10
Filter Feeding

10-1 FILTER FEEDING IN POLYCHAETES

With the increasing development of cell differentiation and coordination that marks the history of the Metazoa, there arose methods of filter feeding much more elaborate than those of sponges. This type of feeding is found only in aquatic animals, the absence of filter feeding from terrestrial forms being largely related to the much lower density of air as compared with that of water, and to the consequent lack of inert organic particles floating in it. However, air does contain an abundant supply of flying insects, the trapping of which by birds and web-spinning spiders can be regarded as the nearest approach to filter feeding on land. Filter feeding in aquatic animals is not easy to understand, yet it is worth while trying to do so, for the mechanisms involved are unexcelled for the precision and beauty of their adaptive organization. The principles involved show a considerable degree of uniformity over a wide range of species; this is to be expected, having regard to the uniform character of the food material and to the limited range of structures that animals can deploy in capturing it.

Good examples occur among the polychaetes. Primitively, these worms were probably free-moving and macrophagous, following the mode of life familiar in such animals as *Nereis* and *Nephtys*. These have an eversible pharynx that is used both for burrowing (p. 165) and for feeding. Prey is seized by the hooked jaws that arise from the lining of the pharynx; these are situated at its tip when the pharynx is fully everted. Microphagous feeding is characteristic of the sedentary species, and involves mechanisms so specialized that it is difficult to see immediately any close relationship between the two modes of life. Yet with feeding, as with other functions, we cannot suppose that such specializations arose already fully organized—they must have evolved stage by stage, under the influence of natural selection. Closer analysis often suggests in such instances that the more primitive forms possessed structures suitable for adaptive modification in a particular direction, even though they may have initially served some quite different function. We have earlier referred to this as pre-

256

adaptation; it is a phenomenon that must have been important in facilitating evolutionary change.

Examples of it occur in the errant polychaetes. Like so many creeping and burrowing animals, they produce over their body surface a mucous secretion which protects the surface and forms temporary linings to burrows. *Nereis diversicolor* sometimes forms this secretion into a net within its burrow; water can then be pumped through this net, so that it can be used for a simple form of filter feeding. Particles collect in the secretion as though in a bag, and from time to time the material is swallowed. We can visualize that the further elaboration of some such mechanism might have been aided by the presence on the head of tentacles and palps, which are used by errant worms for sensory purposes and to assist in the manipulation of food. These structures have given rise in sedentary worms to complex and beautiful systems of tentacular outgrowths, often called gills, or branchial crowns, because they were at one time regarded as primarily respiratory in function. No doubt they do play a part in respiration, but they also provide mechanisms for the collection and sorting of food particles; they are aided in this by the production of mucus, which is distributed over tracts of ciliated epithelium.

With this potentiality as a starting point, ciliary feeding mechanisms could have evolved in the sedentary polychaetes along many independent lines. Terebellid worms (Fig. 10–1), for example, which live in permanent tubes in mud, are deposit feeders; they obtain detritus by extending long ciliated tentacles from their head over the surface of the substratum, the food particles being trapped in mucus and swept along ciliated grooves into the mouth (Fig. 10–1). The tentacles, which are highly mobile, are beautifully adapted for this function. Their shape, as seen in cross-section, varies at different points at any particular moment according to the use to which they are being put. At one point a tentacle will be flattened to form a zone of attachment, distal to which the remainder of the tentacle explores the substratum. Proximally to the attachment point the surface of the tentacle will be folded to form a ciliated groove along which the food is propelled. This propulsion is effected in part by ciliary action, but in part also by muscular contraction.

In complete contrast to this, the lugworm obtains detritus by swallowing the mud in which it is contained. This requires active cyclical movements (p. 305), by which the animal draws into its burrow the detritus deposited on the surface; these animals, therefore, although taxonomically sedentary polychaetes, are more active than most worms of this type. They rely upon the sucking action of the anterior end of the alimentary tract to enable them to swallow, and this, coupled with their burrowing activity, accounts for the absence of tentacles.

Sabella, which presents a contrast to both of the above worms, provides an example of the elegance of adaptation that has been achieved in the feeding mechanisms of the polychaetes. It is a comparatively large animal, found in the littoral zone, where it builds tubes that project in large numbers from the surface of the mud. It is a suspension feeder, extracting its food from water currents, which are created by coordinated cilia. These are set upon the branchial crown (Fig. 10–2), which consists of a large number of cephalic tentacles or filaments, differing from those of *Terebella* in being stiff and pinnate, and in being arranged in two groups of about 30. Each group is united towards its base into a lateral lobe, the two lobes being joined together dorsally but extending back independently on the ventral surface.
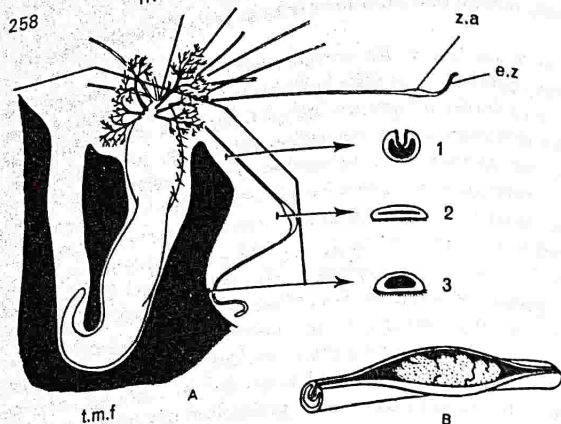
Fig. 10.1. Operation and structure of the tentacles in *Terebella lapidaria*. A, animal in feeding posture within its tube in the silt beneath a rock slab; *z.a*, zone of attachment; *e.z*, exploratory zone; *1*, appearance in cross-section in extended part of tentacle, *2*, at zone of attachment, *3*, in exploratory part. B, conveyance of particles along groove by ciliary action and squeezing by the transverse muscle fibres. C, transverse section of tentacle to show: *coel*, coelomic space; *l.m*, transverse muscles; *t.m.f.*, transverse muscle fibres. From Dales, 1955. *J. mar. biol. Ass. U.K.*, **34**, 55–79.

The branchial crown forms a wide funnel, with the mouth of the animal lying at the base. The problem, therefore, is to secure the food and to direct it towards that point, and it is for this purpose that the cilia are used. Their operation in feeding depends upon two rows of outgrowths, the pinnules, along each filament. These are set in such a way (Fig. 10–3) that a pinnule in one row makes an angle of rather more than 90° with the corresponding pinnule in the other row. The pinnules at the distal end of a filament are separated from the ones on the next adjacent filament, but towards the lower part of the branchial funnel they are brought closer together and finally interlock. As a result, they form a filtering system upon which food particles can be trapped.

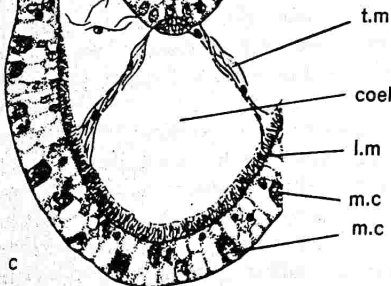**Fig. 10-2.** Ventral view of the base of the branchial crown and the first 12 body segments of *Sabella pavonina* to show the external features × 12. *ab.p*, abdominal parapodium; *b.fd*, basal fold; *b.w*, basal web; *d.b.b*, dorsal bristle bundle; *d.c.f*, dorsal collar fold; *d.l*, dorsal lip; *d.u*, dorsal uncini; *g.f*, gill filament; *g.p*, gill pinnule; *l.l*, lateral lip; *mth*, mouth; *p*, palp; *p.f*, parallel folds; *th.p*, thoracic parapodium; *v.b.b*, ventral bristle bundle; *v.c.f*, ventral collar fold; *v.gr*, ventral groove; *v.g.s*, ventral gland shield; *v.s*, ventral sac; *v.u*, ventral uncini. From Nicol, 1930. *Trans. R. Soc. Edinb.*, **56**, 537–598.

The outer surfaces of the pinnules (Fig. 10–3) bear cilia, the abfrontal cilia, which beat strongly towards the tip of each pinnule. These cilia draw water into the funnel, the process being completed by latero-frontal cilia, which beat inwards, at right angles to the beat of the abfrontal ones. Food particles enter the funnel with
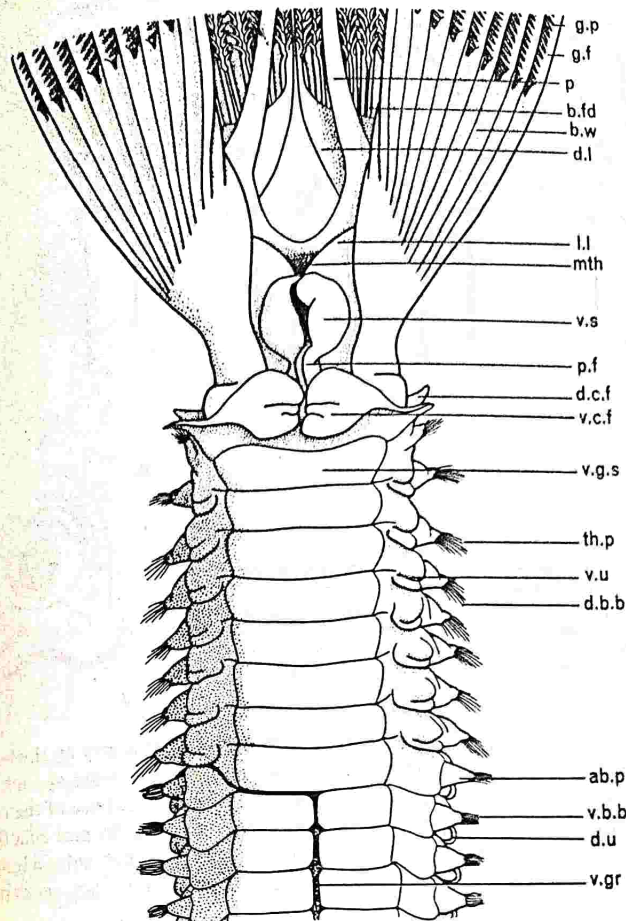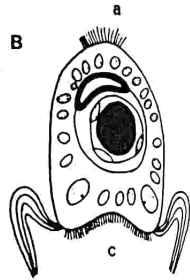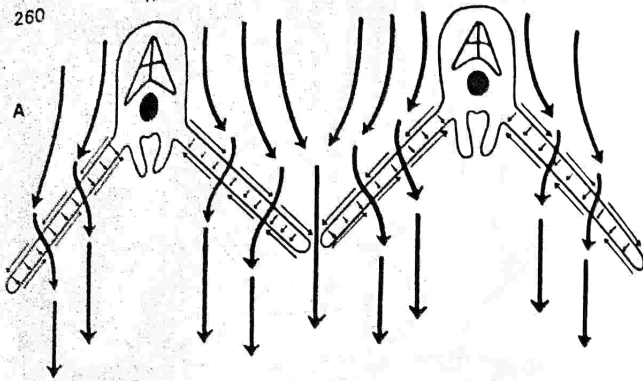
Fig. 10-3. A, diagrammatic section of two gill filaments of *Sabella*, to show the direction of flow of the water entering the branchial funnel, and the direction of beat of the cilia which cause the current. The small arrows indicate the direction of beat of the cilia; the large arrows indicate the direction of flow of the water. B, transverse section through a pinnule to show the ciliation. ×500. a, abfrontal cilia; b, latero-frontal cilia; c, frontal cilia. From Nicol, 1930. *op. cit.*

Fig. 10-4. Diagrams of the base of a gill filament of *Sabella* to illustrate the sorting mechanism. A, lateral lip and base of a gill filament with one basal fold removed to show the tracts of the lower lip, with the relative sizes of particles passing along them, and the direction of beat of the cilia on the basal folds. B, transverse section through a pair of basal folds to show the position of the longitudinal tracts and the relative sizes of particles passing along them. The arrows indicate the direction of beat of the cilia. From Nicol, 1930, *op. cit.*

the steam of water, and are thrown, partly by eddies and partly by the beat of the latero-frontal cilia, onto a groove that runs along the inner edge of each pinnule. In this groove are cilia, the frontal cilia, that beat towards the base of the pinnule in the opposite direction to the beat of the abfrontal ones. The frontal cilia thus drive the food particles to the bases of the pinnules. From here they enter a longitudinal groove than runs down the whole length of each filament, and they are driven along this by the cilia that line it.

Towards the base of each filament the two rows of pinnules pass into two continuous folds, the gill folds or basal folds (Fig. 10–4), which are ciliated on both their outer and inner faces. The cilia mostly beat upwards towards the free edge of the folds, but on their inner surfaces the folds bear three ciliary tracts in which the beat is downwards. This downward beat is directed towards the mouth, which is bordered by a dorsal and two lateral lips (Fig. 10–2); these are formed in part from the bases of a pair of long palps, and in part from the bases of the branchial crown. The lips are ciliated, and, in particular, they bear three ciliary tracts that correspond with the three tracts of the gill folds. These various structures constitute part of the sorting mechanism; we have remarked that this is an essential feature of a highly organized ciliary feeding mechanism, ensuring that only suitable particles are directed into the digestive system.

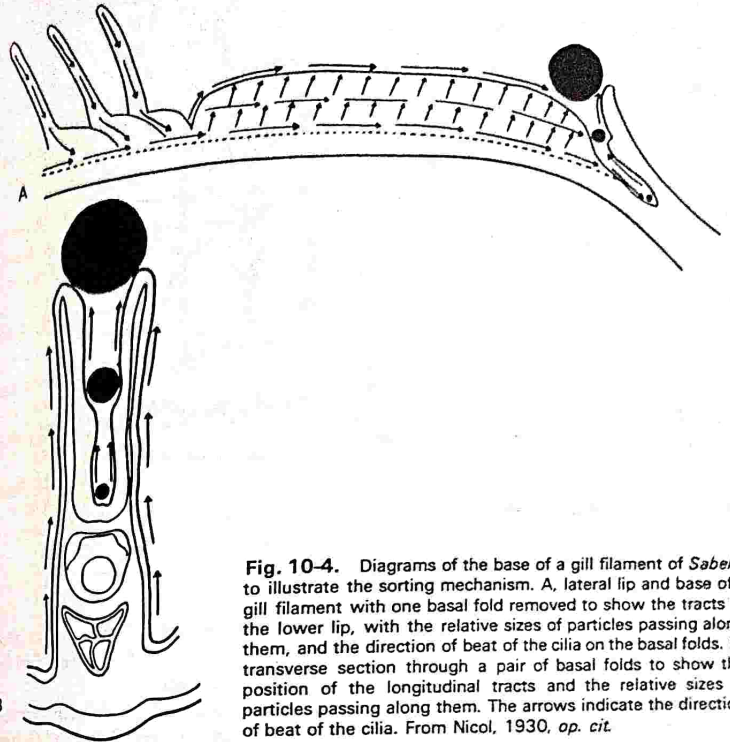Rejection in *Sabella* depends upon the capacity of the sorting mechanism to differentiate between particles of various sizes. The pinnules play some part in this, because large particles falling from above cannot enter the longitudinal grooves of the filaments since these are protected by the overarching of the expanded bases of the pinnules. Lower down a more subtle differentiation is found, permitting the sorting of large, medium, and small particles (Fig. 10–4). The gill folds are arranged in pairs; the members of each pair enclose a basal groove, but their inner surfaces are so close together that large particles cannot enter between them. Such particles, therefore, do not come under the influence of the ciliary tracts that beat downwards towards the mouth. Instead, they are moved away from the mouth towards the edges of the lips. The smallest particles, however, can pass between the inner surfaces of the gill folds into the basal groove, and they are then carried towards the mouth. The medium-sized ones follow yet another course, because, although they can enter between the inner surfaces of the gill folds, they are prevented from proceeding as far as the basal groove owing to the existence of a longitudinal ridge. They thus come under the control of a different ciliary tract, which transports them into two expansions of the lateral lips called the ventral sacs (Fig. 10–5). They do not, therefore,
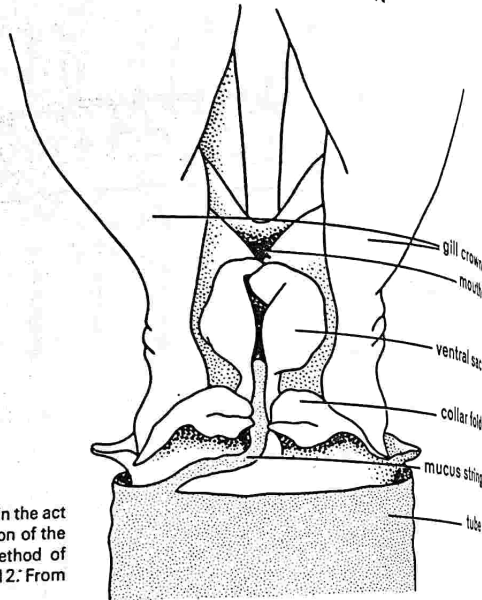
Fig. 10-5. Ventral view of *Sabella* in the act of tube-building, to show the formation of the mucus and sand string and the method of applying it to the edge of the tube. × 12. From Nicol, 1930. *op. cit.*

enter the mouth, but their selection is none the less important. They are used, after being mixed with mucus, for the building of the mud tube. This is formed through the activity of the collar folds that lie just posterior to the mouth.

The large particles are removed from the animal through the action of rejection currents, the cilia of the lips and palps being important in this. Other débris is removed by the same route, together with the faeces that are passed forward from the hind end of the animal in a ciliated groove. Mucus is extensively used in these rejection movements, where it helps the cilia to pass along the discarded material, but it would not be practicable for it to be used in the transport of food, for this depends upon the sorting of individual particles by size. In correlation with this the collection and sorting processes depend largely upon the cilia alone, and upon the currents and vortices that are established by their beat.

There are other polychaetes with feeding mechanisms similar in general principle to that of *Sabella*, but with great variation in detail. One example is *Pomatoceros*, common on rocky shores in its calcareous tubes. The branchial crown, which is very similar to that of *Sabella*, consists of two halves, each of which comprises some 14–20 pinnate tentacles borne on an outgrowth of the prostomium. The two halves are joined by the dorsal and ventral lips, between which lies the mouth. The collection and transport of food is similar in principle to that in *Sabella*, but simpler in detail, perhaps because the animal is smaller and possesses a calcareous tube. In particular, there is no specialized sorting mechanism, so that all particles transported by the pinnules are likely to reach the mouth. Some degree of sorting, however, presumably results automatically from the small size of the animal, for this ensures

that only small particles will be transported by the pinnules in the first instance. If, as may sometimes happen, the filaments become clogged with an excess of material, the tip of a filament will bend over and remove the obstruction; further protection is afforded by rejection currents on the palps, lips, and basal folds.

One other example, which shows the variety of these feeding mechanisms even within the limits of one class, is *Chaetopterus*, a highly specialized worm of bizarre form that lives in sand or mud within a U-shaped tube of parchment-like consistency (Fig. 10-6). In this animal there is no branchial crown. Instead, water is drawn through the tube by the beating of three pairs of fans that are presumably derived from the parapodia of related forms. Farther forward another pair of outgrowths forms two wings that are pressed against the wall of the tube. Mucus secreted by these is drawn backwards by cilia in a ventral groove, and is formed into a conical bag, the apex of which lies within a small cup. Food particles are strained out by this mucous bag, the substance of which is continuously secreted by the wings and rolled up into a pellet in the cup. At intervals the secretory process stops and the cilia in the ventral groove move in reverse; as a result the pellet from the cup, with its contained food particles, is transported to the mouth and swallowed.

In the more advanced invertebrates extracellular digestion tends to replace the intracellular method, for reasons that we have earlier indicated, but the mode of feeding may be decisive in determining how far this tendency proceeds. In annelid worms the situation has been comparatively little studied, but there is evidence that
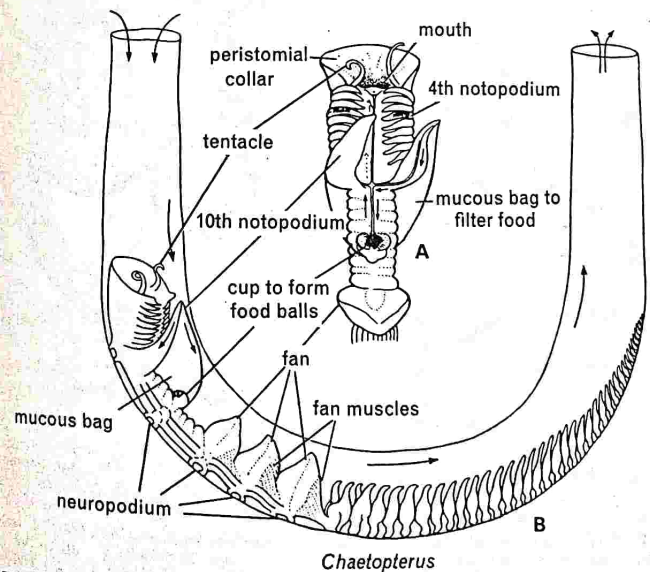

Chaetopterus

Fig. 10-6. *Chaetopterus.* In B, the direction of water is indicated by arrows. From Borradaile *et al.*, 1958. *The Invertebrata* (3rd ed., ed. Kerkut). Cambridge University Press, London.

the extracellular method predominates. Some phagocytosis may, however, take place, as, for example, in *Arenicola marina*, where digestion is completed in wandering amoebocytes that take up from the alimentary epithelium particles that its cells have ingested. It is surprising that digestion appears to be largely extracellular in terebellids, for their filter-feeding habits would seem to favour the persistence of intracellular digestion. In fact, their gut shows considerable regional specialization for extracellular digestion (Fig. 10–7), being differentiated into an oesophagus, a fore-stomach, a muscular hind-stomach which serves as a mixing region, and an intestine. Enzymes are secreted in the fore-stomach and fore-intestine, absorption taking place in the intestine. Arthropods also, incidentally, rely almost completely upon extracellular digestion, even in microphagous forms; intracellular digestion is restricted to the final stages in the digestion of proteins, more especially in arachnids. This contrasts strikingly with the situation that we shall find in the Bivalvia, where microphagy is associated with the retention of a highly specialized form of intracellular digestion.

10-2 FILTER FEEDING AND DIGESTION IN MOLLUSCS

No animals provide better illustrations of filter feeding than do the bivalve (lamellibranch) molluscs, for all the members of this class, with the exception of the secondarily modified septibranchs, obtain their food in this way. As with the polychaetes, we can see that a substantial element of pre-adaptation has been involved, although the course of events has been quite different in the two groups. To judge from the type of feeding found in the chitons and in the most primitive living gastropods, the earliest molluscs must have been microphagous, using a rasping radula to break up encrusting algae, and then transferring particles of these organisms, together with deposits of detritus, into the mouth. We shall see later that the molluscan alimentary tract is highly specialized to deal with the intake of particulate material. What the bivalves have done is to exploit certain potentialities inherent in this molluscan plan of organization. Making use of the protective value of the shell, and of the muscular power of the foot, they have become typically semi-sessile animals, inhabitants of sandy or muddy substrata. Here, with an alimentary system already adapted for microphagy, they have utilized to the full the particulate food resources of their habitats.

Probably ciliated labial palps, lying on either side of the mouth, were the feeding organs of the earliest bivalves, as they are to-day in the members of the order Protobranchia, in which the palps extend into tentacle-like proboscides which probe the substratum. The ciliated gills (ctenidia), initially respiratory in function, would probably have been incorporated later into the feeding mechanism, but it is uncertain how far they are involved in this in the protobranchs, for in these animals the palps are responsible for some quantitative sorting of the particles as well as for their collection. In most other bivalves, however, the ctenidia have become highly specialized for filtering suspended and deposited particles from a current of water, maintained by ctenidial cilia, which enters through an inhalent siphon and leaves through an exhalent one.
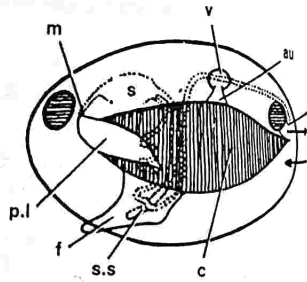
The elongated ctenidia of bivalves (Fig. 10–8) are organized around an axis which bears two demibranchs, each of these being composed of a parallel row of
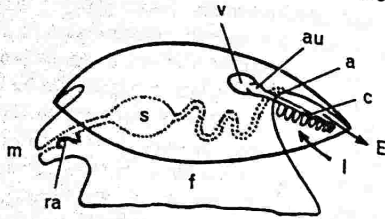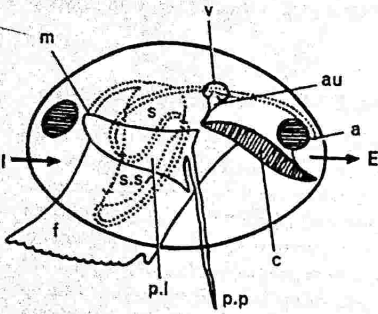
Fig. 10-8. Diagrams illustrating stages in the evolution of the Lamellibranchia, showing significant changes in the orientation of the body, form of the shell, foot, ctenidia, and heart, alimentary canal (stippled), and labial palps. A, structure of hypothetical primitive Mollusca (modified after Pelseneer); B, protobranch stage; C, final eulamellibranch condition without siphons. a, anus; au, auricle; c. ctenidium; f, foot; m, mouth; p.l, palp lamellae; p.p, palp proboscides; ra, radula; s, stomach; s.s, style sac region; v, ventricle. From Yonge, 1939. Phil. Trans. R. Soc. B, 230, 79-147.

filaments. It has been customary to distinguish three grades of arrangement of these filaments (protobranch, filibranch, and eulamellibranch), and to use them as a basis for classification. A different taxonomic treatment is now favoured, but the three terms retain their descriptive value. In the protobranch type the filaments are unfolded, but in the filibranch and eulamellibranch types they are folded so as to form ascending and descending limbs (Fig. 10–9). In the filibranch type (e.g. Mytilus) adjacent filaments are joined by ciliary junctions; in the eulamellibranch types (e.g. Anodonta) they are joined to each other by vascular interfilamental junctions (Fig. 10–10). Each demibranch thus forms a folded lamella, and the ascending and descending plates of this are joined to each other by interlamellar junctions.

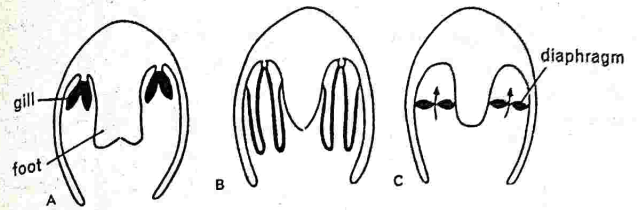In bivalves, as in polychaetes, use is made of cilia that are arranged in frontal

Fig. 10-9. Ventrical section of Bivalvia to show different arrangements of the ctenidia. A, protobranch; B, filibranch and eulamellibranch; C, septibranch, with gills modified into muscular septa. The arrows in C show the direction of water flow through the septum when the latter moves downwards. From Borradaile et al., 1958. op. cit.

and lateral series, but their action is complex, and shows much interspecific variation. In principle, lateral cilia (Fig. 10–10) draw water into the mantle chamber, and from there into the interlamellar and suprabranchial cavities. As the water passes between the filaments, the food particles are filtered out by latero-frontal cirri. These were formerly called cilia, but ultrastructural studies have shown that they are actually ciliary complexes, each consisting of 20–25 pairs of cilia, arranged as a double row, all beating together at right angles to the long axis of the gill filament. The distance between adjacent cirri is about 2.0 to 3.5 μm, but the effective space is smaller than this, since the cilia bend at regular intervals along the cirrus so that they form a meshwork between the cirri and also between adjacent filaments. This remarkable arrangement, which seems to be unique to the bivalves, accounts for the extreme efficiency of their filtration, which permits the retention of a high proportion of incoming particles in the size range 1–3 μm, and virtually a 100% retention of those of 4 μm.

The particles thus trapped by the latero-frontal cirri are thrown onto the frontal cilia, which then sweep them, entangled in mucus, over the surface of the gill lamellae. From here they may pass either into a ventral marginal groove, or into a dorsal groove along the axis of the gill, at the base of the demibranchs. Along one or other of these grooves, depending upon the particular species concerned, the food material is carried to the two pairs of labial palps; these are triangular structures, one pair lying on either side of the mouth.

It would take too long to describe the possible courses of these particles in detail, so complex are the specialized ciliary mechanisms involved, but as far as sorting is concerned this occurs partly on the gills and partly on the palps. It is common to find a differentiation of ciliary tracts on the gills. Some tracts are provided with fine cilia, and are adapted for conveying the fine particles required for food; other tracts have coarse cilia and deal with the rejection of larger particles. Coupled with this simple differentiation, however, are complex and highly diversified patterns of ciliation, associated in their turn with variations in the form of the gills.

For example, the gill lamellae are sometimes folded (plicate), as they are in Pecten and Ostrea, with the ciliary beat on the crests of the folds differing from that in the grooves. The smaller particles required for food are carried chiefly upwards by fine cilia to the dorsal grooves, while coarse particles, such as sand grains, are

Vertical section (T.S.) through
gills of one side

Horizontal section through
two adjacent filaments

Mytilus

Anodonta
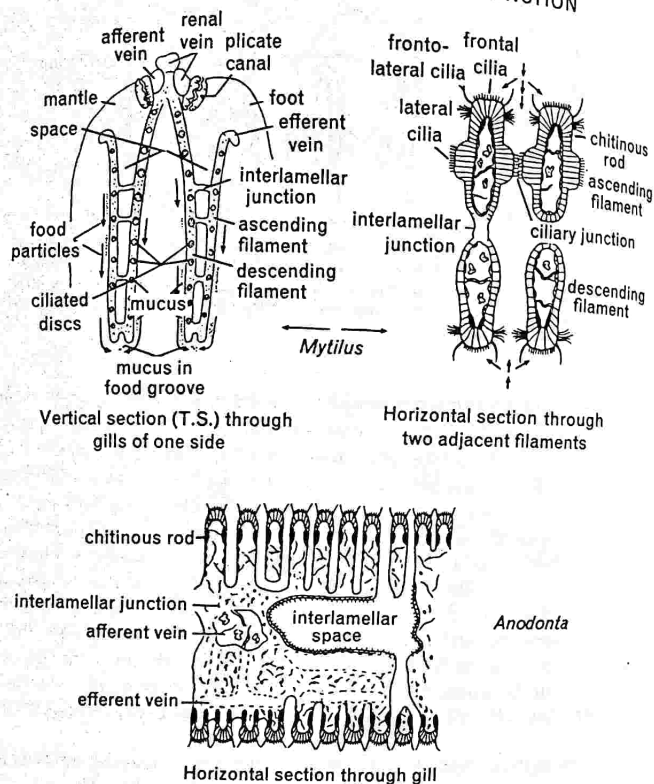
Horizontal section through gill

Fig. 10-10. The ctenidia of the Bivalvia. The arrows indicate the direction of the food current and the path of the food particles it contains. *Mytilus* (filibranch); *Anodonta* (eulamellibranch). From Borradaile *et al.*, 1958. *op. cit.*

carried downwards. The latter tend to drop off from the gill edge (Fig. 10-11), or are shaken off by muscular movements of the demibranchs.

In other forms the ventro-marginal grooves may contribute to the sorting in a way reminiscent of that which we have seen in *Sabella*. For example, they may be divided into a deep channel lined by fine cilia and a superficial one lined by coarse cilia. Fine particles may then be carried into the bottom of the groove, whereas closure of this may cause large ones to be conducted only to its edge, so that they are eventually rejected. As another possibility, long cilia on the edges of the marginal groove may permit the entry of small particles, but prevent the entry of larger ones; this principle operates in *Mya*.

The labial palps (Fig. 10-12) are ciliated structures; their sorting function depends particularly on the structure of their internal faces, which are crossed by a
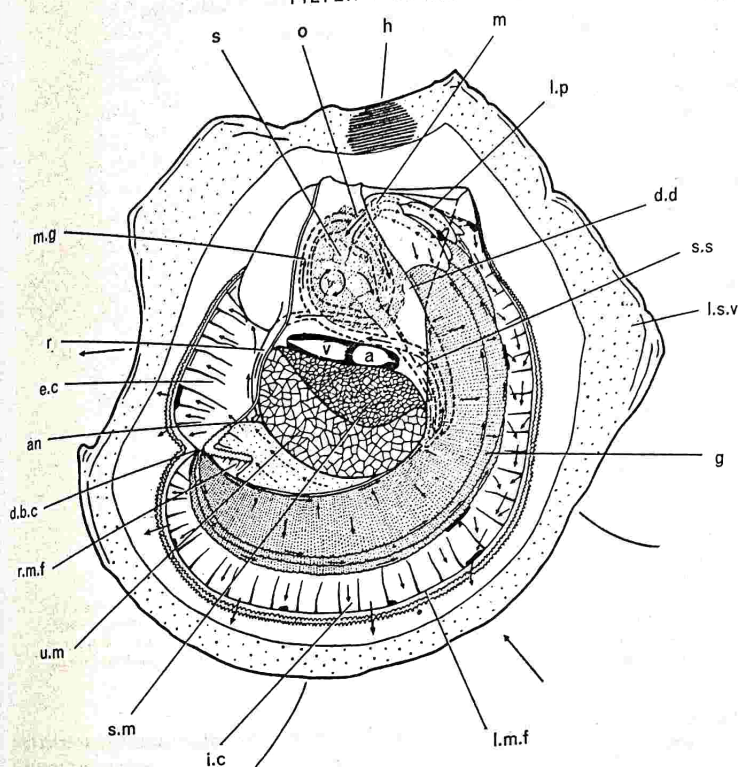
Fig. 10-11. *Ostrea edulis*, right shell valve and mantle removed. *a*, auricle; *an*, anus; *d.b.c*, division between inhalent and exhalent chambers; *d.d*, digestive diverticula; *e.c*, exhalent chamber; *g*, gills; *h*, hinge; *i.c*, inhalent chamber; *l.m.f*, left mantle fold; *l.p*, labial palps; *l.s.v*, left shell valve; *m*, mouth. *m.g*, mid-gut; *o*, oesophagus; *r*, rectum; *r.m.f*, right mantle fold; *s*, stomach; *s.m*, adductor muscle, portion with striated fibres; *s.s*, style sac; *u.m*, adductor muscle, portion with smooth fibres; *v*, ventricle. Large arrows external to shell indicate direction of ingoing and outgoing currents. Broken arrows denote currents on under surfaces. From Yonge, 1926. *J. mar. biol. Ass. U.K.*, 14, 295-386.

series of diagonal folds. These folds overlap each other in the direction of the mouth, all but the uppermost part of one fold being covered by the next adjacent one. The sorting mechanism is here said to depend solely on the weight and not on the size of the particles. Of the particles that are carried over the top of the surface, the heavier ones settle down into the grooves between the slope of one fold and the crest of the next; in this position they come under the influence of a powerful ciliary current that sweeps them to the upper margin of the palp. Lighter ones avoid this current because they do not sink in the same way; as a result, they are swept from one slope to the
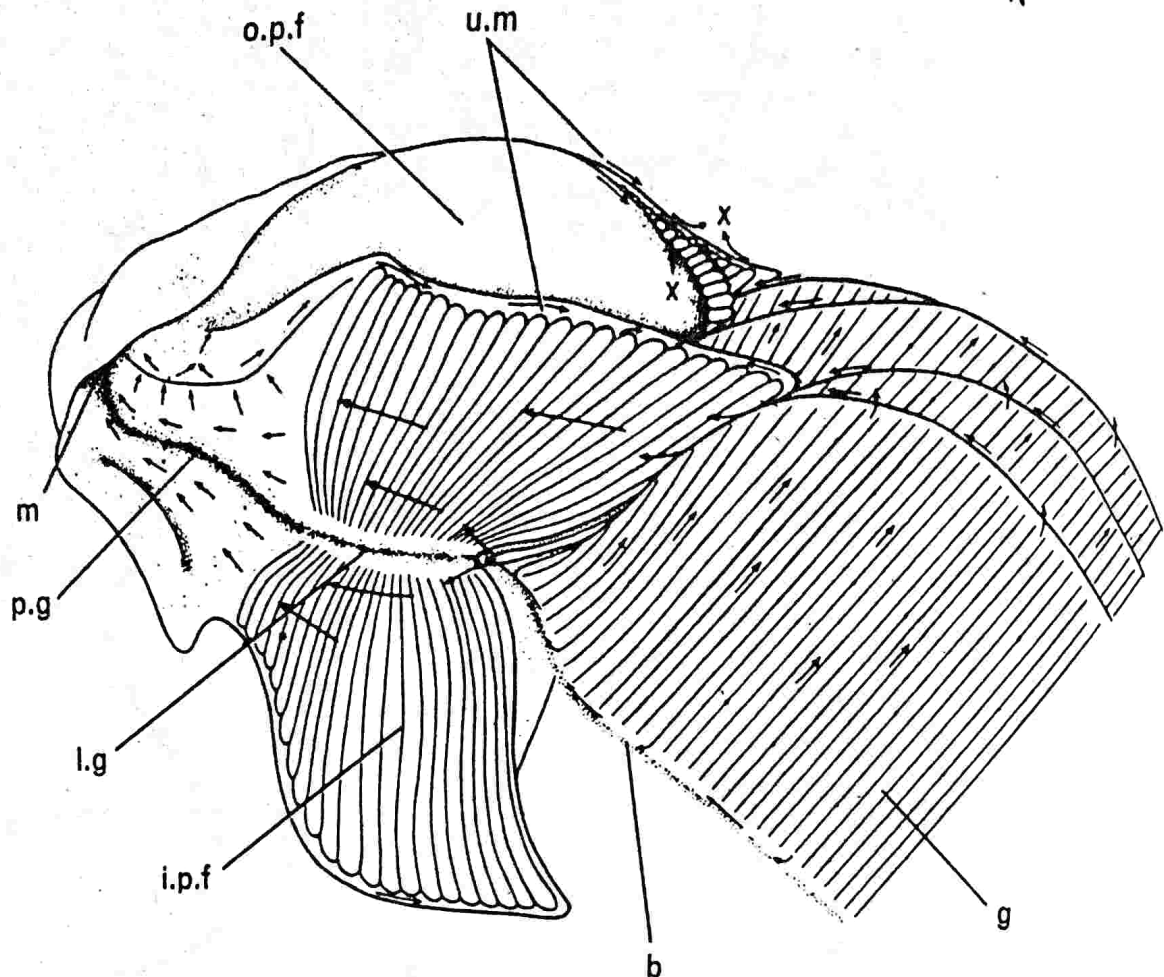
Fig. 10-12. Junction of palps and gills of *Ostrea*, right palps opened out so as to expose inner, ridged surfaces. × 8. *b*, base of demibranch; *g*, gill; *i.p.f*, inner palp face; *l.g*, lateral oral groove; *m*, mouth; *o.p.f*, outer palp face; *p.g*, proximal oral groove; *u.m*, upper margin of palps; *x*, point where material is rejected from palps. From Yonge, 1926. *op. cit.*

next and pass towards the mouth. A similar sorting takes place among particles that pass down between the folds, heavier ones being carried by another current towards the upper margin and lighter ones towards the mouth. Thus these structures have their cilia arranged so as to produce a diversity of ingeniously integrated currents.

We shall follow later the fate of those particles that finally enter the mouth and pass into the alimentary canal. The rejected particles pass onto the ciliated epithelia of the mantle or visceral mass, where the strong ciliary currents produced by these epithelia give rise to vortices. These entangle the particles in mucus to form masses that eventually accumulate below the internal opening of the inhalent siphon. Periodically the animal closes its exhalent siphon and, by a sudden movement of contraction, forces the rejected material (pseudofaeces) out of the inhalent siphon in a current of water.

We have suggested that the rasping method of feeding of primitive molluscs was a pre-adaptation to the evolution of the specialized filter feeding of bivalves. This rasping method is essentially a form of microphagy. Thus the requirements for the handling of small particles must have influenced the organization of the alimentary canal of molluscs from the beginning of their history, and must further have aided the establishment of bivalve feeding methods. Moreover, the ingestion of small particles probably determined the retention of the intracellular method of digestion, which is so widespread in molluscs. Indeed, the group as a whole provides

106: Lateral budding in *Syllis ramosa*.

Trypanosyllis crosslandi develops a of stolons at the posterior end.
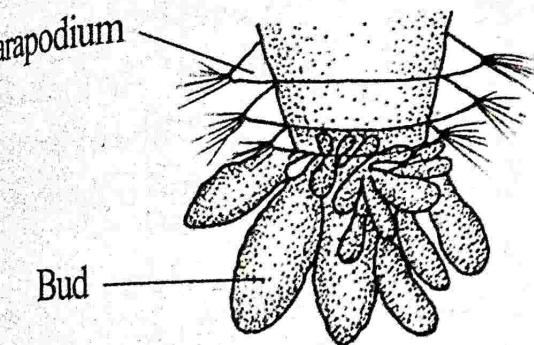

9.107: Budding in *Trypanosyllis*.

Sources of Cellular Material for Asexual Reproduction

Asexual reproduction by fission is closely to regeneration. In both cases, a part body is isolated and reconstructed into a

Feeding is one of the stages in nutrition. It involves the collection and capture of food materials from the medium.

Polychaetes live in different ways. There are *crawling* polychaetes, *pelagic* polychaetes, *burrowing* polychaetes, *tubicolous* polychaetes and *parasitic* polychaetes. Accordingly, they develop different mechanisms for feeding. Based on the mode of feeding the polychaetes are classified into the following types:

1. Raptorial feeders
2. Browsers
3. Sand and mud feeders and
4. Filter feeders.

1. Raptorial Feeders

Raptorial feeders are *carnivores* which capture their prey by chasing. Raptorial animals include some crawling polychaetes (*Nereis, Polynoe, Eunice, Syllis, Autolytus,* etc.), all pelagic polychaetes and a few
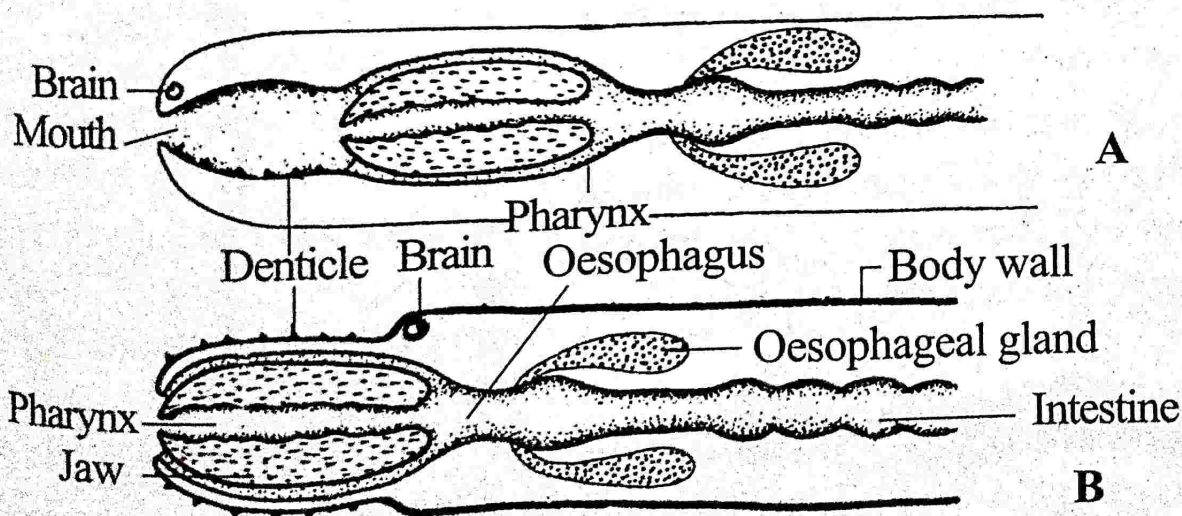

Fig.9.108: Pharyngeal apparatus of a raptorial feeder, Nereis; A. Pharynx retracted; Pharynx protruded.

tubicolous polychaetes. They feed on small crustaceans, molluscs, sponges, etc.

The raptorial feeders have adaptations for capturing their prey. The parapodia are well adapted for active locomotion which is essential for running after the prey. The buccal cavity and pharynx are well armed with teeth and jaws for seizing the prey.

In *Nereis* the inner lining of the buccal cavity is produced into many teeth-like structures called *denticles*. Similarly, the pharynx has two strong, movable jaws. During feeding, the buccal cavity can be everted and the pharynx can be protruded out. The protruded pharynx is called *proboscis*.

When the prey comes closer, the buccopharyngeal region protrudes out through the mouth. The jaws are thrust forward and they open wide to enclose the prey. Then the jaws close together grasping the prey. Then the pharynx is withdrawn inside and the prey is swallowed.

The protrusion of the proboscis is brought out by the working of a set of muscles called *protractor muscles*. Similarly, the retraction is brought out by another set of muscles called *retractor muscles*.

The number of teeth varies in the different polychaetes. *Autolytus* has a circlet of teeth. *Eunice* has a pair of lower jaws and about five pairs of upper jaws.

The length of proboscis also varies in the different polychaetes. *Glycera* has the longest proboscis and it can be protruded to about one fifth of the length of the body.
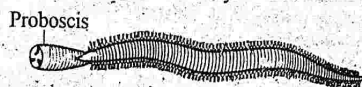
Proboscis

Fig.9.109: Glycera, with long proboscis containing teeth.

2. Browsers

Browsers are *herbivorous* polychaetes feeding on algae. They use their jaws for tearing the algae. Eg. *Some species of Nereis.*

3. Sand and Mud Feeders

The sand and mud of sea bottom contain bacteria, diatoms and other micro organisms. Certain polychaetes depend on these organisms for their food. Such animals are called *mud* and *sand feeders.*

Some sand feeders swallow the mud and sand as such. In the alimentary canal, the micro-organisms are digested and absorbed. The undigested food, mud and sand are eliminated in the form of castings as in earthworm. As the mud and sand contains only a small amount of micro-organisms, the sand feeders should swallow a large quantity of sand. The muscular pharynx helps swallowing. Most of the sand and mud feeders are burrowing polychaetes. Eg. *Arenicola.*

A few tubicolous polychaetes like *Terebella, Amphitrite,* etc. develop a special mechanism to collect the micro-organisms from the sand.
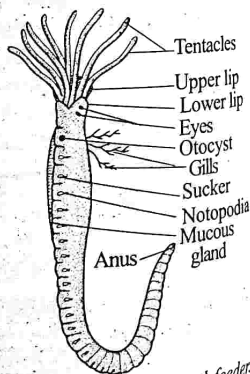

Fig.9.110: Terebella, a sand feeder.
Terebella lives in a tube. The head bears numerous, long, hollow muscular tentacles. The

tentacle can be turned in a variety of ways. One side of the tentacle from the base to the tip is ciliated. This side of the tentacle can be folded to form a ciliated groove along which the food is propelled into the mouth.

The tentacles are beautifully adapted for exploring and transporting the food. Their shape as in cross section, varies at different points at any particular moment according to the use to which they are being put. At one point a tentacle will be flattened to form a zone of attachment; distal to this flattened point, the tentacle explores the mud; proximal to the point of attachment, the surface of the tentacle will be folded to form a ciliated groove along which the food is propelled.

4. Filter Feeders

In filter feeding, the food materials are filtered from the water current which is created by ciliary or other mechanisms. Filter feeding is common in tubicolous polychaetes.

In *Sabella* and *Serpula*, the head bears a crown of filaments (tentacles or gills). Each filament bears two rows of lateral branches called *pinnule* which bear cilia.

These worms live in tubes with the filaments protruded out. In a fully extended form, the filaments can be arranged in the form of a funnel. The mouth is located at the base of the funnel. The pinnules secrete mucous into the funnel. The pinnules and filaments are provided with grooves on the upper or oral surface. The grooves lead into the mouth.

The beating of the cilia of the pinnules draw a water current into the funnel. Food particles also enter the funnel along with the water current. They are trapped in the mucous. The mucous containing the food particles moves along the ciliated groove to the mouth.

Chaetopterus is beautifully modified for filter feeding. It lives in a 'U'-shaped tube. The

body is divided into three regions, namely *anterior, middle* and *posterior.* The middle region is formed of five segments and it is modified for filter feeding. In the first segment of the middle region, a pair of wing-like structures is present. They are called *great wings*. The
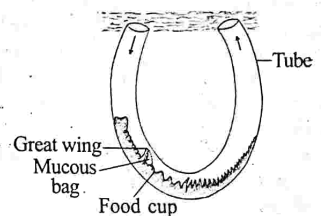

Fig.9.111: Chaetopterus in its tube.

notopodia of the second segment are modified into a cup-like structure called *food cup.* It is ciliated and present on the dorsal side. From the food cup arises a groove called *food groove* which runs forwards and opens into the mouth. The notopodia of the next three segments are fused together to form three *fans.*
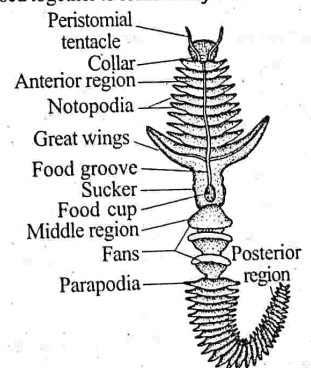

Fig.9.112: Chaetopterus, a filter feeder.

The fans move to and fro and create a water current. The water current enters the tube through the anterior limb of the tube. The

great wings arch over the back of the animal and their tips touch each other to form a ring. Into this ring mucous is secreted by the great wings. The mucous is dragged back by the water current into a membranous conical bag. Food materials are trapped into this bag as the water current passes through it. As the bag is loaded, it is carried into the food cup where it is rolled into a ball. The ball moves along the food groove to the mouth. A new mucous bag is secreted every twenty minutes and about 290 ml. of water passes through each bag.

In *Arenicola marina*, the food is collected by two methods, namely *filter feeding* and *sand feeding*. It lives in a '*J*'-shaped tube. The head lies towards the small limb of 'J'. The worm swallows sand continuously by the proboscis. As more and more sand is swallowed, a funnel-like depression is formed on the surface. Water enters the tube through this funnel, percolating down through the sand which filters food materials (micro-organisms). This organically rich sand is swallowed by the worm. Now and then, the worm moves to the top of the vertical limb and defaecates in the form of castings.
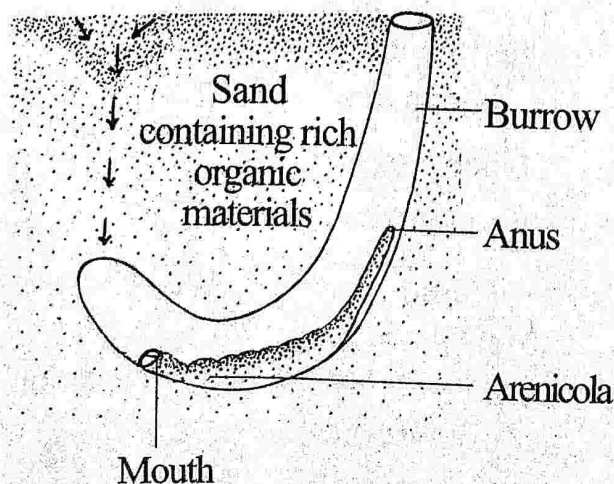

Fig.9.113: *Arenicola exhibiting filter feeding.*