UNIT 1 INTRODUCTION TO CHORDATES

Structure

1.1 INTRODUCTION

We are more familiar with chordates than with any other group in the animal kingdom. The reason for this is obvious in the fact that we as well as several domesticated animals like, cow, sheep, goat, dog etc., are members of this group. Chordates are the most diverse and successfully adapted to various kinds of habitats. However, the basic plan of organisation is more alike among the chordates than it is in several non-chordates groups. The study of chordates continues to be of great importance to biologist because it illustrates the biological principles like development, ancestry, inter-relationships and evolution very well. Many chordates are constructed of hard parts that survive to yield a respectable history in the fossil records which have made them especially useful in defining ideas about evolutionary processes. Advanced chordates are also some of the most intricate animals even to appear. They, therefore, introduce to us questions about the complexity of biological organisation and their evolution.

Objectives

After studying this unit you will be able to:

- enumerate the distinctive characters of chordates and explain how these are characteristically different from the non-chordates,
- classify the chordates giving suitable examples,
- describe the natural history and basic adaptive features of hemichordates and protochordates, and
- outline the affinities, ancestry and evolution of hemichordates and protochordates in relation to other groups in the animal kingdom.

1.2 PHYLUM HEMICHORDATA

Initially hemichordates were considered a subphylum of the chordates. The basis for this was the presence of rudimentary notochord and gill slits. But the hemichordate notochord is in reality a buccal diverticulum and not homologous with chordate notochord. Therefore, the hemichordates are now put as a separate phylum. However, in our course of Diversity we are dealing Hemichordata with the Chordata as it bears certain characters in common with true chordata though lacking a true notochord.

Characteristics of Hemichordata

Hemichordates (Hemi - half + Chorda - chord) are soft bodied, marine animals; bottom dwellers, found usually living in U-shaped burrows in sand or mud in shallow waters; worm like or short and compact with stalk. The body has three parts - proboscis, collar and trunk (protosome, mesosome and metasome). Coleomic pouch is single in proboscis but paired in collar and trunk with buccal diverticulum in posterior part of proboscis. Circulation through dorsal and ventral vessels and dorsal heart; respiration through gill slits; excretion by a single glomerulus connected to blood vessels. Nervous system consists of subepidermal nerve plexus thickened to form dorsal and ventral nerve cord, with connective ring in the collar and the dorsal nerve cord of collar is hollow in some. The phylum Hemichordata consists of two classes: class Enteropneusta and class Pterobranchia.

1.2.1 Class Enteropneusta

Commonly known as acorn worms, these are worm like, sluggish animals that live in burrows or under stones, eg. *Balanoglosus*, *Saccoglossus* (Fig. 1.1) and *Ptychodera*.

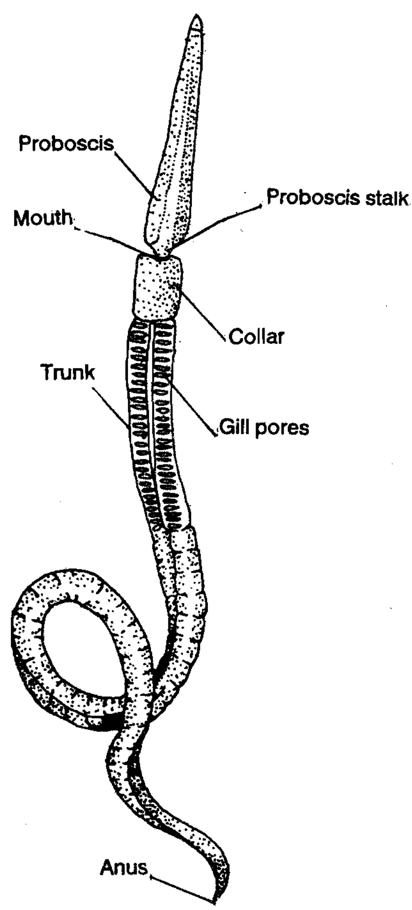

Fig.1.1: External characters of acorn worm *Saccoglossus*.

Body is mucous-covered and divided into a preoral **proboscis**, a round **collar** behind the mouth and a long **trunk**. The proboscis probes its surroundings and collects food in mucous strands on its surface. The food particles are then carried by cilia to the groove at the edge of the collar, directed underside to the mouth and swallowed (Fig.1.2 a). Large particles can be avoided by closing the mouth with the edge of the collar (Fig. 1.2 b). Bottom dwellers use proboscis and collar for building U-shaped mucous-lined burrows.

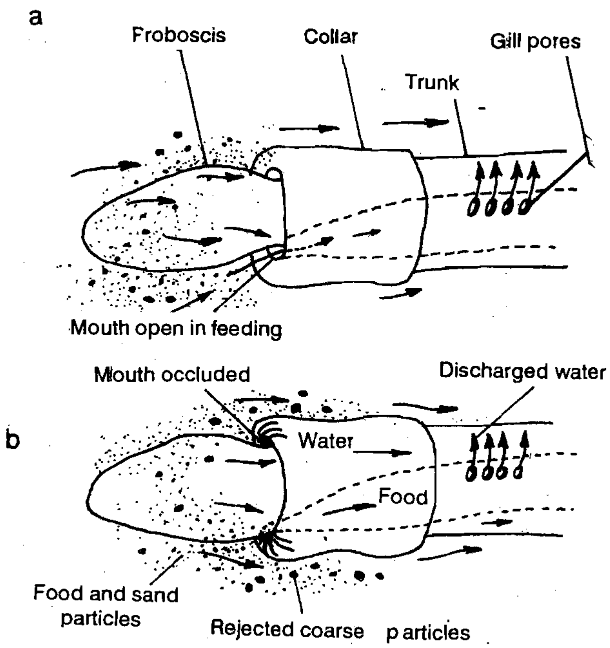

Fig.1.2: Water currents carrying food particles in enteropneust hemichordate. (a) Side view showing the open mouth and direction of currents indicating that food particles are directed towards the mouth and digestive tract. Particles not taken in, move outside the collar and water leave through the gill pores, (b) Mouth is closed and in this state all particles are kept out which pass over the collar.

Buccal diverticulum is a slender blindly ending pouch of gut that reaches into the buccal region. It is this gut part that was formerly considered to be nerve cord.

A small coelomic sac (protocoel) exists at the posterior end of the proboscis into which buccal diverticulum extends. A thin canal connects the protocoel with the proboscis pore and then to the outside. The paired coelomic cavities of the collar also open through pores (Fig.1.3). Water is taken through the pores into the coelomic sacs and the proboscis stiffened in this way is used for burrowing. By contractions of body wall musculature excess water is driven out through the gill slits allowing the animal to move forward, and the food passes into the alimentary canal for digestion.

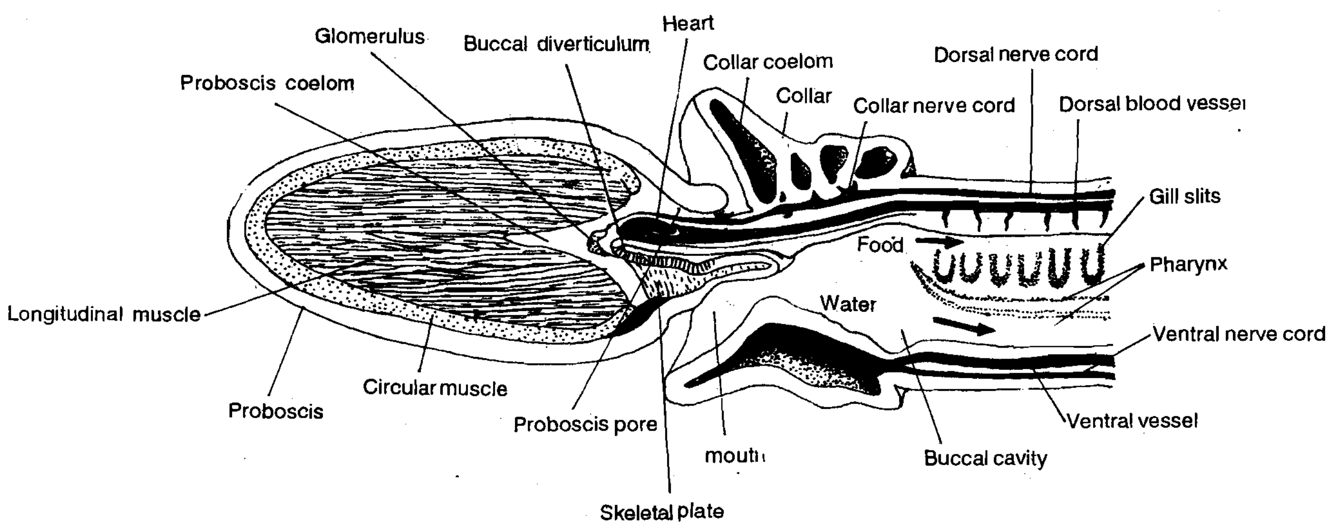

Fig.1.3: Longitudinal section through anterior end of a hemichordate (showing internal structures).

A row of gillpores located dorsolaterally on each side of the trunk open into series of gill chambers that in-turn are connected to a series of gill slits. Gills are absent. Water moves from mouth through the pharynx to the gill slits and branchial chambers and then to out side (Fig.1.2 a). Oxygen is removed from the indrawn water and carbon dioxide released into it. The gaseous exchange occurs in the vascular branchial epithelium and at body surface.

Hemichordates are mainly ciliary-mucous feeders. Pharynx that lies behind the buccal cavity acts as a strainer or filter separating food particles from the water. Food particles, trapped in the mucous are brought to the mouth by the ciliary action on the proboscis and collar. The food particles, then strained out of the water that leaves through the gill slits, pass through the ventral part of the pharynx and oesophagus to intestine where digestion and absorption occurs.

Circulatory system is open and consists of a median dorsal vessel above the gut and a median ventral vessel below the gut, both connected by open spaces. The dorsal vessel expands into heart and a group of sinuses above the buccal diverticulum (Fig.1.3). This group of sinuses is called as glomerulus as it is assumed to have an excretory function. The colourless blood flows anteriorly above the gut in the dorsal vessel, and then posteriorly through the ventral vessel, passing through the extensive open spaces to the gut and body wall.

Nervous system is subepidermal (intraepidermal) consisting of plexus of nerve cells and fibres that are thickened to form dorsal and ventral nerve cords. Both the cords are connected with a ring posteriorly to the collar. The dorsal cord in some species contains one or two cavities and continues in the collar region giving out many fibres in the proboscis. This feature is suggestive of the dorsal hollow nerve cord of chordates, however the nervous system as a whole is simpler than in most of the chordates. Neurosensory cells that are present throughout the epidermis and photoreceptor cells are the sensory receptors.

Sexes are separate. Gonads are arranged in rows, dorsolaterally on each side of anterior part of the trunk. Fertilization is external in sea-water. In some species there is a free swimming, pelagic and ciliated larva called tornaria (Fig.1.4).

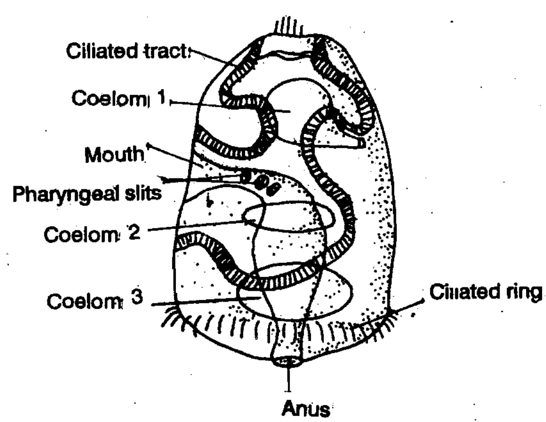

Fig.1.4: Tornaria larva : larval stage of a hemichordate.

1.2.2 Class Pterobranchia

Pterobranchs are sessile, sluggish hemichordates and live in the tube made up of their own secretions. Their size varies from 1 to 7 mm. in length, although the stalk may be longer. The basic plan of class Pterobranchia is similar to that of the Enteropneusta. However, certain structural differences are correlated with the sedentary life style of pterobranchs. Several genera are recognised but details of only two genera *Cephalodiscus* and *Rhabdopleura* are known.

Many individuals of *Cephalodiscus* (Fig.1.5) live together in anastomosing gelatinous tubes, attaching themselves to the walls of the tubes by extensible stalk. The zooids however live independently and can move about their trunk in and out of the tubes. Typical of hemichordates, the body of *Cephalodiscus* consists of three parts — proboscis, collar and trunk. There is only one pair of gill slits. The alimentary canal is U-shaped and the anus is placed near the mouth.

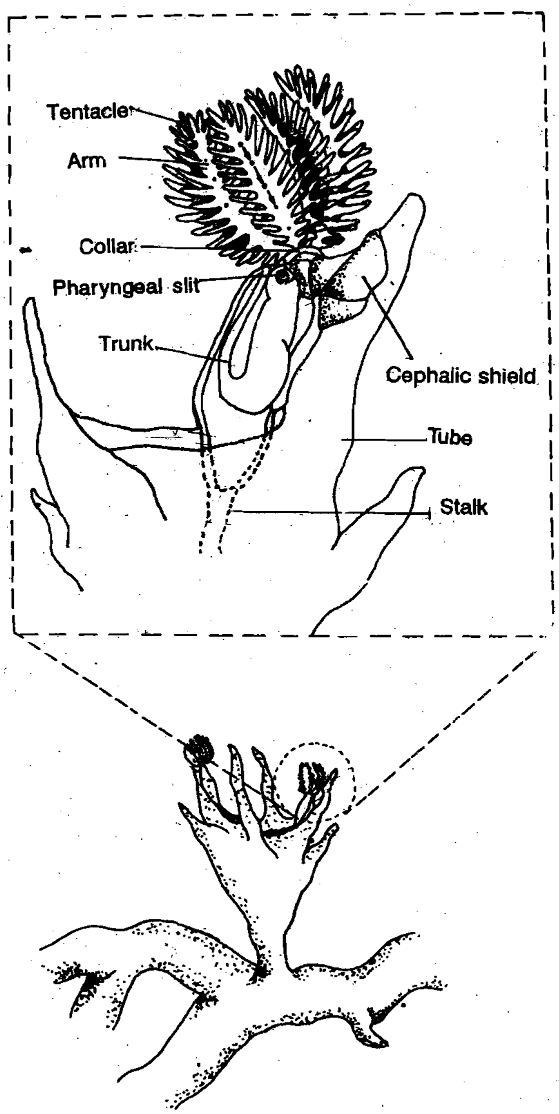

Fig.1.5: Structure of pterobranch hemichordate *Cephalodiscus*, that lives in tubes in which they can move about.

The proboscis is shield shaped. Beneath the proboscis there are five to nine pairs of branched arms with tentacles, containing the coelomic extensions. The animal collects the food with the help of the ciliated grooves present on the arms and tentacles. This whole structure is called Iophophore. Sexes are separate in some species, while some are monoecious. Asexual reproduction, wherever occurs is by budding.

The members of *Rhabdopleura* form a colony of zooids that are connected by a basal stolon and enclosed in the tubes (Fig.1.6 a). Collar contains two branching arms (Fig. 1.6 b). Glomeruli and gill clefts are absent. Nervous system is similar to that in Enteropneusta except for the absence of tubular nerve cord in the collar. Asexual reproduction occurs by budding from the creeping stolon.

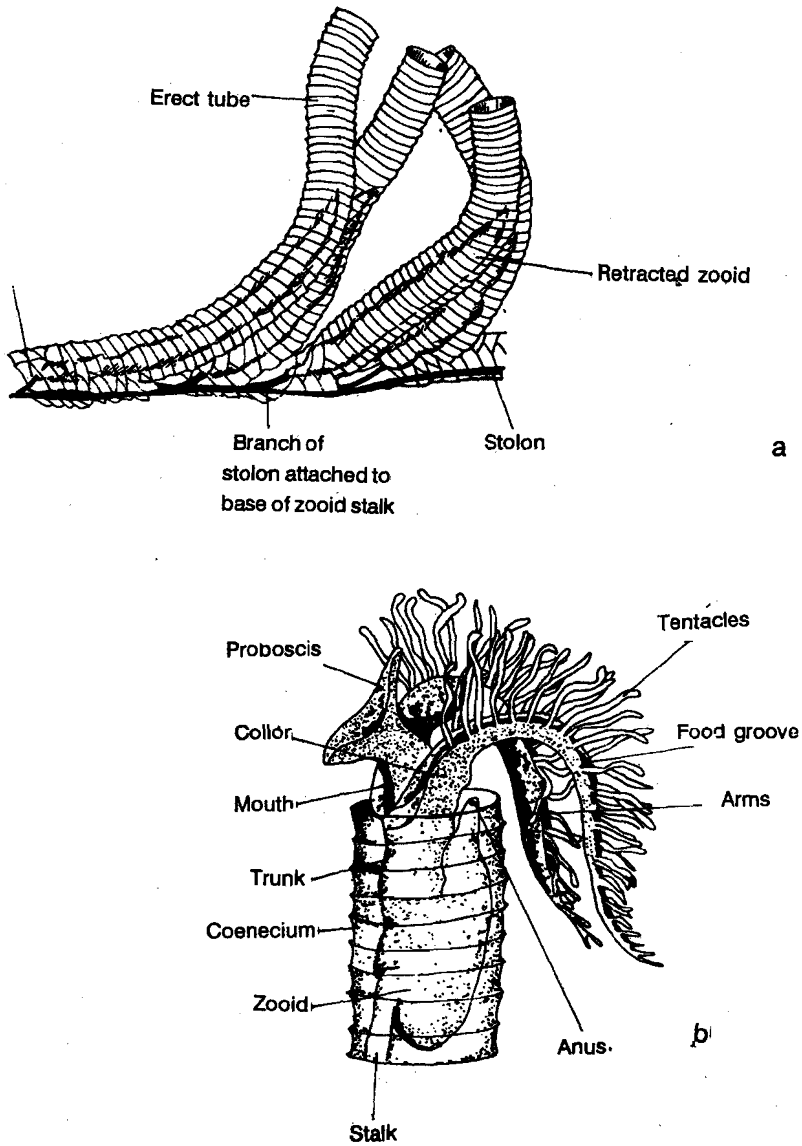

Fig.1.6 : a) Portion of a colony where individuals of pterobranch hemichordate *Rhabdopleura* live in branching tubes connected by stolon; b) structure of *Rhabdopleura*.

SAQ 1

i) List out any three characteristics of Hemichordata.

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ii) Write one major difference between Enteropneusta and Pterobranchia.

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1.2.3 Basic Adaptive Features

The two major groups of Hemichordata are diverse in their habit. The main adaptive feature in the free swimming form is found in the efficiency of proboscis which also aids in burrowing. In a way, life in burrows offers safety from predators. The gill slits are primarily used for filter feeding and secondarily for breathing. The colonies of the sessile forms are well protected by chitinous material. The presence of large, branched lophophore bearing ciliated bands in *Cephalodiscus* and *Rhabdopleura* is very well adapted to feeding and thus contributes to the success of the species. The multiple gonads provide reproductive efficiency. In addition,, the capacity to regenerate the lost parts contributes to the survival of the race. The free swimming larva during the development enables wider distribution and thus contributes further to the success of the species.

1.2.4 Affinities

Let us now consider the inter-relationships of the hemichordates with other members of the animal kingdom. The systematic position and phylogenetic relationship of hemichordates has been a puzzle among zoologists over decades. Hemichordates show following affinities with different phyla.

Affinities with annelids :

1. Bilateral symmetry.
2. Adults with similar morphology, burrowing and feeding habits.
3. In both digestive tract is straight and tubular.
4. Similar mode of blood circulation.
5. Similarities between the tornaria larva of enteropneusts and the trochophore larva of polychaetes including the apical tuft of cilia, apical sense organs and larval gut.

There are, however, serious objections to relate the hemichordates with annelids such as :

1. Annelids do not possess gill slits.
2. Excretion in annelids is carried out by means of nephridia. On the other hand, glomeruli take up the role of excretion in enteropneusts.
3. The coelom is schizocoelous type in annelids while in hemichordates it is enterocoelous type.
4. In hemichordates the cleavage is holoblastic whereas in annelids it is spiral.
5. Nephridia are present only in the trochophore.

In addition complete absence of branchial respiration and notochord argues against any phylogenetic relationship between hemichordates and annelids.

Relationship with Pogonophora :

Hemichordates and pogonophores (beard worms) have many similar structures - such as, 1) tentacular apparatus; 2) septum, separating the mesosome and metasome; 3) intraepidermal nervous system; 4) pericardial sac; 5) gonads in the trunk.

Inspite of the above similarities there are many structural differences. Pogonophora differ in the following characters: 1) tentacles originate from the protosome and protocoel extends in all tentacles. 2) the main component of the nervous system is located in the protosome. 3) absence of gill slits and digestive tracts; 4) the gonopores are ventral in position.

Because of these differences the two groups are treated as separate and their similarities are due to remote connection with the ancestral stalk.

Relationship with Echinoderms :

Among the invertebrates echinoderms seem to be close to hemichordates. Their affinities are : 1) similar feeding habits; 2) the general plan of sub-epidermal nervous system;

3) enterocoelous origin of coelom i.e., the coelom arises as outpocketings of archenteron of the embryo and formation of the anus from the embryonic blastopore. Thus, there is a marked functional similarity between hydraulically operated water vascular system and proboscis-collar coelom; 4) both the groups show relationship in indeterminate cleavage with equipotential blastomeres; 5) marked similarities between tornaria larva and bipinnaria larva. These include presence of similar ciliary bands, sensory cilia at the apical regions, curved gut with ventral mouth and posterior anus. There are also similarities between the auricularia larva of echinoderms and the tornaria larva of hemichordates (see discussion under ancestry); 6) recent studies on the fossil echinoderms *Stylophora* furnished evidence linking echinoderms with chordates. These small nonsymmetrical forms like *Coteurnocystis* have a head resembling a long toed medieval time boot, a series of branchial slits like the gill openings of shark and a post anal tail resembling a notochord, a dorsal nerve cord and muscle blocks. Whether this evidence would sufficiently justify the concept that the echinoderms are the true ancesters of chordates needs to be further examined.

Apart from the above considerations, it is interesting to note that the energy rich compounds phosphocreatine and phosphoarginine which generally characterise vertebrates and invertebrates respectively, are present in Balanoglossus. This is the basis for some authors to postulate that the hemichordates form a connecting link between invertebrates like echinoderms and vertebrates. Subsequently this view lost its credential when both phosphocreatine and phosphoarginine were found in the muscles of many invertebrate phyla.

SAQ 2

Fill in the blanks with appropriate words.

i. Annelids and hemichordates have ______________ ____________ of circulation.

ii. ____________ ____________ in hemichordates provide reproductive efficiency.

iii. Nephridia are ______________ in hemichordates.

iv. Both hemichordates and pogonophora have intraepidermal_________________.

v. The bipinnaria larva of _________________ are similar to tornaria larva.

1.3 PHYLUM CHORDATA - GENERAL CHARACTERS

Notochord is a rod like flexible structure made up of cells enclosed in a fibrous sheath, located along the mid dorsal line between the gut tract and central nervous system where it forms the axis for muscle attachment. It is a primitive endoskeletal structure that is present in all the chordates during embryonic life. In some of the chordates (most protochords and primitive vertebrates) the notochord persists through out the life, but in most vertebrates it is entirely displaced by vertebrae. However, the remains of notochord generally persist between or within the vertebrae.

Chordates retain many of the features of inverteberates such as bilateral symmetry, anterioposterior axis, pattern of arrangement of coelom, metamerism, and cephalisation. Despite these similarities it is difficult to establish clearly the relationship of chordates with invertebrates. The following salient features characterise the chordates:

1. Bilateral symmetry, segmented body, well developed coelom and presence of three germ layers namely ectoderm, mesoderm and endoderm.
2. The body differentiated into head, trunk and tail in majority of the forms.
3. In general all organ systems well developed and specialised in their functions.
4. The presence of a notochord (hence the name "chordate") at some stage or throughout life history in the lower forms and well developed vertebral system in higher forms.
5. A dorsal tubular nerve cord distinct from, but lying first dorsal to the notochord, with its anterior end usually differentiated into brain.
6. Pharynx perforated by numerous slits/pouches at some stage or other. These pharyngeal slits may or may not be functional.
7. Complete digestive system.

8. A ventral heart and better developed closed blood vascular system to carry nutrients from the digestive tract to the liver.
9. Presence of tail in the post anal region at some stage. The tail may or may not persist in the adult.
10. Exoskeleton often present but well developed in some members.
11. The endoskeleton either cartilaginous or bony. The endoskeleton in higher chordates consists of axial and appendicular divisions. The endoskeleton provides protection and support and serves as a frame work for the body. For example, the well developed cranium to protect the brain.

Nerve cord in most invertebrate phyla is solid and ventral to the alimentary canal, but in chordates it is tubular and dorsal to the alimentary canal. The anterior end of the nerve cord becomes enlarged to form the brain. It persists throughout the life in almost all the chordates but degenerates before maturity in some lower forms. The nerve cord in chordates is enclosed between the protective neural arches of the vertebrae and the brain is surrounded by bony or cartilagenous cranium.

1.4 HOW CHORDATES DIFFER FROM INVERTEBRATES

There are several striking differences between chordates and invertebrates. Let us compare the organisation of these two groups.

i) Although both groups have dorsal brain, the nerve cord when present is ventral in higher invertebrates and dorsal in chordates.

ii) The heart is dorsal in invertebrates and ventral in chordates. Blood flows in the dorsal blood vessel posteriorly in vertebrates and anteriorly in invertebrates

iii) Some invertebrates possess skeletal structures to protect their internal organs : however they lack a true endoskeleton. In echinoderms beneath the epidermis there is an endoskeleton of small calcareous plates called ossicles that are bound together with connective tissue. The spines and spicules that make up the spiny surface are projected from these ossicles. In chordates, there is a notochord or highly developed vertebral system. It is noteworthy that among the chordates, all vertebrates possess a frame work of bones inside their body. In some vertebrates the endoskeleton is made up of cartilage. The skeletal system of chordates is designed to perform a wider division of labour than that of any invertebrate.

iv) Initially in lower invertebrates there is single opening for mouth as well as anus, for example in Cnidarians. Later the complete digestive system from mouth to anus is developed in higher invertebrates such as in phylum Nemertina, pseudocoelomates, worms etc. Anal opening in invertebrates terminates at the posterior part of the body. In the larval and adult chordates the anus is situated near the tail anterior to the posterior part of the body. In invertebrates, in general, blastopore becomes anus and in vertebrates blastopore becomes mouth.

v) Invertebrates lack pharyngeal gill slits but chordates possess them.

From the above, it is possible to conclude that the chordates can be easily set apart from the invertebrates by several distinctive characteristics. The four chordate hall marks are notochord, dorsal tubular nerve cord, pharyngeal gill slits and post anal tail (Fig. 1.7). Both higher and lower forms display these characteristics at some stage or the other in their life history.

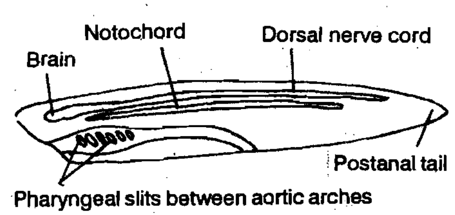

Fig.1.7: Schematic diagram showing four distinctive characters of chordata.

SAQ 3

List out three important differences between chordates and invertebrates.

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1.5 CLASSIFICATION OF PHYLUM CHORDATA

The Chordates are divided into the following groups.

Phylum Chordata

Group - 1: Protochordata (Acrania)

Subphylum 1: Urochordata (Tunicata): Tunicates, marine animals, stalked adults, often colonial and ensheathed in the tunic; notochord and nerve cord only in free swimming larva; the larva shows all the chordate characters (Fig.1.8). The three classes that fall under this subphylum are **Ascidiacea, Larvacea** and **Thaliacea.**

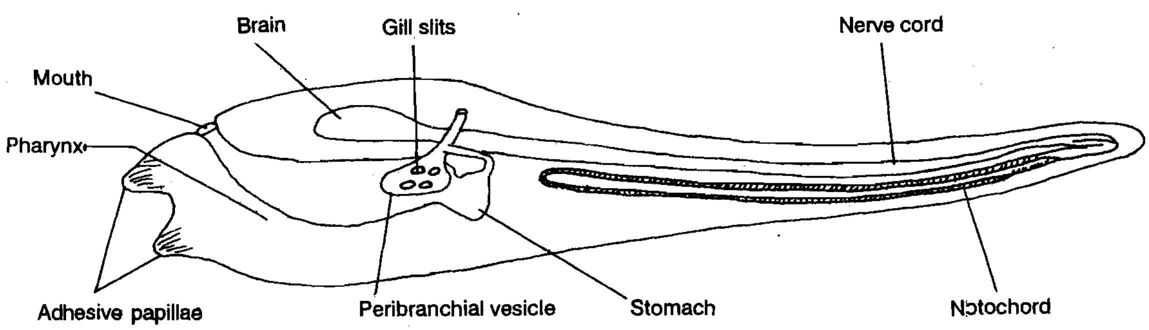

Fig.1.8: Tunicate tadpole larva showing chordate features.

Subphylum 2: Cephalochordata: Popularly known as lancelets (*Amphioxus*) : marine animals; notochord, gill apparatus and nerve cord are well developed in adults; filter feeders; food particles are carried posteriorly to the digestive tract instead of passing through the slits.

Both Urochordates and Cephalochordates are collectively known as **Protochordates.** They lack the cranium and hence they are also called **Acrania.**

Group Craniata

Subphylum: Vertebrata (Craniata) : Include all the chordates with backbone composed of a series of cartilaginous or bony vertebrae surrounding the spinal cord; notochord, dorsal nerve cord, pharyngeal gill pouches and postanal tail present at some stage of life; integument present; coelom well developed and filled with visceral systems; digestive system complete and ventral to spinal column; ventral heart with two to four chambers; closed blood vessel system; excretion by a pair of kidneys; endocrine system present; muscles attached to skeleton for facilitating movement; body consists of head, trunk and postanal tail, neck present in some (Fig.1.9). The group is divided into two superclasses on the basis of the presence of jaws.

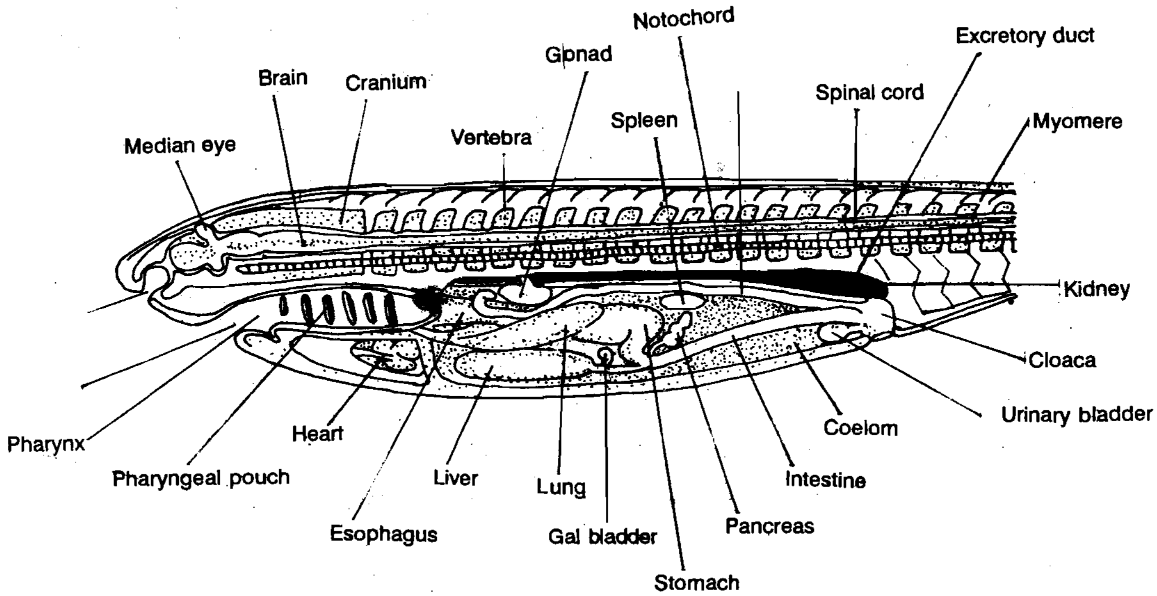

Fig.1.9: A diagrammatic sagittal (median vertical) section of a vertebrate showing the distinctive characters of the subphylum.

Superclass 1: Agnatha (without Jaws) (Cyclostomata): Hagfishes, lampreys. Forms without true jaws or paired appendages. Consists of following two classes.

Class 1: Myxini: Hagfishes. Forms with terminal mouth having four pairs of tentacles; buccal funnel is absent; nasal sac connected to pharynx via a duct; gill pouches about five to fifteen pairs; partially hermaphroditic.

Class 2: Cephalaspidomorphi: Lampreys. Forms with suctorial mouth having horny teeth; mouth not connected to nasal sac; seven pairs of gill pouches

Superclass 2: Gnathostomata: Jawed fishes, all tetrapods. All vertebrates with upper and lower jaws and usually with paired appendages. This group is divided into following classes.

Class 1: Chondrichthyes: Sharks, skates, rays, chimaeras. Body streamlined with heterocercal tail (Fig. 1.10); skeleton entirely cartilagenous; five to seven pairs of gills; gill slits opening directly to the exterior; operculum and swimbladder absent; body covered with placoid scales.

Operculum is a body flap present over the gill outlet which assists in pumping water through the mouth and out from the gills.

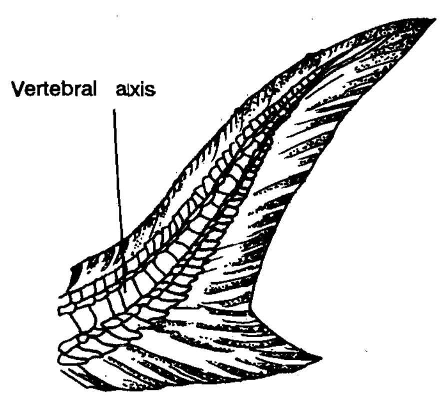

Fig.1.10: Heterocercal tail.

Class 2: Osteichthyes (Teleostomi): Bony fishes. Skeleton mostly ossified (bony); body primitively fusiform; tail outwardly symmetrical or homocercal (Fig.1.11); single gill opening on each side; operculum present; usually swim bladder or lung.

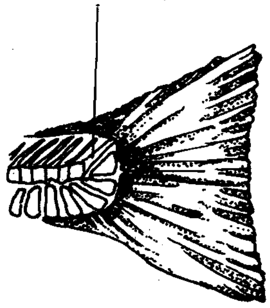

Fig.1.11: Homocercal tail.

Class 3: Amphibia: Amphibians. Ectothermic tetrapods; respiration by lungs, gills or skin; larval stage in the development: skin moist and contains mucous glands; scales absent.

Class 4: Reptilia: Reptiles. Both ectothermic and endothermic tetrapods; pulmonary respiration by lungs; larval stage absent; embryo develops in the shelled egg; dry skin; mucous glands absent; skin covered with epidermal scales.

Tetrapod is the term frequently used for amphibians and other higher four footed animal forms.

Class 5: Aves: Birds. Endothermic vertebrates; body covered with feathers; anterior limbs modified for flight; scales present on feet.

Class 6: Mammalia: Mammals. Endothermic vertebrates; young nourished by mammary glands; body covered with hair; brain well developed; diaphragm separates lungs and pericardium from other viscera.

Amnion is the innermost of the extraembryonic membranes that form fluid-filled sac around the embryo in amniotes

Based on the features of embryonic development, fishes and amphibians are grouped under anamniotes whereas reptiles, birds and mammals are referred to as amniotes. In this unit we will discuss the group Protochordata which comprises of Urochordata and Cephalochordata. About vertebrata you will read more in the following units and blocks. But before that attempt the following SAQ.

SAQ 4

Match the items given in column I with those in column II.

	I		II
a)	Protochordata	i)	Myxini
b)	Vertebrata	ii)	Bony fishes
c)	Agnatha	iii)	Amphibia
d)	Osteichthyes	iv)	Urochordata
e)	Moist skin	v)	Backbone
f)	Endothermic	vi)	Mammals

1.5.1 Subphylum Urochordata

The Urochordata (tail-chordata) comprises about two thousand species of marine chordate animals. Most of them are sessile as adults. The name 'tunicate' is because of the presence of a tough, nonliving tunic or test that surrounds the animal. Tunic is composed of a substance called tunicin which is rather unusual in animals. This is because of the fact that tunicin is very closely related to the cellulose of the plants. In most of the species only the larval form bears all the chordate hall marks. In the adult form the notochord and the tail disappear, whereas the dorsal nerve cord is reduced to a single ganglion. Urochordata are divided into three clases: **Ascidiacea, Larvacea** and **Thaliacea**. These three classes are distinguished based on the number of pharyngeal gill slits, nature of metamorphosis, solitary or colonial habit and organisation of tunic.

Class Ascidiacea: The ascidians include sea squirts and are solitary (eg. Herdmania, Ciona) (Fig.1.12), colonial or compound (eg. Botryllus).

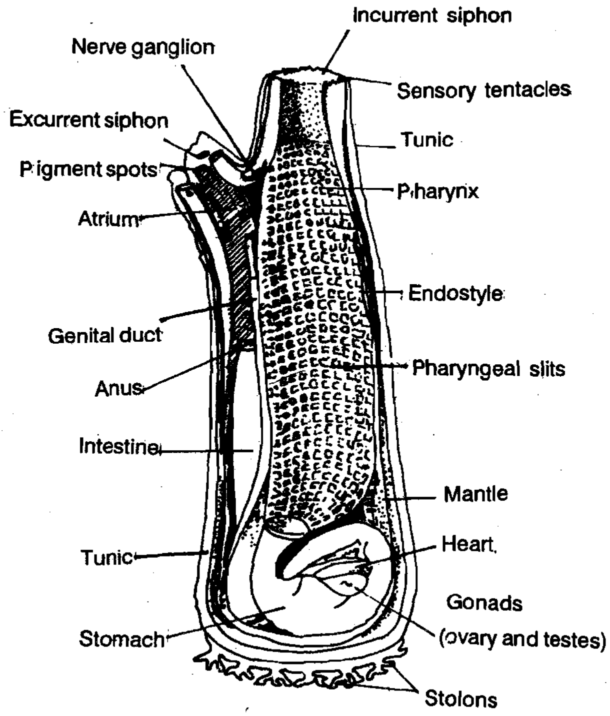

Fig.1.12: Structure of an adult ascidian: *Ciona* species.

The general form is like a vase with a vertical tube, with a terminal growth or branchial opening at its apex and a lateral tube leading to an opening called atrial opening. Water enters at the branchial opening (incurrent siphon or mouth), circulates over the gill basket inside and is ejected through the atrial opening (excurrent siphon). Gill basket is the spacious ciliated pharynx that is minutely subdivided by gill to form an elaborate basket work. During this water circuit, oxygen and food particles are removed from the water and the waste is carried out through the atrial opening. One of the special features of ascidian is the presence of endostyle (a ciliated, glandular groove of the pharynx) on the floor of branchial chamber. This structure secretes mucous in which food particles are trapped. Interestingly, the cilia lining the endostyle pass the mucous upward and over the midline of the pharynx where it is rolled into a mucous rope by a row of tentacles and the rope is then passed to the oesophagus, thence to the stomach and intestine. Nutrients are absorbed in the midgut. Faecal pellets are discharged outside through the anus located near the excurrent siphon. Some believe that the endostyle is the fore-runner of thyroid gland.

Nervous system consists of a nerve ganglion and a plexus of nerves that lie on the dorsal side of the pharynx. Beneath the nerve ganglion is the neural gland containing gonadotropic substances, believed to be analogous to the vertebrate pituitary. One of the striking features of Urochordates is that the tubular heart has pace makers at both the ends which periodically reverse the flow of the blood. Two large vessels on either side of the heart connect to the diffused system of small vessels and spaces that serve to various organs. **Sea Squirts** are hermophrodites and fertilization is internal. Some are oviparous, others viviparous but in forms like **Clavelina** there is a tadpole like larva. The larva is free swimming and does not feed. After some hours the larva fastens itself vertically with the help of adhesive papillae and undergoes metamorphosis to become the sessile adult (Fig.1.13)

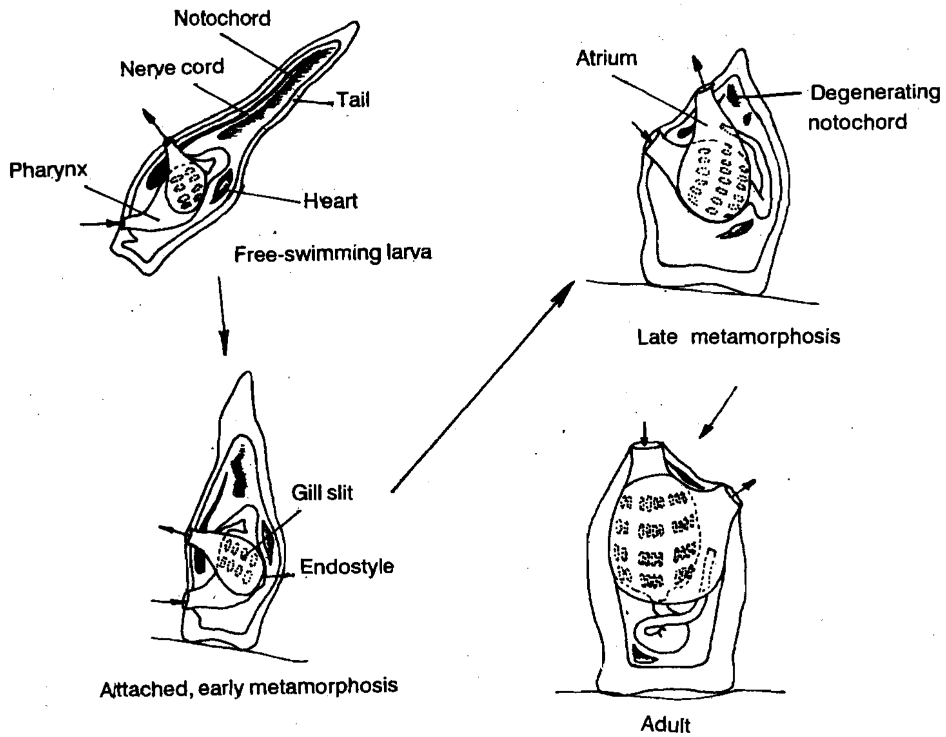

Fig.1.13: Metamorphosis of ascidian larva from a free swimming tadpole larva stage to an adult.

Class Thaliacea: The thaliaceans are barrel-shaped pelagic forms with gelatinous and transparent bodies that are almost invisible in sunlit surface waters. Their body is typically surrounded by bands of circular muscles. The incurrent and excurrent siphons are at opposite ends. The muscular contraction helps the water to pump through the body which is used for locomotion, respiration and a source of food that is filtered out on mucous surfaces. Many species of Thaliacea are luminescent. Some members like *Doliolum* (Fig.1.14) and *Salpa* exhibit alternation of sexual and asexual generation.

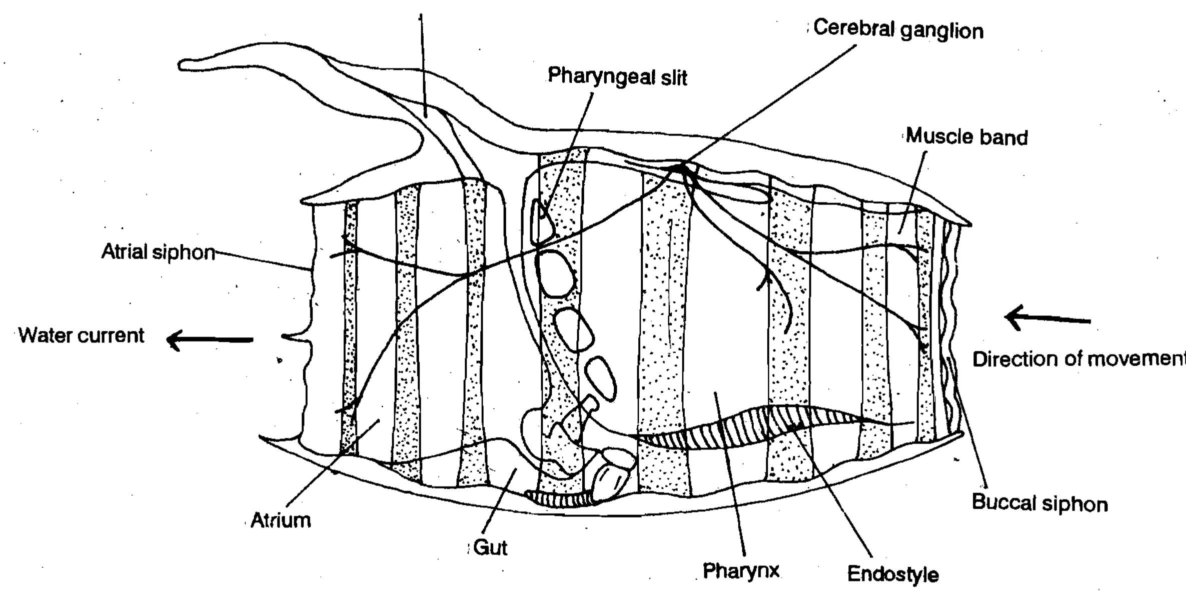

Fig.1.14: The solitary thaliacean *Doliolum*.

Class Larvacea: The larvaceans are pelagic and shaped like a bent tadpole. The test in larvacean is not composed of tunicin. They exhibit an interesting method of feeding. The individual animal builds a house that is a delicate, transparent hollow sphere of mucous interlaced with filters and passages through which the water enters (Fig.1.15). Food particles that are trapped on the feeding filter inside the house is drawn into the animal's mouth through - a straw like tube. After about every four hours, when the filter becomes clogged with waste, the animal abandons its house and builds a new one within a few minutes. The animals are neotenous that is the sexually mature animals have retained the larval body form eg. *Appendicularia, Oikopleura.*

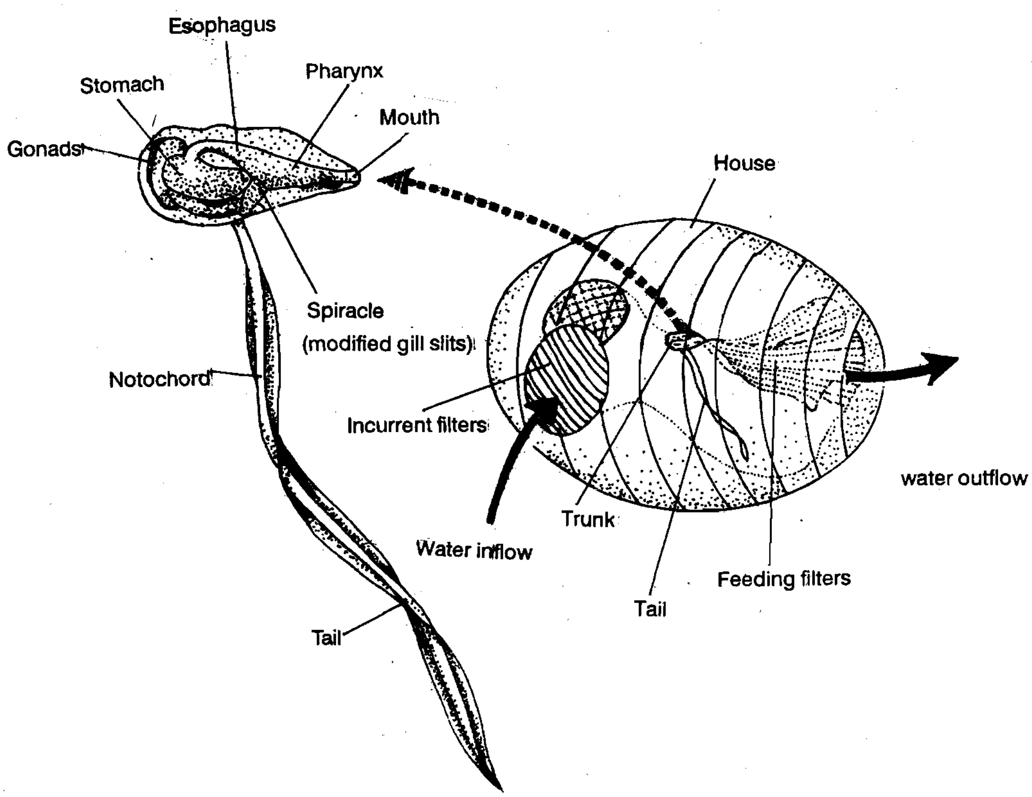

Fig.1.15: An adult larvacean (left) shown in its transparent house (right).

1.5.2 Subphylum Cephalochordata

Cephalochordates are also called as lancelets (Branchiostoma) - *Amphioxus* is the sole representative of the subphylum Cephalochordata. These are slender, laterally compressed and translucent animals about 5 to 7 cm. in length (Fig.1.16).

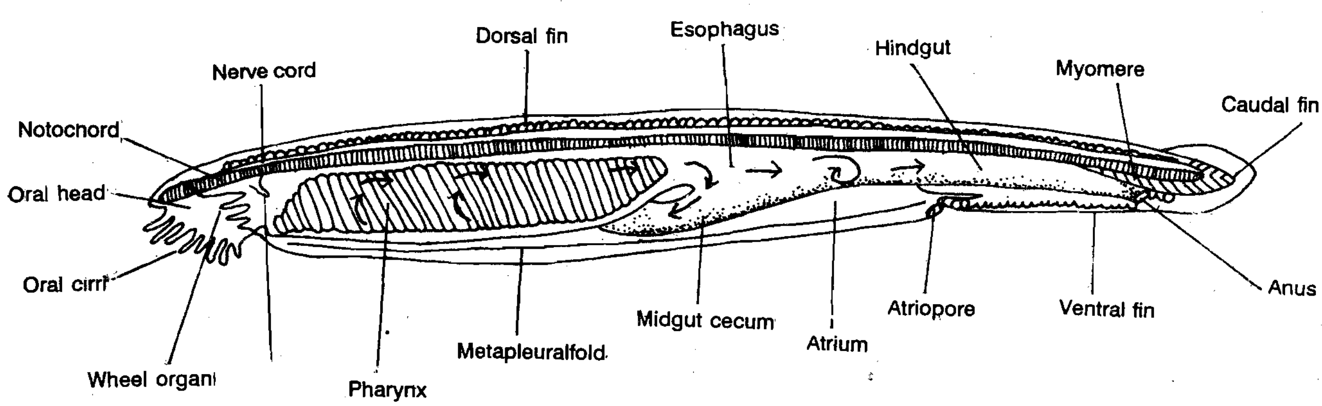

Fig.1.16: External features of *Amphioxus*.

There are about two dozen species of this genus found distributed all over the world. A striking feature of the surface of the body is the presence of V-shaped myotomes or muscle segments visible externally. It burrows in sand and spends most of its time buried tail down in sand with only its head including the mouth exposed above the surface. During breeding season it usually comes out of sand at night and swims about here and there. It feeds upon organic particles and small plankton which are brought to the mouth by the inhalant current of water. During feeding, the cilia lining the oral funnel create an inhalant current. Water is then drawn into the mouth through a membranous velum which bears twelve short tentacles. The current of water passes into a large branchial chamber formed by the pharynx, closely comparable to that of Urochordates. The branchial chamber bears gill slits (Fig.1.17), used for breathing.

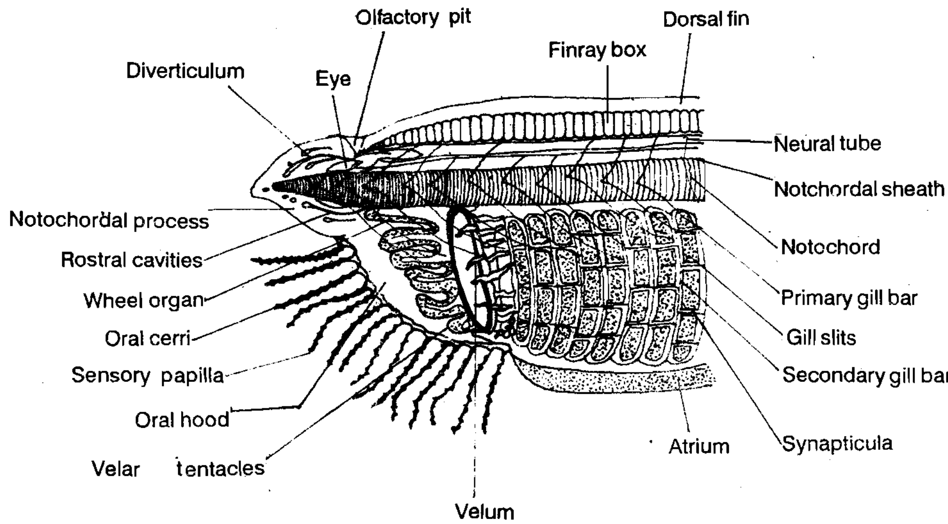

Fig. 1.17: Anterior part of *Amphioxus*.

The cilia lining the gill slits allow water to enter into a groove on the floor of the branchial chamber known as endostyle The food particles present in the water are trapped by the mucous secreted in the endostyle. The mucous then travels through two ciliated grooves to the dorsal side of the pharynx to enter into the intestine. Here the smallest food particles are separated from the mucous and passed into hepatic caecum, where these particles are phagocytized and digested intracellularly. The filtered water then passes into atrium and leaves the body by an atriopore similar to the excurrent siphon of tunicates. Circulatory system is closed and blood flow pattern is similar to that of primitive fishes, although there is no heart. Blood is pumped forward in ventral aorta, then passed upward through branchial arteries (aortic arches) in the gill bars and then to dorsal aortae which terminate into a single dorsal aorta. The blood is then served to the body tissues, collected in the veins which return it to ventral aorta. The blood is devoid of erythrocytes and hemoglobin.

Nervous system consists the nerve cord lying above the notochord. Brain is a simple vesicle at the anterior end of the nerve cord. Pairs of spinal nerve roots emerge at each myometric (muscle) segment of the trunk. Sense organs are the unpaired bipolar receptors present in the various parts of the body. Excretion is by means of nephridia — a feature not usual in chordates. In the lancelets the sexes are separate. Eggs and sperms pass to the exterior through the atriopore. Fertilisation is external and takes place in water during late spring or early summer.

SAQ 5

i. Explain the mode of feeding adopted by a larvacean.

....

....

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....

ii. Fill in the blanks with appropriate words.

a) The tough nonliving covering of urochordates is called ....

b) The three classes of Urochordata are ....,................, and ....

c) In ascidians the food particles are trapped in the .... secreted by ....

d) .... spends most of the time burried tail down in the sand.

e) Excretion is by means of .... in *Branchiostoma.*

f) In lancelets .... are separate and .... is external.

g) Digestion is .... in *Branchiostoma.*

1.5.3 Basic Adaptive Features

Urochordates also present a few important adaptations which contributed to the success of the group. The efficient ciliary mode of feeding compensates very well the disadvantage of sedentary life. Some species have developed the habit of growing as commensals on gastropods and thus they have found a way for wider distribution. Other features which confer upon urochordates, the "adaptive advantage", are large perforated pharynx with its efficient gaseous exchange and a thick leathery protective test to keep away the predators. The tadpole of Herdmania has developed several adaptive features such as streamlined body, tail supported by turgid notochord for locomotion, otoliths for maintaining equilibrium and adhesive papillae for attachment to the substratum.

The cephalochordates are adapted to their surroundings in an excellent manner. Various adaptations encountered in this group can be arranged into following categories. They are: 1) adaptations for swimming; these include the development of streamlined body, turgid notochord and expanded caudal fin in the adult. 2) ciliary mode of feeding adaptations well suited for sedentary life. 3) adaptations which conferred survival value and thereby achieved success are a) life in burrows ensured safety from the predators, b) the multiple gonads that provide means by which large number of gametes are formed and thus increase chances of fertilization. c) large and voluminous pharynx for efficient exchange of gases and d) the free swimming larva for distribution to different ecological niches.

1.5.4 Affinities

Let us now focus our attention to the affinities of urochordates and cephalochordates. The urochordates and cephalochordates show many points of resemblances. They are: 1) ciliary mode of feeding; 2) presence of atrium and endostyle, 3) pharynx perforated with numerous gill slits; 4) similar origin of notochord and neural tube.

But there are also some dissimilarities between the two groups which make it difficult to draw affinities between them. Urochordates differ from cephalochordates in the following respects: 1) the body wall containing tunicin; 2) presence of pericardium; 3) 'U' shaped alimentary canal; 4) absence of nephridia; 5) loss of chordate characters in the adult.

Urochordates show resemblances to the invertebrates like molluscs such as 1) presence of cartilage; 2) presence of chitin, this substance is also present in cephalochordates showing affinity between them; 3) presence of pericardium and pancreatic tissue; 4) ammonia as excretory product. However, tunicate tadpole larva presents several chordate features like notochord, median eye, well developed pharynx with endostyle, and a tail with expanded dorsal and ventral fins.

There are some striking resemblances between cephalochordates and echinoderms also. These are 1) enterocoelous coelom, and 2) symmetrical features in anatomy. However, the affinities with invertebrates are of minor importance. *Amphioxus* is rather peculiar showing several chordate features and specialised characters.

SAQ 6

Match the items given in column I with that of column II.

	I		II
i.	Adhesive papillae	a)	Formation of large number of gametes.
ii.	Multiple gonads	b)	Urochordates and cephalochordates
iii.	Presence of atrium	c)	Tail supported by turgid notochord
iv.	Locomotion	d)	Herdmania Larva
v.	U-shaped alimentary canal	e)	Present in Urochordates

1.6 ANCESTRY AND EVOLUTIONARY TRENDS

When we try to trace the ancestry and evolutionary trends among animals, it is important to analyse once again the organisation and general plan of development common to all the groups. There is sufficient basis for comparison between echinoderms, hemichordates, protochordates and chordates. In all, the blastopore becomes anus and mouth is entirely a new opening. Hence these animals are grouped under deuterostomia (Greek *deuteros*, "second" or "later" and *stoma*, "mouth"); (second mouth). This is in marked contrast to other non-vertebrates where the blastopore forms the mouth (protostomia: primitive mouth) (Greek *protos*, "first" and *stoma*, "mouth").

Protostomes, literally meaning 'first mouth' are animals in which the mouth arises from or near the blastopore. Additionally, they tend to have spiral cleavage, a schizocoelom and a skeleton derived from the surface layer of cells. Deuterostomes, literally meaning "second mouth" are animals in which the mouth arises not from the blastopore but secondarily at the opposite end of the gut. Additionally, embryonic development of deutrostomes includes radial cleavage, an enterocoelom and a calcified skeleton, when present, derived generally from ectodermal tissues.

The origin and ancestry of chordates is not clearly established. There are several view points but they are all largely speculative. It is not certain as yet whether the end products are neotenous, free swimming derivatives of formerly sessile animals or have continuously evolved as active, free swimming animals. We have known earlier that chordates generally resemble echinoderms and their allies. However, there are also certain specialization in echinoderms such as radial symmetry, water vascular system and nerve ring to rule out the possibility that echinoderms are the ancestors of chordates. A similar view is also applicable to hemichordates. Even though hemichordates are placed close to chordates, the proboscis, collar, nature of circulatory system are features which set them completely apart from the higher chordates.

Let us now examine whether or not it is possible to consider primitive urochordates as chordate ancestor. Adults of urochordates are highly specialised : they have lost notochord, nerve cord and coelom and retain non-chordate characterstics, like tunic, atrium and siphon. Thus, these animals hardly fit into vertebrates plan. Tunicates, however, show us a stage in which branchial feeding has fully replaced tentacle feeding in a sessile adult. But they have a fishlike tadpole larva. Perhaps it would be worthwhile to trace vertebrate ancestry based on larval structure of ascidians.

The auricularia theory of Garstang (1894) explains how ascidian tadpole has arisen from auricularia larva. According to this theory the ciliated auricularia larva is evolved into a fish like creature in progressive stages, while the adults, at first sedentary, substituted gill slits and endostyle for the original lophophore. This view seems to be reasonably convincing. The theory enables one to reconstruct the course of events that led the lophophore feeder in streams and in doing so they faced, the drastic physical forces of water currents. In order to overcome the force of water currents flowing towards the sea, expectedly the larvae had to equip themselves with powerful locomotory and sensory systems. In addition necessary modifications would occur in kidney to suit the fresh water life. Around palaeozoic era some selected groups of animals exploited ecological niches of freshwater and among these are the provertebrates and arthropods. Garstang's theory further envisages that *Amphioxus* must have been the early protovertebrate and this returned (migrated) to sea for breeding purpose; and then readopted to filter feeding for marine existence. This theory is supported by authorities like N. Berill and A.S. Romer.

Amphioxus reveals several basic features of chordates, such as the presence of notochord, dorsal tubular nerve cord and pharyngeal gill slits in its organisation (Fig. 1.18). In addition, it shows secondary characteristics like the postanal tail, liver, diverticulum, hepatic portal system and the beginning of a ventral heart. The muscular layer in *Amphioxus* is thickened in the dorsal side as in vertebrates. The metameric condition of muscles bears resemblances to a similar plan in vertebrate embryos. However, some authorities like Hickman (1966) have pointed out that it is close to the primitive fish, Ostracoderm, though it is difficult to settle whether to place it before or after Ostracoderms. Besides, there are also reasons to develop pharynx with gill slits and its larva to have muscles, nerve cord and a nerve tube (Fig.1.19). Thus, the tunicate tadpole larva could be easily derived from an echinoderm larva. The most pertinent question is how vertebrates have eliminated the sea-squirt stage from their life history. According to Haeckel's concept of recapitulation, adult stages of ancestors are repeated during development of their descendents. But this view cannot be accepted as such since there is no sea-squirt stage in the development of any vertebrate. Some believe that the adult ascidians are regarded as degenerate sessile descendants of the ancient chordate form, whereas the ascidian tadpole is considered as relic of an ancient free-swimming chordate ancestor of the ascidians.

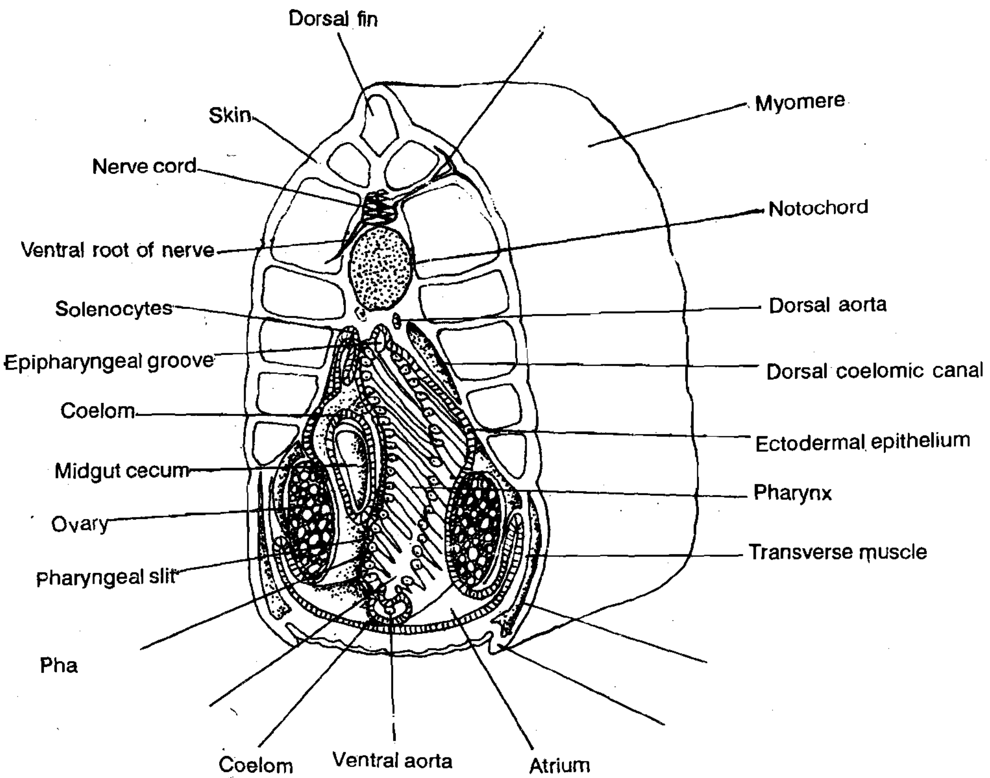

Fig.1.18: Cross section of *Amphioxus* showing chordate features.

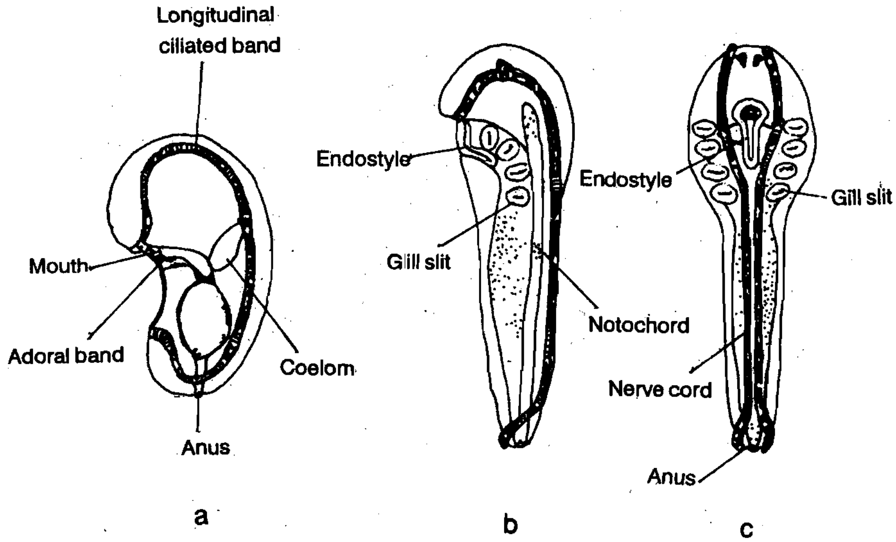

Fig.1.19: Derivation of protochordate (b-lateral view, c-frontal view) from auricularia(a)

Study of ascidian tadpole larva of urochordates further led to many speculations regarding the origin of chordates. According to the ascidian theory of chordates advanced by Garstang (1928) all ancestral chordates were marine, sessile and filter feeders. The ascidians themselves may have taken their origin from sessile hemichordates. Ascidian tadpole with its basic vertebrate organisation then evolved from the sessile form. The larva is pelagic, freeswimming and feeds upon the plankton of the oceanic waters. Soon after freeswimming life, the larva attaches to substratum, undergoes regressive metamorphosis and transforms into a sessile adult form (Fig.1.13). It is believed that some of these larvae, instead of undergoing metamorphosis become sexually mature (neoteny) and enter estuaries and rivers where they can feed upon the organic detritus. Class larvacea of tunicates belongs to this stage of evolution, Firstly, the over development of the notochord is regarded by some as an adaptation to burrowing habit. Secondly, presence of solenocyte type of protonephridia recalls primitive condition seen in polychaetes, and therefore do not bear any resemblances to glomerular-tubular nephron of vertebrates. Colbert, however, emphasises that *Amphioxus* is still the logical structural ancestor of vertebrates overruling the objections of others regarding the specialization of this form.

By and large the widely accepted view is that vertebrates are more closely related to cephalochordates than to urochordates and that the phylum Chordata is close to Hemichordata and Echinodermata. However, no known echinoderm, hemichordate, urochordate and even cephalochordate is in the main line of chordate evolution. Infact, it is difficult to pinpoint that the chordates have evolved from any known animal living or extinct. Some authors believe that the cephalochordates forms a specialized offshoot from a vertebrate ancestor. Even this view could not gain acceptance, since at no time any member of this group ever possessed cranium and features like brain and eyes.

Current view is that echinoderms, hemichordates and chordates must have diverged from a common lineage around 500 million years ago, A possible phylogenetic line suggested the relationships of the hypothetical ancestor, various groups of protochordates and vertebrates is shown in Fig.1.20.

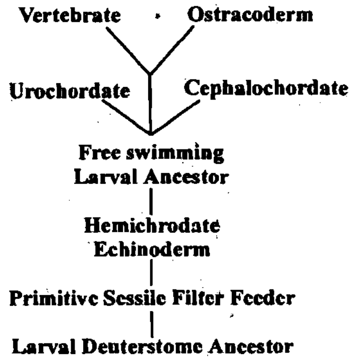

Fig.1.20 : A possible scheme of the phylogency of chordates.

The echinoderms are linked to protochordates by similarity of the echinoderm auricularia to tornaria, of protochordate groups. Further, the palaeontological evidence, as discussed earlier, strengthens the view that both the groups are closely related. These considerations with regard to echinoderm line of phylogeny of chordates are based upon morphological, anatomical, embryological and palaentological evidences. Authors like Geoffrey (1930) in the past and more recently Siliman (1960) have pinpointed several striking similarities between molluscs and chordates. It is rather surprising that the relationship of the chordates with molluscs has not attracted the attention of phylogeneticists, although they resemble each other in several biochemical, physiological and histological characteristics. There are several characters studied by many authors and some of them are listed in Table-1.1

Table 1.1 : The biochemical, physiological and histological characters that were used to compare molluscs, echinoderms and vertebrates (chordates).

Biochemical	Physiological	Histological
Glycosaminoglycans	Respiration	Cartilage
Sialic acid	Circulation	Skeleton
Collagen	Food & digestion	Heart
Epidermal Proteins	Osmoregulation	Blood
Chitin	Nitrogen excretion	Pericardium
Phosphogens	Photoreception	Liver & Pancreas

The criterion that has been adopted in the selection of characters from these is that their presence or absence must be established in all the three main groups namely the echinoderms, molluscs and vertebrates (chordates). The main objective of the study is to determine the degree of closeness between molluscs, echinoderms and vertebrates, based upon the number of above mentioned characteristics. Lovtrup's (1977) phylogeny relies on the above mentioned characters because he considered them more evolutionary stable than morphological characters. For example, any two groups that shared more biological chemicals as compared to others were more closely related.

We finally conclude that the ancestry of chordates is an unsettled issue and any attempt to trace their phylogeny is beset with difficulties. Both the echinoderm and molluscan line of chordate ancestry can be either accepted or rejected.

SAQ 7

Explain the auricularia theory of Garstang. How it is different from his ascidian theory?

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1.7 SUMMARY

In this unit you have learnt that:

- Hemichordates are the group of animals that are characterised by the presence of chordate features i.e. gill slits and rudimentary notochord. However, the hemichordate notochord is in reality the buccal diverticulum and not the true notochord. It is for this reason hemichordates are now considered as a separate phylum.

- The four chordate hall marks are the presence of notochord, dorsal tubular nerve cord, pharyngeal gill slits and post anal tail. Hence they are so very different from invertebrates.
- The members of the phylum chordata are diverse in their habit and organisation.
- Among the invertebrates, echinoderms are close to hemichordates. However, both the groups have their own specialisation.
- There is no known echinoderm, hemichordate, urochordate and even cephalochordate, either living or dead, in the main line of chordate evolution.
- Evidences based upon biochemical, physiological and histological characteristics suggest that the chordates (vertebrates) stem from molluscan lineage but not echinoderm lineage. The available data on the ancestry of chordates is conflicting and the issue is unsettled.

1.8 TERMINAL QUESTIONS

1. What are the four hall marks of chordates?

   ....

   ....

   ....

2. Give atleast three basic adaptive features of hemichordates and urochordates.

   ....

   ....

   ....

3. Describe the mode of feeding in *Branchiostoma*.

   ....

   ....

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4. Explain briefly how cephalochordates have adapted to their surroundings.

   ....

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5. Mention atleast four important affinities between echinoderms and chordates.

   ....

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6. Describe any fossil echinoderm that is believed to be close to chordates.

   ....

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   ....

7. What are the specialisations in the anatomy of adult urochordates?

....

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....

8. What are the lines of evidence to support the molluscan lineage of chordates?

....

....

9. What is the current view of the ancestry and evolution of chordates?

....

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1.9 ANSWERS

Self Assessment Questions

1. i) 1. Body divided into three parts Proboscis, Collar and Trunk.
   2. Gill slits present.
   3. Dorsal nerve cord present. You can write about other characteristics of hemichordates from Section 1.2.

   ii) Pterobranchs live in the gelatinous tube secreted by them whereas enteropneusts live in burrows. You can read about the other differences from sections 1.2.1 & 1.2.2.

2. i) similar mode
   ii) multiple gonads
   iii) absent
   iv) nervous system
   v) echinoderms.

3. i) Nerve cord is ventral in higher invertebrates and dorsal in chordates.
   ii) Pharyngeal gill slits are present in chordates but absent in invertebrates.
   iii) Heart is ventral in chordates and dorsal in invertebrates.

4. a. iv
   b. v
   c. i
   d. ii
   e. iii
   f. vi.

5. i. The food particles coming along with water are trapped on the feeding filter in the house. The filtered food is then drawn into the animal's mouth through a straw like tube. After about four hours when filter is clogged with waste, the animal leaves the house and builds a new one.

   ii. a. tunic
   b. Ascidiacea, Larvacea, Thaliacea
   c. mucous, endostyle

d. *Amphioxus*
e. nephridia
f. sexes, fertilization
g. intracellular

6. i. d
   ii. a
   iii. b
   iv. c
   v. e

7. The auricularia theory of Garstang (1894) explains how ascidian tadpole has arisen from the auricularia larva. According to this theory the ciliated auricularia larva is converted into fish like creature in progressive stages, while the adults, at first sedentary, substituted gill slits and endostyle for the original lopohore. It is expected that larvae have to equip themselves with powerful locomotory system. Garstang's theory further envisages that *Amphioxus* must have been early protovertebrates.

   According to ascidian theory of origin of chordates by Garstang (1928) all ancestral chordates were marine, sessile and filter feeders. The ascidians themselves may have taken their origin from sessile hemichordates. With ascidian tadpole it is believed that some of the larvae, instead of undergoing metamorphosis become sexually mature and entered the estuaries. The class Larvacea of tunicates belongs to this stage of evolution.

Terminal Questions

1. The four distinctive characters of chordates are the presence of notochord, dorsal tubular nerve cord, pharyngeal gill slits and post anal tail.

2. In hemichordata, the efficient proboscis which aids in burrowing, the protection offered by the chitinous material present in the skin and the regenerative capacity of the individuals in the colony are the basic adaptive features which contributed to the success of the group.

   The chief orienting factors which contributed to the success of Urochordates are: 1) The efficient and complex ciliary mode of feeding; 2) Large perforated pharynx; and 3) The active freeswimming tadpole larva.

3. The ciliary mode of feeding in *Branchiostoma* is unique. The cilia of the oral funnel, velum and velar tentacles and the pharynx participate in feeding. The cilia and tentacles set up water current which enters through oral funnel into the pharynx. The gill slits of the pharynx are employed for breathing. The cilia of the gill slits allow the water to enter into the floor of the branchial chamber. The food particles in the water are trapped by the mucous secreted by the endostyle and the food collected in the mucous is then pushed into the intestine for digestion and assimilation.

4. The cephalochordates are adapted to their surroundings in an excellent manner. Some noteworthy adaptations are : 1) Ciliary mode of feeding to suit sedentary life; 2) Streamlined body supported by notochord and expanded fins to aid in swimming; 3) The pharynx which takes up dual function namely respiration and feeding; and 4) The presence of multiple gonads to produce large number of gametes.

5. Echinoderms are close to the chordates. The following are the four important resemblances: 1) Enterocoelous origin of coelom; 2) Indeterminate cleavage with deuterostomes development; 3) Similarities between auricularia and tornaria; 4) Fossil echinoderms like Coteuronocystis with chordate features.

6. A fossil echinoderm of the Ordovician period (450 million years) belonging to the group Stylophora, namely *Coteuronocystis* has been reported recently from Scotland. It is a small non-symmetrical form with a head resembling a long toed medieval boot, a series of branchial slits like the gill openings of shark, a post anal tail with a notochord and nerve cord like structures. All these features bear superficial resemblance to chordates.

7. The main specialisations in the adult urochordates include the loss of chordate features such as notochord, nerve cord, coelom and the retention of non-chordate characteristics like atrium and siphon.

8. The biochemical, physiological and histological lines of evidence support the molluscan lineage of chordates.

9. The origin of chordates is an unsettled issue. The morphological, embryological and palaeontological evidences support the echinoderm ancestry. Equally impressive is the molluscan lineage based on biochemical, physiological and histological evidences.