The mode of feeding of Crepidula, with an account of the current-producing mechanism in the mantle cavity, and some remarks on the mode of feeding in Gastropods and Lamellibranchs.

By

J. H. Orton, A.R.C.Sc., B.Sc.,

Assistant Naturalist at the Plymouth Laboratory.

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I. INTRODUCTION.

The manner in which the slipper-limpet, *Crepidula fornicata*, feeds has apparently puzzled all the naturalists who have interested themselves in this animal, as may be gathered from what follows. Crepidula—like its allies the whelks and other pectinibranchiate Gastropods—has a well-developed radula, a fact which leads one to infer that the animal lives a marauding life. But both Conklin and myself have shown that Crepidula settles down permanently at an early age to a sedentary life, so that after settling down the animal must feed on whatever food happens to be in its immediate neighbourhood.

From my studies of the habits and anatomy of this sluggish animal I had formed a hazy idea that, since the gut is very strongly ciliated throughout, food was probably drawn in at the mouth in a current of water. As a result of this idea, I concluded that the radula in later life was an obsolete organ which the animal possessed merely as a heritage from its ancestors. On my expressing this opinion to Dr. Allen, he pointed out that if Crepidula possessed an obsolete but well-developed radula, then the phenomenon appeared to be a new one, which required to be carefully investigated. Subsequently a careful examination was made of the gut contents of Crepidula, and a comparison established between these and the ingested food of the native oyster, *Ostrea edulis*, taken from the same grounds, namely, off the Essex coast in the Blackwater near West Mersea. It may be here remarked that as Crepidula has spread so rapidly on the oyster grounds off the Kent and Essex coasts as to become a nuisance, it has become a matter of much importance to oyster farmers to have definite information about its food. The examination made of the gut-contents of these two animals revealed a close similarity in the kind of food-material, as far as skeletal remains indicate, and the identity of the most common forms of diatoms found in both animals. The contents of the gut of both these animals are mainly:

1. Sand-grains.
2. Sponge-spicules.
3. Diatom shells.
4. Vegetable debris, Radiolarian, Foraminiferan, and Peridinian tests.

The most common diatoms* present in both animals are:

† *Actinoptychus undulatus*, Bail.
† *Paralia sulcata* (Ehr.).
Navicula aspera, Ehr.
Cocconeis scutellum, Ehr. and a var. parva?
Hyalodiscus stelliger, Bail.
Actinocyclus ralfsii (Wm. Sm.).

Among the less common, but, in the case of some of the larger, equally important forms are several species of †Coscinodiscus, Nitz-

* For the identification of diatoms, works by Van Heurck (3) and Gran (4) were consulted.

† It is not surprising to find these plankton forms amongst the food of these animals. Both Crepidula and oysters were taken from depths of only a few fathoms and not far from the shore. In such a situation as this the plankton will doubtless be much mixed up with bottom-living organisms.

schia, Navicula, and Grammatophora, and occasional specimens of a few other species. As the majority of these forms were found living in the washings from the shells of Crepidula and the oyster, there is no doubt that the animals were feeding on at least most of the forms mentioned. A species of Prorocentrum, probably *P. micans,* was however the organism found in the greatest numbers in the gut of these animals at the time they were examined, i.e. about the month of October, 1911.

It therefore became evident that Crepidula takes the same kind of food as oysters, and as the oyster has no radula, I appeared to have gained my point about the radula of Crepidula, namely, that it is a useless organ. However, while examining Crepidula one evening I detected a current in the mantle cavity, and subsequently observed the mode of feeding, which established beyond doubt both the nature of the food-material and the use of the radula, as will be shown in the following account.

II. THE MODE OF FEEDING IN CREPIDULA.

Crepidula feeds in the same way in principle as the oyster—that is, an ingoing and an outgoing current of water is established in the mantle cavity along a definite pathway, while between the two currents the gill acts as a strainer, retaining even very fine particles of suspended matter which may eventually reach the mouth. The gill consists of a row of free filaments—more than four hundred filaments were counted in the gill of an adult specimen—placed parallel to one another, midway between the dorsal and ventral surfaces. The filaments stand out in a line along the left side of the mantle cavity, extending almost in a horizontal line across this cavity; their tips rest along the edge of the right epipodium anteriorly, but posteriorly on the dorsal surface of the visceral mass. The gill thus forms a sheet across the mantle cavity, which it divides into a left ventro-lateral inhalent chamber, and a right dorso-lateral exhalent chamber. Fig. 1 gives a ventral view of the animal in the act of feeding; the arrows indicate the direction of the food-current. In feeding, the front end of the shell is raised slightly and a current is set up in the mantle cavity by the cilia on the gill-filaments. Water is drawn in along the anterior half of the edge of the shell on the left, passed through spaces between the gill-filaments, and is expelled along the front half of the edge of the shell on the right (see Fig. 1).

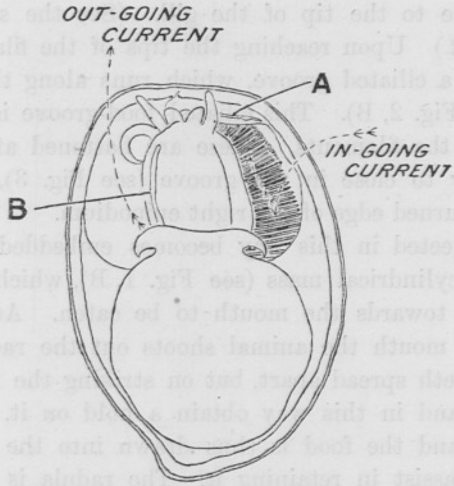


FIG. 1.—Ventral view of Crepidula. The arrows indicate the direction of the food-current. (Drawn from life. × 2.)

A. Food-pouch for the coarse food-particles: the main part of the pouch is hidden from view by the animal's "head."

B. Cylindrical mass of food in the food-groove; seen through the translucent body-wall.

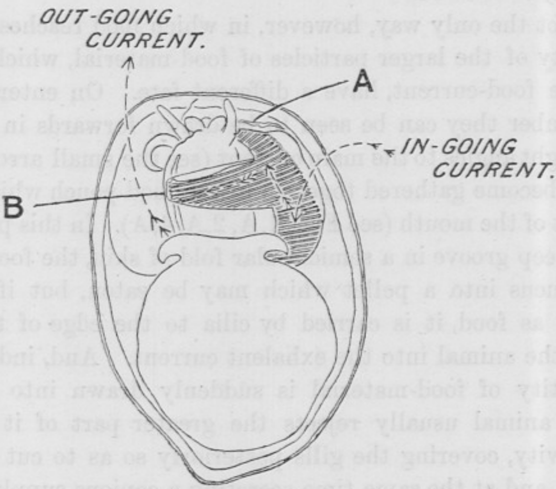


FIG. 2.—Ventral view of Crepidula with a part of the "neck" region supposed to be cut away to show the gill lying over the back of the animal.

A. Food-pouch.

B. The pointer points at the exposed tips of a few gill-filaments, just in front of which can be seen the food-groove in section.

The little arrow between the cut surfaces of the animal indicates the direction in which the fine food-particles travel.

Most of the fine particles of suspended matter are carried by the current against the gills, and being caught by the cilia of the gill-filaments or in the mucus secreted by the gill, are hurried along the ventral face to the tip of the gill. (See the small transverse arrow in Fig. 2.) Upon reaching the tips of the filaments the food is deposited in a ciliated groove, which runs along the right side of the body (see Fig. 2, B). This ciliated food-groove is just roofed in by the tips of the filaments. These are flattened at this point the more effectively to close in the groove (see Fig. 3), and just meet the slightly upturned edge of the right epipodium.

The food collected in this way becomes embedded in mucus and formed into a cylindrical mass (see Fig. 1, B), which is at intervals passed forward towards the mouth to be eaten. As the food-mass approaches the mouth the animal shoots out the radula at it with the marginal teeth spread apart, but on striking the food-mass these teeth close in, and in this way obtain a hold on it. The radula is now retracted and the food is thus drawn into the pharynx where the mandibles assist in retaining it. The radula is then freed and again shot out at another part of the food-mass, grasping and drawing back another length. These operations are repeated until a length of the food-material is broken off from the main mass. The detached piece is then swallowed.

This is not the only way, however, in which food reaches the mouth. The majority of the larger particles of food-material, which are drawn in with the food-current, have a different fate. On entering the inhalent chamber they can be seen to be drawn forwards in a direction almost at right angles to the main current (see the small arrow in Figs. 1 and 2), and become gathered together in the food-pouch which is placed just in front of the mouth (see Figs. 1, A, 2, A, 4, A). In this pouch, which is really a deep groove in a semicircular fold of skin, the food is worked up with mucus into a pellet which may be eaten, but if considered undesirable as food, it is carried by cilia to the edge of the shell or pushed by the animal into the exhalent current. And, indeed, when a large quantity of food-material is suddenly drawn into the mantle cavity, the animal usually rejects the greater part of it by backing into the cavity, covering the gills posteriorly so as to cut off most of the current, and at the same time secreting a copious supply of mucus, in which the intruding material becomes caught, and carried in the current forwards. But instead of passing into the food-pouch, it is carried further forward into a ciliated path which is situated immediately in front of and parallel with the food-pouch and deposited at the extreme front of the shell (see Fig. 4, A). It has been noticed that the food-material gathered in the food-pouch is often rejected, while that in the food-groove is almost always eaten. Thus the food-pouch and forwardly directed current are a means for separating and transferring to the region of the mouth the larger food particles, and at the same time they may be utilized by the animal for getting rid of such heavier undesirable particles as may be taken into the inhalent chamber.

The mode of feeding may be easily observed by inducing individuals to attach themselves to glass, so that if fine particles of some coloured substance be added to the water, the whole of the details of the operations can be seen through the glass. Carmine powder suspended in a solution of methylene blue in seawater gives a good result, as the latter stains the mucus a little, and makes its presence the more easily detected. From the foregoing account of the mode of feeding of Crepidula there remains no doubt that Crepidula takes the same kind of food as the oyster.

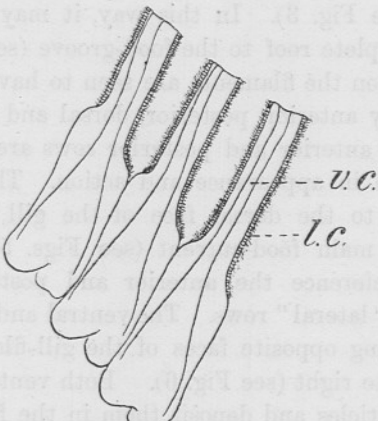


FIG. 3.—Ventral view of the tips of three gill-filaments from the anterior region. (Drawn from the living animal. × about 90.)

v.c. Ventral edge of the filament: the cilia are not represented.
l.c. Lateral cilia.
The notch in the tip of the filament permits the passage of food-particles to the ventral surface.

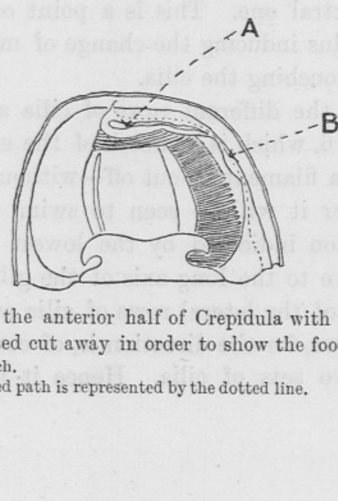


FIG. 4.—Ventral view of the anterior half of Crepidula with the "head" of the animal supposed cut away in order to show the food-pouch.

A. Food-pouch.
B. The ciliated path is represented by the dotted line.

III. MECHANISM CAUSING THE FOOD-CURRENTS IN CREPIDULA.

The main food-current is produced by the lashings of rows of cilia on the anterior and posterior faces of the gill-filaments. The filaments, it has been noted, stand out in a row from the left side of the mantle (seen in Figs. 1 and 2 below the small arrow), being each supported internally by a pair of chitinous rods (see Fig. 5, C). They are free, and placed a little distance apart so that water can pass between them. When examined separately they are seen to be flattened antero-posteriorly (see Fig. 5), except at the tips, where they are flattened dorso-ventrally, so that at this part they touch the adjoining ones (see Fig. 3). In this way, it may be noted, the filaments form a complete roof to the food-groove (see Figs. 1 and 2, B). In transverse section the filaments are seen to have four rows of cilia (see Fig. 5), namely anterior, posterior, dorsal and ventral rows (compare Fig. 6). The anterior and posterior rows are formed by far the stronger cilia both in appearance and action. These lash the water from the ventral to the dorsal face of the gill, and are the chief producers of the main food-current (see Figs. 5 and 6, l.c.). For convenience of reference the anterior and posterior rows may be referred to as the "lateral" rows. The ventral and dorsal rows of cilia lash the water along opposite faces of the gill-filaments towards the tips, i.e. from left to right (see Fig. 6). Both ventral and dorsal rows gather the fine particles and deposit them in the food-groove, but the anterior and posterior rows also assist in this process, as may sometimes be seen when examining a living filament under the microscope, or even when examining the living animal with a lens. Therefore, when cilia of the anterior and posterior rows wash food towards the food-groove, the direction of their lashing is changed from a ventro-dorsal to a laevo-dextral one. This is a point of some interest, and apparently the stimulus inducing the change of motion is supplied by the particles merely touching the cilia.

The way in which the different rows of cilia act may be gathered from a glance at Fig. 6, which is a sketch of the end of a gill-filament.

If such a piece of a filament be cut off—without the flattened tip—and observed in water it will be seen to swim, when unimpeded by mucus, in the direction indicated by the lowest arrow in the figure. This direction, relative to the long axis of the gill, gives some idea of the relative strength of the lateral rows of cilia as compared with the dorsal and ventral rows, for the direction is, of course, the resultant of the action of the two sets of cilia. Hence it is apparent that the lateral cilia are by far the stronger, just as one would expect to find, seeing that they have to draw a current of water through the mantle cavity, while the other rows merely pass on the food-particles.

The ventral rows of cilia lash in a direction from left to right, and, as has already been remarked, are the main collectors of the fine food-particles. The dorsal rows of cilia lash in the same direction as the ventral rows, but on the opposite face of the gill; whatever particles are passed on to them by the lashings of the lateral cilia they wash along the dorsal face of the filament, through a notch in the tip of the latter (see Fig. 3), and round to the large cilia on the ventral surface (see Fig. 6). The dorsal cilia, however, also assist in maintaining the food-current, and in modifying the direction of the current formed by the "lateral" cilia, for a glance again at Fig. 6 will show that the resultant direction of the water current produced by all the cilia on the gill is in a direction opposite to that in which the free filament swims. Thus, in the living animal the effect of the dorsal cilia on the current on its passing through the gills is to turn it towards the right, namely, towards the exhalent aperture (see Figs. 7 and 8). The groups of large cilia on the ventral tips of the filaments are probably the chief agents in pushing the collected food forwards towards the mouth, being assisted in this by the cilia in the food-groove. The tips of the filaments are covered all over with cilia; those on the anterior and posterior faces doubtless assist in interlocking the filaments.

In connection with the gill-filaments, there still remains to be considered the action of those cilia which occur on the floor of the posterior part of the mantle cavity, that is, on that part of the mantle lining the dorsal surface of the visceral mass. In this region the cilia wash particles from left to right into a ciliated path on the right side, which path is continuous with the food-groove (see Fig. 2, B) in the anterior region. The mantle to the right of the ciliated path bears cilia which lash particles into the same path, working however in a direction mainly dorso-ventral.

The cause of the forwardly-directed current at the anterior end of the inhalent chamber is found in the presence of strong and active cilia on the lips of the food-pouch, on the inner side of the mantle, and especially those on the dorsal surface of the left epipodium. The food which is washed forwards by these groups of cilia is directed into the food-pouch chiefly by the cilia on the dorsal lip of the latter, but it is pushed along inside the pouch by cilia, being assisted in this, however, by slow, wave-like pulsations of the side-walls. In the capture of food-particles there is no doubt that the secretion of mucus for entrapping the particles is a very important factor, and a more correct

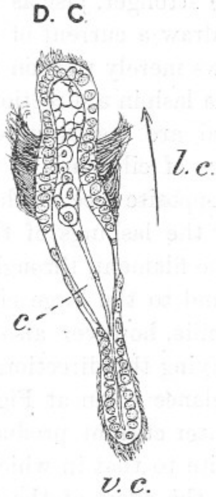


FIG. 5.—Transverse section of a gill-filament of Crepidula from the visceral region. (× about 67.)

D.C. Dorsal cilia; l.c. Lateral cilia, which lash in the direction indicated by the arrow; v.c. Ventral cilia; c. Gill-filament supports.

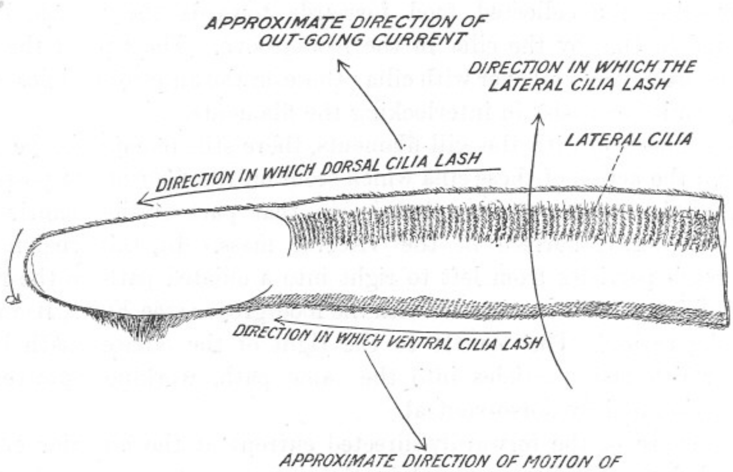


FIG. 6.—Posterior view of a gill-filament of Crepidula. (Drawn from a living filament of Crepidula. × 50.)

idea of the forward movement would be conveyed if one imagined a sheet of mucus bearing the food-particles being both drawn and passed onwards into the food-pouch.

The question now arising as to why the larger food-particles should be caught in mucus and carried forwards, while the finer particles travel onwards to the gill, is easily answered, but it is necessary first to obtain a fair idea of the spacial relation of the inhalent chamber. Fig. 7 is a transverse sectional diagram of the inhalent chamber, and Fig. 8 a longitudinal sectional diagram, A in both figures indicating the position of the forwardly directed stream in the inhalent chamber.

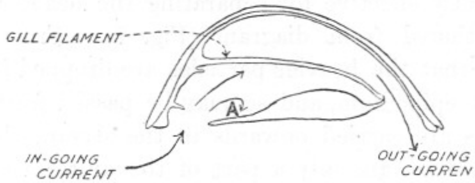


FIG. 7.—Diagram of the special relations of the mantle cavity of Crepidula in transverse section, taken just anterior to the propodium.
A indicates the position of the forwardly directed stream.

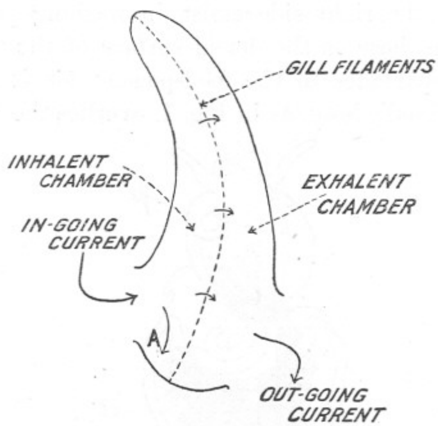


FIG. 8.—Diagram of the general spacial relations of the mantle cavity of Crepidula in median longitudinal section. The inhalent and exhalent apertures are represented, although not actually occurring in the section.
A indicates the position of the forwardly directed stream.

It will be seen that the area of the inhalent aperture is relatively small, and that there is a sudden widening out at this point of the path of the inhalent stream. Consequently, when a current is passing through the mantle cavity the velocity of the stream must fall just inside the inhalent chamber, and as a result the larger particles tend to lag behind and sink in the stream. As they sink they come within the influence of the forward stream caused by the cilia on the food-pouch, mantle and left epipodium, and becoming eventually caught in this stream (see the small arrow A in Figs. 7 and 8) are carried forwards into the food-pouch. From the disposition of the cilia causing the forward stream, it is possible for the coarser food-particles always to be carried forward, no matter whether the animal be placed upside down or any other way, but if the animal be upside down a fairly copious secretion of mucus becomes necessary to capture the particles. In the normal position of the animal, however, that is, with the ventral surface downwards and facing a little to the left, the disposition of the parts is beautifully effective for separating the heavier food-particles, as may be gathered from diagram (Fig. 7). From this diagram it will be seen that the heavier particles are dropped into the ciliated path on the left epipodium, and so may be passed forwards while the lighter particles are carried onwards in the stream above. The cilia on the left epipodium are only a part of the uniform covering of cilia on the dorsal surface of the animal's "head" and "neck." The disposition of the cilia on the remaining parts, and the directions in which these lash, may be gathered from a glance at Fig. 9. It will be noticed that the cilia on the right side assist in washing particles into the food-groove, while those on the dorsal surface of the "head" assist in transferring food-particles to the food-pouch; for it will be remembered that the animal's head, as in Fig. 1, overlies the food-pouch.

FIG. 9.—Dorsal view of a male Crepidula taken out of its shell and drawn from life, with the mantle turned back. The arrows indicate the directions in which the various groups of cilia lash. (Natural size.)
ct. Gill filaments.

IV. SUMMARY OF ACCOUNT OF CURRENT-PRODUCING MECHANISM, AND MODE OF FEEDING IN CREPIDULA.

The mode of feeding in Crepidula is thus seen to be as follows:—A main food-current is produced through the mantle cavity by the lashings of rows of cilia on the anterior, posterior, and dorsal surfaces of the gill-filaments; the current entering the mantle cavity on the left at the front of the shell passing between the gill-filaments and out at the front of the shell on the right. On entering the inhalent chamber, however, the velocity of the stream falls owing to the widening out of its path, so that while the heavier food-particles tend to be dropped out of the current, the lighter particles travel onwards towards the gill. On coming in contact with the gill these particles are either caught by the cilia or in mucus secreted by the gill, and swept by the rows of cilia on the ventral and dorsal faces of the gill-filaments towards the tips of the latter, and deposited in a ciliated groove on the right epipodium, which groove is efficiently roofed in by the flattened tips of the filaments. In the groove the food becomes worked up with mucus into a cylindrical mass which at intervals is passed forwards towards the mouth to be eaten. In the process of eating the food is seized and drawn into the buccal cavity by means of the radula, and there retained by means of the mandibles prior to being swallowed. The heavier food-particles, however, reach the mouth by a different route. On falling out of the main stream they are caught in the forwardly directed stream caused by the combined lashings of several groups of cilia, namely, those on the left dorsal region of the animal's "head" and "neck," those on the face of the food-pouch, and those on the left anterior border of the mantle. This stream is directed into the pocket of the food-pouch by the cilia on its dorsal lip where the captured food becomes worked into a pellet and deposited in front of the mouth for eating. If, however, the animal is not wanting food, the entrance to the food-groove is closed, and the stream is directed out of the mantle cavity by way of a ciliated path parallel to the left anterior edge of the mantle. In front, this ciliated path runs parallel with the pocket of the food-pouch (see Fig. 4, B), but behind, it is placed on a fold of skin somewhat similar to that forming the food-pouch. If a large quantity of foreign material be drawn into the mantle cavity, the ciliated path may be formed into a channel by the infolding of the edge of the fold on which the path lies posteriorly, but in front by the raising up of the mantle along the sides of the path. At the same time, the animal shuts off the food-current by closing the mantle cavity, and by covering the gill by the body, confines the intruding material to the forwardly directed stream, and is then able to reject it. Should large bodies get into the mantle cavity, the animal tries very hard to get behind them, and when it does so, pushes the intruding material bodily in front of the lips and extended tentacles out of the apparently sacred precincts of the inhalent chamber into the exhalent chamber, or even right outside the mantle cavity. Intruding air-bubbles have often been seen to give the animals great trouble in this way. In trying to clear the chambers the animal shows some ingenuity in trying different plans, but apparently also some stupidity in not widening the exits by raising the shell, and so making its task an easy one.

V. FUNCTION OF THE RADULA IN CREPIDULA.

In the process of feeding it will now be seen that the radula plays a very important part; it is used for seizing and conveying to the pharynx all the food that the animal takes; while the mandibles, it may be noted, assist in retaining the food temporarily in the pharynx.

Thus the radula of Crepidula, far from its being, as I thought, an obsolete organ, is one which is in constant use and of the first importance in the life of the animal, but, instead of its being used for rasping, as in its allies and presumably in its ancestors, it is now used for grasping. The function of the radula in Crepidula has therefore changed, and the failure to imagine the probability of such a change led me to a wrong conclusion with regard to its present importance to the animal. The change in function is, however, interesting, as it adds one more instance to the economy practised by nature in making use of the material that is to hand. Signs of degeneration in the radula are nevertheless appearing, as may be gathered from the following independent observations by Haller (5): "Die Auffallende kurze Radula (*of species of Crepidula*) liegt in einem sehr dickwandigen Radularsacke. Der Munddarm und die Buccalmasse ist bei allen von mir un tersuchten Calyptraeiden ungemein klein." Hence one might expect to find among the allies of Crepidula some forms which are evolving out of their radular apparatus a more efficient organ adapted to the present needs; and such a change is the more to be expected as the radula is a specific variant in the group to which the animal belongs.

VI. RESEMBLANCE OF THE FUNCTION OF THE GILL OF CREPIDULA TO THAT OF THE LAMELLIBRANCH GILL.

A change in function—or rather an additional function—has also been taken on by the gill of Crepidula. The ancestral gill was probably mainly an organ of respiration, but now the gill serves also as a food-collector. The gill of Crepidula has, therefore, exactly the same function as that of typical Lamellibranchs. The phenomenon is thus apparently presented of two independent trends of evolution arriving in principle at exactly the same result: both groups of animals having utilized the respiratory organ in a similar way as a water-pump and as a food-sieve.*

VII. THE MODE OF FEEDING IN THE OYSTER AND OTHER LAMELLIBRANCHS.

The mode of feeding in Lamellibranchs has been described by several writers. Stenta (6) described a number of forms fairly fully. Kellogg

* If, however, the gill of the ancestors of Lamellibranchs and Gastropods were already a food-collecting organ—as seems possible from the observations here made on the gill of Nucula and many Gastropods (see pp. 467–73)—then the "convergence" is homogenic and not homoplastic.

(7 and 9) has treated other forms in more detail; and about the same time Herdman and Hornell (10) described the mode of feeding in the Ceylon pearl oyster.

The following description of the mode of feeding in the European oyster contains little that has not already been noted by these writers in similar forms. The native oyster (*Ostrea edulis*) draws a food-current into the mantle cavity between the mantle lobes antero-ventrally. The current does not enter along the whole of the ventral surface, however, when the animal is feeding normally, but only in a small restricted part such as is indicated in Fig. 10. It is only in this part that the ventral edges of the mantle lobes are not apposed, and the opening thus produced forms practically an inhalent aperture. The outgoing current leaves the mantle cavity postero-dorsally (see

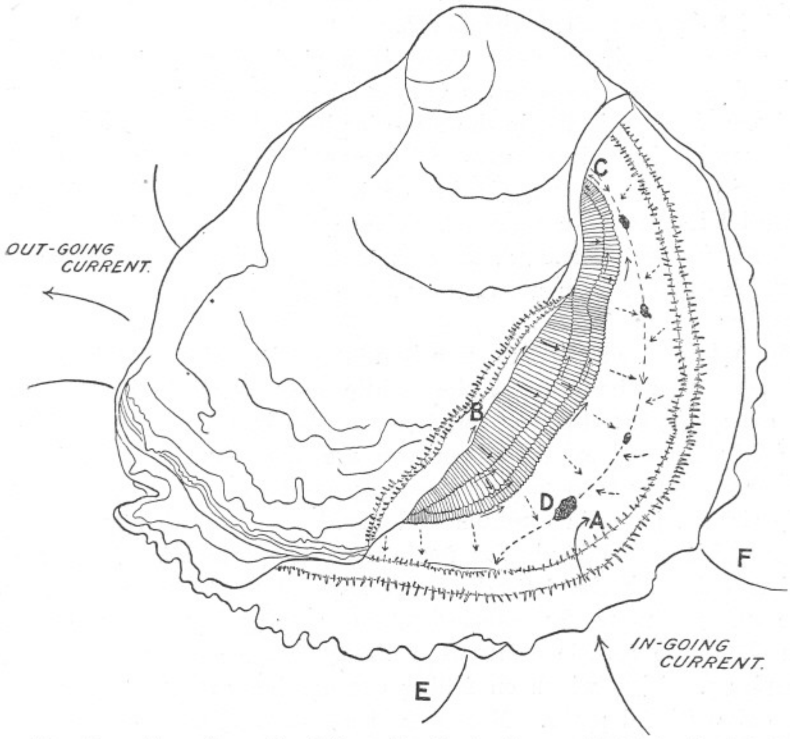


FIG. 10.—View of mantle cavity of the native Oyster (*Ostrea edulis*) from the right side to show the food currents. (Drawn from life, natural size.)

The ingoing current enters the mantle cavity between the points E and F.

The dotted arrows indicate the directions in which the mantle cilia lash.

The arrows on and at the edges of the gill-lamellae indicate the paths of the main food-streams.

A. Point at which the heavier particles begin to fall out of the main food-stream.

B. Minor food-stream at the base of a gill-lamella.

C and D. The ciliated path on the mantle which carries away food-material rejected by the palps and the particles collected from the mantle.

E and F. Region in which the oyster commonly takes in its main food-stream.

Fig. 10). On entering the mantle cavity the path of the ingoing stream is suddenly widened (see Fig. 14) and, as is the case in Crepidula, the heavier particles drop out of the current. These particles, however, are collected by the mantle cilia into a definite ciliated path, the cause of the "untere Rückenström" of Stenta, which conducts them posteriorly to a point in about the middle of the inhalent chamber (see Fig. 10), whence the intruding material is expelled at intervals by sudden flappings of the shell-valves. This stream is protected, or rather rendered possible, by the infolded mantle edges, which shield it from the main stream. Those particles which fall on the mantle in the posterior part of the inhalent chamber are washed ventrally, and are either shot out of the mantle cavity at any point, as indicated by the arrows in Fig. 10, or are caught up by the gill and carried forwards towards the mouth.

In the American oyster there is a similar, posteriorly-directed ciliated path on the anterior half of the mantle, but according to Kellogg (7) there is also in the posterior half of the inhalent chamber a forwardly-directed current, which carries intruding bodies forward to the point where the current in the anterior part deposits whatever material it may have collected. The whole of the foreign particles collected by the mantle are then expelled at the point where the two paths meet, that is, in about the middle of the edge of the inhalent chamber.

In Mytilus and Cardium (see Stenta, 6) the ciliated path collects particles from the whole of the mantle and washes them posteriorly into the exhalent chamber, but here, as also in *Glycimeris glycimeris*, the inhalent and exhalent apertures are more definite than in the oyster, both apertures, however, being posterior (see Figs. 11 and 12). The ciliated paths in Cardium and Mytilus are excellently arranged for expelling intruding bodies, for in the natural feeding position these animals lie with the ventral surface apposed to the substratum, and the current enters the mantle postero-ventrally. Hence the whole length of the mantle cavity is utilized for the weeding out of the heavier particles, which on falling out of the current drop straight into the ciliated paths. Moreover, there is in Mytilus in the dorsal angle of the inhalent aperture a fold of epidermis forming a sort of curtain (see Fig. 11, B) which prevents the ingoing current from impinging directly on to the gills by directing it ventrally. In this way there doubtless results a more effective selection of the coarser particles. In Cardium a semicircular fold of the mantle between the inhalent aperture and the posterior ends of the gills (see Fig. 12, B) doubtless assists in the automatic selection of the heavier food-particles in the same way as the "curtain" in Mytilus. In Pecten water is drawn into the mantle cavity along the whole of the ventral and part of the anterior surface, but chiefly in two restricted areas. One of these areas is indicated by the large arrow pointing to B in Fig. 13, and the other is shown approximately by the large arrow passing near A, Fig. 13. The ciliated path on the mantle in Pecten collects particles from the whole of the ventral region of the mantle (see the dotted line C A B in Fig. 13) and washes them anteriorly to the edge of the mantle (see Fig. 13, B), whence they are expelled along with the material rejected by the palps.

While the heavier particles are dropped out of the current just inside the mantle cavity in the oyster, the finer particles travel onwards in the stream until they reach the gill, which retains them while allowing the current to pass onwards into the exhalent chamber. The food-particles drawn against the gill-filaments are caught in the mucus secreted by the gill and washed to the distal edges of the gill-lamellae, where they are formed into a cylindrical mass. This mass is then pro-

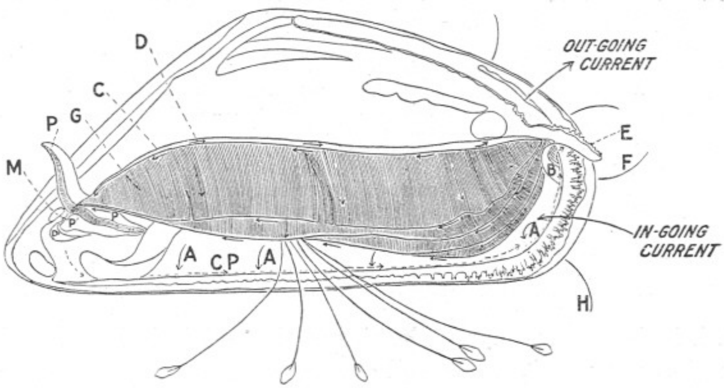


FIG. 11.—View of the mantle cavity of the common mussel, *Mytilus edulis*, from the left side to show the food-currents. (Drawn from life, about natural size.) The arrows on and at the edge of the gill-lamellae (G) indicate the paths of the main food-streams.

C.P. The dotted arrows and line at the ventral edge of the mantle indicate the ciliated path which carries the material rejected by the palps and that collected from the mantle to the point indicated by the arrow above B in the figure. Here the rejected material is pushed into the exhalent current.

A. Arrows indicating the paths of the heavier particles settling out of the main food-stream.

B. A sort of curtain hanging from the dorsal part of the inhalent aperture.

C. The line of attachment of the mantle to the body-wall.

D. Arrows in the supra-branchial chamber indicating the direction of the exhalent current.

E. Uplifted left border of the inhalent aperture to show the curtain, B.

F.H. Points between which the main food-current is drawn into the mantle cavity.

G. Left outer gill-lamella.

P.P. Left palps between which the edges of the left gill-lamellae may be seen to end.

P^1P^1 Right palps.

M. Locus of the mouth.

pelled along its somewhat precarious journey towards the palps by the cilia in the open food-groove which is found along the distal edges of the gill-lamellae of the oyster, and indeed of most other Lamellibranchs (compare Figs. 14 and 15).

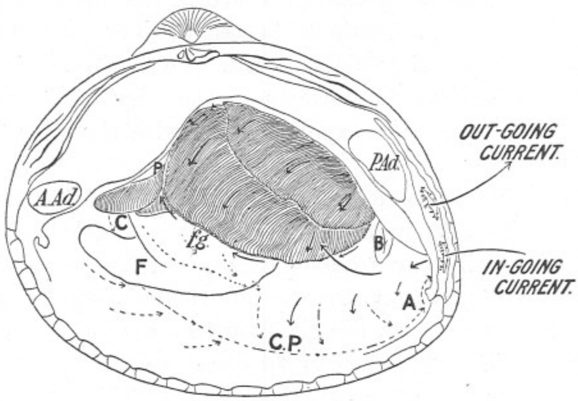


FIG. 12.—View of the mantle cavity of the common cockle, *Cardium edule*, to show the respiratory current and the currents connected with the mode of feeding. ($\times \frac{3}{2}$.)

C.P. Ciliated path on mantle which carries away the material rejected by the palps and that collected from the mantle.
A. Point at which heavier particles begin to drop out of main stream on to mantle, and also the region on the mantle whence the material collected by the ciliated path is finally shot out of the mantle cavity.
B. Gill-shield directing the ingoing current ventral-wards.
C. Point at which material is passed from the palps to the mantle.
fg. Food-groove at the ventral edge of the inner gill-lamella.
P. Left outer palp, below the base of which lies the mouth.
A. Ad. Anterior adductor. P. Ad. Posterior adductor.
The dotted arrows on the mantle and foot indicate the directions in which the cilia lash.
The arrows on and at the edge of the gill indicate the paths of the food-streams.

Such food-streams occur at the tips of the four lamellae, at the bases of and between the lamellae, and also between the outer lamellae and the mantle (see Fig. 14). The particles in the basal streams are mostly washed to the tips of one or other of the gill-lamellæ before reaching the palps, but in any case the streams on each side of the body eventually pour their burdens on to the palps, whence they are conveyed either to the mouth or directed into the ciliated paths if deemed undesirable as food (see Figs. 10 and 14). If the food is accepted, the palps separate so as to allow it to pass between. The cilia on the inner surfaces of the palps then quickly wash the food into the mouth. If the food is rejected, the palps remain apposed, and the cilia on their outer surfaces direct the food-mass on to the ciliated path on the mantle whence it is conveyed outside the mantle cavity.

In Pecten and Mytilus the upturned edges of the outer gill-filaments touch the mantle during feeding, and in this way form at this point a temporary food-groove. Otherwise the food-streams in these forms are similar to those of the oyster. In Cardium the frontal cilia on the outer gill-lamellae lash towards the edge of the gill on the outer faces

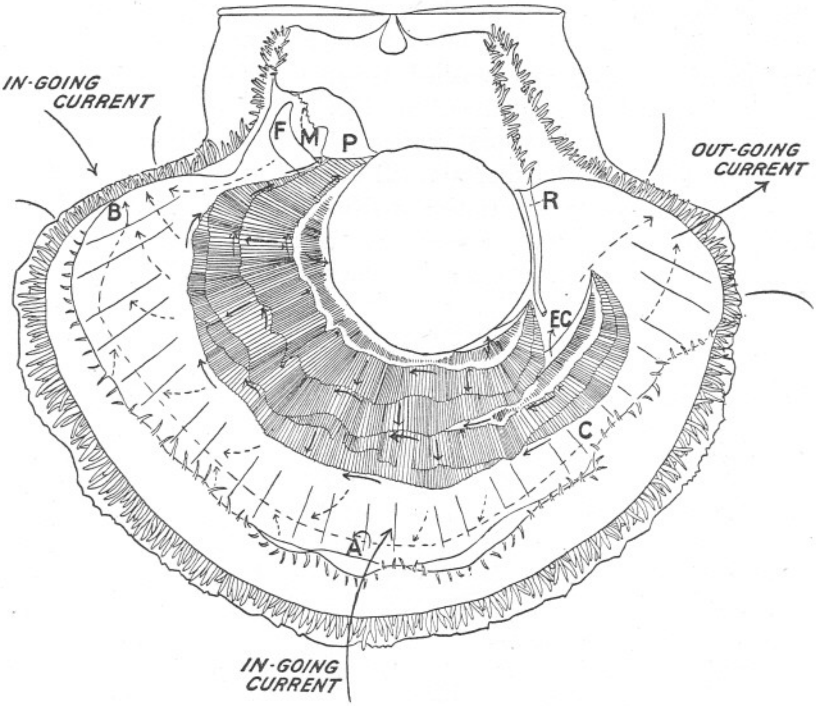


*FIG. 13.—View of mantle cavity of the scallop, *Pecten maximus*, to show the food-streams, seen from the left side with the mantle supposed to be cut away. (Drawn from life, natural size.) The posterior ends of the gills are somewhat retracted. In feeding, these spread across to the edge of the mantle and divide the cavity into inhalent and exhalent chambers.

The *dotted arrows* indicate the directions in which the mantle cilia lash, and the dotted line on the ventral part of the mantle between A and B indicates the ciliated path.

The *small arrows* at the edges of the gill-lamellae and of the reflected filaments indicate the paths of the main food-streams which lead to M, the region of the mouth. The arrows at the proximal ends of the gills, as at E C, indicate the direction of the exhalent current.

A. Point at which the heavier particles settle out of the main food-streams.
B.C. The ciliated path on the mantle.
E.C. Exhalent currents.
F. Foot.
M. Region of mouth.
P. Left outer palp.
R. Rectum.

* I am indebted to Mrs. Orton for this drawing, for assistance in the drawing of the oyster (Fig. 10) and also Fig. 14.

but towards the base of the gill on the inner faces. On the inner lamellae the frontal cilia on both faces lash particles towards the free edge of the gill into a well-defined food-groove. In Pecten, Kellogg has described that in the troughs of the gills particles are lashed towards the base of the gill, while on the crests particles are lashed towards the edge. On the other hand, Stenta has shown that in Anodon food-particles are washed towards the bases of the outer lamellae but to the tips of inner lamellæ. All these different modes of food collection and transportation may be indicated in diagrammatic form as in Fig. 14. This diagram will also indicate the mode of food-collection and food-transportation in Nucula. I find that in Nucula the gills divide the posterior region of the mantle cavity into infra- and supra-branchial chambers as in the higher Lamellibranchs. The

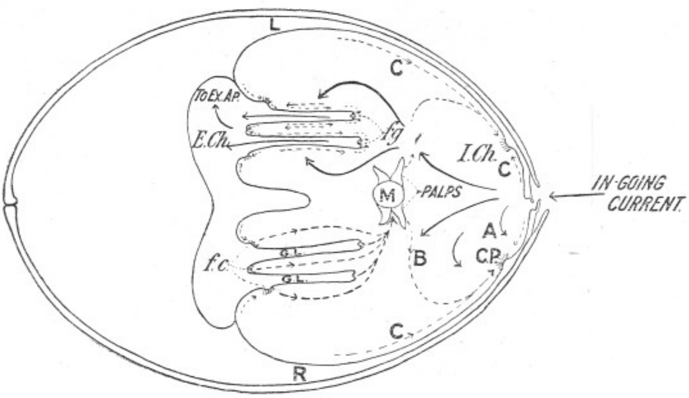


FIG. 14.—Diagram of the general mode of feeding in Lamellibranchs.

The large thick-lined arrows indicate the paths of the main respiratory and food-current.

The dotted thin-lined arrows indicate the directions in which the mantle and gill cilia wash the food-streams. The dotted thick-lined arrows leading from the right gill-lamellae indicate the paths of the main food-streams towards the mouth.

Food-collection is indicated on the left gill-lamellae, and food-transportation on the right gill-lamellae.

A. Point at which the heavier particles begin to settle out of the current.

B. The ciliated path on the mantle which carries away material rejected by the palps, and that collected from the mantle.

C.P. The ciliated path seen in section on the mantle.

C. The subsidiary mantle streams.

L. & R. Left and right valves of shell, and the beginning of the left and right mantle lobes.

f.g. Main food-grooves.

f.c. Food-channels at bases of gills.

I.Ch. Inhalent chamber.

E.Ch. Exhalent chamber.

G.L. Gill-lamellae.

M. Mouth.

To Ex. Ap. To exhalent aperture.

inner edges of the inner leaflets are apposed and kept interlocked by groups of large cilia (see Fig. 18, I.c.d., p. 468). The outer edges of the outer leaflets and the posterior ends of the gills effect similar ciliary junctions with the mantle by means of groups of large cilia (see Fig. 18, O.c.d.). In this way a complete partition of the mantle cavity is effected, and the ventral surface of this partition is utilized as in the higher Lamellibranchs for food-collection. Food-particles brought to the gill in the main current are arrested by the gill and washed along the edges of the leaflets from the outer leaflet to the inner (see Fig. 18). At the ventral end of the inner leaflets of both sides the collected food is washed anteriorly towards the mouth. Food-particles collected from the gill in this way appear to be gathered up by the appendages of the palps and transferred to the palps, which pass it along into the mouth. Food-particles may be rejected by the palps in Nucula in the same way as in other Lamellibranchs. Rejected food is pushed off the posterior end of the palps on to the foot, and off the posterior face of the foot on to the mantle. The mantle cilia in Nucula collect particles into anterior and posterior ciliated paths which converge at the middle ventral edge of the mantle just as in the American oyster. The observations on the mode of feeding in Nucula are still being carried on. In the light of the observations already made on Nucula, and especially of those on the ciliation of the gill (see page 467), it would be worth while to re-examine the mode of feeding in Yoldia. Drew (11, pp. 15 and 16) was unable to find out whether Yoldia uses its gills otherwise than for pumping water. If, however, the whole gill be examined alive while feeding it with carmine, the secret would soon be out. It is possible that the gill in this form may not be used for food-collecting, and if not, the condition is more interesting than if it is so used. However, from one of Drew's figures of the gill of Yoldia, although a general view (11, Fig. 20), there is good reason for believing that food-collecting occurs in the same way as is described here for Nucula.

VIII. AN EXPLANATION OF THE DIRECTION OF EVOLUTION IN LAMELLIBRANCHS.

The mode of feeding in Lamellibranchs, it will now be seen, necessitates the sedentary habits which are exhibited by most members of this group. Moreover, there can be no doubt that adaptation to the mode of feeding has been at least one of the main factors in determining the direction of evolution in Lamellibranchs. From the foregoing account of the gill of Nucula, it is clear that the gill in this form presents an early stage in the adaptation of the original respiratory organ to a food-collecting organ; and further, recent work (see Pelseneer, 12, pp. 253–4, and Ridewood, 13) has confirmed the conclusion that the higher Lamellibranchs have evolved mainly on the principle of folding and consolidating the originally simple free gill-filaments to form gill-lamellae. It will now be seen to be highly probable that this complication and fusion of the gill-filaments is an adaptation for the purpose of obtaining a more efficient feeding organ. Folding of the gill-filaments dorso-ventrally into demibranchs and—incipiently—antero-posteriorly into crests and troughs has increased the food-collecting surface, while fusion of the filaments first by ciliary junctions and afterwards by organic connections has rendered the food-collecting organ less liable to derangement. In the Filibranchs there is much danger of the gill-filaments becoming separated, whereby the continuity of the food-grooves at their tips is broken. As a result the animal may have difficulty in feeding, and its nourishment be thus seriously interfered with. Hence adaptations which ensure a firm gill would undoubtedly be advantageous—other things being the same—in preventing interference with the feeding process. The folding of the gill in an antero-posterior direction is also an adaptation in perfecting the feeding process, for by this means the food-collecting surface of the gill is further increased (see various figures by Ridewood, 13, pp. 242–263); moreover, greater opportunity is thereby given for effectively sieving the food-current, which has necessarily to pass more obliquely over the surface of the filaments to pass onwards into the exhalent current, thus giving the frontal cilia of the gill-filaments a better chance of capturing food-particles. It will also be seen that this folding results in the formation of secondary food-channels, thus the principal and apical filaments which occur in the troughs and crests respectively of the folds of the gills of many Lamellibranchs (see Ridewood, 13, p. 163) probably function mainly as the bearers of subsidiary food-grooves.

Along with the evolution of a more efficient food-collecting gill in Lamellibranchs there have occurred a gradual fusion of the ventral edges of the mantle lobes and a development of inhalent and exhalent siphons. It is highly probable that this fusion of the mantle lobes is primarily an adaptation of the same nature as the gill folding, that is, tending towards perfecting the mode of feeding. For in Mytilus, Glycimeris, and Ostrea, and doubtless also in many other forms, there is an attempt to limit the ingoing current to a definite area, and the effect obtained is that of limiting the area over which the heavier particles settle out of the food-stream to a part of the mantle adapted for expelling the undesirable material. In siphonate forms with the mantle fused ventrally such as the higher Eulamellibranchs, the whole of the ventral region of the mantle lobes may be utilized as a settling area from which undesirable material can be removed without interfering unduly with the normal feeding process.

IX. THE CURRENT-PRODUCING MECHANISM IN LAMELLIBRANCHS.

With regard to the cause of the main food-current in Lamellibranchs most writers are vague. Herdman and Hornell (10), however, have investigated *Margaritifera vulgaris* and state cautiously that in this species " the respiratory current is apparently due to the normal rhythmic lashing of the cilia on the large cells at the edges of the filaments; while the collection or the rejection of particles in the water seems to be the result of special action stimulated apparently by the irritation. Particles arrested by the branchial filter are caught up by the nearest cilia, which by local reversed lashing carry them outwards to the free ventral edge of the lamella."

In Crepidula it is easy to make out with certainty the direction in which the several rows of cilia are working, as the filaments—relative to those of Lamellibranchs—are large. In Nucula, Anomia, Mytilus, Glycimeris, Arca, Modiola and Pecten, I also find that it is fairly easy to make out that, as in Crepidula, the lateral cilia which lash across the length of the filaments (see Figs. 15 and 16) are the chief cause of the inhalent current, and that the "frontal" cilia which lash towards the free edge of the gill, collect the food-particles and wash them onwards towards the food-grooves at the edge of the gill (see Figs. 15 and 16).

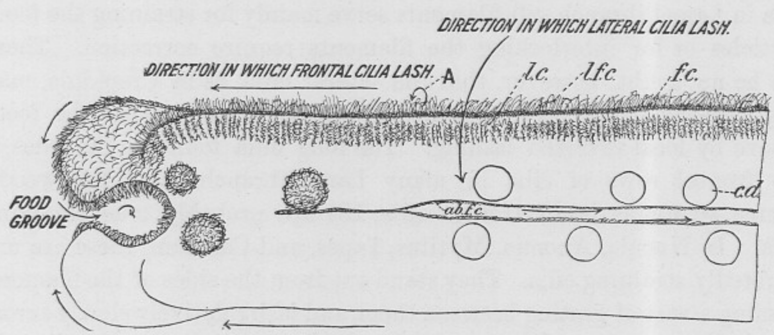


FIG. 15.—Lateral view of a living filament of the left outer lamella of the gill of *Mytilus edulis*. (× about 84.)

l.c. Lateral cilia. l.f.c. Latero-frontal cilia. f.c. Frontal cilia.
ab.f.c. Ab-frontal or inner cilia. c.d. Ciliated disc.
A. Arrow indicating roughly the direction in which the latero-frontal cilia lash.

In Mytilus there are also on the "inner"* or ab-frontal side of the filament cilia which lash in a direction opposite to that of the frontal cilia; they therefore help in producing the main current as in Crepidula. These cilia doubtless also assist in keeping clean the inner surfaces of the gill-filaments. The examination of living filaments of Mytilus revealed inaccuracies in the existing figures of the gill-cilia in this form (see Peck, 14) and Ridewood (13, Fig. 11, c, p. 201). Sections were therefore prepared from well-preserved material, and a drawing of one of these made for Fig. 17 (p. 467).

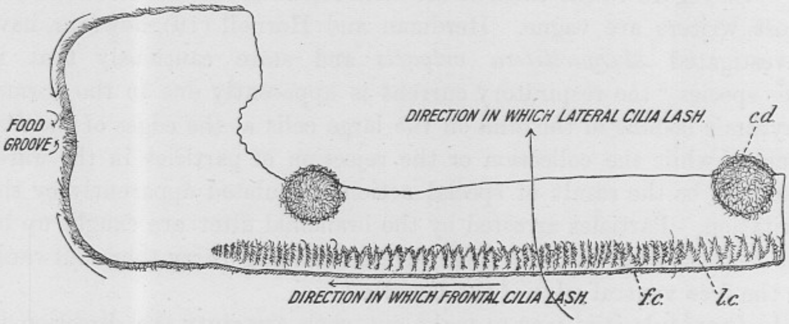


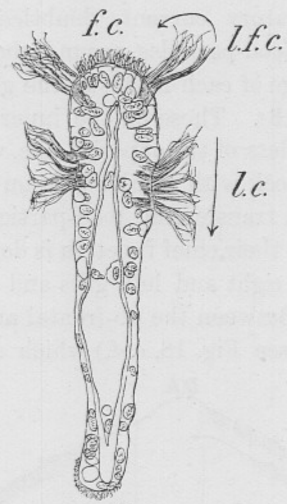
FIG. 16.—Lateral view of living filament of left outer lamella of gill of *Pecten maximus*. (× about 130.)
l.c. Lateral cilia. f.c. Frontal cilia. c.d. Ciliated disc.

On now comparing the ciliation in Ostrea, Tapes and Cardium, with that in the aforementioned forms, there can remain no doubt that the lateral cilia here also produce the main current by lashing across the length of the filament, while the frontal cilia collect the food-particles by lashing towards the free edge of the gill. Therefore the statements by Kellogg (9, pp. 416–423, see also 7, p. 36), and Pelseneer (12, p. 230) that the lateral cilia in Lamellibranch gill-filaments serve mainly for straining the food-particles or for interlocking the filaments require correction. There can be no doubt, however, that the lateral cilia, as in Crepidula, may help occasionally if necessary in washing particles towards the food-groove by local reversed lashing. The long cilia found at the sides of the frontal rows of cilia in many Lamellibranchs (see Ridewood's figures *passim* as latero-frontal cilia, 13) are probably true straining cilia. In Nucula, Anomia, Mytilus, Tapes, and Cardium, these are undoubtedly straining cilia. They stand out from the sides of the filament, forming a sort of grating between them, and lash relatively slowly across the length of and towards the middle of the frontal face of the filament (see Figs. 15, 17, and 18). Thus Nucula and Mytilus have four kinds of cilia, the lateral cilia producing the main current, the frontal for

* That is, the side away from the exposed face of the gill-lamella.

collecting and transporting the food, the fronto-lateral, which assist in food-collecting, and the ab-frontal or inner cilia, which help in producing the main current, in collecting food, and in cleaning the filaments.

Since the ciliation of the gill-filaments in all Lamellibranchs is essentially the same (see Ridewood, 13, p. 163) doubtless in all Lamellibranchs the main food and respiratory current is caused by the lateral cilia, while the collecting and transporting of food-material is done mainly by the frontal cilia, assisted by the latero-frontal cilia when these are present.



* FIG. 17.—Transverse section of gill-filament of outer left gill-lamella of *Mytilus edulis* taken near the free end of the lamella and between the ciliary junctions. (× 418.)

l.c. Lateral cilia which lash in the direction indicated by the arrow alongside.
l.f.c. Latero-frontal cilia which lash in the direction indicated by the arrow.
f.c. Frontal cilia.
ab.f.c. Ab-frontal cilia.

X. CILIATION OF THE GILL OF NUCULA.

The ciliation of the gill-plates of Nucula is, I find, essentially the same as that of the gill-filaments of Mytilus (compare Figs. 15 and 18). The lateral cilia are well developed, and, as in the other Lamellibranchs examined, produce the main current through the mantle cavity. The frontal cilia collect and lash food-particles from the tip of the outer towards the tip of the inner leaflet on both gills. The larger frontal

* This section was obtained from material preserved in Bouin's Picro-formol (see 19, p. 76) and stained in borax-carmine and picro-nigrosin solutions. Picro-nigrosin after picroformol or corrosive-acetic is an excellent stain for cilia.

cilia on the tips of the inner leaflets lash the collected food anteriorly towards the mouth. The latero-frontal cilia are also well developed and, as in Mytilus, stand out between the filaments, acting as strainers and lashing across the length of the filament away from the inter-filamentary spaces. These cilia are very large, and, *as in the case of all the cilia on gill-filaments, it is necessary to see them living to obtain an accurate idea of their size and function. And indeed all figures of gill-cilia ought to be corrected where necessary by comparison with the living object.* The ab-frontal cilia lash mainly towards the tip of each leaflet as indicated in Fig. 18, and besides helping in producing the main food and respiratory current, doubtless also assist in food-collecting, by lashing food-particles around the tips of either leaflet. On the outer dorsal edge of each leaflet of the gill of Nucula is a group of large cilia (see Fig. 18). Those on the inner leaflets interlock with similar cilia on the leaflets of the opposite side, while those on the outer leaflets doubtless interlock with similar cilia on the mantle. Probably these large cilia help in transferring food-particles from the dorsal to the ventral surface, but their chief function is doubtless that of effecting a junction between the right and left gills and between the gills and mantle respectively. Between the ab-frontal and lateral rows of cilia occur patches of cilia (see Fig. 18, *c. d.*) which are more numerous on

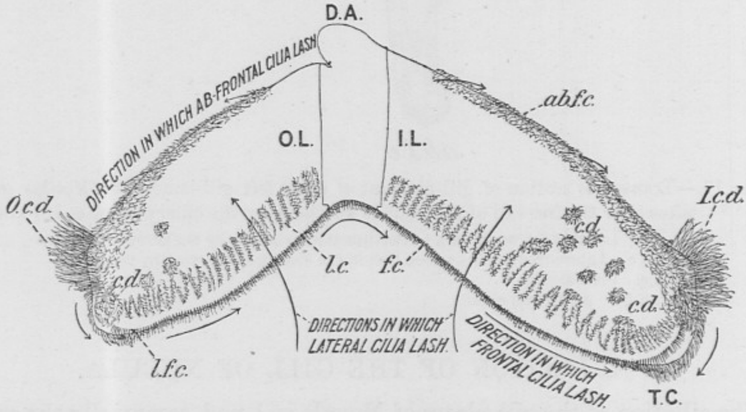


FIG. 18.—Anterior view of a living pair of leaflets of the right gill of Nucula. (× about 65.) The leaflets anterior to the pair depicted were cut away.

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.c.d. Cilia effecting a junction with the mantle.
T.C. Cilia which transport collected food forwards.

the inner than on the outer leaflets, and indeed are apparently often absent from the outer leaflets. These cilia arise from little spurs of tissue and have the same curious rotary motion as those which occur in patches on the gill-filaments of the Filibranchs. The action and distribution of these patches of cilia leave no doubt that they effect ciliary junctions between the leaflets in the same way as those of the Filibranchs effect junctions between filaments. There are also similar patches of larger cilia immediately below and to the side of the groups of the inter-locking cilia on the tips of each leaflet (see Fig. 18, c.d. below O.c.d. and I.c.d.). Doubtless these have also the function of interlocking the leaflets, and are similar to those occurring on the tips of the gill-filaments of Yoldia (see Kellogg, 9, Fig. 78) and *Anomia aculeata.* It is therefore evident that the gill of Nucula is undoubtedly less primitive as compared with the gill of other Lamellibranchs than has formerly been thought. A fuller investigation of this gill is being made.

XI. THE BEARING OF THE GILL CHARACTERS OF NUCULA ON THE RELATIONSHIPS OF THE PROTOBRANCHIA.

It is clear from the foregoing description that the gill of Nucula—and indeed those of Yoldia and Solenomya may be included—cannot now be regarded as being so primitive and unique as to justify the classification of the Protobranchia as a group co-equal with the Filibranchia. Ridewood has shown that the gill of *Anomia aculeata* consists on each side of two rows of filaments whose only difference from the leaflets of Nucula lies, I find, in their being narrow and filamentous instead of broad and lamellate. This obviously constitutes only a minor difference. Indeed, the occurrence of ciliated discs on the gill-lamellae of Nucula might fairly be advanced as evidence of higher specialization —along orthodox Lamellibranch lines—than occurs in the gill of *Anomia aculeata,* since the filaments of this species of Anomia appear to be without ciliated discs excepting at the tips. Further, the ciliated discs at the tips of the Anomia filaments are matched by similar ones in the gill-leaflets of Nucula, and the action and function of the various rows of cilia is, I find, the same in both animals. Moreover, the frontal cilia on the filaments of Anomia occur on the ventral surface as in Nucula, and those on the outer filaments lash in the same direction as in Nucula (see Fig. 18). Ridewood (13, p. 194) has shown that in this species of Anomia the posterior end of the gill on each side is free and that the inner filaments of each side interlock, and that the outer filaments form a junction with the mantle by means of cilia. All these features are found in the gills of Nucula (see Fig. 18).

Thus the one feature of Protobranchia regarded by Pelseneer as unique—the occurrence of gill-leaflets—is undoubtedly robbed of its glamour—and cannot now be reasonably regarded as of such great taxonomic value as formerly. Another supposedly unique feature of the Protobranchs, namely, the absence of a subdivision of the mantle cavity (see Sedgwick 15, p. 345), must be abandoned, for Drew has already shown that in Yoldia (11, p. 14) there is a subdivision of the mantle cavity into inhalent and exhalent chambers, as is here described for Nucula, and as will no doubt be found in all the Protobranchs. With regard to the other primitive or special features of Protobranchs, such as the occurrence of distinct pleural ganglia, a plantar surface to the foot, free communication between the cavities of the gonad, pericardium, and kidneys, and other features—with regard to these, Pelseneer has already shown (12, *passim*) that they are matched in some adult members of the Filibranchs with the exception of separate pleural ganglia, which at present are only known in the developmental stages of other forms (as Modiolarca, Dreissensia, etc. See Pelseneer 12, p. 234). It is therefore clear that the Protobranchs cannot now be classified as a group equivalent to the Filibranchs. We must therefore be prepared to degrade —or rather elevate—the Protobranchia to a subordinate position in the Filibranchia of Pelseneer, or in the Eleutherorhabda of Ridewood. It is a matter of much interest that Palaeontologists (16, p. 359) should already have classified together the Protobranchia and the remainder of the Filibranchs into the order of Prionodesmacea, whose diagnosis is concerned mainly with shell characters. As we may now take for granted that Lamellibranchs have evolved mainly on the principle of perfecting the gill as a feeding organ, it is clear—from the closely similar results attained by Palaeontologists and modern zoologists—that there is a close correlation between shell characters and gill characters. Whether the shell characters are capable of any functional explanation, similar to that of the gill characters, my knowledge of the group does not yet enable me to say. It is probable that such an explanation may now be possible.

XII. A COMPARISON OF THE MODE OF FEEDING IN LAMELLIBRANCHS AND CREPIDULA.

In Lamellibranchs, as in Crepidula, it has been noted that there is an arrangement whereby an automatic selection of the heavier particles takes place just inside the inhalent chamber. Thus the forwardly directed stream in the inhalent chamber in Crepidula is equivalent to that caused by the ciliated path on the mantle of Lamellibranchs; the purpose of the stream in both animals being that of expelling undesirable material from the inhalent chamber. There is this difference, however, that Crepidula, unlike the oyster, has the option of ingesting the automatically selected heavier particles. On the other hand, in the oyster and other Lamellibranchs the fringes of tentacles on the edge of the mantle form a coarse sieve by interlacing at the entrance to the mantle cavity, and in this way prevent the entrance of coarse particles; it is possible, however, that the particles collected on the mantle in Lamellibranchs might be picked up by the gill and conveyed to the mouth, as probably happens in the posterior region of the inhalent chamber of the oyster and the scallop. Both animals have still another opportunity for selecting their food-material, namely, by refusing the food-masses which are brought by the gills to the mouth. It has been observed that both animals do at times refuse such food, so that selection of food-material is undoubtedly exercised in this way. From my preparations of the gut contents of these two animals, I received the impression that those of the oyster were the finer, but as I have examined comparatively few specimens, it is doubtful whether that observation has any significance. It would be necessary to examine and compare a larger number of individuals to obtain a significant result. The fine food-particles are collected on the gill in both Crepidula and Lamellibranchs, and conveyed along food-grooves to the mouth, but Crepidula may be regarded as having gained an advantage over Lamellibranchs by closing in its food-groove, and thus ensuring the capture of the food. If disturbed while feeding an oyster would be much more liable to lose its food than Crepidula.

There is, however, an interesting difference in the position of the lateral cilia on the filaments in Crepidula and Lamellibranchs. In Crepidula these cilia are nearer the exhalent chamber (see Fig. 6, l.c., p. 452), while in Lamellibranchs they are nearer the inhalent chamber (see Fig. 18, l.c., p. 468). An explanation of these phenomena will probably be offered when more Gastropod gills have been studied.

It will now be apparent how remarkably similar Crepidula, its allies, and Lamellibranchs are in the details of their modes of feeding. The closeness of the resemblances they offer may fairly be regarded as an expression of the similar tendencies they have derived from their common origin.

XIII. THE MODE OF FEEDING IN THE ALLIES OF CREPIDULA.

The nearest allies of Crepidula doubtless all feed as Crepidula itself does. Such a deduction may fairly be drawn at once from the similarity in the mode of life of those animals and the general similarity of their organs in the region of the mantle cavity. I have examined *Calyptraea chinensis* alive, and find that it feeds in exactly the same way as does Crepidula, collecting food both in its epipodial food-groove and in a food-pouch.

Capulus hungaricus exhibits an interesting variation of the same manner of taking food. In this animal there is no epipodium nor food-pouch. But instead of the former the lips have become elongated in the form of a grooved proboscis, which appears to be held along the right side of the animal to collect the food-particles from the tips of the gills when the animal is feeding. The forwardly-directed stream is present on the edge of the mantle in the inhalent chamber, but the stream is relatively weak. There is an outgrowth of the foot between the propodium and the "neck" region, known as the "operculum," which appears to be used partly for side-tracking the food-current into the exhalent stream when the animal is not feeding, but I have not yet had the opportunity for investigating Capulus fully, and so must defer a detailed account until later.

The Hipponycidae are so similar in structure to the Capulidae as to have been placed with them at one time in the same Order, and as they live a sedentary life, it is almost certain that they will be found to feed in some similar manner to that of Capulus. There is, therefore, little doubt that all the Calyptraeidae feed in the same way as Crepidula, and that the Capulidae feed in a similar manner: thus there is good reason for suspecting that all sedentary Pectinibranchs may obtain their food in the same or in a similar manner.

XIV. THE CURRENT-PRODUCING MECHANISM IN OTHER GASTROPODS.

After seeing the gills of Crepidula, Calyptraea, and Capulus, and especially the latter, whose gill is very similar to that of most Gastropods, I was stimulated to examine all the sedentary forms to be had. But, on seeing Pelseneer's figures of sections of the gills of some Aspidobranchs (17, Figs. 99 to 104), I was induced to examine all the Gastropods available. It was found that in all the forms examined, namely, Fissurella, Haliotis, Calliostoma, Gibbula, Murex, Purpura, Nassa, Buccinum—in all these—the gill-filaments are ciliated in essentially the same way as those of Crepidula. There are generally present lateral, frontal and ab-frontal cilia, and the gill-filaments, or rather gill-leaflets, closely resemble those of the Protobranchs. The lateral cilia in all the forms examined produce the main current in the mantle cavity. The occurrence of frontal and ab-frontal cilia in all these forms is a matter of much interest. In all cases these cilia collect plankton from the ingoing current, but whether such collected food is eaten I am not yet able to say. It seems probable that all these forms may be found to feed partly on plankton. A research into this matter is being made. In some cases (namely, Fissurella and Buccinum) the gill undoubtedly divides the mantle cavity into inhalent and exhalent chambers as occurs in Crepidula and its allies. At the tips of the filaments in all these forms there are interlocking cilia similar to those at the tips of the gill-leaflets of Nucula. These cilia doubtless serve to effect a junction between the gill and the opposite wall of the mantle. Thus there can be no doubt that most Gastropods on further investigation will be shown to have the mantle cavity divided by the gill into two chambers.

A point of some interest presents itself at once on comparing the gill-filaments or gill-leaflets of the Aspidobranchs and many Pectinibranchs with the gill-filaments of Crepidula and Calyptraea, namely, that the gill-leaflets of the former bear the same relation to the filaments of the latter that the gill-leaflets of Nucula bear to the gill-filaments of the Filibranchs. Thus the Pectinibranchs already present the same range of gill-features that I propose should be united in the Filibranchiate Lamellibranchs. It may here be remarked that the similarity in the structure and function of the gills in Gastropods and Lamellibranchs shown by the foregoing observations, emphasizes that close relationship between these groups, which Pelseneer has already pointed out (17).

A cursory examination of the gills of Chitons indicates that rows of lateral cilia on the gill-leaflets produce the main current through the mantle cavity in a manner similar to that in Gastropods and Lamellibranchs.

XV. SIGNIFICANCE OF CHAIN FORMATION IN THE MODE OF FEEDING OF CREPIDULA.

It is well known that Crepidula has the curious habit of forming long chains by one individual settling on the back of another; as many as fourteen individuals may be found holding together in such a manner, and usually there is a gradation in size from the largest at the bottom to the smallest at the top.* Each individual does not sit in the *middle* of the back of the one immediately below, but with the right anterior edge of the shell touching the same part of the shell next below. As a result each animal topples over a little to the right of the one below it, so that the chains really form spirals (see Fig. 19). This arrangement has some relation to the mode of feeding, for by the toppling over to the right each individual is given a maximum area of water to draw on from the left side for its food-current, which it will be remembered is drawn in at the left. Moreover, the approximation of the right sides of all the individuals of a chain results in a combination of the exhalent currents, which must give excellent results in removing effete products from the chain. The combined exhalent currents will doubtless also assist the smaller individuals in the chain by reducing the pressure of the water in the region of the exhalent aperture, and thus enabling them to pass a greater volume of food-bearing water through their mantle cavities than they otherwise could.

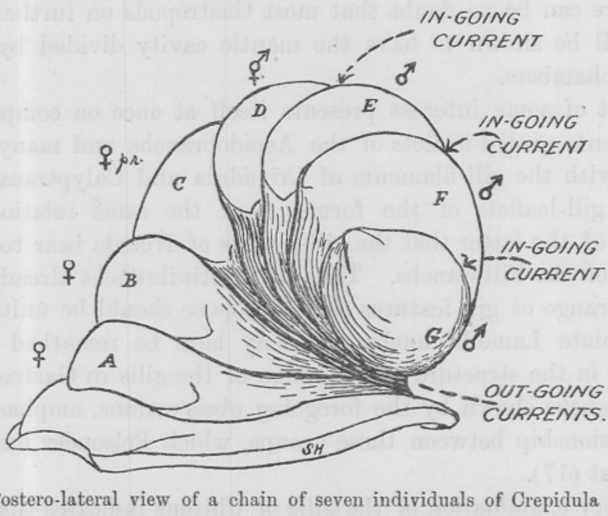


FIG. 19.—Postero-lateral view of a chain of seven individuals of Crepidula to show the separate ingoing and the combined outgoing current of all the individuals in the chain. (Natural size.)

These advantages of chain formation are to be added to those already noted (2, p. 479), and it may be remarked that the copulation of the smaller with the larger individuals there suggested as probable has now been observed a good many times, and contrary to what Prof. Conklin has suggested (1, p. 16), several times by the same individuals, and by individuals separated from each other by one or two of their fellows. These observations, however, are still being carried on.

* See (2) pp. 469–80 for a fuller description of chain phenomena.

In connection with the feeding habits of whole chains, an interesting adaptation has many times been observed: when a number of chains have established themselves on a surface of limited extent, as on a valve of an oyster-shell, the chains are to be found with their anterior ends towards the edge of the oyster-shell and their posterior ends all converging on the middle. Thus the animals are again found to be making the best use of the space at their disposal for ensuring an equally good respiratory and food-current to each member of the group.

From a consideration of the mode of feeding of Crepidula its habits are easily explained, and it is now easy to understand why all individuals but small ones run a great risk of death if they become dis-enchained, or detached from their surface of attachment. A detached individual with its mantle cavity exposed is unable to produce an effective respiratory and food-current, which along with some unknown cause which gives rise to the general discomfort usually exhibited eventually results in death. Moreover, if a new surface of attachment is offered, it is necessary for the animal to be able to fit its shell fairly well to it in order to have a chance of living. If, however, an animal be offered a surface to which it is able to accommodate its shell, I find that it is usually able to accept it, especially if the surface offered is smooth.

XVI. THE MANDIBLES OF CREPIDULA.

The location of the mandibles of Crepidula appears to have given so much difficulty that even Troschel confesses (18), "Die beiden Kiefer habe ich nur einmal bei *Crepidula fornicata* gefunden. Sie Können also leicht übersehen werden. Der eine Fund beweist dass sie vorhanden sind, und dass die Meinung diese Familie sei kieferlos welcher ich lange Zeit gehuldigt hatte, irrthumlich war."

During the foregoing research, however, a clue was given from the mode of feeding as to the probable position of the mandibles, so that it was possible to make a preparation to demonstrate them at once. As Crepidula in eating takes food into the mouth between the roof of the mouth and the dorsal surface of the radula, one would expect to find the mandibles in the dorsal wall of the buccal cavity. If this region be exposed after dissecting out the radula and its muscular apparatus, the mandibles are to be found lying transversely on a prominence near the mid-dorsal line and just behind the mid-dorsal anterior edge of the buccal cavity as in Fig. 20. They are easily found by following the above directions after soaking the head region in glycerine.

Troschel describes the mandibles and gives a drawing of them in the work cited. They are very small, being about ·7 mm. long and ·16 mm. wide in the widest part.

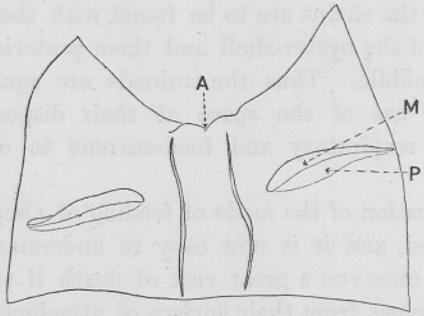


FIG. 20.—Ventral view of the roof of the mouth of Crepidula. (× 25.)

A. Middle part of anterior edge of the roof of the mouth.
M. Mandible.
P. Prominence on which the mandible is situated.

SUMMARY.

The gut-contents of Crepidula and the English oyster are similar with regard to skeletal remains, and the commonest diatoms found in both animals are the same.

Crepidula is a marine Pectinibranch which settles down at an early age to a sedentary life.

Crepidula feeds in the same way, in principle, as the oyster, i.e. a food-current of water is set up in the mantle cavity, while between the entrance and the exit of the current the pectinate gill acts as a food-sieve. The food-particles arrested in the inhalent chamber reach the mouth in one of two ways: the fine particles by way of a food-groove on the right side of the body, the coarse particles by way of a food-pouch placed in front of the mouth.

The radula is used for grasping the food-masses and conveying them into the mouth; its function has therefore changed from a rasping to a grasping organ, hence adaptational developments of the radula may be expected to occur in the allies of Crepidula.

The mode of feeding may be easily observed in detail by inducing animals to fix on glass and feeding them with carmine granules suspended in methylene blue solution in sea water.

The main food-current is caused chiefly by rows of cilia, the lateral cilia, on the anterior and posterior faces of the gill-filaments: the food-streams are caused by rows of cilia on the dorsal and ventral faces of the gills, by cilia on the dorsal surface of the animal, and by cilia on the inside of the mantle.

The gill of Crepidula, like that of Lamellibranchs, is at the same time a respiratory organ, a water-pump and a food-sieve.

The food-streams of Crepidula are comparable to those of Lamellibranchs.

A partial selection of the coarser food-particles is effected in the oyster—and Lamellibranchs generally—in the same way in principle as in Crepidula.

There are special morphological arrangements in Mytilus and Cardium to assist in the automatic selection of the finer food-particles.

The main food and respiratory stream in Lamellibranchs is caused by the "lateral" cilia on the gill-filaments, while the collection and transportation of food is effected mainly by the frontal cilia of the filaments. The latero-frontal cilia in Nucula, Anomia, Mytilus, Tapes, and Cardium, and therefore probably in all the Lamellibranchs in which they occur, are true straining cilia.

The gill-leaflets of Nucula and most Protobranchia possess similar cilia having a similar function to those on the gills of higher Lamellibranchs, and those of *Nucula nucleus* have also ciliated discs.

The gill of Nucula divides the mantle cavity into infra- and suprabranchial chambers, and the ventral surface of the gill is used for food-collection in the same way as in higher Lamellibranchs. Thus the gill of Nucula is essentially similar to that of some Filibranchs—for example, some species of Anomia and Dimya.

Hence the Protobranchia cannot now be considered as a group co-equal with the Filibranchia, and should be elevated to a sub-division of the Filibranchia.

Evolution in Lamellibranchs, which has occurred mainly on the principle of folding and consolidating the gill-filaments, comprises a series of adaptations tending towards a more perfect mode of feeding.

Calyptraea chinensis feeds in exactly the same way as Crepidula, and *Capulus hungaricus* feeds in a similar way.

Doubtless, therefore, all the Calyptraeidae, all the Capulidae, and there is reason to suspect that all sedentary Pectinibranchs, feed in the same or in a similar manner.

Most Gastropods have gill-filaments essentially the same in structure and function as those of Lamellibranchs, i.e. lateral cilia occur generally and produce the main current in the mantle cavity; frontal and ab-frontal cilia are found, and these collect food-particles from the ingoing current. In many Gastropods, and probably in most branchiate forms, the mantle cavity is divided by the gill into inhalent and exhalent chambers.

The manner of chaining in Crepidula is adapted to securing a good food and respiratory current.

The mandibles in Crepidula are to be found just behind and a little to either side of the middle of the anterior border of the roof of the mouth.

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