Neanthes : Nereis virens

SYSTEMATIC POSITION

Phylum	Annelida
Class	Polychaeta
Subclass	Errantia
Family	Nereidae
Genus	*Neanthes* or *Nereis*
Species	*virens*

HABITS AND HABITAT (ECOLOGY)

Nereis is a cosmopolitan marine polychaete, usually found on sandy shores between tidemarks. It remains overlooked by casual observers because of its secretive habits. Most of the time it lives in burrows, which it forms with the help of its jaws. Burrow is U-shaped, up to 60 cm deep and coated with mucus, secreted from body, which binds together fine particles of sand. Worm maintains a constant current of water through the burrow by dorso-ventral undulations of its body. Water current brings oxygen for respiration. Worm is nocturnal and carnivorous. At night it keeps its head protruded out of the burrow in search of prey, which is usually a small crustacean, mollusc or annelid. Prey is captured by protruding the pharynx provided with chitinous teeth and jaws, dragged into burrow and then devoured. Occasionally, the worm leaves its burrow and creeps about beneath stones and rocks or among seaweeds, in search of food. During breeding season, the worm leaves its burrow permanently and swims about actively in surface layers of water. At this stage, it is known as *Heteronereis*.

Clamworms are frequently used for fish bait. In Greek mythology, nereids were sea-nymphs or beautiful human figures who sometimes lured sailors into captivity.

EXTERNAL MORPHOLOGY

1. Shape, Size and Colour

Body is elongated, slender, bilaterally symmetrical, somewhat broad anteriorly and tapering posteriorly. It is slightly flattened dorso-ventrally, dorsal surface being convex, while ventral surface flat or even somewhat concave. Length of adult worm varies from a few to about 40 cm or even more. Different species are differently coloured. *N. pelagica* is brownish, *N. cultrifera* greenish and *N. virens* steel blue. But colour may vary with age and sexual maturity. Cuticle imparts an iridescent sheen to the surface.

2. Body Divisions

Body of *Nereis*, as in other annelids, is metamerically divided into a number of **metameres** or **segments** arranged in a linear series. Adjacent metameres are demarcated externally by circular grooves. Number of segments is fairly constant for a species; about 80 in *N. cultrifera* and *N. dumerilli* and about 200 in *N. virens*. Three distinct regions can be identified in the body : (i) head, (ii) trunk, and (iii) pygidium.

[I] Head

Nereis possesses well-developed head because of its active life and predaceous habit. It lies at the anterior end and consists of two parts : (i) **peristomium**, and (ii) **prostomium**.

1. Peristomium. Peristomium is the first segment of body, distinct from others. It is large, ring-like and surrounds the ventral, transversely elongated slit-like **mouth**, hence its name (Gr., **peri**, around + **stoma**, mouth). It is formed by the fusion of first two embryonic segments during cephalization. It differs from a trunk segment in being longer, in lacking **parapodia** and in the presence of two pairs of thread-like **peristomial cirri** on each side. The dorso-lateral pair of cirri is longer than the ventro-lateral pair. Peristomial cirri are homologous with the

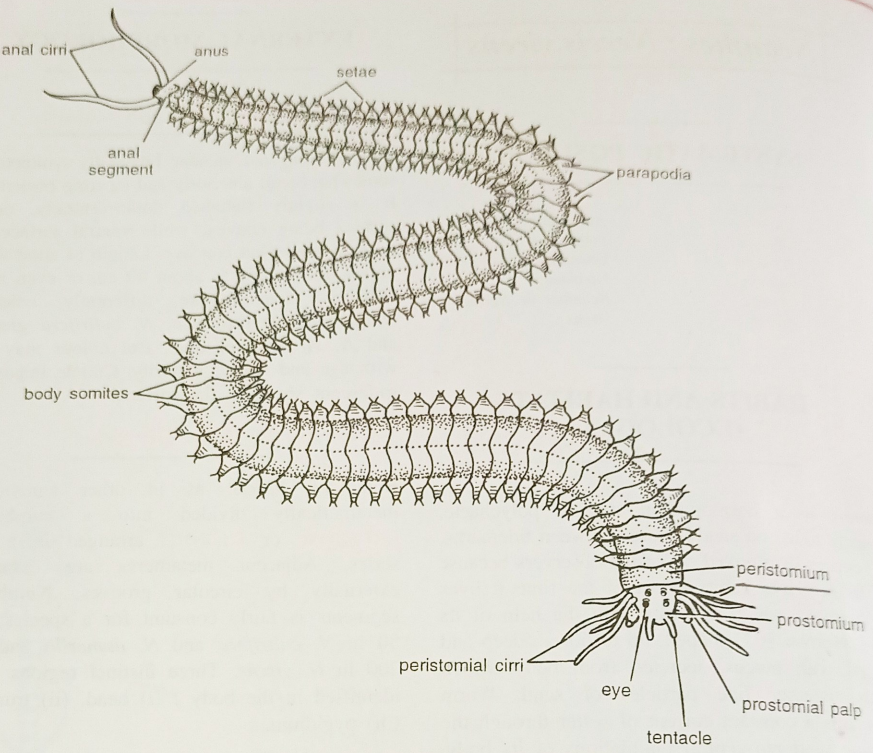


Fig. 1. *Nereis.* External features in dorsal view.

notopodial and neuropodial cirri of parapodia of trunk segments. Each cirrus is a long, slender, tactile structure, having a short proximal joint and a long distal joint.

2. **Prostomium.** It is not a true segment of body but rather dorsal, anterior projection of peristomium, presumably of its first fused segment. It is a roughly triangular, dorso-ventrally flattened, fleshy lobe lying above and in front of **mouth** (Gr., **pro**, anterior + **stoma**, mouth). It bears two pairs of simple pigmented **eyes** on dorsal surface, a pair of short cylindrical, sensory **prostomial tentacles** anteriorly, and a pair of short, stout, fleshy, and two-jointed **palps** ventro-laterally. Palps are somewhat contractile and their small distal joints can be retracted into their large proximal joints.

Tentacles, palps and cirri, all serve as sensory organs.

[II] Trunk

It comprises practically the entire body excluding head and last body segment or **pygidium.** It consists of 80-200 similar segments, each broader than being long and characterized by the presence of a **parapodium** on each lateral side.

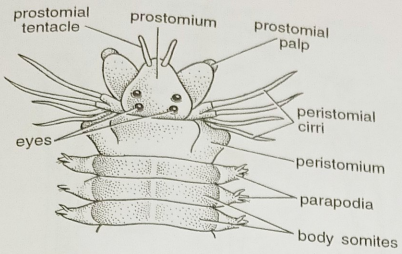


Fig. 2. *Nereis.* Head in dorsal view.

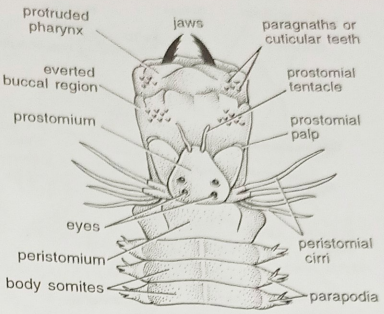


Fig. 3. *Nereis.* Head in dorsal view with everted proboscis.

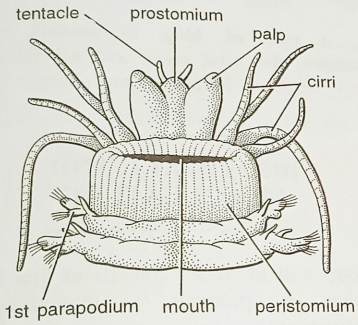


Fig. 4. *Nereis.* Head in ventral view.

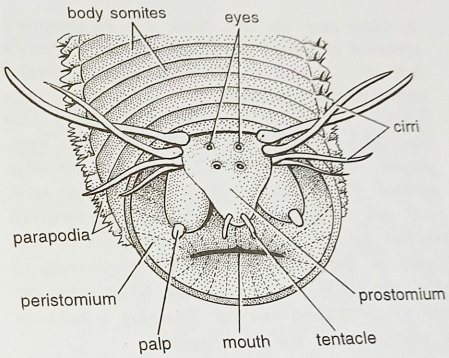


Fig. 5. *Nereis.* Head in frontal view.

1. Parapodia. Parapodia (Gr., **para**, beside + **podos**, foot) are flattened, fleshy, vertical flap-like outgrowth of body wall on lateral sides of trunk segments. They are hollow structures enclosing coelom which is continuous with that of trunk segments. Structurally, a parapodium is typically **biramous**, consisting of a proximal **basal region** bearing distally two rami or parts, a dorsal **notopodium** and a ventral **neuropodium**. Each part or ramus is further subdivided into two leaf-like lobes or **ligulae**, a dorsal **superior ligula** and a ventral **inferior ligula**.

Each part bears at its base a slender, tentacular process known as **cirrus**. Notopodial or **dorsal cirrus** is slightly larger than neuropodial or **ventral cirrus**. Each part is supported internally by a deeply-embedded, long, stout and black chitinous rod, known as **aciculum**. It also serves for attachment of **setal muscles**, thus serving as a sort of endoskeleton. Each part also bears a bundle of long, fine, stiff, chitinous bristles, the **setae** or **chaetae**, which project beyond its margin. Each seta is lodged in a **setal** or **setigerous sac**, formed by an inpushing of epidermis and arises from a single **formative cell**, lying at the base of sac. New setae are continuously produced by setal sac

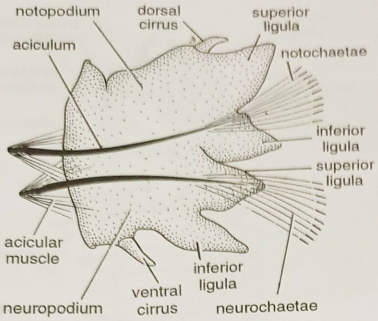


Fig. 6. *Nereis.* Parapodium.

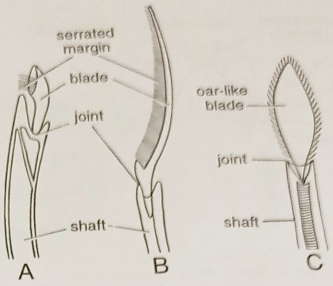


Fig. 7. *Nereis.* Kinds of setae. **A.** Typical. **B.** Long-bladed. **C.** Oar–shaped of heteroneries.

as older ones are lost. Setae can be protruded, retracted or turned in various directions with the help of **setal muscles**. Each seta is a two-jointed structure with a proximal **shaft** and a distal **blade**. Setae of *Nereis* are generally of two types. One type (long-bladed) has a small shaft and a long, slender, straight and pointed blade with one edge serrated. Other type (typical) has a large stout shaft and a short, stout blade with an incurved notched tip. A third type (oar-shaped) of seta occurs in the sexual phase or *Heteronereis* in which the blade becomes oar-like. Sharp setae are used for protection and for obtaining a hold on the smooth inner walls of burrow.

Parapodia near the middle region of trunk are the largest and gradually decreases in size towards the two ends. All parapodia are essentially similar except that the first two pairs lack notopodial setae. Parapodia serve the dual purpose of locomotion and respiration.

2. Nephridiopores. These are minute excretory pores through which the nephridia communicate with the exterior. Each parapodium of a nephridia-bearing segment bears a nephridiopore near the base of its ventral cirrus.

[III] Pygidium

This is represented by the last body segment, also known as **tail** or **anal segment**. It bears a terminal **anus**, a pair of long filamentous, ventral appendages, the **anal cirri**, and several minute **sensory papillae**. Parapodia are absent.

BODY WALL AND MUSCULATURE

The body wall of *Nereis* consists of four layers : (i) cuticle, (ii) epidermis, (iii) musculature, and (iv) peritoneum.

[I] Cuticle

It is the outermost, thin, tough and chitinous layer, with a system of intersecting striations which impart iridescence to it. It is secreted by the underlying epidermis and is perforated by numerous minute openings of epidermal gland cells.

[II] Epidermis

It lies beneath cuticle and rests on a thin **basement membrane**. It consists of a single layer of tall columnar **supporting** cells and some scattered **glandular** and **sensory cells**. Epidermis on ventral surface, especially near bases and on lobes of parapodia, is somewhat thicker and more glandular. Epidermal gland cells secrete **mucus**,

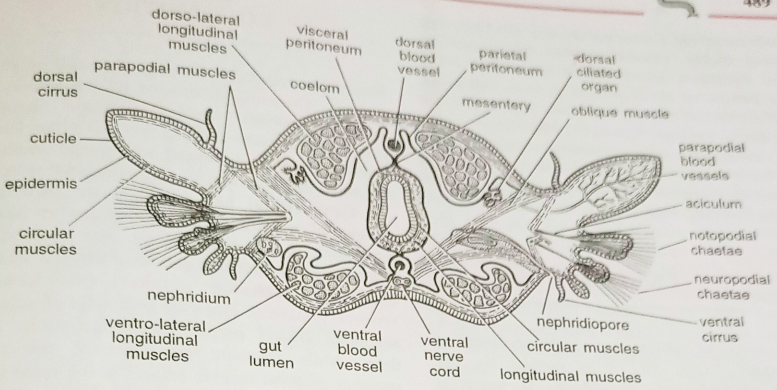


Fig. 8. *Nereis.* T.S. of a segment.

which lines the U-shaped tube in which the worm lives.

[III] Musculature

Nereis has a well-developed musculature consisting of (i) **circular**, (ii) **longitudinal**, and (iii) **oblique** muscles. These are composed of unstriped muscle fibres.

1. Circular muscles. These form a continuous layer beneath epidermis, which is slightly thicker on ventral side. In parapodia, circular muscles are modified to form a complicated system of parapodial muscles comprising the **protractor** and **retractor** muscles. Protractors radiate from bases of setigerous sacs to the layer of circular muscles on all sides. Retractors extend from outer part of setigerous sacs to the dorso-lateral body wall.

Contraction of circular muscles make the body longer and thinner, while that of protractors and retractors causes respectively the protrusion and retraction of parapodial acicula and lobes.

2. Longitudinal muscles. These do not form a continuous layer beneath circular muscles, but occur in four powerful longitudinal bundles, two **dorso-lateral**, one on either side of dorsal blood vessel, and two **ventro-lateral**, one on either side of ventral nerve cord. Contraction of longitudinal muscles causes shortening and thickening of body.

3. Oblique muscles. These lie in each segment in two pairs. First pair is situated at the level of anterior limit, and second at the level of posterior limit of parapodia. Each oblique muscle arises between ventral nerve cord and a bundle of ventro-lateral longitudinal muscles. It soon bifurcates into a dorsal and a ventral branch, each extending to the base of corresponding parapodium.

Oblique muscles are responsible for bending movements of parapodia and their complete retraction.

[IV] Peritoneum

Muscles are lined internally by a thin, delicate layer of **coelomic epithelium** or peritoneum. This layer also lines the coelom externally and is thus also described as the somatic or parietal layer of coelomic epithelium. It secretes the coelomic fluid.

[V] Functions of Body Wall

Body wall of *Nereis* performs a variety of functions, (i) Cuticle protects the body against

desiccation and mechanical injuries. (ii) Epidermis, being highly vascular, serves for respiration, (iii) Epidermal glands secrete mucus for lining the burrow so as to prevent it from collapsing, (iv) Epidermal sensory cells are responsible for perceiving external stimuli, (v) Musculature helps in various types of movements, (vi) Setae serve for locomotion, (vii) Peritoneal cells lining coelom secrete the coelomic fluid and give rise to gonads during breeding season.

COELOM

Body cavity of *Nereis* is a true coelom of schizocoelic origin, *i.e.*, it is formed by the splitting of embryonic mesoderm. It forms a spacious perivisceral cavity between the body wall and alimentary canal. Numerous membranous transverse **septa** or **coelosepta** divide the entire coelom into a linear series of compartments, each corresponding to a segment of body. Septa correspond in position to the external intersegmental grooves. They are perforated and each is composed of connective tissue and muscles sandwiched between two layers of coelomic epithelium. Coelom of each segment is further divided into right and left compartments by dorsal and ventral mesenteries. The latter, however, disappears in older segments.

Coelom is filled with a colourless coelomic fluid containing amoeboid corpuscles (leucocytes) and, during breeding season, numerous reproductive cells in various stages of development. It is internally lined by thin, delicate **coelomic epithelium** divided into two layers : a **parietal layer** beneath body wall and a **visceral layer** covering the alimentary canal. Coelom communicates with the exterior through nephridia. Coelomic fluid acts as an **hydrostatic skeleton** and for transportation of digested food, gases and waste materials.

LOCOMOTION

Nereis can crawl on substratum as well as swim actively. **Crawling** is affected by the activity of parapodia alone, while **swimming** involves parapodial activity as well as snake-like lateral undulations of body which are brought about by the wave-like contractions of longitudinal muscles.

Gray (1939) has described the pattern of parapodial activity during locomotion in *Nereis*. According to his observations, each parapodium behaves like a miniature paddle, alternately beating backwards (**effective stroke**) and forwards (**recovery stroke**). Opposite parapodia of adjacent segments always perform the same stroke at a time, while opposite parapodia of the same segment perform reverse strokes at the same time. Movements of parapodia are controlled by oblique and parapodial muscles and coelomic fluid which may be forced into, or withdrawn from them.

DIGESTIVE SYSTEM

[I] Alimentary Canal

It is a straight tube extending from anterior to posterior end of the body suspended in the body cavity by the dorsal mesentery and the intersegmental septa. It is open at both ends, the anterior opening is the **mouth** and posterior opening, the **anus**. It can be distinguished into three distinct regions : (i) **stomodaeum** or **foregut** comprising buccal cavity and pharynx, (ii) **mesenteron** or **mid-gut** comprising oesophagus and stomach-intestine, and (iii) **proctodaeum** or **hind gut** comprising rectum. Foregut and hind gut are lined internally by ectodermal epithelium and cuticle which is continuous with those of body wall, while the mid-gut is lined by endodermal epithelium.

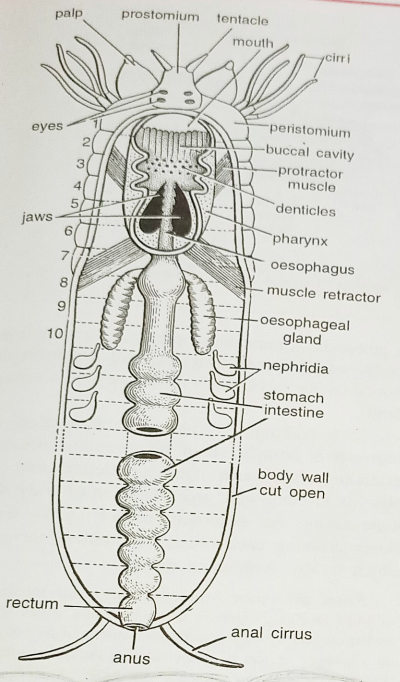


Fig. 9. *Nereis.* Diagrammatic view of the anterior and posterior ends dissected dorsally to show the alimentary canal.

1. Mouth. It is a transversely elongated slit, opening ventrally below prostomium and bordered by peristomium. It leads into buccal cavity.

2. Buccal cavity and pharynx. **Buccal cavity** is a wide chamber succeeded by the highly muscular **pharynx**. Cuticle-lining their lumen is thickened at places to form **denticles** or **paragnaths** or **teeth**, which have fixed numbers and specific arrangement in each species. Posterior part of pharynx has a thick muscular wall and a narrow lumen. Embedded laterally in the wall of this region (sometimes called **dentary region**), is a pair of stout, mobile and dark, chitinous **jaws**. Each jaw has a hollow **base** and an incurved, pointed, somewhat notched **apex**. Inner margins of jaws are serrated. Buccal cavity and pharynx are wrapped in a common muscular coat and together they extend up to 4th or 5th trunk segment. They can be fully everted to form a **proboscis** or **introvert**. This operation exposes tips of jaws for capturing prey.

3. Oesophagus. Pharynx narrows posteriorly to lead into oesophagus. It is a narrow tube extending through 5 segments behind pharynx. A pair of long, unbranched, sacculated glandular pouches, the **oesophageal glands** or **caeca**, open into it laterally at the anterior end. They probably secrete proteolytic enzymes. Oesophagus is followed by the stomach-intestine. Opening between the two is guarded by a sphincter muscle. A distinct stomach is absent.

4. Stomach-intestine. It is a segmentally constricted, straight, thin-walled tube extending up to the last trunk segment. Epithelial lining of mid-gut contains scattered **gland cells** which secrete digestive enzymes.

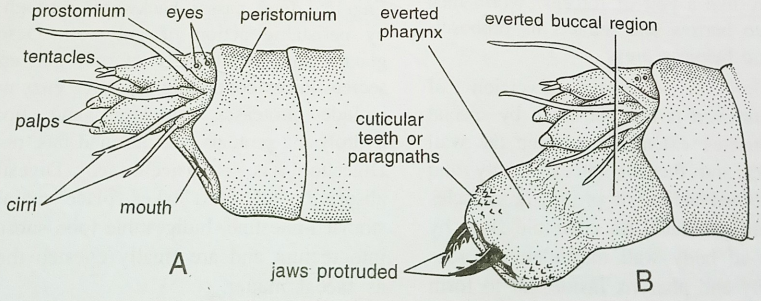


Fig. 10. *Nereis.* Anterior end in lateral view. **A.** Pharynx retracted. **B.** Pharynx everted.

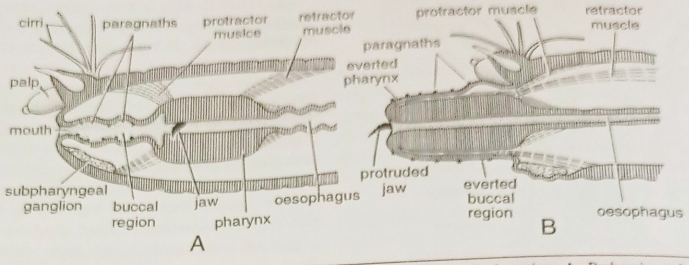


Fig. 11. *Nereis.* Diagrammatic representation of the action of introvert in sagittal section. **A.** Proboscis or introvert at rest. **B.** Introvert protruded.

5. **Rectum.** Rectum or hindgut occupies the last body segment or pygidium and opens to the exterior through a terminal **anus**.

[II] Histology of Alimentary Canal

Gut wall consists of : (i) an outermost layer of **visceral peritoneum**, (ii) a layer of **longitudinal muscles**, (iii) a layer of **circular muscles**, (iv) an **enteric epithelium** which is endodermal in case of mid-gut but ectodermal in fore- and hind guts, and (v) a layer of **cuticle** in fore- and hind guts.

[III] Food and Feeding Mechanism

Nereis is **carnivorous** and a raptorial feeder. It preys upon small crustaceans, worms, larvae, etc., which are actively captured by the exposed jaws of proboscis. Worm lives in the burrow with its head protruded and suddenly everts its proboscis to capture any minute creature passing by. Jaws seize the prey like a pair of forceps. Worm then withdraws into burrow and retracts its proboscis to swallow the helpless prey.

1. **Eversion of pharynx.** Eversion of proboscis or introvert is brought about by special **protractor muscles**, extending between the wall of peristomium and that of buccal cavity and pharynx. Combined action of protractor muscles and the pressure generated on coelomic fluid by the contraction of body wall musculature forces the buccal cavity and pharynx inside out to form a proboscis. A muscular diaphragm extending from body wall between 2nd and 3rd segments to buccal cavity checks the eversion beyond a certain limit.

2. **Retraction of pharynx.** Retraction of introvert is brought about by **retractor muscles** extending backwards from posterior end of pharynx to body wall, and relaxation of body wall musculature. As proboscis retracts, jaws come closer crossing each other and holding the prey which is also withdrawn inside.

Nereis diversicolor frequently exhibits the mechanism of **filter feeding**. It secretes a **mucous cone** at one end of its burrow and by dorso-ventral undulations of its body sets up a constant current of water entering the burrow through that end and leaving through the other. Mucous cone, behaving like a strainer, holds up the food particles. Food-laden mucous cone is finally ingested by the worm.

[IV] Digestion, Absorption and Egestion

Engulfed food passes backwards through midgut by peristaltic action of gut wall. Oesophageal glands and gland cells of mid-gut epithelium secrete juices containing digestive enzymes which include proteases, amylases and lipases for hydrolysing proteins, starches and fats, respectively. Digestion is **extracellular**. Digestion and absorption of food takes place mainly in the stomach-intestine. Indigestible food substances pass into rectum and are finally egested through anus as faecal matter.

RESPIRATION

Gills or any other special organs of respiration are lacking in *Nereis*. However, respiration is carried on by the whole body surface, but more specially by the thin, flattened lobes of parapodia, which possess extensive capillary-networks, lying very close to the surface. Blood running through them gives up carbon dioxide collected from tissues and receives oxygen dissolved in surrounding water. Water is constantly renewed by gentle dorso-ventral undulations of body which cause a steady current to flow through the burrow.

BLOOD-VASCULAR SYSTEM

Transportation of materials in annelids and higher animals is brought about by a specialized system, the **circulatory** or **blood vascular system**. It consists of a fluid tissue, called **blood**, which circulates throughout the body through a system of closed tubes or **blood vessels**. This type of blood-vascular system is called **closed type**.

[I] Blood

It consists of a fluid medium called **plasma** containing numerous nucleated, colourless amoeboid cells or **corpuscles** and dissolved **haemoglobin**, which serves as the respiratory pigment and imparts bright red colouration to blood. Blood circulates in body throughout life of the animal (hence the name **circulatory system**) and brings about transportation of gases, food, excretory materials, etc.

[II] Blood Vessels

There are three main longitudinal blood vessels, *viz.*, **dorsal**, **ventral** and a **peri-neural**.

1. Dorsal vessel. It runs above the alimentary canal, through dorsal mesentery, from hind end forward to the fifth segment. Its walls are highly contractile and surrounded at several places by rings of muscles. Strong peristaltic waves pass from its posterior to anterior end, driving blood anteriorly. Behind oesophagus, it acts as a **collecting vessel** receiving blood from body wall, parapodia, nephridia and alimentary canal. In the region of oesophagus, it bifurcates and each branch forms a **capillary meshwork** to supply the oesophageal wall. Here, it acts as a **distributing vessel**. Blood from capillary meshwork in oesophageal wall is collected by a single median vessel which opens into the ventral vessel.

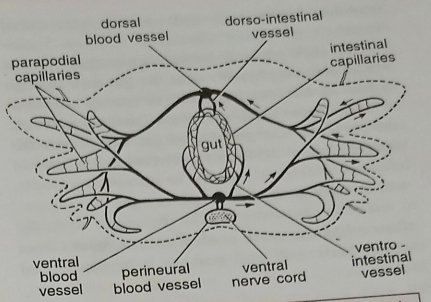


Fig. 12. *Nereis*. Blood-vascular system, representation in T.S. of a segment.

2. Ventral vessel. It runs mid-ventrally below alimentary canal almost the entire length of body. Its walls have little contractility and hence peristalic waves do not pass through it. Blood flows in it from anterior to posterior end. It is a **distributing vessel** except at the anterior end, where it collects blood from the oesophageal wall. In the last segment, it communicates with dorsal vessel by a simple **circum-rectal ring**.

In each segment, behind the oesophagus, the ventral vessel is connected with the dorsal vessel by a pair of loop-like **lateral commissural vessels**. Each of these vessels shortly divides into **afferent** branches (afferent cutaneous, afferent nephridial and afferent parapodial) which carry blood to the body wall, nephridium and parapodium of its side. In these organs, the afferent branches break up into a network of capillaries which reunite to form the corresponding **efferent** branches. The efferent

branches finally unite and open into the dorsal vessel.

In each segment behind oesophagus, ventral vessel also supplies blood to the gut wall through a pair of **afferent intestinal** or **ventro-intestinal vessels**. These break up into a capillary network, the **peri-intestinal plexus**, in gut wall. From this network blood is finally collected by a pair of **efferent intestinal** or **dorso-intestinal** vessels, which carry it to the dorsal vessel.

3. **Peri-neural vessel.** It runs ventrally surrounding the nerve cord. It collects blood from ventral body wall and conveys it to the ventral vessel.

EXCRETORY SYSTEM

[I] Excretory Organs

Excretion is brought about by **nephridia**, one pair of which is found in each segment except a few anterior and a few posterior ones.

Each nephridium is distinguished into a somewhat oval, curved **body** and a narrow **neck**. Body lies somewhat transversely in the ventro-lateral aspect of segment, while neck penetrates the intersegmental septum in front and extends a short distance into adjacent anterior segment. Body

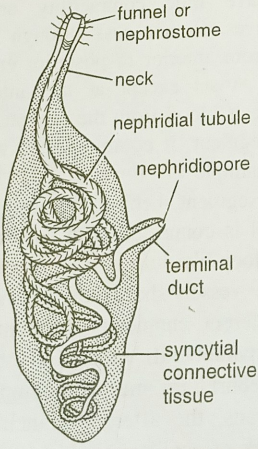


Fig. 13. *Nereis.* A single nephridium.

of nephridium consists of a syncytial mass of connective tissue, containing a coiled **excretory** or **nephridial tubule** open at both ends. One end of tubule runs through neck and opens into coelom of adjacent anterior segment by a funnel-like **nephrostome**. Margin of nephrostome is produced into a number of long, delicate processes provided with **cilia**. A nephridium possessing such a ciliated nephrostome is termed **metanephridium**. Behind nephrostome the excretory tubule becomes much coiled in the body region and finally forms the **terminal duct**, which opens to the exterior through **nephridiopore**, situated near the base of ventral cirrus of parapodium. Nephridiopore is guarded by a sphincter. Excretory tubule is ciliated at most places. Terminal duct is without cilia.

[II] Physiology of Excretion

Excretion is carried out in two ways. Outer surface of nephridium is densely covered by blood capillaries. Gland cells, forming the wall of ciliated excretory tubule, remove waste material from blood and finally discharge it through nephridiopores. Nitrogenous waste is mainly ammonia (**ammonotelic**). Ciliated funnels of nephridia, opening into coelom, also remove dead or dying coelomic corpuscles which have eaten up, or have been destroyed by foreign bodies such as bacteria. Any useful substance entering the excretory tubule is reabsorbed by its cells and returned to the blood capillaries. This is known as **selective resorption**.

NERVOUS SYSTEM

Correlated with its active predaceous life, *Nereis* possesses a well-developed nervous system. It is bilaterally symmetrical, metamerically segmented and distinguished into **central**, **peripheral** and **visceral** nervous systems.

[I] Central Nervous System

Cerebral ganglia or **brain** is a large bilobed mass located dorsally in prostomium. It consists of nerve cells surrounding a centrally-placed mass of nerve

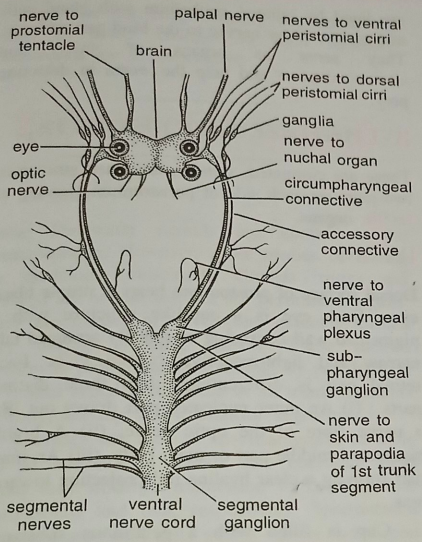


Fig. 14. *Nereis.* Nervous system.

fibres. In brain, three **centres** are mainly recognised. These are **anterior**, **middle**, and **posterior centres**. Middle centre bears a pair of small lobes called **corpora pedunculata**. These are **association centres** that coordinate all impulses entering the brain.

A **sub-pharyngeal** ganglion, formed by fusion of two pairs of ganglia of ventral nerve cord, lies ventrally below the pharynx in first trunk segment. Brain is connected with sub-pharyngeal ganglion by a pair of stout nerve strands or **circum-pharyngeal connectives**, running one on either side of pharynx, forming a nerve collar or nerve ring. Connectives bear small ganglia near their points of attachment with brain. These ganglia probably represent nerve centres that were originally located in ventral nerve cord but have shifted to their present position due to cephalization.

Ventral nerve cord runs posteriorly from sub-pharyngeal ganglion throughout body along the mid-ventral line, immediately beneath the ventral blood vessel. It is actually formed by the fusion of two very closely apposed cords enclosed in a common sheath of connective tissue, and joined together by segmental cross connections. Its dual nature is revealed by a careful examination of its transverse section. In each segment, nerve cord is dilated into a **segmental ganglion** which actually represents a pair of ganglia very closely fused together. A segmental ganglion occupies about two-third of the length of a segment. Cell bodies of nerve cord are confined to the segmental ganglia.

Throughout the length of ventral nerve cord run 5 **giant fibres** or **axons**, 3 central and 2 lateral in position. These fibres are very thick and long, some extending the entire length of nerve cord without synapses. Through such fibres impulses travel very fast, about 25 cm in a hundredth of a second, as against 25 cm in 10 seconds in case of the usual ventral nervous system that has several ganglion and synapses. Such giant fibres, found in most annelids (including earthworm), enable the worm to respond to an alarm by sudden violent shortening of the entire body.

[II] Peripheral Nervous System

It consists of nerves connected to brain, circum-pharyngeal connectives and segmental ganglia of ventral nerve cord. Brain gives out : (i) from its anterior centre, a pair of short nerves to prostomial palps, (ii) from its middle centre, two pairs of stout nerves to eyes and a pair of nerves to prostomial tentacles, and (iii) from its posterior centre, a pair of slender nerves to nuchal organs. Ventral pair of peristomial cirri receives nerves from ganglia on circum-pharyngeal connectives. Sub-pharyngeal ganglion gives out anteriorly a pair of long nerves, the **accessory connectives**, which run parallel to the circum-pharyngeal connectives through much of their course and supply the dorsal pair of peristomial cirri. Each accessory connective, before giving out a pair of nerves to peristomial cirri, swells into a ganglion. It lies close to the corresponding ganglion on circum-pharyngeal connectives, and like the latter, represents the nerve centre of ventral nerve cord. Posteriorly, the sub-pharyngeal ganglion gives out

a pair of nerves to body wall and parapodia of third segment (first trunk segment).

Each segmental ganglion gives out four pairs of peripheral nerves. I and IV pairs supply the longitudinal muscles and body wall. II pair supplies the parapodia, and III pair is composed of fibres from proprio-receptors in muscles. Each peripheral nerve contains afferent and efferent fibres.

[III] Visceral Nervous System

It consists of a network of fine nerves (stomogastric nerves) and a few ganglia supplying the dorsal and ventral walls of pharynx (proboscis). These are involved in the motor control of proboscis. Dorsal and ventral networks are connected with the ganglia and ventral ends of circum-pharyngeal connectives, respectively.

Nereis possesses a slight power of learning including finding its way and avoiding unpleasant stimuli. However, when brain is removed, the ability to retain learnt behaviour is greatly reduced.

SENSE ORGANS

[I] Prostomial Tentacles

These are a pair of small, cylindrical projections from anterior border of prostomium. They are probably tactile. Surface of tentacles bears numerous sensory spiral organs, each consisting of about 100 photoreceptive cells, spirally arranged within a cuticular pit.

[II] Prostomial Palps

These are a pair of stout highly muscular, two-jointed structures arising one from each ventro-lateral aspect of prostomium. Proxima or basal joint is large, while distal one is small and can be retracted into the former. In addition to serving as lateral lips, the palps probably serve as organs of touch, taste and smell.

[III] Nuchal Organs

These are a pair of small pits on the posterior dorsal surface of prostomium behind eyes. Pits are lined by ciliated epithelium with gland cells and connected by nerves to the hind part of brain. They serve as organs of smell and chemoreception and help the worm in detecting prey.

[IV] Peristomial Cirri

These are elongated, slender, unjointed structures, two pairs on each side of peristomium, serving as tactile organs.

[V] Eyes

Dorsal surface of prostomium bears 4 simple black eyes. Each eye is a cup-like structure with a pigmented wall consisting of radially arranged tall, narrow and light-receptive retinal cells. Each retinal cell is differentiated into three distinct parts : (i) An outer nucleated part drawn out into a nerve fibre of the optic nerve, (ii) A highly pigmented middle part or main body, (iii) An inner part forming a clear hyaline rod projecting towards lens.

Cup is filled with a gelatinous substance forming the lens which, according to Andrews, is secreted by the retinal cells. Outer exposed surface of eye is covered by a layer of flattened epidermal cells and a transparent protective cuticular layer, together forming the cornea. Retinal cells are modified ectodermal cells and become continuous with epidermis at the edges, so that the small opening of cup towards cornea functions as a pupil.

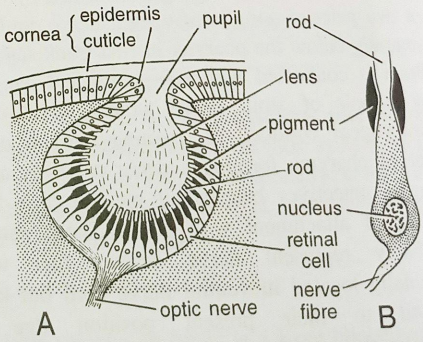


Fig. 15. *Nereis.* Eye. **A.** Entire eye in V.S. **B.** An isolated retinal cell.

Eyes are not image-forming but enable the worm to detect changes in light intensity. Clamworms are photonegative.

REPRODUCTIVE SYSTEM

[I] Gonads

Some freshwater nereids are known to be hermaphrodite. However, most species of *Nereis* are dioecious (unisexual). Gonads (testes and ovaries) are neither distinct nor permanent organs. They are masses of developing gametes formed only during breeding season. These masses develop as projections of swellings by proliferation of ventral septal peritoneum in all trunk segments of body, leaving a few anterior segments.

Gametes are shed as **spermatogonia** in male and as **oogonia** in female into coelomic fluid where they undergo maturation to develop into spermatozoa and ova, respectively. Spermatozoa or sperms are small cells with a minute rod-shaped head and a long vibratile tail. Ova are somewhat large and rounded and packed with yolky globules. In a mature worm, coelom remains packed with gametes.

[II] Gonoducts

In *Nereis* there are no gonoducts. Ripe sperms and ova are discharged to outside sea water mostly through metanephridia by the action of cilia borne by nephrostomes and nephridial tubules. Goodrich (1945) proposed the name **nephromixia** or **mixonephridia** for such nephridia, acting both as excretory and genital ducts. In some species, gametes are liberated by the breakdown of body wall. After the rupture of body wall the adults die.

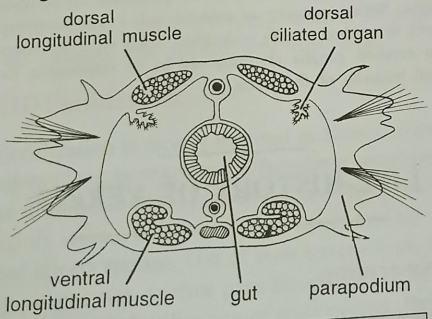


Fig. 16. *Nereis.* T.S. of a segment to show the ciliated organs.

[III] Dorsal Ciliated Organs

A pair of dorsal ciliated organs occurs in each segment in close relation to the dorsal longitudinal muscles. Each ciliated organ is a ciliated tract of coelomic epithelium appearing as a short and much folded funnel with a wide opening into body cavity but lacks an opening to the exterior. They resemble the **coelomoducts** of other polychaete annelids. Formerly regarded as excretory organs, they are now looked upon as gonoducts. It has been said that during sexual maturity, funnels open to the exterior by temporarily acquired minute apertures opposite to them in body wall. But due to lack of adequate evidence, the real function of ciliated funnels remains controversial.

HETERONEREIS

[I] Epitoky

At sexual maturity, most of the posterior segments, filled with gametes, exhibit morphological and anatomical differentiation. These constitute the sexual region or **epitoke** of worm. Few anterior segments which do not take part in gamete-formation, constitute the asexual region or **atoke**. Sexually mature worm with these two regions is known as *Heteronereis* and the phenomenon involving transformation of non-sexual individual into sexual individual is referred to as **epitoky**.

In *N. virens* and some other species, the sexually mature phase differs so widely from the immature phase that it has long been considered to be a member of a separate genus, which was given the name *Heteronereis*. Its correct identity was known only after **Malamgren** recognized it as merely the sexual individual of *Nereis*.

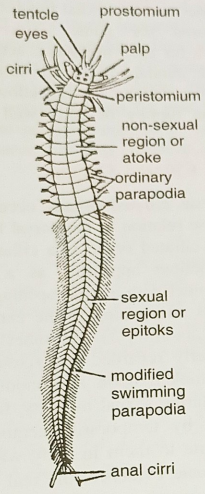


Fig. 17. *Heteronereis.*

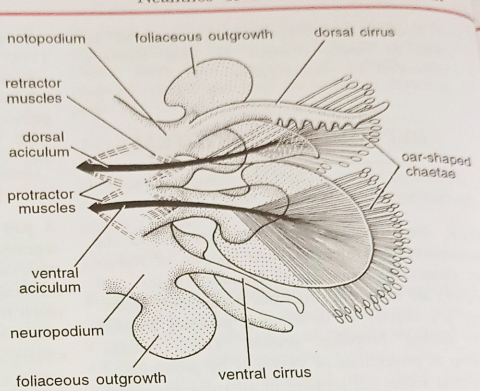


Fig. 18. *Heteronereis.* Parapodium.

[II] Characteristic Features of *Heteronereis*

(1) Instead of creeping about on sea bottom or living in burrows like *Nereis*, the *Heteronereis* swims actively in surface waters.

(2) Body of *Heteronereis* is divisible into two distinct regions : an anterior asexual **atoke**, and a posterior sexual **epitoke**.

(3) Parapodia of posterior sexual region becomes larger, more vascularized and develop flattened leaf-life outgrowths for more rapid respiration. Their normal setae are replaced by flattened oar-shaped setae arranged in a fan-like manner, to offer a larger surface for swimming. Dorsal cirri are altered. Leucocytes break down and digest the original parapodial muscles and new muscles are formed.

(4) The eyes become greatly enlarged and conspicuous.

(5) Prostomial palps and tentacles become reduced, but peristomial cirri become longer.

(6) Intestine becomes compressed and functionless due to much developed gonads.

(7) Sensory projections become shrunken while pygidium or anal segment develops special sensory papillae.

(8) In some species, such as *Nereis virens*, *Heteronereis* shows sexual dimorphism, male having less unaltered anterior segments than female.

It has been shown by **Durchon** that immature worm is prevented from metamorphosing into *Heteronereis* by inhibitory action of neurosecretions produced by cerebral ganglia. Sexual maturity is attained only when secretory activity in cerebral ganglia is declined. Some other hormones from cerebral ganglia are supposed to be responsible for sexual maturity of the worm.

LIFE-HISTORY OF *NEREIS*

[I] Swarming

Sexually mature individuals or *Heteronereis* swim to the surface of sea water in order to shed sperms or ova. This behaviour is called **swarming**. It generally occurs at night and some species, while

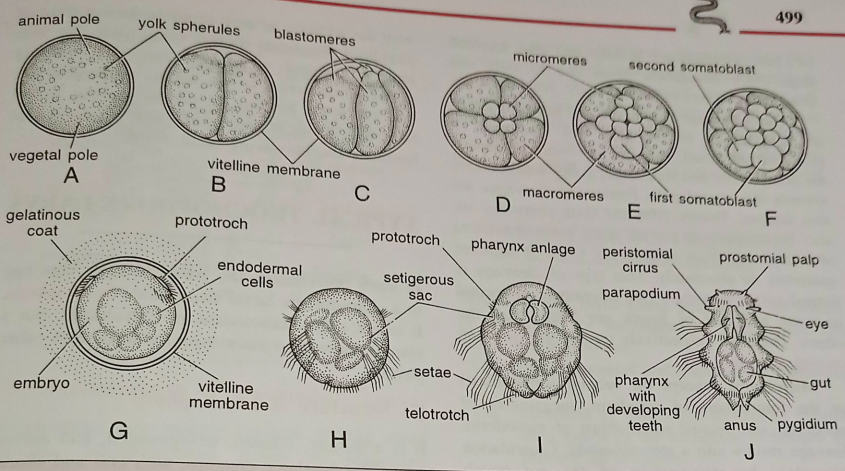


Fig. 19. *Nereis.* Stages in development.
A. Fertilized egg. **B.** Two-cell stage. **C.** Four-cell stage. **D.** Eight-cell stage. **E.** Ist somatoblast formed. **F.** 2nd somatoblast formed. **G.** Young trochophore before hatching. **H.** Post-trochophore or nectochaete larva with three setigerous segments. **I.** Older larva. **J.** Later larva after three weeks.

swarming, perform a nuptial dance in which both males and females swim rapidly in a circle. Females produce a substance, called **fertilium**, which attracts the males and stimulates shedding of sperms, which in turn excites the females and stimulates shedding of eggs. In case of *N. succinea,* males first swim to the surface and wait for females. When the latter appear, males swim around them shedding sperms. In response, the females get excited and shed ova.

[II] Fertilization

Fertilization is mostly external in *Nereis virens* and takes place in sea water. *Platynereis megalops* has an altogether different mechanism. The male wraps tightly around female, inserts his anus into her mouth and injects sperms. Gut of both having been eroded by phagocytes, sperms pass directly into coelom of female where fertilization of eggs occurs. Fertilized eggs are shed at once from the posterior end of female's body. This mechanism of internal fertilization has probably evolved in *Platynereis megalops* because its eggs become unfertilizable just after 30 seconds contact with sea water. In case of *N. diversicolor,* which does not attain epitokous form, fertilization occurs in burrow of female into which male enters, or on the surface of mud.

[III] Development

Development of *Nereis* comprises three distinct periods :

1. Pre-larval period. Unfertilized Egg of *Nereis* contains numerous yolk spherules and oil droplets. It is covered by a thick, radially striated membrane, called **zona radiata**, which in turn has another thin delicate membrane around it. Outside these membranes is a thick gelatinous coating. Soon after fertilization, zona radiata disappears, yolk spherules from animal pole move into vegetal pole (**telolecithal** condition), egg extrudes two polar bodies, and undergoes cleavage.

First two cleavages of zygote are **equal** and **vertical** and result in four cells or **blastomeres**, lying in the same plane. Cleavage is **determinate**,

i.e., fate of blastomere is fixed and after four-cell stage, each blastomere gives rise to only one quadrant (quarter) of embryo.

Third cleavage is unequal and horizontal, *i.e.*, at right angles to the first two cleavages. It produces four small, yolk-free **micromeres** towards the animal pole and four large, yolky **macromeres** towards the vegetal pole. Remaining cleavages are also unequal. Fourth, fifth and sixth cleavages are also horizontal and cut off three more quartettes of micromeres from megameres. Cells of adjacent quartettes lie alternately. This type of cleavage is termed **spiral cleavage**. One micromere of second quartette and one of fourth are larger than the others. These are respectively termed the **first** and **second somatoblasts**.

Micromeres (except the second somatoblast) are the forerunners of ectoderm, megameres of endoderm, and second somatoblast of mesoderm. Cleavage results into a stereoblastula. Gastrulation takes place by invagination of the gut pouch resulting in a ciliated gastrula.

2. Larval period (Trochophore). After gastrulation, ciliated embryo rapidly develops into a larval stage, called **trochophore** or **trochosphere**. Only after 24 hours of development, the trochophore structure begins to appear. Embryo takes up a top-like form. Ringing the larva just above its equator develops a girdle of ciliated cells, called **prototroch** or **preoral ciliated band**.

A typical trochophore larva does not occur in *Nereis*. Instead, trochophore stage is embryonic and passed inside the egg membrane. It differs from a typical trochophore in the absence of a blastocoel. Newly hatched larva of *Nereis* is termed **post-trochophore** larva or **nectochaete**. It possesses three segments with bristles and is without greatly developed larval structures.

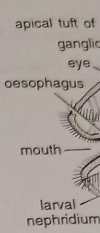
3. Post-larval period or metamorphosis. Post-trochophore larva swims actively for a few days, feeding on microorganisms. While swimming it undergoes metamorphosis to change into the adult. Its preoral apical portion develops into the **prostomium** of adult. First segment becomes the **peristomium** and the last segment the **pygidium**. Ciliary bands disappear and larva grows in size with the addition of new segments just in front of pygidium. Segments soon develop parapodia with long provisional or larval setae. The resulting young worm settles to the bottom at the low tide line and starts forming its tubular burrow. In the burrow it grows further adding new segments and becomes the burrowing adult worm.

TYPICAL TROCHOPHORE LARVA

In some polychaetes, the young hatches from egg in a characteristic larval stage called **trochophore**. It is not only characteristic of polychaetes, but a similar larva also occurs in molluscs and other phyla.

[I] Structure of Trochophore

It is a minute, ciliated, unsegmented, and almost pear-shaped pelagic creature, with oral and aboral surfaces recognizable. In a full grown typical trochophore larva, there is a sensory **apical organ** or **plate** bearing a **tuft of cilia**. Brain rudiments, as a **ganglion**, are usually evident beneath the apical organ. A characteristic feature of trochophore is the presence of a preoral ciliated girdle of cells, just above equator, and called **prototroch**. Digestive tract is complete. **Mouth** lies ventrally just beneath the prototroch and **anus** is near the lower apex. A **pastoral ciliated band** or **metatroch** lies behind the mouth, and in some there is also a, **telotroch** just infront of anus. These ciliated rings help in feeding and locomotion. Gut is regionated into oesophagus, stomach and intestine. Mesoderm is a pair of undifferentiated masses of cells located in the lower cone. Lying beside these is a pair of protonephridia that develop from ectoderm. Trochophore, at its early stage of development, lacks a coelom. Its body is composed primarily of an outer ectoderm with ectodermal derivatives (nervous tissue and scattered ectodermal elements), and inner endoderm forming the gut. Space enclosed between gut endoderm and ectoderm is called **blastocoel**.



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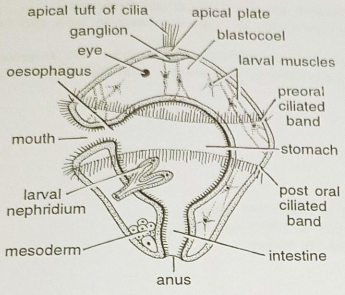

Fig. 20. A typical trochophore larva.

[II] Metamorphosis of Trochophore Larva

Trochophore is a pelagic creature drifting about in sea. Metamorphosis results in immediate termination of planktonic existence, and loss of many larval structures, such as protonephridia, ecto- mesodermal muscle bands and ciliated girdles. Cells of apical plate form the prostomium and brain. Larva gradually grows in length with the formation and development of trunk segments in front of the terminal pygidium. Formation of body segments is marked externally by the development of setal sacs and setae. Mouth region fuses with the first trunk segment to form the peristomium without setae. Larva eventually sinks to the bottom to complete post larval development and assume the habits of the adult.

[III] Significance of Trochophore

Trochophore larva serves for dispersal of the species. Besides, it has great phylogenetic significance. A trochophore larva appears in the development of animals belonging to several phyla, such as Annelida, Mollusca, Bryozoa, etc. This led **Hatschek** (1878) and other embryologists to conclude that these groups of animals are all descended from a common hypothetical ancestor called a **trochozoon**. This is known as **Trochophore theory**. However, strong arguments have been given both for and against this theory.

ADAPTATIONS OF *NEREIS*

Structural and behavioural adaptations of *Nereis* or *Neanthes*, for its burrowing and carnivorous habits are as follows :

(1) Body elongated and flattened for burrowing in mud.

(2) Secretion of mucus for cementing together sand grains in the formation of burrow and prevent its collapse.

(3) Burrowing and nocturnal habits protect from predators.

(4) Eversible pharynx and chitinous sickle-shaped jaws help in capture of fast-moving prey.

(5) Needle-like setae on flat oar-like parapodia help in swimming and crawling.

(6) Thin and highly vascular integument of parapodia serves for gaseous exchange, in the absence of respiratory organs.

(7) Head with sense organs well-developed corresponding to its active mode of life.

(8) Nervous system well-developed correlated with active predaceous life.

(9) Swarming of sexually mature individuals (*Heteronereis*) ensures fertilization of ova.

(10) Occurrence of free-swimming trochophore larva in development serves for far and wide dispersal of species.

Important Questions

➤➤*Long answer type questions*

1. Describe the external morphology of *Nereis*. Compare it with that of *Heteronereis*.
2. Give an account of the feeding mechanism of *Nereis* and explain clearly the physiology of digestion in this animal.
3. Give an account of the process of reproduction and development in *Nereis*.