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Balanoglossus : A Tongue Worm

SUBPHYLUM - HEMICHORDATA

Hemichordata (Gr., **hemi** half; **chorde**, cord), till recently treated as a subphylum of the phylum Chordata (or Protochordata), are now regarded to be an independent phylum of invertebrates close to Echinodermata. It includes deuterostome animals with enterocoelous coelom, pharyngeal gill-slits, a buccal diverticulum (considered earlier as 'notochord' and a vermiform body divisible into three regions : proboscis, collar and trunk. Hemichordates includes a small group of soft, marine and primitive chordates, commonly called the 'acorn worms' or 'tongue worms'.

BALANOGLOSSUS : TONGUE WORM

SYSTEMATIC POSITION

Phylum	Chordata
Subphylum	Hemichordata
Class	Enteropneusta
Family	Ptychoderidae
Genus	*Balanoglossus*

Most familiar hemichordate genus is *Balanoglossus* which belongs to the class Enteropneusta. Other closely related genera are *Saccoglossus (=Dolichoglossus), Glossobalanus, Ptychodera, Spengelia,* etc.

DERIVATION OF NAME

Balanoglossus clavigerus was recorded and named by **Delle Chiaje** in 1829. Its generic name was derived from two Greek words, **balanos** and **glossus**. Term **balanos** means an 'acorn' (fruit of oak) and refers to the proboscis projecting from collar looking like an acorn-nut, hence the common name 'acorn worm'. Term **glossus** means 'tongue' and refers to the shape of its proboscis, collar and genital wings bearing a close resemblance to an ox tongue, hence the common name 'tongue worm'. Local fisher-men call *Balanoglossus* by the name 'ox tongue'.

GEOGRAPHICAL DISTRIBUTION

Balanoglossus, like all other hemichordates, is a marine animal having a world-wide distribution. About 120 species occur all over the world especially in the tropical and subtropical seas. However, 12 species occur in India. Some species are *B. australiensis* (Australia), *B. carnosus* (Indo-Pacific), *B. misakiensis* (Japan),

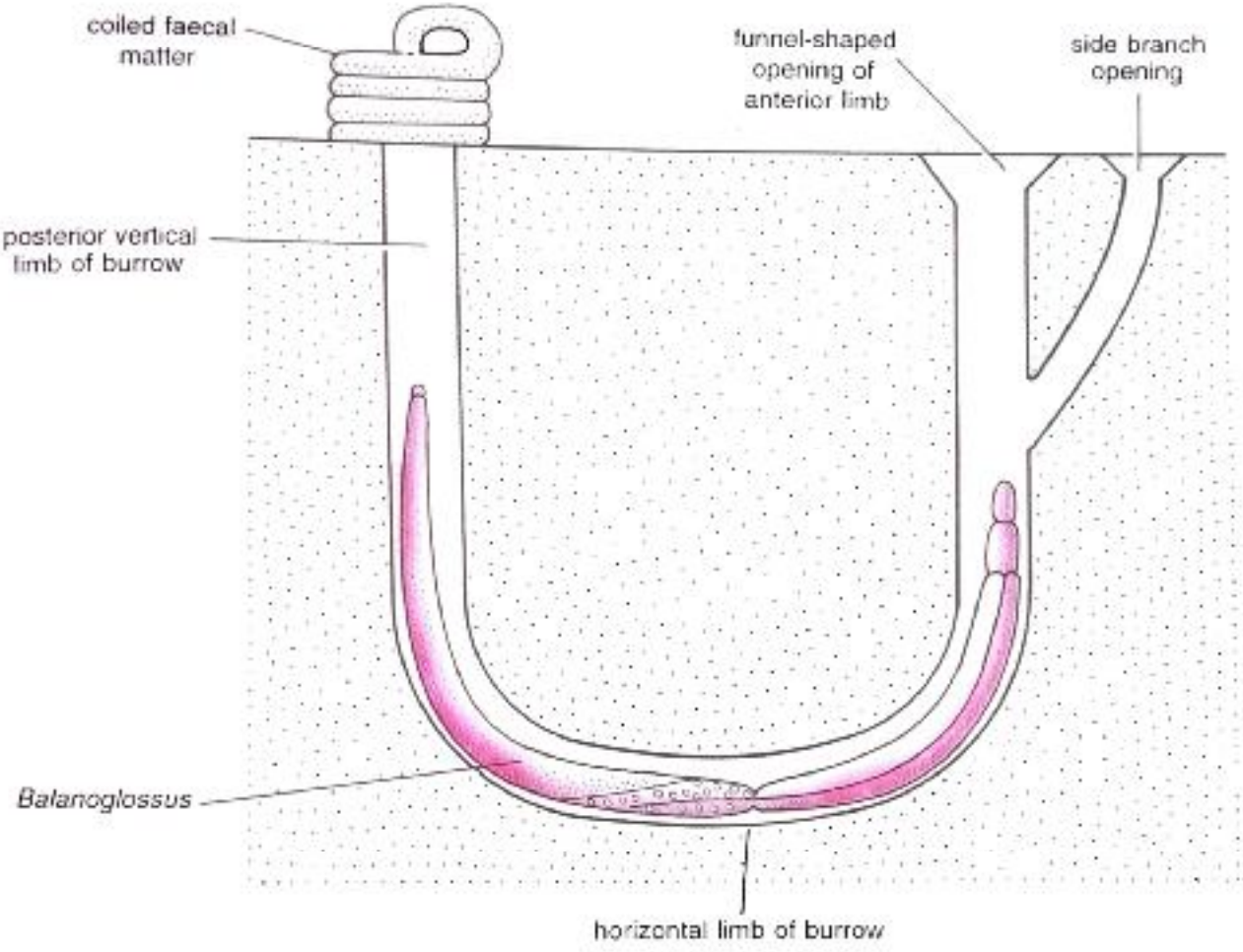

Fig. 1. *Balanoglossus clavigerus* in U-shaped burrow.

B. jamaicensis (West Indies), *B. gigas* (Brazil), *B. capensis* (South Africa) and *B. clavigerus* (Mediterranean and British isles).

HABITS AND HABITAT

Balanoglossus is a marine, tubicolous or burrowing hemichordate inhabiting shallow coastal waters of intertidal zone, but a few occur in deeper water.

Burrow. The animal may conceal under stones or sea weeds or excavate its own burrow in the bottom of sand or mud. *B. clavigerus* lives inside a U-shaped tube or burrow with the two vertical limbs, 50-75 cm deep and the two openings 10-30 cm apart. In some species (*Saccoglossus*), body of the animal and tube are twisted, whereas the anterior and posterior extremities remain straight. Anterior opening of the burrow is funnel-shaped and exposed. Anterior vertical limb may give out side branches each having its independent funnel-like opening (Fig. 1). Posterior opening of the burrow is rounded and concealed below the spirally coiled faecal matter of the animal.

Protective device. Inner wall of the fragile tube is smoothly lined by sand particles cemented together into a tough cast with sticky mucus secreted by the skin mucous glands of the animal. This prevents the collapse of the burrow and protects the delicate animal from burial in loose sand. Another protective device is the secretion of a foul-smelling odour similar to iodoform. One species shows phosphorescence.

Movements. Worm is sluggish and little affected by external stimuli. It moves in its burrow by cilia covering its body surface. Most active part of the body is proboscis. It elongates and shortens by muscular activity and helps in burrowing. When the tide recedes, the tongue worm protrudes its anterior end out of the burrow to explore the surroundings, or its posterior end to cast out faecal matter.

Feeding and breeding. It swallows sand or mud to obtain diatoms, protozoans, other microorganisms and organic detritus on which it feeds. Sexes are separate. Males and females, living in separate tubes, shed their gametes in seawater where fertilization occurs. Life cycle includes a free-swimming planktonic ciliated larva, the **tornaria larva**. Tongue worm does not reproduce asexually, but its fragile body has considerable power of regeneration.

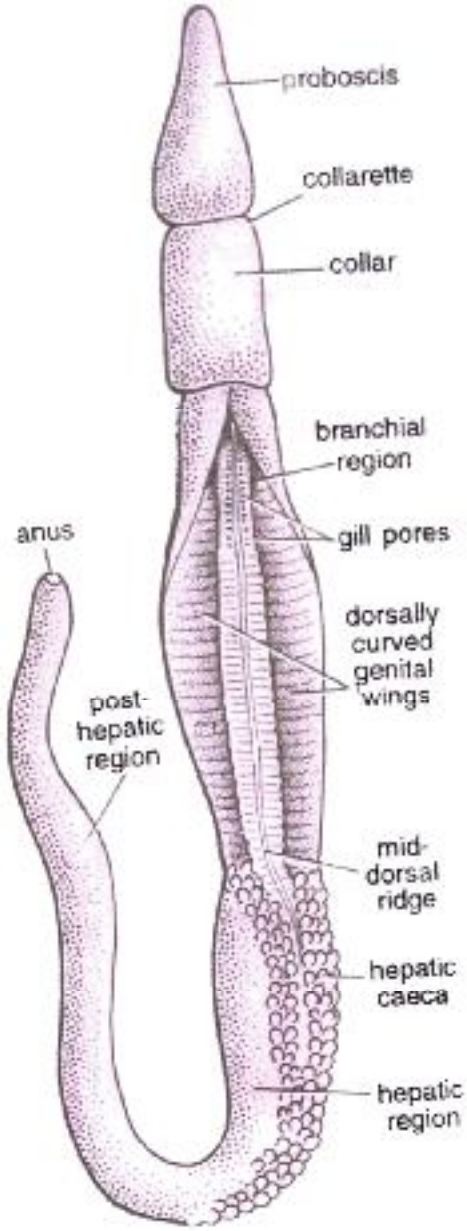

Fig. 2. *Balanoglossus*. External features in dorsal view.

EXTERNAL MORPHOLOGY

Shape, size and colouration. Body is soft, elongated, worm-like, cylindrical and bilaterally symmetrical. It measures 10 to 50 cm in length, according to species. *B. gigas* attains a length of

1.8 m (**Sawaya**, 1951) or 2.5 m (**Spengel**, 1893). Colour is bright or drab with reddish or orange tints. Body is uniformly ciliated and without any exoskeleton or external appendages.

Division of Body

Body is unsegmented but divisible into three distinct regions or parts : (i) **proboscis**, (ii) **collar** and (iii) **trunk**.

[I] Proboscis

Proboscis or **protosome** is the anteriormost part of the body. It is short, club-shaped or conical and circular in cross-section. It has thick muscular wall and is hollow within. Its cavity or proboscis coelom communicates with the outside through a minute **proboscis pore** situated mid-dorsally near its base. In some species the proboscis pore ends blindly or there are two pores. Posteriorly, the proboscis narrows into a slender **neck** or **proboscis stalk** which is attached to the collar. Below the stalk, the base of proboscis bears a U-shaped ciliated epidermal depression, called the **preoral ciliary organ**, which tests the quality of food and water entering the mouth.

[II] Collar

Collar or **mesosome** is the middle, short and cylindrical part. Its flap-like or funnel-like anterior margin, termed **collarette**, completely surrounds and conceals the proboscis stalk and the posterior part of proboscis. Ventrally, below the proboscis stalk, the collarette or collar-rim encloses a permanently open wide aperture, the **mouth**. It opens into buccal cavity inside the collar. Posterior end of collar is well demarcated from the trunk by a circular constriction. Wall of collar is thick, highly muscular and encloses a cavity, the **collar coelom**. It opens to outside through a pair of **collar pores** into the first pair of gill pouches.

[III] Trunk

Trunk or **metasome** is the posterior and largest part of the body. It is rather flat and appears annulated due to circular constrictions on the surface. All along its length, trunk bears a **mid-dorsal** and a **mid-ventral ridge**, each accommodating its corresponding nerve and blood vessel. Trunk is further differentiated into three regions : an anterior **branchiogenital**, a middle **hepatic** and a posterior **post-hepatic**, **abdominal** or **caudal** region.

1. **Branchiogenital region.** Anterior or branchiogenital region of trunk is marked by a pair of lateral, thin, flat and longitudinal flaps, the **genital wings**, containing the **gonads**. **Gonopores** are microscopic and cannot be seen by the unaided eyes. Anterior half of branchiogenital region bears two longitudinal rows of small **branchial apertures** or **gill pores**. One row of gill pores is mounted on a prominent longitudinal ridge on each side of the mid-dorsal ridge. Number of gill pores increases with the age of the animal. Two genital wings can be curved to meet mid-dorsally so as to conceal the gill pores. In some species, a posterior prolongation of the collar, called the **operculum**, may cover the anterior-most gill pores.

2. **Hepatic region.** Middle or hepatic region of trunk is somewhat smaller than the genital region. It is greenish in colour and its dorsal surface marked by the presence of numerous irregular intestinal sacculations or **hepatic caeca**.

3. **Post-hepatic region.** It is the posterior-most and the longest part of the trunk also called **abdomen** or **caudal region**. It is more or less uniform in diameter but its posterior end slightly tapers and bears a **terminal anus**.

BODY WALL

Body wall is composed of epidermis, musculature and peritoneum.

1. **Epidermis.** Outermost layer or epidermis consists of a single layer of mostly tall, slender, columnar and ciliated cells. Three kinds of gland cells secreting mucus are present. **Goblet gland cells** are flask-shaped with fine granules. **Reticulate gland cells** have vacuolated cytoplasm. **Mulberry** or **granular gland cells** contain coarse granules and also secrete amylase. Gland cells are more abundant in the collar region. Besides, **neuro-sensory cells**, which stain darker, are

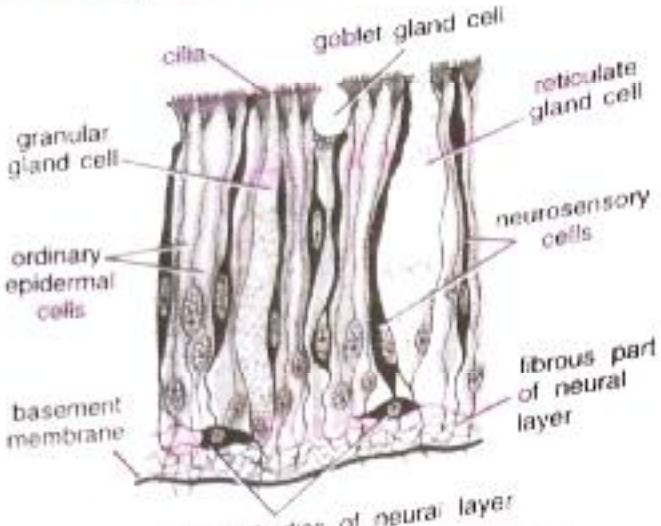

Fig. 3. *Balanoglossus*, V.S. of epidermis.

present in the epidermis of proboscis and anterior part of the collar. Dermis is absent. Below the epidermal cells is a thick **nervous (neural) layer** consisting of a network of nerve cells and nerve fibres. Below the neural layer is a thick **basement membrane** which supports the epidermis and serves for attachment of the underlying musculature.

2. Musculature. Muscles are smooth, weak and mostly longitudinal. Proboscis and the anterior end of collar (collarette) have an outer layer of circular muscle fibres and an inner layer of longitudinal muscle fibres. In the trunk region, only longitudinal muscle fibres are present.

3. Peritoneum. Coelom is lined by the parietal coelomic epithelium or peritoneum which covers the inner surface of the body wall musculature.

Functions of body wall. (i) Body wall shields the soft internal organs from mechanical injuries, (ii) Mucus produced by epidermal gland cells adheres sand particles for lining the burrow in which the worm lives, (iii) Foul smell of mucus is protective, (iv) Neuro-sensory cells serve to receive the external stimuli, (v) Musculature helps in body movements.

COELOM

Balanoglossus has a spacious coelom lined by coelomic epithelium and is enterocoelous in origin. Coelomic cavities of proboscis, collar and trunk are completely separated from one another. However, in the adult, the original coelom is greatly obliterated by connective tissue and muscle fibres derived from coelomic epithelium which becomes inconspicuous and irregular. Adult coelom is represented by five separate cavities which originate as independent pouches from the archenteron of the embryo. These include one cavity in proboscis, two in collar and two in the trunk.

1. Proboscis coelom. Unpaired **proboscis coelom** or **protocoel** is greatly obliterated by connective tissue and muscle strands except for a small central space which is occupied by the **proboscis complex**. Latter includes the buccal diverticulum, central sinus, heart vesicle and glomerulus. Proboscis coelom communicates with the outside through a **proboscis canal** and a **proboscis pore** situated mid-dorsally at the base of the proboscis stalk (Fig. 4).

2. Collar coelom. Collar coelom or **mesocoel** is represented by two narrow lateral cavities, one on each side between the collar wall and buccal tube. Two cavities are partitioned by incomplete mid-dorsal and mid-ventral mesenteries. Collar coelom does not communicate with the proboscis coelom, but posteriorly, its each cavity opens into the first gill sac of its side by a **collar canal** and a **collar pore**. Collar coelom is greatly obliterated by the collar musculature and connective tissue (Fig. 5).

3. Trunk coelom. Trunk coelom or **metacoel** is represented by a pair of closed cavities between the body wall and gut wall. Two cavities are separated by an incomplete dorsal and a complete ventral mesentery. In the branchiogenital region

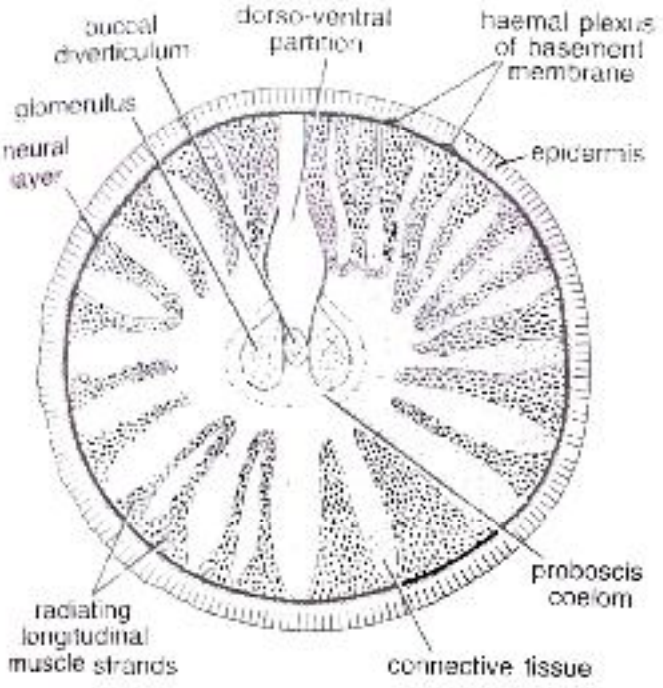

Fig. 4. *Balanoglossus*. T.S. through proboscis.

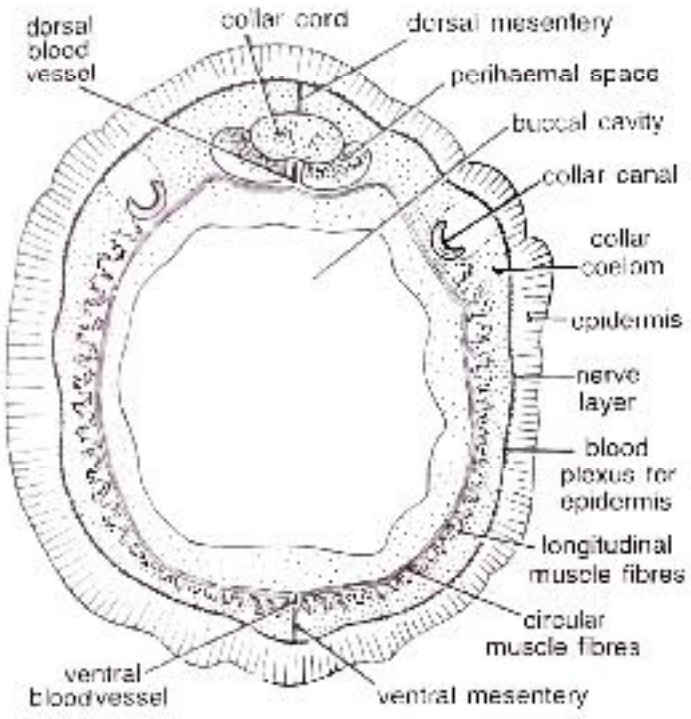

Fig. 5. *Balanoglossus*. T.S. through collar region.

each cavity is further divided by a **lateral septum** into a dorsal-lateral and ventro-lateral compartment. Trunk coelom is partitioned from the collar coelom by a **collar-trunk septum**. Trunk coelom is obliterated by the trunk musculature.

Coelomic Fluid

Proboscis and collar coelom communicate with the exterior and are largely filled with sea water which keeps them turgid. Trunk coelom is filled with a watery coelomic fluid containing amoeboid **coelomocytes**, each with a single large vacuole. Coelomocytes originate from the coelomic epithelium. According to **Spengel**, they behave like leucocytes by secreting a membrane around any foreign body that may invade the animal.

ENDOSKELETON

Balanoglossus has no definite endoskeleton of bone or cartilage. However, the following four stiff structures are present : (i) **Buccal diverticulum**, (ii) **proboscis skeleton**, (iii) **branchial skeleton**, and (iv) **pygochord** (Fig. 6).

1. Buccal diverticulum. From the roof of buccal cavity (lying inside collar region), a short stiff, thick-walled, hollow projection extends forward through the proboscis stalk into the proboscis coelom. Its wall is composed of a single layer of tall, slender, vacuolated endodermal cells. For a long time it was considered a **notochord** (**Bateson**, 1885), or **stomochord** (**Willey**, 1899 and **Dawydoff**, 1948). Histologically as well as developmentally, it is quite different from the true notochord of other chordates, but resembles the wall of the buccal cavity. To most modern workers it is only a preoral extension of buccal cavity, so that, Hyman preferred to use the non-committal term **buccal diverticulum** for this tubular outgrowth of buccal cavity.

2. Proboscis skeleton. Proboscis or **nuchal skeleton** is a Y-shaped chitinous structure formed by the thickening of the basement membrane. It consists of a broad, flat, roughly rectangular **median plate** produced ventrally into a **keel** and posteriorly into two diverging **horns**. Median plate lies below the buccal diverticulum in the proboscis

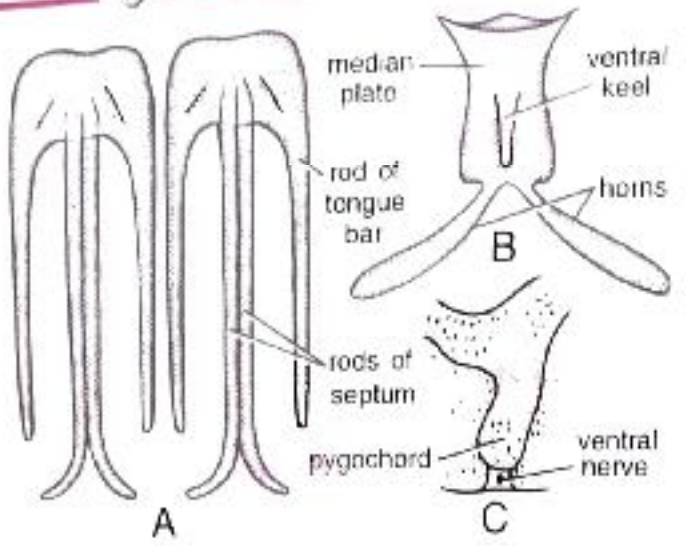

Fig. 6. *Balanoglossus.* Skeletal elements. **A.** Branchial skeleton. **B.** Proboscis skeleton. **C.** Pygochord.

stalk while the two horns extend backwards into the roof of the buccal cavity. Median plate remains embedded in a reticulum of stiff **chondroid tissue** which resembles vertebrate cartilage.

3. Branchial skeleton. It is also formed by the thickening of the basement membrane. It consists of numerous M-shaped chitinous skeletal rods that lie in the wall of the pharynx and support the U-shaped gill-slits that perforate it. Middle arm of the skeletal rod is thicker than the others and bifurcated at the free end which indicates that it is formed by the fusion of two arms of two adjacent 'inverted U-shaped' rods that join to form the M-shaped rod.

4. Pygochord. In the post-hepatic region of the trunk, mid-ventrally between the intestine and body wall, develops a rod-like thickening called **pygochord**. Its cells are vacuolated. It supports the post-hepatic region of the body but probably also performs some other function not yet understood.

DIGESTIVE SYSTEM

[1] Alimentary canal

Alimentary canal is a complete and straight tube running between the mouth and anus. It is supported throughout its length by the dorsal and ventral mesenteries. Its wall is made up of ciliated epithelium covered externally by a basement membrane, but peculiarly, muscle layers are absent. Alimentary canal comprises : (i) **Mouth**, (ii) **buccal cavity**, (iii) **pharynx**, (iv) **oesophagus**, (v) **intestine**, and (vi) **anus** (Fig. 7).

1. Mouth. It is wide and circular opening situated ventrally in a groove between the proboscis stalk and collarette. According to **Knight-Jones** (1952), it can be closed or opened and does not remain permanently open as previously supposed. It has two sets of muscle fibres, the radial fibres to open it and the concentric fibres to close it. Mouth leads into buccal cavity.

2. Buccal cavity. Short buccal cavity occupies the collar region. Its epithelial wall contains glandular goblet cells. Anteriorly its dorsal wall forms a short, stiff and hollow **buccal diverticulum** that projects into the proboscis coelom. Posteriorly it extends up to the collar-trunk septum behind which it continues into the pharynx.

3. Pharynx. It lies in the branchial region of the trunk. Externally its wall bears a longitudinal constriction along each lateral side. These lateral constrictions project into its lumen as ridges, called **parabranchial ridges**, consisting of tall columnar cells. These ridges incompletely divide the pharynx into a dorsal **respiratory** or **branchial portion** and a ventral **digestive portion**. Dorsal branchial portion is perforated dorso-laterally by two rows of U-shaped gill-slits, and is concerned with respiration. Ventral digestive portion, lined with ciliated epithelium with gland cells, helps in food concentration (Fig. 8).

4. Oesophagus. Behind the last pair of gill-slits the pharynx continues into the short **oesophagus**. Dorsal and ventral divisions of pharynx continue for some distance into oesophagus. In this region, the dorsal part is called **postbranchial canal** which possesses thick, folded and glandular epithelium. Posterior part of oesophagus reduces in diameter and has deeply furrowed epithelium (Fig. 9).

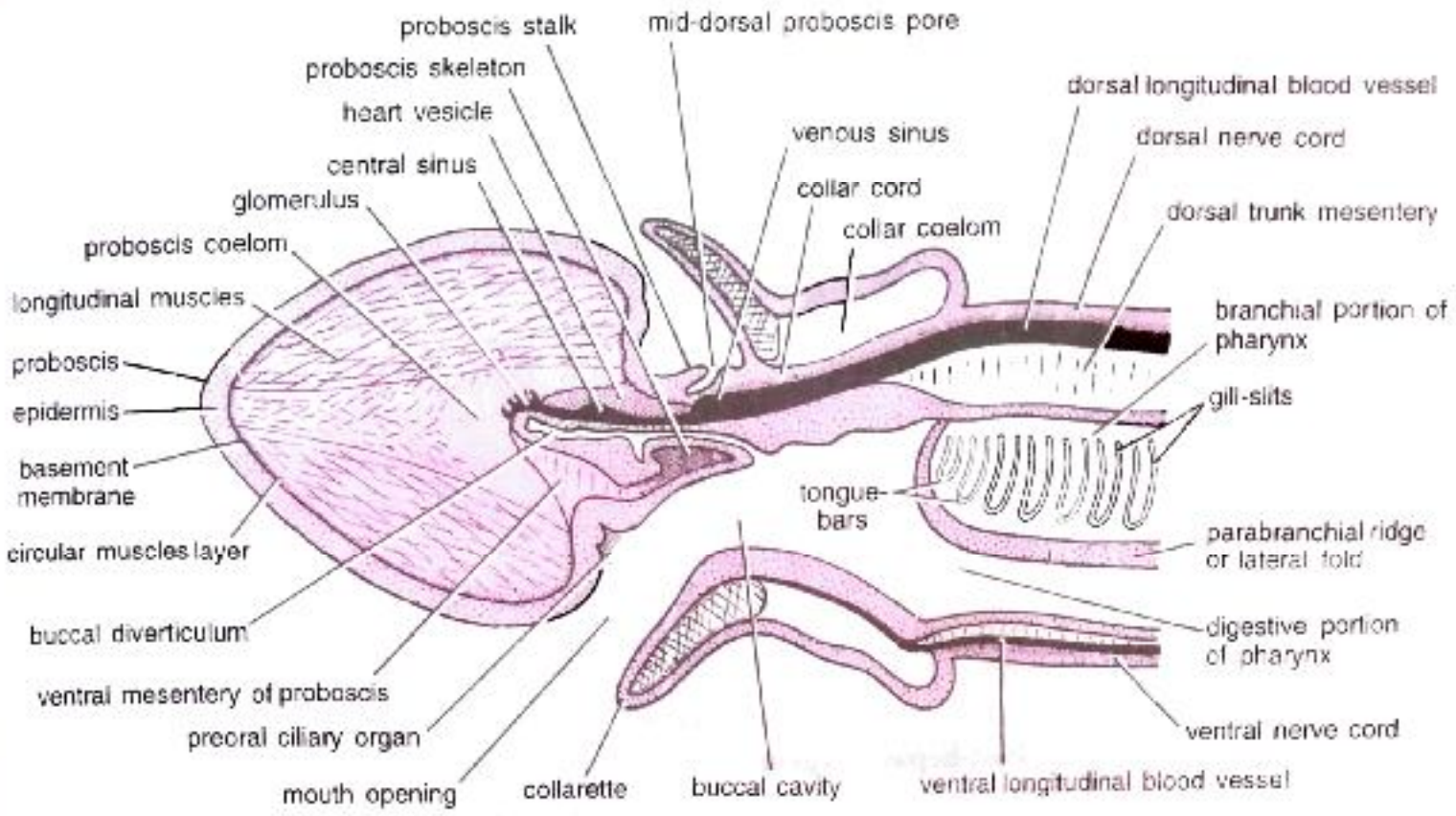

Fig. 7. *Balanoglossus.* V.L.S. Anterior region to show the alimentary canal.

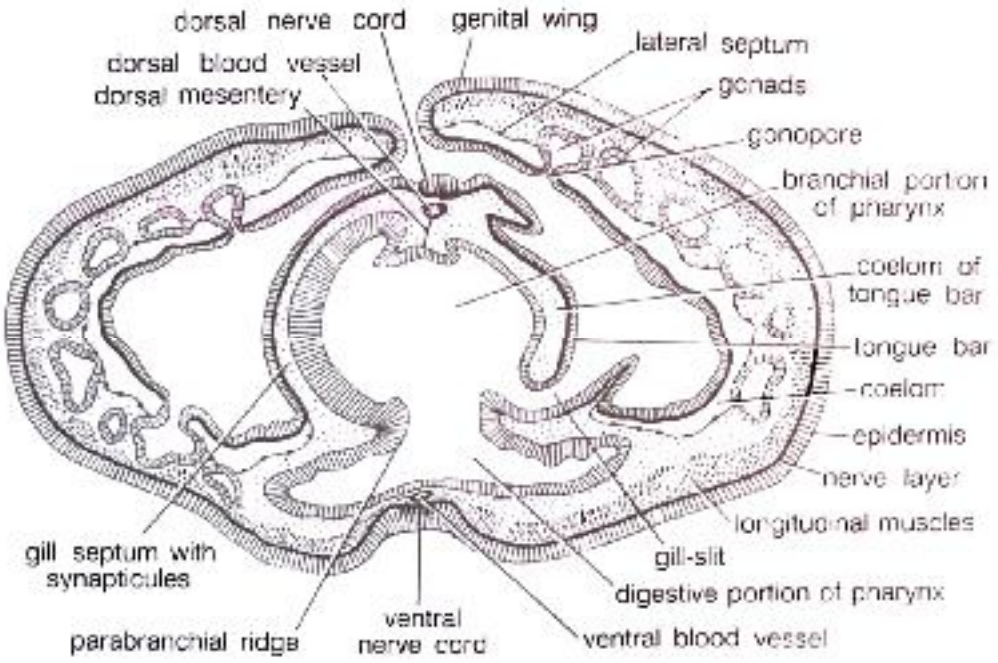

Fig. 8. *Balanoglossus.* T.S. through pharyngeal or branchio-genital region.

5. **Intestine.** It occupies the hepatic and post-hepatic regions of trunk. **Hepatic region** of the intestine is highly vascular. Its epithelial cells are dark green or dark brown, and its dorsal wall forms numerous sacculations called **hepatic caeca.** Intestinal wall lies in close contact with the body

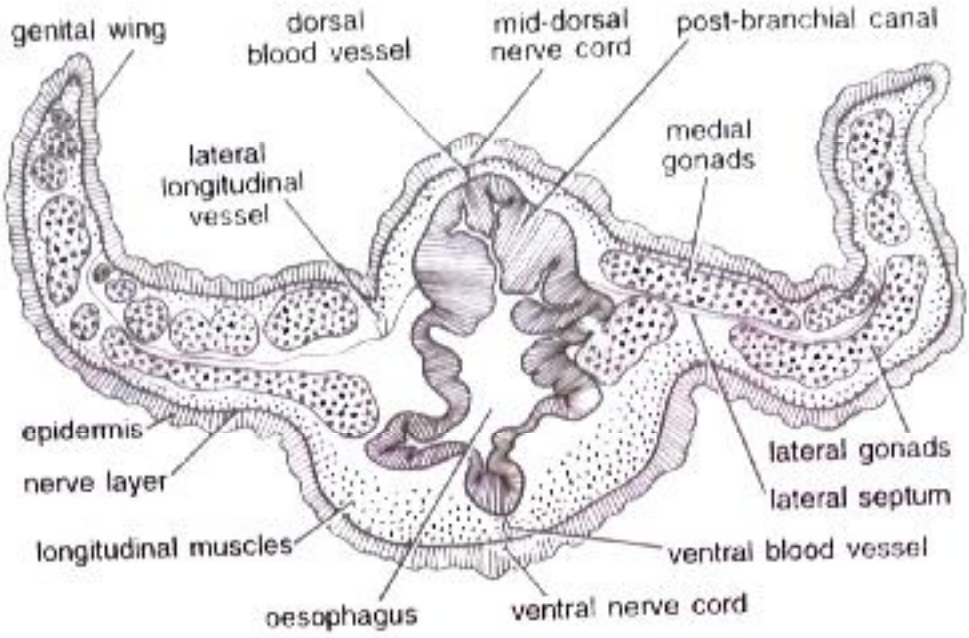

Fig. 9. *Balanoglossus.* T.S. through oesophageal region.

wall, so that the intestinal sacculations correspond with those of the body wall. **Post-hepatic region** of intestine is connected with the ventral body wall by the pygochord described earlier. It is a simple and straight tube bearing a pair of dorso-lateral grooves lined by tall epithelial cells with long cilia (Fig. 10).

6. Anus. Posteriorly, the intestine opens to the exterior by a terminal circular aperture, the **anus** at the tip of the trunk. It is often surrounded by a sphincter muscle.

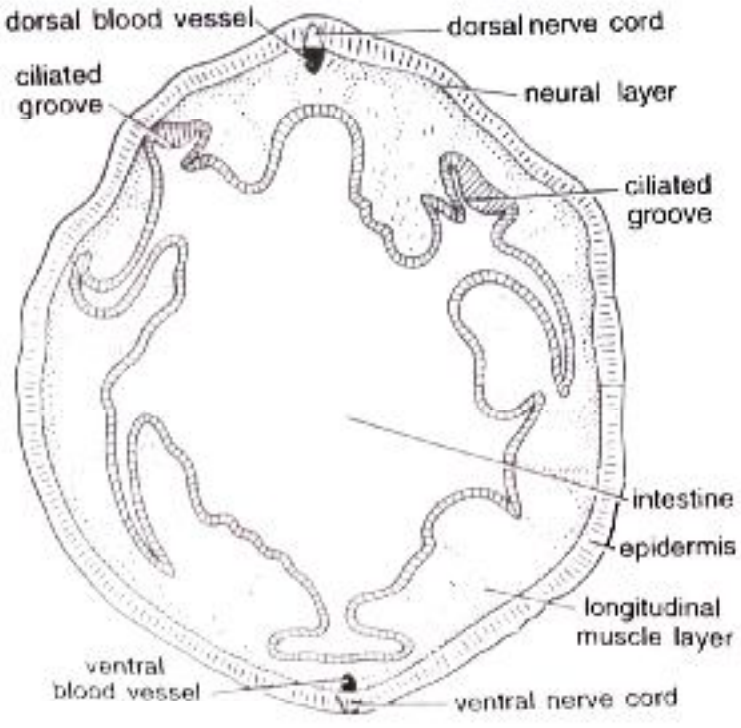

Fig. 10. *Balanoglossus.* T. S. through post-hepatic region of intestine.

[II] Food, feeding and digestion

Balanoglossus is a 'ciliary feeder'. Its food comprises of microscopic organisms and organic particles present in water and the bottom sand in which it makes its burrows. Lateral cilia lining the gill-slits set up a current of water which enters through the mouth, takes its course through the buccal cavity, pharynx, gill-slits and branchial sacs, and leaves through the gill pores. This is the **respiratory-cum-food current.** Some food particles directly enter the mouth with this current while some come in contact with the proboscis and get entangled in the mucus that covers it. Mucus is secreted by the gland cells of the proboscis epithelium. Cilia covering the proboscis direct the

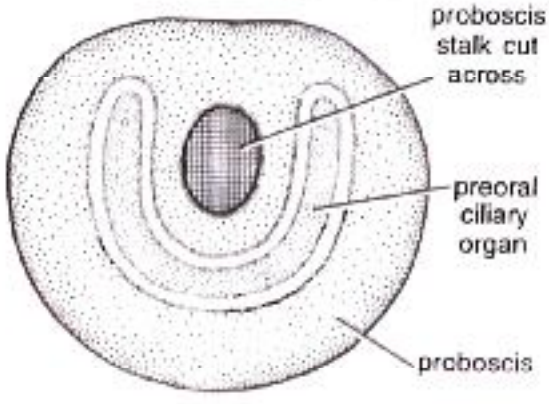

Fig. 11. *Balanoglossus.* Posterior view of proboscis.

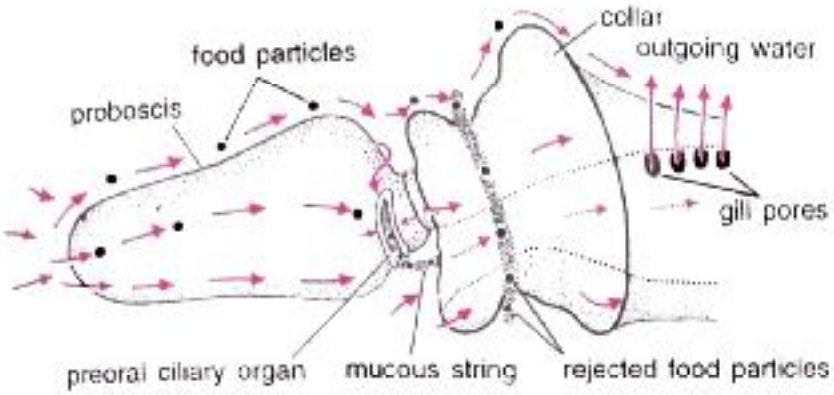

Fig. 12. *Balanoglossus.* Anterior end of body showing feeding current in lateral view. Arrows indicate the direction of the water current.

mucous string, containing food particles, towards the pre-oral ciliary organ at the base of the proboscis. From here the mucous string is passed back into the mouth by the action of the proboscis cilia, aided by the main water current entering the mouth. Organic particles present in the sand are ingested directly along with the latter at the time of burrowing.

U-shaped **pre-oral ciliary organ**, at the base of proboscis stalk, tests the quality of food and water entering the mouth. Undesirable substances are prevented from entering the mouth by the ventral part of the collarette which does so by covering the mouth. Thus, the rejected particles, instead of entering the mouth, pass back over the collar.

Backward movement of food through the alimentary canal is maintained by the cilia lining its walls. In the pharynx, the food moves through the ventral digestive portion. Digestion is brought about by enzymes secreted by gland cells of the pharynx, oesophagus and hepatic region of the intestine. Exact process of digestion in *Balanoglossus* is not known. Undigested substances, along with sand and silt, pass out through the anus as 'castings'.

RESPIRATORY SYSTEM

Respiratory apparatus of *Balanoglossus* comprises : (i) **branchial portion of pharynx** bearing **gill-slits** and (ii) **branchial sacs** that open out through **gill-pores**.

[I] Branchial pharynx

As already described, two lateral longitudinal **parabranchial ridges** divide the pharyngeal cavity into a ventral digestive portion and a dorsal respiratory or **branchial portion**. Dorsolaterally, on each side, the branchial portion is perforated by a longitudinal series of numerous U-shaped openings, the **gill-slits**. Their number varies and increases as the animal grows older. To start development a gill slit is a broad oval slit. Later, a hollow projection of dorsal pharyngeal wall, called **tongue bar**, grows into the slit making it U-shaped. Hollow tongue bars enclose coelomic cavity and do not touch the ventral side of gill-slits. Portions of the pharyngeal wall between two adjacent **gill-slits** are termed **gill septa**. They are solid, without enclosing coelom. A tongue bar is connected with adjacent gill septa by short transverse or horizontal connections, the **synapticula**. Development and arrangement of gill-slits is identical with that found in *Branchiostoma*.

As described earlier, the tongue bars and septa are supported internally by a chitinous skeleton forming M-shaped rods. A septum contains the middle arm of a M-rod which is bifurcated at its lower free end. Lateral arms of M-rod lie in

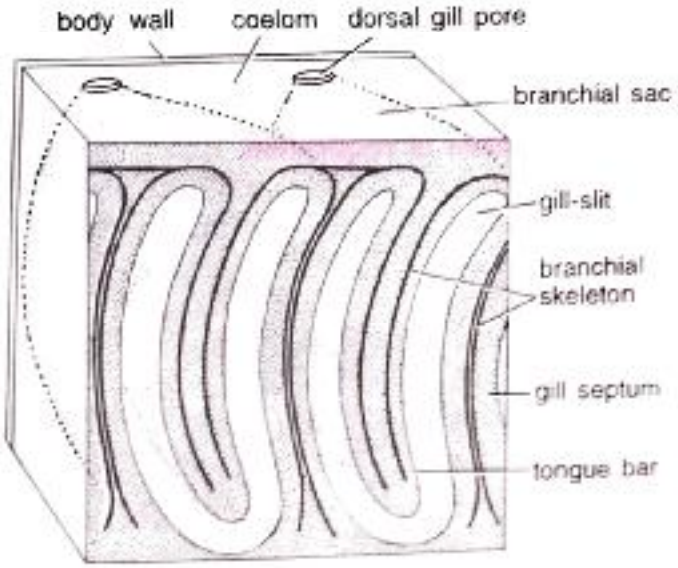

Fig. 13. *Balanoglossus.* Diagrammatic 3-dimensional view of two gill-slits and two branchial sacs.

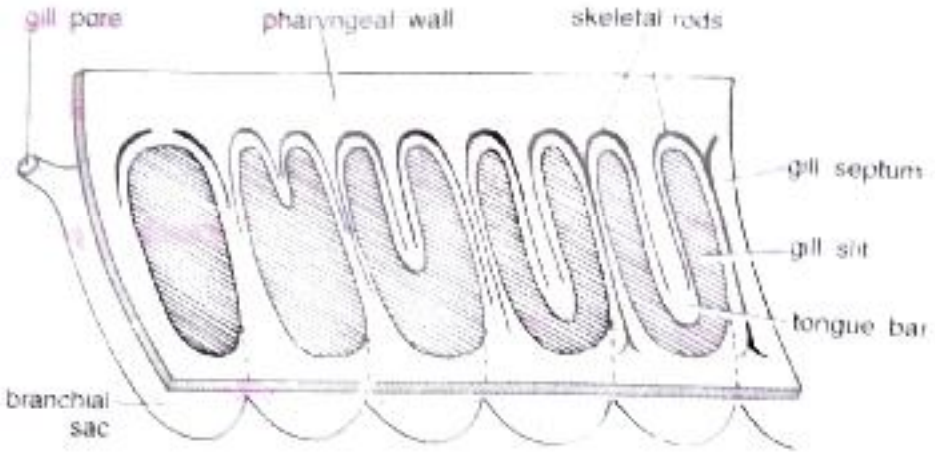

Fig. 14. *Balanoglossus.* Development of tongue bars.

adjacent tongue bars so that each bar contains two arms of two adjacent skeletal rods. Gill-slits are richly lined by cilia, called lateral **cilia**.

[II] Branchial sacs

Gill-slits do not open directly outside. Each gill-slit opens into a gill pouch called **branchial sac**, which lies between the body wall and the pharynx. Each branchial sac in turn opens to the exterior by a small, independent **gill pore**. However, in one species (*B. misakiensis*) the first four pouches become united to open by a common gill pore to outside. Collar coelom also communicates with the common branchial sac of its side through a **collar canal**. Gill-pores are visible externally in two longitudinal rows one on each side of the mid-dorsal ridge in the branchiogenital region of the trunk.

Mechanism of respiration. Lateral cilia lining the gill-slits set up a food-cum respiratory current of water. It enters the pharynx through mouth, then passes through gill-slits into the branchial sacs and finally leaves through the gill pores. Tongue bars are richly vascular and participate in gaseous exchange. Blood of their capillary network takes up the oxygen dissolved in water and returns carbon dioxide to it.

BLOOD VASCULAR SYSTEM

Blood vascular system of *Balanoglossus* is of the **open** or **lacunar type**. It consists of : (i) a colourless **blood**, (ii) a **central sinus** and a **heart vesicle**, (iii) distributing vessels or **arteries** and **sinuses**, and (iv) collecting vessels or **veins**.

[I] Blood

Blood is colourless fluid containing few white corpuscles which are possibly detached endothelial cells. A respiratory pigment is probably absent.

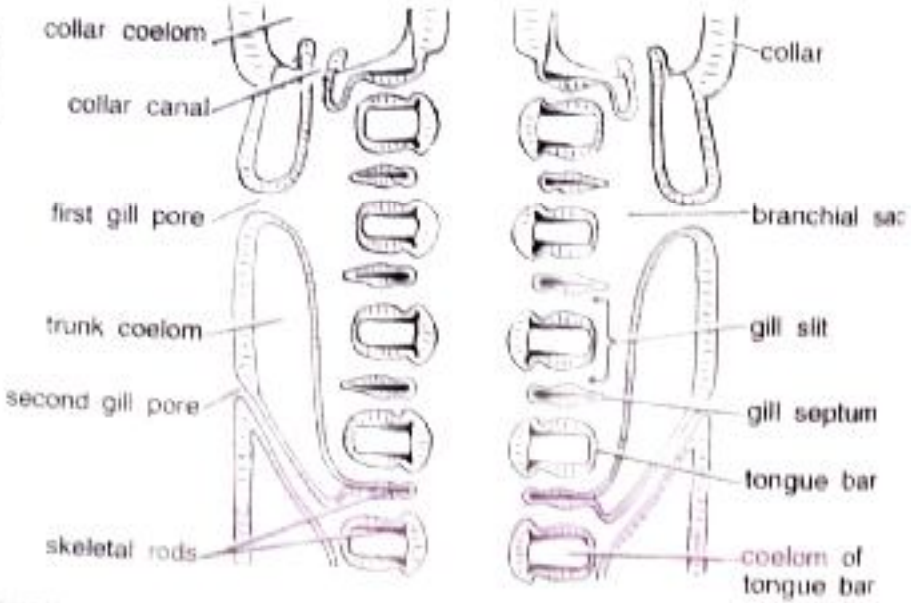

Fig. 15. *Balanoglossus misakiensis.* H.L.S. of branchial portion of pharynx to show first four gill-slits opening by a common gill pore.

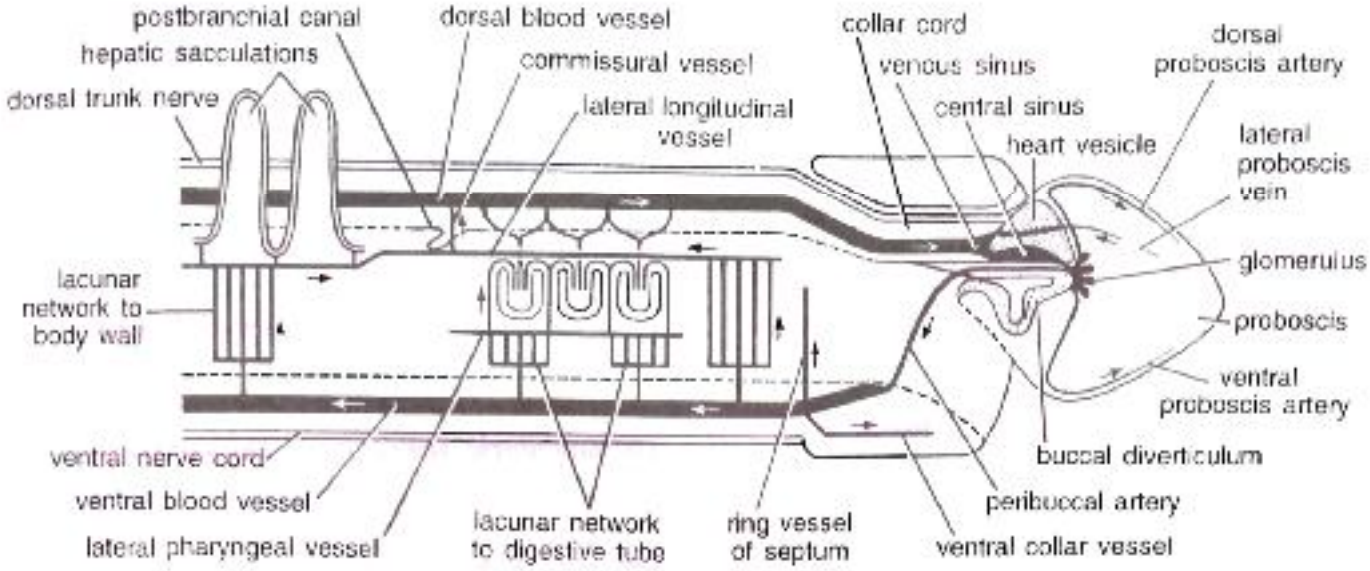

Fig. 16. *Balanoglossus*. Blood-vascular system in anterior end in lateral view.

Functioning of the circulatory system is not properly understood.

[II] Central sinus and heart vesicle

Central sinus is a small elongated non-contractile sinus situated in the proboscis just above the buccal diverticulum. Just above it is a closed triangular **cardiac sac** or **heart vesicle**. Its ventral wall is muscular and contracts rythmically thereby producing pulsations in the central sinus that help in the circulation of blood. Central sinus receives blood from collecting vessels that open into its posterior end. Anteriorly, it pumps its blood into several **afferent vessels** which form a plexus in the **proboscis gland** or **glomerulus**, lying in front of it. In glomerulus the blood gets rid of its excretory wastes.

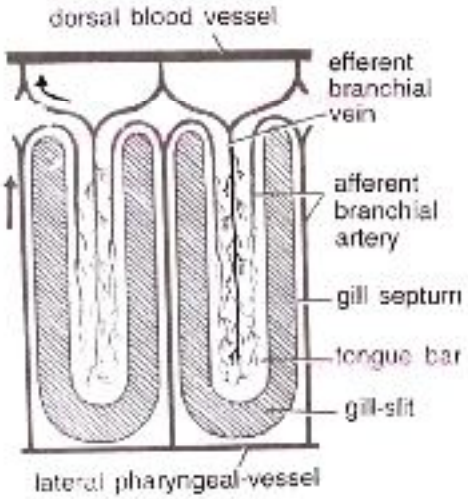

Fig. 17. *Balanoglossus*. Lymph sinuscids in a portion of the branchial wall.

[III] Distributing vessels or arteries

Blood from the glomerulus is carried away by four arteries. Of these, two arteries, a **mid-dorsal proboscis artery** and a **mid-ventral proboscis artery**, supply the proboscis. Other two, called **efferent glomerular arteries**, run backward along the two sides of buccal diverticulum, encircle the buccal tube as **peribuccal vessels** (which are actually of the nature of blood plexuses) and unite in a single longitudinal **ventral vessel** that runs up to the posterior end of the body through the ventral mesentery. On its way, the ventral vessel gives out a **ventral collar vessel** to the collar, a **ring vessel** to the collar-trunk septum and an **afferent branchial artery** to each gill septum in which it bifurcates to supply two adjacent tongue bars. All these branches break up into a system of sinuses in their respective structures. All along its length, the ventral vessel also supplies the body wall and gut wall by an elaborate network of sinuses. Ventral vessel has muscular contractile walls and the blood in it flows backwards.

[IV] Collecting vessels or veins

Blood from body wall, gut wall and branchial apparatus (**efferent branchial vessel**) is collected by a single median **dorsal vessel** which runs through the dorsal mesentery, from posterior end upto the collar. It has muscular and contractile

wall and the blood flows in it forwards. At the anterior end of collar, the dorsal vessel dilates a little to form a **venous sinus**. Latter receives a lateral **proboscis vein** from each side of proboscis and then opens into the central sinus.

EXCRETORY SYSTEM

Excretory organ is **glomerulus** or **proboscis gland** lying in front of the central sinus and projecting into the proboscis coelom. It is made up of several blind tubular projections formed by the peritoneum covering the buccal diverticulum, central sinus and heart vesicle. Tubular projections contain blood confluent with that of central sinus. Excretory peritoneal cells of glomerulus contain yellow or brown granules, probably of excretory substances. From glomerulus the excretory substances pass on into the proboscis coelom and finally to the exterior through the proboscis pore.

NEURAL SYSTEM

Neural (nervous) system is of primitive type resembling that of coelenterates and echinoderms.

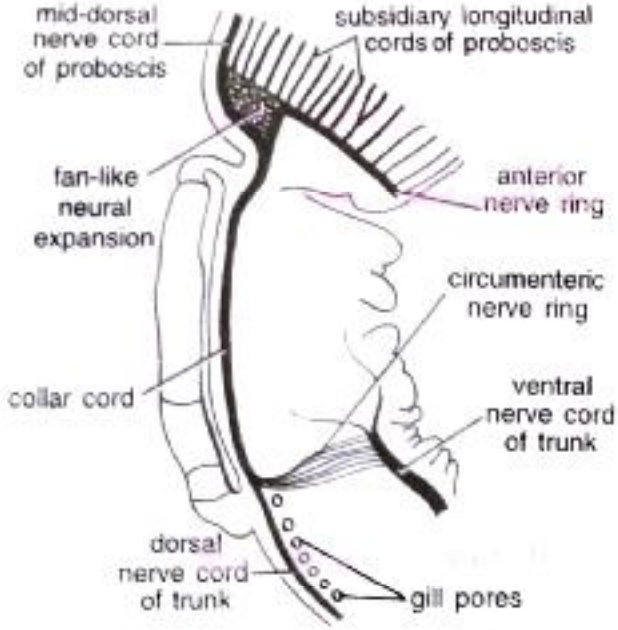

Fig. 18. *Balanoglossus*. Nerve cords in the anterior region of the body.

Throughout the body a plexus or layer of nerve cells and nerve fibres lie just below the epidermis. Nerve fibres are traversed by the filamentous basal portions of epidermal cells, and form synapses with the processes of nerve cells. Neural layer is thickened along definite strands to form two main **nerve cords**, one **mid-dorsal** and other **mid-ventral** which run along the entire length of the trunk. **Ventral cord** extends upto collar-trunk septum where it is connected with the dorsal cord by a circular strand, called **circumenteric nerve ring**. **Dorsal cord** extends anteriorly upto the base of proboscis where it is connected with another circular strand called **anterior nerve ring**. In collar region, dorsal cord leaves the epidermis and traverses the collar coelom as **collar cord**. It is supposed to be the neural centre of the animal. But unlike brain, it has no concentration of nerve cells and also does not give out nerves. However, it contains some giant nerve cells which help in transportation of impulses over the body and in reflexes. Collar cord contains a cavity called **neurocoel**.

Sense organs of *Balanoglossus* are simple and comprise : (i) **neuro-sensory cells** in the epidermis of proboscis and anterior part of collar, sensitive to touch and light; and (ii) **preoral ciliary organ** situated ventrally at the base of proboscis, which is a chaemoreceptor.

REPRODUCTIVE SYSTEM

Asexual reproduction. Asexual reproduction is rare in enteropneusts. **Gilchrist** (1923) has described it in one species, *Balanoglossus capensis*, which lacks hepatic caeca. During summer the young worms (juveniles) cut off small pieces from tail end, each regenerating into a complete sexual adult in winter.

Regeneration. *Balanoglossus* shows great power of regeneration. Proboscis, collar and isolated pieces from trunk can regenerate the lost part of the body completely.

Sexual reproduction. Sexes are separate. Males and females cannot be identified externally

except for the difference in colour of the ripe gonads in the living specimens. Testes of male and ovaries of female are similar. They are sac-like bodies occurring in several longitudinal rows in the genital wings, on either side of the alimentary canal. Each gonad has a narrow neck or ductule that opens out through a gonopore. All gonopores are situated outer to the gill pores. Ova are small with poor yolk content.

DEVELOPMENT

Development of *Balanoglossus* is described in Chapter 42 in the section 'Vertebrate Embryology'.

AFFINITIES & SYSTEMATIC POSITION OF *BALANOGLOSSUS* (HEMICHORDATA)

Group *Enteropneusta*, to which *Balanoglossus* belongs, was established by Gegenbaur in 1870. Bateson (1885) proposed the name Hemichordata in place of Enteropneusta. Since then, due to their peculiar anatomical organisation and embryology, the Hemichordata (or *Balanoglossus*) have been considered closer to the Chordata as well as most non-chordate phyla by different workers from time to time. Some of these views regarding the phylogenetic relationship (affinities) and taxonomic position of the Hemichordata are summarized below.

[I] Affinities with chordata

Some earlier workers, such as William Bateson (1885), proposed closer affinities between Hemichordata and Chordata. Their resemblance was based on the presence of the three fundamental chordate characteristics in Hemichordata, that is, (i) a notochord, (ii) a dorsal hollow nerve cord and (iii) the pharyngeal gill-slits (pharyngotremy).

Affinities with Urochordata. Hemichordates are nearest to Urochordata, as they exhibit many close resemblances with them. The structure and function of pharynx and branhial apparatus in hemichordates are similar to those of urochordates. Also, the development of the central part of neural system is quite similar in both.

Affinities with Cephalochordata. Besides similarities in the structure and function of the branchial apparatus, the hemichordates also show similarity with cephalochordates in the arrangement of coelomic sacs and in development.

Due to these similarities Hemichordata had been considered as a subphylum of the phylum Chordata till recently, representing its lowest group, and probably having a common ancestry.

Objection. However, the hemichordates are no longer included under chordates because they do not possess chordate characters in a typical condition. The main objections are :

(1) A true notochord does not occur in hemichordates. Unlike that of the chordates, the so-called 'notochord' is very short, confined to proboscis and without any supporting function. It is ventral to the main (dorsal) blood vessel and not covered by sheaths. Instead of being solid and made of vacuolated cells, it is hollow and lined by epithelial cells. It does not originate from the roof of larval archenteron but as a forward hollow projection of the foregut. Instead of being called notochord (**Bateson**, 1885) it is now termed the **stomochord** (**Willy**, 1899). Hyman prefers to name it **buccal diverticulum**.

(2) Neural system is distinctly of the invertebrate type being intra-epidermal in position and having a ventral nerve cord and a circumenteric nerve ring which are absent in chordates. In *Balanoglossus*, the dorsal tubular nerve cord is confined to the collar region only.

(3) Gill-slits of *Balanoglossus* are numerous and dorsal in position, whereas they are 5 to 7 and lateral in higher chordates.

Other differences. Hemichordates further differ from the chordates in :

(1) Lacking metameric segmentation, cephalization, paired appendages, postanal tail, exoskeleton, living endoskeleton, dermis, liver, haemoglobin, red blood corpuscles, etc.

(2) Having peculiar division of body and coelom (into proboscis, collar and trunk), single-layered ciliated epidermis, hepatic caeca, dorsal heart, open neurocoel, colourless blood, numerous gonads, etc.

[II] Affinities with Rhynchocephalia (Nemertinea)

Feeding and burrowing habits are similar in *Balanoglossus* and Nemertinea. Body in both is elongated, vermiform, without external metamerism, with terminal anus, with smooth skin containing unicellular glands and ectodermal nerve plexes, and having metamerically arranged simple gonads. But Nemertinea differ in lacking a dorsal nerve cord and in having lateral nerve cords and a protrusible proboscis.

[III] Affinities with Phoronida

Some zoologists like **A.T. Masterman** (1897) advocated relationship of *Balanoglossus* with *Phoronis* on the following grounds :

(1) Similar nature of epidermal neural system.

(2) Paired gastric diverticula of *Phoronis*, like the **buccal diverticulum** of *Balanoglossus*, forming so-called notochord.

(3) Actinotroch larva of *Phoronis* has several enteropneust features of tornaria such as similar disposition of coelom, anus surrounded by a ciliary ring, presence of a proboscis pore and a sensory apical plate with cilia and eye spots.

(4) Both have great power of regeneration.

Objection. But, the chordate features of *Balanoglossus* like pharyngeal gills, are absent in *Phoronis* which also differs in having paired metanephridia. Moreover, **Selys-Long Champ's** (1948) account of development of *Phoronis* does not corroborate Masterman's observations, so that relationships of these two groups are rejected.

[IV] Affinities with Pogonophora

Marcus (1958) tried to relate Hemichordata with Pogonophora due to following similarities :

(1) Enterocoelous formation of coelom.

(2) Body and coelom divided into three regions.

(3) Mesosome and metasome separated by a septum.

(4) Neural system intra-epidermal.

(5) Pericardial sac in some pogonophores.

(6) Gonads found in trunk.

Objection. But pogonophores differ in having protocoelic nephridial coelomoducts and lacking an alimentary canal. Moreover, neural system is concentrated in protosome in Pogonophora, but in mesosome in Hemichordata.

[V] Affinities with Annelida

Spengel (1893) first suggested affinities of Annelida and Hemichordata as follows :

(1) Body vermiform and coelomate.

(2) Burrowing habit, tubicolous life and ingesting mud which is passed out as castings through anus.

(3) Collar of *Balanoglossus* similar to **clitellum** of earthworm.

(4) Proboscis and prostomium similar and preoral.

(5) Similar arrangement of blood vessels with blood flowing anteriorly in dorsal vessel and posteriorly in ventral vessel.

(6) Dorsal position of heart.

(7) Tornaria larva of *Balanoglossus* shows several structural resemblances with the trochophore larva of Annelida in being pelagic, ciliated, with apical plate, eye spots, sensory cilia and well developed alimentary canal with similar parts.

Objection. However, the two groups show striking differences as follows :

(1) Annelids do not have pharyngeal gill-slits, stomochord or buccal diverticulum and dorsal tubular nerve cord found in *Balanoglossus*.

(2) *Balanoglossus* does not have double and solid ventral nerve cords and nephridia found in annelids.

(3) In tornaria larva of *Balanoglossus*, preoral or proboscis coelom is present, nephridia are absent and blastopore becomes anus of the adult (Deuterostomia). In trochophore larva

of annelids, preoral coelom is absent, nephridia present and the blastopore becomes the mouth (Proterostomia).

Thus, compared to their great fundamental differences, the similarities of the two groups are only superficial and quite insignificant indicating probably a convergent evolution due to similar habits and habitat.

[VI] Affinities with Echinodermata

Adult resemblances. Adult hemichordates and echinoderms are structurally quite different and it is difficult to suspect any phylogenetic relationship between them. They show few resemblances such as :

(1) Enterocoelic origin of coelom and its division into three successive parts filled with sea water to serve a hydraulic mechanism.

(2) Heart vesicle and glomerulus of enteropneusts are considered homologous to the dorsal sac and axial gland of echinoderms. Both the structures are related and combine vascular and excretory functions.

(3) Neural system is poorly developed and forms epidermal nerve plexus.

(4) Proteins and phosphagens present in hemichordates closely resemble those of echinoderms.

(5) Common habits and ecological niches and remarkable power of regeneration.

Larval resemblances. Two groups show a strong affinity on embryological ground as the tornaria larva of *Balanoglossus* has a striking structural similarity with an echinoderm larva, in particular the bipinnaria larva of asteroids. In fact, the tornaria was regarded an echinoderm larva for a long time by **Johannes Muller** (1850), **Krohn** (1854), **Agassiz** (1864), etc., till **Metschnikoff** (1870) proved it to be an enteropneust larva. Larvae of the two groups possess the following common features :

(1) Small, pelagic, transparent and oval.

(2) Identical ciliated bands taking up a similar twisted course.

(3) Enterocoelic origin and similar development of coelom.

(4) Proboscis coelom opening to outside by proboscis pore of tornaria comparable to hydrocoel of echinoderm dipleurula.

(5) Blastopore becomes the anus (Deuterostomia) and digestive tract is complete with mouth, anus and same parts.

Objection. However, the tornaria larva shows presence of apical plate with sensory hairs and eye spots and telotroch which are absent in echinoderm larvae. Protocoel is single in tornaria but paired in echinoderm larva. This raises doubts about the echinoderm affinities of hemichordates. **Fell** (1963) and others believe that their larval similarities are only because of convergent evolution due to same mode of habits and habitat.

[VII] Systematic position and phylogeny

Peculiar anatomical organisation of *Balanoglossus* or hemichordates makes their systematic position uncertain and controversial. Earlier workers (**Bateson**, 1885) placed them as a **subphylum** under the phylum Chordata representing its lowest group. But the only chordate feature shown by them is the presence of pharyngeal gill-slits. Therefore, some recent workers like **Van der Host** (1939), **Dawydoff** (1948), **Marcus** (1958) and **Hyman** (1959) have chosen to remove hemichordates from the phylum Chordata and treat them as an **independent invertebrate phylum.** Since the group comprises only about 80 species, it is included in the category of a **minor phylum.**

The name Hemichordata (Gr. *hemi*, half; *chorde*, cord) means they are 'half' or 'part' chordates, a fact that is undisputed. Therefore, in the present work, Hemichordata has been retained as a subphylum of Chordata to avoid any controversy.

Regarding phylogeny, the close affinities of Echinodermata, Phoronida, Pogonophora, Hemichordata and Chordata have led to the conclusion that they have arisen from a common ancestral stock, probably the dipleurula larva (**Bather**, 1900). But **Berril** (1955), **Whitear** (1957), **Carter** (1958), **Marcus** (1958), **Hyman** (1959, **Bone** (1960) and many others do not contribute to this view. **Barrington** (1965) has

interpreted their views based on the deuterostome line of chordate evolution. According to his explanation, the Echinodermata deviated greatly from the ancestral stock and formed a blind branch. Hemichordata also did not stand on the direct line of ancestry but formed a divergent offshoot from the main line of chordate evolution. Since the hemichordates arose from the ancestral line after the divergence of the ancient Echinodermata but before the rise of the true chordates, they are often called the **prechordates**.