

The Ciliary Mechanisms on the Gill and the Mode of Feeding in Amphioxus, Ascidians, and *Solenomya togata*.

By

J. H. Orton, A.R.C.Sc., B.Sc.,
Naturalist in the Plymouth Laboratory.

With Figures 1-11 in the Text.

TABLE OF CONTENTS.

	PAGE
Introduction	19
The Mode of Feeding in Amphioxus	20
The Ciliary mechanisms on the gill of Amphioxus	22
The Ciliation of the Endostyle	24
The function of the Wheel Organ and the peri-pharyngeal bands in Amphioxus	25
Recapitulation of the account of the food and respiration currents in Amphioxus	27
The function of the Pharynx in Amphioxus	28
The Mode of Feeding in Ascidians	30
Food-collection in various Ascidians	31
Ciliary mechanisms on the gill of Ascidians	33
Comparison of the Mode of Feeding in Amphioxus and Ascidians	35
The Function of the gland and its ciliated tract in the Branchial Openings of Amphioxus and Ascidians	36
The Maintenance of the Pharyngeal spaces in Ascidians and Amphioxus	37
The Ciliation of the gill of Balanoglossus	37
Observations on the Ammocoete of <i>Petromyzon fluviatilis</i>	38
The Mode of Feeding in <i>Solenomya togata</i>	38
The ciliation of the gill of <i>Solenomya</i>	40
Resemblance of the ciliation of the gill in <i>Solenomya</i> and <i>Nucula</i>	43
Summary of the account of the ciliary currents in <i>Solenomya</i>	44
The function of the gill in Lamellibranchs	44
Appendix	45
Summary	47

INTRODUCTION.

IT is well known that Amphioxus obtains its food by straining off the nutritive particles contained in the current of water which is taken in continuously at the mouth and expelled at the atriopore. It is also well known that the cilia on the gill cause this continuous current, and that in some way a separation of the food-particles is effected.

The existing explanations, however, of the manner in which these two processes are effected are either very vague or only partially true and

misleading. It is to clear up our ideas on this matter that the present account is written.

It is generally stated that the current through the pharynx of *Amphioxus* is effected by the cilia on the gill-bars, and that the food-particles are collected in the endostyle which conducts them forwards to the peri-pharyngeal bands (1, 2, and 3). The latter are then described as conducting the collected food to the dorsal groove, which in turn conducts it backwards to the intestine. These statements are vague and wrong and misleading, inasmuch as there are on the gill-bars at least two sets of cilia which function in quite different ways, and the endostyle does not conduct food-particles forwards, as will be seen from the following description:—

MODE OF FEEDING IN AMPHIOXUS.

While the animal is at rest a current of water is being taken in continuously at the mouth and expelled at the atriopore. This current serves for the nourishment of the animal, and doubtless is also a main factor in its respiration. If an *Amphioxus** be placed in water containing fine particles of carmine in suspension or in water containing diatoms and dissolved methylene blue, a mass of particles embedded in mucus very soon collects in the dorsal groove of the pharynx and is passed on into the intestine. The living animal after being fed in this manner has the appearance indicated in Fig. 1.

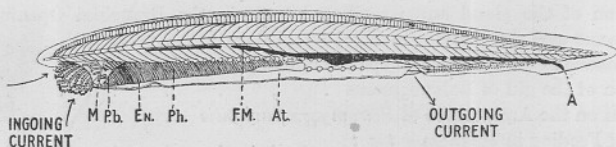


FIG. 1.†—View of a living *Amphioxus* shortly after being fed with carmine particles, to show the collection of food in the dorsal groove and the intestine, and the course of the main current through the body (\times about $\frac{5}{8}$).

- F.M. Food masses in the dorsal groove of the pharynx and in the intestine.
 M. Mouth, between which and the end of the arrow indicating the ingoing current is situated the buccal cavity. The outgoing current leaves the animal at the atriopore.
 At. The Atrium, the space between the pharynx and the body wall through which the current passes after leaving the pharynx, Ph.
 Ph. The pharynx or branchial sac.
 En. The endostyle.
 P.b. The peri-pharyngeal band of the left side.
 A. Anus.

* The observations recorded in this paper were made on the species *Branchiostoma lanceolatum*. The general similarity in structure of the species of this genus, however, renders it highly probable that the processes here described will apply to all the group.

† I am indebted to Mrs. Orton for the drawing for this figure, and also for assistance with Figures 6, 8, and 9.

If the animal is examined closely by means of a microscope when feeding it is easy to make out a strong current entering at the anterior end of the animal between the buccal tentacles. Thence the current can be followed successively through the buccal cavity, the mouth, the pharynx,

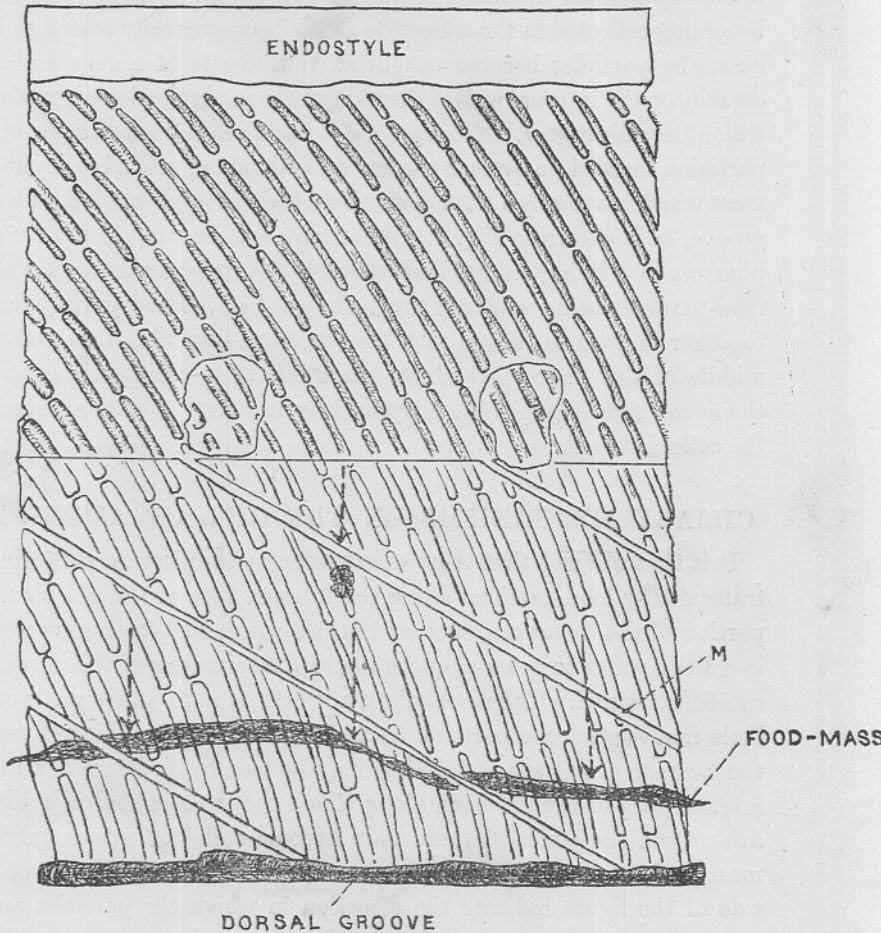


FIG. 2.—View of a portion of the body wall and pharynx of a living entire *Amphioxus* at about the level of the posterior two-thirds of the pharynx.* (Drawn as seen through a microscope, \times about 37.)

- D.Gr. Dorsal groove in which becomes collected a mass of food particles embedded in mucus.
 F.M. Cylindrical mass of mucus with embedded food-particles being transported away from the endostyle towards the dorsal groove, as is indicated by the overlying vertical arrows.
 M. The boundary of adjacent myotomes.

* It was found the most convenient for this examination to view the animal laid on its right side. Thus in this view the main current passes from the reader's right to the left.

and the atrium ; it is finally seen to pass out of the animal at the atriopore. If now the pharynx of the living animal be examined carefully while feeding is going on the process of collection of the food-particles may be watched. As particles pass along the pharynx they may be seen to be drawn up against the internal wall of this organ. Instead, however, of becoming collected in the endostyle as has been generally stated to be the case, the particles become caught in thin sheets of mucus and travel *dorsally* on the internal wall of the pharynx towards the dorsal groove, into which they disappear. If the animal is taking in a large number of food-particles, these often become worked up with mucus into a long cylindrical mass which travels as a whole away from the endostyle towards the dorsal groove, as is shown in Fig. 2. This figure is a drawing of a view of the pharynx of a living animal seen through the transparent body wall, the food-particles being visible through the gill-bars. Food-particles massed together in various shapes may also be seen—like that depicted in the middle of this figure just above the food-mass—all travelling towards the dorsal groove, which in this way becomes very quickly charged with the collected food.

CILIARY MECHANISMS ON THE GILL OF AMPHIOXUS.

It is thus obvious that there exists some mechanism for collecting and transporting food-particles along the internal face of the gill-bars. If a portion of the living gill, such as that shown in Fig. 3, be now observed in a little water in a watch-glass under the microscope, this mechanism can be examined. The mechanism, however, is more easily made out if a little finely powdered carmine be added to the water. Very soon after the carmine grains are added they may be seen to be drawn towards the internal face of the gill-bars, along which they are hurried in a direction away from the endostyle, and may become collected into a cylindrical mass such as is shown on the right side in Fig. 3. The arrows on this side of the figure indicate the direction in which the particles and the collected mass travel. Individual particles may be seen to travel at an angle across the bars, i.e. in a ventro-dorsal direction, as is indicated also by the arrows. The mechanism which causes the movement of these particles across the gill-bars cannot be made out easily when examining the gill from this point of view, but when a single gill-bar is examined in side view, highly magnified (see Fig. 4), it is seen that on the internal face of the bar there is a row of relatively short cilia (Fig. 4, *fc.*) which lash rapidly along the length of the bar and thus effect the translation of such particles as are drawn against it. That the particles are drawn against the

bars is very easily seen even in a view like that of Fig. 3, and if the lateral, i.e. the anterior and posterior, faces of the gill-bars be focussed carefully, rows of long, rapidly moving cilia are to be seen lashing across the length of the bars. In Fig. 4 this direction is indicated by the large arrows. In a view of a portion of the pharynx, as shown in Fig. 3, these lateral cilia—as they may be called—lash in the direction shown by the arrows

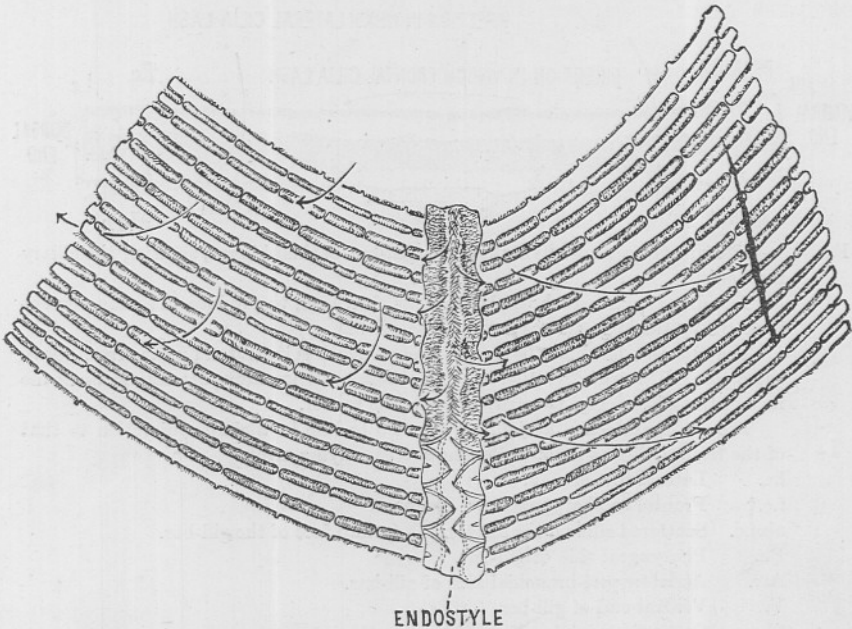


FIG. 3.—View of a portion of the pharynx of *Amphioxus* to show the cilia producing the main current (on the left) and the collection and transportation of food-particles (on the right). The portion consists of a piece of the endostyle with gill-bars attached. (Drawn from the living object, \times ca. 32.)

The arrows on the reader's left indicate the direction in which the main current is drawn by the lateral cilia on the gill-bars. These cilia are shown bordering the gill-slits. The arrows on the reader's right show the direction in which the frontal or pharyngeal cilia on the gill-bars are transporting a mass of food-particles away from the endostyle towards the dorsal groove. The upper arrow on the right-hand side of the figure points to the food-mass. The small arrows in the middle of the figure on the endostyle show the direction in which the outer, i.e. lateral cilia, on the endostyle transport particles out of the endostylar groove on to the gill-bars. The supporting rods of only a few of the gill-bars are shown.

on the reader's left-hand side, and thus draw water with suspended particles against the side of the gill. Water is actually lashed between the gill-bars, as is indicated by the lower arrow on the extreme left of this figure, while the suspended particles are caught in mucus on the face of the gill-bars, and, as we have already seen, are carried away from the endostyle towards the dorsal groove (see Fig. 3 again on the right). In the

lateral view of a gill-bar or a gill-filament, shown in Fig. 4, scattered cilia can be seen on the atrial epithelium. These cilia appear to lash in the direction shown by the arrow on the atrial side of the bar, and by comparison with a gill-filament of a Lamellibranch, may be called ab-frontal cilia. They probably help in a small way in producing the main current and also in cleaning the atrial surface of the gill-bar.

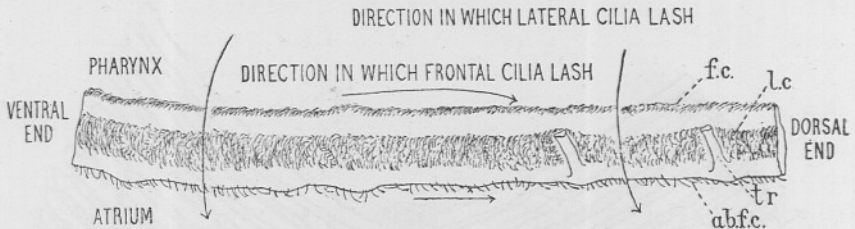


FIG. 4.*—Side view of a single living primary gill-bar of *Amphioxus*, showing the ciliary mechanisms.

The direction in which the lateral cilia, l.c., lash, to produce the main current is shown by the large arrows crossing the gill-bar.

The direction in which the frontal cilia, f.c., lash is indicated by the arrow above these cilia. The true direction in which these particles transport cilia is along the face of the gill-bar and upwards towards the reader.

The ab-frontal cilia, ab.f.c., appear also to lash in a similar direction to that of the frontal cilia as is shown by the accompanying arrow.

- l.c. Lateral row of cilia.
 f.c.† Frontal or pharyngeal row of cilia.
 ab.f.c. Scattered cilia on the atrial or ab-frontal face of the gill-bar.
 Ph. Pharyngeal side of gill-bar.
 Atr. Atrial or peri-branchial side of gill-bar.
 V. Ventral end of gill-bar.
 tr. Connexions joining the gill-bar to others.

CILIATION OF THE ENDOSTYLE.

There still remains for examination the ciliation on the endostyle. Under a low power in such a view as Fig. 3, particles suspended in the water may be observed to be lashed rapidly out of the endostyle on to the face of the gill-bars in the direction denoted by the small arrows in the middle of the figure (i.e. on the endostyle). Examination of the endostyle under a high power brings out the presence of three main sets of cilia, two outer or lateral sets and one median. The cilia on these lateral rows are short and lash rapidly across the length of the endostyle. These are the cilia which throw particles out of the endostyle on to the gill-bars. The median cilia on the endostyle are long and appear only to shake with

* I am indebted to Mr. L. R. Crawshaw for the lettering in this figure, and also for that in Figures 2, 3, and 5.

† The short cilia figured by Benham (15, Plate 6) have not yet been seen in the living filament, although they have been carefully looked for. Further observations, however, will be made on this point.

a wave-like motion which begins at the attached end. Particles may indeed be observed to rest on these cilia for some time, but such particles are eventually worked towards the lateral sets of cilia, which soon transport them to the gill-bars. In the passage of the particles from the median to the lateral cilia on the endostyle one can often make out that the particles have become embedded in mucus. It is therefore doubtless the function of the median cilia on the endostyle to pass on mucus secreted by the endostyle to the lateral endostyle cilia and thence to the gill-bars. This mucus, along with that doubtless secreted also by the pharyngeal epithelium of the gill-bars, serves to entrap food-particles and render the transportation of these easier.

Between the median and lateral sets of cilia on the endostyle a narrow ciliated groove can be made out on either side (see Fig. 3). Particles are frequently caught in these grooves, but they can be seen to be passed quickly on to the lateral endostyle cilia and generally on to those portions of the endostyle overlying a primary bar, and thence to the gill-bars.

Before passing on to a recapitulation of the ciliary mechanisms and their function in *Amphioxus*, it will be convenient to examine the ciliary arrangements so well known in the anterior end of the animal, namely those in the buccal cavity, the wheel organ, and Hatchek's pit, and the peri-pharyngeal bands.

THE FUNCTION OF THE WHEEL ORGAN, AND THE PERI-PHARYNGEAL BANDS IN AMPHIOXUS.*

The action of these organs can be made out by examining the anterior end of the living animal through a microscope while it is feeding. During the act of feeding the buccal tentacles are kept folded over one another. In this way these tentacles act as a sieve, allowing only the finer suspended particles to pass on into the buccal cavity. The efficiency of the buccal tentacles in straining, when held in this manner, is increased by the presence along the sides of the tentacles of conical papillæ which subdivide the spaces between the tentacles, as is shown in Fig. 5. In this manner the larger particles carried along in the ingoing current become arrested on the buccal tentacles, only the finer particles being allowed to pass onwards. A selection of the finer food-particles is thus effected.

From the buccal tentacles the main current with the suspended particles passes through the buccal cavity, the mouth and onwards into the pharynx.

In the buccal cavity, however, some particles fall out of the main stream as a result of the occurrence of slack waters in the periphery of

* See Appendix on page 45 for an account of Andrew's work on feeding in *Amphioxus*.

this region, and become drawn against the wall of this cavity by the sets of cilia which are known collectively as the wheel organ. These sets of cilia are shown on the wall of the buccal cavity in Fig. 5. They are really ciliated grooves running antero-posteriorly in the posterior part of the buccal cavity. Around the mouth these paths are connected together by a circular ciliated path, which is stated by V. Wijhe (4) to be

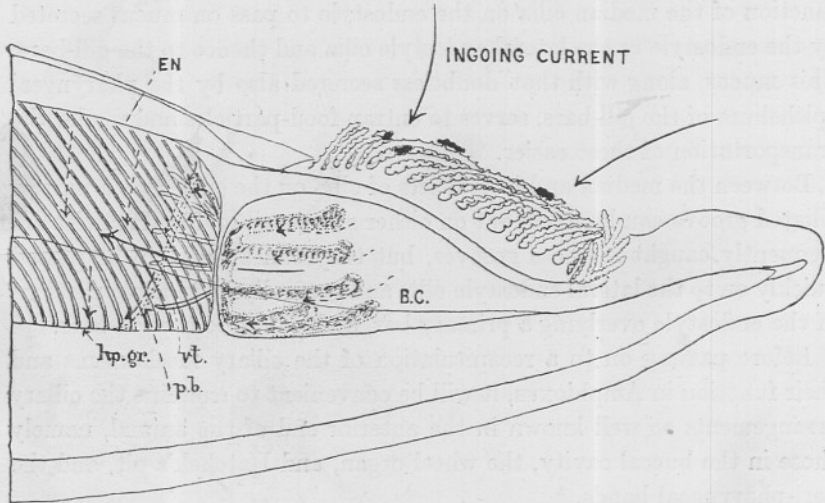


FIG. 5.—View of the anterior end of a living *Amphioxus* (drawn as seen through a microscope, \times ca. 27), after keeping the animal in a dilute solution of methylene blue in water. This view shows the action of the buccal tentacles in sieving off the coarser food-particles at the entrance to the buccal cavity, the action of the ciliated grooves (the Wheel Organ) in the wall of the buccal cavity, and the collection of food-particles from this region of the body into the peri-pharyngeal bands.

b.c. Buccal cavity.

hp. gr. Dorsal or hyperpharyngeal groove.

p.b. Peri-pharyngeal band.

v.t. Velar tentacles.

EN. Region of the endostyle.

The arrows in the buccal cavity lie alongside the ciliated grooves, along which food-particles are lashed towards the mouth in the direction indicated by the arrows. The large arrow passing through the mouth from the buccal cavity into the pharynx indicates the course of the main stream.

sometimes complete and sometimes incomplete. These ciliated paths have been said to be "an organ for creating currents in the mouth back to the pharynx." There can be little doubt about their function, however, if they are watched while the animal is feeding. As particles drop out of the main current in the buccal cavity they very quickly become caught in the anterior end of one or other of these ciliated paths and rapidly whirled along the groove towards the mouth, becoming rolled into a

mass with mucus on the way. A large number of these minor food-masses, however, are swept into the main stream as they approach the oral aperture and pass onwards into the pharynx. Some particles, however, appear to pass between and sometimes along the velar tentacles on to the internal surface of the pharynx, whence they are passed on to the peri-pharyngeal grooves. It is well known that there are no gill openings anterior to the peri-pharyngeal grooves. Thus the part of the pharynx anterior to the peri-pharyngeal grooves serves as a collecting ground for the food-particles which have been caught in the buccal cavity. Most of the particles, however, appear to pass around the ventral part of the mouth to the peri-pharyngeal groove; while others appear to pass dorsally straight into the dorsal groove. There is also, however, a steady dribble of particles into the peri-pharyngeal groove from a position immediately ventral to it. These particles are probably collected from the extreme anterior portion of the endostyle, by which they are ejected in the same way as we have seen at other parts. Doubtless these minor streams have been the cause of the erroneous views which are current on the mode of feeding in *Amphioxus*. If a little methylene blue is added to the water from which an *Amphioxus* is feeding the edges of the ciliated paths in the buccal cavity stain blue, which doubtless indicates the presence of mucus glands at these points (see Fig. 5). The anterior end of each ciliated groove can now be easily seen to form a pit-like depression around which the cilia are lashing vigorously. As particles are caught by the cilia they are seen to be passed along in the middle of the groove towards the mouth, as has been described above.*

RECAPITULATION OF THE ACCOUNT OF THE FOOD AND RESPIRATORY CURRENTS IN AMPHIOXUS.

The main food and respiratory current in *Amphioxus* is produced by the lashing of the lateral rows of cilia on the gill-bars or gill-filaments (see Fig. 4, l.c., Fig. 3, and Fig. 6). These lateral cilia lash across the length of the filament from the cavity of the pharynx to that of the atrium. In the adult *Amphioxus* there are about 180 gill-filaments on each side of the body (Willey, 1. p. 17). Each of these carries two long rows of lateral cilia, hence in all there are about 720 rows of long cilia acting like oars lashing water through the body of the animal. These are indeed powerful enough to produce the strong current that is to be observed.

* If a stronger solution of methylene blue is used the whole of the wheel organ as well as the pharynx stains a deep blue, and a surprising amount of detail can be made out over the whole of the body.

The main cilia which collect and transport the food-particles are those on the pharyngeal surface of the gill-filaments, namely, the frontal cilia (see Figs. 4 and 6, f.c., and Fig. 3). These cilia lash in a direction which is chiefly along the length of the bars, but actually at an angle to the bars in a ventro-dorsal direction (see the arrows on the right side of Fig. 3). The gill-bars, it is to be remembered, run in the living animal in an antero-dorsal to postero-ventral course, as is shown in Figs. 1, 2, and 3. Food-collection is effected in the following manner. Mucus is secreted by the endostyle and passed on to the gill-bars in a thin sheet by the cilia on the lateral portions of the endostyle. Probably mucus is secreted also by the pharyngeal epithelium of the gill-bars. Food-particles are drawn against the gill-filaments by the lateral cilia on those filaments, as we have already seen; the particles become entangled in the mucus in which they are hurried along the face of the gill-bars into the dorsal groove by the frontal or pharyngeal cilia. The actions of these different mechanisms are depicted in the accompanying diagram, Fig. 6.

It is thus evident that feeding in *Amphioxus* occurs automatically as in the Lamellibranchs. *Amphioxus*, however, has an advantage over most Lamellibranchs in being able to swim away from a region where the water is laden with innutritious or undesirable particles. And, indeed, the occurrence of *Amphioxus* mainly on shelly or gravelly grounds may be due largely to the desire of the animal to seek out grounds where the water is relatively free from undesirable, i.e. innutritious particles.

A food-collection of minor importance is also effected, as we have seen, in the buccal cavity. Food-particles are collected into the ciliated grooves on the wall of this cavity and transported in mucus through the mouth to the peri-pharyngeal bands, often, however, these particles are drawn into the pharynx in the main stream at the oral aperture.

These ciliated grooves in the buccal cavity doubtless lend some small aid to the lateral cilia of the gill-filaments in producing the main current, as probably also do the ab-frontal cilia of the filaments. Short cilia have also been observed on the atrial epithelium overlying the gonads. These cilia lash ventrally, and thus help somewhat in producing the main current.

THE FUNCTION OF THE PHARYNX IN AMPHIOXUS.

It is generally stated that the gill of *Amphioxus* functions mainly as a respiratory and only secondarily as a feeding organ. In the light of the present researches, however, it would appear that the pharynx functions

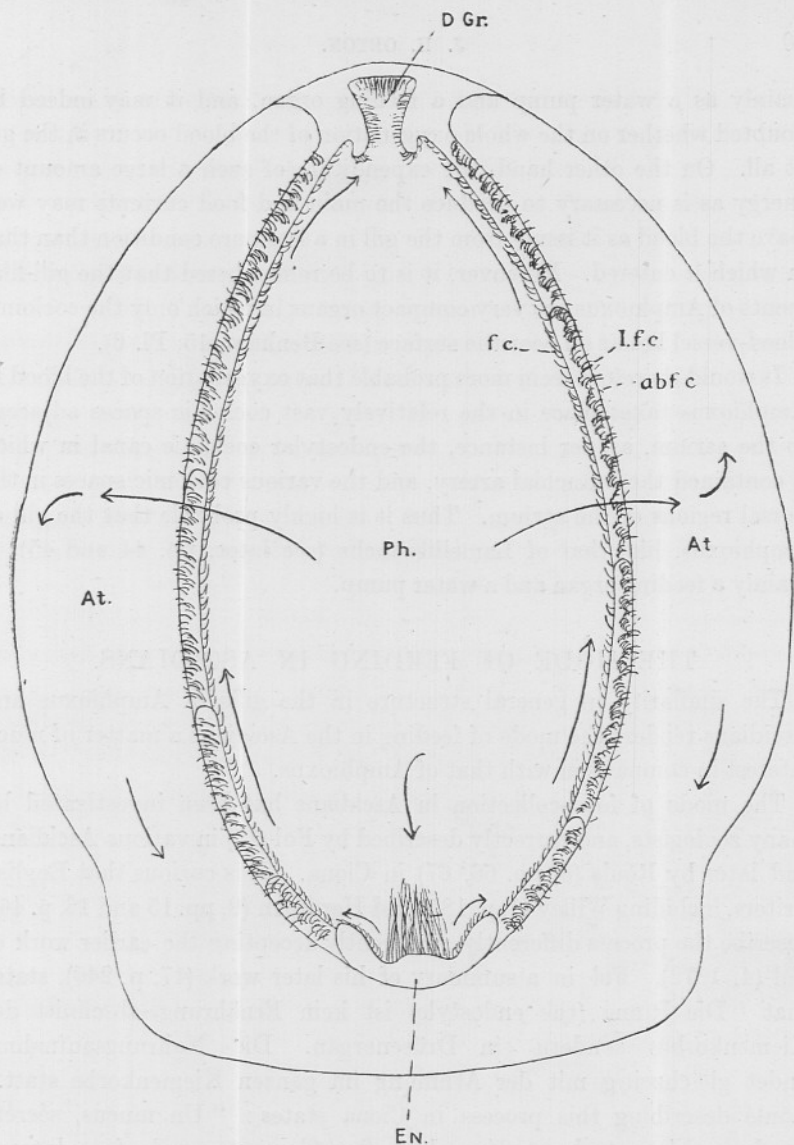


FIG. 6.—Diagram of a transverse section of the pharynx and atrium of *Amphioxus* to show the ciliary mechanisms on the gill, which produce the main current and collect and transport food-particles. (This diagram serves equally well also for *Ascidians*.)

Ph. Pharynx, in the walls of which are shown several gill-bars.

At. Atrium.

En. Endostyle, the lateral cilia of which pass on mucus and food-particles from the median cilia to the gill-bars.

D.Gr. Dorsal groove of pharynx.

l.f.c. Lateral cilia on the gill-bars.

These produce the main current which passes across the gill from the pharynx to the atrium in the direction indicated by the large arrows which cross the gill-bars about the middle of the figure. (These cilia should have been denoted in the figure by the letters l.c.)

f.c. Frontal or pharyngeal cilia. These cilia are the chief collectors and transporters of food-particles, which become caught in the mucus passed on to the gill from the endostyle. The captured food-particles are transported towards and into the dorsal groove, as indicated by the arrows along the inside of the gill-bars.

mainly as a water pump and a feeding organ, and it may indeed be doubted whether on the whole oxygenation of the blood occurs in the gill at all. On the other hand, the expenditure of such a large amount of energy as is necessary to produce the main and food currents may well leave the blood as it issues from the gill in a less pure condition than that in which it entered. Moreover, it is to be remembered that the gill-filaments of *Amphioxus* are very compact organs in which only the coelomic blood-vessel lies at all near the surface (see Benham, 15, Pl. 6).

It would therefore seem more probable that oxygenation of the blood in *Amphioxus* takes place in the relatively vast coelomic spaces adjacent to the atrium, as, for instance, the endostylar coelomic canal in which is contained the branchial artery, and the various coelomic spaces in the dorsal regions of the atrium. Thus it is highly probable that the gill of *Amphioxus*, like that of Lamellibranchs (see later, pp. 44 and 45), is mainly a feeding organ and a water pump.

THE MODE OF FEEDING IN ASCIDIANS.

The similarity in general structure in the gills of *Amphioxus* and Ascidians renders the mode of feeding in the Ascidians a matter of much interest in comparison with that of *Amphioxus*.

The mode of food-collection in Ascidians has been investigated by many zoologists, and correctly described by Fol (17) in various Ascidians, and later by Roule (8, pp. 66, 67) in *Ciona*. It is curious that English writers, including Willey (1, p. 185) and Herdman (9, pp. 15 and 16, p. 46), describe the process differently, apparently accepting the earlier work of Fol (4, 1872). Fol, in a summary of his later work (17, p. 240), states that "Die Rinne (the endostyle) ist kein Ernährungs-abschnitt des Kiemenkorbes sondern ein Drüsenorgan. Die Nahrungsaufnahme findet gleichzeitig mit der Athmung im ganzen Kiemenkorbe statt." Roule describing this process in *Ciona* states: "Un mucus, sécrété par le raphé ventral, est déversé en fins filaments sur la face interne de la paroi branchiale; là, ces filaments agglutinent tous les petits corpuscules, amenés par l'eau, qui passent à leur portée; puis, entraînés par les mouvements des cils vibratiles des papilles, ils se dirigent obliquement en haut et en arrière, de telle sorte que les filaments les plus antérieurs se rassemblent en une seule masse qui suit le raphé dorsal pour pénétrer dans la bouche œsophagienne, tandis que les postérieurs y parviennent directement." On the other hand, English writers describe food-collection as occurring in the endostyle and peri-pharyngeal grooves; the former groove conducting mucus with contained particles forwards to the latter,

which in turn carries the food-mass upwards into the dorsal groove, and at the same time assists in capturing food-particles. Delage and Herouard (3, p. 144) point out the differences in the descriptions of this process, and cautiously give only a general account.

FOOD-COLLECTION IN VARIOUS ASCIDIANS.

Observations have been made on a number of Ascidians, namely, *Ascidiella aspersa*, *Phallusia mamillata*, *Ascidia mentula* and *virginea*, *Ciona intestinalis*, *Clavellina lepadiformis*, *Leptoclinum (Diplosoma) gelatinosum* and a species of *Morchellium*, with the result that the process of food-collection has been found to be the same in all these animals as that described by Fol and Roule.

When carmine particles are added to the water in which one of these animals is living, for example, *Ascidia mentula*, the particles may be observed with a hand lens to be drawn into the branchial cavity and against the wall of the gill. Particles approaching the endostyle, however, are seen to be immediately lashed out of this groove on to the wall of the pharynx, just as is the case in *Amphioxus*. These particles become rolled into a mass with mucus, and are transported *across* the branchial sac to the dorsal lamina. All the particles entering the endostyle are washed out on to the pharynx in this way, and no mass of collected food has ever been seen—in any of the animals examined—to be passed forwards along the endostyle. An examination of the endostyle through a microscope shows further that the lateral rows of cilia on this organ lash in a direction across the endostyle, and from the endostyle on to the pharynx, and no transference of food-particles along the endostyle is seen. The food-particles drawn against the pharynx become caught in mucus and gradually transferred across the wall of the pharynx to the dorsal lamina, becoming rolled into cylindrical masses with mucus on the way. This process of food-collection and transportation is very well seen in the Compound Ascidian *Leptoclinum (Diplosoma) gelatinosum*, as shown in Fig. 7, which is a drawing of one living zooid in the act of feeding. In such a small animal as this one is able to keep the whole animal in the field of a microscope, and so to follow the course of even small food-particles in the pharynx. The particles entering the branchial cavity sometimes fall on to the pharyngeal wall close to the peri-pharyngeal grooves, but in none of the animals examined have the particles posterior to the grooves been observed to be drawn into these grooves. On the contrary, in *Ascidiella aspersa* especially these food-particles become collected in masses some distance posterior to the peri-pharyngeal groove

as though the cilia in this region were lashing away from the groove. The particles falling on to the region between the buccal tentacles and the peri-pharyngeal grooves, however, are washed into these grooves by cilia in a manner somewhat similar to that observed in *Amphioxus*.

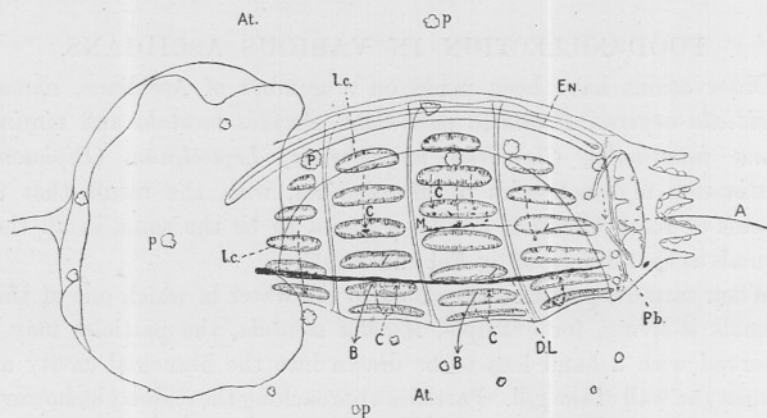


FIG. 7.—View of one entire zooid of the compound Ascidian, *Leptoclinum gelatinosum*, to show the currents produced by the ciliary mechanism on the gill and the mode of food-collection.

(Drawn from the living animal seen through the microscope, \times about 60.) The large arrows indicate the direction of the main current, and the dotted ones the course of food-particles which have been captured and are being transported to the dorsal lamina. Only the gill slits on the upper surface are shown.

- A. Arrow indicating the direction of the inhalent current produced by the lateral cilia, l.c.
- l.c. Lateral cilia on the sides of the gill slits: these produce the main current by lashing from the pharynx towards the atrium.
- B. Arrows indicating the current passing through the gill slits into the atrium.
- C. Dotted arrows indicating the paths of the food-particles, as at M, captured in mucus and travelling away from the endostyle towards the dorsal lamina, DL.
- DL. Dorsal lamina filled with collected food-particles seen through the wall of the transparent pharynx.
- En. Endostyle.
- M. Food-particles embedded in mucus being transported by the frontal cilia on the gill towards the dorsal lamina.
- P. Pigment spots scattered about the surface of the colony.
- At. Common atrium of the colony.
- P.b. Peri-pharyngeal band.

When *Leptoclinum* (*Diplosoma*) is fed with a large amount of carmine particles the process of feeding occurs extremely rapidly. Within a few seconds from adding particles to the water the dorsal lamina becomes full of the particles embedded in mucus ready to be passed into the œsophagus. *Clavellina* can be observed through the microscope to feed in the same way, and almost as rapidly as *Leptoclinum*. *Asciidiella* and *Ciona* feed

more quickly than the other simple forms, which feed relatively slowly. The process of food-collection at the anterior end of the pharynx in *Ascidia mentula* is shown in Fig. 8. At the posterior end of the pharynx in this animal the cilia in the dorsal groove lash food-particles *forwards* to the cesophageal opening. This process can be easily observed by cutting from the test a window, through which the processes can be followed distinctly.

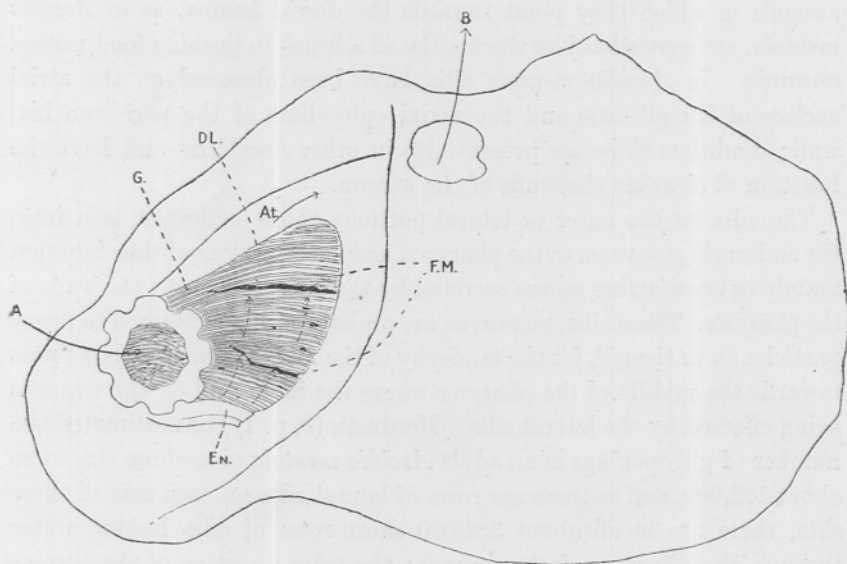


FIG. 8.—A view of the anterior end of *Ascidia mentula* to show the mode of feeding. Drawn from the living animal, as seen through a hand-lens. A part of the pharynx is drawn as though the test were transparent. (\times ca. $\frac{4}{3}$.)

- A. Arrow indicating the direction of the inhalent current.
 B. Arrow indicating the direction of the exhalent current.
 At. Arrow in the atrium showing the direction of the main current after passing through the gill slits.
 En. Endostyle.
 D.L. Locus of the dorsal lamina.
 F.M. Food-particles collected into a cylindrical mass with mucus being transported across the gill-bars and away from the endostyle towards the dorsal lamina, as indicated by the dotted arrows alongside.
 G. One of the longitudinal bars of the gill.

CILIARY MECHANISMS ON THE GILL OF ASCIDIANS.

The main current through the branchial cavity of all the Ascidiæ examined is produced by the lashings of the cilia on the sides of the gill-bars, as has been observed by Herdman for *Ascidia mentula* (10, p. 47). Food-collection is effected by the cilia on the pharyngeal surface of the

gill-bars and the cilia on the papillæ on the bars. These cilia lash across the length of the pharynx from the endostyle towards the dorsal lamina, but are not specially active nor specially powerful in the simple Ascidiæ, and food-collection is accelerated by the waving of the longitudinal bars in a transverse direction. In this way the food masses are pushed on as well as lashed onwards towards the dorsal groove. The papillæ of the gill-bars thus assist in food-collection, and in those animals in which they point towards the dorsal lamina, as in *Ascidia mentula*, act somewhat like the bristles of a brush in pushing food masses onwards. In *Ascidia mentula* cilia have been observed on the atrial surface of the gill-bars and the atrial epithelium of the peri-branchial wall; doubtless these are present also in other Ascidiæ, and have the function of cleaning the walls of the atrium.

The cilia on the outer or lateral portions of the endostyle lash from the endostyle groove on to the pharynx, and in this way doubtless function mainly in transferring mucus secreted by the endostyle on to the walls of the pharynx. These cilia, moreover, are probably seldom required to throw particles on to the gill, for the tendency of the main stream will be to pass towards the middle of the pharynx where the main pull on the water is being effected by the lateral cilia. Herdman (9, p. 17) has estimated the number of gill openings in an adult *Ascidia mentula* of medium size to be about 192,000, and as there are rows of lateral cilia on each side of these slits, there are in all about 384,000 short rows of cilia lashing water through the pharynx of the animal; the main direction of the current thus produced (see Figs. 7 and 8) is away from the endostyle. It is therefore curious that this groove can ever have been regarded as an important food-collecting organ. On the outer edge of the endostyle of *Ciona* there are definite short transverse grooves in which the cilia are specially powerful, and lash from the endostylar groove on to the pharynx.

The median ciliated tract of the endostyle bears cilia up to two millimetres in length. Roule (8) describes the cilia as having a very slow movement directed along the length of the groove and consisting of a series of undulations beginning at the base of the cilia. I have not yet been able to detect any movement in these cilia, and am therefore in some little doubt as to their function. Since, however, food-particles are not transported in the endostylar groove, these cilia do not appear to have any transporting function. This view is further supported by the fact that transporting cilia in Gastropods, Lamellibranchs (see 5, *passim*), and Amphioxus are always relatively very short and vibrate

rapidly. Perhaps the function of these cilia may be detected by examining their action through a microscope in the whole living and feeding animal, and an attempt will be made to find an animal in which this is possible. It is probable that they assist in passing mucus on to the walls of the pharynx, as has been suggested for the similar cilia in *Amphioxus*.

Examination of the peri-pharyngeal bands through a microscope shows that the cilia in these grooves lash from the endostyle towards the dorsal lamina. These grooves serve to collect and transport to the dorsal lamina such particles as fall out of the main stream at the entrance to the pharynx.

COMPARISON OF THE MODE OF FEEDING IN AMPHIOXUS AND ASCIDIANS.

From the foregoing description it will be seen that there is an exact correspondence in the mode of feeding in *Amphioxus* and *Ascidians*. In these animals the lateral cilia on the gill-bars are the main factors in producing the main current; mucus is passed on to the gill-bars by the outer tracts of cilia on the endostyle, and food-particles are collected and transported to the dorsal region of the gill by the pharyngeal or frontal cilia on the gill-bars. The food collected in the dorsal wall of the pharynx is transported backwards, to be passed into the digestive tract. Thus the diagram of the ciliary mechanism on the gill of *Amphioxus* (see Fig. 6) will serve equally well for *Ascidians* in general. The cilia in the peri-pharyngeal bands in both of these groups of animals lash from the endostyle towards the dorsal groove, and collect and transport to the dorsal groove those particles which fall out of the main stream at the entrance to the pharynx. The process of feeding in both *Amphioxus* and *Ascidians* is automatic, but at the same time these animals are able to select from the food-stream the finer food-particles by means of their buccal tentacles. *Ascidians*, moreover, have been observed to reject food after it has been collected in masses on the gill by suddenly contracting the walls of the pharynx and expelling the whole mass. It is also not improbable that the pharyngocloacal slits observed by Garstang in *Ascidians* (18, p. 132), may be exits from the pharynx used for relieving that organ when overburdened with undesirable matter. On the other hand *Amphioxus* is obliged to ingest all that passes beyond the oral aperture.

THE FUNCTION OF THE GLAND AND ITS CILIATED TRACT
IN THE BRANCHIAL OPENINGS OF AMPHIOXUS AND
ASCIDIANS.

In the anterior region of these animals there are also similar organs which have doubtless a similar function, and a function in connexion with the mode of feeding. These organs are a gland, and a ciliated tract connecting the gland with the pharynx, namely, the sensory pit or Hatchek's pit, and the Wheel Organ in *Amphioxus*, and the neural gland and the dorsal tubercle in *Ascidians*. It has been suggested by V. Wijhe (7, p. 121) and Andrews (14, p. 227) for *Amphioxus*, and by Herdman (10, p. 52), Hartmeyer (11, p. 303), and Seeliger and Neumann (12, p. 61) for *Ascidians*, that this gland may have the function of secreting mucus which is passed on to the pharynx by the ciliated tract. The observations here made on these groups of animals support these views. The gland probably merely secretes mucus which is passed on to the food-grooves by the ciliated tract to serve for entrapping or embedding food-particles and rendering the transportation of these easier than it otherwise would be. Thus it is not improbable that the great variations observed in the openings of the dorsal tubercle of *Ascidians* may be a means of distributing mucus in various ways to the pharynx in correlation with minor differences of food-collection on the pharynx; such differences as may be due to the well-known differences in structure of the pharynx.

From the occurrence of sensory cells in Hatchek's pit in *Amphioxus* it would seem that this organ is also in some way sensory, as V. Wijhe (7, p. 120) has pointed out. In the light of the present researches it is suggested that possibly this sensory pit may govern in some way the supply of mucus from the gland itself and the endostyle, for the capture of food-particles depends to a great extent on the amount of mucus passing over the pharynx. Thus when a large amount of food-particles is passing into the pharynx—as might be first appreciated by the sensory cells in Hatchek's pit—a large amount of mucus would be required to capture the food-particles. It is therefore not improbable that the supply of mucus may be regulated by means of this sensory pit. Whether any similar function is exercised by the neural gland in *Ascidians* is perhaps more doubtful, but both Herdman (10, p. 52-3) and Seeliger and Hartmeyer (11, p. 303) suggest that the dorsal tubercle in these animals may have a sensory function. It may also be pointed out here that if the neural gland in *Ascidians* is an organ for secreting mucus which is passed on to the pharynx by the cilia in the dorsal tubercle,

then this mucus must be passed straight into the dorsal groove. The cilia on the dorsal tubercle of *Ciona* when examined under a microscope appear to lash away from the body-wall towards the lumen of the branchial opening. Thus in the whole animal it is not improbable that thin sheets of mucus are constantly passing from the dorsal tubercle into the dorsal groove. These sheets would serve to entrap food-particles in the same way as the ciliated tracts do in *Amphioxus*. It is hoped, however, to complete these observations on a suitable animal and to obtain more definite information on this subject.

THE MAINTENANCE OF THE PHARYNGEAL SPACES IN ASCIDIANS AND AMPHIOXUS.

The maintenance of a current of water through the body of these animals is dependent upon the maintenance of a continuous open passage through the animal as well as upon the action of the gill as a water pump. In *Ascidians* doubtless the main function of the test is to maintain a cavity for the branchial sac. The body wall in *Ascidians* is maintained in close contact with the test by organic connexions, so that the branchial sac lies free in a cavity—the peri-branchial cavity—which the expanded pharynx does not quite fill. Thus a cavity in communication with the pharynx and the exterior is maintained outside the pharynx. The pharynx in *Ascidians* is kept open by the intercrossing of longitudinal and transverse bars of a sufficiently rigid consistency. In *Amphioxus* the pharyngeal bars are supported, as is well known, by definite skeletal rods. The peri-branchial cavity in *Amphioxus*, however, is maintained by dorso-lateral sheaths of connective tissue arising from the notochordal sheath (see Lankester, 16, Plate 36) held in position above the pharynx and connected to the lateral surface of the notochord and dorsal skeletal system by the myotomes. A glance at a pharyngeal section of this animal indicates at once how the attachment of the myotomes to the dorsal region of the body and the dorso-lateral sheaths in the wall of the peri-branchial cavity maintains this cavity. Indeed, the shape of the myotomes in *Amphioxus* may have been directly influenced by their function of assisting in maintaining a cavity in the ventral region of the body.

THE CILIATION OF THE GILL OF BALANOGLOSSUS.

Up to the present it has been possible to examine only sections of the gill of this animal, but it is hoped that observations may be made on the living animal later. Examination of sections of the gill-bars of *Balano-*

glossus (a species of Ptychodera) shows the presence of well-marked lateral cilia and smaller frontal or pharyngeal cilia. From the foregoing observations it is a fair deduction that these lateral cilia produce the main current of water through the body of the animal, and that the frontal cilia are concerned in some way in food-collection. It is also highly probable that observations on this group of animals may now demonstrate the function of the mucus, which is doubtless secreted by the dorsal diverticulum, the gland in this group of animals corresponding to Hatchek's pit in Amphioxus and the neural gland in Ascidians.

OBSERVATIONS ON THE AMMOCOETE OF *PETROMYZON FLUVIATILIS*.

Some observations have also been made on rather late stages of the Ammocoete of *Petromyzon fluviatilis*. It is well known that this larva closely resembles Amphioxus in some respects. I have also learnt from fishermen that these larvæ will live in captivity for even a year by merely changing regularly the water in which they are kept. It was therefore thought probable that they might feed on Plankton in the same way as Amphioxus. Two specimens were fed on carmine particles and then preserved in 90% alcohol. On opening the branchial portion of the alimentary canal it was found that the carmine particles had become entrapped in mucus and were collected along the gill-bars and roof of the pharynx. No particles, however, were found in the intestine. Nevertheless sufficient evidence was obtained to indicate that further observations on the mode of feeding in younger forms might be highly interesting, and an effort will be made to make such observations.

THE MODE OF FEEDING IN *SOLENOMYA TOGATA*.

In view of the observations formerly made on the mode of feeding in *Nucula* (see 5, pp. 467-70), similar observations undertaken upon any other Protobranch promised to be interesting. Acting upon a happy suggestion made by Sir E. Ray Lankester, I obtained living specimens of *Solenomya togata* from Naples at the second attempt, and made the following observations. An examination of this delicate little animal through a microscope in water containing carmine particles readily showed that as in *Nucula* the mantle cavity is divided into two chambers when the animal is feeding. The food-current is drawn into the mantle cavity at the antero-dorsal end and expelled posteriorly (see Fig. 7). During the process of feeding the gills are extended so that their posterior

ends touch the mantle postero-ventrally (see Fig. 7), and the lower portions of the gill on each side also meet ventrally, while the tips of the upper lamellæ complete the partition of the mantle cavity by forming a junction with the mantle dorsally. Thus a large anterior inhalent chamber and a smaller posterior exhalent one are formed (as shown in Fig. 9), in the same way as in *Anomia aculeata* and the higher Lamellibranchs. This subdivision of the mantle cavity is of some importance, as it has been regarded by some authors (for example, Sedgwick, p. 345) as occurring only in the higher Lamellibranchiata. It will thus be seen that the whole of the gills of *Solenomya* resemble generally one lamella of the gill of a mussel for example.

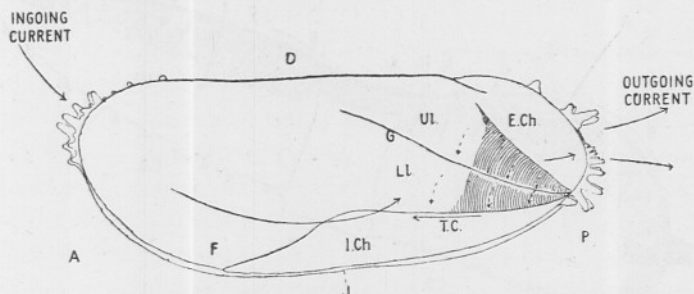


FIG. 9.—View of a living specimen of *Solenomya togata* to show the relations of the gill and the inhalent and exhalent chambers. (\times ca. 10.)

- G. Left gill.
- I.Ch. Inhalent chamber.
- E.Ch. Exhalent chamber.
- A. Anterior end.
- P. Posterior end.
- D. Dorsal surface.
- U.L. Upper lamellæ of gill.
- L.L. Lower lamellæ of gill.
- J. Anterior end of the fused portion of the mantle.
- T.C. Region where collected food is transported forwards as shown by the arrow.

The gill of *Solenomya*, it will be remembered, has the outer and inner leaflets of the same side placed vertically, the one over the other, so that both appear to form one leaflet with a shallow groove along the median lateral line (see Fig. 9). These leaflets are arranged on an axis on each side at the posterior end of body with only the thin edges of the leaflets showing in a side view. The shape of a pair of leaflets may be seen in Fig. 10.

On feeding the animal with carmine grains it was observed that the food-particles collected on the outer faces of the gills were transported quickly to the ventral edges—even from the upper leaflets—and thence carried forwards towards the mouth to be eaten. The collection and

transportation of food-particles are effected by means of sets of cilia, but in order to make out the actions of these different sets it is necessary to examine separate living leaflets.

THE CILIATION OF THE GILL OF SOLENUMYA.

When two of the living leaflets (comprising a single pair) of *Solenomya* are examined microscopically they are seen to resemble in general characters those of *Nucula* (see Figs. 10 and 11). As in *Nucula* the main current through the mantle cavity is produced by the

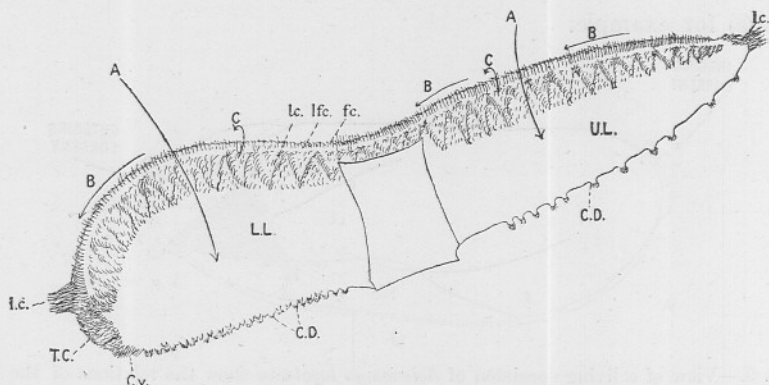


FIG. 10.—View of a pair of living leaflets of *Solenomya togata* taken from about the middle of the gill, to show the directions in which the different sets of cilia lash. (\times ca. 60.)

The arrows marked A indicate the direction in which the lateral cilia lash to produce the main current; those marked C indicate the direction of lashing of the latero-frontal cilia which act as food-strainers; while those marked B show the direction in which food-particles are lashed by the frontal cilia.

U.L. Upper lamella.

L.L. Lower lamella.

l.c. Lateral cilia forming a broad band on the side of the gill.

l.f.c. Latero-frontal cilia.

f.c. Frontal cilia.

C.D. Ciliated knobs.

I.c. Cilia interlocking with the mantle.

T.C. Cilia which transport food along the ventral edge of the gill towards the mouth.

C.v. Cilia interlocking with similar ones on the adjacent leaflet.

lashings of the large lateral cilia on the anterior and posterior faces of the leaflets (see Fig. 10, l.c. and the arrows marked A). Food-particles are collected by the latero-frontal cilia (the presence of which in this species has recently been doubted, see Ridewood, p. 193) and frontal cilia, but transported solely by the latter (see Fig. 10, l.f.c. and f.c.). The latero-frontal cilia lash in a direction across the length of the edges of the leaflets, i.e. away from the spaces between the leaflets

(see the arrows marked C in Fig. 10). They catch the food-particles which tend to be drawn between the leaflets in the main current and pass them on to the frontal cilia. The latter lash in a ventral direction, and thus send particles along the edges of the leaflets to the ventral surface (see Fig. 10, f.c. and the arrows marked B). Here a group of cilia now lash the food-particles anteriorly towards the mouth to be eaten. As the food-particles are lashed along the face of the gill they become embedded in mucus, which is doubtless secreted by the epithelium of the gill. The

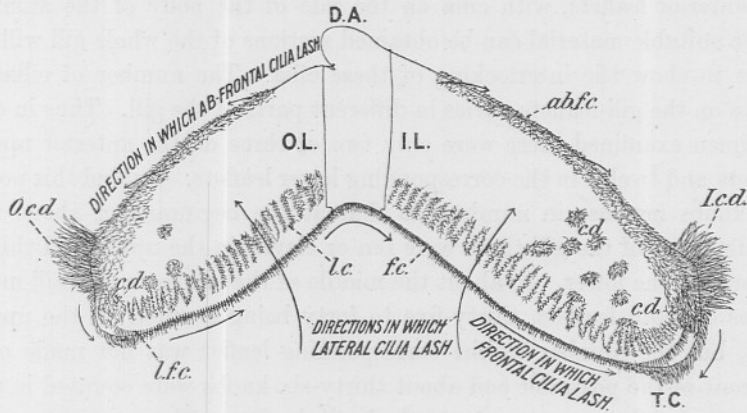


FIG. 11.—Anterior view of a living pair of leaflets of the right gill of *Nucula*. (\times about 65.)

The leaflets anterior to the pair depicted were cut away.

- ab.f.c. Ab-frontal cilia.
- c.d. Patches of cilia on the inner and outer leaflets.
- D.A. Dorsal surface of gill about the 30th pair of leaflets from the posterior end of gill.
- f.c. Frontal cilia.
- I.c.d. Cilia effecting a junction with similar cilia on the left gill.
- I.L. Inner leaflet of gill.
- l.c. Lateral cilia.
- l.f.c. Latero-frontal cilia.
- O.L. Outer leaflet of gill.
- O.e.d. Cilia effecting a junction with the mantle.
- T.C. Cilia which transport collected food forwards.

secretion of mucus on the Lamellibranch gill is indeed a matter of considerable importance in the feeding process, and it is hoped to investigate the matter more fully later.

The examination of single living leaflets reveals a feature of much interest in the ciliation of the gill. On the inner edges of the leaflets, that is, on the ab-frontal surfaces, there occur numerous ciliated knobs (see Fig. 10, c.d.). These ciliated knobs have cilia whose motion is like that of the ciliated discs on the gill-filaments of the Filibranchia (for example see the Fig. of Mussel, Orton, 5, p. 465). This motion may be

compared to that of the bristles of two brushes when the brushes are rubbed together slowly in a rotary manner with the bristles interlocking. To get the proper effect one brush should be started rotating before the other, and the bristles should be regarded as vibrating at the same time with a slow wave-like motion which begins at the attached end.

The function of these ciliated knobs is doubtless the same as that of the ciliated discs of the Filibranchia, namely, to interlock with similar discs on the leaflets of the gill on the other side of the body; or, in the case of the anterior leaflets, with cilia on the side of the body of the animal. When suitable material can be obtained sections of the whole gill will be made to show the interlocking of these cilia. The number of ciliated knobs on the gill-leaflets varies in different parts of the gill. Thus in one specimen examined there were only two or three on the anterior upper leaflets and twelve in the corresponding lower leaflets. Behind this point the knobs increase in number, so that at the beginning of about the middle third of the gill there were ten or eleven in the upper and thirty to forty in the lower. In about the middle of the gill there are still more knobs on both leaflets, thirty-five to forty being counted on the upper ones, but the number on the corresponding leaflet was not made out. In front of the posterior end about thirty-six knobs were counted in the upper and eighteen to twenty in the lower leaflets. There are thus more knobs in the middle of the gill and fewer at the anterior and posterior ends, and more in the lower leaflets in the anterior end than in the upper ones in this position, but more in the upper than in the lower at the posterior end. These differences are doubtless explained by the facts that at the anterior ends of the gills the upper leaflets appear to lie against the body, while the lower ones meet below, and thus require a better interlocking arrangement, while at the posterior end of the gill the upper leaflets are longer than the lower ones.

Besides these ciliated knobs there are also other interlocking cilia at the tips of the upper and at the ventro-lateral edges of the lower leaflets (see Fig. 10, I.c.). These cilia doubtless effect a junction with the mantle, and an attempt will be made to obtain sections of the gills and mantle to show these connexions.

On the anterior and posterior faces of the ventral edges of the lower leaflets there are patches of cilia which also have the rotary motion characteristic of interlocking cilia. These probably serve—like the similar patches on the gill leaflets of *Nucula* (see Fig. 11, c.d.)—to hold the tips of the leaflets together. Thus the living gill of *Solenomya* is a very compact organ, which, however, like that of *Pecten*, can be contracted

into a small compass so as to leave the inhalent and exhalent chambers continuous.

The characters of a transverse section of a gill-leaflet of *Solenomya* can now be recognized. Ridewood (p. 193) in describing the ciliation of the gill remarks, "Cilia are confined to the thickened edge, and appear to form a continuous investment of it, not differentiated into frontal and lateral tracts. The material available is not sufficiently well preserved to allow of a definite statement upon this point, but it is worthy of remark that no gap between the frontal and lateral cilia is shown in the figures (of the transverse sections) given by Pelseener, Kellogg, and Stempell. The cilia extend as far as the level of the outer edge of the thickened chitin bands, and the shortest are those on the frontal surface. Pelseener shows large latero-frontal cilia, but this is possibly an error."

The foregoing examination of the living leaflets shows that Pelseener's depiction of large lateral cilia (the latero-frontal cilia) is correct, and that all figures err in depicting a continuous covering of cilia at the tip of the gill (see Fig. 10), thus justifying Ridewood's cautious remarks in this respect. A transverse section may or may not show cilia on the ab-frontal face according as the section passed through a ciliated knob or not. An attempt will be made to make preparations from well-preserved gills and to figure a transverse section.

RESEMBLANCE OF THE CILIATION OF THE GILL IN SOLENOMYA AND NUCULA.

From the above description of the ciliation of the gill of *Solenomya* it will be seen that there is a close resemblance to that obtaining in *Nucula* (see Fig. 11). If the frontal surfaces of these gills be compared a complete resemblance in this part is seen; frontal, latero-frontal, and lateral cilia occurring in both and having the same function in both. The ab-frontal cilia of the gill of *Nucula*, however, are absent from that of *Solenomya*, and are replaced by ciliated knobs. The small patch of interlocking cilia on the lateral faces of the leaflets of *Nucula* have not been seen in *Solenomya*, but a patch of interlocking cilia is present on the ventro-lateral portion of the inner leaflets of both gills (see Figs. 11, c.d., and 10, c.v.). Cilia interlocking with the mantle are present in both forms at the tips of both leaflets; those in *Solenomya* are, however, nearer to the frontal surface than in *Nucula* in correlation with the difference in position of the gill in the former. On the whole, therefore, the ciliation of the gill of *Solenomya* bears a very close resemblance to that of *Nucula*.

SUMMARY OF THE ACCOUNT OF THE CILIARY CURRENTS IN SOLENOMYA.

The main current through the mantle cavity is effected by means of the lashings of the lateral cilia on the gill-leaflets. This current is drawn in at the antero-dorsal region of the shell and expelled in the posterior region. The food-particles brought to the gill in this current are arrested on the gill by the latero-frontal and frontal cilia, the former passing on particles to the latter. The frontal cilia transport the food-particles along with mucus, which is doubtless secreted by the epithelium of the gill, on to the ventral edges of the lower leaflets, whence a special group of cilia transport the collected particles and mucus towards the mouth to be eaten.* Ciliated knobs occur on the ab-frontal edges of the leaflets which serve to interlock with similar knobs on the fellow-leaflets on the other side of the body. Long interlocking cilia also occur at the dorsal ends of the upper leaflets and the ventro-lateral edges of the lower ones. These cilia serve to effect a junction of the gills with the mantle during feeding, and so divide the mantle cavity into an inhalent and an exhalent chamber.

On the whole, therefore, it is seen that the gill of *Solenomya*, like that of *Nucula*, is essentially similar to that of the higher Lamellibranchs. Indeed the presence of numerous ciliated knobs must rank this gill as a more highly specialized one than, for instance, that of *Anomia aculeata*, which has only interlocking arrangements at the tips. Apart from the narrowness of the filaments in *A. aculeata*, there is almost an exact-resemblance between the gills of this species and those of *Nucula* and *Solenomya togata*. Thus the gross structure and the function of the gills in the Protobranchia and the Filibranchia have been shown to be essentially similar, and there can be very little doubt from the published accounts of the gills of other Protobranchia that these may be regarded as essentially similar to those of *Solenomya* and *Nucula*.

THE FUNCTION OF THE GILL IN LAMELLIBRANCHS.

The gill in all groups of Lamellibranchs has now been shown to be a feeding organ. Generally, however, this organ is regarded as being chiefly a respiratory and only secondarily a feeding organ. In the light

* Since this account was sent to the printer, a paper by E. S. Morse on *Solenomya* in the current number of the *Biological Bulletin*, Woods Hole, has come to hand. This paper gives an account of observations on living *Solenomya velum* and *S. borealis*. Morse has observed the palps being used for transferring food from the gill to the mouth, which fact, added to those given above, completes our knowledge of the mode of feeding in *Solenomya*.

of recent researches on the function of the gill, however, it would appear that the order of importance in which these functions have been regarded must be at least reversed. The expenditure in the gill of the relatively large amount of energy necessary to produce the main current and food currents must enormously outbalance the aerating effect of these currents on the gill. For it is to be remembered that in the gill-filaments of Lamellibranchs the blood is not contained in a capillary plexus, but usually in a blood vessel sunk well below the epidermis. This conclusion with regard to the function of the Lamellibranch gill has indeed already been arrived at, from a morphological point of view, by Dakin (6, pp. 52-3), who states that in the genus *Pecten* "It seems certain, from the development of vessels in the mantle, that the great function of the gills is to produce currents of water for aeration, nutrition, and the carrying away of waste products, and the only parts of the gills performing any really important duty in respiration are the branchial expansions of the principal filaments." There is little doubt that this statement might now be made similarly of the whole of the higher Lamellibranchs. It is of interest, however, that there is one important difference in this respect in the gills of the Protobranchia. In this group the gill-filaments are broad and lamellate, and contain an extensive space between the two surfaces (see Ridewood, p. 193) over which we have seen the current passes. Doubtless with this type of gill a much greater proportion of the whole respiration is effected in the gill than is the case in the forms with narrow compact filaments. But even here it may be doubted whether respiration is effected to the same degree in the gill as in the mantle. It would be highly interesting in these respects if a ready means could be found of detecting the relative amounts of waste products in any particular part of the body at any particular instant. Such an experiment may perhaps not be an impossibility, as some of these animals can be observed living through a microscope.

APPENDIX.

Some of the observations made in the section on the function of the Wheel Organ and Peri-pharyngeal bands in *Amphioxus* (p. 25) have already been noticed by Andrews in the *Bahamas Amphioxus*, as will be seen from the following quotation. It was unfortunately not possible to refer to Andrews' work in the general text, as some difficulty was experienced in obtaining his paper, which only became available after the text had gone to the printer.

Andrews (4) obtained living specimens of the *Bahamas Amphioxus*

(*Asymmetron lucayanum*) about which he observes: "As the animal is small and translucent, the course of food and carmine granules may be traced through most of the digestive tract. The strong current of water setting into the pre-oral chamber seems to be controlled by the longitudinal, ciliated ridges of Müller's 'Räderorgan' which pass forward from the velum on the inside of each lateral wall of the pre-oral chamber. Thus the carmine granules pass rapidly along these ridges towards the velum, where they are turned inward towards the aperture, mouth, at the centre of the velum. The granules pass along in strings as if held together by a thin mucus; once through the mouth they do not pass out through the pharyngeal slits, but continue along the median dorsal pharyngeal groove, the hyper-pharyngeal groove, still adhering to one another in strings. In actual longitudinal and cross sections these strings of granules may still be recognized in the ciliated hyper-pharyngeal groove.

"This groove leads into what may be called the stomach, within which the current of granules, or the granule containing mucous strand, turns abruptly downwards and forwards as indicated in the above diagram, yet does not enter the diverticulum, but, still under the control of the active cilia lining the digestive tract, passes back again through the centre of the stomach. It is now revolving rapidly in a constant direction from right to left, and continues to do so throughout the next division of the digestive tract, the first or larger section of the intestine. In this part of the intestine the granules, diatoms, etc., collect into clumps separated by the clear part of the continuous mucus-like strand. In this region the intestinal epithelium is especially modified in a zone that became very prominent when staining reagents are used.

"The second, final and smaller part of the intestine, contains pellets of detritus that become successively larger towards the anus, where they have the form of elongated, not spherical, masses that are discharged from the anus as the anal sphincter relaxes from time to time. The mucous strand is here broken, the granular aggregates becoming isolated from one another. These balls or pellets move along but slowly, and give up the revolving motion seen in the first part of the intestine and in the stomach.

"The time elapsing from the addition of carmine to the water to the discharge of carmine containing pellets may be much less than one hour."

It will thus be seen that Andrews has described some of the processes in the subsidiary method of feeding in the Bahamas Amphioxus which

is doubtless the same as in the Plymouth Amphioxus. He gives the impression, however, that this is the main method of feeding, but such is not the case, as will have been seen from the foregoing description.

SUMMARY.

The mode of feeding in Amphioxus is effected by—

- (1) The maintenance of a stream of water through the pharynx by rows of lateral cilia on the gill-bars.
- (2) The throwing out of mucus from the endostyle on to the gill-bars to serve for entrapping food-particles.
- (3) The collection of food-particles by rows of cilia on the pharyngeal surface of the gill-bars; these cilia work up the food-particles with mucus into cylindrical masses and transport such masses dorsally into the dorsal groove which carries the collected masses backwards into the digestive tract.

Thus the ciliary mechanisms on a gill-bar of Amphioxus are exactly the same as those on the gill-filaments of some Lamellibranchs, as Pecten, and some Gastropods, as Crepidula.

A subsidiary mode of food-collection is effected in the buccal cavity of Amphioxus by the ciliated tract known as the wheel organ, and Hatched's pit, which supplies mucus for entrapping food-particles. These particles are passed on to the peri-pharyngeal bands which conduct them in turn into the dorsal groove.

The gill of Amphioxus functions mainly as a feeding organ and a water pump, and probably not at all as an organ for aerating the blood.

The mode of feeding in Ascidians is almost exactly the same as that described above for Amphioxus. Food-collection, however, in Ascidians is effected by cilia on the papillæ and similar outgrowths on the gill, and is also helped in some forms by transverse waving of the longitudinal bars, by which process the food is pushed as well as lashed towards the dorsal region of the pharynx.

The observations here made lend support to the view that the neural gland in Ascidians is an organ for secreting mucus, which aids in the capture and transportation of food-particles, and that the dorsal tubercle of Ascidians is an organ for passing mucus on to the pharynx; the corresponding structures in Amphioxus, namely, Hatched's pit and the wheel organ, are here shown to effect food-collection in the buccal cavity.

The cavity in the body of Ascidians through which the food stream

can pass is maintained by the test, and in *Amphioxus* by the expansion of stout connective sheaths over the dorsal region of the pharynx held in place by muscular attachments to the dorsal region of the body.

The ciliation of the gill-bars of *Balanoglossus* is essentially the same as that of *Amphioxus*. Hence the current of water through the body of the animal is doubtless effected by the lateral cilia and a mode of food-collection effected by the frontal cilia.

Observations on late Ammocoete larvæ indicate food-collection on the gill-bars and the roof of the pharynx, as occurs in *Amphioxus*. An attempt will be made to complete these observations.

The mantle cavity of *Solenomya togata* is divided into inhalent and exhalent chambers by the gill in the same way as in other Lamellibranchs, namely, *Anomia* and *Pecten*.

The ciliation of the gill of *Solenomya* closely resembles that of *Nucula*: the lateral cilia produce the main current, the latero-frontal and the frontal cilia collect food-particles, and the latter transport them to the ventral surface of the gill, whence they are conducted forwards by special transporting cilia towards the mouth to be eaten.

Numerous small ciliated knobs occur on the ab-frontal face of the gill-lamellæ and serve to interlock with their fellows on opposite leaflets.

These ciliated knobs correspond to the ciliated discs of the gill-filaments of other Lamellibranchs, for example, the Mussel.

Interlocking cilia occur on the edges of the upper and lower leaflets of the gill and serve to lock the gill to the inner wall of the mantle, and thus to partition the mantle cavity.

The function of the Lamellibranch gill is probably mainly that of a food collector and a water pump, and except in the Protobranchs is probably not an organ in which aeration of the blood occurs.

REFERENCES.

1. A. Willey. *Amphioxus* and the Ancestry of the Vertebrates. Macmillan & Co. 1894.
Feeding of Amphioxus, pp. 9, 39. *Feeding of Ascidians*, p. 185.
2. A. Sedgwick. Student's Text Book of Zoology, Vol. II. London, 1905, p. 22.
3. Delage and Hérouard. *Traité de Zoologie concrète* VIII. Prochordés p. 113, p. 144, *Ascidians*.
4. H. Fol. Études sur les Appendiculaires du détroit de Messine. *Mém. de la Société de Phys. et d'hist. natur. de Genève*. T. XXI. 2. 1872.

5. J. H. Orton. Journ. M.B.A., Vol. IX, No. 3. 1912. *Gill of Nucula*, pp. 467-70.
6. W. J. Dakin. L.M.B.C. Memoir XVII. Pecten. 1909. pp. 52-3.
7. J. W. van Wijhe. Beiträge zur Anatomie der Kopffregion des *Amphioxus lanceolatus*.
Petrus Camper I, p. 121. 1901-2.
8. L. Roule. Recherches sur les Ascidies simples des côtes de Provence (Phallusiadées), p. 66.
Ann. du Mus. d'Hist. Nat. de Marseille. Zoologie. Tome II. Mem. No. 1. 1884.
9. W. A. Herdman. Cambridge Nat. Hist., Vol. VII. Fishes, Ascidians, etc., 1904, p. 45 *feeding*, p. 47 *lateral cilia*, pp. 52-3, *neural gland and dorsal tubercle*.
10. W. A. Herdman. L.M.B.C. Memoir, Liverpool. 1. *Ascidia*. pp. 14, 15 *endostyle*.
11. O. Seeliger and R. Hartmeyer. Bronn's Tier-reich, III. Supplement, I Abteilung. 1893-1911, pp. 302-3.
12. O. Seeliger and C. Neumann. Bronn's Tier-reich III. Supplement, II Abteilung. 1913, p. 61.
13. W. G. Ridewood. Phil. Trans. Roy. Soc. London. B. Vol. 195. 1903, p. 193.
14. E. A. Andrews. Studies from the Biol. Lab. of the Johns Hopkins Univ., Vol. 5, No. 4. 1893.
15. W. Blaxland Benham. Q.J.M. Sci., Vol. XXXV, p. 9, Plate 6, Figs. 1 and 2. 1893.
16. E. Ray Lankester. Q.J.M. Sci., Vol. XXIX, Plate XXXVI. 1889.
17. H. Fol. Ueber die Schleimdrüse oder den Endostyl der Tunicaten, Morphologisches Jahrbuch. Bd. I. 1876.
18. W. Garstang. Journ. M.B.A. Vol. 2. N.S. 1891-2, p. 132.