardate type, forcipate type, incudate type, ramate type, uncinate type, fulcrate type. The trophi consist of 7 main pieces, the unpaired fulcrum and the paired rami, unci, and manubria.

The salivary glands are 2 to 7 in number, occur in the mastax wall in many rotifers as uninucleate or syncytial masses with granular or vacuolated cytoplasm.

The function of the salivary glands is presumably concerned with ingestion or digestion. The mastax is followed by the oesophagus lined with cuticle or ciliated throughout or at the posterior end only. The oesophagus is devoid of glands. The oesophagus is followed by the stomach. It is an enlarged thick-walled sac or tube.

The stomach has a muscular layer consisting of muscle cells. At the junction of oesophagus and stomach occurs a pair of syncytial gastric glands having a constant number of nuclei and opening into the stomach by a simple pore on each side. The secretion comprises droplets or granules aggregated around the pore and are presumably enzymatic. The stomach is followed by the intestine. In one case the intestine is tubular and in the other, bladder-like. The stomach and intestine are attached to the body wall by the usual cutaneovisceral muscles.

Nervous System of Rotifers

The nervous system of rotifers consists of a bilobed rounded, triangular, or quadrangular brain or cerebral ganglia lying dorsal to the mastax, some sensory and motor nerves, some additional ganglionic masses and 2 main ventral nerve cords.

From the various sense organs of the head, the eyes, the sensory bristles and pits on apical field, the rostrum and the dorsal antenna, several paired sensory nerves extend to the brain which sends motor nerves to the anterior parts of the various muscles, as the dorsal, lateral, central retractors, and to the salivary glands.

The ganglionated cords that are the main ventral nerves, spring from the sides of the brain and proceed backward in latero-ventral position into the foot. They bear an anterior ganglion near the brain and a geniculate ganglion farther posteriorly. The ventral cords terminate posteriorly in ganglia serving as the urinary bladder and foot. These ganglia may be fused in one mass, called the cardiovascular ganglion.

Sensory Structures of Rotifers

In rotifers, the sensory cells and sense organs occur abundantly on the anterior end in the form of sensory membranelles, styles, ciliated pits, sensory papillae, etc. The sensory membranelles or styles are single stiff bristles situated near the inner edge of the circumapical band and named from their position as dorsolateral, lateral, and ventrolateral styles.

Similar apical styles occur on the apical field and oral styles may be present near the mouth. These styles seem to be tactile organs and each is underlined by one or two sensory nerve cells from which fibres go to brain. Paired ciliated pits are chemo-receptors occurring on the apical field. Conical or finger-like palps tipped with sensory hairs or without hairs are present on the apical field. Ocelli, seen as red pigment spots, are of common occurrence.

A single, less often paired, cerebral eye is embedded in the dorsal and ventral surface of the brain. Cerebral and apical or cerebral and lateral eyes may be present simultaneously. The dorsal antenna or tentacle is a movable papillae or finger-like projection provided at its tip with one or more tufts of sensory hairs.

Excretory System of Rotifers

The excretory system of rotifers consists of a pair of protonephridia and tubules provided with flame-bulbs which open posteriorly into a common urinary bladder. The main tubules fork into an anterior and a posterior branch and extend lengthwise the animal, one on each side.

The flame bulbs are two to eight in number on each side and open into a ciliated capillary that enters the end of the main tubule or its branches and may run alongside the main tubule for some distance.

Huxley's anastomosis, a similar capillary runs transversely between the anterior terminations of the main tubules and receive additional flame bulbs. The flame bulbs vary in shape from a tubular to a flattened triangular form and contain a slender to triangular membrane kept in constant motion.

The thickened cap-like end frequently bears one to several protoplasmic filaments. These filaments anchor the bulb mostly to the body wall. The flame bulbs are not cells and are enucleated but are part of the general nephridial syncytium. Posteriorly the tubules open separately into a urinary bladder situated ventral to the cloaca or they unite to a common stem that enters the ventral wall of the cloaca.

Reproductive System of Rotifers

The rotifers are exclusively dioecious and show a marked sexual dimorphism. In the order floscularaceae and collothecacea, the free-swimming males are one-tenth or less the size of the females and have a simple ciliated anterior end in place of the elaborate coronal lobes of the female.

The reduction of males is most pronounced in pelagic and sessile rotifers and appears to be adaptated to ensure fertilisation under these environmental conditions. The minute size of males is because they come from smaller eggs and do not grow after hatching.

In most of rotifers, the female reproductive system consists of a single multinucleate ovary and vitellarium that are bound together in a common membrane that continues to the cloaca as a simple tubular oviduct. The male reproductive system consists of a single large sac like testis from which a ciliated sperm duct receives a pair or more of prostatic glands that proceeds to the genital pore.

The posterior end of the sperm duct is eversible as cirrus which is lined with hardened cuticle; or it may bear a cuticular tube protrusible as a penis. Copulatory organ is formed by the body wall around the gonopore that assumes a tubular form.

Affinities of Rotifers

The rotifers have been allied in turn to almost every invertebrate group, specially the arthropods and annelids.

Resemblances to Arthropods Include:

- The body surface is cuticularized.
- Apparent segmentation in the body
- The appearance of jaws
- The discovery of pedalia with movable bristle bearing arms suggests the appendages of a crustacean larva.

Hatschek propounded his trochophore theory which states that the living rotifers are closely related to the ancestral mollusca, annelida and certain other groups. This theory compares rotifers with the trochophore larva concluding that rotifers are simple annelids that have remained in a larval state. This hypothesis is based chiefly on the rotifer trochosphaera whose ciliary girdle, bent intestine and excretory organs resemble the similar parts of the trochophore topographically.

On the other hand, the primitive corona was a large ventral ciliated field in no way resembling the ciliary circlets of the trochophore. The annelid theory must, therefore, be regarded as without foundation, as concerns the trochophore resemblance.

The embryology of rotifers suggests that these animals are primitive, not derived by the retrogression on higher forms.

No trace is seen in the development of a coelom or an entero-mesoderm. The anatomy and embryology both incline to the origin of the rotifers from some low-grade creeping bilateral type such as a primitive flatworm. The primitive type of corona may be the remnant of a former complete or ventral ciliation such as found in the turbellaria.

The formation of cuticularised parts as the trophi is common among the Turbellaria. The strongest point of resemblance between rotifers and turbellarians is the protonephridial system which is practically identical with that of the rhabdocoels which precludes the derivation of the rotifers from any higher group since none of the higher groups have protonephridia with flame-bulbs.

The retro-cerebral organ is homologous with the frontal organ of turbellaria. The division of the female gonad into ovary and vitellarium is another resemblance to flatworms. The rotifers differ from flatworms in the presence of anus and the lack of a sub-epidermal muscle sheath and of the sub-epidermal nerve plexus which is characteristic of the Turbellaria. The nervous system bears some similarity to that of flatworms.

The small size of rotifers probably makes an accessory nerve plexus unnecessary. The rotifera show a great resemblance to the turbellaria and relate the aschelminthes to the platyhelminthes. The rotifers display an amazing variety in structure and do not resemble any one group of animals. Hence, the status of an independent phylum to rotifers is justified.

(2) Acanthocephala

Members of Phylum- Acanthocephala are vermiform, slightly flattened, Bilaterally symmetrical worms. They are thorny-headed worms, or spiny-headed worms, characterized by the presence of an eversible proboscis, armed with spines, which it uses to pierce and hold the gut wall of its host. They act as endoparasites. Adults reside as parasites in the intestine of vertebrates. Larvae live in insects and crustaceans. The major diagnostic feature of the phylum is the presence of organ of attachment comprising of an invaginable proboscis that forms the anterior end. The proboscis is armed with rows of recurved hooks. Body has more than two cell layers, tissues and organs.

The body wall consists of cuticle, syncytial epidermis permeated with spaces and sub-epidermal musculature. In connection with the proboscis apparatus the epidermis forms two elongated bodies termed lemnisci that hang down into the trunk. Body covered by a syncitial epidermis with a few giant nuclei. Body cavity is a pseudocoelom. Mouth, anus and digestive tube are absent.

Circulatory system is absent. Respiratory organs are absent. Excretory organs when present are of the nature of protonephridia and open into the terminal part of the reproductive system. The nervous system is present. It consists of a ganglion near the proboscis as well as two lateral cords extending posteriorly from the ganglion along with numerous minor nerves.

The sexes are separate i.e., dioecious. Females are generally larger than the males. Males are provided with a copulatory apparatus and the terminal part of the female apparatus is also somewhat complicated. Reproduction is sexual and gonochoristic, with viviparous embryos. The eggs develop within the maternal body into a larva that requires an intermediate invertebrate host for its further development.

There are over 500 known species. Echinorhynchus is the chief genus of acanthocephala and it is described below in detail.

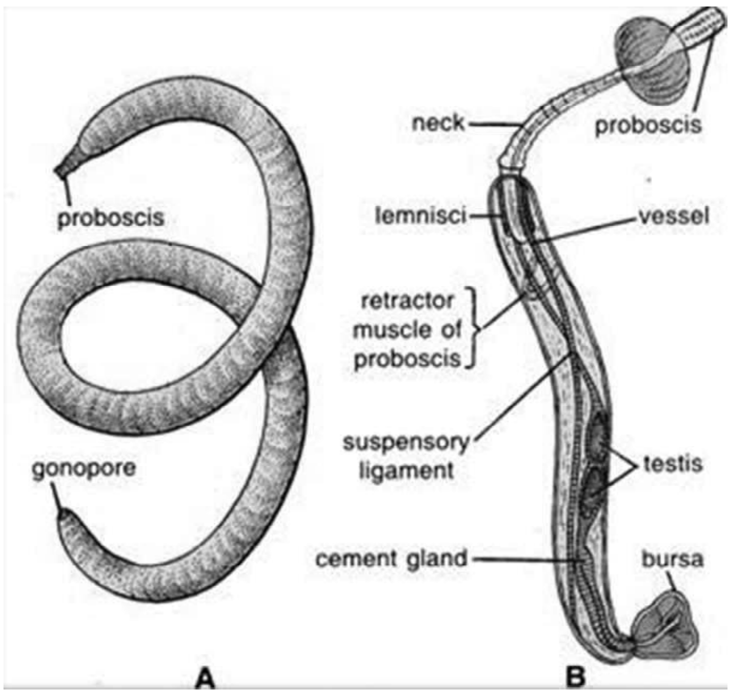

Fig. 4.16 *Echinorhynchus gigas. A) Male; B) Female*

Classification of Acanthocephala

Phylum Acanthocephala, consist of about 1150 species, that have been placed within three classes by Ruppert and Barnes (1994).

I) Class Archiacanthocephala

i. Several lacunar canals are dorsal as well as ven-tral.

ii. Presence of eight uninucleate cement glands

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iii. Trunk spines are absent.
iv. Proboscis receptacle with single muscle layer, often with ventral cleft.
v. Protonephridia are present but only in one family.
vi. Ligament sacs break down in reproduc-tive females.
vii. Adults are parasite on birds and mam-mals, while the centipedes, millipedes and insects form the intermediate host.

For instance: macracanthorhynchus, moniliformis, oligacanthorhynchus.

II) Class Eoacanthocephala

i. Main lacunar canals are dorsal as well as ventral.
ii. Single syncytial cement gland with giant nuclei is present.
iii. Presence of trunk spines
iv. Proboscis receptacle closed, with single muscle layer
v. Excretory structure protonephridia are absent.
vi. Ligament sacs persist in reproductive females.
vii. Adults parasitize on fishes, some amphibians and reptiles, while the crus-taceans form the intermediate host.

For instance: Neoechinorhynchus

III) Class Palaeacanthocephala

i. Main lacunar canals are lateral.
ii. Two to eight multinucleate cement glands are present.
iii. Presence of trunk spines
iv. Proboscis receptacle is present as closed sac and usually with two muscle layers.
v. Excretory structures protonephridia are absent.
vi. Ligament sac breaks down in reproductive females.
vii. Palaeacanthocephala represents the largest as well as the most diverse group where the adult parasitizes on all vertebrate classes and crustaceans form the intermediate host.

For instance: Polymorphus, Acanthocephalus, Echinorhynchus, Leptorhynchoides.

Habit and Habitat of Acanthocephalans

The genus echinorhynchus is a common parasite present in the intestine of mammals, birds, reptiles, amphibians as well as fishes.

External Characters of Acanthocephalans

Acanthocephalans have cylindrical bodies and ends in front in a protrusible portion, the proboscis, which is armed, i.e., covered with rows of recurved chitinous hooks. The body bears an external segmentation due to the presence of rings or constriction at regular intervals. The neck is generally short but sometimes much elongated. The trunk region may be cylindroid, flattened, curved or coiled having a smooth, wrinkled or segmented surface. In several genera, phylum Acanthocephala, the trunk is visibly differentiated into a broader fore trunk and a slender hind trunk in variable proportions in different species. There is no trace of mouth, anus as well as that of excretory pore. The gonopore occurs at or near the posterior extremity.

Body Wall of Phylum Acanthocephala

The body wall of species belonging to phylum Acanthocephala is covered with firm cuticle of homogeneous structure. Epidermis of hypodermis is present below the cuticle. The epidermis is composed of a thick layer of fibrous syncytial construction comprising three fibrous strata namely: an outer layer which is slightly thicker than the cuticle and is composed of parallel radial fibres; a middle thick layer consisting of layers of fibres running in different directions and finally an inner layer of radial fibres. The inner layer is highly thick. The inner radial layer is also composed of nuclei as well as lacunar system. The number of nuclei is approximately constant for each species, at least in early stages, and in many families throughout the life (Van Cleave, 1914). The shape of the nuclein varies from globose or oval to rosette, amoeboid or highly branched forms and are of relatively large size up to 2 mm or more in length. The lacunar system comprised of two longitudinal vessels with evenly spaced transverse connections. The lacunar system is present only in the epidermis and it does not communicate with the exterior or with any other body structure. The lacunar system holds a highly nutritious fluid and thus the primary function of this system is to act as food distributing channels. The movement of the nutritious fluid is synchronized with that of animal's body movement. Beneath the epidermis, a thin layer of dermis is present. The dermis permeates the underlying musculature. The thin muscle layer is composed of both outer circular and inner longitudinal fibres. No definite lining membrane bounds the body wall from the pseudocoel.

Proboscis Apparatus of Acanthocephala

The shape of the everted proboscis varies from a short cylindrical to globose shape to a long cylinder. Proboscis is composed of a single muscle layer or two layers in some species. The proboscis is armed with firm recurved chitinous spines/ hooks. Hooks are covered with cuticle The armed spines are usually arranged in alternating radial rows but may be concentric or irregular. The total number of hook's rows, the number of hooks present per row, as well as the size pattern of the hooks are constant for each species. Hooks serves as important taxonomic characters of the phylum. The proboscis is invaginable in nature and withdraw-able into a muscular sac known as the proboscis receptacle that is fixed firmly in a circle to the inner surface of the proboscis wall and hangs into the body cavity i.e. pseudocoel. Proboscis as well as receptacle are operated by special muscle bands. Muscle bands are inserted on the receptacle wall and also passes via this wall to continue as the dorsal and ventral receptacle retractors that finally halt on the trunk wall. Neck retractors also encircle the proboscis and insert on the trunk. From the posterior part of the neck region, a pair of projections of inner radial layer of epidermis referred to as lemnisci extends into the trunk pseudocoel. The lemnisci are well supplied by vessels of the lacunar system. The primary function of the lemnisci is to act as reservoirs for the fluid of the lacunar system of the presoma when the proboscis is invaginated.

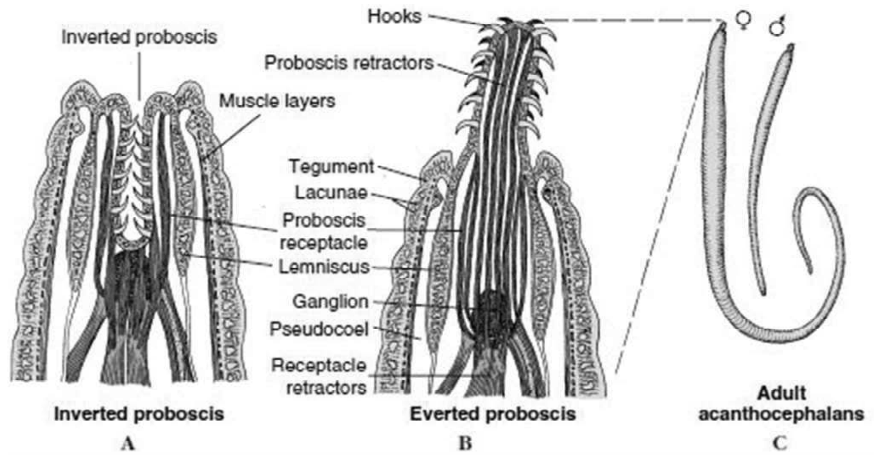

Fig. 4.17 *A) Inverted Proboscis B) Everted Proboscis C) Adult Acanthocephalans*

Nervous System of Acanthocephala

Nervous system of Acanthocephala consists of the cerebral ganglion, the branches from cerebral ganglion and in the male a pair of genital ganglia with branches. The cerebral ganglion is a large cellular mass enclosed within the proboscis receptacle and is in contact with its ventral walls. It contains of a central fibrous mass consisting of ganglion cells. For instance:- Genus *Macracanthorhynchus* consist of 86 ganglionic cells and its cerebral ganglion gives off two single and three pairs of nerves. Cerebral ganglion of *Macracanthorhynchus* gives off an anterior median and a ventral anterior nerve to the musculature and sensory papillae of the proboscis, a pair of lateral anterior nerves to the lateral protrusors, a pair of lateral medial nerves to the receptacle wall, and the pair of main lateral posterior nerves that proceed to the posterior end of the animal.

Sense Organs of Acanthocephala

Specialized sense organs are absent owing to its parasitic mode of life. However, three sense organs are present in the proboscis whereas male bursa and penis consist of multiple sense organs.

Feeding and digestion in Acanthocephala

Acanthocephalans lacks digestive system; however, they selectively absorb nutrients from the host's intestine across their tegument. A few studies are conducted on feeding and digestion in acanthocephalans till date. Based on that, it is concluded that the major substrate for acanthocephalan metabolism is carbohydrate, with ethanol being the main end product. Uptake of monosaccharides appears to involve active transport mechanisms (active transport mechanism involves expenditure of energy). A few Acanthocephalans are known to store glucose in the proboscis receptacle muscle as well as in the cytoplasmic core of the hollow muscles. However, it is yet not known whether the hollow muscles acts as a storage site or helps in distributing nutrients throughout the body. The plasma membrane present at the surface of the tegument exhibits hydrolytic activity and tegumental surface crypts within which various enzymatic activities have been localized. The primary function of the crypt is to increase the absorptive surface area and are considered to be extra-cytoplasmic digestive organelles. A lot of amino acids are also known to be absorbed via tegument, however, their function in metabolism is not known. The main channels of absorption keep on varying with amino acid. Lipids are absorbed and then stored for future use in the lemnisci, however, it is still not clear whether the primary site of lipid absorption is the body wall or the neck/proboscis region. Even though, a large amount of lipids may be deposited in acanthocephalans, they are not thought to be used in metabolism.

Excretory Organs of Acanthocephala

Excretory organs of most Acanthocephalans comprise of a pair of small bodies, protonephridia, situated at the posterior end near the genital aperture. Each protonephridium is comprised of a branching mass of flame bulbs attached to a common stem. The total number of flame bulbs in each protonephridium varies from varies from 250 to 700. The flame bulbs are lined by a row of cilia. In genera like *Oligacanthorhynchus* and *Nephridiorhynchus*, the flame bulbs open directly into a sac from which the nephridial canal leads (Meyer, 1931).

Ligament Sacs and Ligament Strand of Acanthocephala

Ligament sacs are exclusively present in Acanthocephalans. The ligament sacs are hollow tubes of connective tissue with or without accompanying muscle fibres that run interiorly along the length of the body and enclose the reproductive organs. In males, only dorsal ligament sac is present whereas ventral sac is missing. The dorsal sac encloses the testes and the cement glands. In females, both dorsal as well as ventral ligament sac are present. The medial walls of dorsal and ventral ligament sacs make contact in the frontal plane and communicate anteriorly by an opening.

Pseudocoel of Acanthocephala

True body cavity is absent in acanthocephalans. Instead, a pseudocoel body cavity is present. The pseudocoel is not bounded by membranes and is present between the body wall and the ligaments. The pseudocoel is filled with a clear fluid.

Reproductive System of Acanthocephala

Species of phylum Acanthocephala are dioecious, i.e., the male and female sexes are separate. The female is generally longer than the males of the same species. Much of the body is occupied by the reproductive organs. In both the sexes the gonads and their ducts are connected with a ligament strand which extends backwards from the end of the proboscis sheath.

A male comprises two oval shaped, rounded or elongated testes enclosed in the ligament sac and attached to the ligament strand. A sperm duct from each testis proceeds posteriorly inside the ligament sac. A group of variably shaped (rounded, pyriform, clavate or tubular) unicellular gland cells referred to as cement glands open into the sperm duct shortly behind the more posterior testis. The ducts of these cement glands unite to form a single or two main duct and then opens into the sperm duct. All these structures, i.e., sperm ducts, the cement ducts and the protonephridial canals (when present) are all enclosed within a single muscular tube, the genital sheath. The two sperm ducts unite together inside the genital sheath to form a single sperm duct. The urogenital (consisting of both excretory and reproductive parts) canal so formed penetrates the centre of the penis, a short conical protrusion. The penis projects into hemispherical or elongated cavity the bursa that is eversible to the exterior and grasps the rear end of the female in copulation. The final sperms are long filaments without definite heads.

In female reproductive system, the original single or double ovary breaks up into fragments referred to as ovarian walls that float freely in the dorsal ligament sac but as the latter sac soon ruptures the balls occupy the pseudocoel. The ligament sacs lead to the first part of the female canal termed the uterine bell. The funnel shaped uterine bell is a highly muscular structure that exhibits peristaltic contractions (wave like muscular contractions). The peristaltic contractions help in engulfing the developing eggs and passes them onward. The spherical shaped immature eggs pass into the pseudocoel via the ventral opening of uterine bell. The bell constricts at its posterior end to form a uterine tube. The uterine tube is composed of several large cells with conspicuous nuclei and bearing two bell pouches that extend anteriorly. This uterine tube finally enters into the uterus. Uterus of acanthocephalans is a muscular tube and is followed by the short non-muscular vagina opening to the exterior. The mature ova are elliptical and surrounded by a membrane.

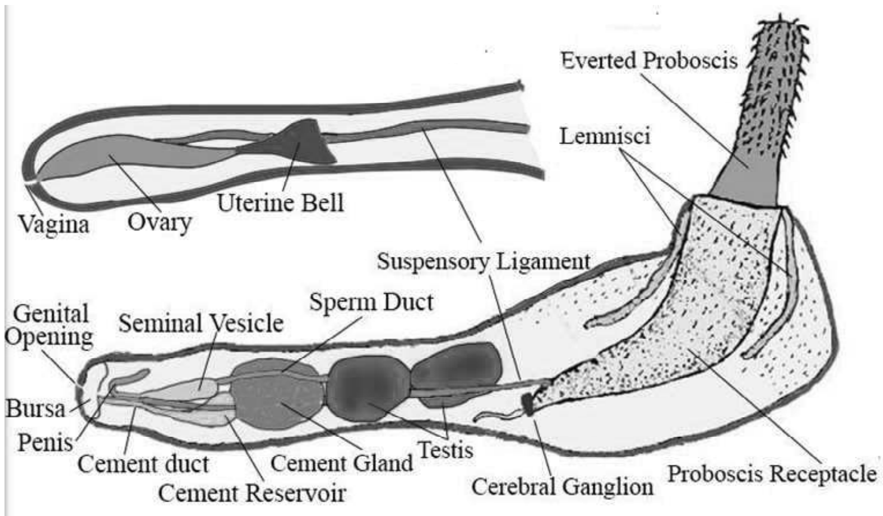

Fig. 4.18 *Male and Female Reproductive Structures of Acanthocephalan*

Copulation and Development of Acanthocephala

Fertilisation is internal, i.e., it takes place inside the body cavity and after fertilisation a membrane arises inside the original egg membrane. During copulation, the everted male bursa of acanthocephalans holds the posterior end of the female and the male penis enters the female vagina and discharges long filamentous sperm without a definite head into the uterus. The secretion of cement glands acts as a plug in the gonopore and thus prevents the escape of sperms. The eggs keep on continuing their development in the pseudocoel until a larval stage provided with a rostellum armed with hooks is reached. These acanthor larvae are engulfed by the uterine bell and passed towards the uterine tube. However, the larvae which are not developed sufficiently are passed back into the pseudocoel via the ventral bell opening. The mature larvae move further into the bell pockets and then along the uterus and vagina and finally to the external surroundings. These acanthor larvae needs to be ingested by the invertebrate host for their further development.

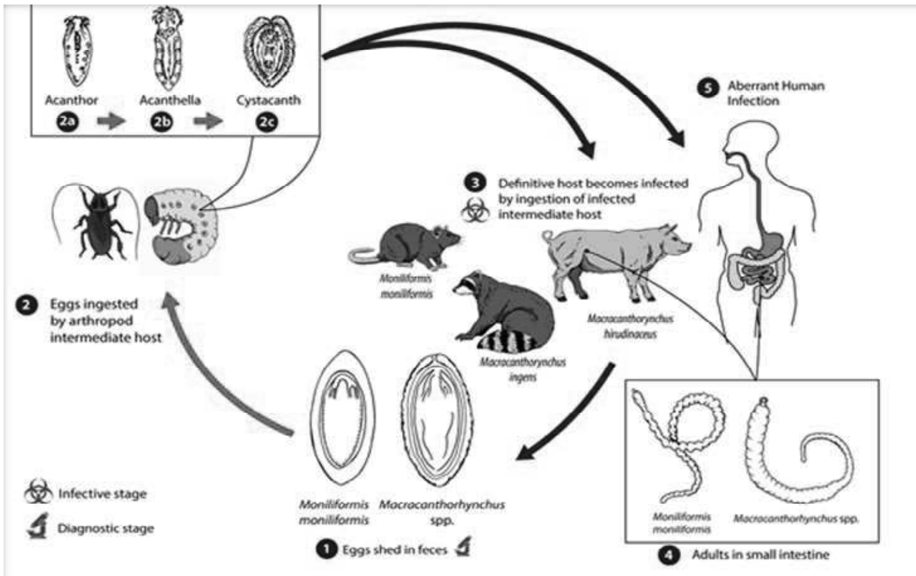

Fig. 4.19 *Life cycle of an Acanthocephalan*

- Eggs are shed in the feces of the definitive hosts.
- The eggs contain a fully developed acanthor larva when shed in feces. The liberated eggs are ingested by an intermediate host like insect.
    - o Within the hemocoelom of the insect, the acanthor larva molts.
    - o After molting, it forms a second larval stage called an acanthella.
    - o After 6–12 weeks, the worm reaches the infective stage called a cystacanth.
- The definitive host becomes infected upon ingestion of intermediate hosts containing infective cystacanths.
- In the definitive host, liberated juveniles attach to the wall of the small intestine, where they undergo final maturation and mate in about 8–12 weeks.
- In humans, the worms rarely develop to full maturity or produce eggs.

Affinities of Phylum Acanthocephala

The acanthocephalan worms were first observed at the beginning of the 18th century but were clearly distinguished from other intestinal worms until 1771 when Koelreuther proposed the name Acanthocephalus for one obtained/isolated from fish. In 1776, Zoega and O.F. Muller, without knowledge of Koelreuther's work proposed the name Echinorhynchus to a similar fish parasite. In 1803, Zeder gave these worms a common name "*Haken wurmer*" (hooked worms) and Rudolphi (1809) changed this into the form Acanthocephala (Greek, akantho = spiny; kephalo = pertaining to the head) by which the group has since been known.

The position of the Acanthocephalans is still not clearly understood. At the present time, there are two dominating views, one associating the Acanthocephala with the Platyhelminthes and the second one associating them with Aschelminthes. In the following section, we shall discuss the similarities and dissimilarities between the three groups.

Similarities of Acanthocephala with Platyhelminthes

- Presence of a proboscis armed with spines occurs in certain cestodes and the proboscis of Trypanorhyncha (Phylum-Platyhelminthes, Class- Cestoda) and Acanthocephala is very similar as far as the shape and arrangement of hooks is concerned.
- Cuticle and syncytial nucleated epidermis are precent.
- Musculature with both circular as well as longitudinal fibres are present.
- Excretory system consists of Protonephridia of flame-bulbs.
- Reproductive system, particularly in male bear resemblance to that of Platyhelminthes.
- Embryology in Acanthocephala is similar to that of cestodes.
- Serological tests also show a relationship of Acanthocephala with cestodes rather than nematodes.

Similarities of Acanthocephala with Aschelminthes

- The partition of the body into the presoma and the trunk as observed in priapulids and the gordiacean larva.
- Presence of a proboscis armed with spines is found among the Aschelminthes in echinoderids, priapulids and gordiacean larva.
- Presence of superficial segmentation, at times involving musculature, is also visible in rotifers, echinoderids, priapulids and nematodes, etc.
- Body is covered with cuticle.
- Body covered by a syncytial epidermis with a few giant nuclei.
- A pseudocoel cavity in present.
- Reduction of gut to a strand as observed in male rotifers.
- Presence of flame-bulb protonephridia
- A close relationship of nephridial and reproductive systems has also been observed in priapulids and rotifers.

Differences of Acanthocephala from Nematoda

(1) Presence of proboscis in Acanthocephala, however it is absent in nematodes

(2) Digestive tract is absent in Acanthocephala, however, a complete digestive tract is present in nematodes.

(3) Presence of circular muscles in Acanthocephala, however, they are entirely absent in the body wall of nematodes

(4) Presence of ciliated excretory organs

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(5) Marked differences have been observed in the Peculiarities and complexities of reproductive system.

Thus, it is difficult to conclude whether the Acanthocephala are allied to the Platyhelminthes or to the Aschelminthes. The general structure of Acanthocephala exhibits more resemblance to Aschelminthes whereas embryology of Acanthocephala exhibits resemblance with the Platyhelminthes. Hence, on the basis of available evidences, Acanthocephala have been assigned an independent phylum.

(3) Nemertins

- The Nemertea are commonly known as ribbon worms or proboscis worms due to the presence of long proboscis. The proboscis is eversible lying in a sheath on the dorsal side of the gut.
- Body is slender, worm-like, soft, highly contractile and un-segmented.
- Adult worms' range in size from a few millimetres to several centimetres in length.
- Most nemertean are pale yellow, orange, green or red in colour.
- Most species of phylum Nemertea are marine, predominantly benthic or bottom dwellers, with an estimated 900 species known.
- However, a few species of nemertines have been recorded from freshwater and terrestrial habitats as well.
- They are triploblastic, i.e., having three germ layers namely ectoderm, mesoderm and endoderm.
- They are acoelomate animals lacking a true body cavity.
- They are bilaterally symmetrical unsegmented worms. (Bilateral symmetry-Symmetrical arrangement of an organism or part of an organism along a central axis, so that the organism or part can be divided into two equal halves. Bilateral symmetry is a characteristic of animals that are capable of moving freely through their environments.)
- They possess a ciliated epidermis containing mucous glands.
- Body musculature forms two or three layers.
- They have complete digestive tract with lateral diverticula and terminates in posterior anus.
- Most nemerteans are carnivores, feeding on worms, clams, and crustaceans.
- Some species are scavengers, and some nemertini species, like *Malacobdella grossa*, have also evolved communalistic relationships with some molluscs.
- True respiratory organs are absent.
- They have closed circulatory system.
- Excretory structures are paired, excretory tubules provided with flame cells.
- Nervous system is well developed and comprises cerebral ganglion, longitudinal nerve cords, and transverse commissures.

- A pair of ciliated pits are also connected with the brain.
- Nemertins are dioecious, i.e., sexes are separate.
- Both male and female gonads are simple sac-like structures.
- Development is either direct or indirect consisting of a free-swimming pilidium larva.
- Asexual reproduction occurs by fragmentation.
- The nemertines are non-parasitic worm like organisms.
- Nemerteans have almost no predators and two species are sold as fish bait.

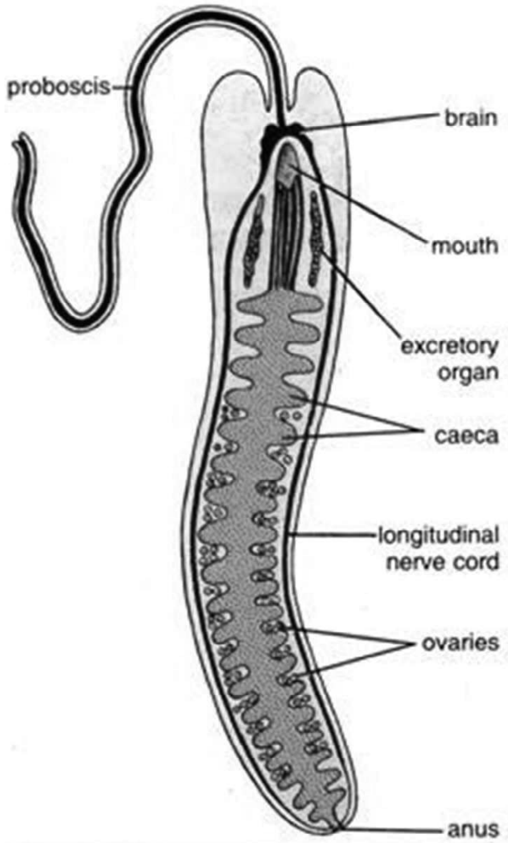

Fig. 4.20 *Generalized Structure of a Nemertine*

Classification of Phylum Nemertea

The phylum Nemertea is divided into two classes:

I) Anopla

II) Enopla

Class 1. Anopla

1. Mouth of the species belonging to the Class Anopla is located at the back of the brain.
2. Stylet is absent in the proboscis region.

   Class Anopla comprises two orders.

Order 1. Palaeonemertea

1. Body wall musculature comprises two to more layers.
2. Larval stage is absent in the life cycle.

   Examples: *Carinoma, Tubulanus*

Order 2. Heteronemertea

1. Body wall musculature is three layered.
2. Life cycle consist of Pilidium larva.

   Examples: *Cerebralutus, Micrura, Lineus*

Class 2. Enopla

1. Mouth is situated at the front of brain.
2. Stylet is present in the pro-boscis region.

   Class Enopla consist of two orders

Order 1. Hoplonemertea

1. Stylet is present in the proboscis region.
2. Mostly of freshwater and terrestrial forms.

   Examples: *Prostoma, Ototyphlonemertes, Gononemertes*

Order 2. Bdellonemertea

Stylet is absent secondarily.

For instance, single genus ***Malacobdella***. Most species belonging to this genus reside in the mantle cavities of some marine bivalves.

Structure of Nemertine

The body of a nemertine is mostly narrow, elongated, cylindrical or depressed, un-segmented as well as devoid of appendages. The length of a nemertine varies from a few millimetres to approximately twenty-seven metres. A prominent/distinct head is absent, however, in few cases, a short narrow posterior region or tail is present. The ectodermal surface is covered with vibratile cilia and often the integument is brightly coloured. The epidermal gland cells secrete a mucus secretion which acts as a protective sheath for the animal. The mouth is located at the anterior end on the ventral side. A long hollow muscular organ known as proboscis protrudes out via a small opening present near the mouth.

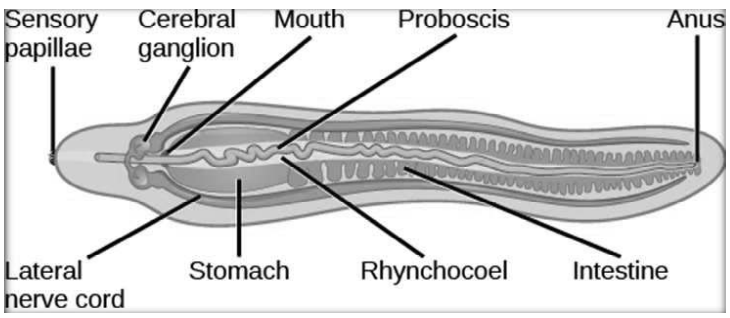

Fig. 4.21 *General Anatomy of a Nemertea*

Body Wall of Nemertine

Body wall of a Nemertea is composed of epidermis, dermis, circular as well as longitudinal muscle layer. The outermost epidermal layer of the body wall of a Nemertea is composed of columnar cells. These cells are ciliated. Epidermal layer also contains unicellular glands arranged in clusters. The gland cells are scattered irregularly between the narrower portions of the ciliated columnar epidermal cells. The secretion of the unicellular glands i.e., mucus forms a protective sheath or tube on the surface of the organism. A thin basement membrane is present beneath the epidermis. Epidermis is followed by dermis forming a connective tissue. A thick muscular layer is present beneath the dermis. In few species of nemertines, only two layers of muscle fibres i.e., an outer circular and an inner longitudinal is present. However, in other species, apart from these two, a third (longitudinal) layer is also there. Apart from unicellular glands, several nemertines also possess packet glands. The packet glands may be included within epidermis as observed in paleonemertines or these packet glands may sink into the sub-epidermal tissue as observed in heteronemertines.

Proboscis of Nemertine

Nemertines are commonly known as ribbon worms or proboscis worm due to the presence of long, coiled, hollow muscular organ known as proboscis. The proboscis is the most characteristic feature of nemertines. The proboscis is retractile in nature and lies in a sheath on the dorsal side of the gut. When the proboscis is retracted, it lies within the body inside a fluid-filled cavity known as rhynchocoel which is completely shut off from the exterior. The muscular walls of the rhynchocoel form the proboscis sheath. The epithelial cells of the proboscis, in majority of the species, secrete rods which is identical to the rhabdites of Turbellaria. The blind end of proboscis is attached to the posterior end of the sheath with the help of the retractor muscle which prevents the eversion of the proboscis beyond a certain point, and by means of which also it is retracted. The part of the proboscis present in front of the brain is referred to as rhynchodaeum which opens to the exterior via proboscis pore. The proboscis may be armed with styles at the tip in some species or it remains unarmed. The lining epithelium of the proboscis closely resembles the surface epidermis from which it has been derived. The musculature of proboscis as well as that of proboscis sheath is exactly similar to body wall musculature. The proboscis comes out with great force as muscular contraction exerts pressure in the fluid of the rhynchocoel. Due to this, the proboscis turns inside out (everts) and protrudes. Withdrawal of the proboscis is brought about by retractor muscles.

Digestive System of Nemertine

A definite head is absent. The mouth is located at the anterior end on the ventral side. A long hollow muscular organ known as proboscis protrudes out via a small opening present near the mouth. The digestive tract is complete. It is a simple ciliated tube which runs throughout the length of the body from the mouth to the anus. The anterior part of the digestive tube is generally a simple tube-oesophagus (stomodaeum), however, it may be more complex in some species and is divided into various regions, occasionally with paired diverticula. Posteriorly, it opens into the intestine. The intestine may be a simple unconstricted tube in some species while in others it might be slightly constricted at intervals by the paired gonads. In most species, the constrictions corresponding to the gonads are very deep so that the intestine comes to be provided with two rows of lateral diverticula or caeca which may be branched. The lateral diverticula or caeca are separated from each other via incomplete transverse septa composed of dorsoventral muscular fibres. This arrangement of the caeca and septa along with the alternately arranged gonads brings about an appearance of imperfect metamerism as observed in flatworms or Platyhelminthes. The intestine finally opens to the exterior via anal aperture at the posterior end of the body. The nemertines usually feed at night on living or dead animals mostly annelids, molluscs, crustaceans and fishes, etc.

Circulatory System of Nemertine

The circulatory system of nemertine consists of three principal vessels: - longitudinal trunks, a median dorsal and two lateral blood vessels. The longitudinal trunks lie in the parenchyma, one on each side of the intestine and one just above it. These lateral blood vessels have branched tributary. The lateral vessels communicate with each other both anteriorly and posteriorly by spaces lined by only delicate membranes respectively known as cephalic lacuna and anal lacuna. The contractions of the walls of the large vessels propel blood. Blood is colourless and consist of rounded or elliptical cells. are observed in some species. However, in few species blood is red in color due to the presence of respiratory pigment i.e., haemoglobin. Heart is absent in them. Blood does not circulate as such due to lack of pumping organ. However, blood circulation is brought out by the general movement of the body.

Excretory System of Nemertine

The excretory system of nemertine comprises a pair of longitudinal vessels which sends off branches. Each longitudinal vessel opens to the exterior via nephridiopore on each side. The fine terminal branches of the excretory system are associated with ciliary flames.

Respiratory System of Nemertine

Specialized respiratory structures are absent. However, recent studies suggest that respiration is performed by taking in and giving out of water via the mouth by the oesophagus. Respiration also takes place by the diffusion of oxygen through the general body surface.

Nervous System of Nemertine

The nervous system comprises brain. The brain itself is composed of two pairs of ganglia, dorsal and ventral. The dorsal ganglia is situated above and the ventral ganglia. The dorsal and ventral ganglia of each pair are connected together by commissures. From the brain, a pair of thick longitudinal nerve cords pass backwards. These nerve cords run throughout the length of the body. Usually, these nerve cords are lateral in position. The lateral nerve cords usually meet posteriorly in a commissure situated above, however as an exception in a genus, it meets below the anus. A third median dorsal nerve of smaller size than the lateral nerve cords extend backwards from the dorsal commissure of the brain. The position of brain and lateral nerve cords, or the system of commissures and nerve branches varies in different groups.

Sense Organs of Nemertine

Sense organs comprised of sensory nerve cells, sensory pits as well as eyes. Specialized sense organs are confined to the anterior region of the body; however, the sensory nerve cells are scattered in the epidermis of both anterior and posterior ends. The sensory nerve cells are slender-like in appearance. Each sensory nerve cell bears a hair-like process on the outer side. These hair like process are tactile (connected with sense of touch) in function. Sensory pits are present all over the body. Eyes are present in majority of nemertines and in the more highly organised species occur in considerable numbers. The structure of the eye varies with species. In some species, it has a simple structure; however, in other cases eye is a highly developed structure, having a spherical refractive body with a cellular vitreous body as well as a retina comprising of layer of rods bounded in a sheath of dark pigment. Each rod has a separate nerve branch connected with it. A few nemertines also possess statocysts containing statoliths. The statocyst is a balance sensory receptor present in some aquatic invertebrates, including bivalves, cnidarians, ctenophorans, echinoderms, cephalopods, and crustaceans. The statocyst consists of a sac-like structure containing a mineralised mass (statolith) and numerous innervated sensory hairs (setae).

Locomotion of Nemertine

The adult nemerteans glide on a trail of mucus Cilia and peristaltic contractions of body muscles provide the propulsive forces.

Reproductive System of Nemertine

Most nemertines are dioecious, i.e., sexes are separate, however, a few may be hermaphroditic. The gonads (both male and female gonads) are simple, tubular, sac-like structures, located in the intervals between the intestinal caeca. The sac like male and female gonads are lined by cells which give rise to germ cell i.e., ova or spermatozoa respectively. Each sac like gonad opens via a narrow duct leading to the dorsal, rarely to the ventral surface, or which it opens by a pore to release the mature germ cell.

Development of Nemertine

Nemertines shows two different types of development, i.e.,

a) Direct

b) Indirect

Pilidium is the characteristic larval form of nemertines. This is a helmet/hat-shaped larvae having side lobes like ear-lappets, and a bunch of cilia representing a spike. During metamorphosis, numerous ectodermal invaginations growing inwards around the intestine, fuse together to form the integument as well as the body wall of the future worm, which then frees itself and develops into the adult form. In other nemertines, there is another ciliated creeping larva known as Desor. Desor's Larva (named for the Swiss scientist E. Desor, 1811-1882), a pelagic or benthic larva of certain nemerteans that develop without the pilidium stage. Desor's larva undergoes metamorphosis accompanied by the formation of the so-called imaginal disks, from which the skin and body of the young nemertean form. The larval skin eventually falls off.

Affinities of Nemertine

It is very difficult to determine the phylogenetic position of nemertines. They exhibit affinities with lower chordates, vertebrates as well as the Platyhelminthes.

Similarities of nemertines with lower chordates

Nemertines exhibits several characters in common with a typical lower chordate like *Balanoglossus.*

- Elongated vermiform body
- External metamerism is absent.
- Skin is smooth and composed of unicellular glands.
- Presence of Ectodermal nerve plexus.
- Anus is terminal in position.
- Simple metamerically situated gonads
- Retractile proboscis of nemertines is equivalent to the non-retractile proboscis of Balanoglossus.

Similarities of nemertines with Vertebrates

Nemertines are generally considered to be the ancestral forms of vertebrates due to following similarities:

- Dorsal nerve of Nemertines resembles the spinal cord of vertebrates.
- Lateral nerves resemble the nerves of lateral lines of fishes.
- Cerebral ganglion resembles the brain of vertebrates.
- Proboscis sheath suggests the notochord of vertebrates.

Similarities of nemertines with Platyhelminthes

- Like Platyhelminthes or flatworms, the general shape of the body is flat, ribbon-like or tape-like without any external segmentation.
- Body is entirely covered with a ciliated epithelium comprising of gland cells.
- Thick, highly contractile muscles are present beneath the cuticle
- The space between the body wall and the gut is filled with mesenchyme.
- Absence of coelom
- Excretory system consists of flame cells.
- Nervous system is similar to that of flatworms.

Differences of nemertines with Platyhelminthes

- Presence of a defined body wall

- Presence of a complete digestive tract with a second opening i.e., the anus
- Vascular system present is of higher organisation
- Higher organisation as well as complexity of organs and tissues in general
- Presence of a massive brain forming a ring around the digestive tract
- Presence of proboscis independent of the gut

Thus, it is difficult to conclude whether the nemertines are allied to the Platyhelminthes or to the lower chordates or vertebrates. Hence, on the basis of available evidences, Nemertea have been assigned an independent phylum.

(4) Entoprocta/Endoprocta

Let us study the structural organization and affinity of phylum Entoprocta/ Endoprocta.

Structural Organization and Affinity of Phylum Entoprocta/Endoprocta

This group represent a cluster of tiny, sedentary and marine animals which are either solitary or colonial forms. Superficially, these animals resemble the phylum 'hydroidea' and 'bryozoa'. In the past, this group was placed under bryozoa (ectoprocta), however, recently they have been excluded from phylum 'Bryozoa' and included them under the phylum 'entoprocta'. Almost all their forms are marine, excepting the fresh-water form, called the 'urnatella'.

The stalked cup-like body of the entoprocta is called calyx which bears a crown of tentacles at its free edge. The hollow or cavity of this cup is called atrium or vestibule and it include both mouth as well as anus. The digestive tube is curved to form a U-shaped structure. They are acoelomate as the empty space between the body wall and the digestive tube is filled up with parenchyma. The excretory system consists of a pair of ciliated intracellular tubes which represent protonephridial type of excretory organs. Each excretory tube begins with a flame cell. The two excretory ciliated intracellular tubes may open individually or may fuse together to form a common duct opening into the cloaca. The nervous system is characterized by a sub-oesophageal ganglion which is bilobed in 'Loxosoma'. The sexes may be united or separate (gonochoristic). In the solitary form (loxosoma), the body is divided into a calyx and a stalk which possesses a foot-gland at the base, whereas in the colonial forms (pedicellina and urnatella) the body of each zooid is separated from the stalk by a diaphragm. Asexual reproduction takes place by the process of budding from any part of the body and the buds stay attached to the parental body forming colony. Development is indirect and the cleavage is of 'spiral' type forming a free swimming ciliated larva. It is a trochophore type larva which feeds on planktonic organism. After a brief swimming phase, the larva fastens itself to the free surface of some other animal with the assistance of an attachment organ located at the postero-ventral position and then transforms into the zooid form. Based on development, it is presumed that they are linked to those groups that have trochophore larva during their development and most likely have evolved from a common ancestor, shared with the coelomate bryozoans.

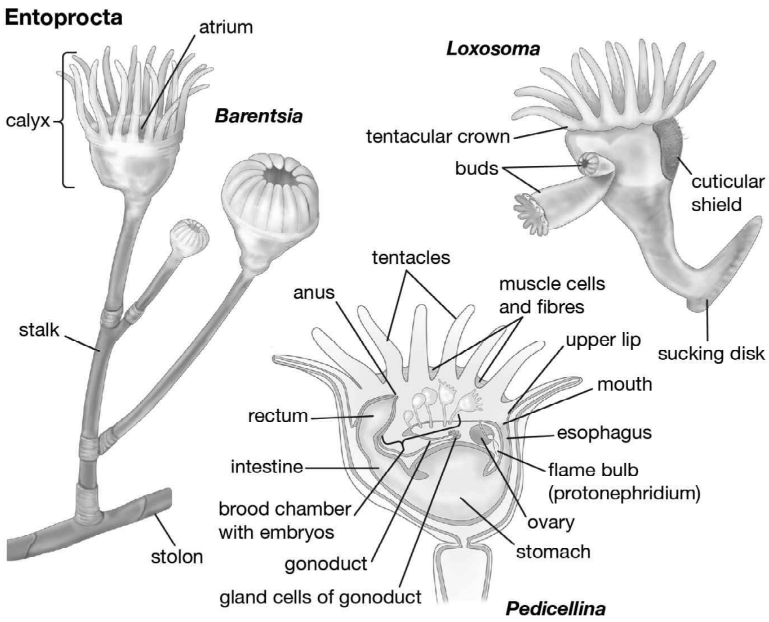

Fig. 4.22 *Entoprocta*

Distinctive Characters of the Phylum

- Phylum entoprocta are tiny, sedentary mostly marine animals.
- They are either solitary or colonial forms.
- They exhibit bilateral symmetry.
- They are un-segmented acoelomate (lacking a coelom) animals.
- Body of phylum entoprocta is divided into three parts calyx, stalk, and stolon.
- The mouth and anus of the animal open inside the circlet of tentacles, hence, called entoprocta.
- They have a U-shaped alimentary canal.
- They lack both circulatory and respiratory organs.
- The excretory system is protonephridial.
- They are hermaphrodites.
- The cleavage is spiral and determinate.
- Development leads to a ciliated planktotrophic trochophore larva. For example – pedicellina, myosoma, loxosoma, urnatella.

Affinities of Phylum Entoprocta With Ectoprocta

Previously both entoprocta and ectoprocta were grouped under a single phylum—Ectoprocta as the two groups bear several similar features:

- Existence of a crown of ciliated tentacles.
- Presence of U-shaped alimentary canal in both the phylum.
- The larva of entoprocta seemingly resembles the 'cyphonautes' larva of ectoprocta.

Dissimilarities

- Entoprocts are acoelomates but Ectoprocts are coelomate (having a coleomic cavity) animals.
- In Ectoprocts, the anus and mouth are situated within the circlet of tentacles but in Entoprocts, anus remains at the outside of circlet of tentacles and the mouth is only located within the crown of ciliated tentacles.
- The protonephridia and gonoducts are present in Entoprocts but both the structures are absent in Ectoprocts.

Phylogenetic Relationship of Phylum Entoprocta

Brien and Papyn concluded that the entoprocts differ unquestionably from the entoprocts in their embryology, metamorphosis, adult anatomy, and consequently support their separation as two distinctive phyla. Hyman (1951) and Barnes (1980, 1987) supported the above view. Further, colonial entoprocts exhibit superficial resemblance with bryozoans. Hence, some scientists consider that bryozoans might have evolved from entoprocts. Molecular studies of 18S RNA genes indicate that Entoprocts are protostomes (group of animals in which mouth develops from blastopore).

B. Coelomate: Phoronida, Brachiopoda and Bryozoa/Ectoprocta

Let us study them in detail.

1. Phoronida

Let us study the structural organization and affinity of phylum phoronida in detail.

Structural Organization and Affinity of Phylum Phoronida

The phoronids are a very important group of the lophophorate coelomates. In 1888, Hatschek first coined the name of the group as phoronid. Another name, Phoronidea, proposed by Lang has not/been accepted universally.

Before the establishment of this group, many zoologists used to study the biology of phoronids. In the year 1847, J. Muller and his student Wegener observed several free-swimming animals on the surface of the sea. Both mistakenly assumed them as adult forms and named them Actinotroch Abranchiate; but, their larval nature was correctly pointed out by Gagenbaur in 1854.

Wright (1856) was the first one to observe an aggregate of many adult worms inhabiting the tubes and called these animals as phoronis. By observing the developmental sequences, Kowalevsky (1867) and Metschnikoff (1871) established the fact that the actinotrocha larva metamorphosed into adult phoronis. This observation established the fact that the Phoronis is the adult worm whereas the actinotrocha is its larval stage. To date, two genera (namely: *Phoronis and phoronopsis*) with 10 species are known.

Characteristic Features of Phoronids

- They are exclusively marine.
- Bilaterally symmetrical, sedentary coelomate worms with trimeric construction

NOTES

- Sessile, vermiform body that is enclosed in a leathery tube
- Body is differentiated into three distinct parts:
  - o Prosome
  - o Mesosome
  - o Metasome, each consisting its coelomic cavity

The epistome is formed by the prosome. The mesosome bears the lophophore with the mouth and two rows of tentacles. The metasome or trunk is slender and cylindrical in shape with a bulb-like posterior end known as ampulla.

- Horse-shoe shaped lophophore with spirally coiled lateral cornu.
- Alimentary canal is U-shaped with anus present outside lophophore.
- Closed blood vascular system having red blood corpuscles with haemoglobin.
- Distinct heart is not seen.
- Excretory system composed of a pair of metanephridia with ciliated nephrostome which are located on either side of intestine.
- Nervous system consists of nerve fibres and nerve cells that are present within epithelial tissue.
- Hermaphrodite or monosexual but also can reproduce asexually.
- Indirect development.
- Cleavage type is holoblastic, equal, and radial.
- Actinotroch larva forms during development.

Description of Phoronis Bhadurii Species

One of the phoronids classified as *Phoronis bhadurii species* were collected at Digha coast from tubes covered with sand small fragments of molluscan shell. The body of the animal is long, cylindrical and stout. The total length of the body is approximately 59 to 94 mm. The breadth of body below the ionophore is 2mm whereas at posterior end it is around 1 mm. The number of tentacles is approximately 1406 with tentacle having a length of 6.5mm to 8mm. The cuticle is transversely striated. The mouth of the animal is surrounded by several ciliated tentacles.

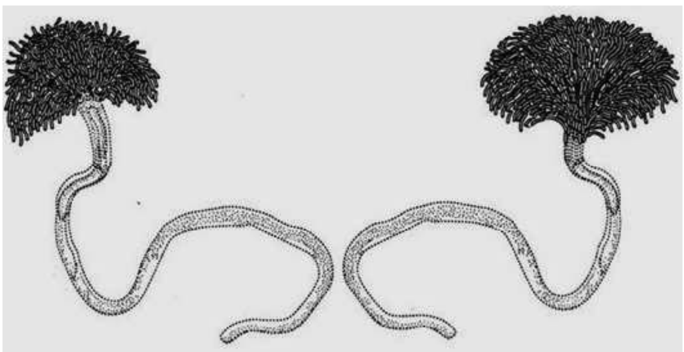

Fig. 4.23 *Diagrammatic Representation of Phoronis Bhadurii sp.*

Affinities of Phoronids

The biological status of the phoronida in the animal kingdom is controversial due to the peculiar anatomical organization and structural resemblances with other groups since its discovery. Amongst all other groups, brachiopoda and Ectoprocta resemble the phoronida very closely.

The lophophorate coelomates is the term given collectively to phoronida, brachiopoda and ectoprocta. Based on their structural similarities, these three groups were referred by earlier zoologists, chiefly by Milne-Edwards (1843) and T. H. Huxley (1853) as a single phylum molluscoidea. However, due to their major structural divergences and absence of mutual relationships, the format has been totally abandoned. In 1882, Caldwell, also tried establishing the relationship between these three groups. Hatschek (1888) instead placed them in different classes under the phylum tentaculata. Similar attempts of combining them under one phylum seem to be inappropriate though. Later on, Hyman gave another name, lophophorata for these groups due to the presence of lophophore. Despite all efforts that were made to inculcate them under one common group, it is improper to figure out any definite affinity between them, as they consist of several structural differences. This fact will be clear from the subsequent discussion:

Relationship with Brachiopoda

The phoronida show close resemblances with brachiopoda.

Similarities

- Similarly constructed horseshoe-shaped lophophore
- Epistome present
- Alimentary canal U-shaped
- Presence of a coelomic septum separating the mesosome and metasome, although not so well developed in brachiopoda, except on crania where the septum is complete
- Sub-epidermal nervous plexus that forms a nerve centre in the mesocoel present
- Presence of a pair of metanephridia
- These serves as coelomoducts of metacoel which also act as gonoducts
- In both of them, the mouth originates directly from the blastopore, *i.e.,* they are protostomes.
- The dorsal surface between mouth and anus is extremely shortened in both.

Dissimilarities

The phoronida and brachiopoda have many structural differences too which do not support the supposed affinities. These are:

- Supraenteric nerve centre in phoronida but subenteric in brachiopoda.
- Two sets of tentacles are present in phoronida namely: larval set and definitive set. However, in brachiopoda, larval tentacles are absent.
- The brachiopod shell cannot be compared to the exoskeleton of phoronida.

NOTES

- The chitinous setae present in larval and adult brachiopoda lack corresponding match in phoronida.
- Phoronida has a more developed circulatory system than brachiopoda. The blood vascular system consists of closed blood vessels in phoronids, whereas it is of open type in brachiopods.
- The cleavage pattern is spiral in phoronida which is not the case in brachiopoda

Despite of all the similarities in cases, the anatomy and development are still quite different for which the two groups should not be included under a common group. But according to Nicolson (1985), the phoronids are often told as the ancestor of brachiopods because of the somewhat similar embryology of these two lophophorate phyla and presence of mono-ciliated tentacular cells within upstream ciliary collecting system in both.

Relationship with Ectoprocta

Caldwell (1882) also emphasised the relationship between phoronida and Ectoprocta.

The similar features which gave rise to this idea are:

- Presence of nerve centre in mesocoel in both
- Supraenteric kind of nerve centre
- Horseshoe-shaped lophophore
- Presence of epistome
- Alimentary canals bent to form a U-shaped tube in both
- Similar disposition of coelom and a septum that separates the mesocoel from the metacoel

Dissimilarities

A detailed study of the two groups shows much organizational dissimilarity between the two. They differ greatly from both anatomical and embryological viewpoint. The following characteristics act as obstacles to sketch the relationship between them:

- Different origin of coelom as it is of endomesodermal in origin in phoronida, while in Ectoprocta, it is ectomesodermal.
- The region between the mouth and anus is dorsal in Phoronida whereas in ectoprocta it is ventral.
- Circulatory system and nephridia are lacking in ectoprocta but in phoronida both the systems are present as well as well developed.
- The developmental progression differs quite greatly.

Thus, the relationship between ectoprocta and Phoronida cannot be justified because of the presence of wide structural differences.

Among the three lophophorate coelomates, the phoronids are closer to the lophophorate ancestor due to the following reasons:

- Presence of muscular vermiform body with cresentic lophophore.
- A septum between an anterior lophophore bearing part and a posterior trunk.

- Closed type circulatory system with dorsal and ventral vessels.
- Trochophore larva having protonephridia.

Relationship with Annelida

NOTES

The larval similarities form the basis of relationship between annelida and phoronida. This is because of their resemblances, the actinotrocha is referred as a modified trochophore larva by many authors.

The points of resemblances are:

- The tentaculate lophophore of phoronida can be compared to the tentacular crown of sipunculus.
- The nephridia is the source of mature germ cells in both annelida and phoronida.
- The actinotrocha larva and the Trochophore larva share several common features:
    - o The larval forms of both are free-swimming ciliated pelagic forms with distinct pre-oral lobe.
    - o The ciliary band gives rise to the girdle of larval tentacles. The cilia that borders the preoral lobe of actinotrocha represents the metatroch and prototroch of trochophore respectively. Both have a similar disposition of the telotroch.
    - o The apical plate of Trochophore (sometimes bearing eyes) is represented be a thickening of the ectoderm of the preoral lobe in Actinotrocha.
    - o Presence of a pair of solenocytic nephridia in both
    - o The alimentary canal is similarly placed and has similar divisions in both the larval forms.

After all these similarities, a closer examination discloses that the annelida and phoronida are essentially different in their organisation.

1. The most significant difference lies in the development of mesoderm.
2. Actinotrocha have an endomesodermal mesoderm.
3. The body of phoronida is unsegmented whereas in annelida segmentation is the major characteristic feature of their organisation.
4. In Trochophore, mesoderm is orderly arranged in the form of teloblastic bands.

Therefore, the connection between annelida and phoronida cannot be reasoned by critical examination; however, the larval resemblances are quite outstanding. These larval similarities may be present due to their adaptive convergence.

Relationship with Hemichordata

Many zoologists like A. Masterman (1897) tried to establish the relationship between phoronida and hemichordata. The relationship is chiefly based on the similarities in the larval forms, i.e., the actinotrocha larva and the tornaria larva of hemichordata.

Similarities

- The body division of hemichordata (proboscis, collar and trunk) can be compared to the body division of the phoronida (epistome, mesosome and trunk or metasome).

NOTES

- A pair of glandular pockets which open into the proximal end of the stomach of phoronida is supposed by to be the paired notochord.
- Existence of a septum between the middle and posterior sectors of the body in both hemichordates and phoronids.
- The position of the tentaculate lophophore corresponds to the tentaculated arms of cephalodiscus, a member of hemichordata.
- Superficial similarities in the disposition of larval coelom are observed.

Dissimilarities

A methodical examination exhibits much dissimilaritics such as:

- The embryological data does not justify the three divisions of the body of phoronida. Phoronida has two divisions in the body as the epistome of phoronida is not considered a body region and lack coelom like that of proboscis of hemichordata.
- The mesocoel of phoronida opens to the exterior through metanephridia which are lacking in hemichordata.
- The coelom in actinotrocha is separated into three compartments whereas; the collar coelom and trunk coelom are present in paired condition in Trochophore.
- The notochordal nature of the glandular pockets in phoronida is hard to interpret.

From the above discussion it is quite clear that most of the opinions made to establish the relationship between the phoronida and Hemichordata are not substantiated by the embryological facts.

Majorly, the resemblances are based on presumptions except for the septum present between the middle and posterior sectors of the body and the similarity between the tentaculate lophophore and the tentacular crown in cephalodiscus. Consequently, it may be suggested that the two groups inherited these features from a remote common ancestor.

2. Brachipoda

Let us study brachipoda in detail.

General characteristic of Brachiopods

1. The Brachiopoda are commonly known as ”lamp-shells”.
2. Brachiopods are exclusively marine. They are present in all seas from the intertidal zone to the deep sea (about 5000 meters).
3. Brachiopods are bilaterally symmetrical animals.
4. Body of Brachiopods is un-segmented body.
5. Brachiopods are encased within a bivalve shell having dorsal and ventral valves.
6. The shells are calcific or chitinophosphatic.

7. Brachiopods are triploblastic animals.
8. Brachiopods are sedentary or sessile coelomate ani-mals.
9. Brachiopods are attached to the substratum via an elongated muscular stalk, called pedicel or peduncle.
10. The lophophore of the Brachiopods is a horseshoe-shaped structure which surrounds the mouth.
11. The lophophore consists of a pair of coiled or folded arms bearing ciliated tentacles.
12. A true spacious coelom is present in Brachiopodes.
13. The alimentary canal of the Brachiopods is a U-shaped gut with anus present either outside lophophore or it is entirely absent.
14. Digestion is intracellular (e.g., Lingula) or extracellular.
15. The blood vascular system is of open type. Circulatory system consist of a contractile heart vesicle and ciliated blood vessels/channels.
16. Excretory system consist of one or two pairs of metanephridia. It also serve as gonoducts.
17. Nervous system of Brachiopods consist of an extensive nerve net as well as a circumoesophogeal nerve ring.
18. Brachiopods are dioecious, i.e., sexes are separate.
19. In Brachiopods, gametes become mature in the coe-lom and exit via metane-phridia.
20. Fertilization is external.
21. Cleavage is holoblastic and radial in nature.
22. Coeloblastula is present.
23. Coeloblastula transforms into gastrula by the process of emboly.
24. Coelom formation is either enterocoelous or schizocoelous.
25. Blastopore becomes anus. The terms “deuterostomes” and “protostomes” are originally defined as distinct ways of forming the mouth from the blastopore, a depression that appears in an early stage of the embryo. However, some “protostomes” forming the mouth using a process more like that typical of deuterostomes. Hence forming the mouth via a deuterostome-like process does not imply that brachiopods are affiliated with deuterostomes.
26. The life cycle consists of a ciliated trochophore-like free-swimming larva.

Classification of Brachiopods

The phylum Brachiopoda is divided into two classes—

1) Ecardines or Inarticulata

2) Testicardines or Articulata

1) Ecardines or Inarticulata

- Shell valves of species belonging to class Inarticulata are not united by hinge but by muscles only.
- No shelly loop supports the lophophore.
- Anus is present.

The class is further divided into two orders:

a) Atremata

b) Neotremata

a) Atremata

- The shell is majorly composed of calcium phosphate.
- The foramen, via which the pedicle passes out, is formed by both the shell valves.
- For instance: Lingula, Glottidia.

b) Neotremata

- The shell may be composed of calcium carbonate.
- The pedicle foramen is generally restricted to the ventral shell valve alone.
- For instance: Crania, Craniscus, Pelagodiscus, Discina, Discinisca.

2) Testicardines or Articulata

- Shell valves are united by hinge apparatus
- Shelly loop supports the lophophore
- Intestine terminates blindly, i.e., the anus is absent in species belonging to the class Articulata
- For instance: Megellania, Lacazella, Thecidellina, Rhynchonella, Terebratulina, Chlidonoyhora, Dyscolia.

In the following discussion, we shall discuss the *Magellania* as a typical example of the phylum Brachiopoda.

Habit and Habitat of Brachiopoda

Brachiopods are present exclusively marine found at different depths between tide marks to 2900 fathoms. A very large number of Brachiopods lives at moderate depths, down to 500 or 600 fathoms. Magellania is a marine and benthonic animal similar to other brachiopods. Magellania comprises several species which are extensively distributed, however, they are quite plentiful off the coast of New Zealand. These species remain attached by peduncle to rocky ground. They are ciliary feeders (It is the mode of feeding where the movement of cilia generates a current of water to be drawn towards and through the animal, and the food particles in the water are filtered out by the cilia) with lophophore serving as the food catching apparatus. Food particles comprises minute marine organisms specially diatoms.

NOTES

External Structures of Phylum Brachiopoda

a) Shell

The body of the Brachiopod is completely covered by an oval shaped bivalved shell. It is slightly pink in colour. The valves are different in size and are dorsal and ventral in position. Both dorsally and ventrally positioned valves are deeply concavo-convex and their colour varies from pinkish to brown on outside, however, these shells are whitish in colour from inside. The ventral valve is bent posteriorly into a beak like structure ultimately terminating in a foramen for the peduncle. The distal margin of the foramen is left incomplete by the shell proper however it is closed by a small double plate, the deltidium. Directly anterior to the beak is present the curved hinge-line along which the valve articulates with its fellow. On the other hand, just anterior to the hinge-line, the inner surface of the shell is bent/produced into a pair of massive irregular hinge- teeth. Shallow depressions are also observed on the inner surface of the valve towards its posterior end. They must be playing a role in making the attachments of muscles.

The dorsal valve lacks beak like structure, however, its posterior edge forms a hinge-line which is bent in the middle to form a strong cardinal process having a folded surface. When both the dorsally and ventrally located valves are in position, this cardinal process fits perfectly in between the hinge-teeth of the ventral valve, the hinge-teeth in their turn being received into depressions located on each side of the cardinal process. The inner surface of the dorsal valve is produced to form a median ridge or septum. This ridge or septum continues posteriorly with the cardinal process. Two ends of a delicate calcareous ribbon are present on either side of the base of the cardinal process. These calcareous ribbon or shelly loop projects freely into the cavity enclosed between the two valves. The shelly loop has the form of a simple loop bent upon itself. The inside of the dorsal valve consists of muscular impressions. At the external surface of shell, a series of concentric ridges that represents the lines of growth can be observed. The shell of Brachiopods is composed of prismatic rods or spicules of calcium carbonate positioned obliquely to the external surface. The calcareous spicules are separated from each other via a thin layer of membrane. Further, the shell is crisscrossed by perpendicularly disposed delicate tubules closed on the outer surface.

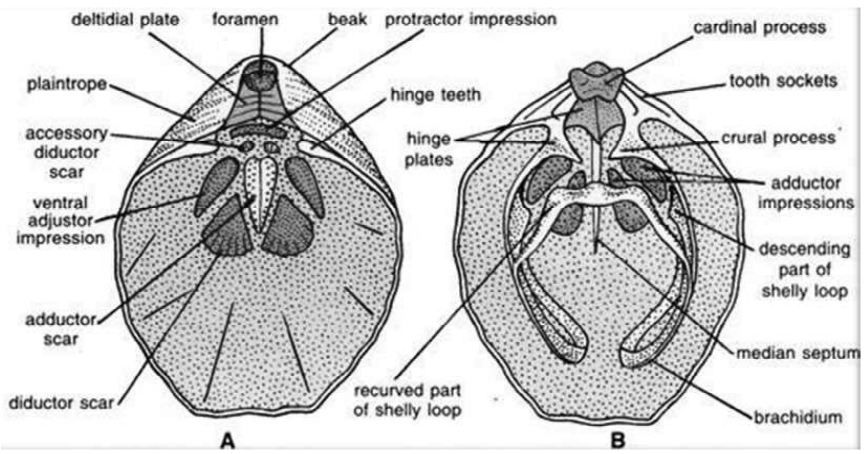

Fig. 4.24 *Shell of Magellania. A- Interior View of Ventral Valve; B- Interior View of Dorsal Valve*

Internal Structures of Phylum Brachiopoda

(a) Mantle

The body proper is positioned inside the posterior end of the shell. Integumentary folds i.e, the dorsal and ventral mantle lobes are observed just below the shell valves or sometimes they are closely associated to the shell valves. A wedge-shaped cavity referred to as mantle cavity is present between the dorsal and ventral lobes. The outer surface of mantle lobes send-off hollow processes which extend into the tubules of the shell. The margin of the mantle lobes is bordered with minute setae lodged in muscular sacs like structures of chaetopods. The mantle lobes are formed by reduplication of the body wall.

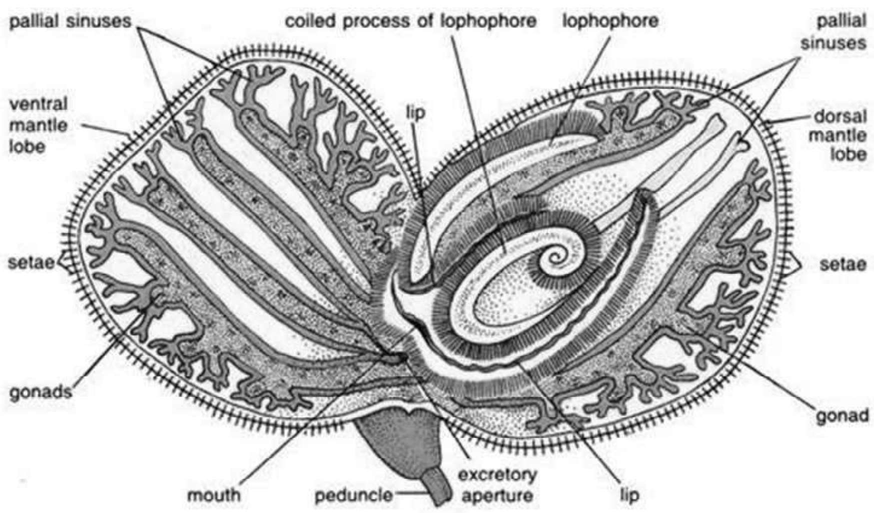

Fig. 4.25 *Internal Structure of Magellania (Shell Removed)*

(b) Body Wall

The body wall of the Brachiopods comprises three layers namely:- an outer epidermis comprising of single layer of cells; a middle layer comprising of connective tissue (more or less cartilaginous at most places) with changing thickness, and a third layer of ciliated coelomic epithelium lining the body-cavity.

(c) Body-Cavity or Coelom

The body-cavity is the true coelom. The body cavity is quite spacious and is further divided into three compartments namely protocoel, mesocoel and metacoel. All these three compartments are incompletely separated from each other. The coelom comprises mesenteries as well as muscles. The mesocoel also send off a large arm canals to the lophophore. The metacoel comprises the main body cavity holding major part of the alimentary canal, shell muscles, nephridia as well as other structures like gonads, etc. It is also continued into the mantle lobes as mantle canal. The coelom is lined by a ciliated epithelium. Body cavity or the true coelom is filled with a coelomic fluid containing several types of free coelomocytes. The coelom communicates to the exterior via a pair of metanephridia.

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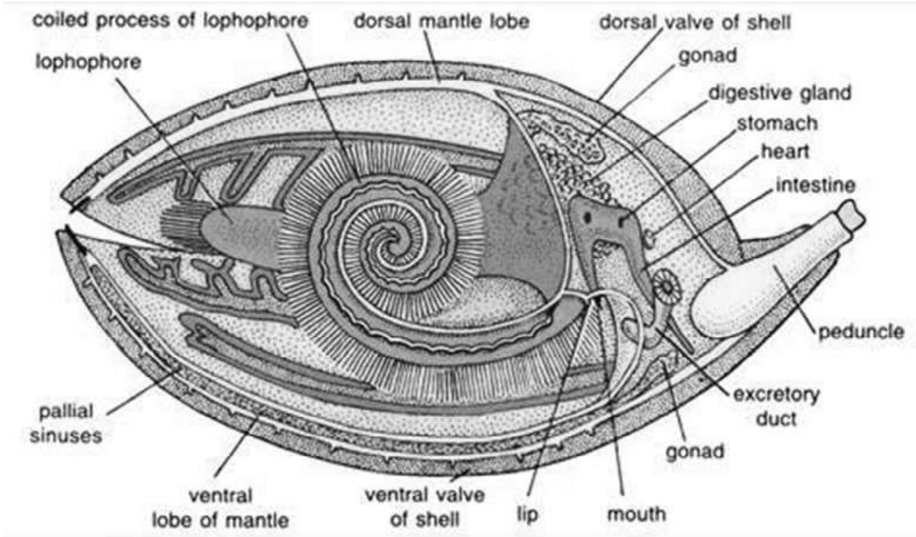

Fig. 4.26 *Longitudinal Section (L.S) of the Entire Animal*

(d) Lophophore

The mantle cavity of the animal is mostly occupied by a large lophophore. The lophophore is basically an outgrowth of the anterior body wall that projects into the mantle cavity. Lophophore almost completely fills the mantle cavity and is fairly voluminous as compared to the size of the animal's body. The lophophore is a prominent horse-shoe-shaped structure comprising of two spirally coiled tentacular arms. The two spirally coiled tentacular arms of the lophophore curve inwards and coil to fit inside the mantle cavity. The middle of the concave edge, which is dorsal in position, is produced to form a spirally coiled offshoot, and is situated coiled towards the dorsal side between the two arms. Internally, the lophophore is hollow and contains a spacious cavity or sinus. The two tentacular arms of the lophophore also receive continuations of the coelom into which project the digestive glands. The lophophore is bordered all over with long ciliated tentacles. These long ciliated tentacles form the outer boundary of a ciliated food-groove, bounded on the inner side by a wavy ridge or lip. Due to action of cilia, microscopic particles (especially diatoms) are swept along the food-groove to the mouth. The lophophore is supported by internal skeleton referred as the brachidium or brachial support. The brachidium consist of a pair of prongs known as the crura. Inside the lophophore, the crura are continued forward as calcareous ribbon to form a loop. This long curve loop is present on the dorsal side and is not attached with the dorsal valve. The lophophore is supported by calcareous structure developing from the inner lamina of the dorsal mantle lobe.

Muscular System of Brachiopoda

Brachiopodes comprises a well-developed muscular system. Two large adductor muscules arise on each side from the dorsal valve. These adductor muscles pass downwards and unite with one another to have a single insertion on the ventral valve. The action of these muscles is to approximate the valve and also to close the shell. A large as well as a small pair of divaricators arise from the ventral valve and get inserted into the cardinal process, which they depress, as this process is positioned posteriorly to the hinge-line. Its depression raises the rest of the dorsal valve and thus open the shell. Two pairs of muscles arise, one from the ventral and the second from the dorsal valve, and inserted into the peduncle referred to as adjusters. The peduncle is fixed in its position, the function of the adjustors is to alter or adjust the position of the animal as a whole by turning it in several directions.

Digestive System of Brachiopoda

The alimentary canal of a Brachiopoda is an U-shaped structure and is lined with ciliated epithelium. The mouth is a narrow crescentic slit-like aperture present in the middle of the lophophore. Mouth is circumscribed dorsally by the brachial fold also known as lip and ventrally by the tentacular fringe of the lophophore. The mouth leads into the oesophagus which ultimately opens into a large stomach. A large branched digestive gland or liver is present on each side of the stomach. It opens into the stomach via a duct. The stomach opens into a narrow and straight structure known as intestine. Intestine is directed downwards and backwards towards the ventral surface and ends blindly. The anus is absent.

Circulatory System of Brachiopoda

Circulatory system of a Brachiopode is simple and of open type. Circulatory system consists of a contractile vesicle known as heart and is found attached to the dorsal mesentery. Various parts of the body are supplied by blood channels arising from the heart. Blood channels are merely spaces inside the mesenteries. These blood channels lack definite wall. The blood flowing inside the blood channels is a colourless and cell free fluid. It is coagulable in nature.

Excretory System of Brachiopoda

Excretory system of a Brachiopod comprises a pair of large metanephridia positioned in the metacoel. Each metanephridium is a tubular structure, one end of which opens into the coelom via wide funnel- shaped nephrostome, whereas the other end extends anteriorly and opens into the mantle cavity via the nephridiopore, positioned one on each side of the mouth. The metanephridia also serve as gonoducts.

Nervous System of Brachiopoda

The nervous system of Brachiopodes consists of a supra-oesophageal ganglion present in front of the mouth as well as a larger infra- oesophageal ganglion present behind the mouth. Both supra-oesophageal ganglion and infra- oesophageal ganglion are connected by oesophageal connective. The infra- oesophageal ganglion sends off nerves to the dorsal mantle, dorsal arms as well as to the adductor muscles and two small ganglia which supply the ventral mantle lobe and the muscles of the peduncle. The ganglia along with the commissures are in direct contact with the ectoderm. No special sense-organs are present in Magellania, however, sense organs like statocysts, eyes and sensory patches can be seen in other brachiopods.

Reproductive System of Brachiopoda

Brachiopodes are dioecious i.e., male and female sexes are separate. The gonads are irregularly shaped structures/organs. Two pairs of gonads are present i.e., one pair of dorsal and one pair of ventral present near the intestine. Gonads sends off branches into the pallial sinuses. When the gametes become mature, they are discharged into the metacoel from metacoel they are conveyed to the exterior via metanephridia which serves as gonoduct.

Fertilisation is external in Brachiopodes. The cleavage is holoblastic and occurs along the radial plane. A coeloblastula is formed as a result of complete radial cleavage (even or uneven). Coeloblastula refers to the stage of embryonic development; a type of blastula. The coeloblastula is typical of certain Coelenterata, lower Arthropoda, Echinodermata, Tunicata, Acrania, Brachiopoda, Cyclostomata, Acipenseridae, and most Amphibia. Coeloblastula resembles a bubble filled with fluid. Coeloblastula eventually forms a gastrula by the process of emboly. Coelom is enterocoelous in origin. Mesoderm differentiates as a single sac structure which becomes separated off from the posterior end of the archenteron by a developing partition. After consequent developmental stages, a free-swimming ciliated larva emerges out which closely resembles to the annelidian trochophore larva. After a brief swimming phase, the larva fixes itself to the substratum by the peduncular region and metamorphoses into an adult.

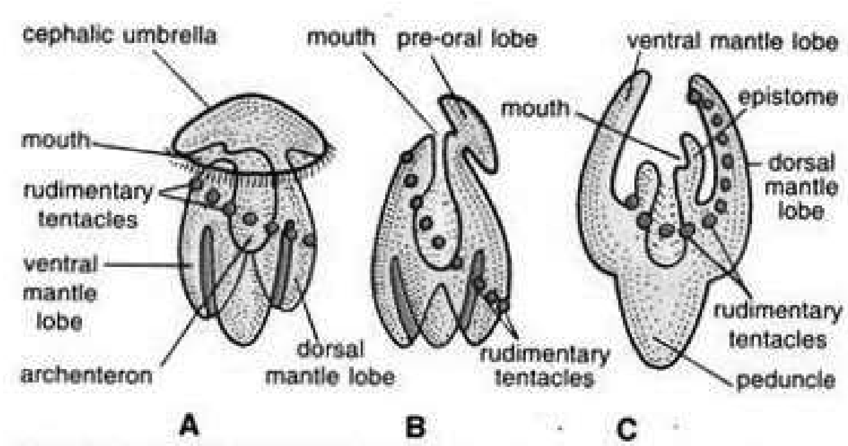

Fig. 4.27 *Stages in metamorphosis.* ***A-*** *Free Swimming Larval Stage;* ***B-*** *Intermediate or Transitional Stages with Reduced Preoral Lobe;* ***C-*** *A Young Brachiopod after the Turning Forward of a Mantle Lobe.*

Affinities of Brachiopoda

Brachiopoda shows affinities with several phyla namely Mollusca, Annelida, Ectoprocta, Chaetognatha and Phoronida. In the following discussion, we shall discuss them one by one.

Affinities with Mollusca

- In both Phyla, bivalve shell and mantle lobes surrounding the body are present. However, shell valves are dorsal and ventral in Brachiopoda whereas shell valves are lateral in Mollusca.
- Presence of a trochophore-like larval form.
- Apart from the two above mentioned similarities, species of both phyla differ in peduncle, internal structure of arm as well as embryology, hence their affinities cannot be supported.

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Affinities with Annelida

Species of phyla Brachiopoda and Annelida share several structural similarities.

Similarities of Brachiopoda with Annelida

- Presence/Indication of segmentation of body. The larval segmentation is comparable in both the Annelida and Brachiopoda.
- Presence of setae in both species of Brachiopoda as well as Annelida.
- Presence of a well-developed perivisceral coelom in both species of Brachiopoda as well as Annelida.
- Presence of metanephridia which also act as gonoducts.
- Presence of a trochophore-like larval form

Due to the presence of above-mentioned similarities, the Brachiopoda may be considered as segmented annelids like Cephalobranch or Oligonereis which have become fixed and transformed their tubes into a pair of calcareous scales (valves) adhering to the epidermis.

However, segmentation of brachiopods is superficial and limited. Segmentation of the body cavity or genital organs or nervous system or segmental organs in the adult is absent. Hence, the resemblances of both phyla i.e., Annelida with Brachiopoda is not much supported.

Affinities with Ectoprocta

The following section discuss the similarities between Brachiopoda and Ectoprocta.

Similarities of Brachiopoda with Ectoprocta

- Species of, i.e, Brachiopoda and Ectoprocta have similar kind of body plan.
- In both the phyla, a coelomic septum is present between mesocoel and metacoel.
- In both the phyla, U-shaped alimentary canal is present.
- The bivalve shell of cyphonautes larva of Ectoprocta is similar/equivalent or comparable to the shell of Brachiopoda.

Differences between Brachiopoda and Ectoprocta

- In Ectoprocta, nervous centre is mainly supra-enteric, however, it is sub-enteric in Brachiopoda.
- The shell of the Brachiopoda cannot be compared to the exoskeleton of Ectoprocta.
- In Brachiopoda the shell is dorso-ventrally placed, however, it is laterally placed in Ectoprocta.
- The chitinous setae are present in the brachiopods, however, setae are absent in Ectoprocta.
- The coelomic septum is poorly developed in most brachiopods.
- The anus is lacking in some brachiopods.

Affinities with Chaetognatha

- The affinities between Chaetognatha and Brachiopoda Lemeere are based mainly on the presence of longitudinal, dorsal and ventral mesenteries.
- The mode of origin of coelom and mesoderm is enterocoelic in both Chaetognatha and Brachiopoda. However, only the outer appearance of mesoderm exhibit some kind of similarity between Chaetognatha and Brachiopoda, but the further development as well as organisation of the adult is quite different in both phyla.

Similarities between Brachiopoda and Phoronida

- Presence of similar lophophore in both phyla.
- Epistome represents the anterior segment of the body in both phyla.
- Presence of U-shaped alimentary canal in both phyla.
- Presence of septum separating the mesocoel and metacoel.
- Presence of a subepidermal nerve plexus.
- In both the phyla, excretory system consist of a pair of metanephridia in the metacoel. It also serves as gonoducts.
- Mouth is derived from the blastopore i.e., both are protostomes.
- The dorsal surface between the mouth and the anus becomes greatly shortened.

Differences between the Brachiopoda and Phoronida

- In Phoronids, the nerve centre is supra- enteric whereas it is sub-enteric in Brachiopoda.
- Two sets of tentacles are present in Phoronids however in Brachiopoda only one set of tentacles is present.
- The shell of Brachiopoda is not comparable to the exoskeleton of phoronida.
- The chitinous setae in Brachiopoda have no counterparts in phoronida.
- In Brachiopoda, circulatory system is of open type, however, in phoronida it is of closed type.
- Phoronids exhibits spiral type of cleavage, however, it is not so in brachiopoda.

Due to the above-mentioned differences both the groups are placed in separate phyla. The similar features are mainly due to distant connection with the ancestral stalk. The current knowledge of the anatomy as well as development of brachiopods suggests that the group may be allotted the rank of an independent phylum.

3. Bryozoa/Ectopracta

Bryozoa are also referred to as the Polyzoa as well as Ectoprocta. They are commonly known as moss animals. The terms "Polyzoa" as well as "Bryozoa" were introduced a year apart, in 1830 and 1831 respectively. As soon as they are named, another group of animals was discovered whose filtering mechanism appears to be quite similar, hence it was included in Bryozoa until 1869, however, further research conducted by the zoologist provided strong evidences that the two groups were very different internally. This new group was given the named entoprocta, while the original Bryozoa were called ectoprocta. Disagreements about terminology persisted well into the 20th century, but "Bryozoa" is now the generally accepted term. Bryozoa represent a phylum of simple, aquatic invertebrate animals. Nearly, all the species belonging to the phylum live in sedentary colonies. Bryozoans are about 0.5 millimetres ($^{1}D_{64}$ inch) long and possess a special feeding structure called a lophophore. Lophophore represents a "crown" of tentacles used for the purpose of filter feeding. Most marine bryozoans live in tropical waters, but a few are found in oceanic trenches and polar waters.

General Characters of Bryozoa

1. Bryozoans are commonly known as moss animals.
2. Most marine bryozoans live in tropical waters, but a few are found in oceanic trenches and polar waters.
3. They are Un-segmented, bilaterally symmetrical animals.
4. Bryozoans are sessile, colonial coelomate animals of trimeric construction except Monobryozoon which lives in solitary state.
5. Body has more than two cell layers, tissues and organs.
6. The individuals or zooids of the colony are connected by organic substance.
7. Each zooid of the colony is covered by a cup-shaped exoskeletal case, called zoecium which is calcareous or chitinous and gelati-nous in freshwater species.
8. Usually, each zooid of the colony is about 0.5 mm in length.
9. Polymorphism is a common feature seen in Bryozoans and physiological exchange takes place via the pores of the walls among the colony zooids.
10. Colonies take a variety of forms, including fans, bushes and sheets.
11. Single animals, called zooids, live throughout the colony and are not fully independent. These individuals can have unique and diverse functions.
12. All colonies have "autozooids", which are responsible for feeding, excretion as well as for supplying nutrients to the colony through diverse channels.
13. Some classes have specialist zooids like hatcheries for fertilized eggs, colonial defence structures, and root-like attachment structures.
14. Cheilostomata is known to be the most diverse order of bryozoan, possibly as its members have the widest range of specialist zooids.
15. They have mineralized exoskeletons and form single-layered sheets which encrust over surfaces, and some colonies can creep very slowly by using spiny defensive zooids as legs.
16. Body cavity is a true coelom.
17. The digestive system consists of a U-shaped gut with an anus.
18. The body of the animal is enclosed in a calcareous, chitinous or gelatinous box, tube or communal matrix.

19. The Nervous system of the animal is composed of a central ganglion with a circum-oesophagal ring.
20. It lacks both specialized circulatory system as well as respiratory systems or gaseous exchange organs.
21. The animal also lacks specialized excretory oragns.
22. The animal possesses a lophophore. Lophophore represents a "crown" of tentacles used for the purpose of filter feeding.
23. The animal feeds on fine/minute particles present in the water.
24. Bryozoans are hermaphrodites.
25. Gonoducts are lacking in Phylum Ectoprocta.
26. Sperms are released into the coelom and exit through the pores in the lophophore tentacles.
27. Fertilization takes place both in sea water or in the metacoel.
28. Development takes place in sea water or in the special brood chambers of the colony (e.g., Cheilostome sp.).
29. Cleavage is biradial in Phylum Ectoprocta.
30. A lecithotrophic larva, called cyphonautes is typically present in Phylum Ectoprocta.
31. Species of phylum Entoprocts are also filter-feeders and appear somewhat like bryozoans however, in practice, they are different from Bryozoans. For instance:- the lophophore-like feeding structure of Entoprocts has solid tentacles, their anus lies inside rather than outside the base of the "crown" and they have no coelom.

Classification of Bryozoa

The Phylum Bryozoa is divided into two classes:

(1) Gymnolaemata or Stelmatophoda

(2) Phylactolaemata or Lophophoda

(i) Gymnolaemata or Stelmatophoda

- The members of this class are charac-terised by the presence of a circular lophophore as well as by the absence of epistome.
- The musculature in the body wall is absent.

Class Gymnolaemata or Stelmatophoda includes five orders:

1. Order Ctenostomata

- Zoecia are membranous.
- Ovicells and avicularia are absent.
- For instance: Nolella, Victorella, Zoobotryon, Clavopora, Paludicella.

2. Order Cheilostomata

- Box-like zoecia are present which are chitinous or calcareous.

- Both Ovicells and avicularia are present.
- For instance: Labiostomella, Membranipora, Conopeum, Callopora, Bugula.

3. Order Cyclostomata or Stenostomata

- Tubular zoecia are present which are calcareous in nature.
- Both the avicularia and operculum are ab-sent.
- For instance: Tubulipora, Stomatopora, Diplosolen, Berenicea.

4. Order Trepostomata

- Order Trepostomata includes the fossil forms.
- The zoecia are elongated, tubular and traversed by horizontal partitions.
- They are colonial forms with massive bodies.
- For instance: Heteropora, Batostoma.

5. Order Cryptostomata

- Order Cryptostomata represent an extinct order of the class Gymnolaemata.
- The zoecia remain hidden at the bottom of the vestibule.
- For instance: Rhombopora, Fenestella.

(ii) Phylactolaemata or Lophophoda

- Class Phylactolaemata comprises exclusively freshwater forms.
- These forms possess horse-shoe-shaped lophophore.
- Epistome as well as body musculature are present.
- For instance: Fredericella, Pectinatella, Lophopus, Cristatella, Plumatella, Stolella.

Meaning of Bryozoa/Ectoprocta

Bryozoa/Ectoprocta are tiny, un-segmented, sessile, colonial animals that are firmed permanently in exoskeletal cases or gelatinous material of their own secretion. They bear a circumoral ring with crescentic lophophore and a U-shaped alimentary canal bringing the anus close to the mouth but lacking nephridia and circulatory system. The Ectoprocta form colonies which are commonly referred to as "Corallines" or "Sea-mats".

Habit and Habitat of Bryozoa/Ectoprocta

The Bryozoa/Ectoprocta are strictly benthonic animals but are pelagic only during larval stages. Bugula avicularia, one of the most striking example of Ectoprocta, commonly known as Bird's Head Coralline occurs in brown or purple bushy tufts, it is usually 5.0 to 7.0 cm long, found attached on rocks or piles of jetties or similar positions on the shore throughout the world. It is a ciliary feeder and lives on small micro-organisms, especially the diatoms.

External Structures of Bryozoa/Ectoprocta

A 'zoarium' or a complete ectoproct colony superfi-cially resembles to a hydroid coelenterate though it exhibits much higher level of organisation. This colony is made up of several units or individuals known as zooids. There are colonies which consist of dichotomously branched narrow stem, which are rooted by a number of slender root filaments. One example of such a colony is that of a 'Bugula'. Each stem has a number of elements, the zooecia of the colony, which in turn are closely united together and arranged in four longitudinal rows. The zooecia are of cylindrical shape, but broader distally than proximally, five times as long as broad. They have, near the distal end, a wide crescentic aperture, the mouth of the zooecium, on either side of which lies a short blunt spine. The ooecium is a rounded structure which lies in many parts of the colony in front of each zooecium. Except a few, on each zooecium, there is a remarkable appendage, the avicularium. The avicularium appears like a bird's head supported on a very short stalk. The chitinous wall of the zooecia is made up of hardened and thickened cuticle of zooids which has a soft body wall beneath it. An introvert is formed by the anterior region of the body of the zooid. When the introvert is everted it is seen that its anterior end bears a circlet of usually fourteen long, slender, filiform tentacles on a circular ridge or lophophore surrounding the zooid mouth. The tentacles are ciliated densely except along their outer surfaces. The function of cilia of the tentacles is to vibrate in such a way as to drive currents of water and with them food particles towards the mouth. The tentacles have the capability of being bent in various directions. A narrow prolongation of the coelom lies in the interior of each tentacle. The tentacles are tactile and thus also act as organs of respiration. When retracted they get enclosed by the walls of the introvert or by a sheath known as the tentacle sheath. The parietovaginal muscles, a pair of bands of muscle fibres passing to the introvert from the body wall perform the function of retracting the introvert tentacles. The trunk is the main body of the zooid which is immovably attached inside the zooecium. It consists of the coelom and other internal organs.

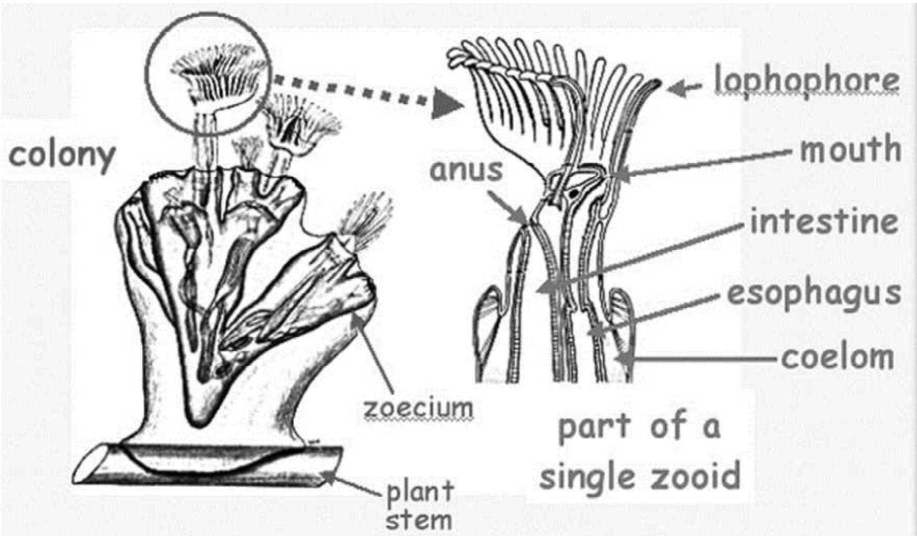

Fig. 4.28 *Bryozoa with Magnified Zooids*

NOTES

Body Wall of Bryozoa/Ectoprocta

The body wall is made up of cuticle, epidermis, two muscular layers and parenchyma. The cuticle is the covering of the zooecium. The epidermis composed of a single layer of large flattened cells lies beneath the cuticle. Muscle layers are there in some genera, while absent in others. When present there are two layers, the outer one is circular and the inner one is longitudinal. The innermost layer is composed of peritoneal cells in some cases or of irregular cellular tissue or parenchyma in others.

Coelom of Bryozoa/Ectoprocta

It has quite an extensive coelom which is incompletely divided into two parts by an incomplete septum: a smaller anterior coelom called the ring coelom. The ring coelom is present at the base of the lophophore and extends into the tentacles. The space between the body wall and the alimentary canal is occupied by the large trunk coelom. It is traversed by 20-40 pairs of muscle fibres which are referred as the displaced muscles of the body wall. There is a large double strand that passes from the proximal or aboral end of the alimentary canal to the aboral wall of the zooecium. This is known as the funiculus. The coelom is internally by visceral layer of the same tissue, ensheathing the alimentary canal lined and externally either by the parietal layer of parenchyma or ciliated peritoneum. There are numerous radiating strands of spindle-shaped cells crossing the coelom. The coelom is filled with a colourless fluid which contains several kinds of suspended coelomocytes.

Digestive System of Bryozoa/Ectoprocta

The alimentary canal of Ectoprocta is a U-shaped tube. The mouth is present at the centre of the lophophore. The mouth paves way into a wide chamber the pharynx which in turn passes into the oesophagus. The oesophagus thereafter leads into the stomach. The stomach gives off a long conical prolongation or caecum which passes towards the aboral end of zooecium to which it is attached by the funiculus.

Mouth $\rightarrow$ pharynx $\rightarrow$ oesophagus $\rightarrow$ stomach $\rightarrow$ caecum $\rightarrow$ funiculus $\rightarrow$ aboral end of zooecium

The oral aspect of the stomach gives off the intestine. The intestine gets terminated in a rounded anus which is situated near the mouth but outside the lophophore. The entire alimentary canal is lined by an epithelium that is ciliated throughout except in a portion of the stomach. A pair of slender muscles passing from the body wall to the stomach functions as retractors of the alimentary canal when the introvert is drawn back.

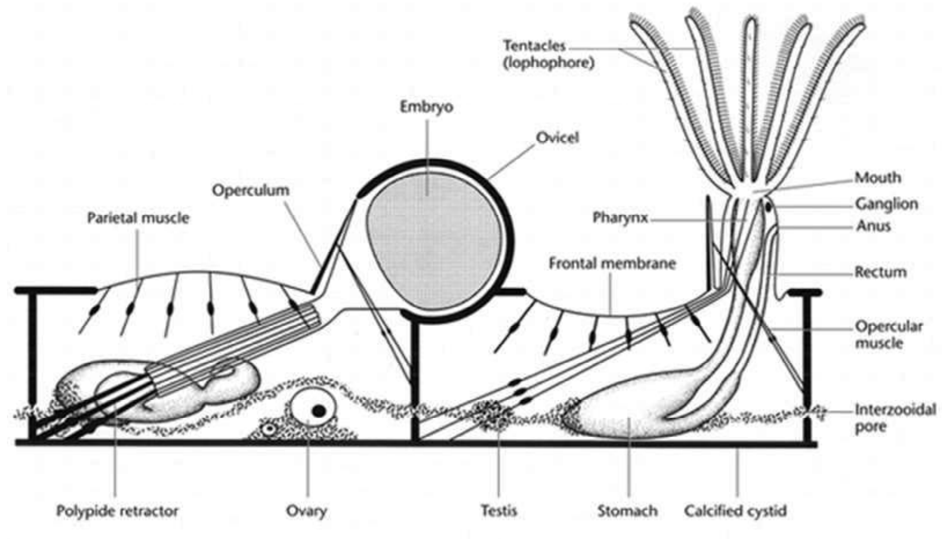

Fig. 4.29 *Digestive System of a Representative Bryozoan*

Circulatory, Excretory and Nervous System of Bryozoa/Ectoprocta

There are no blood vessels present in the ectoprocts and the circulatory system is completely absent.

Excretory System of Phylum Bryozoa/Ectoprocta

Definite excretory organs are not seen in ectoprocts. The cells of the funicular tissue and the leucocytes perform the function of excretion (i.e., the collection of nitrogenous waste matters).

Nervous System of Phylum Bryozoa/Ectoprocta

The nervous system is made up of a small round ganglion which is situated in the ring coelom between the mouth and anus. This ganglion gives off nerves to various parts. The ganglion is continuous with the nerve ring which surrounds the pharynx. The nerve ring gives two ganglionated sensory and motor nerve fibres to each tentacle. Special organs of sense are not present.

Reproductive System of Bryozoa/Ectoprocta

Bugula is a hermaphrodite i.e., ovary and testis occur together in the same zooid. Specially modified cells of the parenchyma, either of the funiculus or of the body wall form both testis and ovary. The testis develops from the cells of the funicular tissue and gives rise to the spherical masses of cells known as the spermatidia which develop into sperms having very long motile tails. These become detached from one another and move about in the body cavity or in its prolongations into tentacles. There is no sperm duct present and therefore it is highly doubtful if the sperms pass to the exterior. The ovary is like a small rounded body which is formed from the parietal layer of the parenchyma about the middle of the zooecium. It is made up of only a small number of cells and among which only one at a time becomes a mature ovum, certain smaller cells forming an enclosing follicle. The mature ovum is fertilised in the coelom and passed into the interior of a rounded outgrowth of the zooecium, the ooecium lined with parenchyma forming a sort of brood pouch in which it will undergo development. Ectoprocta reproduce asexually by various methods: budding statoblasts, hybernacula, brown bodies and regeneration.

Development of Bryozoa/Ectoprocta

Bugula do undergo self-fertilisation. A holoblastic (complete) and nearly regular cleavage is seen in the fertilised egg. Cleavage is of radial type. A coeloblastula is formed which eventually undergoes delamination to transform into a gastrula. Four elongated cells cut off into the blastocoels during the process of production of 64-128 blastomeres. These endo-mesodermal cells give endoderm and mesenchyme. The larva is known as cyphonautes. The cyphonautes larva in bugula has some specialised features, viz., oval shape, absence of alimentary canal and delimitation of the apical organ by a circular groove.

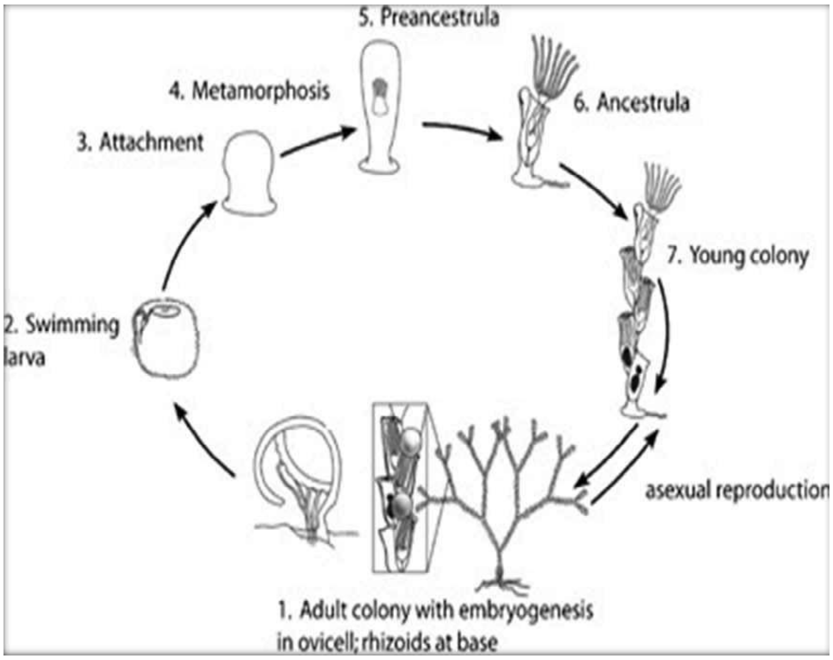

Fig. 4.30 *Life Cycle of a Bryozoan*

Affinities of Phylum Bryozoa/Ectoprocta

The phylogenetic relationships of Ectoprocta are uncertain and a topic of debate. The controversy arises due to their structural similarities with other groups of animals.

Affinities with Phoronida

Caldwell (1888) emphasised the affinities between Phoronida and Ectoprocta. This idea was based on various similarities:

- Both have horse-shoe-shaped lophophore.
- Epistome is present.
- Alimentary canal is U-shaped.
- Disposition of the coelom is similar and a septum separating the mesocoel and metacoel is also present.
- The nerve centre is supraenteric and is present in the mesocoel.

Though, a detailed study also showed many structural differences between them. They differ greatly in their anatomical organisation. The embryology too exhibits a number of differences.The noteworthy differences are:

- The origin of coelom
- The region present between the mouth and the anus is dorsal in position in Phoronida and ventral in ectoprocta.
- The circulatory system and nephridia are not present in Ectoprocta while they are in case of phoronida.

Because of the above-mentioned differences the affinities between Ectoprocta and Phoronida cannot be established.

Affinities with Brachiopoda

There are quite a few similarities between Bryozoa/Ectoprocta and Brachiopoda

- Similar body organisation
- The bivalved shell of cyphonautes larva of ectoprocta which can be compared to the shell of Brachiopoda
- Coelomic septum between the metacoel and mesocoel
- U-shaped alimentary canal

There are also many structural differences between them. These are:

- The brachiopod shell is in no comparison to the exoskeleton of Ectoprocta.
- In Brachiopoda, the shell is placed dorso-ventrally while in an ectoproct larva the shell is placed laterally.
- The chitinous setae are present in Brachiopoda but absent in Ectoprocta.
- The nervous system is mainly supraenteric in ectoprocta while subenteric in brachiopoda. The affinities between these two groups cannot be established because of lack of specific relationships between them.

Affinities with Endoprocta

Earlier ectoprocta and endoprocta were linked together as two classes under the phylum Bryozoa or Polyzoa because of the following similarities:

- Crown of ciliated tentacles.
- Looped alimentary canal.
- Similarity in larval stages.

But these features are common in all the sessile animals. A careful examination of the structural organisation shows that these two groups are fundamentally different from each other. The main differences are as follows:

- Only the mouth is surrounded by the tentacular crown in ectoprocta, but in endoprocta both the mouth and anus are enclosed by the tentacles.
- The Ectoprocta has true coelom, whereas in endoprocta there is no true coelom.
- The nephridia and gonoducts are not present in ectoprocta, while in endoprocta both of them are there.

NOTES

If we look at these features it is quite apparent that Ectoprocta is highly organised than the endoprocta.

All the information of anatomy and embryology present for Ectoprocta leads us to place the Ectoprocta under a separate phylum having phylogenetic relationship with the two other lophophorate coelomates, i.e., phoronida and brachiopoda.

The larval forms of all classes in echinodermata will demonstrate general resemblance. However, the crinoidea larva diverge from this pattern. In general, all the larvae exhibit that they might have arrived from same ancestor. Hence, the common ancestor is a coelomate, free swimming and bilaterally symmetrical animal. These larvae also show resemblance with toronaria larvae of balanoglossus. Thus, the study of echinoderm larva has a phylogenetic significance.

Check Your Progress

6. What do you mean by ganglionated cords?
7. Define ectoprocta.
8. Define ooecium.
9. What do you understand by trunk?
10. What is the shape of the alimentary canal of ectoprocta?

4.4 ANSWERS TO 'CHECK YOUR PROGRESS'

1. Crustaceans are the arthropods whose body is protected with a chitinous exoskeleton covering.
2. Nauplius Larva is the first fundamental stage in all the crustaceans and was discovered by Muller in the 18th century.
3. The nauplius larva transforms into metanauplius in some branchiopods like apus. It is slightly larger than the nauplius and possesses cephalothorax, abdomen and a caudal furca.
4. Protozoea larva hatches from the eggs of marine prawns and lobsters. It has a large cephalothorax and an elongated unsegmented abdomen with a caudal fork and a pair of small uropods.
5. Echinopluteus is the only larval stage in echinoidea.
6. The ganglionated cords that are the main ventral nerves, spring from the sides of the brain and proceed backward in latero-ventral position into the foot.
7. Ectoprocta are tiny, un-segmented, sessile, colonial animals that are firmed permanently in exoskeletal cases or gelatinous material of their own secretion.
8. The ooecium is a rounded structure which lies in many parts of the colony in front of each zooecium.
9. The trunk is the main body of the zooid which is immovably attached inside the zooecium. It consists of the coelom and other internal organs.
10. The shape of the alimentary canal of ectoprocta is U- shaped.

4.5 SUMMARY

- The invertebrates comprise about 90 percent of the total number of animals inhabiting the surface of earth.
- The invertebrates are so vast and heterogeneous that every group has certain structural and functional peculiarities and a distinct classification system.
- Currently, there are 30 known invertebrate phyla which are defined by a unity of basic structural pattern, i.e., though the members in each phylum may differ in external features; the anatomical characteristics have developed similarly in several respects.
- Evolutionary studies have established that all the individuals of a phylum have been derived directly or indirectly from a common primitive ancestor.
- The invertebrate phyla are broadly divided into two, i.e., major and minor phyla. The concept of major and minor phyla is based on two factors:
- Crustaceans are arthropods whose body is protected with a chitinous exoskeleton covering.
- Every moult results in larval form which is entirely different from the previous one.
- Crustaceans go through various stages of larvae before becoming an adult.
- Nauplius larva is the first fundamental stage in all the crustaceans and was discovered by Muller in the 18th century.
- The nauplius larva transforms into metanauplius in some branchiopods like apus. It is slightly larger than the nauplius and possesses cephalothorax, abdomen and a caudal furca.
- Protozoea Larva hatches from the eggs of marine prawns and lobsters. It has a large cephalothorax and an elongated unsegmented abdomen with a caudal fork and a pair of small uropods.
- Zoea Larva is the most common larva found in decapods hence it has a lot of variants in different species.
- In some Malacostraca, zoea transforms to metazoea which develop abdominal appendages for performing swimming action.
- Zoea transforms into Mysis larva in shrimps and some lobsters. It resembles Mysis and has a cylindrical, elongated body with a cephalothorax and an abdomen with 6 segments.
- Schizopoda Larva is found in some crustacean decapods, such as, homarus, nephrops. It is like megalopa and mysis larva in general features.
- Pleopods are present on the abdomen. These are biramous and are used for swimming.
- In spiny lobsters, egg hatches to form phyllosoma larva. The body of the larva is divided into head, thorax and abdomen. It has a pair of compound eyes present on a stalk.

- The rotifers are the most common inhabitants of freshwaters that are also found in small numbers in brackish water bodies such as the ocean and on land in damp sites.
- Rotifers are also called wheel animalcules, which are minute animals ranging from 0.04 to 2 mm in length.
- The body of Rotifers is covered with yellowish cuticle which is ringed throughout or in certain regions.
- In some groups of rotifers, the enlargement of the cilia along both margins of the apical band, results in two circles of cilia or membranelles that is trochus, an inner or anterior circlet and cingulum, an outer or posterior one.
- The adult females of the genera Atrochus, Cupelopagis and Acyclus have no corona but it is present in normal form in the males and young females of these genera.
- In Rotifers, the sub-epidermal muscles are circular and longitudinal muscles and found in different parts of the body.
- The mouth is ventral, rounded, slit-like or triangular. The cingulum forms a definite lower tip beneath the mouth.
- The nervous system of Rotifers consists of a bilobed rounded, triangular or quadrangular brain or cerebral ganglia lying dorsal to the mastax, some sensory and motor nerves, some additional ganglionic masses and 2 main ventral nerve cords.
- The rotifers are exclusively dioecious and show a marked sexual dimorphism.
- The ectoprocts are strictly benthonic animals but are pelagic only during larval stages.
- The body wall is made up of cuticle, epidermis, two muscular layers and parenchyma.
- The Ectoprocta have quite an extensive coelom which is incompletely divided into two parts by an incomplete septum. The smaller anterior coelom is called the ring coelom.
- There is a large double strand that passes from the proximal or aboral end of the alimentary canal to the aboral wall of the zooecium. This is known as the funiculus.
- The nephridia and gonoducts are not present in Ectoprocta, while in Endoprocta both are there.

4.6 KEY TERMS

- **Crustaceans:** These are the arthropods whose body is protected with a chitinous exoskeleton covering.
- **Nauplius Larva:** This larva is the first fundamental stage in all the crustaceans and was discovered by Muller in the 18th century.

- **Metanauplius Larva:** The nauplius larva transforms into Metanauplius in some Branchiopods like Apus. It is slightly larger than the nauplius and possesses cephalothorax, abdomen and a caudal furca.
- **Zoea Larva:** It is the most common larva found in decapods hence it has a lot of variants in different species.
- **Mysis Larva:** Zoea transforms into Mysis larva in shrimps and some lobsters. It resembles Mysis and has a cylindrical, elongated body with a cephalothorax and an abdomen with 6 segments.
- **Cypris Larva:** Nauplius larva transforms into cypris larva in subclasses ostracoda and cirripedia.
- **Pentacrinoid:** Pentacrinoid is a sedentary larva having an attachment plate to adhere to the substratum.
- **Trochus:** In some groups of rotifers, the enlargement of the cilia along both margins of the apical band, results in two circles of cilia or membranelles that is trochus.
- **Echinopluteus:** It is the only larval stage in echinoidea.
- **Ganglionated Cords:** The ganglionated cords that are the main ventral nerves, spring from the sides of the brain and proceed backward in latero-ventral position into the foot.
- **Ectoprocta**: Ectoprocta are tiny, un-segmented, sessile, colonial animals that are firmed permanently in exoskeletal cases or gelatinous material of their own secretion.
- **Ooecium:** The ooecium is a rounded structure which lies in many parts of the colony in front of each zooecium.
- **Trunk:** The trunk is the main body of the zooid which is immovably attached inside the zooecium. It consists of the coelom and other internal organs.

4.7 SELF-ASSESSMENT QUESTIONS AND EXERCISES

Short-Answer Questions

1. What do you understand by the larval forms in invertebrates?
2. What do you understand by exoskeleton?
3. State the importance of larval stage.
4. Define the significance of the echinoderm larva.
5. State the key difference between the major and minor phyla.
6. Where are the rotifers found?
7. What do you understand by the corona of rotifers?
8. What do you understand by the body wall?

Long-Answer Questions

1. Describe the various larval forms found in invertebrates.
2. Explain the significance of the larval stage in invertebrates in detail.
3. Mention the differences between the major and the minor phyla in detail.
4. Describe the characteristic features of rotifera.
5. Explain the affinity of rotifers with other invertebrates.
6. Describe the habit and habitat of ectoprocts.
7. Explain the physiology of ectoprocts.
8. Explain the differences between the coelomates and non-coelomates in detail.

4.8 FURTHER READING

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