21 Published Articles on Zoology

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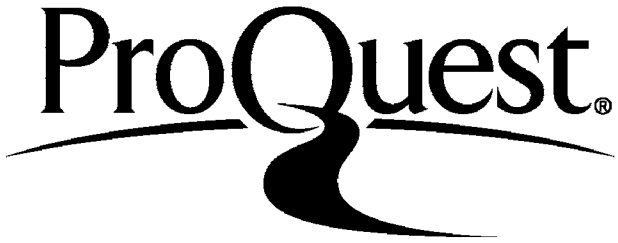

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Nature, vol. 117, 1926, pp. 415-6.

On Nocturnal Colour Change in the Pea-crab (Pinnotheres veterum).

While investigating the moulting stages of pea-crabs, a nocturnal colour change — analogous to that described by Gamble and Keeble in Hippolyte (Quart. Journ. Micros. Sci., 1900; Phil. Trans. Roy. Soc.,B, 1903,1905) - was observed by me in what is apparently Pinnotheres veterum. Last June I received from the Marine Biological Association, Plymouth, an ascidian (A.mentula) which had been dredged off the Mewstone, and from the branchial chamber of which a pea-crab had been found attempting to escape. By the time it reached me two crabs had escaped, a male and a berried female. These are most probably P.veterum.

P.veterum is the pea-crab which inhabits the Pinna of the Mediterranean and is also found in the large Pinna of the Salcombe Estuary in Devonshire. It has been recorded as well from parts of the Irish coast in Pinna and Modiola. P.veterum, however, is much less common than P.pisum, the pea-crab which is found living within the mussel (Mytilus edulis), as well as in other bivalve molluscs.

It so happened that the paper lining of the lid of the jar in which the ascidian and crabs travelled from Plymouth had become sodden and had fallen into the water in numerous small pieces. After the contents of the jar had been turned into a

bowl and allowed to rest for a while, it was noticed that the crabs had hidden themselves beneath the paper. When uncovered they proceeded to hide themselves again, sidling under the fragments, and throwing them on to their backs with their legs. The female being of considerable size (11 mm. in width) had more difficulty in hiding itself and made more use of its legs in placing pieces of paper on its back. Occasionally it was seen holding there fragments of paper, and once a tiny empty bivalve shell. The last two or three pairs of legs were used in these operations, and not the chelipeds, as perhaps one might have expected. The dactyli of the legs of this crab are long and curved. When in hiding the antennules were withdrawn.

At night the crabs came out of hiding and were very active. The female appeared at dusk; the male some while, an hour or an hour and a half, later. The nights being very short in June, the crabs were only active for a few hours out of the twenty-four. The more tardy male never showed itself until 10.30 P.M., and was hidden again soon after daybreak, about 5 A.M. Summer Time.

If at night the crabs were brought into the light they almost immediately made efforts to hide themselves. Their activity in the dark was accompanied in the male by loss of colour. In daylight or in a lighted room the dorsal surface of the male crab was a golden brown, shaded with dark brown, and more richly

coloured anteriorly than posteriorly. This coloration was due to the presence of orange and dark brown chromatophores, which in this condition were so expanded and their pigment so diffuse as to be almost invisible with a low power of the microscope. In the dark the male became pallid and transparent, the food in the stomach and intestine showing black and the testes white. This loss of colour is due to the retraction of the pigment in the chromatophores induced by the onset of darkness. When the chromatophores were quite contracted some faint yellow diffuse pigment was visible towards the centre of the carapace.

The orange pigment appeared to have a quicker rate of flow than the dark brown, and contracted to a smaller area; it is probable that it is lodged in a smaller cell than the dark brown. It appeared as irregular patches of reddish brown or deep orange pigment near the more dendritic or stellate dark brown chromatophores. The ventral surface of the male crab was pale, with very few chromatophores.

The female P.veterum had a dirty appearance, but seemed to have no definite colour, and after being in the dark there was no appreciable change in its appearance. I was unable to make out chromatophores in this female, though I have seen them in other adult females which had a definite brown colour.

It is interesting that the male P.veterum which suffered

nocturnal loss of colour only came out of hiding after it had been really dark some considerable time, while the female appeared at dusk.

During the day the experiment was tried of covering the crabs' bowl with something dark. This was done several times, and on a few - but not all - occasions the crabs came out of hiding in about forty to sixty minutes, the male gradually losing colour during this time. When the bowl was uncovered and the crabs exposed to light, the male took about the same time to recover its colour.

The crabs were kept under observation for about forty days. The conditions were unfavourable, for they were kept without change of water and without the addition of food. After about a month the male P.veterum failed to react to the stimulus of light, the chromatophores remained expanded at night and the crabs did not hide themselves during the day. It is hoped to continue the observations in the near future.

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The Moulting Stages of the Pea-Crab (*Pinnotheres pisum*).

By

D. Atkins.

D.Sc. Zoology 1939.

With Plates I–V and 4 Figures in the Text.

Reprinted from the Journal of the Marine Biological Association of the United Kingdom.
Vol. xiv., No. 2. August, 1926.

The Moulting Stages of the Pea-Crab (*Pinnotheres pisum*).

By

D. Atkins.

With Plates I–V and 4 Figures in the Text.

Pinnotheres pisum is a small crab with a carapace between about 2·1 and 18 mm. wide. The females are commonly found parasitic in the mussel, *Mytilus edulis*, though they have been recorded from other bivalves. The males are free-swimming and are comparatively rarely found in mussels. These small crabs are never abundant, and not more than one female has ever been found in a mussel.

Sexual Dimorphism.

It is well known that there is a marked sexual dimorphism in *P. pisum*. This is, no doubt, due to the difference in the mode of life of the two sexes, the male being active and free swimming, while the female is parasitic. Contrary to what usually occurs in the Brachyura, the adult male is much smaller than the adult female. The male has a carapace varying in width between 3·6 and 7·7 mm., while that of the female may reach a size of 18 mm.

Description of the Male.

Normally the males, young and adult, are of one form (Plate I, Figs. 1 and 2). A few abnormal crabs, however, have been found, and it is hoped to refer to them in a later paper.

The carapace of the male *P. pisum* is almost circular; very strong and hard and for the most part glabrous. It is very light grey or fawn in colour, with a conspicuous pattern of pale yellow areas outlined with darker yellow or yellowish orange. There is a slight variation of the pattern in different males; in the larger crabs the yellow areas increase in size and fuse to cover the greater part of the dorsal surface of the carapace. Lines and areas of colour also occur on the chelipeds and legs, while on the ventral surface are a few, more or less symmetrically placed,

pale yellow spots. There are frequently numerous black, with an occasional red, chromatophores scattered over the body.

The chelipeds (Plate IV, Fig. 15) are hairy ; the palms broad and rather swollen. There are two rows of setæ beneath the chela ; one reaches from the base of the palm to the tip of the finger, while that which is visible on the inner surface extends only slightly beyond the base of the immovable finger. These two rows are widely apart at the base of the palm, but converge distally. In the longer row the setæ, which point towards the tip of the finger, are stout and curved. A large tooth is present near the base of the dactylus, and fits a slight notch in the propodial finger. This notch has a small tooth at either end. Both biting surfaces bear stiff setæ, and towards the tips of the fingers small, closely set, spines. In some males the small teeth on the propodial finger are absent, as well as the curved spines from both fingers.

The walking-legs (Plate IV, Figs. 17, 19, 21) are strong, somewhat flattened, and exceedingly hairy, the long hairs being plumose. The second and third legs are especially hairy, the three distal segments bearing two thick fringes of very long hairs, one attached on the lower margin and one near the upper margin on the posterior surface. The extreme hairiness of the legs, as well as their flattened form, assists in maintaining a free swimming existence. The second and third legs are subequal in length, the second being slightly the longer. The first leg is the next in length, and the fourth leg the shortest. The short, curved dactyli end in short, horny tips.

The abdomen is narrow and tapering. Two small, transversely ridged, nodules of chitin are present on the fifth thoracic somite, and these fit into two pockets on the sixth segment of the abdomen. By this arrangement the abdomen is securely fastened to the thorax.

The copulatory organs of the male (Text Fig. 1) are large ; the first appendage is blade-like and hairy, with the tube, or rather the closed groove, running along its inner side. Numerous rosette glands are present round the lower portion of the groove. The second appendage is rod-like with a swollen base. The distal portion is normally carried within the groove of the first appendage. This stylet, unlike the first, is almost hairless, and is without glands.

Growth Stages of the Female.

The female occurs under two forms : the young female is almost indistinguishable from the male, while the next and subsequent stages are entirely different in appearance, and are what may be considered typically female in form. This change in form occurring between Stage I and II would appear to be related to the change in the mode of life, though

it would seem that it can only take place after copulation. One exception has been found among the material so far examined; a Stage I female more nearly resembling the female form than the male though with empty spermathecæ.

After the typically female form is assumed in Stage II, the further growth stages are mainly a development of those structures connected with reproduction, together with a general increase in size. Somewhat similar growth stages have been described for the female *Hapalocarcinus* by Potts (**6**).

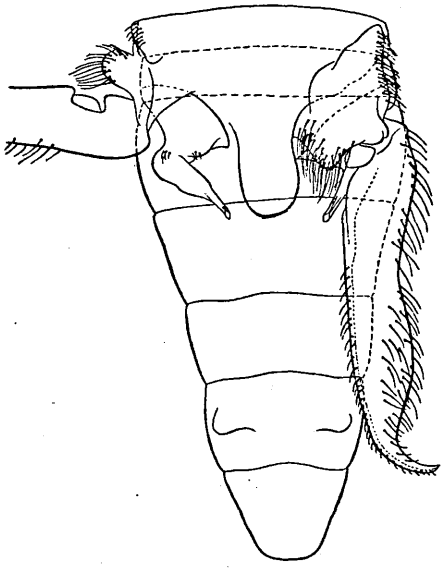

FIG. 1. Male abdomen and copulatory appendages. The first appendage of the right side is turned aside to expose the second appendage. Magnification, ca. 16⅔.

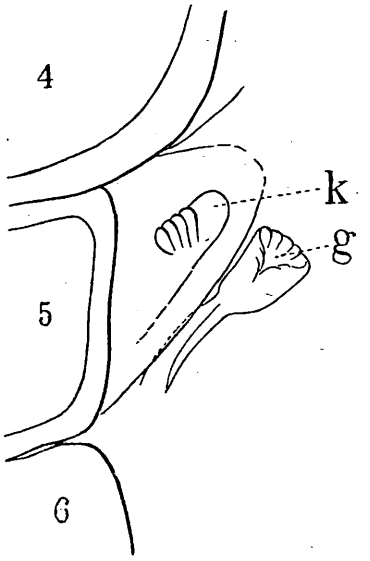

FIG. 2. Genital aperture and chitinous knob of right side of a Stage I female. g = genital aperture, k = chitinous knob; 4, 5, 6 = 4th, 5th, 6th thoracic somites. Magnification, ca. 71.

The female crab becomes parasitic in the mussel, *Mytilus edulis*. The parasitic life has exerted a considerable influence on the structure of the female, which is modified to a certain extent. It is large and extremely passive; the carapace with the rest of the exoskeleton being no longer needed for protection is soft and membraneous; the eyes are very minute, and in the fully adult crab invisible from the dorsal surface.

As noted by Orton (**4**) the female only reaches its adult form after passing through a number of growth stages. The greater part of the work recorded in this paper has been to determine these stages. The majority of them have been verified by a series of moults.

Stage I (Plate II, Figs. 3, 4). The young Stage I female, which has been found with a carapace varying in width between 2·1 and 4·9 mm., can only be distinguished from the male by the genital openings and the abdominal appendages. Indeed, the resemblance is so close that Orton (**4**) records that, on obtaining a female form moulted from a supposed male crab, he thought that he had a case of protandry until careful examination of the moult revealed the presence of the full number of abdominal appendages characteristic of the female. There is an exceedingly slight difference in the shape of the abdomen, which is a very little broader, and does not taper quite so much as in the male, while the sides of the segments are slightly convex. The locking apparatus is as well developed as in the male, and is very close to the oviducal apertures, which are on the sixth thoracic somite (Text Fig. 2). All four pairs of pleopods characteristic of the female are present, though not fully developed. The first two pairs (Plate V, Figs. 23, 24) are distinctly biramous, though there is not such a difference in length between the exopodite and endopodite of the first pair as there is in the adult. The third and fourth pairs are uniramous as in later stages. There are, at this stage, very few hairs on these appendages.

The ovary exists as paired narrow tracts of oocytes anteriorly ; these join in the thorax, then divide again to extend into the abdomen. The ovary at this stage is not visible externally.

Similar male-like females have been recorded by Rathbun (**7**) as occurring in the American species, *P. maculatus*, *P. margarita*, *P. taylori*, and *P. concharum*. These hairy, male-like females are probably at first free swimming, but after a time enter a mussel where copulation takes place.

Females of this stage have been found with spermathecæ full of sperm, others with spermathecæ empty (Plate II, Fig. 4), while again some have been found with one spermatheca full and one empty (Text Fig. 3). In this stage the oviducts are narrow and their external apertures very small, so that the accurate adjustment of the tips of the long first copulatory appendages of the male during copulation must be a process of considerable difficulty, as evidenced by the occurrence of Stage I females in which insemination is not complete, one spermatheca being empty. One of the crabs found in this condition was a tiny one with a carapace measuring only 2·1 mm. across (Text Fig. 3). The difficulty of the process must be increased by the great discrepancy in size which often exists between individuals of a pair.

It would appear, therefore, that copulation takes place during this stage ; that *P. pisum* is peculiar in copulating precociously at an extremely early age. The majority of the larger females examined have been found to have their spermathecæ full of mature sperm, but occasionally an

adult occurs with the spermathecæ almost if not quite empty. It is extremely probable that sperm from the first copulation is sufficient to fertilize several batches of eggs. The occurrence of an occasional adult female with empty spermathecæ, would seem to point to the possibility that copulation may take place more than once. Males have been found all the year round within the same host as females of all stages, including those in berry, though it has been found that " a newly moulted female (adult) appears to have no charm for a male " (**4**).

There would appear to be no relation in age and size between the male and female of a pair ; there is often a great difference, for young males

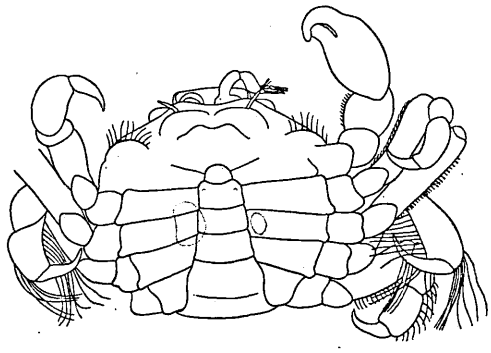

FIG. 3. Stage I female (carapace 2·1 mm. in width), with one spermatheca full and one empty. Stained with alum carmine and cleared in oil of winter green.

have been found with large adult females while the opposite may occur, though, of course, cases occur where there is little difference in size between individuals of a pair.

Orton (**4**) notes that : " It would appear that copulation normally takes place inside the host, and that the males visit mussels in their search for females, since unwary male crabs have been found with their legs or bodies trapped by the mussel closing its shell before the crab could get inside. These crabs survive the rough treatment by reason of their extraordinarily strong carapaces, and creep inside the mussel later when it must perforce relax and open its shell in order to breathe. The male-like female has a similarly hard carapace which prevents the animal being crushed to death if unluckily trapped by the mussel destined to become a host. Individual crabs have been found to be lacking a leg which might very well have been lost in this dangerous operation."

The change from the male-like female to the next stage is very striking. It undoubtedly depends upon and follows copulation, in this, offering a striking difference to Cancer (**5**), in which " ecdysis will not take place in

the female so long as there is a supply of spermatozoa in the spermatheca."

Stage II (Plate II, Figs. 5, 6). Females of this stage have been found with a carapace varying in width between 3·3 and 5·8 mm. The carapace is more or less circular ; thin and membraneous. It is translucent whitish or yellowish, without a colour pattern, although there are usually a few pale yellow spots on the ventral and dorsal surface. The front is as advanced, and the eyes are as well developed, as in the male and male-like female.

In this and the following stages the chelipeds (Plate IV, Fig. 16) are slender, the palms being reduced in width, and there is only one row of setæ on the lower edge of the chela. The walking-legs (Plate IV, Figs. 18, 20, 22) are more slender than those of the preceding stage, not so flattened and with very few hairs, though the degree of hairiness varies somewhat. The relative length of the legs is the same as in the male. The second and third legs bear only a scanty fringe of short hairs, attached near the upper margin on the posterior surface of the last three segments, which represents the much thicker and longer fringe present in the male.

The abdomen has increased in width, and is now more than half the width of the sternum. Anteriorly it extends beyond the chelæ sterna, but is very little further forward than in Stage I. The locking apparatus has disappeared. The pleopods are further developed and more hairy (Plate V, Figs. 25, 26).

There is a certain amount of variation between individuals of the same stage, which may be due to differences in general conditions. Three specimens (one crab and two moults) have been taken with the abdomen rather narrower than that of the specimen figured, but with no other difference.

All specimens so far obtained, belonging to this stage, have been found to have the spermathecæ densely packed with sperm.

Stage III. In this stage the abdomen has increased still further in width, and reaches further forward. The pleopods (Plate V, Fig. 27, 28) are rather more hairy than in the preceding stage.

Two variations of this stage occur :—

(*a*) The abdomen has increased greatly in width ; at its middle it overlaps the sternum, but anteriorly extends very little if any further forward than in Stage II. Two crabs, with carapace 5·0 mm. and 4·75 mm. wide respectively, having these characters have been obtained moulted from crabs of the previous stage. The one with carapace 5·0 mm. across is figured in Plate II, Figs. 7, 8.

(*b*) The abdomen is only slightly wider than in Stage II, but reaches further forward. The two specimens which have these characteristics

are both 5·0 mm. wide. The field note on the specimen figured in Plate II, Figs. 9, 10, is "trace of gonad seen through carapace." The second one showed no sign of gonad externally. It is thought that these two crabs should be placed in Stage III, but they have not been verified by moults.

Stage IV (Plate III, Figs. 11, 12). Females of this stage have a carapace varying in width between 6·5 and 16 mm. The carapace is rather wider than long; smooth, shining, and rather stiffer than in the preceding stages. Some specimens have yellow spots on the ventral surface and legs, others are without them. The spots appear to consist of three or four cells in a stellate arrangement. There may also be scattered black and red chromatophores on the dorsal and ventral surfaces, but in none of the stages after Stage I is there any indication of a colour pattern such as Bell (1) both describes and figures for the adult female of *P. pisum.*

The front is less advanced than in Stage III, and though the eyes are very small they are still visible from the dorsal surface.

The abdomen in this stage reaches just posterior to the propodites of the outer maxillipeds, when the latter are covering the mouth. The abdomen is broad and overlaps on to the coxopodites of the legs. It is deeply hollowed, as is also the thorax, though to a less extent. The abdominal appendages are well developed and hairy (Plate V, Figs. 29, 30). The exopodite is rudimentary in the first pleopod, but very long and blade-like in the second. Hairs are present along the edge of the abdomen and sternum, and there is also a slight growth of hairs stretching in a semicircle across the thorax between the chelipeds, following the outline of the terminal segment of the abdomen. Scattered rosette glands occur on the pleopods and on the inner surface of the abdomen.

The degree of development of the ovary, of course, varies in different crabs. In specimens in which there are a considerable number of yolk-laden eggs, the ovary shows a deep red through the carapace, and where it has attained its full development it occupies the greater part of the body space, and almost the entire dorsal surface of the carapace appears of a deep red colour. The ovary extends nearly to the tip of the abdomen.

Stage V (Plate III, Figs. 13, 14). Females of this stage have been found between 9 mm. and 18 mm. wide. The carapace is wider than long, and often rather quadrilateral in shape. The front is very narrow, about one-fifth the width of the carapace, and is hardly visible from the dorsal surface. The eyes are feebly developed, being very minute and quite invisible from above.

The abdomen is rather larger than in the preceding stage. Laterally it overlaps on to the basipodites of the legs, while anteriorly it completely covers the mouth parts, reaching just posterior to the eyes. When the crab is feeding the last segment of the abdomen is bent rather sharply

inwards, so that the mouth is uncovered. The abdomen is deeply hollowed, as is also the thorax. Longer and more numerous hairs are found at this stage, on the edge of the abdomen and of the sternum, between the bases of the chelipeds and on the pleopods.

There is not a very great difference between Stage IV and Stage V; some crabs have been found with the abdomen reaching as far forward as in Stage IV, but as wide as in Stage V and vice versa. The variation in the degree of concavity of the abdomen may account for this difference, or it is possible that reproduction may take place in Stage IV, and that growth may go on after reproduction has commenced.

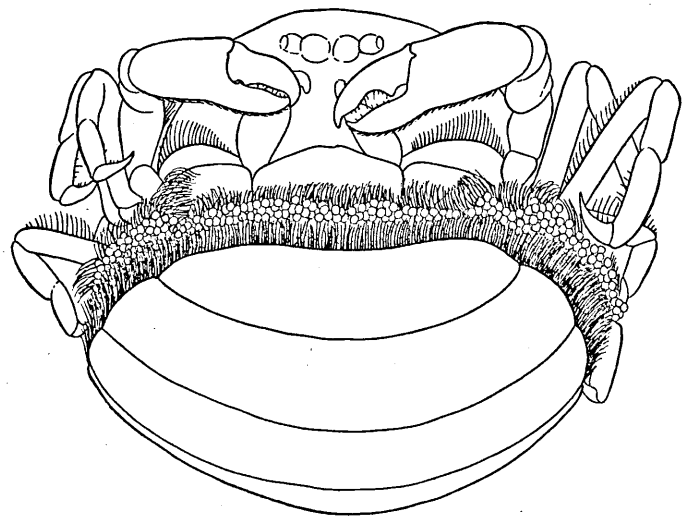

FIG. 4. Ovigerous female. Magnification, ca. $4\frac{1}{3}$.

Ovigerous Female (Text Fig. 4). The smallest berried female found had a carapace 7·5 mm. wide. The very numerous eggs are carried in the cavity formed by the hollowed thorax and deeply hollowed abdomen. The space between the side of the abdomen and the thorax besides being very small, is well guarded by long fringing hairs. The long blade-like exopodite of the second pair of pleopods, fringed with long and numerous hairs, fits along the inside of the gap as far forward as the fifth segment of the abdomen, and gives a double protection to the eggs.

In a good many instances the size of the pea-crab and its host was noted, and the figures are given in the accompanying table. It will be seen that there is a rough relationship in size between the female crab and its host, the larger crabs being found in the larger mussels. Hornell and Southwell (**3**) have noted this for *P. placunæ* found in the window-

pane oyster (*Placuna placenta*) from the coast of Okhamandal in Kattiawar. They say : " Immature shells, as is natural, less frequently revealed the presence of commensal pea-crabs ; when they did occur the crabs were more or less immature. It would seem that the crabs grow towards maturity concurrently with their hosts."

Dr. Orton tells me that judging from the size of the mussels from which Pinnotheres have been taken, it is probable that the female crab attains sexual maturity easily in its first year. Additional evidence in favour of this is the scarcity of the early stages which would seem to point to the probability that the female passes through the various growth stages very rapidly. Of the first three stages, Stage I is perhaps the least scarce. It may be that a pause occurs here before a male enters the mussel and copulation takes place. During this time growth and moulting probably go on, but without a change of form, females of this stage having been found varying in size between 2·1 and 4·9 mm.

TABLE OF MEASUREMENTS OF FEMALE *Pinnotheres pisum* AND HOST (*Mytilus edulis*).

Stage.	Pea-crab mm. in width.	Mussel mm. in length.	Stage.	Pea-crab mm. in width.	Mussel mm. in length.
Stage I (abnormal)	4·0	41	Berried	10·0	58
I	4·9	62	,,	10·0	65
III	5·0	60	,,	10·0	67
IV	6·5	80	,,	10·0	68
IV	6·5	82	,,	10·0	68
IV	7·5	56	,,	10·0	68
IV	7·5	58	,,	10·0	70
IV	7·5	68	Stage V	10·5	68
Berried	7·5	90	V	10·5	73
,,	8·0	53	IV	10·5	84
,,	8·0	58	Berried	11·0	75
,,	8·5	65	,,	11·0	76
,,	9·0	60	Stage IV	11·5	79
,,	9·0	65	V	12·0	80
,,	9·0	69	IV	12·0	79
,,	9·5	73	V	15·0	104
Stage V	9·5	72	V	15·0	90

The work recorded in this paper was undertaken at the suggestion of Dr. J. H. Orton, to whom I am indebted for advice, help, and information. I should like to express my thanks to him for sending me some of his

material as well as arranging for a further plentiful supply. The material came through the Marine Biological Association, Plymouth; a great deal of it from the Tollesbury and Mersea Native Oyster Fishery, Essex, through the kindness of Mr. French, and some from the Yealm Oyster Fisheries, Devon.

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EXPLANATION OF PLATES I TO V.

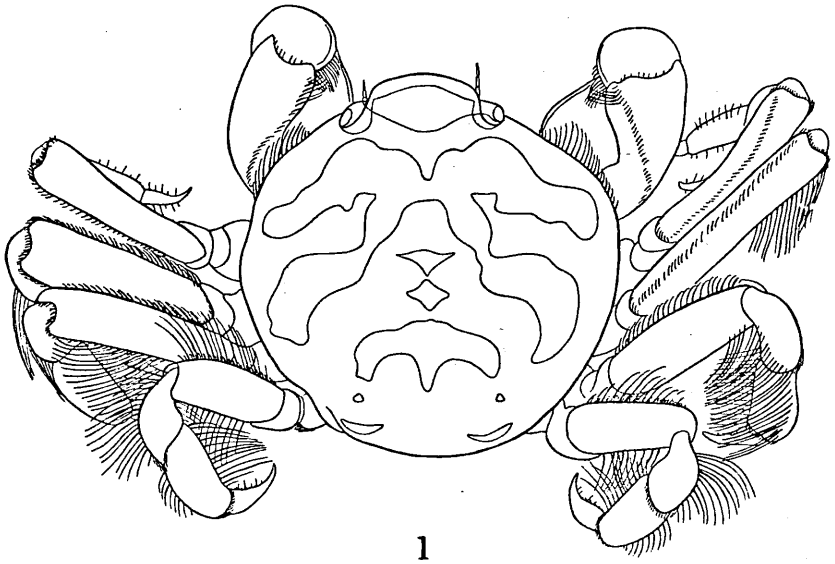
The outlines of the drawings were made with camera lucida.

PLATE I.

Pinnotheres pisum, male × ca. 8½.

Fig. 1. Dorsal view. The colour pattern is indicated.
Fig. 2. Ventral view.

PLATE I.



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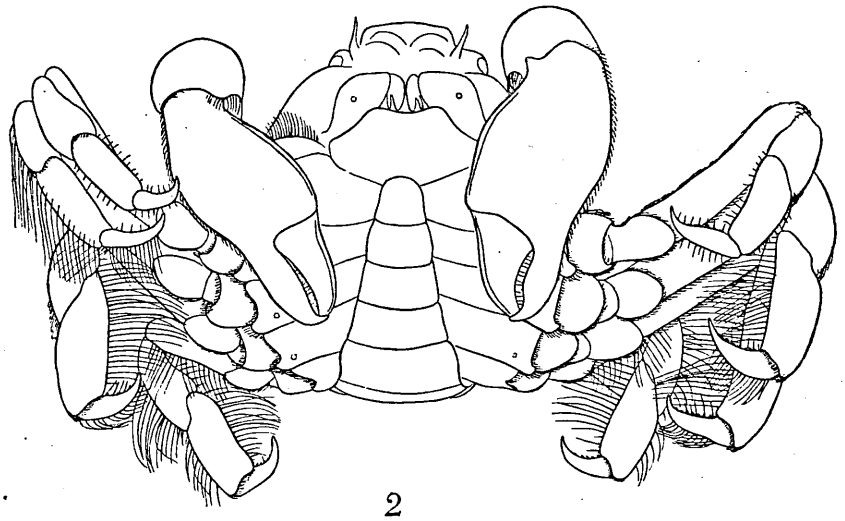

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DEL. D. A.

PLATE II.

Pinnotheres pisum, female × ca. 5.

The crabs figured in this plate and in Plate III were first drawn in outline, then soaked in acid alcohol, stained with alum carmine and cleared in oil of winter green.

FIG. 3. Stage I, dorsal view. The colour pattern is indicated.

FIG. 4. Stage I, ventral view. The empty spermathecæ are shown by dotted lines.

FIG. 5. Stage II, dorsal view.

FIG. 6. Stage II, ventral view. The full spermathecæ and the pleopods are shown by dotted lines.

FIG. 7. Stage III (a), dorsal view.

FIG. 8. Stage III (a), ventral view.

FIG. 9. Stage III (b), dorsal view.

FIG. 10. Stage III (b), ventral view.

PLATE II.

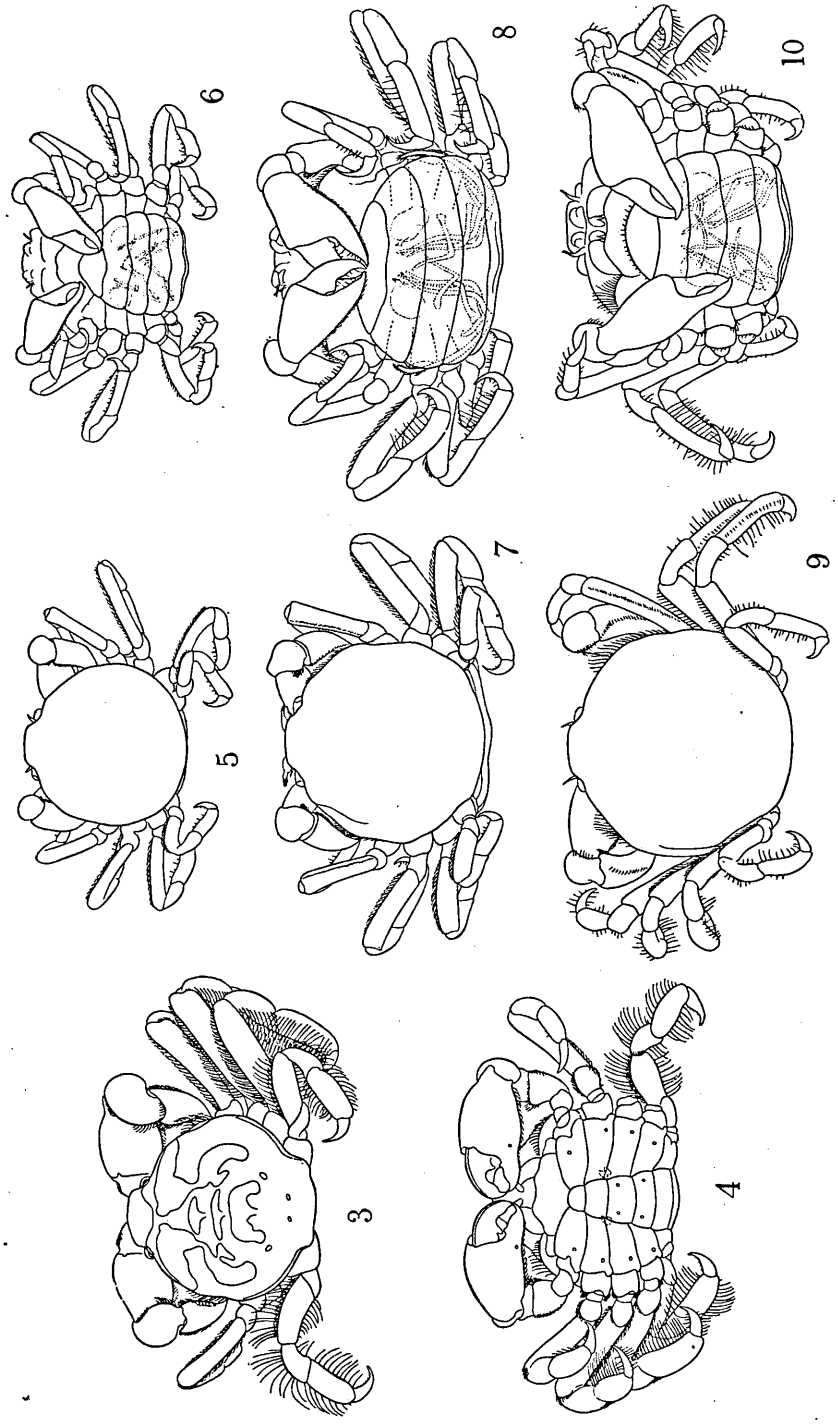

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PLATE III.

Pinnotheres pisum, female, × ca. 5.

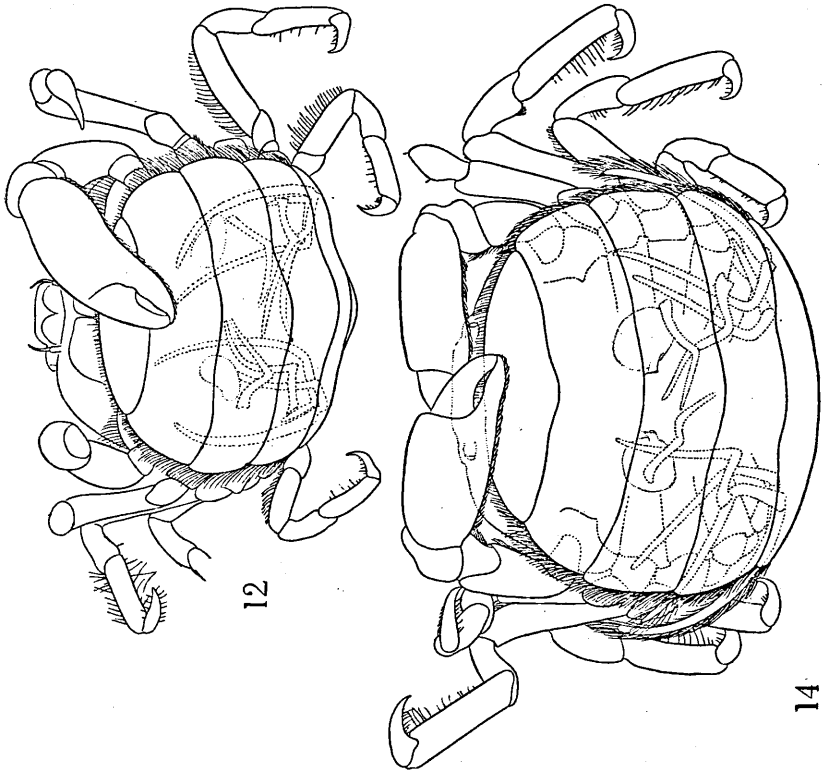
FIG. 11. Stage IV, dorsal view.

FIG. 12. Stage IV, ventral view. The spermathecæ and the pleopods are shown by dotted lines.

FIG. 13. Stage V, dorsal view. The gonad is shown in outline. The abdomen is seen extending beyond the bases of the legs.

FIG. 14. Stage V, ventral view.

PLATE III.



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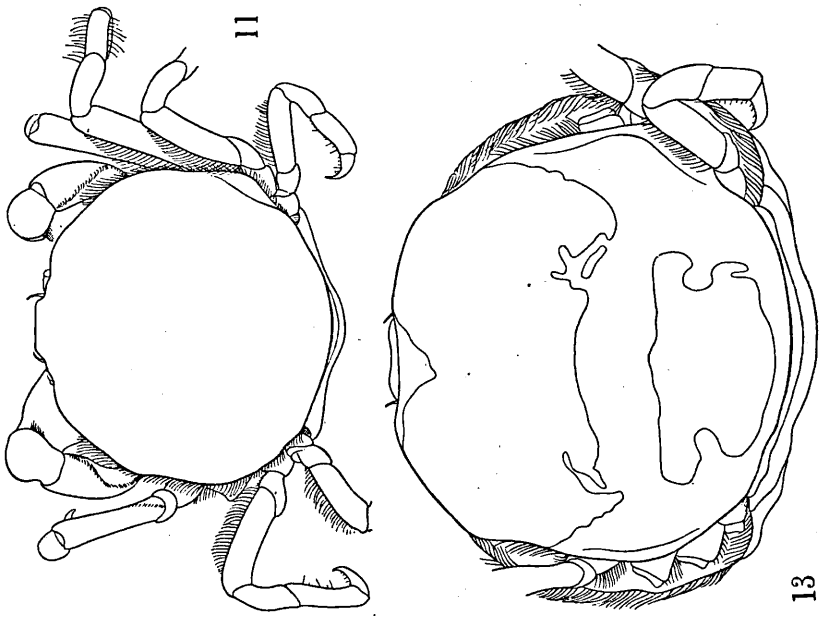

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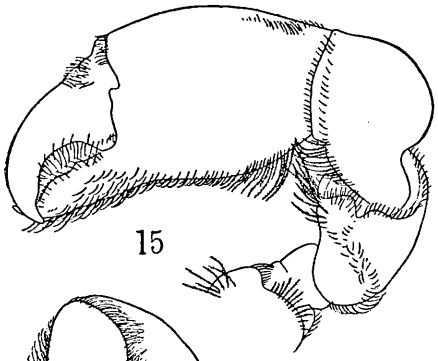
DEL. D. A.

PLATE IV.

Peræopods of right side of male and Stage II female, dorsal view, × ca. 14.

FIG. 15. Cheliped of male.
FIG. 16. Cheliped of Stage II female.
FIG. 17. First walking leg of male.
FIG. 18. First walking leg of Stage II female.
FIG. 19. Third walking leg of male. The second walking leg is very similar, but slightly longer.
FIG. 20. Second walking leg of Stage II female. The third walking leg is very similar, but slightly shorter.
FIG. 21. Fourth walking leg of male.
FIG. 22. Fourth walking-leg of Stage II female.

PLATE IV.



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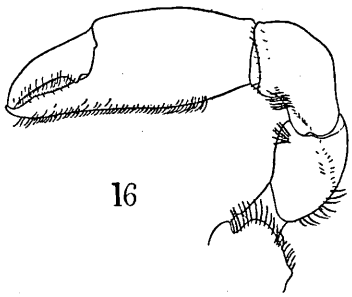

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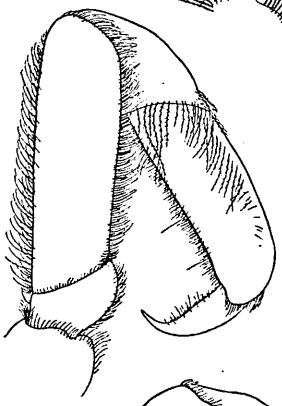

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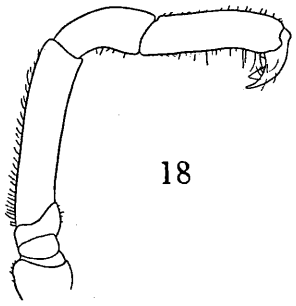

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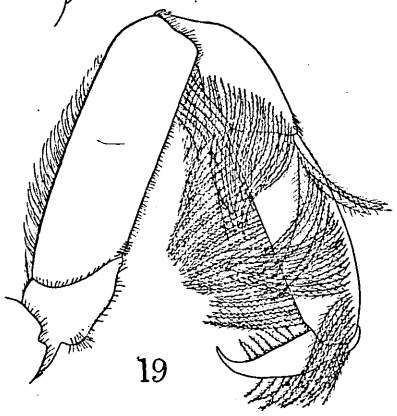

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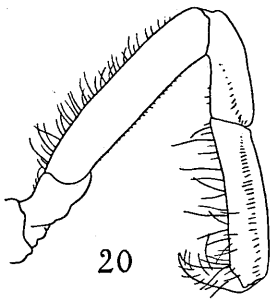

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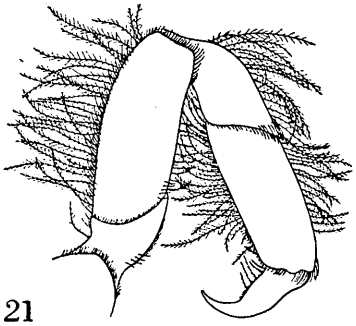

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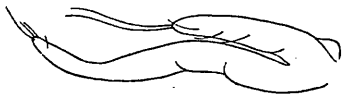
DEL. D. A.

PLATE V.

First and second right pleopods of female.

FIG. 23. Stage I female. First pleopod—drawn from a moult—× ca. 57¼.
FIG. 24. Stage I female. Second pleopod „ „ „ × ca. 57½.
FIG. 25. Stage II female. First pleopod, × ca. 17½.
FIG. 26. Stage II female. Second pleopod, × ca. 17½.
FIG. 27. Stage III female. First pleopod, × ca. 17½.
FIG. 28. Stage III female. Second pleopod, × ca. 17½.
FIG. 29. Stage IV female. First pleopod, × ca. 12½.
FIG. 30. Stage IV female. Second pleopod, × ca. 12½.

PLATE V.



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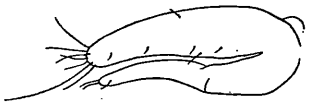

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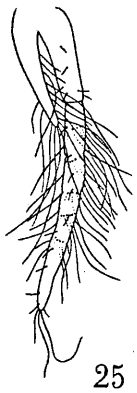

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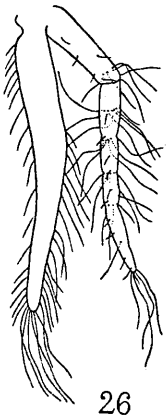

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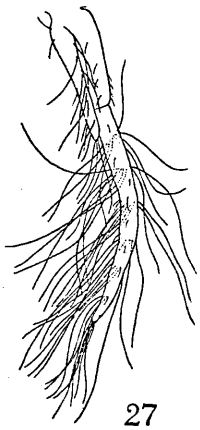

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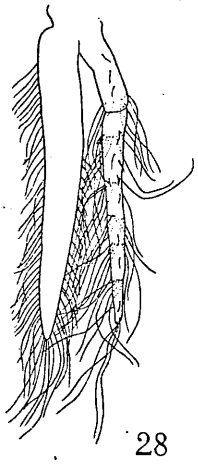

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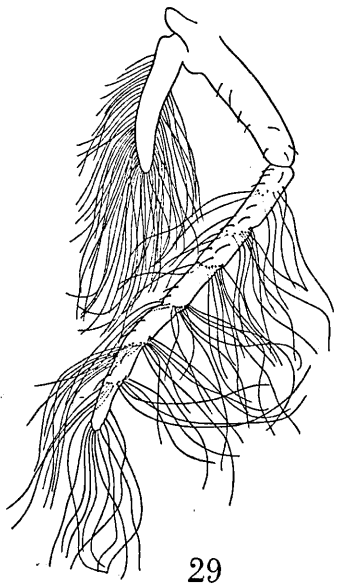

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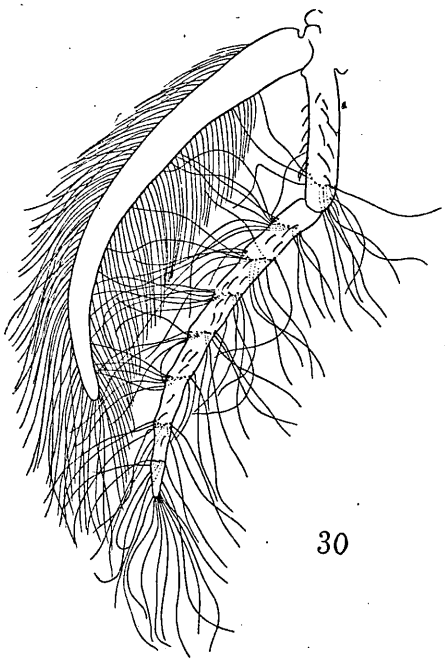

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DEL. D. A.

A New Habitat for *Loxosoma phascolosomatum* Vogt.

By

D. Atkins.

With 4 Figures in the Text.

Reprinted from the Journal of the Marine Biological Association of the United Kingdom.
Vol. xiv., No. 3. March, 1927.

A New Habitat for *Loxosoma phascolosomatum* Vogt.

By

D. Atkins.

With 4 Figures in the Text.

Loxosoma phascolosomatum was first described under that name by Vogt (**6**) in 1876 when he discovered it at Roscoff on the posterior extremity of *Phascolosoma elongatum* and *P. margaritaceum*, where it forms a small tuft. It had probably been observed previously by Norman (**4**), and described by him in 1861 (**3**) as tentacular appendages of "Strephenterus claviger"; he found it on gephyreans dredged in 1858 from Bantry Bay. Barrois (**2**, p. 8) mentions that he also saw this species in 1874–75, before the publication of Vogt's paper, at Roscoff, where it was abundant on sipunculids. Since then it has been recorded as occurring on Phascolion by Andersson (**1**) in East Greenland, and by Norman (**5**) in East Finmark.

While I was working on Loxosoma at Plymouth, in September, 1923, Dr. Orton brought to my notice some organisms attached to the outer surface of the shell of certain minute bivalves, *Lepton clarkiæ* and *Montacuta bidentata*. These proved on examination to include acinetarians, *Perigonimus* sp., and a species of Loxosoma, which is almost certainly *L. phascolosomatum*.

L. clarkiæ and *M. bidentata* occur associated with *Phascolosoma pellucidum*, being found in their burrows in the mud of the Salcombe Estuary; the former is the more common. These bivalves may occur either free in the burrows, partly embedded in the walls, or loosely attached to the gephyreans (Orton, J. H., "Nature," Vol. 112, Dec. 15, 1923, p. 861). It was found that if the *Lepton clarkiæ* were placed in a bowl of sea-water with a gephyrean for twelve hours or more some became attached; the attachment was of a slight kind, for when the water was changed the current from the syphon detached the shells. Of thirty-four specimens of Lepton and Montacuta all but five carried the Loxosoma. They were most frequently found round the edge of the shell, where they might be supposed to derive the greatest benefit from the current of water passing between the valves of the mollusc, but in some cases much of the surface of the shell was covered with the polyzoan (Fig. 1).

The large individuals are usually seen lying along the edge of the shell with the long stalk looped or curved (Fig. 2); it is generally the younger forms only in which the stalk is straight, standing out beyond the shell margin (Fig. 3). The chief movement of the Loxosoma is twisting or bending from side to side. The stalk is rarely seen extended to its full length; it is usually somewhat contracted when it may be very broad, in some cases nearly as broad as the calyx. Vogt says of his specimens that the lower extremity of the stalk was pointed like the nib of a pen, and there was no special organ of attachment; in his Fig. 1, Pl. I, it is

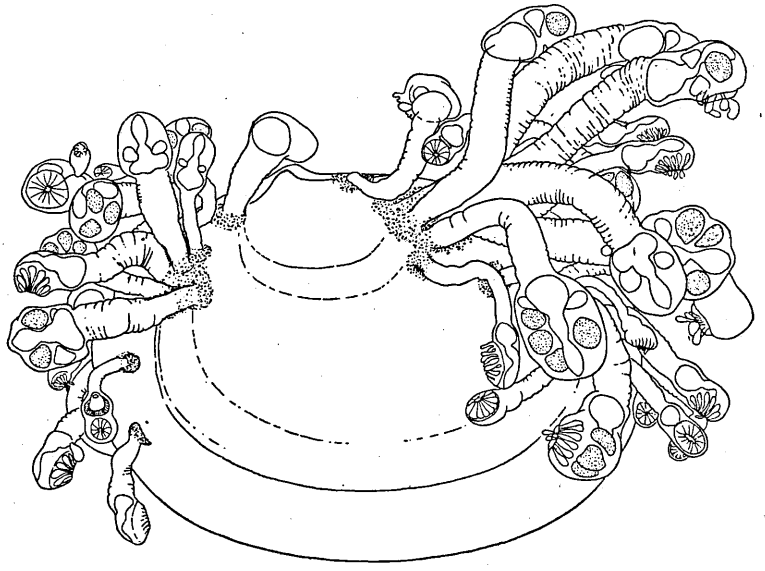

FIG. 1.—Sketch of *Loxosoma phascolosomatum* on shell. The individuals are mostly female, some with embryos in the vestibule. They are somewhat contracted, the cuticle of the stalk is ringed. Small particles are seen adhering to the secretion by which the foot is attached to the shell. Alum carmine, oil of winter green. × *ca.* 41½.

shown ending in a curious bisected extremity; in the specimens from Lepton and Montacuta the stalk ends in a small disc of attachment.

It is difficult to obtain measurements of large individuals owing to their generally curved condition; some measurements of rather small living specimens with straight stalk are as follows:—

Total length in mm.	Length of calyx in mm.	Length of stalk in mm.	Breadth of calyx in mm.
·5	·23	·27	·18
·69	·27	·42	·21
·78	·22	·56	
1·01	·29	·72	

The lophophore is large and very oblique. The tentacles are extremely difficult to count, as they are usually more or less retracted, and even when most fully extended are somewhat bent; this peculiarity was noted by Vogt. The number of tentacles in the adult appears to be twelve or more.

On either side of the calyx, slightly above the lower level of the lophophore, are the sense organs, one on either side, which are characteristic of *L. phascolosomatum*. These are often practically invisible, they contract and sink below the surface when their position is only marked by a slight elevation of the cuticle.

FIG. 2.—Sketch of a specimen lying along the edge of a shell. × 63.

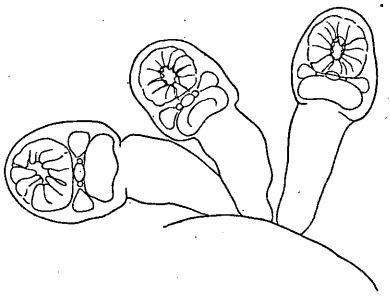

FIG. 3.—Three rather small male individuals attached near the edge of a shell, and standing out beyond the shell-edge. × 63.

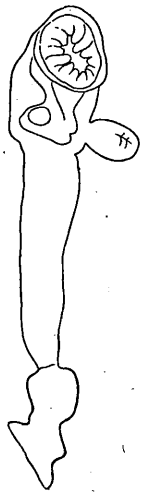

FIG. 4.—A specimen with a bud on either side. The cuticle of the lower part of the stalk is thickened, and was yellowish in colour. × 63.

Ciliary movement was seen near the outer and lower border of the rather conspicuous dumb-bell shaped nerve ganglion, presumably indicating the position of nephridia.

Both male and female individuals were seen; the individuals of a colony are, as observed by Vogt, mostly of one sex (Fig. 1). In the living animal the testes and seminal vesicle of the functionally male individual are very conspicuous, the latter having the appearance of a tangled skein. Many of the females carried a varying number of embryos in the vestibule. The larva is like that figured by Vogt.

Many of the Loxosomas, both male and female, had buds (Fig. 4); the number of buds is apparently small, but not restricted to two, as Vogt supposed; the greatest number seen was five—three on one side,

one of which was very small, and two on the other. The buds have a large foot gland and duct or groove (pedal body and pedal gland respectively of Vogt). In the larger buds still attached to the parent that part which is traversed by the groove of the gland is sometimes strongly curved, the bud twisting backwards and forwards.

So far as I have been able to ascertain this is the first Loxosoma described as occurring on a mollusc; it is curious that though the gephyreans (*P. pellucidum*) were carefully searched, none were found on them; but Mr. Nunn told me he had sometimes found, when preserving *Phascolosoma pellucidum* at Plymouth, a few stray Loxosoma actually on the gephyreans. *L. phascolosomatum* is also, as is well known, found on the caudal extremity of *Phascolosoma vulgaris* in the Salcombe region, but this gephyrean is now apparently rare in the Estuary, though formerly it could be taken in good numbers in particular situations (Journ. Mar. Biol. Assoc., Vol. II, N.S., 1900, p. 164).

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4

REPORT ON THE MYZOSTOMIDA COLLECTED BY MR. F. A. POTTS IN TORRES STRAIT, TOGETHER WITH A DESCRIPTION OF A SPECIES OBTAINED BY PROFESSOR J. STANLEY GARDINER FROM THE MALDIVES.

By DAPHNE ATKINS, B.Sc. (from the Pilcher Research Laboratory, Bedford College for Women).

[*From the* Proceedings of the Zoological Society of London, 1927.]

[Published July 12th 1927.]

[*Reprinted from* PROC. ZOOL. SOC., *Part* 2, 1927.]

Report on the Myzostomida collected by Mr. F. A. Potts in Torres Strait, together with a Description of a Species obtained by Professor J. Stanley Gardiner from the Maldives.

By DAPHNE ATKINS, B.Sc. (from the Pilcher Research Laboratory, Bedford College for Women).*

(Plates I.–II.†; Text-figures 1–15.)

CONTENTS.

The Myzostomida described in the following report were, with one exception, collected by Mr. F. A. Potts from Crinoids obtained at Murray Island at the north end of the Great Barrier Reef of Australia, and Badu, one of the western islands of Torres Strait, during the latter part of 1913. The collection was sent to Prof. C. L. Boulenger, who very kindly handed it over to me for examination while I was working under his direction in the Pilcher Research Laboratory at Bedford College in 1923.

The material consisted of ten tubes containing about 65 specimens, all of which proved to belong to species so far undescribed. Whilst the majority of the specimens were in an excellent condition, a few had unfortunately deteriorated so as to be unsuitable for description; altogether six new species were recognised.

The collection is especially interesting because it was accompanied by notes made by Mr. Potts on the colours of the living animals, and previous records of this description are all too few. Some of the specimens were extremely beautiful and many had very striking colour-patterns, in a few cases retained in the preserved state.

The Myzostomida of this collection belong mainly to two types. In one the body is circular and thin, the more delicate forms being almost transparent, while the marginal cirri are well developed, numbering ten pairs or more. In this type the colour-pattern takes the form of rings, either broken or complete. A striking form belonging to this type had a very pronounced pattern of alternating dark and unpigmented rings; it was found

* Communicated by Prof. C. L. BOULENGER, M.A., D.Sc., F.Z.S.

† For explanation of the Plates see p. 357.

on the dark green or black varieties of *Comanthus annulatus*, but though so conspicuous when seen apart from its host, when in its natural habitat was comparatively inconspicuous, the unpigmented rings being transparent.

In the second type the body is stout and thick, and the cirri are inconspicuous or absent. In this type the dorsum, although sometimes smooth, is frequently ornamented with radiating ridges of a lighter colour than the rest of the body, the ridges occasionally being thrown further into relief by encircling lines of dark pigment either black or purple; such forms were found on Crinoids of a colour closely approaching that of the general ground-colour of the Myzostomids. In the two forms in which sculpturing is absent the dorsum was covered with a dark pigment, in one case relieved by a white line down the middle. These were found on dark Crinoids.

I have included in this report the description of a new species of *Myzostoma* collected by Prof. J. S. Gardiner from Crinoids of the Hulula Malé Atoll, in the Maldives. These were handed over to me by Prof. Boulenger together with Mr. Potts's collection.

The descriptions in this report are based on external features only. Sections were not cut of the material as the specimens belong to the more normal types of the genus, and especially as there were only a few individuals of the more important species, and the results likely to be obtained did not seem to justify their destruction by section-cutting.

I should like to express my thanks to Prof. Boulenger for submitting to me for examination such interesting and valuable material, and also for help given throughout.

MYZOSTOMA POLYCYCLUS, sp. n. (Pl. I. figs. 1–3.)

Twenty-two specimens of this extremely handsome and striking Myzostomid occur in Mr. Potts's collection; nineteen were obtained from *Comanthus annulatus* at Murray Island, the remainder being collected at Badu.

The body varies in diameter from 1 to 4·8 mm., it is approximately circular, flat and thin, increasing only slightly in thickness towards the centre. Where the quantity of pigment is not great the body is transparent from the parapodial bases to the margin, the smaller specimens being extremely membranous.

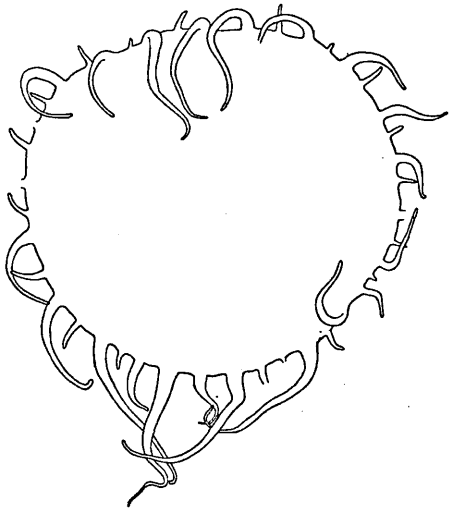
The dorsal surface is ornamented with concentric dark and unpigmented rings; these vary in width in different individuals, and the contrast between them is much more marked in some specimens than in others. The two worms figured represent extremes in the development of the rings (Pl. I. figs. 1, 2), practically every intermediate form occurring in the series; two specimens, moreover, were uniformly pale in colour with the pattern only just distinguishable. As a general rule in the young forms the pigmentation is more diffuse and the rings less

distinct than in the adults. According to a sketch by Mr. Potts, the living Myzostomid possessed also a definite dark streak running longitudinally down the middle of the dorsum; this has almost completely disappeared in the preserved specimens.

The ventral surface of the body is uniformly pigmented except in the marginal zone, which corresponds to the outer light ring of the dorsal side; in the majority of specimens the suckers, parapodia, male papillæ, and pharynx, are unpigmented and show up conspicuously against the dark background (Pl. I. fig. 3).

In referring to the colour-pattern of the living worm and its relation to that of the host, Mr. Potts remarks: "the alternate

Text-figure 1.



Myzostoma polycyclus, sp. n.

Sketch to show the arrangement of the cirri in a small specimen 1·1 mm. long and 1·2 mm. broad.

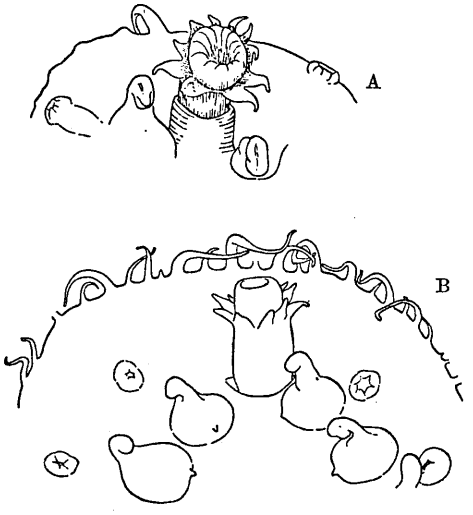
black and non-pigmented rings are in vivid contrast, but the Myzostomid is thin and the non-pigmented parts are so transparent as to be inconspicuous against the dark ground of the host. This species seems to occur only on the darker Crinoids" (6).

In the larger individuals the margin bears numerous slender cirri, apparently indefinite in number and arrangement, those on the lateral margins, however, being slightly shorter than those at the anterior and posterior ends. In the smaller specimens, where the cirri are less numerous and comparatively longer than in the adults, some sort of arrangement can be made out; there appears in these to be a posterior median cirrus and ten pairs

of long primary cirri between which nine or more pairs of shorter secondary cirri are developed (text-fig. 1); the latter grow and are added to as the worm increases in size, until finally all traces of the division into primary and secondary cirri disappear.

The parapodia are well developed, their bases being connected with the central muscular mass by distinct radial ridges. The terminal portions are slender although the actual tips are enlarged. The thick basal portion of each parapodium bears a minute unpigmented cirrus on its under surface, a character which has so far only been described in four other species, *M. cirripedium*

Text-figure 2.



Myzostoma polycyclus, sp. n.
Sketches of extended pharynx with subterminal circlet of small tentacles.
A × ca. 53; B × ca. 18.

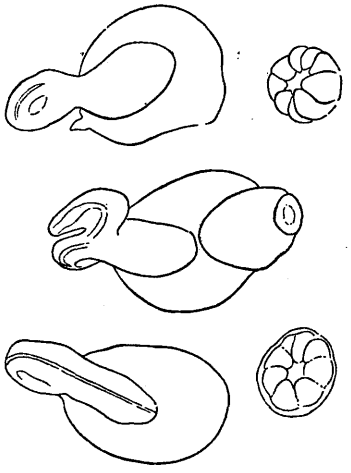
v. Graff (4), *M. circinatum* Wheeler (8), *M. metacrini* McClendon (5), and *M. vincentinum* v. Reichensperger (7). McClendon suggests that this cirrus may be homologous with the neuropodial cirrus of the Polychæta. The tip of the parapodium appears to be bent over; this is, however, an optical effect due to the shadow thrown by the curved hook within it.

The four pairs of suckers are large, and being unpigmented appear prominent against the dark background; they are raised on muscular prominences and consist of radially folded walls surrounding a small central boss.

Mouth and cloaca are both on the ventral surface, the former

lying a little further in from the margin than the suckers. The pharynx when extended shows a subterminal circlet of ten small tentacles (text-fig. 2 A and B). The intestinal diverticula can

Text-figure 3.



Myzostoma polycyclus, sp. n.
Sketch of abnormal double parapodium and male papilla.

be seen in the smaller more transparent individuals; they extend only slightly beyond the level of the suckers, leaving a narrow marginal zone. The position of the cloacal papilla appears to

Text-figure 4.

Myzostoma polycyclus, sp. n.
Sketch of abnormal double sucker.

vary with the state of contraction of the body; it is, however, approximately on the same level as the suckers.

The male papillæ which are noticeable on most of the specimens are large and have the shape of tall cones with broad bases.

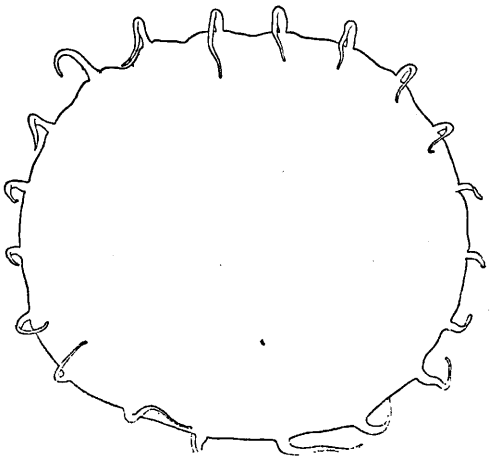
Among the individuals in the collection several abnormalities were met with; a few specimens have less than the normal number of parapodia, one has an abnormal third parapodium on the left side, the distal portion being double (text-fig. 3), while another has a sucker missing, and in another there is a peculiar double sucker (text-fig. 4).

MYZOSTOMA STOCHOEIDES, sp. n. (Pl. I. fig. 4.)

This is another beautiful species, of which five specimens were obtained from *Comanthus annulatus* collected at Badu.

The body is almost circular with an average diameter of 1·5 to 4·5 mm.; the breadth is, however, very slightly greater than the length, this being most noticeable in the smallest specimen (text-fig. 5). The worms are flat, and very thin and membranous, being semitransparent except where the quantity of pigment is

Text-figure 5.



Myzostoma stochoeides, sp. n.

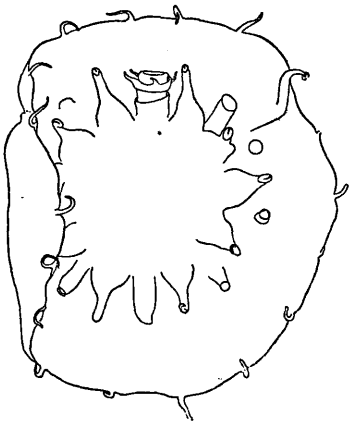
Sketch to show the shape of the body in a young specimen approximately 1·5 mm. in breadth.

greatest; the body disc is slightly thickened from about the level of the parapodial bases to the centre, where the dorsum shows a slight concavity.

The colour-pattern resembles that of *M. polycyclus* in that the dorsal surface is ornamented with concentric darker and lighter rings (Pl. I. fig. 4); these are caused partly by change in the ground-colour, and partly by intensification and reduction respectively of the numerous dark pigment spots which occur over practically the whole surface. The broad outer ring has a

pale grey appearance to the naked eye; the ground-colour is whitish, speckled with dark pigment spots increasing in number towards the inner margin. The next ring, which appears to be nearly cream in tint, is narrow and marks the position of the extended tips of the parapodia; it has a pale yellow ground-colour and the dark spots are much finer and less numerous. The central area is darkest in colour, but has a light streak running through it antero-posteriorly; the ground-colour is pale yellowish-brown and the dark irregular flecks of pigment are very numerous, especially towards the periphery and bordering the light streak; they are arranged roughly in radiating lines giving a slightly streaky appearance to the dorsum. In the smallest individual the rings are not noticeable, the coloration being much more diffuse.

Text-figure 6.



Myzostoma stochoeides, sp. n.

Ventral aspect of specimen 3·65 mm. in length. Only nine pairs of cirri are present.

The central muscular mass, together with the parapodia, suckers, rectum, and pharyngeal region are unpigmented and stand out conspicuously against the surrounding greyish pigmented part of the ventral surface.

There are only ten pairs of marginal cirri; these are slender and longest at the anterior and posterior ends of the body, the fifth and sixth pairs being the shortest (text-fig. 5).

The parapodia are arranged almost in a circle, they are well developed and have much the same structure as those of the preceding species but are, however, relatively larger and their bases are without cirri (text-fig. 6). Conspicuous radial ridges mark the position of the muscles passing from the parapodia to the central muscular mass.

The four pairs of suckers are situated rather far from the margin, they are not extremely conspicuous, but the size varies according to their state of contraction; when well extended their borders appear to be prolonged into a tube-like continuation with very thin walls. The radial muscles running to the suckers are fairly well developed.

The mouth and the cloacal papilla are on the ventral surface about equidistant from the margin and just within the outstretched tips of the parapodia. The pharynx when extended is seen to be crowned with a subterminal circlet of small tentacles, of which five can be counted from the ventral side (text-fig. 6). The cloacal papilla is quite conspicuous. A rounded median longitudinal ridge marks the position of the pharyngeal region and the rectum.

A well-developed male papilla is visible on the left side of a small individual.

Two of the animals have less than the normal number of parapodia, and one of these has only three suckers on one side. The specimen drawn in text-fig. 6 is imperfect in that it has only nine pairs of cirri.

MYZOSTOMA INSIGNE, sp. n. (Pl. II.)

Mr. Potts's collection contains one specimen of a magnificent Myzostomid found on a green form of *Comanthus annulatus*.

The animal, which is roughly circular, is stout and massive with a maximum thickness of about 2·5 mm. The diameter is approximately 8 mm., but, owing to the fact that the right side is considerably contracted, it is impossible to obtain exact measurements. The dorsal surface is vaulted, the thick body thinning out gradually to the narrow, rather translucent margin. The margin is inconspicuously notched, the processes so formed being irregular in size and having swollen bases; there are about twenty of these processes.

The dorsum (Pl. II. fig. 1) is ornamented with marked, clearly defined, truncated ridges, with nearly parallel sides; each ridge is surrounded at some little distance by a line of intense black pigment, giving to the animal a remarkably striking appearance. The lines encircling some of the ridges are not complete towards the periphery. Running antero-posteriorly down the middle line of the worm is a median ridge incompletely divided into four unequal pieces, all enclosed within a single black line. Radiating outwards are five pairs of primary costæ and between them four pairs of much shorter secondary ones, corresponding to the positions of the parapodia and suckers respectively. The costæ leave a semicircular space clear of ornamentation on either side of the long median ridge. When more highly magnified the dorsal surface between the ridges is seen to be divided by a series of furrows into irregular polygonal areas, larger and more clearly marked towards the margin; they are, however, probably due to

contraction and therefore of no systematic importance. The ventral surface is concave.

As mentioned previously this worm was found on a green form of *Comanthus annulatus*, and Mr. Potts states that "It resembled its host closely and was comparatively inconspicuous. The general colour was a bright green; the ridges appeared greenish white, darker at the edges owing to the addition of a granular pigment and round each there was an intense black line" (6). The underside was a vivid blue-green, brownish in the centre; in the preserved state it is of a uniform dirty cream colour. From the collector's field-notes it appears that "the animal moved with a quick jerky movement over the disc" of the Crinoid.

The parapodia are very well developed, extremely strong, and muscular; they are inserted about two-thirds of the radius from the margin. Each parapodium consists of a basal and a much smaller terminal portion. The basal part ends distally in a flattened, rather horseshoe-shaped area, lighter in colour than the rest of the parapodium; from it rises the narrow cone-like terminal portion, provided on the ventral surface with a well-marked groove. The hooks project some little distance, the tips are pale amber in colour, while the shafts are very dark brown.

The four pairs of prominent suckers are at about the same distance from the margin of the body as the distal extremities of the parapodia; they have definite apertures with radially folded walls. They are extremely muscular and are elevated on broad papillæ: rounded ridges connect them with the central muscular mass. Under a higher magnification the muscle-fibres running to the suckers are clearly visible beneath the body-wall (Pl. II. fig. 2).

The mouth and cloaca are ventrally situated close to the margin of the body, though the former is about twice as far from the margin as is the latter. The almost completely retracted pharynx bears a circlet of small tentacles of which eight can be counted. A peculiar elongated tubercle-like process is applied to the ventral surface of the very conspicuous buccal region. The cloacal papilla is extremely prominent, and a broad elevation marks externally the position of the cloaca.

Two specimens taken from a darker variety of *Comanthus annulatus* collected on the reef facing Dauer either belong to the same species or are very closely related. Their preservation is not good, and the original colour is quite lost. One worm measures 5·35 mm. in diameter and about 2·2 mm. in thickness, while the other, which is slightly damaged, has a diameter of about 5 mm.

The sculpturing of the dorsum closely resembles that of the type-specimen; the ridges are broader and not so clearly defined, but this may be due to contraction and also to poor preservation. The arrangement of the small elevations occurring along the middle line is slightly different, and from a sketch of the

collector's it would appear that there was a dark line encircling each of these elevations and not one encircling them all as in the type-specimen. In all three worms the ridges have a peculiar truncated appearance and are not gently rounded as in *M. rubrofasciatum* v. Graff (2, 1). The margin in the last two specimens is entire and without indication of cirri.

Mr. Potts records in his notes a slight difference in coloration between these last two specimens; in one the ridges were yellow, surrounded by a dark line, and the dorsum was brown with an intensification of the colour between the ridges; in the other the ridges were white, surrounded by a purple line, and the colour of the dorsum was a granular brown. The chief difference in colour between these Myzostomids and the type-specimen is in the ground-colour; in the two former it is brown, in the latter green. Such a difference in coloration alone seems insufficient for the creation of another species. Von Graff (2) quoting as examples *M. horologium* and *M. glabrum*, the only two species of which he had abundant material, says how greatly the colour may vary among individuals of the same species and "how unsafe it is, therefore, to fix the limits of a species by its colour. And this is owing to variations in the living animals and not merely to the fact that they are mostly known only by spirit specimens, in which case it is impossible to decide how much of the colour is caused by the alcohol which contains the dissolved pigment of its host."

MYZOSTOMA POTTSI, sp. n.

The single example of this species was found on a young stage of an unidentified Crinoid, which it did not match in colour.

The stout body is nearly circular in outline, with a diameter of about 4 mm. The dorsal surface is vaulted, thinning out gradually to the semi-translucent margin. The ventral surface is very slightly concave, but the margin tends to curve dorsally. The dorsum (text-fig. 7) is ornamented with rounded ridges; each of these bears on its summit a lower truncated ridge, with nearly parallel sides, giving to the rounded ridges a crested appearance. Running down the middle of the animal are three ridges in linear series. The anterior one is very slight and indefinite in form; the middle and largest one is much higher and broader; the posterior one is small but well-marked. Radiating from the central elevation are five pairs of primary costæ, and between them four pairs of much shorter secondary ones, corresponding to the positions of the parapodia and suckers respectively. The whole dorsum is much furrowed, due no doubt to contraction and the action of alcohol.

In the living animal the depressions between the radial ridges were dark green in colour, those between the middle elevations and the radial ridges black-green. The middle ridge was cream in colour, with a streak of white with green granules on either

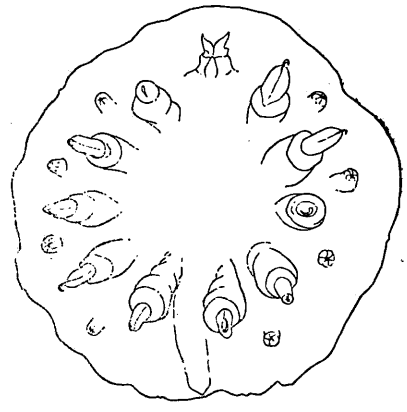
side. The colour of the preserved animal is a dirty brownish-green, with the centre of the under surface more green than brown.

Text-figure 7.

Myzostoma pottsi, sp. n. Dorsal view.

The margin is irregular; there would seem to be indications of two cirri at the hinder extremity, perhaps others may have been lost by abrasion.

Text-figure 8.



Myzostoma pottsi, sp. n. Ventral view.

The structure and position of the parapodia and suckers are essentially the same as in *M. insigne*; the two forms would

appear to be somewhat closely related. Radial ridges connect the parapodia and suckers with the central muscular mass.

The mouth and cloaca are both ventral in position (text-fig. 8), the former being about the same distance from the margin as are the suckers. Applied to the ventral surface of the buccal region is an elongated tubercle-like process as in *M. insigne*. Small tentacles, which probably belong to the partly retracted pharynx, project from the mouth-opening. The cloacal papilla is some distance posterior to the last pair of parapodia and close to the hinder extremity of the body. A longitudinal median rounded ridge on the ventral surface, especially prominent anteriorly and posteriorly, marks the position of the pharyngeal region, stomach, and rectum.

MYZOSTOMA ATRUM, sp. n.

The three examples of this species were collected at different times; two were taken together on October 22nd, 1913, from the purple crinoid *C. pectinata*, while a third and smaller individual was found at a later date.

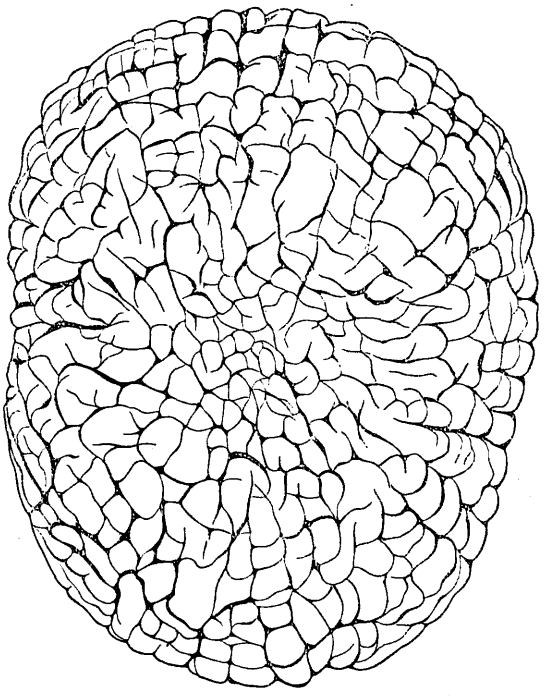
One specimen (text-figs. 9, 10), which is only slightly contracted, has a length of 6·65 mm., a breadth of 5·3 mm., and a maximum thickness of 2 mm. The animal is probably circular in shape, but its true form is somewhat concealed owing to the lateral margins being bent slightly downwards. In the preserved state it appears approximately oval, with broadly rounded anterior and posterior ends. The body is very stout, coarse, and thick, thinning only gradually towards the margin, where it is still of considerable thickness and not at all translucent. The margin is irregular and corrugated but bears no cirri. The dorsum is vaulted; it has rather the appearance of the rough bark of a tree, irregular radial and circular furrows forming irregular areas which are continued on to the peripheral part of the ventral surface. The ventral surface is slightly concave.

Of the remaining two specimens one has a diameter of 4·6 mm. and a maximum thickness of 2 mm., the other a diameter of 4 mm. with a maximum thickness of 1·5 mm. These measurements, however, by no means indicate the size of the living animals, as in the preserved state they are violently contracted, the margin is bent down all round so sharply that it is almost at right angles to the dorsal surface, and the worms appear circular in shape with a down-turned rim, which is very thick, rounded, and corrugated (text-fig. 11). The bent-down margin is furrowed both externally and internally, but the central part of the ventral surface is comparatively smooth, the muscle-fibres passing from the suckers and parapodia to the central muscular mass are visible beneath the body-wall. The dorsal surface is almost smooth, furrows only occurring in a central depression and in two narrow areas running from the anterior to the posterior margin and from left to right. Ten broad cone-shaped prominences

or bosses, corresponding to the insertion of the parapodia, occur round the edge; owing to the animals being in a state of extreme contraction the proximal part of the hook apparatus almost pierces the dorsum and appears at the apex of each prominence as a dark spot (text-fig. 12).

These three specimens illustrate very clearly to what a great extent the general shape and furrowing of the animal depend on

Text-figure 9.

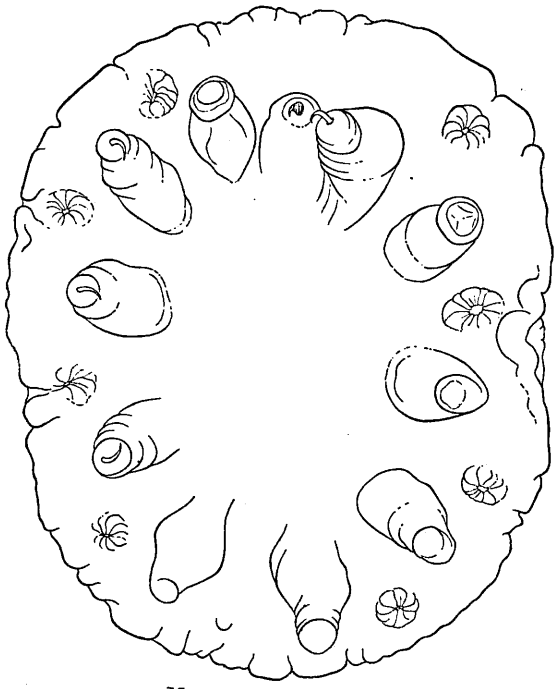


Myzostoma atrum, sp. n.
Dorsal aspect of specimen about 6·65 mm. in length.

the state of contraction it is in when death occurs, and how cautious one should be in using sculpturing as a means of identification.

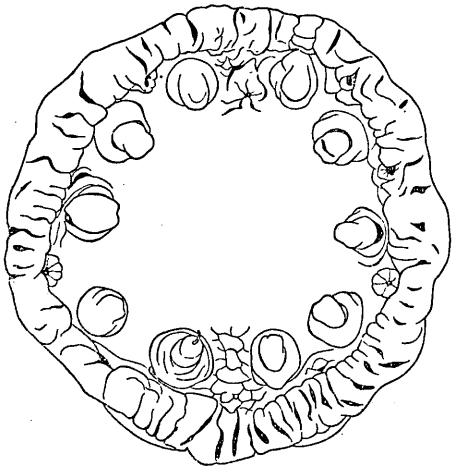
From the collector's notes it appears that the dorsum was black or dark purple; he found that on washing in water, after fixing in corrosive sublimate, a fine purple pigment came from the animal.

Text-figure 10.



Myzostoma atrum, sp. n.
Ventral aspect of specimen drawn in text-fig. 9.

Text-figure 11.

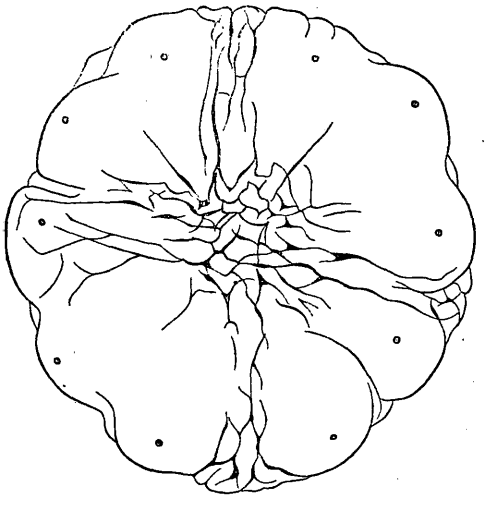


Myzostoma atrum, sp. n.
Ventral view of strongly contracted specimen with a diameter of 4·6 mm.

The parapodia are inserted about a third of the radius from the margin. They are not clearly divisible into two parts, are very stout and clumsy with strongly built hooks. In the smaller contracted specimen the middle parapodium of the right side is reduced to a mere stump.

The four pairs of suckers are situated rather close to the margin; they have definite apertures which have very thick lips with radially folded walls. Owing to the fact that they are not

Text-figure 12.



Myzostoma atrum, sp. n.
Dorsal view of specimen shown in text-fig. 11.

raised on papillæ and are of the same colour as the rest of the ventral surface, they are not very conspicuous; indeed, some of the suckers are rather difficult to make out, as they have become involved in the folds of the body.

The inconspicuous cloacal papilla is on the ventral surface about the same distance from the margin as are the suckers, while the mouth is about twice as far. The position of the pharyngeal and cloacal regions is marked by two slight ridges.

MYZOSTOMA VIRIDE, sp. n.

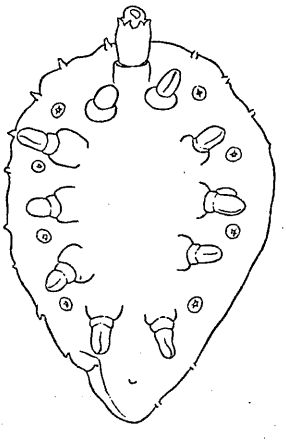
In Mr. Potts's collection are four specimens of a Myzostomid taken from *Comanthus annulatus*.

Three of the worms measure 2·6 mm. each in length, while a fourth and larger one is 3·7 mm. long with a maximum breadth of 2·55 mm. The breadth of the three smaller individuals could

not be ascertained, as they are contracted with the sides sharply incurved ventrally (text-fig. 14); in these the anterior and posterior margins are broadly rounded. The large specimen (text-fig. 13) tapers almost to a point posteriorly, but this may be abnormal, as the right side is slightly faulty. The body is stout and fairly thick, increasing slightly in thickness towards the middle line, while there is only a very narrow semi-translucent margin. The dorsum of the uncurled specimen has a few irregular folds, due no doubt to artificial causes.

In the living animal the dorsal surface was a dark green, only relieved by a white line down the middle; the extended pharynx was red. The colour in the preserved state is a light brown with a paler streak running down the middle of the dorsum.

Text-figure 13.



Myzostoma viride, sp. n.

Sketch of the ventral surface of uncurled specimen.

There are twenty marginal processes, finely pointed and triangular in shape. These are rather inconspicuous in the uncontracted worm but clearly visible in the curled up individuals.

The parapodia are well developed; each consists of a short, broad, very muscular basal portion and a narrower terminal portion, grooved ventrally. The distal end of the basal portion encircles the terminal part like a tightly fitting, thin collar. The parapodia, when extended, reach almost to the body-margin. The muscle-fibres from each are gathered into well-defined bundles, which rise above the surface as sharp ridges, and pass into the central muscular mass.

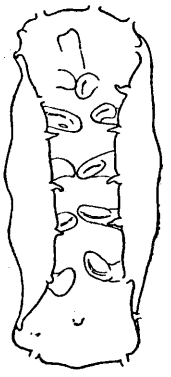
The four pairs of fairly conspicuous suckers are in the normal position; their rather indistinct apertures appear as slight

depressions; when more highly magnified they are seen to have radially folded walls.

The mouth and cloaca are ventral and subterminal. The extremely strong and muscular pharynx bears a circlet of small triangular tentacles, of which four are visible from the ventral side. The inconspicuous cloacal papilla lies well behind the last pair of parapodia. A rounded median longitudinal ridge marks the position of the stomach and rectum.

A male papilla is visible in the large worm just anterior to the third parapodium on the left side.

Text-figure 14.



Myzostoma viride, sp. n.
Sketch of curled specimen.

This species resembles *M. wheeleri* McClendon (5) in its general shape and size, and to a less extent *M. folium* v. Graff (2) and *M. nanseni* v. Graff (3). *M. wheeleri* had "its lateral margins bent downwards, probably to grasp the pinnæ, making the dorsal surface very convex and the ventral very concave" (5). This also occurs in three out of the four specimens of *M. viride*, but here may be due to contraction on killing. *M. viride* is clearly distinguishable from *M. wheeleri* by the presence of suckers, by the much stouter pharynx, and the shorter cirri.

MYZOSTOMA GARDINERI, sp. n.

Prof. J. Stanley Gardiner obtained the two specimens of this species from an unidentified Crinoid collected from Hulula Malé Atoll in the Maldives.

The larger specimen (text-fig. 15) has a length of 3·9 mm. and a breadth of 2·8 mm.; the smaller a length of 2 mm. and a breadth of 1·17 mm. The worm is oval in shape, the body thin, and in the smaller specimen almost transparent, even the larger

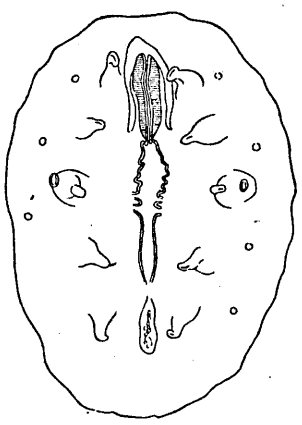
one being so to a certain extent, especially near the margin. The dorsal surface is slightly convex, without ridges, and the ventral slightly concave.

The dorsum in the preserved animal is a pale sepia brown fading towards the margin; a light coloured streak marks the middle line.

The margin of the larger specimen is somewhat irregular, but it is impossible to make out any cirri; their absence is probably due to abrasion, for in the smaller worm the bases of at least six cirri remain on one side.

The feebly developed parapodia are arranged in two almost parallel rows; they are not clearly divided into two parts and are not grooved.

Text-figure 15.



Myzostoma gardineri, sp. n.

Sketch made from the larger specimen cleared in cedar-wood oil.

The suckers are very indistinct, being extremely difficult to find; in the smaller specimen they appear to be absent altogether, although a careful search was made for them, and in the larger one the fourth sucker on the right side could not be discovered.

The position of the mouth is very near the anterior end of the body; the strong pharynx is retracted. The aperture of the cloaca is about twice as far from the posterior end as the mouth is from the anterior. The intestinal diverticula extend almost to the margin of the body, leaving only an extremely narrow, clear border. On the ventral surface a rounded and pale-coloured median longitudinal ridge marks the position of the stomach and rectum.

This is a very generalized form; it has some resemblance to *M. viride*, but is not nearly so stout and strong, the parapodia

and especially the suckers being relatively feebly developed. As the pharynx is retracted in both specimens it is impossible to ascertain whether it bears papillæ as does that of *M. viride*.

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EXPLANATION OF THE PLATES.

Plate I.

Figs. 1–3. *Myzostoma polycyclus*, sp. n. Figs. 1 and 2 dorsal views showing extremes in the development of the rings. Fig. 3, ventral view of a third specimen. × ca. 14.

Fig. 4. *Myzostoma stochoeides*, sp. n. Dorsal aspect. × ca. 14.

Plate II.

Figs. 1–2. *Myzostoma insigne*, sp. n. Dorsal and ventral aspects. × ca. 11.

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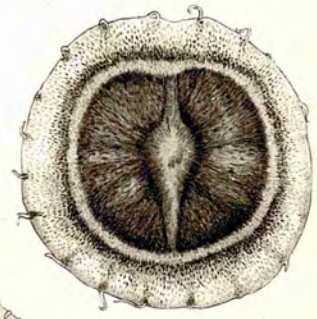

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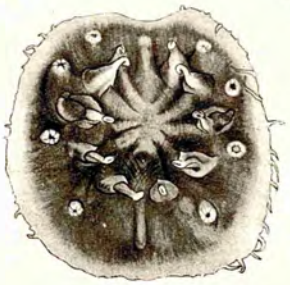

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1-3 MYZOSTOMA POLYCYCLUS, sp. n.
4 MYZOSTOMA STOCHŒIDES, sp. n.

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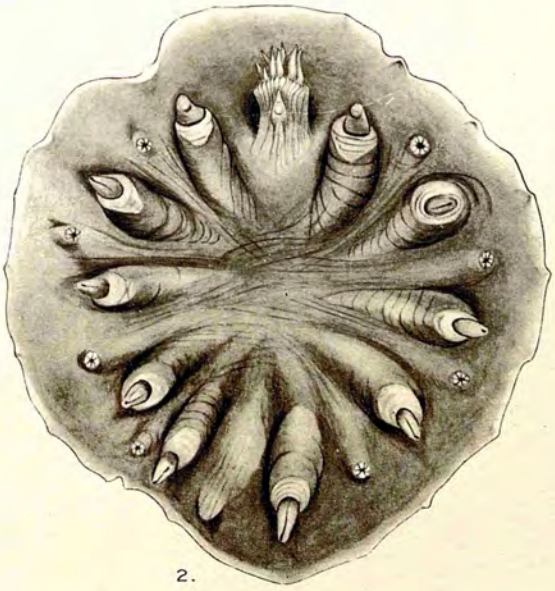

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MYZOSTOMA INSIGNE, sp. n.

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On a Fungus Allied to the Saprolegniaceæ found in the Pea-crab *Pinnotheres.*

By

D. Atkins, B.Sc.

With 13 Figures in the Text.

Reprinted from the Journal of the Marine Biological Association of the United Kingdom, Vol. xvi., No. 1. May, 1929.

On a Fungus Allied to the Saprolegniaceæ found in the Pea-crab *Pinnotheres.*

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Introduction.

In the course of work on *Pinnotheres*, a fungus, which from its general characters would appear to be allied to the Saprolegniaceæ, was noticed in pea-crabs taken from mussels (*Mytilus edulis*) coming from beds in the estuary of the Camel near St. Issey Cliff (Padstow), from the estuary of the Yealm, and from near the junction of the Tamar and Tavy (Weir Point). Although the pea-crab lives in estuarine situations where the water is brackish, yet it may be taken in bivalves dredged in rather deep water on the coast (**1**, p. 123); those in the Laboratory were kept in the sea-water in ordinary circulation in the tanks and it was under these conditions that the fungus was seen to grow and produce reproductive elements. This fungus therefore attacks a marine invertebrate and, as far as I have been able to ascertain, it is the first member of the Saprolegniaceæ which has been so described. Some members of the family which occur on living freshwater fish are *Saprolegnia parasitica* Coker* on salmon, trout, etc.—stated by Patterson (**13**, p. 5) to be unable to grow in sea-water—*Achlya Hoferi* Harz on Bohemian mirror carp (**8**, p. 201; **2**, p. 145), *A. Nowickii* Raciborski on a sink carp (**2**, p. 147), and *A. polyandra* and *A. prolifera* on various fish (**9**, p. 108), while two which are found on freshwater plankton-crustaceans are *Leptolegnia caudata* de Bary on *Leptodora Kindtii* in Denmark (**14**, p. 511) and *Pythiopsis cymosa* de Bary on *Holopedium gibberum* in Lake Malmagen in Sweden (**14**, p. 511).

The mycelium of the *Pinnotheres* fungus may penetrate deeply into the body of the pea-crab, surrounding the organs, and may occasionally extend into the appendages, mouth parts, and even the eye-stalks, while it is generally found in the gills (Fig. 1). Such deep penetration of the tissue of the host would appear to be somewhat unusual among the Saprolegniaceæ, but it may also be effected by the salmon fungus where

* Coker (**2**, p. 58) considers that the fungus described from salmon and certain other fish as *Saprolegnia ferax* is distinct from that species, and he names it *S. parasitica*.

the way is prepared by *Bacillus salmonis pestis*, the bacteria breaking down the tissue which the fungus is then able to invade (**13**, p. 7), and by *A. Hoferi* of the Bohemian mirror carp, which is also probably preceded by bacteria (**2**, p. 145 ; **8**, p. 201). In these cases the fungus may penetrate the entire dermis with the exception of the muscles. The mycelium of *L. caudata* which attacks and kills *Leptodora* in large numbers, sometimes almost exterminating them from certain lakes in

FIG. 1.—Photograph of a gill infested with the fungus, fixed in Flemming's fluid. × ca. 29.

Denmark, is said by P. E. Müller to envelop the organs. Petersen (**14**, p. 512) thinks that the mycelium usually enters round the mouth opening and, spreading rapidly, kills the animal, while it finally envelops both the mother individual and the eggs with a thick meshwork of hyphæ.

DESCRIPTION OF THE FUNGUS.

Mussels were obtained from Padstow on the following consecutive dates, November 25/27, February 24/28, April 25/28, August 1/28, and September 14/28, and a certain number of the pea-crabs taken from them on arrival at the Station either showed signs of the disease at the time or developed it later, but crabs obtained from mussels from the same place on October 11/28 were apparently free, for they did not develop it although many were kept together in bowls for about 6 weeks. Crabs which also developed the disease were obtained from near the junction of the Tamar and Tavy on March 22/28, April 10 and 20/28, and from the Yealm on July 21/28. The fungus would therefore seem to attack crabs during the greater part of the year in the comparatively mild climate of the south-west of England and is not restricted to the period of July to about the middle of September as are apparently the attacks of *Leptolegnia* on *Leptodora* in Denmark (**14**, p. 512). In some few instances it is certain that the crabs were already infected when taken from the mussels on arrival from the beds, and against the possibility of their acquiring the infection from the water circulating in the tanks in the Laboratory is the fact that crabs kept for over a year separately in mussels for rearing experiments have not developed the disease.

The presence of the fungus is mostly indicated some days before the death of the crab either by opaque white patches showing through the chitin of its body and abdomen, or else more rarely by the opaqueness of the gills, though a crab may die of the disease without any outward indication. The patches in the body generally occur over the gill chamber, especially the posterior region, though as the disease progresses the whole of the roof of the gill chamber may become involved. A white line is sometimes seen along the junction of the carapace with the

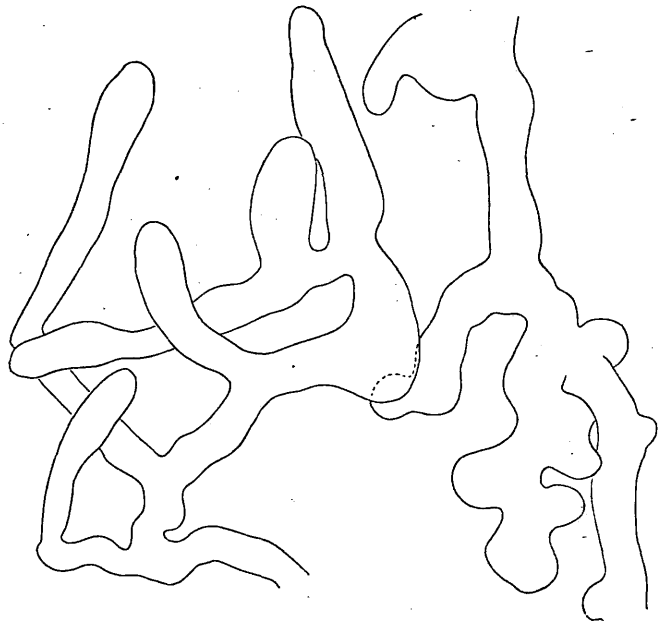

FIG. 2.—Broad, uncrowded hyphæ from roof of gill chamber. The protoplasmic contents are not shown, they were very finely granular with indication of vacuoles. × ca. 253.

This figure and all following ones were drawn from living material.

abdomen, and patches may also occur in the abdomen, where they are generally to be found round the junction of two segments. The white appearance due to the presence of the fungus can readily be distinguished from that due to parasitisation by a Sarcosporidian identified by Dr. Pixell Goodrich; in the latter case the muscles only become an opaque white. The white patches of the fungus probably surround the original point of infection, and from their position it will be realised that the fungus enters the crab either where the chitin is extremely thin or along the fine chitinous membrane which unites the segments of the abdomen, and the posterior border of the carapace to the abdomen. The white patches are

an intricately branched felt-like mycelium of fine hyphæ averaging about 9μ in width; occasionally very broad, uncrowded hyphæ up to about 32μ in width are found in the roof of the gill chamber (Fig. 2).

It appears that when the fungus enters through the exceedingly fine chitin roofing the gill chamber, it spreads for some distance in the tissue between it and the thicker chitin of the dorsal surface of the carapace, while it sends branches into the gills and sometimes the mouth parts. The fungus is most easily seen in these situations, but probably in some,

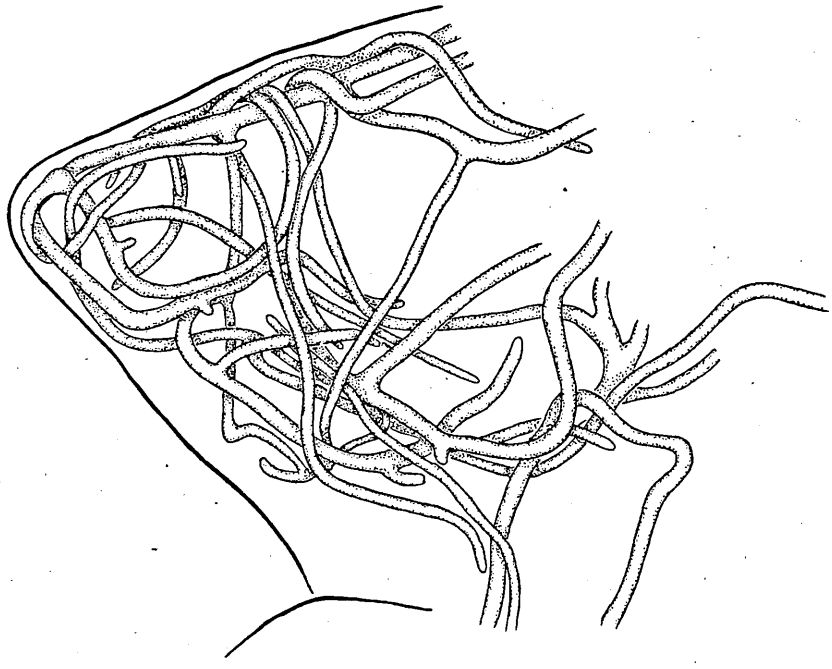

FIG. 3.—A rather heavy growth of the fungus in one of the larger leaflets near the base of a gill. × ca. 114.

if not all cases, it also extends into the body of the crab. Perhaps the easiest way of following the hyphæ, but only possible if the crab is small and thin-shelled, is to lift off the carapace, puncture the abdomen in several places, and fix the animal in Flemming's fluid. The oil globules, often present in great numbers in the hyphæ, are blackened by the osmic acid, and the branches of the fungus can be traced after clearing the crab in glycerine. By this means the fungus was seen without dissection in the body of three small crabs.

When the fungus has once entered the gills it soon absorbs the tissue and death of the pea-crab is rapid. It is an interesting possibility that in this case death may be due to asphyxiation.

In examining crabs for the presence of the fungus, when the white patches are absent, an inspection of the gills only has usually been relied on. A crab may die, however, when only one gill out of the six is infected, and therefore it would appear that in such a case there must be a considerable growth of the fungus in the body, unless laboratory conditions, which possibly included for these crabs shortage of food, markedly weakened them.

The fungus is most easily studied in the gills where the delicate chitinous

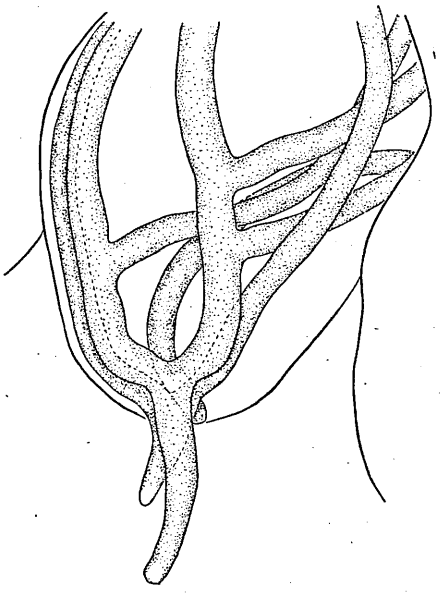

FIG. 4.—Sketch to show the very regular mode of growth of the hyphæ within the gill leaflet. The papillæ for discharging the spores are well developed but intact. The protoplasm is indicated by stippling, but no attempt has been made to show its structure. The thick lines show the outline of the gill leaflets. × ca. 253.

covering is so thin as to be transparent (Fig. 1). The hyphæ would seem to enter through the base of the gill from the infection area in the roof of the gill chamber and pass down the axis of the gill, giving off branches into the gill leaflets, both the axis and the leaflets soon becoming crowded with richly branched hyphæ (Fig. 3). At least in the young stages of the fungus the hyphæ keep within the leaflet, passing up one edge, curving very regularly round the tip, and passing down the other edge and so into the main axis, giving off branches on the way.

The whole of the contents of the hyphæ in the gills of the host gradually

divide into zoospores and no marked sporangia are formed. This fungus resembles *Aphanomyces* (**2**, p. 160) and *Leptolegnia* (**14**, p. 522) in that the sporangia are formed from unchanged hyphæ. Cross walls arise, but the portion cut off may be of considerable length with several branches; it may include a length running along the axis of the gill with loops into the gill leaflets, but apparently with only one exit. When the abdomen of

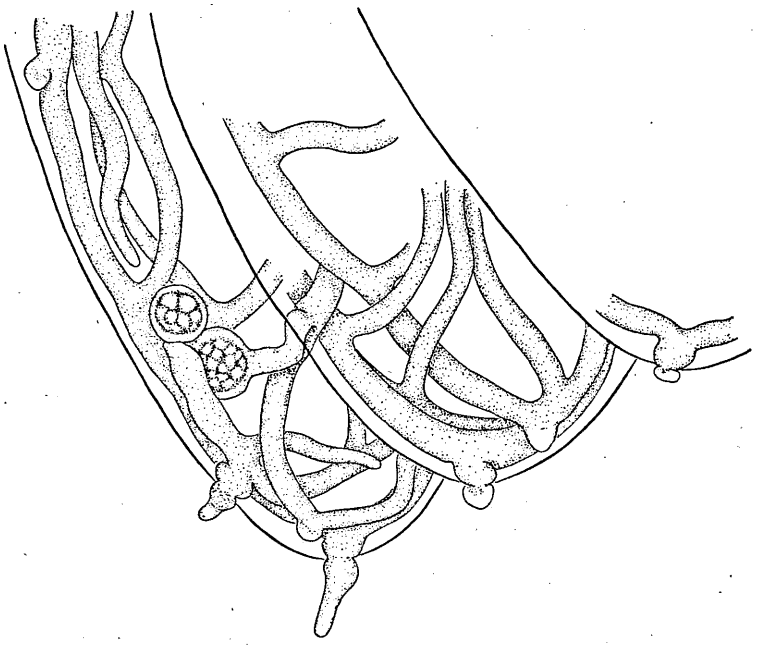

FIG. 5.—Sketch to show the fungus in three overlapping gill leaflets. Discharging papillæ are developing and show a bulge at the point of penetration of the chitin of the gill. The sketch was made at 8 p.m.; the next morning the filaments were empty, as was also the larger of the two reproductive bodies; the smaller, which had a wall dividing it from the hypha, was still full. The protoplasm is indicated by stippling, but no attempt has been made to show its structure, except in the two round reproductive bodies. The thick lines show the outline of the gill leaflets. × ca. 253.

the crab has areas of infection, hyphæ may pass into the pleopods and there become sporangia. A characteristic of this fungus is that the spore-producing filaments occur within the crab, though they would appear to be restricted to the gills and pleopods, the hyphæ in the roof of the gill chamber and in the body being purely vegetative. The reproductive hyphæ are generally stouter than the vegetative and are remarkably regular, tapering gradually to the tip with very clear and definite outline (Fig. 4). They vary in width from about 10μ to 20μ. Gills and pleopods

may be seen with a network of hyphæ empty except for a comparatively few spores which, unable to escape for some reason, have encysted there. The tissue of such gills and pleopods generally has disappeared entirely. It would seem that the filaments which enter these structures are entirely reproductive, though where infection takes place directly on the gill there is a tiny opaque patch of vegetative hyphæ. It may be that in the comparatively confined space of the gill or pleopod the tissue is soon consumed, and under these conditions spore formation naturally follows.

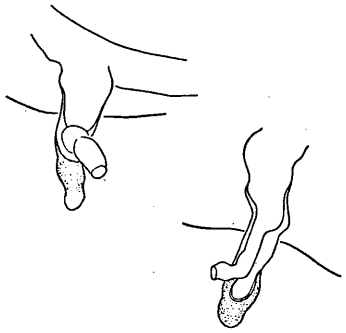

FIG. 6.—Sketches to show the development of a secondary discharging papilla when the tip of the first one has not given way. × ca. 342½.

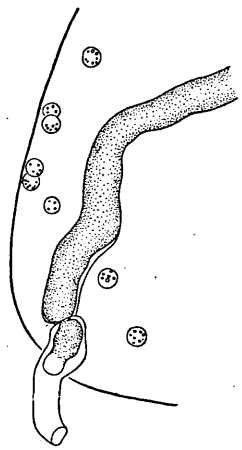

FIG. 7.—Hypha growing up within an old sporangium after the *Saprolegnia* type of proliferation; it is much reduced in size where it penetrates the gill chitin. The tip of the hypha is of almost clear protoplasm. A few spores are lying free on the surface of the gill leaflet, the outline of which is shown by a thick line. × ca. 342½.

Klebs in 1899 showed that sporangia are formed only when the food-supply is quickly and markedly decreased (**15**, p. 484).

When spore formation is about to take place a small branch or papilla arises either from the end of a hypha (Figs. 7, 8A) or along its length (Figs. 4, 5, 9, 12) and the tip becomes applied to and penetrates the chitin. There is a slight bulging of the tip of the papilla, before the chitin is penetrated (Fig. 5). The branches to the exterior are mostly quite short, ranging between 0·03 mm. to 0·12 mm. It is by these short branches or papillæ that the zoospores pass to the exterior and, with very few exceptions, this is the only part of the fungus which extends into the sea-water. In one interesting case where the long blade-like exopodite of the second

pleopod of one side was infected, the long hairs were absent towards the tip, only their circular bases remaining, and the tips of the hyphæ were protruding through the centre of these cup-like bases. Branched discharging papillæ may occur where the tip of the original papilla has apparently failed to give way and a lateral branch has arisen through which discharge has taken place (Fig. 6).

Occasionally a new sporangium may grow up within an old one, as sometimes occurs in *Leptolegnia* (2, p. 157) and is typical in *Saprolegnia*, but the most that has been seen is one within another (Fig. 7).

The details of spore formation have not been observed. A gill which when pulled from a dead crab at night shows no sign of spore formation or of the discharging papillæ will the next morning be seen with a quantity of empty sporangia and with others in the process of discharging spores; spore formation, however, occurs in gills in situ. Spore discharge seems most commonly to occur at night. The number of spores in a row in a sporangium varies with the width, from several to one or two.

The tip of the discharging papilla is mostly rounded; it would seem to be forced off by the pressure of the zoospores packed behind it; in one instance, however, the tip was flattened, with a fine membrane across it which appeared to dissolve. When the tip first gives way the zoospores pour out in a rapid stream, but when pressure is relieved they swim out singly; once liberated, they swim off rapidly. Zoospores within the sporangia may be seen trying the various branches until they find the exit. If the exit should be blocked by an encysted spore, or if the sporangium is very long and branched, a considerable number of spores may be retained, becoming encysted.

The time during which the first zoospores may remain active varies considerably. They are apparently very susceptible to changes in the environment, for the placing of a cover-slip over a drop containing motile spores, just out of a sporangium, causes rapid encystment. Both within the sporangium and outside, zoospores may come to rest while still irregular in shape; this is probably due to sudden change in the environment, such as increasing salinity on the slide. On the other hand, zoospores seen coming from a sporangium at 9.30 p.m. were taken up in a fine pipette and put on a cover-slip as a hanging drop; many were still active 50 minutes later. The length of time during which the zoospores may remain active seems unusually long for the first zoospores, which in the Saprolegniaceæ apparently encyst after 5 to 15 minutes.

The first zoospores are of two sizes, large and small, as in *S. anisospora* de Bary (2, p. 33); the small are, however, comparatively rare. The small ones are about 8μ in length, the large about 14μ. Fig. 8 A and B shows sporangia from different parts of the same gill, one containing a few small zoospores, the other containing large ones; the smaller appear to be more

regular in shape. Zoospores of intermediate size occur. The zoospores within the sporangia vary considerably in shape, especially in different sporangia. They may be oval, pear-shaped, or very elongated, almost rod-shaped, and may be rather irregular in outline, while some have a distinct protoplasmic tail. The zoospores appear capable of changing their shape to some extent, are slightly amœboid (Fig. 9). They are considerably flattened, as may be seen when they turn up an edge in swimming. It is probable that when free in the water they become a

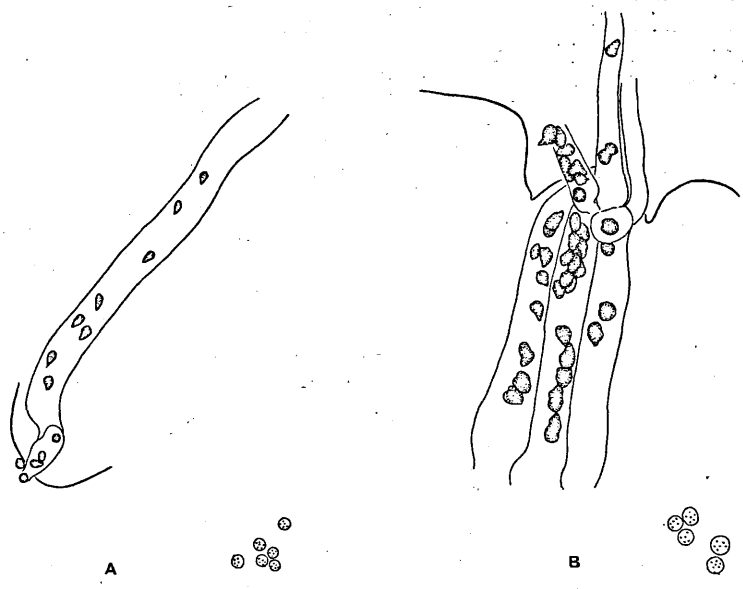

FIG. 8,—A. Zoosporangium with small zoospores. In the lower right-hand corner are cysts formed from some of these spores within the sporangium. B. Zoosporangium with large zoospores. In the lower right-hand corner are cysts formed from some of the spores within the sporangium. × ca. 253.

more regular pear-shape. Zoospores swimming in the sporangia always keep the same end foremost, but in some cases the fore end is blunt, in others rather pointed, though generally all in the same sporangium swim with the same end foremost. The free zoospores have many shining droplets, and a small vacuole near the apex; they are biciliate but swim rapidly enough to make the number of the cilia and their attachment very difficult to discern. They move with the pointed end foremost and tend to swim in wide circles. The smaller zoospores, which seem to have a more regular shape, swim in a more straightforward manner and more rapidly. They often swing round in their tracks; this *volte-face* could be more easily understood if there were an anteriorly and a

posteriorly directed cilium. One apically attached cilium can be seen clearly, a second is sometimes glimpsed but is much more difficult to distinguish. A possible explanation is that this one, though also apically attached, is normally posteriorly directed and therefore often hidden by the body of the zoospore. In an attempt to make certain of the point of attachment of the cilia, zoospores were fixed in vapour of glacial acetic acid, then treated with iodine, but drops of sea-water containing the zoospores were also swarming with bacteria, which were particularly thick round the spores and often tended to arrange themselves on fixing, end to end in crinkled lines, sometimes touching the spores, so that any cilia were entirely hidden.

An interesting case was noted of spores emerging from a sporangium

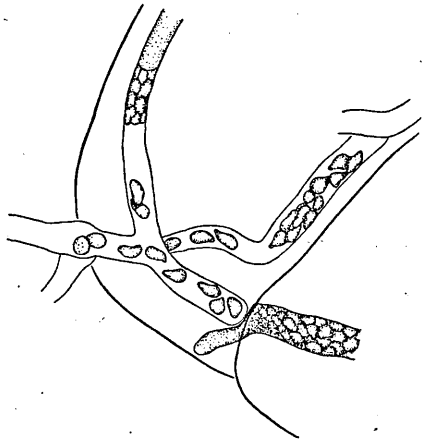

FIG. 9.—Sketch showing slightly amœboid zoospores within sporangia. A spore has encysted in the discharging papilla of one sporangium making it difficult for the zoospores to pass. × ca. 342½.

by way of a tiny discharging papilla which was markedly constricted where it penetrated the chitin of the gill. The emerging zoospores took a considerable time to pass through, they were almost pinched in half and detained there for perhaps 30 seconds. After passing through they halted at the exit for a few seconds as though held up by a posterior cilium or protoplasmic process adhering to the wall of the papilla; they would fling themselves sideways in an effort to become free.

As mentioned previously the length of time before encystment varies considerably, as does also the time taken actually to encyst. They may take several minutes in the process, swinging round and round in small circles and becoming more and more rounded until at last movement ceases; or a zoospore may stop abruptly when swimming rapidly, and,

as it were, tucking in the pointed end, become rounded in a second. When rounded the spore often swings round for a short time, and at least one cilium can be seen lashing. The spore comes to rest, a shining droplet appears on the tip of the cilium as it gradually shortens, and while still of some length it breaks off and floats away. This process of events was seen very clearly perhaps a dozen times and the path of the drifting cilium followed for a second or so. Generally only one cilium has been clearly seen during this process. The shortening of the cilia with the appearing of a droplet was noted by Butler in the encysting zoospores of *Pythium de Baryanum* Hesse (Pythiaceæ) (**6**, p. 94). On one occasion a zoospore of the *Pinnotheres* fungus, seen when about to encyst, had two

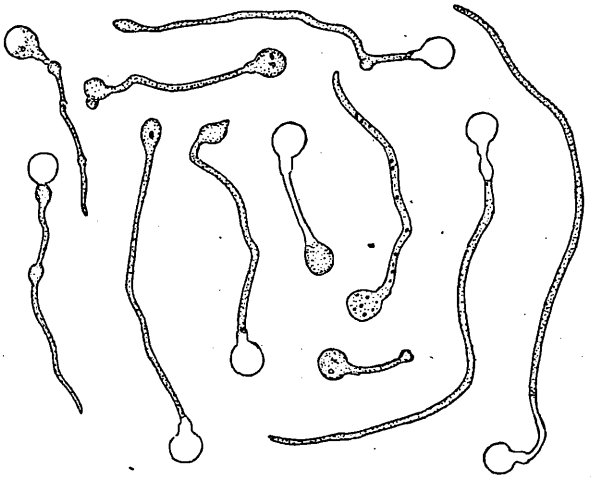

FIG. 10.—Germinating cysts. Some have small swellings along the length of the germ tube and one seems to be attempting to re-encyst. × ca. 685.

apical cilia which curled in towards each other, then broke off and floated away. The cysts vary from about 6μ to 10 or 11μ in diameter; they contain several shining globules. A fine germ tube is put out, but since no nutritive medium was supplied, as the tubes grew in length the part next the cysts was gradually left empty and after a time the plant died. Small swollen structures occur along the germ tube (Fig. 10), some nearly as large as the original cyst, as though there was an attempt at re-encystment (**3**, p. 283).

The question of the structure of the zoospores and as to whether there are two motile phases has had to be left, at least for the present, in a very unsatisfactory state. Owing to lack of time no attempt was made to obtain pure cultures and, as already mentioned, it was found impossible otherwise to obtain a drop containing zoospores that was not swarming

with bacteria, hiding the cilia. A second zoospore has not been observed emerging from a cyst, all that can be brought forward in favour of the existence of two motile phases in this fungus is, firstly, the finding of empty cyst cases with tiny exit tubes: the empty cases showed up quite clearly owing to the thick zone of bacteria collected round them. Secondly, the occurrence of a few zoospores of a definite bean-shape with two cilia which appeared to be laterally inserted, answering to the description of the second zoospores of the Saprolegniaceæ. These came from a sporangium, but may have emerged from spores encysted there.

Difficulty was experienced with growing the fungus in hanging drops of sea-water; it was found that the development of the fungus in the

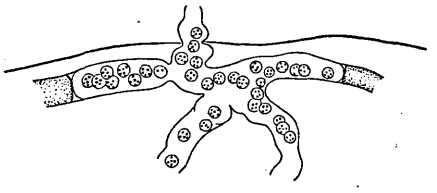

FIG. 12.—Sketch to show part of a branched sporangium with a single aperture; a number of zoospores have encysted within it. The thick line shows the outline of the gill leaflet. × ca. 253.

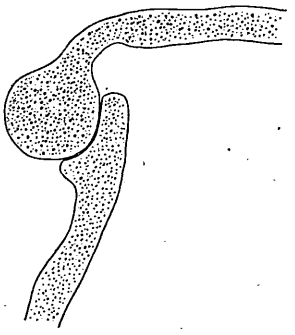

FIG. 11.—Young oogonium with applied antheridium (?). × 400.

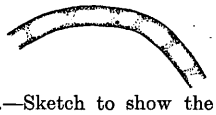

FIG. 13.—Sketch to show the highly vacuolated nature of the protoplasm in hyphæ which very occasionally grow out from the gill into the sea-water. × ca. 342½.

gills in such drops was arrested after a day or two, but that development would go forward and spores form if they were changed into a bowl of sea-water, even if growth had been at a standstill for 14 or so days. A somewhat similar state of affairs has been described by Lechmere (**11**, p. 318) for a species of *Saprolegnia*. The cysts formed in some of the hanging drops, probably owing to artificial conditions, did not develop and after a few days became enlarged, while their contents shrunk away from the wall, in some cases stretching in a band across the cell.

The infection and death was observed of a tiny nematode worm which had accidentally become fixed by its posterior extremity near the edge of a hanging drop made with an infected gill. The spores settled in the first place on the motionless tail of the worm; the rest of the body was writhing vigorously for over 16 hours.

Sexual organs have not been definitely identified. Fig. 11 shows what

appears to be a young oogonium about 32μ in diameter with an applied antheridium of diclinous origin. In gills fixed in Flemming's fluid a very few round bodies containing many black globules of varying size have been seen. Similar bodies are shown in Fig. 5 which was sketched from fresh material. They appeared as shown at night, the next morning the larger one and the hyphæ were empty, the smaller still full. On two or three occasions two round bodies have been seen in proximity as in this figure. There is a possibility that they may be oogonia or gemmæ, but in any case they are exceedingly rare and are formed on spore-producing hyphæ.

Life-History (so far as known).

The mycelium enters the pea-crab in places where the chitin is extremely thin, and round the point of infection the hyphæ form a densely woven patch. In cases where the entrance is effected through the roof of the gill chamber, some strands pass into the body while hyphæ invade the gills and mouth parts. When the tissue of the gills is partly absorbed and the death of the crab is imminent, the hyphæ in these parts turn into zoosporangia, swarms of zoospores being liberated. These remain active under laboratory conditions for a period of a few up to at least 50 minutes, when they encyst. After encystment a second motile period may occur. Infection probably occurs during one or other of the motile phases. Organs which have been recognised as possibly sexual would appear to be rare.

Discussion of Relationships.

The *Pinnotheres* fungus has the general characters of the Saprolegniaceæ, the hyphæ, which are freely branched and unconstricted, are aseptate until the approach of the reproductive stages, and the asexual spores are biciliate. The zoosporangia are formed from unchanged hyphæ, as in *Aphanomyces* (**2**, p. 160) and *Leptolegnia* (**14**, p. 522); they are mostly branched (Fig. 12) as Coker (**2**, p. 159) observed for the sporangia in old cultures of *Leptolegnia* which may become very complex from the extension of a single sporangium into a number of adjoining branches. In both *Aphanomyces* and *Leptolegnia*, however, the spores are typically formed in a single row, while in the *Pinnotheres* fungus the number varies with the width of the sporangium. Very occasionally a second sporangium is formed within an empty one, a feeble development of the "nested" arrangement found in *Saprolegnia* and sometimes in *Leptolegnia* (**2**, pp. 22, 157). The biciliate zoospores on emerging from the sporangia swim actively away as in *Saprolegnia*, *Leptolegnia*, and *Isoachyla* (**2**, pp. 22, 157, 81; **6**, p. 83), and it is possible that after encystment a second zoospore emerges as also occurs in those genera. As previously mentioned, the first

zoospores are probably of two sizes, large and small, with intermediate sizes as in *S. anisospora* de Bary.

The *Pinnotheres* fungus is distinguished from species of Saprolegniaceæ growing on freshwater animals and apparently from all other members of the family (**6**, p. 82) by being almost entirely an internal parasite, the discharging papillæ of the sporangia only, with very rare exception, penetrating the chitin of the host and reaching the exterior. It is extremely rare for there to be any growth of the fungus, apart from the discharging papillæ, external to the host, but an exceedingly slight external growth was noticed on three occasions on gills. Such filaments are very different in appearance from the normal internal hyphæ from which they arise, they are very fine and exceedingly vacuolated, the squarish vacuoles stretching across the width of the hyphæ (Fig. 13). Similar very slender, highly vacuolated hyphæ were seen extending from a few well-developed embryos of *P. pisum;* the hyphal threads radiating from the embryos had the appearance of a halo. These were found on August 21st and 12 days later the female, which was carrying the embryos, was found dead with white opaque patches on the abdomen and with the gills infested with the usual fungus.

Dead infected crabs, left in sea-water, show no external growth of the fungus and it seems probable that it dies soon after the crab. This is in striking contrast to the heavy external growth formed by *S. parasitica* on dead salmon and other fish, dead flies, beetles, etc. (**10**, pp. 321, 331), indeed this latter species is said by Patterson (**13**, p. 1) to show a richer growth on dead than on living salmon, indicating that dead tissue is much more suitable for its growth than the living fish. The apparent inability of the *Pinnotheres* fungus to form a growth on dead crabs may seem to argue in favour of its truly parasitic nature, but putrefaction of *Pinnotheres* is somewhat rapid and it may be that the number of bacteria, etc., present, check the growth of the fungus and kill it (**14**, p. 506 ; **10**, p. 331).

The question as to whether it is a true parasite or only invades tissue which has been broken down by parasitic bacteria, as does *S. parasitica* of the salmon (**13**, pp. 2, 7 ; **4**, p. 200 ; **7**, p. 29) and perhaps *A. Hoferi* of the Bohemian mirror carp (**2**, p. 145), has not been gone into : there is quite a possibility that this may be so, for gills infested with the fungus are almost always swarming with bacteria of several kinds. If it is a true parasite it would seem to be ill adapted to its host, for its penetration into the gills must soon cause the death of the host.

It is very probable that death occurs more rapidly under laboratory than under natural conditions. In the case of the crabs, of which details are given in Table I, they had been taken from mussels, being themselves parasites (**12**), and were isolated free in batches varying in number from

TABLE I.

MORTALITY OF PEA-CRABS, INFECTED WITH THE FUNGUS, WHEN KEPT TOGETHER IN BOWLS.

Number of crabs in a bowl, all of which died with the infection.	Date of placing in bowl.	Date of 1st and of last death.		Number of days before 1st death.	Number of days between 1st and last death.	Number of days between placing in bowl and last death.
5 (4 adult ♀+1 ♂) from Weir Point, April 10/28	April 10, 1928	April 28	May 18	18	20	38
12 (♀ adult) from Padstow, April 25/28	April 25	May 22	June 6	27	15	42
13 (♀ adult) from Padstow, April 25/28	April 27	May 12	May 25	15	13	28
7 (♀ adult) from Padstow, April 25/28	May 8	May 26	June 8	18	13	31
3 (♀ berried) from Padstow, April 25/28	May 8	June 4	June 13	27	9	36
7 (♀ adult) from Padstow, April 25/28	May 9	May 28	June 15	19	18	37
21 (♀ adult) from Padstow, April 25/28	May 10	May 22	June 11	12	20	32
18 (♀ adult) from Padstow, Sept. 14/28	September 17	October 6	October 20	19	14	33
				Average 19·4	Average 15·2	Average 34·6

5 to 21 in bowls of sea-water and therefore possibly able to obtain little food. When a number of crabs were kept together in a large glass dish, as in the eight instances given in Table I, they gradually died of the disease, one after the other succumbing. Mortality was very much lower among those crabs kept singly in finger bowls, indicating that the disease is extremely infectious. All crabs in the Laboratory had their water renewed every day or every other day.

The death of the host is generally sufficiently rapid, at least in the Laboratory, for the gonad—so far as appears outwardly—not to be affected. This is a condition contrary to that which occurs in infection by a Sarcosporidian identified by Dr. Pixell Goodrich, and in infection by *Pinnotherion vermiforme* Giard and Bonnier (**5**). In some few cases, mostly crabs which when taken from the mussels were seen to be infected, the crabs were rather orange or milky orange in colour. This possibly indicates that they may resist the fungus longer under natural conditions and there is time for them to draw on the gonad. In one dead crab examined, which had been a milky orange for some time, the fungal threads were found among degenerating ova in the gonad. The main axis of each of the gills was full of a bright yellowish orange substance, which looked like yolk globules, but did not blacken with the osmic acid in Flemming's fluid, and was doubtless derived from the degenerating ova.

SUMMARY.

A fungus, most probably allied to the Saprolegniaceæ, has been found infecting *Pinnotheres*. Pea-crabs so infected always die, but there is not as yet sufficient evidence to determine whether the fungus is pathogenic or only invades tissue which has been destroyed by parasitic bacteria. Although having the general characters of the family it apparently differs from all members so far described in that it occurs in a marine invertebrate and is almost entirely internal in habit, the zoosporangia occurring within the tissue of the host.

ACKNOWLEDGMENTS.

The work was carried out at Plymouth while holding a Miss Busk studentship of Bedford College. I wish to thank the College authorities for allowing me to work at the Marine Station, and the London University for granting me the use of their table. My thanks are also due to the Director and Staff for their kindness, and I am especially indebted to Dr. J. H. Orton for criticism and advice throughout the work. Miss G. L. Naylor most kindly read the manuscript. I am in addition indebted to several members of the Staff, and especially to Mr. A. J. Smith for the photograph in Fig. 1.

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On Abnormal Conditions of the Gills in *Mytilus edulis*. Part I. On Permanent Natural Reversal of the Frontal Cilia on the Gill Filaments of *Mytilus edulis*.

By

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With 35 Figures in the Text.

Reprinted from the Journal of the Marine Biological Association of the United Kingdom, Vol. xvi. No. 3. May, 1930.

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CONTENTS.

Introduction.

A HEAVY percentage of the mussels obtained from various parts of the Fal Estuary, during October and November, 1927, had the gills in an exceedingly abnormal condition (31·8% among 1488 recorded). Occasional mussels from other localities (Padstow, Teignmouth, Yealm, Saltash) have been observed to have slightly abnormal gills, though perhaps in the majority of these the condition was due to the presence of a large female pea-crab, *Pinnotheres pisum*. In the Fal Estuary mussels the abnormal conditions were doubtless correlated with some factor in the environment, the percentage of pea-crabs in these being so low (4·8%) that their presence could have no relation to the abnormal condition of the gills.

These abnormal conditions will be described in some detail as they are thought to be of considerable general interest for experimental work.

The present paper will be restricted to a description of the permanent reversal of the frontal cilia on the gill filaments. In a further paper it is hoped to deal with: (1) folding over of the free edge of the gill with concrescence, (2) fusion of filaments side by side, and (3) enlargement of filaments.

The Permanent Natural Reversal of the Frontal Cilia on the Gill Filaments of *Mytilus edulis*.

Perhaps the most interesting of the abnormal conditions for experimental work is the occurrence of supernumerary food grooves on the surface of the gill (see Fig. 2, p. 921), accompanied in most cases by a permanent reversal of the frontal cilia, generally on that part of the lamella between the main and secondary grooves. The supernumerary

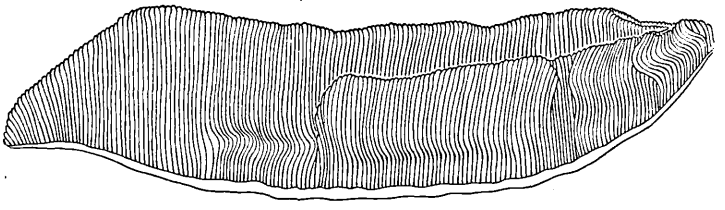


Fig. 1.—Sketch of the right inner gill of an uninfected* *Mytilus edulis* from Trelissick Reach, Fal River, showing a large fold—composed of three folds in series—on the ascending lamella. From preserved material. ×3.

groove may be set directly on the frontal surface of the lamella, as in Fig. 7, III, p. 930, or may be raised on a slight projection (Fig. 23, p. 948), or the lamella may be produced into a tiny fold (Fig. 35, II, p. 963), passing in some cases into a pocket (Fig. 30, II, p. 954). Food collected in any of these secondary grooves is passed eventually into the main grooves without interfering with the normal functioning of the gill.

These conditions were of rather rare occurrence among the Falmouth mussels, and—when found in mussels from other localities—are undoubtedly in most cases, as will be shown later, due to injury caused by the presence of a large female *Pinnotheres pisum*.

There is considerable range of variation in the size of the folds or pockets. The greatest development of pockets—indeed they are so large as almost to merit the term secondary gills—occurred on the gills of a small uninfected* mussel, 5·1 cm. long, from Trelissick Reach, Fal River. The gills were roughly 33 mm. long and 8 mm. deep; the secondary gills occurred on the ascending or reflected lamellæ of the inner

* "Infected" and "uninfected" means infected and uninfected with *P. pisum*.

gills,* that on the left gill was about 24 mm. long and 4 mm. deep ; that on the right about 18 mm. long and 4 mm. deep was composed of three pockets in series (Fig. 1). The descending or direct lamellæ of these gills were nearly normal, only a very little fusion of filaments side by side occurring. (The nomenclature employed for the gill filaments is that figured on p. 226, *Treatise of Zoology*, Vol. V, Mollusca, edited by E. Ray Lankester.) The ascending lamella of the left outer gill had a pocket about 7 mm. long and 3 mm. deep near the posterior end, and near the anterior end a simple secondary groove about 9 mm. long running into the main groove very near the mouth. A pocket about 10 mm. long and

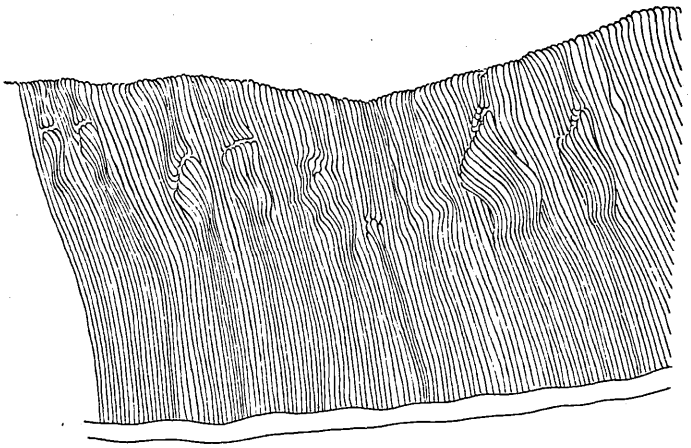


FIG. 2.—Sketch of part of a gill of an uninfected Mytilus from Trelissick Reach, Fal River, showing a series of small folds or pockets on the ascending lamella. From preserved material. ×4.

5 mm. deep, and a simple secondary groove about 13 mm. long occurred on the right outer gill in similar positions to those on the left. The descending lamellæ of both gills were nearly normal, a very little fusion only occurring. The supernumerary pockets and grooves were arranged in such a symmetrical manner as to make it appear doubtful whether they were due to abnormal conditions in the environment.

Figure 2 is a sketch of a series of small pockets on the gill of another mussel from Trelissick Reach, Fal River, which again did not contain a pea-crab.

The gills of a Padstow mussel harbouring a female *P. pisum* (12 mm. carapace width), had numerous secondary grooves, which were almost entirely restricted, in an unusual manner, to the descending lamellæ of all four gills, as though the crab had been scrambling between the two gills of each side (Fig. 3).

* For convenience in description the two demibranchs on each side of the body are considered as two gills.

Possible Cause of Formation of Secondary Grooves and Folds.

Owing to pressure of other work at the time the Falmouth mussels were received they were preserved after no more than a cursory examination. The following observations on the structure of secondary grooves and folds and their ciliation have been made on those which may occur exceedingly rarely on gills of normal, healthy, uninfected mussels, but

Fig. 3.—Photograph of a mussel (10·0 cm. long) from Padstow, showing numerous secondary food grooves on the descending lamellæ of the gills. In some places the free edge of the two right gills is permanently folded over. From preserved material.

more frequently on the gills of mussels which harbour a large female *P. pisum.*

In working on Pinnotheres since October, 1927, a look out had been kept for any possible direct harmful effect of the crab on its host, and it had been noticed that the gills of mussels containing large specimens were sometimes injured, though it has not been found so far that the pea-crab injures the mantle causing the nacreous layer to be dissolved away, as described by Wright (**43**, p. 145). Mussels with injured gills and containing crabs, have been obtained from the River Yealm, the estuaries of the Hamoaze (Saltash), Padstow, and Teignmouth ;

those from the Fal were so commonly abnormal that it was impossible to distinguish abnormality possibly due to the presence of a pea-crab. No careful record of the frequency of injury, however, had been kept until the last two batches of mussels from Padstow were examined. These gave the following results :—

Date. 1929	Total number of mussels.	(a) No. of mussels with large pea-crabs.	No. of gills of (a) affected.	(b) No. of mussels with small pea-crabs.	No. of gills of (b) affected.	Gills abnormal, no crabs present.
June 6	944	88 (crabs with carapace width 9·0–14·0 mm.; eight were accompanied by males)	65 (73·86 %)	85 (crabs with carapace width 1·45–7·25 mm.)	0 (0·0 %)	12 (1·56 %)
Aug. 9	508	34 (crabs with carapace width 8·0–13·0 mm.; three were accompanied by males)	29 (85·29 %)	86 (crabs with carapace width 2·0–7·0 mm.	4 (4·65 %)	3 (·77 %)

Included under gills affected are mussels with (1) gills simply short, (2) gills folded over slightly at the free edge, (3) fusion of filaments, and (4) secondary grooves and folds. It may be pointed out that where gills are abnormal in mussels containing only a small pea-crab or none, there is the possibility that the injury may be due to a previous infection.

A large *Modiolus modiolus* from the Salstone, Salcombe, containing a female *P. pisum*, about 13 mm. carapace width, had not only the gills of both sides injured but also the mantle of one side. In Modiolus, however, the mantle is much thinner than is usual in healthy *Mytilus edulis*, for it appears that in the former the gonad does not encroach on the mantle.

Judging by the usually restricted area of injury—it is extremely rare for the gills of both sides to be damaged—it would seem that large pea-crabs move about very little in a mussel. On opening a mussel they are generally found on one of the inner gills mostly near the base of the foot, but just beyond the reach of the outstretched palps, and backing on the visceral mass. Beneath the crab the inner gill of the infected mussel is often considerably narrower than normal; sometimes the outer one may also be slightly narrow in this region. The shortness may be restricted to a small semicircular area (Figs. 13, I, p. 937, and 17, I, p. 943), or may extend for almost the entire length of the inner gill (Figs. 7, I, p. 930; 20, I, p. 946; 22, I, p. 947). In some cases, except for the shortness, the gill appears normal, in others the food groove is very irregular, and a slight folding over of the edge may occur with some fusion to the lamella (Fig. 4); in some places a food groove may be entirely absent for a short distance so that food collected posterior

to the break will not reach the oral end of that gill, possibly however at the break food strings will be carried on to the deeper outer gill and reach the palps that way.

In connection with the shortening of the gill there are, in perhaps the majority of cases, to be found small secondary grooves and folds or pockets. They may occur on the inner much shortened gill and on the inner face (descending lamella) of the outer gill, where it is exposed to possible injury by the pea-crab, owing to the shortness of the inner gill (Figs. 12, I, p. 936 ; 17, I, p. 943), but are not always restricted to these areas and may occur on gills of normal depth (Fig. 14, I, p. 938). The secondary grooves vary much in length, a tiny one involving only one grooved filament is shown in Figure 13, II (p. 937), while one 16 mm. long has been seen.

It is thought that these secondary grooves arise in some way as the

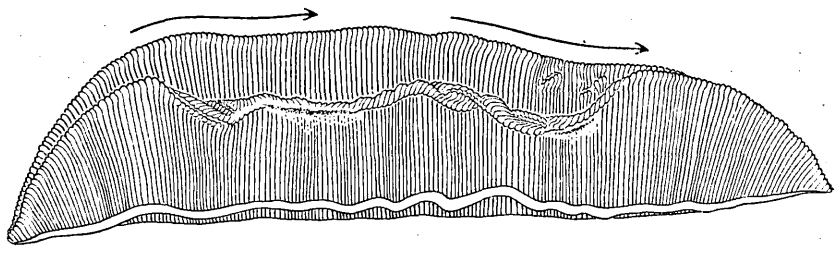


FIG. 4.—View of gills of the right side of a Padstow mussel, which harboured a large ♀ *Pinnotheres pisum*. The inner gill is short for most of its length, the free edge is in part folded over ; in one place a food groove is wanting and considerable fusion of the filaments has occurred, while elsewhere secondary food grooves are present. Three short secondary grooves are present on the descending lamella of the outer gill. The arrows indicate the direction of the current in the main food grooves at the free edges of the gills. Drawn from life. × 2.

result of injury caused by the presence of the pea-crab. A pea-crab is often very difficult to remove from a gill without injury to itself or the gill, as when disturbed it hooks the pointed claw-like tips of its legs well into the gill. Whether the pockets are caused by the pea-crab hooking its claws into the gill and drawing it up into folds, which become permanent, or whether the folds grow as the result of wound stimulus, following a simple tear, can only be determined by experiment. The pockets or folds, however, are permanent. In all those examined it has been found that only the lamella on which the groove occurs is involved in the groove or fold : in some of the folds there is a bend in the non-groove-bearing filament (Figs. 23, p. 948 ; 35, II, p. 963) which seems to point to the possibility that the filaments on which the pocket occurs have been mechanically pulled into a fold, or that growth of the filament in its normal

direction has been restricted or has ceased, while that of the uninjured filament has proceeded normally. In connection with pockets and secondary grooves there is often considerable growth of inter-filamentar junctions, which of course does not occur normally in *Mytilus edulis*. (Cf. *Margaritifera vulgaris* **20**, p. 227, and *Avicula argentea* **38**, p. 155, with ciliated discs and inter-filamentar junctions.) This makes the stripping of such pockets, filament by filament, impossible without careful micro-dissection, which was not attempted, only those with little inter-filamentar growth being examined thoroughly. The two filaments of a fold are not only often strongly connected with each other, but a filament may be connected with one in the opposite lamella other than its pair; also there may be fusion of filaments side by side. In fact, wherever there is a fold or secondary groove on a gill there is a strong tendency for fusion and inter-filamentar, as well as inter-lamellar, growth to occur, especially in pockets the filaments of which are somewhat askew.

In some instances it would seem that originally deep pockets have become fused with the main lamella, little more than the secondary groove remaining, along with a greater width of the filaments and a greater number of ciliated discs for a certain distance dorsal to the secondary groove, to indicate what has occurred. Stages in this possible process are shown in Figures 5, I–II; 26 (p. 950); and 5, III. In Figure 5, I, the pocket is distinct, in Figure 5, II, the two contiguous filaments, one belonging to the main lamella and the inner one of the secondary pocket, have fused for a certain distance so that it appears that there are three filaments. In Figure 26 (p. 950) the fusion has gone a step further, and in Figure 5, III, there are only two filaments, except for a short distance, but by the structure it may be seen that the part of the filament which is dorsal to the secondary groove is formed by the fusion of filaments. This type of pocket will be referred to again in connection with its ciliation.

The cavity of pockets has always been found to face toward the free edge of the gill, but when the secondary groove is carried on only a slight elevation of the lamella it has been noticed, once or twice, that there may be a slight tendency for the process to slope dorsally (Figs. 3, p. 922); 22, II, p. 947).

When a secondary groove occurs very near the main groove it is often found joining the latter at one end, and that most usually the anterior end. In Figure 35, I (p. 963), however, a secondary groove is shown which joined the main groove and then diverged. Secondary grooves near the main groove may very occasionally join the latter at both ends.

In secondary grooves on the surface of the gill one or two filaments at either end of the groove are usually raised into a projection in continuation of the groove (Fig. 10, II, p. 934), though rarely the secondary groove

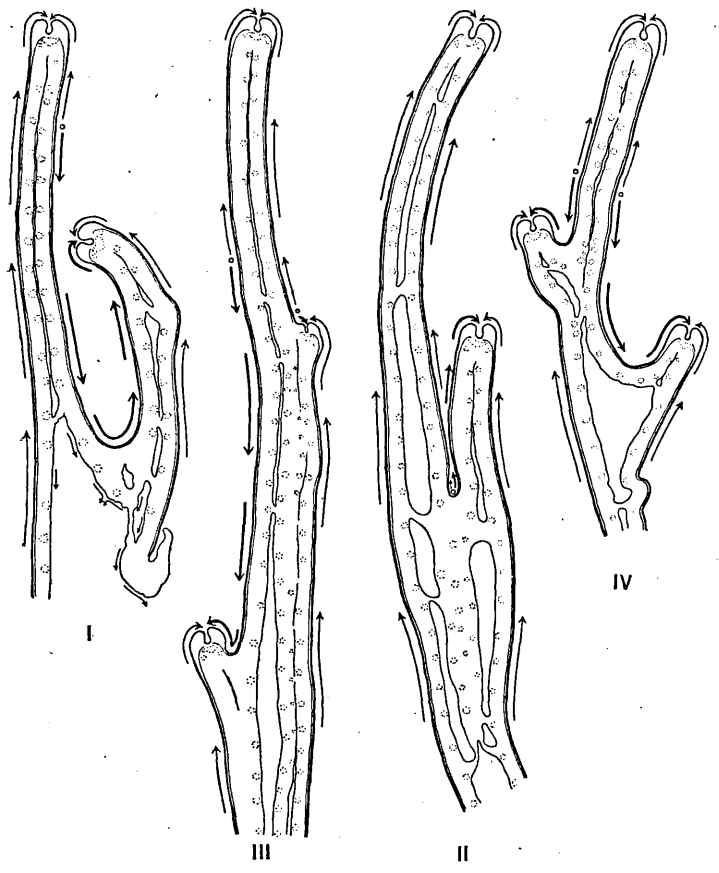


FIG. 5.—Lateral views of living filaments, bearing secondary grooves and folds, from four specimens of Mytilus from Padstow. The direction of beat of the frontal cilia is shown by arrows; heavier arrows are used when the direction is the reverse of normal. × ca. 9.

I. Filament from a deep fold or pocket on the ascending lamella of a left inner gill. The fold was near the posterior end of the gill, near the posterior adductor muscle.

II. Filament from a fold on the ascending lamella, inner gill of a Mytilus, which did not harbour a pea-crab. The fusion of adjacent parts of the filament has caused partial obliteration of the fold.

III. Filament from an outer left gill with secondary food grooves on the descending and ascending portions of the filament. That on the ascending filament (to the right) was apparently originally at the edge of a deep fold, but almost complete fusion of the filaments forming the fold has taken place.

IV. Filament from a left inner gill with secondary folds on the descending and ascending parts of the filament.

begins and ends abruptly, the preceding and following filaments being perfectly normal.

Gills have very occasionally been found with secondary grooves on the descending and ascending lamellæ of the same gill, a certain number of filaments being common to both (Fig. 5, III–IV, p. 926). Two secondary grooves one above the other on the same lamella are shown in Figures 20 (p. 946) and 22 (p. 947), while in Figure 3 (p. 922) several occur in series across the depth of the gill.

General Ciliation of Filaments Bearing Secondary Grooves.

Gills bearing a secondary groove show, over a certain area of the lamella between the main and the secondary groove, in the majority of cases, a reversal in the direction of food transportation caused by a reversal of the frontal cilia. Food particles drawn on to the gill surface instead of passing in the normal direction towards the main groove at the ventral edge of the gill, for a certain distance ventral to the secondary groove pass in a reversed direction into the secondary groove (see Fig. 9, I, p. 932). (For the ciliation and currents on the gill of *Mytilus edulis* see Orton, **29**.)

In the secondary groove the food current is always in the same direction as that of the main groove, that is towards the oral end of the gill. In secondary grooves, which do not join the main groove at their anterior end, particles debouching on the first filament with normal ciliation are carried along it into the main groove. Secondary food grooves on a gill therefore interfere little, if at all, with the efficient working of the gill.

There is not the slightest doubt of the fact of the permanent reversal of the frontal cilia. In all cases stripped filaments were examined at a magnification of 280 or 506 diameters and in many cases the reversal of the current was also demonstrated by carmine particles.

The frontal cilia on the gill filaments of Mytilus are brought to rest at the beginning of their preparatory stroke by increase in osmotic pressure (see Gray, **18**, **19**, p. 54). Presumably owing to increase in osmotic pressure, due to increasing salinity in a preparation by evaporation on a slide, the frontal cilia were found to come to rest at the beginning of their preparatory stroke; it was then seen very clearly that those on either side of the line at which reversal occurs were lying in opposite directions. This would appear to be evidence in favour of the effective stroke being reversed. Gray (**19**, p. 63) remarks that: "It is difficult to imagine how the frontal cilia of *Mytilus*, . . ., could perform any appreciable amount of work during their recovery strokes; but if a cilium is of such a type that there is not much difference between the form of the two strokes it is conceivable that the nett effect of the beat could be reversed

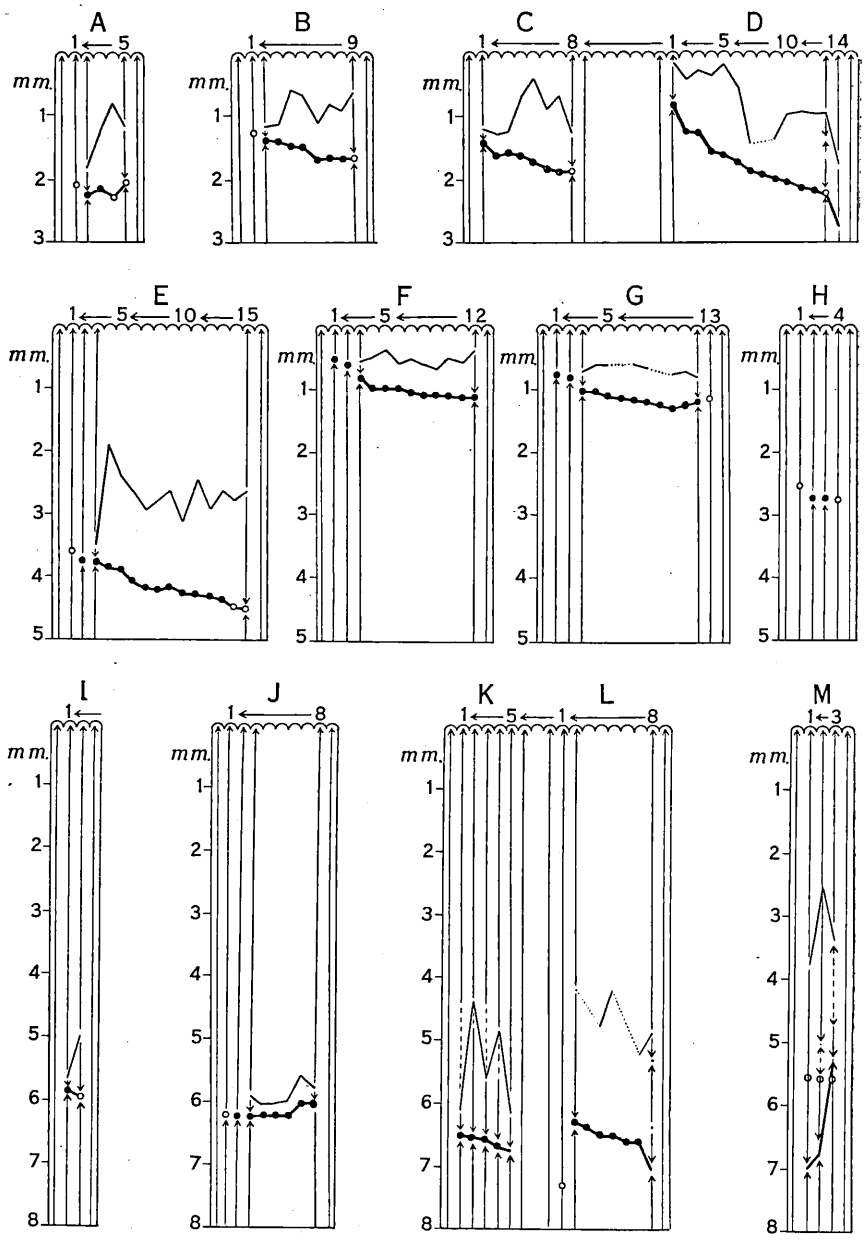


FIG. 6 (description opposite).

by quickening the recovery stroke and slowing the effective stroke as appears to be the case in some protozoa." Parker (**31**, p. 12) suggested that the reversal of Metridium cilia was effected by a system of flexor and extensor elements, placed on the opposite sides of a supporting axis, and his view was elaborated by Williams (**42**).

In *Mytilus edulis*, as in Metridium (**31**, p. 9), the metachronal wave is reversed with the reversal of beat of the frontal cilia.

When the surface of a gill bearing a secondary groove was supplied with carmine particles it was seen that the point of division was by no means always at the same level, or nearly the same level, on adjacent filaments, but as it was thought at first that there might be a simple or direct relation between the influence of the main and the secondary groove, it was decided to strip parts of gills bearing secondary grooves of as many types as possible, to measure the distance from the main groove at which reversal of the beat of the frontals occurred, and to plot the results as a graph.* The results show that if there is a relation between the influence of the main and the secondary groove it is by no means simple: it also appears as though the influence of the secondary groove is exerted as a whole over the adjacent part of the lamella, rather than that the ciliation of each filament is effected only by its own supernumerary groove.

LEGEND FOR FIGURE 6.

FIG. 6.—Graphs showing the relation of the distance of a secondary groove—set directly on the surface of the lamella—from the main food groove, and the points of reversal of the frontal cilia on filaments composing the secondary groove. The direction of beat of the frontal cilia on filaments adjacent to the secondary groove is shown. (Mainly of the gills of *Mytilus edulis*.) The filaments are numbered antero-posteriorly; arrows between the numbers show the direction of the current in the main groove. Distance from the main groove is shown in mm. Semicircles ◠ denote the main food groove at the free edge of the gill. Filled-in circles ● denote a well-formed secondary groove on a filament. Circles o denote a slight groove or a projection of the frontal surface of a filament. When a projection bears cilia beating anteriorly, the arrow showing the direction of beat of the frontal cilia stops dorsal to the projection and begins again ventral to it; when the projection is clothed with short frontal cilia beating ventrally, there is no break.

A broken arrow — — —➢ is used in those instances where the direction of beat of the frontals was somewhat erratic, but the direction of the current was mainly as indicated. A double-headed and broken arrow ≤— — —➢ is used when particles at different times passed in opposite directions.

Inner right or left direct or descending lamella = R2 or L2.
Inner right or left reflected or ascending lamella = R1 or L1.
Outer right or left direct or descending lamella = R3 or L3.
Outer right or left reflected or ascending lamella = R4 or L4.

A was on R3, B „ R3, C „ R3, D „ R3 } of one Mytilus.

E was on L3, F „ L3 } of different specimens of Mytilus.
G „ L3, H „ L3 } of one Mytilus.

I was on R1, J „ R1 } of a *Modiolus modiolus*.

K was on R1, L „ R1, M „ R1 } of one Mytilus.

* The measurements were made with a Leitz eye-piece micrometer, No. 2 eye-piece, and a No. 3 objective.

The basis of these observations is given in the following detailed description :—

Ciliation of Filaments Bearing Secondary Grooves Set Directly on the Face of the Lamella.

Graphs of the change of ciliary current on the filaments comprising a series of short secondary grooves, in which the groove is set directly on

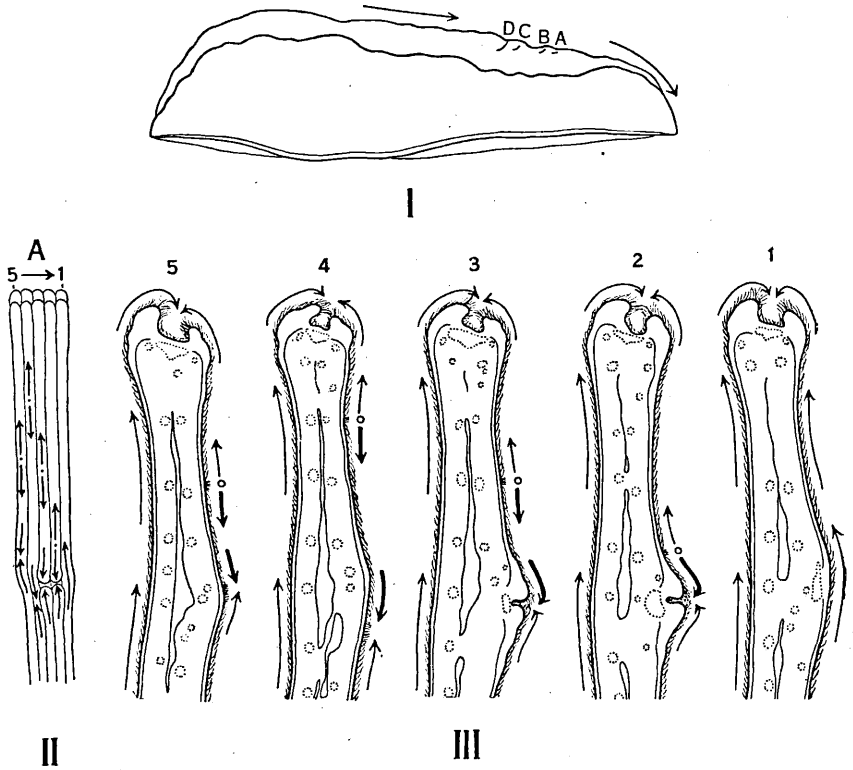


Fig. 7.—I. Sketch of gills of the right side of an infected Mytilus to show the position of the secondary food grooves A–D. The arrows indicate the direction of the current in the main food groves. From life, natural size.

II. Surface view of filaments composing secondary groove A with arrows showing the direction of beat of the frontal cilia. The filaments involved are numbered antero-posteriorly—this order is adhered to in all the figures—and the arrows between the numbers show the direction of the current in the main groove. All figures of surface views, unless otherwise stated, have been constructed from sketches and measurements.

III. Lateral views of single living filaments composing secondary groove A, showing the direction of beat of the frontal cilia. The outline of the filaments, in this and all figures, was traced by the aid of camera lucida. The fine inner line indicates the distribution of the latero-frontal and lateral cilia. The arrows show the direction of beat of the frontal cilia ; heavier arrows are used when the direction is the reverse of normal. I–II × 18¼.

the frontal face of the filament, are shown in Figure 6 (p. 928). The filaments are numbered antero-posteriorly, and where necessary have been so arranged that the first filament is always on the left (in the graphs) from which it follows that the direction of the current in the main and secondary grooves is from right to left.

The graphs in Figure 6, A, B, C and D, are of secondary grooves forming a series on the descending lamella of the right, outer gill of one mussel (Fig. 7, I) where the shortness of the inner gill exposed it to injury by the pea-crab. They were near the main food groove—within 3·0 mm.—and towards the anterior end of the gill.

The secondary groove A (Fig. 7, II), that nearest the anterior end of the

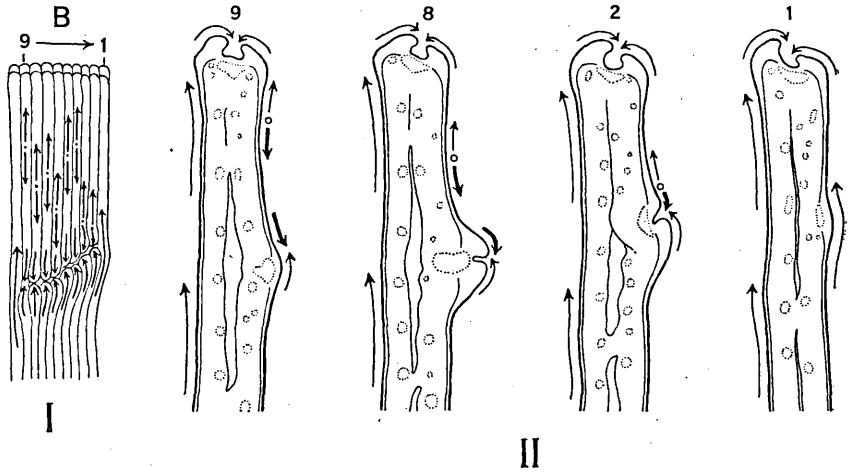


FIG. 8.—I. Surface view of filaments composing the secondary groove B (see Fig. 7, I).
II. Lateral views of representative living filaments. I–II × 18¼.

gill, was composed of only two grooved filaments and all the filaments involved in the abnormality have been drawn (Fig. 7, III). The filament (Fig. 7, III, filament 1) preceding the first grooved filament was nearly normal, there was a break in the rows of latero-frontal and lateral cilia where there was a large elongated ciliated disc, but the length and direction of beat of the frontals was normal. The first grooved filament (Fig. 7, III, filament 2) had a change of ciliary current very near the secondary groove; in the second grooved filament the change occurred further from the secondary groove. The following filament though practically normal in structure had a change in the direction of the beat of the frontals which was here only 0·82 mm. from the main groove: filament 5 was similar, but the change was 1·2 mm. from the main groove. On both these filaments the cilia at the point of meeting of the currents

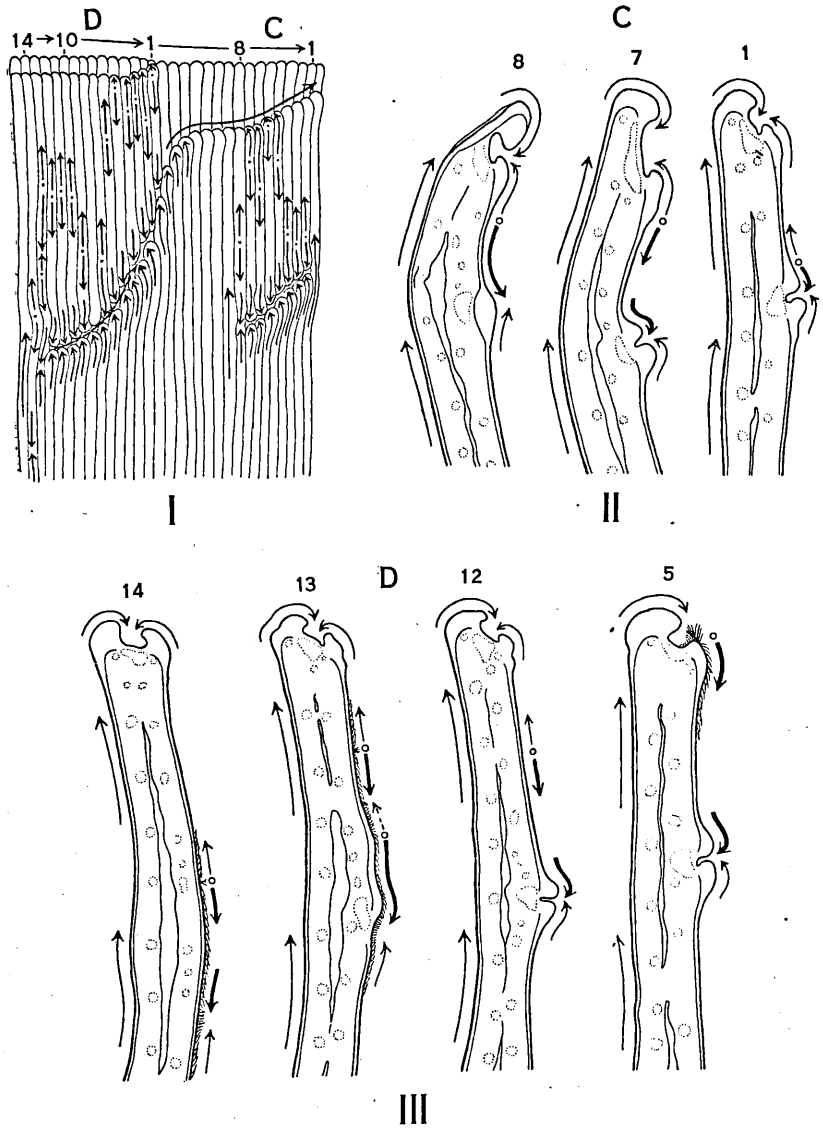


FIG. 9.—Secondary grooves C and D of the gill sketched in Fig. 7, I × 18¼.

I. Surface view of filaments composing the secondary grooves. Owing to the accidental crushing of filament 8 of D, the point of reversal of the frontal cilia could not be determined.

II. Lateral views of representative living filaments of secondary groove C.

III. Lateral views of representative living filaments of secondary groove D. The broken arrow denotes a stretch with cilia uneven in appearance, though the current was in the direction indicated. On filament 5 an arrow, which should have pointed into the main grove, has been omitted.

were of the normal length of frontal cilia, but the direction of their beat was towards the anterior end of the gill, that is at right angles to their normal direction. The following filaments were normal in structure and ciliation.

Secondary groove B (Fig. 8, I), next in the series, was composed of seven grooved filaments and sloped slightly towards the main groove anteriorly. The filament (Fig. 8, II, filament 1) preceding the first grooved one was slightly abnormal in structure, but the direction of beat of the frontals was normal. The first and last grooved filaments only are figured (Fig. 8, II, filaments 2 and 8). The frontal surface of the filament following the last grooved one was raised into a slight projection in continuation of the secondary groove, and there was a break in the rows of latero-frontal and lateral cilia; the reversal of the frontal cilia was only 0·61 mm. from the *main* groove. The next filament was normal both in structure and ciliation.

Secondary grooves C and D (Fig. 9, I) were separated by only seven filaments. In both grooves the slope anteriorly towards the main groove was noticeable, D actually joining the main groove, the sides of which were here very unequal. The filament preceding the first grooved filament of C was normal in structure and ciliation. The point of reversal of the frontals was close to the secondary groove on the first grooved filament (Fig. 9, II); it was nearest to the main groove on the fifth filament. Filament 8 following the last grooved filament, although possessing no groove, only a raised area, showed a change in beat of the frontal cilia. The frontal cilia on the projection, where the ciliary currents met, were of normal length but were beating anteriorly. The following filament was normal in structure and ciliation. Filaments from secondary groove D are shown in Figure 9, III. The fact that a reversal of beat occurred on filament 1 (Fig. 9, I), which is unusual, may perhaps be due to the main groove anterior to this filament being very unequally sided, and therefore possibly continuing the influence of the secondary groove. Filament 13 (Fig. 9, III), although grooveless, had two changes in ciliary beat; the part marked with a broken arrow was rather uneven in beat. Filament 14 was structurally normal, yet had a reversal of the frontal cilia 1·8 mm. from the main groove. On both these filaments the frontal cilia at the meeting of the currents were of normal length, but the direction of their beat was towards the anterior end of the gill. The following filament was normal in structure and ciliation. Filament 8 in groove D could not be measured as it was inadvertently crushed.

Figure 10, I, is a surface view of a secondary groove (E) on the descending lamella of a left outer gill, where it was exposed owing to the shortness of the inner gill. It was between 3·6 mm. and 4·5 mm. from the main groove and sloped slightly ventralwards anteriorly. Figure 6, E (p. 928), is

the graph of this groove and separate filaments are shown in Figure 10, II. The first grooved filament showed no change in beat of the frontals; there was just the break caused by the groove with its long terminal cilia. The filament (Fig. 10, II, filament 14) following the last grooved filament had a distinct projection of its frontal surface, carrying long cilia beating

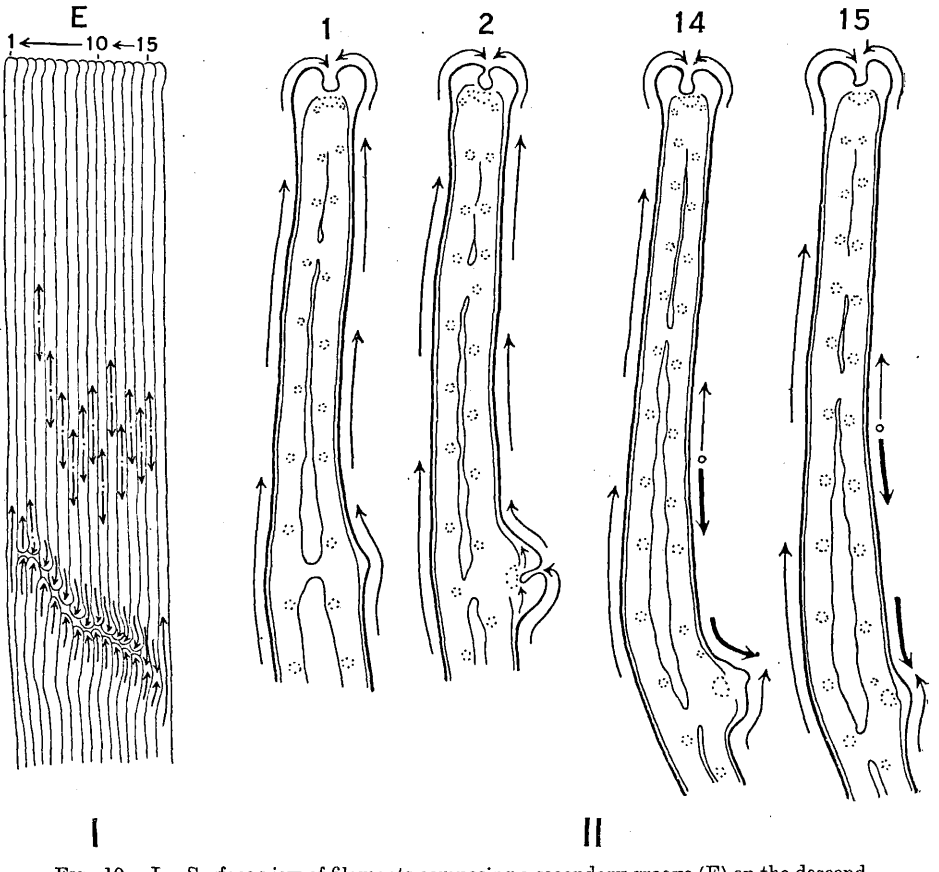


FIG. 10.—I. Surface view of filaments composing a secondary groove (E) on the descending lamella, left outer gill of an infected Mytilus.
II. Lateral views of certain of the living filaments.
I–II × ca. 18¼.

anteriorly, in continuation of the secondary groove, and reversal of ciliary current occurred. Filament 15 had a very slight projection and yet ciliary reversal again occurred: the following one was altogether normal. This secondary groove shows in a definite way the tendency, which is evident from most of the graphs, for the reversal of beat of the frontal cilia to occur nearer the secondary groove at the anterior than at the posterior

end, and that while a grooved filament at the anterior end of a secondary groove may have no reversal of ciliary current, at the opposite end filaments almost normal or normal in structure may yet have ciliary reversal.

Figure 11, I, is the surface view of a short secondary groove (F) on the descending lamella of a left outer gill, exposed by the shortness of the inner gill, and which at the anterior end joined the main groove. No change of beat of the frontal cilia occurred until the third grooved filament and none occurred on that following the last grooved filament (Figs. 6, F, p. 928; 11, I–II); this filament was slightly bent permanently, as were also the next few in the series.

Figure 12, I, is a rough sketch of the two left gills of a mussel with several short secondary grooves on the descending lamella of the outer

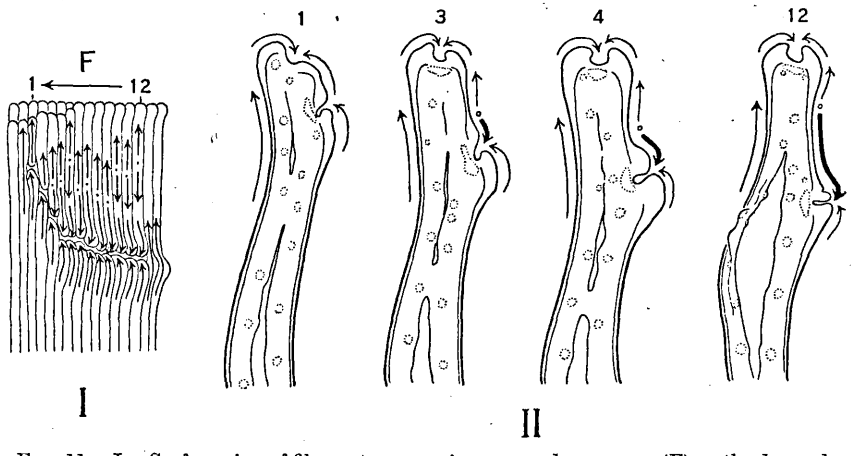


FIG. 11.—I. Surface view of filaments composing a secondary groove (F) on the descending lamella, left outer gill of an infected Mytilus.
II. Lateral views of representative living filaments.
I–II × 18½.

gill. That nearest the anterior end of the gill was composed of twelve grooved filaments (Figs. 6, G, p. 928; 12, II); it was difficult to strip, as many inter-filamentar connections occurred near the secondary groove, holding several filaments together. Apparently no change occurred—but this is a little doubtful as the first two filaments stuck together—until the third grooved filament (Fig. 12, III, filament 3). The last, though slightly grooved, had no ciliary change, and the cilia clothing the groove were short and were beating ventrally.

On the same gill three tiny incipient grooves occurred in series. That marked H in Figure 12, I, is shown in surface view in Figure 12, IV, and its graph in Figure 6, H (p. 928). The two grooved filaments (one shown in Fig. 12, V) showed no ciliary reversal, only the groove with its long

terminal cilia interrupting the food current. It is interesting to compare this secondary groove with that composed of the same number of grooved filaments of Figures 6, A (p. 928), and 7, I–III (p. 930). The filaments of the remaining two tiny secondary grooves, of about four and six

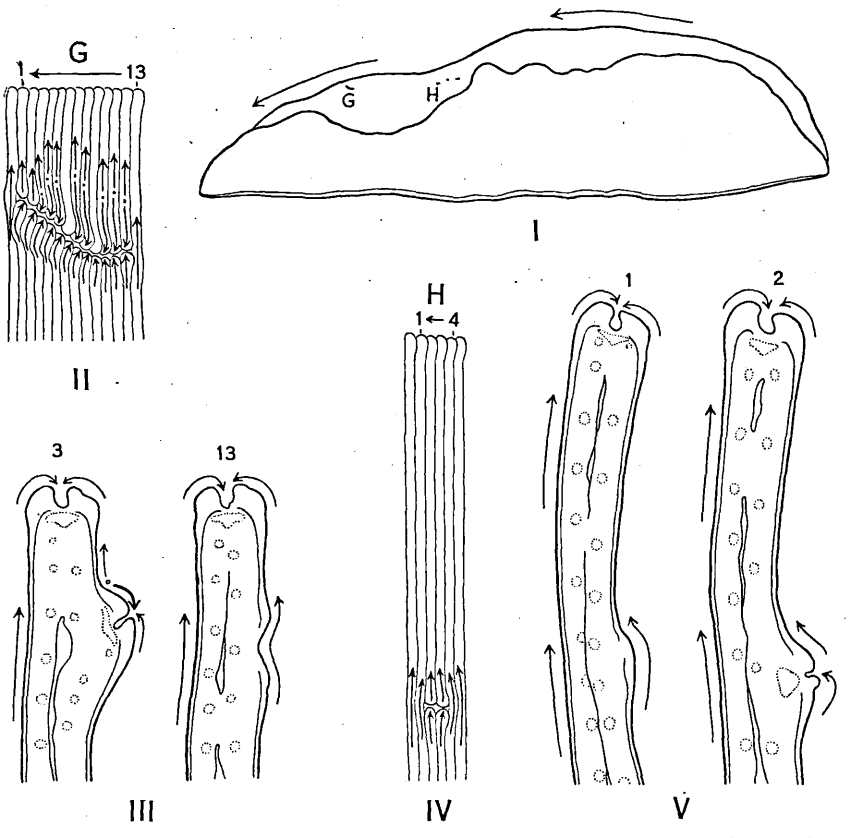


Fig. 12.—I. Sketch of gills of the left side of an infected Mytilus, showing the position of secondary grooves (those investigated are lettered) on the descending lamella of the outer gill where it was exposed owing to the shortness of the inner gill. From life.
II. Surface view of filaments composing secondary groove G. Owing to the fusion of filaments the point of reversal of beat of the frontal cilia on filaments 6 and 9 could not be determined.
III. Lateral views of two living filaments of secondary groove G.
IV. Surface view of filaments composing secondary groove H.
V. Lateral views of two living filaments of secondary groove H.
II–V × 18¼.

filaments respectively, were mostly like the first filament of group H (Fig. 12, V), though some were slightly grooved; there was no reversal of beat of the frontal cilia.

The gills of a *Modiolus modiolus* containing a pea-crab were found to be

affected; those on the right (Fig. 13, I) more than those on the left. The inner right gill was very short in a small V-shaped area, with several short secondary grooves and some crumpling of the filaments near the

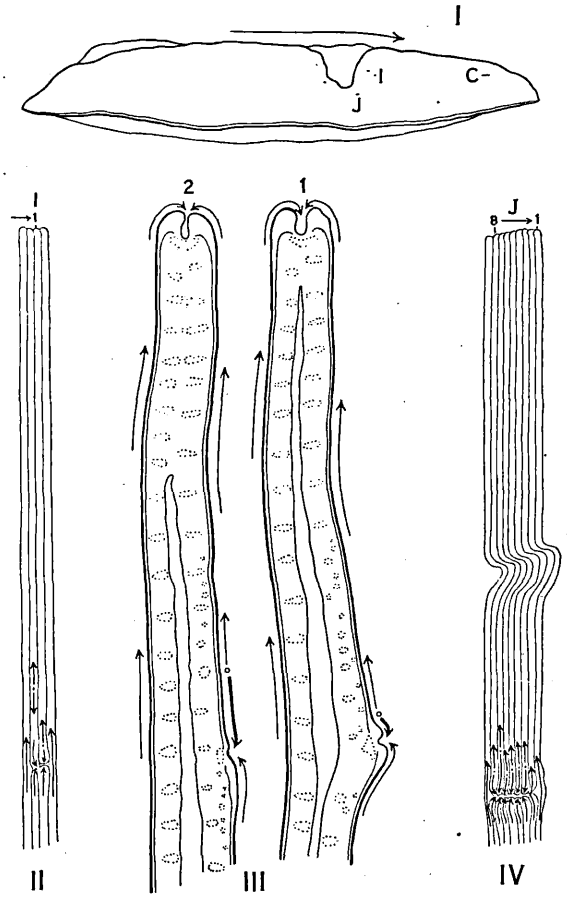


FIG. 13.—I. Sketch of gills of the right side of a specimen of *Modiolus modiolus*, which harboured a large female Pinnotheres, showing shortness of the inner gill in a small V-shaped area and several secondary grooves: those investigated are lettered; I and J are on the ascending lamella of the inner gill, and C indicates the position of a secondary groove on the ascending lamella of the outer gill. Drawn from life. × ⅔
II. Surface view of filaments composing secondary groove I.
III. Lateral views of the two filaments composing secondary groove I.
IV. Surface view of filaments composing secondary groove J.
II–IV × ca. 12.

edge; the crumpling made the filaments very difficult to strip, as where it occurs there is generally considerable fusion of the filaments side by side. (In the normal gill of *Modiolus modiolus*, as in that of *Mytilus*

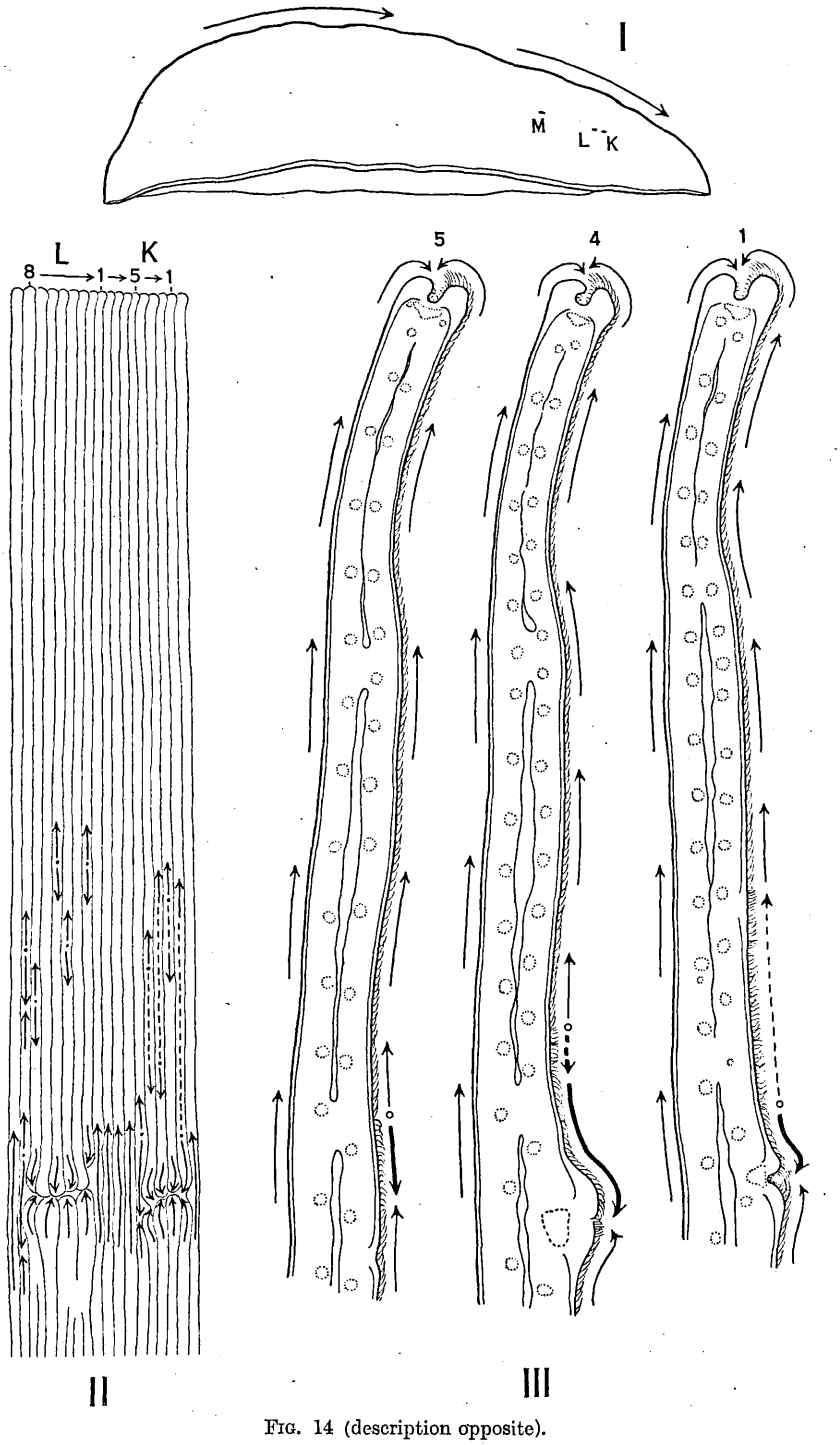


FIG. 14 (description opposite).

edulis,* there are no organic inter-filamentar connections, only ciliary junctions, and in the former most of the filaments have no inter-lamellar junctions, but an occasional filament has an inter-lamellar septum; the septa vary in height.) In secondary groove I (Figs. 6, I, p. 928; 13, I and II) with only one grooved filament, that preceding the grooved one was normal in structure—except for a few extra ciliated discs—and ciliation. On the grooved filament (Fig. 13, III, filament 1) there was ciliary change very near the secondary groove: filament 2 with only a slight groove, which did not bear long terminal cilia, had reversal about 0·95 mm. from it. The following filament was normal except for a few extra ciliated discs. This secondary groove of one grooved filament would seem to show that the influence of the groove is by no means confined to the filament on which it occurs.

Measurements of the filaments forming the secondary groove J (Fig. 13, I) were difficult to obtain as ventral to the supernumerary groove they were permanently bent. The groove was of the same type as the previous one and the approximate changes in direction of the food current are shown in surface view (Fig. 13, IV) and in the graph (Fig. 6, J, p. 928). No ciliary reversal occurred until the second grooved filament and then was very near the secondary groove. This secondary groove shows the very unusual feature of the occurrence of the point of reversal on the last grooved filament very near (0·25 mm. from) the secondary groove. The frontal cilia on the following filament beat normally. Other secondary grooves—but of another type—on the gills of this specimen of Modiolus will be described later.

The division-line between the cilia beating in opposite directions is mostly definite and clear, with usually a few cilia beating in no definite direction. The three secondary grooves, therefore, on the right inner gill sketched in Figure 14, I, are of special interest in that certain filaments

LEGEND FOR FIGURE 14.

FIG. 14.—I. Sketch of right inner gill of an infected Mytilus, showing the position of three small secondary grooves K, L, and M on the ascending lamella. From life, natural size.

II. Surface view of filaments composing secondary grooves L and K. The broken arrows denote stretches over which the direction of beat of the frontal cilia was somewhat uncertain, but was mainly in the direction indicated. Note the fusion of certain filaments dorsal to the secondary groove L; owing to the fusion the point of reversal of beat of the frontal cilia could not be determined on filaments 3 and 6.

III. Lateral views of three living filaments from secondary groove K. The small area with broken outline near the secondary groove of filament 4 denotes an area of fusion with the next filament.
II–III × 18½.

* The difference between Modiolus and Mytilus in the shape of the ciliated discs might be noted (cf. Figs. 13 III and 12 III and V) and the possibility of the use of this character in taxonomy.

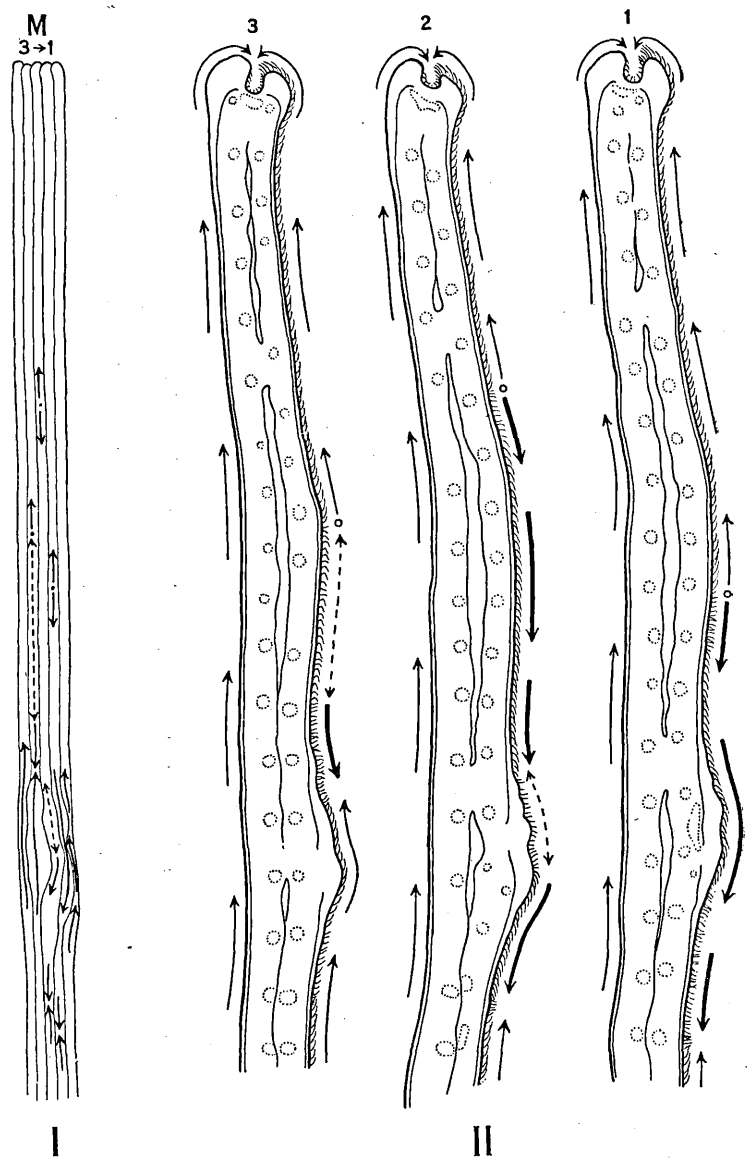


FIG. 15.—I. Surface view of filaments composing the region of enlarged filaments M (see Fig. 14 I). The double-headed arrows indicate stretches over which the current caused by the frontal cilia passed at different times in opposite directions.
II. Lateral views of three living filaments of this region.
I–II × 18¼.

from them showed a considerable area over which the frontals appeared to be somewhat uncertain in the direction of their beat. The cilia of these areas had a rough appearance and, when the separate filaments were supplied with powdered carmine, particles were first drawn on to the frontal surface, then flew off, though there was a general tendency for particles to travel in one direction or the other. The supernumerary grooves K and L (Fig. 14, II) which were between 6·0 mm. and 7·0 mm. from the main groove were separated by only four filaments of normal ciliation. The first grooved filament of K, preceded by a normal one, had a stretch of rough-looking cilia between 4·45 mm. and 6·15 mm. from the main groove over which the general direction of the ciliary current was towards the main groove (Fig. 14, III). The second grooved one had a similar stretch, between 4·4 mm. and 4·75 mm. from the main groove, but the direction of particles was chiefly towards the secondary groove. In filament 3 the corresponding area of irregularity was between 4·45 mm. and 5·6 mm. and the direction of the current was chiefly towards the main groove. Filament 4 was slightly grooved; the stretch of irregular cilia was between 4·9 mm. and 5·6 mm. (Fig. 14, III). The following filament (Fig. 14, III, filament 5) was practically normal in structure, though ciliary reversal occurred between 6·15 mm. and 6·75 mm. from the main groove; the cilia over this stretch were somewhat rough in appearance, but the direction of the ciliary current demonstrated by the movement of carmine particles was definitely in the reverse direction to the normal. The filaments in this supernumerary groove stripped singly with ease, those forming groove L, however, stuck badly owing to some fusion just dorsal to the groove (Fig. 14, II) and it was impossible to tell whether there were stretches of uncertain beating. Filament 1 came off singly; there was no reversal of current, the frontal cilia, however, appeared to be absent, or almost so, for a short distance (between 5·55 mm. and 6·75 mm. from the main groove) and particles collected dorsal to this stretch. The next six filaments tore off in two groups of three; the line of division between cilia beating in the normal and in the reversed direction was at 4·2 mm. and 4·8 mm., and 4·2 mm. and 5·2 mm. respectively from the main groove on the outer filaments of the two groups. The last filament, which stripped off singly, is of much interest; although structurally normal two changes of ciliary current occurred (Figs. 6, L, p. 928; 14, II).

The group of filaments M (Fig. 15, I) could not be termed grooved and the elevations of the frontal surfaces did not bear long terminal cilia. In the first two filaments (Fig. 15, II) the area of reversal extended for some short distance dorsal to the abnormal region as though independent of it. On filament 2 for a short distance, between 5·1 and 5·6 mm. from the main groove, there was a tendency for particles to fly off the surface

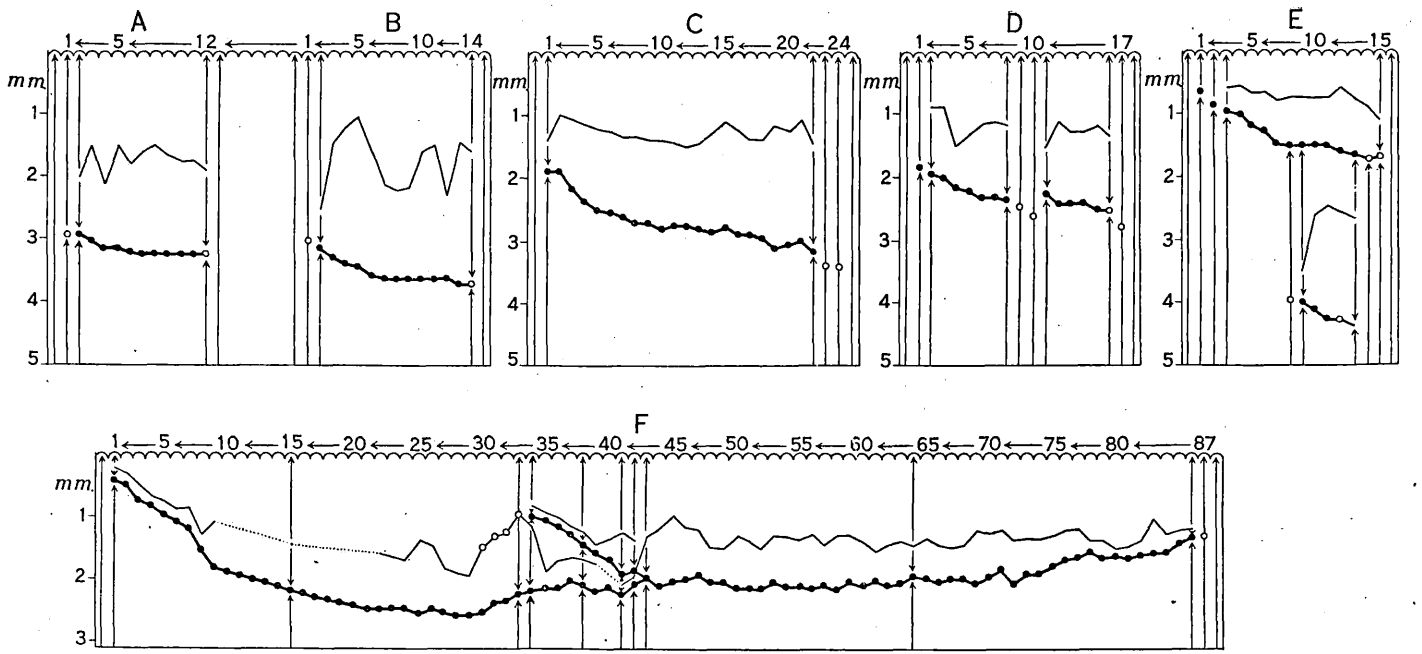


FIG. 16.—Graphs showing the relation of the distance of a secondary groove—raised on a slight projection above the surface of the lamella—from the main food groove, and the points of reversal of the frontal cilia on filaments composing the secondary groove. The direction of beat of the frontal cilia on filaments adjacent to the secondary groove is shown. (Mainly of the gills of *Mytilus edulis*.) The signs used are as in Fig. 6, p. 928.

A and B were on L3 of one Mytilus.
C was on R4 } of one specimen of *Modiolus modiolus*.
D „ L4 }
E „ L1 } of different specimens of Mytilus.
F „ L3 }

of the filament, but they occasionally passed first in one direction, then in the other. Between 3·4 mm. and 4·75 mm. from the main groove on filament 3 although particles mostly passed dorsally, at times they passed up and down. On all three filaments there were small stretches over which the cilia looked irregular in appearance, but particles passed more or less

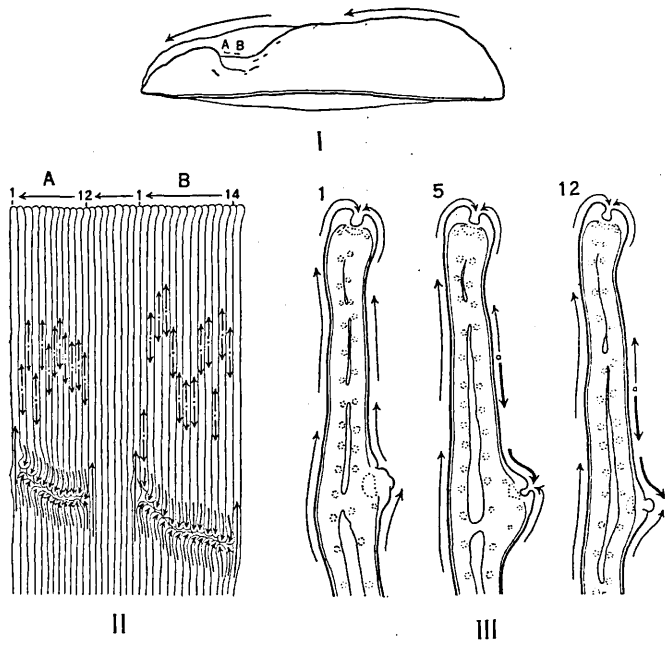


FIG. 17.—I. Sketch of gills of the left side of an infected Mytilus, showing shortness of the inner gill and several secondary food grooves. The two investigated, A and B, are on the descending lamella of the outer gill where it is exposed owing to the shortness of the inner gill. From life, $\times \frac{2}{3}$.
II. Surface view of filaments composing secondary grooves A and B.
III. Lateral views of three living filaments from secondary groove A.
II–III × ca. 12.

definitely in one direction. This apparent uncertainty in the direction of beat of the frontal cilia, over a short length of the filament between two areas in which cilia are definitely beating in opposite directions, is suggestive of the irregularity in beat during ciliary reversal of amphibian embryos described by Twitty (**40**, p. 331), and the impression obtained from the secondary grooves on this gill was that the reversal was unsettled.

Ciliation of Filaments Bearing Secondary Grooves Raised somewhat above the Surface of the Lamella.

In the group of graphs given in Figure 16 have been included those secondary grooves which show slightly more structural alteration of the filaments.

The secondary grooves A and B (Fig. 17, I) on the descending lamella of the left outer gill of a mussel, where it was exposed owing to the

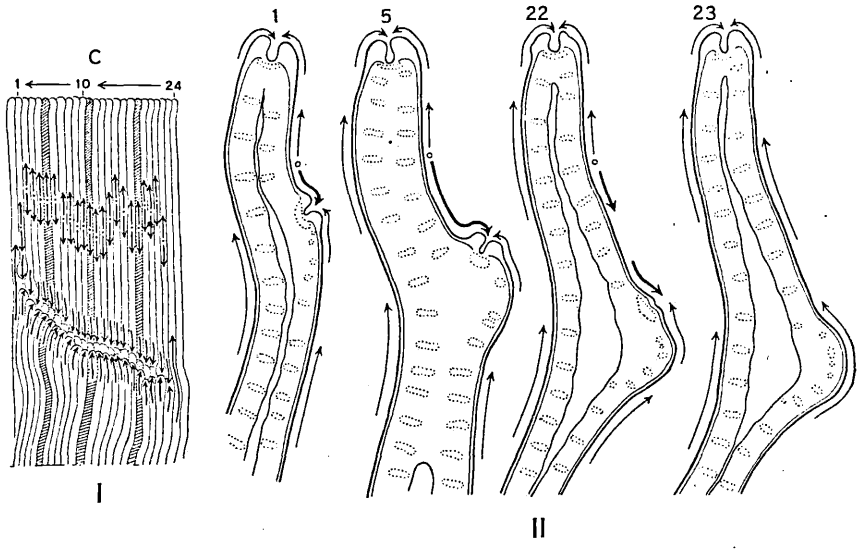


Fig. 18.—*Modiolus modiolus.*

I. Surface view of filaments composing the secondary groove C (see Fig. 13 I, p. 937).
The septate filaments are indicated by shading.

II. Lateral views of representative living filaments.
I–II× ca. 12.

shortness of the inner gill, were separated by only seven normal filaments ; they both showed the characteristic ventral slope anteriorly (Fig. 17, II) and in both the filaments were slightly widened—from frontal to abfrontal surface—beneath the secondary grooves (Fig. 17, III, filament 5). Ciliary reversal occurred on the first grooved filament of A (Fig. 17, I and II, filament 2) ; the preceding one—although having long terminal cilia beating anteriorly—had no reversal (Fig. 17, III, filament 1), on the other hand, reversal occurred on a very similar filament (Fig. 17, III, filament 12) following the last grooved one. The appearance and ciliation of groove B may be gathered from Figures 16 and 17, II.

Two supernumerary grooves of a similar type were present on the gills

of the specimen of Modiolus previously mentioned. The position of groove C on the ascending lamella of the outer right gill is indicated in the sketch in Figure 13, I, p. 937. Groove D was in a similar position on the ascending lamella of the outer left gill. The form of the secondary groove C and the ciliation of the filaments may be gathered from the surface view of the entire groove (Fig. 18, I), the representative separate filaments (Fig. 18, II) and the graph (Fig. 16, c, p. 942). The filament preceding the first grooved one was normal in structure and ciliation.

In groove D ciliary reversal did not occur until the first well-grooved

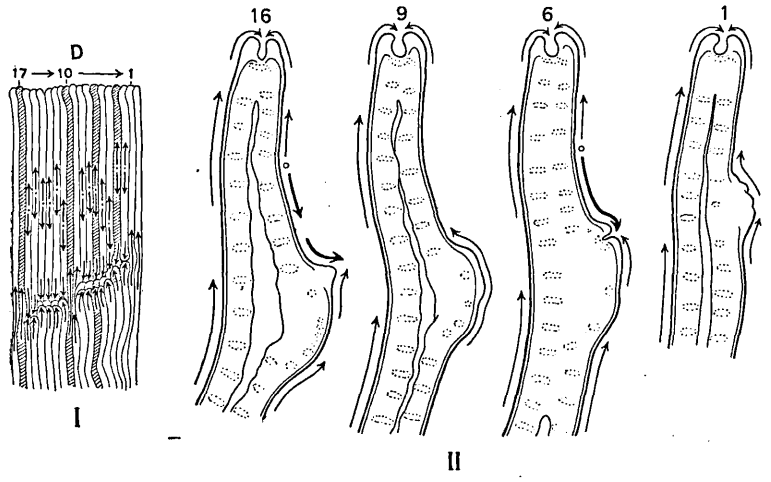


FIG. 19.—*Modiolus modiolus.*

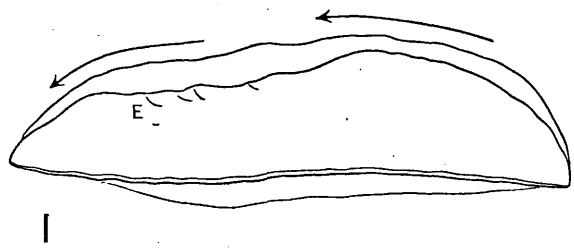
I. Surface view of filaments composing secondary groove D. This was on the ascending lamella of the outer left gill in a similar position to that of secondary groove C on the right gill (see Fig. 13 I, p. 937). The septate filaments are indicated by shading.

II. Lateral views of representative living filaments.

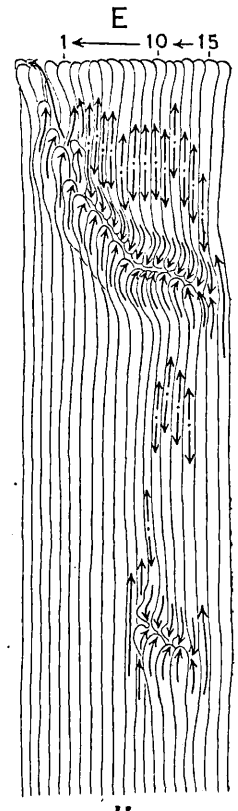
I–II× ca. 12.

filament, although the previous one had long terminal cilia, beating anteriorly, on a projection which was slightly grooved (Fig. 19, II, filament 1). Two grooveless filaments, but with a projection of the frontal surface, occurred between the eighth and eleventh filaments and most unexpectedly there was no reversal of stroke of the cilia on these ; they were very similar in structure and one is shown in Figure 19, II, filament 9. Figures 19, I–II, and 16, D (p. 942), sufficiently indicate the structure and ciliation of this groove.

Gills which have secondary grooves one above the other involving the same filaments would appear to have a possibility of as many changes of ciliary current as there are secondary grooves. In a gill with two secondary grooves one above the other (Figs. 20, I–II ; 16, E, p. 942) reversal occurred



I



II

FIG. 20.—I. Sketch of left gills of a Mytilus showing secondary grooves. The two, one above the other (E), were investigated. From life, natural size.
II. Surface view of filaments composing the secondary grooves.
× ca. 18½.

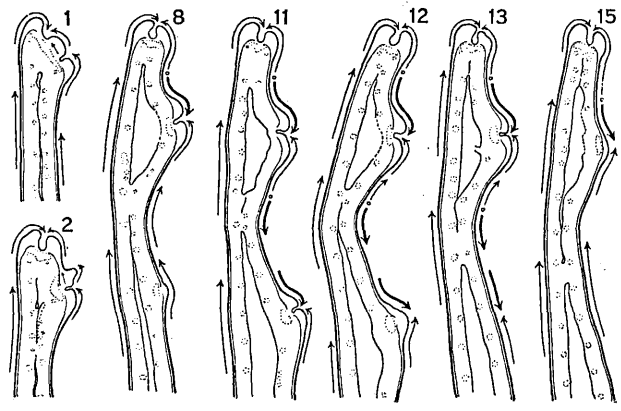


FIG. 21.—Lateral views of certain of the living filaments from the secondary grooves E (see Fig. 20). × ca. 9.

on certain filaments between them, as well as between the main groove and the more ventral secondary groove. The ventral and longer of the two grooves joined the main groove at the anterior end; the tiny—more dorsal one—also sloped in the same direction. In the longer secondary groove no ciliary change occurred until the third grooved filament, while beyond the opposite end of the groove it occurred on filaments 14 and 15, which had merely a projection of the frontal surface (Fig. 21, filament 15). In the tiny more dorsal groove reversal of stroke occurred on the first

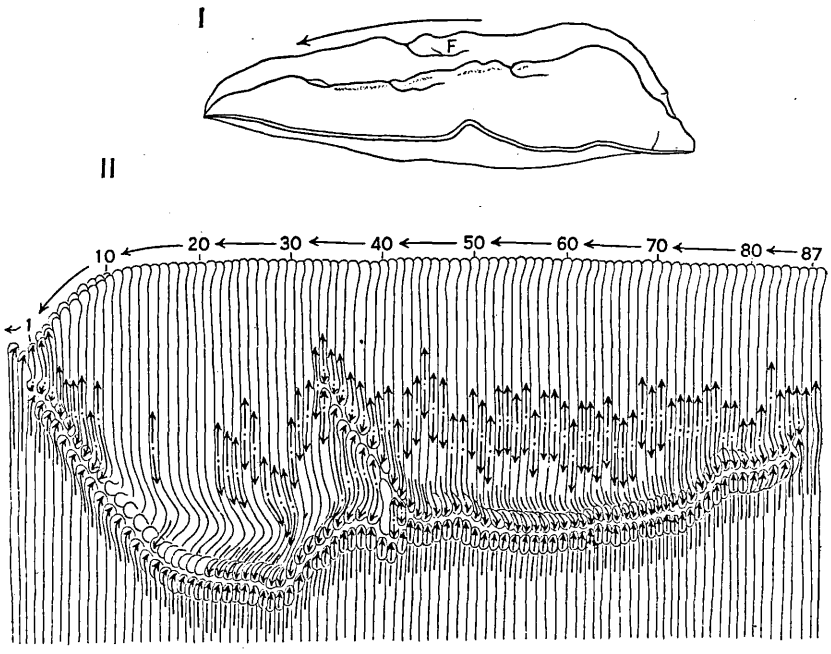


FIG. 22.—I. Sketch of left gills of an infected Mytilus, showing secondary grooves; that marked F was investigated. The stippling indicates abnormally heavy pigmentation. From life, natural size.

II. Surface view of filaments composing the secondary groove. Owing to fusion of certain of the filaments the point of reversal of beat of the frontal cilia could not be determined for filaments 10–14, 16–21, and 40. × ca. 18½.

grooved filament and at the opposite end occurred not only on filament 12, which had a projection bearing long terminal cilia beating anteriorly, but also on the following one (Fig. 21, filament 13), which was normal so far as this secondary groove was concerned.

A long secondary groove involving 87 filaments and joining the main groove anteriorly had, roughly about the middle of its length, a short secondary groove leading from it (Fig. 22, I–II). The chief secondary groove was borne on a slight projection of the lamella, which over parts

of the groove faced dorsally, and is in this respect rather unusual. The filaments of this secondary groove stripped on the whole easily, but as will be seen from the graph (Fig. 16, F, p. 942) filaments 10 to 14 and 16 to 21 pulled off together; a few others also gave trouble. It is interesting to compare filaments 33 and 34 (Fig. 23); on the former a division of the ciliary current occurs at the slight groove, while on the latter at about the same position two currents meet in the definite groove. The filaments composing this secondary groove showed a tendency for the non-groove-bearing ones (the ascending filaments) to be longer than those (the

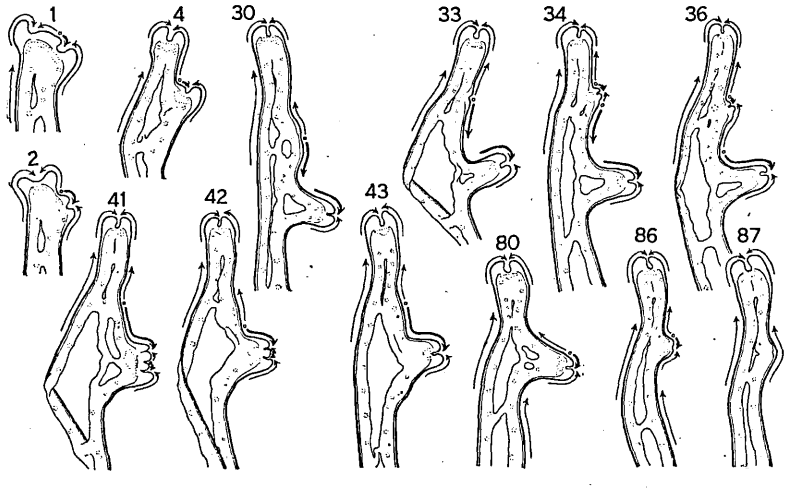


FIG. 23.—Lateral views of representative living filaments of secondary groove F (see Fig. 22). There was a tendency for the non-groove-bearing filament to be longer than that bearing the secondary groove, which made the spreading of the filaments on the slide for examination difficult. × ca. 9.

descending filamen's) bearing a groove and to be bent outwards; this made the spreading of some of the filaments on a slide for examination a little difficult. Figures 16, F (p. 942); 22, I–II; and 23 sufficiently explain the structure and ciliation of this groove.

CILIATION OF FILAMENTS BEARING SECONDARY GROOVES ON THE EDGE OF SECONDARY FOLDS.

The group of secondary grooves from the gills of one mussel (Fig. 25, I), the ciliation of which is shown graphically in Figure 24, had most of them —with the exception of A, E, and F—in surface view the appearance of deep pockets, but single filaments showed that the appearance was deceptive, the groove being set directly on the surface of the lamella. The structure of some of them would appear to indicate that at one period of

their existence they had been deep pockets (see p. 925). In the secondary groove D from the ascending lamella of the right inner gill of this mussel (Figs. 25 and 24) the pocket must have reached almost to the lower food

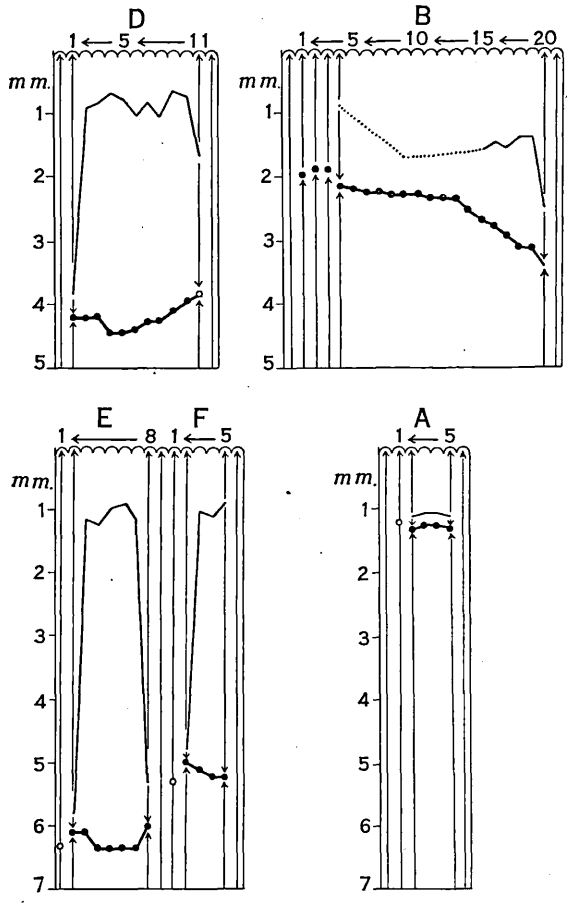


FIG. 24.—Graphs showing the relation of the distance of a secondary groove—on the edge of a secondary fold—from the main food groove on the gill of *Mytilus edulis*, and the points of reversal of the frontal cilia on filaments composing the secondary groove. The direction of beat of the frontal cilia on filaments adjacent to the secondary grooves is shown in most instances. The signs are those used in Fig. 6, p. 928.

A, B, and D are on R1, and E and F on R3 of one Mytilus.

groove. The filament at either end of the groove was of about normal width—from frontal to abfrontal surface—but filament 1 had an extra number of ciliated discs. The filaments towards the middle of the groove, however, such as filament 5 (Fig. 26), showed fairly clearly the probable

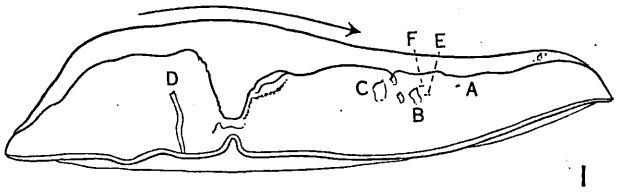
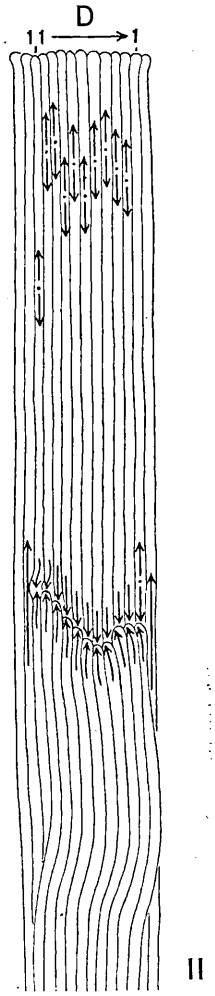


FIG. 25.



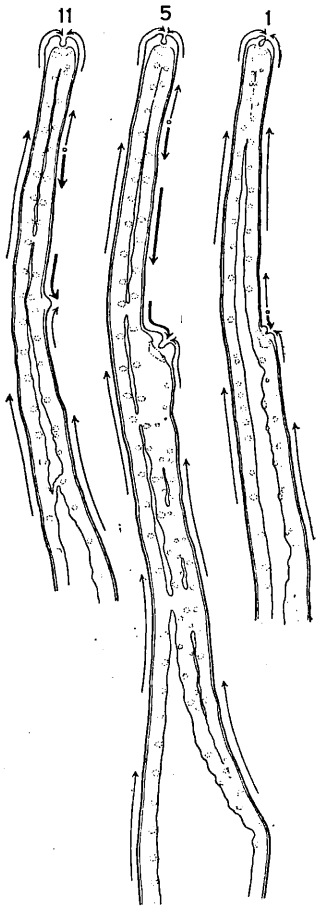


FIG. 25.—I. Sketch of gill of right side from an infected Mytilus, showing shortness of the inner gill and several secondary grooves and folds. Those investigated are lettered; E and F indicates the position of two secondary grooves on the descending lamella of the outer gill. The stippling indicates abnormally heavy pigmentation. Drawn from life, natural size.

II. Surface view of filaments composing secondary groove D. $\times 18\frac{1}{4}$.

FIG. 26.—Lateral views of representative living filaments of secondary groove D (see Fig. 25). $\times$ ca. 9.

previous history of the groove. With the exception of filament 1 the point of ciliary reversal on the filaments composing the secondary groove was much nearer the main than the secondary groove.

Grooves E and F (Figs. 24, p. 949; 25, I, p. 950; 27, I) from the descending lamella of the outer right gill of the same mussel are perhaps of a similar

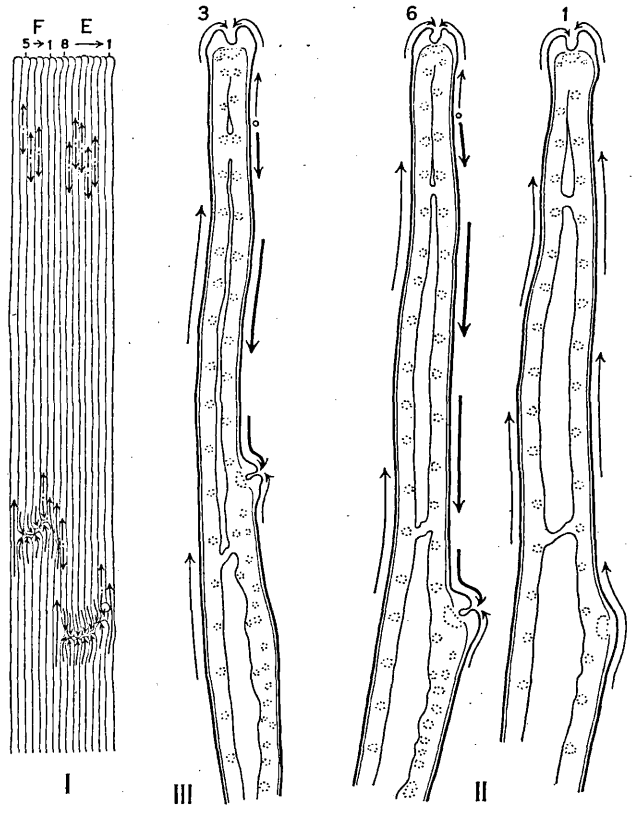


FIG. 27.—I. Surface view of filaments composing secondary grooves E and F (see Fig. 25 I, p. 950).
II. Lateral views of two living filaments from secondary groove E.
III. Lateral view of living filament from secondary groove F.
I–III × ca. 12.

type to groove D, though fusion of the filaments has gone considerably further, and the irregularity in position and number of the ciliated discs is all that remains to indicate their possible origin. The two grooves were separated by only two filaments of normal ciliation but were not on the same level. Their structure and ciliation is evident from Figure 27, I–III.

It is characteristic of both of them, as of the groove previously described, that except for the first grooved filament in each and the last grooved one of E, the reversal of stroke of the frontals occurred close to the main groove. Filaments 2 and 3 of secondary groove E were fused for a short distance dorsal to the groove (Fig. 27, I).

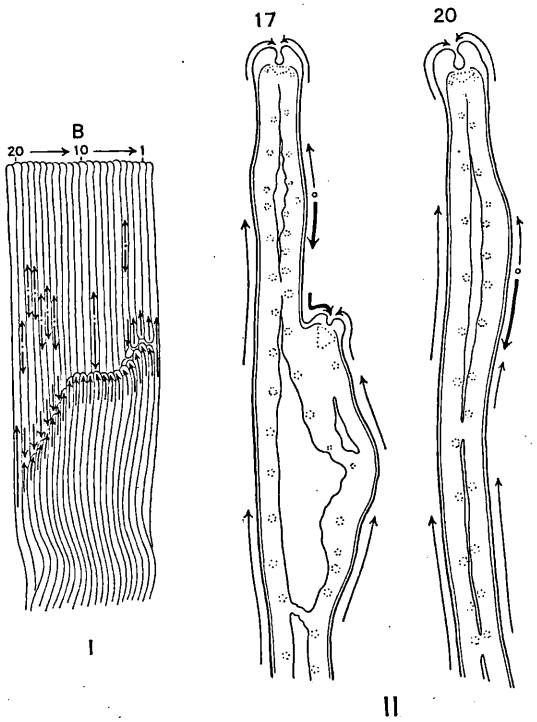


FIG. 28.—I. Surface view of filaments composing secondary groove B (see Fig. 25 I, p. 950).
Owing to the fusion of certain of the filaments the point of reversal of beat of the frontal cilia was not determined for filaments 5–8 and 10–14.
II. Lateral views of two living filaments from secondary groove B.
I–II × ca. 12.

Groove B (Figs. 24, p. 949; 25, I, p. 950; 28) is apparently structurally of a similar type to secondary grooves D, E, and F, but so far as could be judged from very scanty data—the filaments stripped very badly owing to a great deal of fusion occurring—it would not have given the same type of graph as the three previous grooves. Filament 20, following the last grooved one (Fig. 28, II), is interesting in that although structurally normal, ciliary reversal of the frontals occurred.

Groove A (Figs. 24, p. 949; 25, I, p. 950; 29, I–II) was possibly of

the same type structurally as the preceding grooves. Reversal of stroke of the frontal cilia occurred very near the secondary groove on the four filaments composing it, though the point of division on the fourth and fifth filaments is somewhat uncertain as they stuck together.

The 19 or 20 filaments of groove C (Fig. 25, I, p. 950) were of the type drawn in Figure 29, III, and probably the groove was originally a deep pocket. So much fusion occurred between the filaments that no attempt was made to strip the groove systematically. The point of reversal at least

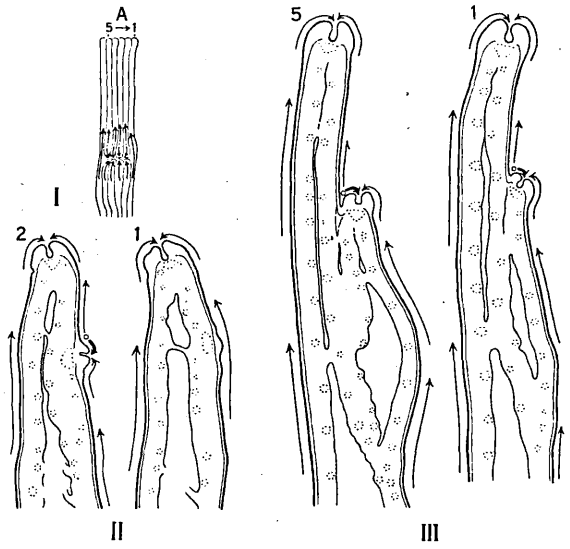


FIG. 29.—I. Surface view of filaments composing secondary groove A (see Fig. 25 I, p. 950).
II. Lateral views of two living filaments of secondary groove A.
III. Lateral views of two living filaments of secondary groove C (see Fig. 25 I).
I–III × ca. 12.

on the first five grooved filaments was exceedingly close to the secondary groove (Fig. 29, III, filaments 1 and 5), so that it is unlikely that it would have given a graph anything approaching the type of D, E, and F.

It is evident from the foregoing observations that the ciliation of filaments bearing secondary grooves, which—from the structure of the filaments composing them—would appear to have been at one time at the edge of deep pockets, is not always of the striking type shown in the graphs of D, E, and F (Fig. 24, p. 949) in that reversal occurred close to the secondary groove. (Fusion of the 'pocket' will bring the point of reversal apparently nearer the secondary groove.)

A deep pocket near the posterior end of the right outer gill of another mussel, the groove of which joined the main groove and then diverged, is shown in the rough sketch in Figure 30, I. It is probable that pockets of this type and in this position, that is near the posterior adductor muscle, are not due to injury caused by a pea-crab, even when one is present. Figure 5, I, p. 926, shows a filament from a pocket of similar type and position. The filaments of the secondary fold shown in Figure 30, I, were not systematically stripped; filament A was the first grooved filament,

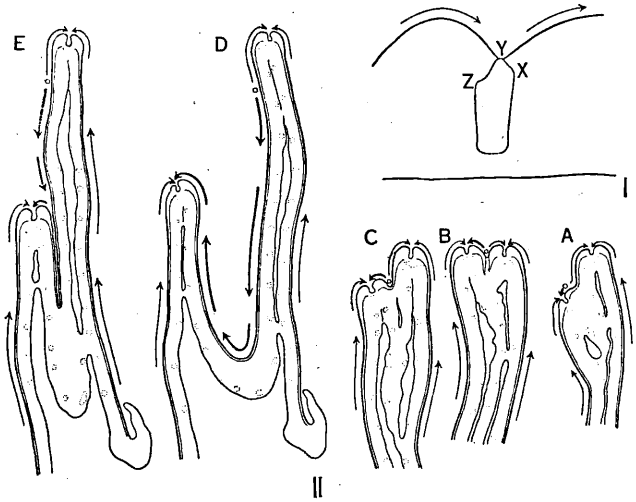


FIG. 30.—I. Rough sketch of a secondary fold or pocket on the descending lamella of the right outer gill of a Mytilus, near the posterior adductor muscle.
II. Lateral views of living filaments from the fold. Filament A was from position X, filament B from about the position Y, and filaments C, D, and E from between Y and Z. × ca. 9.

filament B was from about the position of Y where the secondary groove was on the same level as the main food groove, and filaments C, D, and E were from between Y and Z (Fig. 30, II). Considerable fusion had occurred except between Y and Z, so that the pocket was obliterated as indicated by filaments A, B, C, and E; at some point between Y and Z an open pocket existed as shown by filament D; filament E is from near the posterior edge of the pocket (i.e. near Z). The point of reversal of stroke of the frontals on filaments D and E perhaps lead one to expect that if the filaments had been stripped consecutively the graph would have been of the type of D, E, and F, Figure 24 (p. 949).

Ciliation of Filaments Bearing Secondary Grooves on the same or nearly the same Level as the Main Groove.

The position of a secondary groove of fourteen filaments on the descending lamella of a left inner gill is shown in Figure 31, I. It was so near the main groove that it might be described as a double main groove (Fig. 31, II), and yet ciliary reversal occurred on all the filaments except

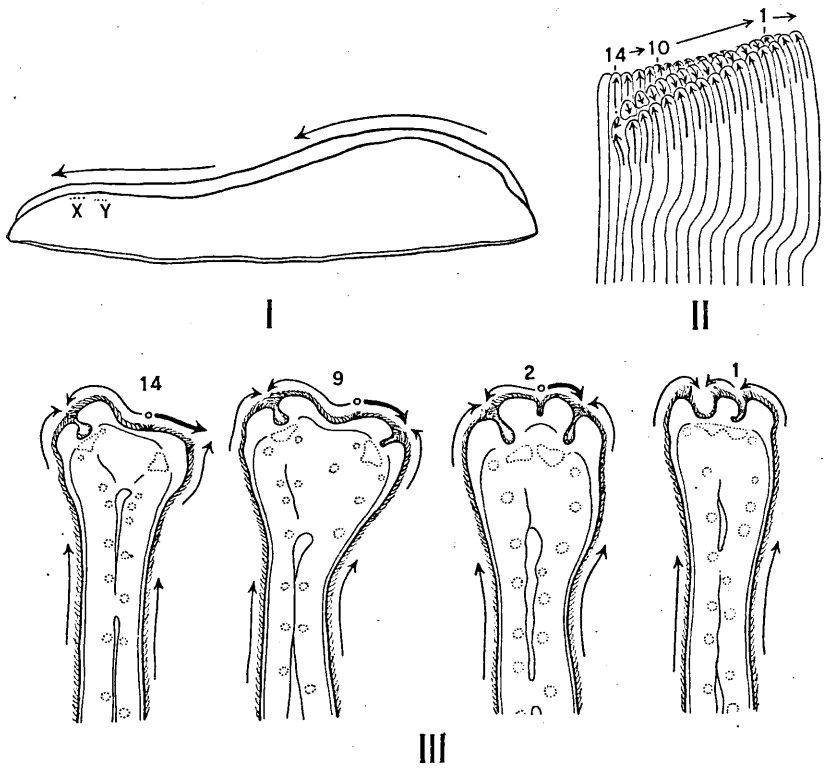


Fig. 31.—I. Sketch of left gills of a specimen of Mytilus: X indicates the position of a secondary groove on the descending lamella of the inner gill, and Y the position of one on the descending lamella of the outer gill. (Secondary groove Y was not investigated.) Drawn from life, natural size.
II. Surface view of living filaments composing secondary groove X. Camera lucida outline.
III. Lateral views of representative living filaments from secondary groove X. II–III × 18¼.

the first; it occurred on the filament (Fig. 31, III, filament 14) following the last grooved filament. On filaments 8 to 12 the point of division between cilia beating in the normal and the reversed direction tended to move slightly towards the secondary groove. Ciliary reversal does not always occur on grooves of this type (see Fig. 35, II, filaments 18–21, p. 963).

Ciliation of Filaments Bearing Secondary Grooves at the Free Edge of the Gill.

As previously mentioned, when a gill is short owing to injury by a large pea-crab the edge is occasionally slightly folded over with some fusion to the lamella (Figs. 4, p. 924; 32, I). In such cases very occasionally a secondary groove is present at what is now the free edge of the gill, and a change in the direction of the current caused by reversal of the frontal cilia may occur between the two grooves. Figure 32, II, is the surface view of

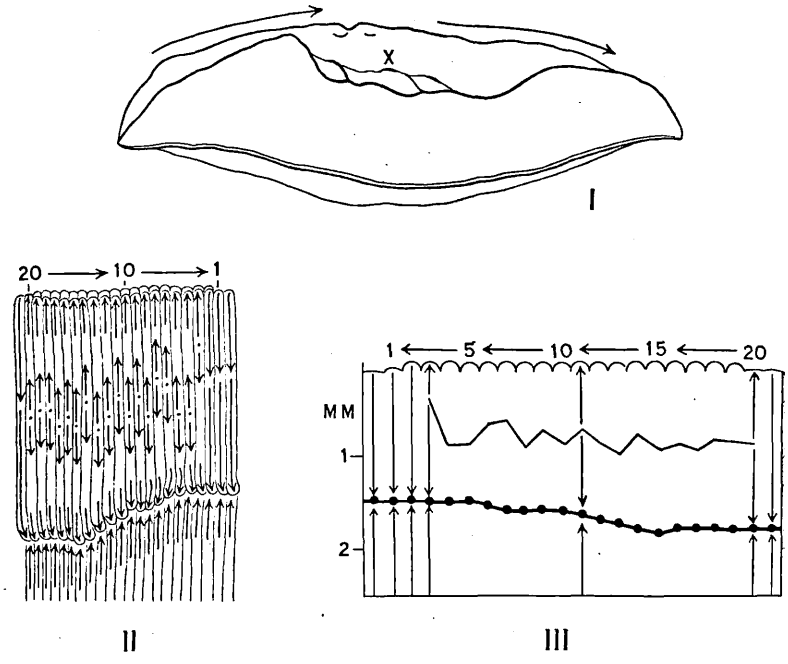


Fig. 32.—I. Sketch of gills of right side of an infected Mytilus, showing shortness of the inner gill and folding over of the free edge with, in certain places, the formation of secondary grooves at what is now the free edge of the gill. The part marked X was investigated. Two secondary grooves are present on the descending lamella of the outer gill. From life, natural size.

II. Surface view of filaments composing the secondary groove X. The secondary groove is at the free edge of the gill, the main groove being folded over. $\times 18\frac{1}{4}$.

III. Graph showing the relation of the distance of a secondary groove X, at the free edge of the gill, from the main groove, which, owing to folding, runs across the surface of the gill, and the points of reversal of the frontal cilia on filaments composing the secondary groove. The direction of beat of the frontal cilia on filaments adjacent to the secondary groove is shown. The main groove in this figure is denoted by filled-in circles, and the secondary groove at the free edge of the gill by semicircles. The arrows at the free edge of the gill show the direction of the food current in the secondary groove and also in the main groove. Distance from the free edge of the gill is marked in mm.

that part of the gill marked X in Figure 32, I, with the change in ciliary beat on the filaments indicated by arrows. From the graph (Fig. 32, III) it will be seen that although the secondary groove is in this instance at the free edge of the gill, there is still a tendency for the change to occur nearer the secondary groove at the anterior than at the posterior end; that while at the posterior end there is change of ciliary current although

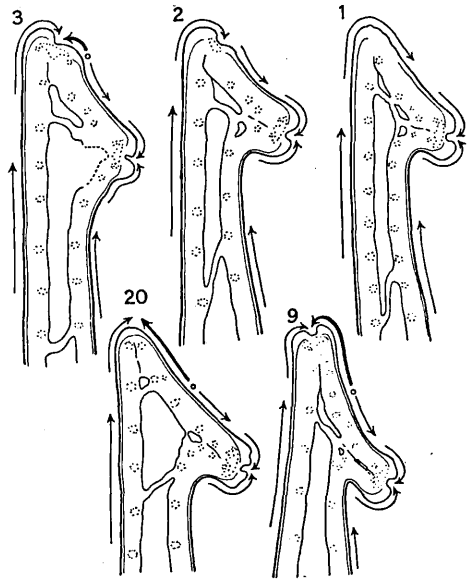


FIG. 33.—Lateral views of representative living filaments from secondary groove X (see Fig. 32). × ca. 12.

there is no groove at the free edge of the gill (filament 20), anteriorly on filament 1, which is enlarged at the edge, and filament 2, which has a shallow groove, there is no change (Fig. 33).

REVIEW OF LITERATURE ON CILIARY REVERSAL.

Known cases of the reversal of ciliary movement in the metazoa are rare, and considerable doubt exists with regard to some at least of those recorded. Purkinje and Valentin in 1835 (**35**) and Engelmann in 1868 (**13**, quoted by Parker, **31**) described reversal of ciliary current on the labial palps of mussels, while Grave (**15**) described it for the labial palps of the oyster; later writers (**1**, p. 129; **2**, p. 233; **22**; **28**, p. 167; **45**, p. 330), however, agree that on the palps of Lamellibranchs there are two permanent ciliated tracts in close proximity which beat in opposite directions and do not reverse their action, muscular movement

determining which set are effective (**1**; **2**; **28**; **41**). Parker (**31**) quotes some case of ciliary reversal in other animals.

Reversal of ciliary current on the lips of the sea anemone *Metridium marginatum* caused by the application of meat extract, potassium ions, etc., but not by mechanical means, has been described in detail by Parker (**30**; **31**). He states that the reversal is strictly local and lasts only as long as the stimulating substance is present, and that there is no evidence for assuming that it is under any form of nervous control.

Elmhirst (**12**) working on *Actinoloba dianthus* observed that "Longitudinal grooves run down the gullet, and when food is being swallowed the inflow is along the grooves; conversely a ciliary out-flow runs up the ridges, for example, when a bolus of waste is discharged it is passed out by the cilia on the ridges aided by a certain amount of contraction of the stomodæal wall. At times there is a vortex in the gullet when both sets of cilia are in action at once" (**12**, p. 151).*

In view of this Gray (**19**, p. 60) suggested that "since the oral disc of Metridium is ridged and its muscles are extremely sensitive to mechanical stimulation, one would like to be quite certain that the reversal of the currents observed by Parker is not due to two separate series of cilia which beat in opposite directions on the ridges and in the furrows."

Parker and Marks (**33**) have therefore repeated the experiments with Metridium. They hold that reversal most certainly occurs both of the ridge and groove cilia, though more easily effected in the case of the latter, and that while the cilia of the ridges ordinarily beat outwards and those of the groove beat commonly inwards, there is no evidence of a double system of cilia, one beating constantly outwards and the other constantly inwards on the lips of Metridium.

In a lecture delivered in the summer of 1928, at the Marine Biological Laboratory, Woods Hole, Gray (**19a**, p. 81) mentioned that he had seen "the convincing demonstration by Dr. Parker that a true reversal of the same ciliary current does actually occur" (in Metridium). He said "perhaps it is just possible to imagine that the reversal is due to a change in the 'tone' of the cilia. For such a suggestion there is some slight experimental evidence."

Torrey (**39**) described reversal of cilia on the lips and œsophagus of *Sargartia davisi*, effected in this instance by mechanical means. Here again the reversal was temporary.

Twitty (**40**) has described the reversal of ciliary action in amphibian embryos, induced by the application of the proper mechanical stimuli.

* Parker (**31**, p. 3) says: "So far as my experience extends, the application of various stimuli to the tentacles has never resulted in a reversal of the effective stroke of their cilia, and the same is true of the siphonoglyphs."

" Those found effective were : intimate contact of the epithelium with a foreign surface, e.g. the floor of a wax or glass dish ; immersion of the embryo in a dense, resistant medium ; contact with the egg membranes in which the embryo develops " (**40**, p. 327). He concluded that the cilia beat in the direction in which they encountered the least resistance. If the stimulus was removed the beat of the cilia returned to the normal after a certain time, which was longer than it had taken to reverse. He remarks that " one often gets the impression that the preference of normal over reversed action is remarkably slight if the conditions are arranged at all suitably " (**40**, p. 329).

The reversal of the beat of the frontal cilia of the gill filaments of *Mytilus edulis* is of a permanent nature. The filaments forming a secondary groove (Fig. 10, p. 934) were stripped one evening and the distance of the point of reversal from the main groove measured. The filaments were carefully kept in order in covered watch glasses and remeasured the next morning. The slight differences in the measurements were such as to be most probably due to error in measuring filaments which are, to a certain extent, contractile. If the ciliary action had been easily reversible, it might have been expected that the dissociation of a filament from its normal position in the gill might have induced a return to the normal direction of beat.

The only attempt to induce a return to the normal direction of beat by cutting off the secondary groove was made on two filaments of the type in Figure 5, I (p. 926), the secondary groove together with the folded part of the filament forming the outer wall of the pocket being cut off. When examined $3\frac{3}{4}$ hours later the points of division, which were 2·6 mm. and 4·1 mm. respectively from the main groove, were in exactly the same position ; when examined again after a further interval of 2 hours there was no change. More experiments of this kind are, however, required.

The possibility must not be overlooked that the ciliated epithelium of the gill filament over which reversal occurs, may have been formed by growth after the production of the secondary groove. If this should occur, the secondary groove would then probably have exerted some influence over the newly formed tissue, causing the cilia as they grew to beat towards it ; in this case it is realized that true ciliary reversal could not then be said to occur. In this connection the gills of the spat of *Mytilus edulis* up to about 3·4 mm. long have been examined and it was found that before the formation of a definite food groove—while there is merely a long tuft of cilia beating anteriorly at the ventral edge of the filaments—the frontal cilia on the very short ascending filaments beat ventrally. The following facts, however, would appear to be against the possibility of the ciliated epithelium over which reversal occurs, having

been formed entirely by new growth after the formation of the secondary groove :

1. The point of ciliary reversal on adjacent filaments is not at the same level ; graphs bring this out clearly.
2. The point of ciliary reversal is at some distance from secondary grooves set directly on the surface of the gill.
3. Ciliary reversal occurs on structurally normal filaments.
4. Little or no reversal of beat of the frontals may occur on all the filaments composing some secondary grooves, even when the filaments are produced into slight folds (Fig. 35, p. 963).

The type of ciliation of filaments forming secondary grooves such as D, E, and F in Figure 24 (p. 949), in which reversal occurs very much nearer the main than the secondary groove—with the exception of the first filament of each and also the last of E—would appear to be a strong indication that cilia, beating originally in the normal direction, had come to reverse the direction of their effective beat.

FIG. 34.

Lateral view of a living filament of a secondary fold on a Mytilus gill. The two food grooves are almost on the same level, and the change of current on the frontal surface of the filaments occurs at the depth of the fold. × ca. 9.

Figures 5, II (p. 926), and 34 show folds or pockets with the change of ciliary beat at the bottom of the pockets ; such might appear to have been formed subsequent to the secondary groove. Unfortunately these pockets were not stripped—a great deal of fusion occurring among the filaments—only one filament from about the middle being examined, so possibly the position of the point of division between cilia beating in the normal and in the reversed direction varied.

Detailed information on the growth (after the early stages studied by Rice, etc.) and the regeneration of the gill of Mytilus, however, will be needed before the origin of the folds or pockets can be decided. Bloomer (**5**), from observations on malformed specimens of *Anodonta cygnea*, concluded that though the animal is able to repair even extensive damage to the mantle-lobes, the gills are not regenerated, the animal being capable of living and thriving with very much aborted gills.

As a rough test as to whether regeneration of the gills of Mytilus occurred, a specimen was wedged open on June 5th, 1929, and several small pieces—more or less triangular in shape—were snipped from the ventral edges of the gills ; it was then allowed to close and put under

circulation in a tank. On September 26th (112 days later) the mussel was opened and the gills examined: they were found to have wedge-shaped pieces—roughly as large or larger than the pieces previously removed—missing from their ventral edges. In all cases, however, where the filaments had been cut across, new food grooves had formed. The mussel when opened was in very good condition, that is well fished, so that the non-occurrence of regeneration—with the exception of the food groove—could not be attributed to lack of food.

The result in this case may be regarded as an indication that a food groove only is regenerated after injury, at least at the free edge of the gills; conditions governing growth and regeneration on the surface of the gills may, however, be different from those governing growth at the free edges.

Mussels are not infrequently found having gills with very jagged ventral edges.

One of the pieces cut from the gill had caused a state of affairs of some interest. It was in the shape of a long, narrow wedge, slanting very much antero-posteriorly, in such a way that the ventral ends of 13 filaments—forming a small triangular area—had been severed from organic connection with the gill, and apparently were only connected with each other by ciliary junctions, while the longest piece, forming the base of the triangle, was connected in the same manner with a normal filament. There is the possibility that organic inter-filamentar junctions may have been formed owing to compression by the cutting, but any such were not obvious and it is improbable that all filaments would have been so connected. The gill was preserved without pulling the filaments apart.

The dorsal cut ends of these apparently organically isolated pieces of filaments had in some cases rounded off and in others had formed a rough food groove, but all, except the shortest and the longest, had developed long terminal cilia, beating anteriorly, at the cut ends. Owing to the triangular shape of the piece the direction of the current produced by these was roughly anterior and dorsal, and met the current from the posterior part of the gill at the depth of the cut. There appeared to be no reversal of the ciliary current on these pieces of filaments, with the possible exception of some very tiny areas near the new groove on some of them, over which particles seemed to pass towards the groove; the current, however, may have been caused by the newly formed terminal cilia.

The 13 pieces of filaments after 112 days were slightly swollen, as filaments of a gill cut from a mussel will generally become after several days in a finger-bowl of sea-water; the cilia, however, were beating vigorously. These, most probably, organically isolated pieces of filaments had therefore in some cases at least regenerated a food groove by the transformation of material, and all with the exception of the shortest and

the longest had grown long terminal cilia beating in the same direction as those along the main food groove at the ventral edge of the gill. It is hoped to repeat this experiment.

Discussion on the Possible Causes of Ciliary Reversal.

From an analysis of the graphs of various secondary grooves it is evident that there is a distinct tendency for the change of ciliary current to occur nearer to the secondary groove at the anterior end of the groove than at the posterior end. In fact at the anterior end a filament with a definite groove may show little or no reversal, particles dorsal to the groove passing into and along it, but all particles ventral to it passing into the main groove. On the other hand, not only is the point of change generally further from the secondary groove at the posterior end, but there may be reversal of cilia on a filament with only a slight projection of the frontal surface, and in a very few instances on a filament perfectly normal except for the ciliary reversal. Cases such as shown in Figure 6, D and L (p. 928), where there are two changes of ciliary current on structurally almost normal filaments are very difficult of explanation, the only possibility seeming to be that the direction of beat is unsettled.

It would appear that the ciliary change is due to the effect of the secondary groove as a whole, and that the change does not occur on a filament entirely independent of its neighbours.

Lillie (**24**, p. 428) has explained the waves of co-ordinated beating such as occur in the rows of swimming plates of ctenophores in the following way: "... increased ciliary activity in one area excites adjoining areas to increased activity, so that a certain synchrony tends to be preserved between neighbouring cells. If ciliary activity, like other forms of contractility, is due to variations of electrical polarization at the surfaces of the contractile elements, an action-current must accompany each ciliary stroke, and its stimulating influence will be transmitted through the medium for some distance."

Wyman (**44**, p. 558) working on the gills of Unio observed that: "The transmission through the gill of the effects of warmth applied locally is apparent through increased rate of ciliary beat on adjacent gill tissue in all directions from the region of application." He offers an explanation similar to that of Lillie that: "The phenomenon might be explained by the stimulating effect of the action-current of the directly excited cilia on the neighbouring relatively quiet cilia," but remarks that "such an explanation, though in accord with the work on Unio, is inconsistent with certain of the observations of Kraft (**23**) on the tissue from the frog's pharynx."

Whether there is any possibility of an action-current being sufficiently

strong to reverse the beat of the frontal cilia of Mytilus, experiments will be necessary to determine.

The suggestion is also very tentatively made that the reversal of beat may be due to the mechanical resistance of a water current, set up by the

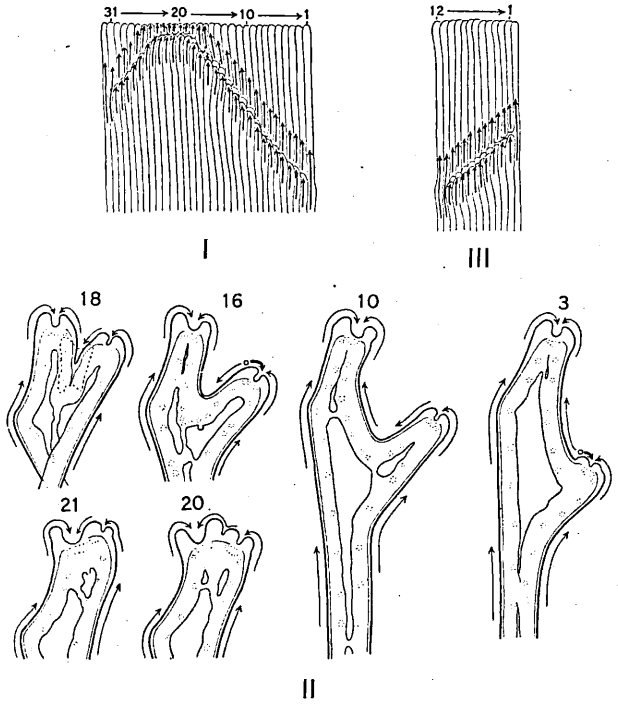


FIG. 35.—I. Surface view of filaments (Mytilus gill) composing a secondary groove which joined the main groove and then diverged. Little or no change of current occurred on the filaments.

II. Lateral views of representative living filaments from the groove. In filaments 3 and 10 especially, the outward bend—due to its greater length—of the non-groove-bearing filament is noticeable. In filament 18 the broken outline indicates an area of fusion with the next filament.

III. Surface view of filaments composing another secondary groove from the gill of the same mussel. They were of the type of filaments 3 and 10 of II, and little or no reversal of beat of the frontals occurred.

I–III× ca. 12.

long terminal cilia beating along the secondary groove. This suggestion would seem to account for the fact mentioned above that the change is generally closer to the secondary groove at the anterior than at the posterior end of the groove. Examination for a current set up by the

terminal cilia of the secondary groove, by means of powdered carmine, however, only revealed what appeared to be a weak one over the surface of the gill at the level of the secondary groove. This current was drawn into the groove at an acute angle.

That in some instances the change is very near the main groove indicating that the secondary groove appears to have more influence than the former, may perhaps be due to the fact that the secondary groove is on the surface of the gill and therefore any current set up by its long cilia would have more effect over the surface of the gill than would the main groove at its free edge.

One would expect the change in direction of beat to be a gradual and increasing one, and secondary grooves which have caused little or no change in direction of beat of the frontal cilia of the filaments of which they are composed, could be explained by assuming their recent formation. Examples of such grooves are those in Figure 35. After filament 18 of that in Figure 35, I, the secondary groove was almost on the same level as that of the main one for several filaments, then gradually diverged from it until at the 31st and last filament it was 0·8 mm. from the main groove. The filaments composing the secondary groove shown in Figure 35, III, were very similar in structure to filaments 3 and 10 in Figure 35, II. Particles on the gill dorsal to these secondary grooves passed into and along them, while those drawn on to the surface of the gill ventral to them passed almost entirely into the main groove.

The fact that experiments in transplanting pieces of ciliated epithelium from the roof of the mouth of the adult frog (**6** ; **25**) and from the trachea of the dog and the cat (**21**), reversing them in direction, have shown that the cilia on the transplanted pieces do not come to beat in the direction of the surrounding cilia of the host, the water current set up by them apparently having no effect, would seem to vitiate the possibility of the reversal of the frontal cilia of the gill filaments of Mytilus being due to the resistance set up by a water current. In Mytilus, however, the long terminal cilia of the grooves are considerably longer than the frontals, and might be expected to produce a stronger current, more likely to overcome the resistance of the frontal cilia.

Nervous control of ciliary action, chiefly of locomotor cilia, is known in certain forms (**8** ; **9** ; **10** ; **11** ; **26**) and Merton (**27**) contends "that reversal is always a manifestation of such regulation. He would thus class reversal as one of the spontaneous or voluntary responses of the organism" (quoted from Twitty, **40**, p. 326). Nervous control of the branchial cilia is said to occur in *Doliolum mülleri* (**14**). Grave and Schmitt (**16**) have described the presence of nerve-like structures lying immediately beneath, and parallel to the ciliated cells of the latero-frontal epithelium of Lampsilis, and in the epithelium itself a series of inter- and intra-

cellular fibrils with a suggested co-ordinating function. Bhatia (**4**) from an investigation of the latero-frontal cells of Mytilus has pointed out that in all probability the inter-cellular fibrils are cell walls, which, owing to the plane of the sections, are not seen in their entirety. Up to the present it has been found impossible to detect the operation of nervous elements in the epithelium or in the cells themselves of the gills of Mytilus (see Gray, **18**, p. 108); it would therefore appear to be unlikely that reversal of beat of the frontal cilia is due to nervous control.*

The work was done at Plymouth while holding a Miss Busk Research Studentship, 1927–28, and an Amy, Lady Tate Scholarship, 1928–29, of Bedford College. I wish to thank the College authorities for allowing me to continue to work at the Marine Station; the London University for granting me the use of their table; and the Director and Council of the Marine Biological Association for facilities. My thanks are also due to Miss Sexton for bringing to my notice an important reference to the literature, and to Mr. A. J. Smith for the photograph in Figure 3. And, finally I should like to express my deep indebtedness to Prof. J. H. Orton for the interest he has taken in the work, and for his advice and criticisms.

SUMMARY.

Permanent reversal of the frontal cilia on the gill filaments of *Mytilus edulis* has been found to occur naturally in the majority of cases where secondary or supernumerary food grooves are present on the gill. Such secondary grooves possibly arise as the result of injury; in some localities they are strongly correlated with the presence of a large female *Pinnotheres pisum* in the mussel. In these cases there is strong presumptive evidence that the secondary grooves are caused by mechanical injury from the claws of the crab. Considerable growth of inter-filamentar junctions, together with fusion of the filaments side by side, is common in secondary grooves and folds, and is especially marked in folds the filaments of which are somewhat askew.

The cavity of a fold or pocket practically always faces ventrally, and there is a definite tendency for the secondary grooves to slope ventrally and anteriorly.

The cavity of pockets would appear to be sometimes obliterated by

* While this account was in the press an interesting paper by S. B. Setna on "The Neuro-muscular mechanism of the gill of Pecten" was published in the *Q.J.M.S.*, Vol. 73, pp. 365–391, February, 1930. In describing the innervation of the gill and in connection with an unsuccessful attempt to determine the function of the subsidiary branchial nerve, he remarks: "While its sensory function cannot be denied, another possibility is that the cilia on the palps and the gills may be under nervous control. . . . On cutting the subsidiary branchial nerve, however, there is no evidence of reversal either on the gills or on the palps, nor does mechanical stimulation alter the direction of the ciliary stroke." (p. 382).

the concrescence of the filaments forming them; illustrations of the stages in the possible process are given.

Generally one or two filaments at either end of a secondary groove are raised into a projection in continuation of the groove; such projections may occasionally bear long terminal cilia beating anteriorly (i.e. at right angles to the normal direction of the frontal cilia), or may be covered with frontals of normal length, in some instances beating anteriorly and in others beating ventrally, according as to whether reversal does or does not occur on the filaments.

About 27 secondary grooves have been investigated, and it has been found that the reversal of beat of the frontal cilia of the gill filaments occurs over a variable distance between the secondary and main grooves. Particles drawn on to that part of the gill over which cilia beat in a reversed direction are carried dorsally into the secondary groove and along it until they reach a filament with normal ciliation, along which they are passed into the main groove. The direction of the current is the same in the secondary as in the main food groove, that is towards the mouth.

The metachronal wave is reversed with the reversal of stroke of the frontal cilia.

The point of division between cilia beating in the normal and in the reversed direction is not at the same level on adjacent filaments forming a secondary groove. Reversal is usually nearer the secondary groove at the anterior than at the posterior end of the secondary groove, and ciliary reversal may even occur on the following one or two ungrooved—and very rarely even on perfectly normal—filaments at the posterior end of the secondary groove; the graphs show this clearly. From a consideration of the graphs it seems apparent that the influence of the secondary groove is exerted as a whole over the adjacent part of the lamella and each filament is not influenced by its own groove independent of its neighbour.

The ciliation of filaments composing certain secondary grooves, which from their structure would appear to have been originally at the edge of deep pockets, is of interest in that the point of division between cilia beating in the normal and in the reversed direction is much nearer the main than the secondary groove, with the exception of certain few filaments. This type of ciliation would appear to be a strong indication that cilia beating originally in the normal direction had come to reverse the direction of their effective beat.

The possibility is not overlooked that the epithelium bearing cilia beating in the reversed direction may be partly formed anew after the production of the secondary groove, whence the probability would be that the influence of the secondary groove may have caused cilia from the very beginning of their appearance to beat towards it (i.e. in the

reversed direction to the normal), in which case there would have been no true reversal.

Possible causes of the ciliary reversal in Mytilus are discussed. A little experimental work has been attempted, and it is suggested that a full explanation of the phenomena observed must await the result of an extended series of experiments.

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On Abnormal Conditions of the Gills in *Mytilus edulis*. Part II. Structural Abnormalities, with a Note on the Method of Division of the Mantle Cavity in Normal Individuals.

By

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With 27 Figures in the Text.

Note on Some Abnormalities of Labial Palps and Foot of *Mytilus edulis*.

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With 7 Figures in the Text.

Reprinted from the Journal of the Marine Biological Association of the United Kingdom.
Vol. xvii. No. 2. June, 1931.

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CONTENTS.

INTRODUCTION.

IN Part I of this paper (2) the presence of secondary grooves and folds on the gills of *Mytilus edulis* especially was described, together with the occurrence of permanent natural reversal of the frontal cilia on the gill filaments composing the majority of these grooves and folds. The present paper is concerned with certain, chiefly structural, abnormalities of the gills, namely: (*a*) folding over of the free ventral edge of the gill with concrescence, (*b*) fusion of the gill filaments side by side, (*c*) enlargement of the gill filaments and (*d*) concrescence of the two gills of one side. The mussels in which the first two of these conditions were observed, were almost entirely from various parts of the Fal Estuary, the average percentage with abnormal gills being 31·8% among 1398* recorded from October 28th to November 25th, 1927, and 44·4% among 162 examined in March, 1930. In no other locality from which mussels have been obtained, was anything approaching these conditions seen, though a very

* Given in error as 1488 in (2) Part I, p. 919.

occasional specimen might have abnormal gills. Batches of mussels have been examined from the Estuaries of the Hamoaze, mostly from near Weir Point (1291 between October 8th, 1927, and February 17th, 1928); the Estuary of the Yealm (296 between October 10th, 1927, and August 3rd, 1928); the Estuary at Teignmouth (9262 between December 6th, 1927, and February 26th, 1929); the Estuary of the Camel, near St. Issey Cliff, Padstow (10,866 between November 8th, 1927, and August 9th, 1929); and from the Promenade Pier, Plymouth (340 December, 1927, and September, 1928).

The widespread abnormal conditions of the gills of the Fal Estuary mussels would seem to be correlated, most probably, with some factor or combination of factors in the environment and not to be due to injury, though several cases of accessory palps, divided palps, and accessory feet possibly had a traumatic origin. The percentages of pea-crabs (*Pinnotheres pisum*) in the Fal Estuary mussels of 1927 were so low (see Table I, p. 517) that their presence could have no relation to the abnormal conditions of the gills, and in the 1930 sample from that locality, mussels containing pea-crabs, of a size likely to cause injury, have been omitted from the total on which the percentage of 44·4 is based. In a certain few cases—about three in March, 1930—in which the gills were exceedingly narrow, or nearly missing, for a short distance, the injury could be almost certainly traced to an old boring by the whelk-tingles, Murex or Purpura. Apart from these few cases, it is suggested that the abnormal conditions of the gills of the Fal Estuary mussels are correlated with some peculiar factor or combination of factors in the environment, though it is by no means clear why mussels from the estuaries of the Hamoaze, Yealm, Teign, and Camel are so little affected.

A consideration of abnormality in the gills of Mytilus is of some importance in regard to the problem of purification of this mollusc for consumption (**12**).

DESCRIPTION OF STRUCTURAL ABNORMALITIES OF THE GILLS.

(*a*) Folding over of the Free Ventral Edge of the Gill, with Concrescence.

This abnormal condition of the gills was restricted to the Fal Estuary mussels, except for its occurrence, in a much modified degree, in a few mussels from other localities, which were inhabited, in practically all instances, by pea-crabs. The deep and regular folding over of all four gills,* as shown in Figure 1, has been observed to occur only in the Fal

* As in Part I (**2**), for convenience in description the two demibranchs on each side of the body are considered as two gills.

mussels, a number of which had the gills permanently folded over lengthwise, the fold in some cases extending up to two-thirds of the length of the gill. The extreme anterior and posterior ends of the gills were very rarely involved in the fold. It is peculiar that with few exceptions (one exception only noticed) the gills were folded away from each other, the inner gill of either side being folded inwards, and the outer gill outwards (cf. the direction of upward folding of the ventral tips of the descending filaments during development). The filaments in the folded over portion tend to become fused or concresced in varying degree with those beneath them;

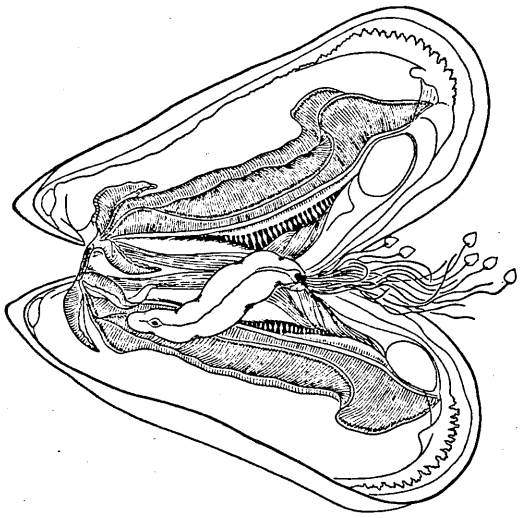

FIG. 1.—Sketch from life of a mussel from the Fal Estuary, October 28th, 1927, showing folding over of the four gills. The folded portion of the left inner gill alone was entirely fused; that of the other three gills could be raised almost to the bend. Natural size.

various stages in the process were observed. In the very early stages the entire fold can be raised, though when placed in water the gill will not straighten out. Fusion first occurs near the bend of the fold and the major part can be raised; in later stages the folded over portion has become entirely fused with the lamella beneath. In the mussel sketched in Figure 1 the fold of the left inner gill alone was entirely fused, those of the other three gills could be raised almost to the bend.

The appearance in surface view of a small part of a gill in which the fold had become completely fused, is shown in some detail in Figure 2 (p. 492). The main food groove now runs across the surface of the lamella (at G), and just dorsal to it there is a narrow zone in which fusion of the filaments side by side, and considerable irregular proliferation of the frontal surfaces

of the filaments has occurred. Fusion of the filaments has also taken place along a narrow region ventral to the food groove, as well as near the bend of the fold, at what is now the free edge of the gill. The occurrence of fusion of the filaments laterally, added to the fact that the folding is

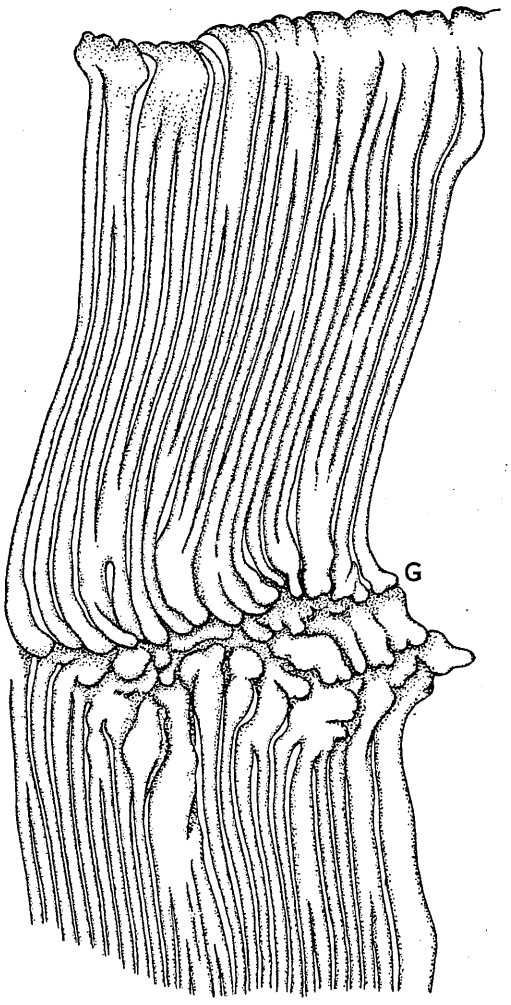

FIG. 2.—Surface view of a small area of a gill of which the folded portion had entirely fused, the main ventral food groove (G) now running across the surface of the lamella. The fusion of the gill filaments side by side is shown, and the irregular growth of the frontal epithelium in a narrow region dorsal to the fused food groove. The ventral and folded edge of the gill is at the top of the figure. From a mussel from East Bank, Fal Estuary, November 23, 1927. From preserved material. × ca. 24⅓.

usually slightly oblique—a filament generally being folded over on to one posterior to it in the series—makes it difficult to separate a single filament, or even a few filaments, to examine in side view.

Figure 3 shows in side view small groups of filaments from gills

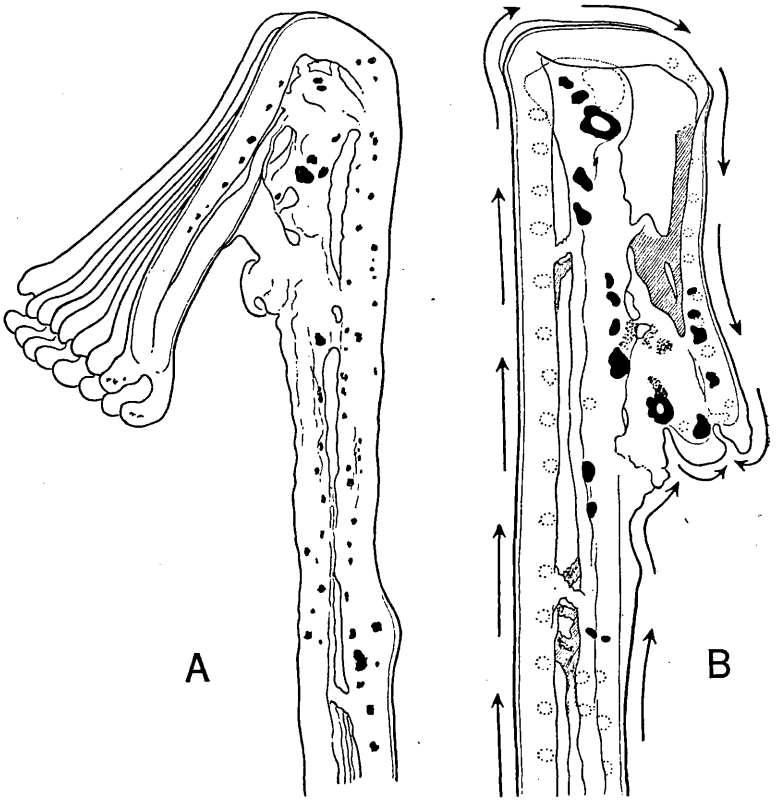

FIG. 3.

A. Side view of a small group of filaments from a gill of Mytilus in which the folded over portion had fused at the bend only. Considerable fusion of filaments side by side had occurred, and the surface sketched showed no ciliated discs, while lateral and latero-frontal cilia were absent for the most part, indicating presumably that fusion with the next filament in the series had already begun. The accumulation of brown pigment in masses is shown. From a mussel from East Bank, Fal Estuary, November, 1927.

B. Side view of a small group of filaments from the same gill as that of Fig. 2, showing complete fusion of the folded over portion of the gill with the ascending lamella. The two inner arms of the fold have apparently fused and are undergoing degeneration: masses of brown pigment are indicated. There is some fusion of the ascending filaments laterally, dorsal to the food groove, with slight enlargement of the frontal surfaces of the filaments. The arrows, showing the direction of the ciliary current on the frontal surface, have been added from a living gill, which showed a similar fold and fusion.

A–B, from preserved material. $\times 18\frac{1}{4}$.

with different degrees of fusion of the folds. Figure 3, A, was from a gill where the fold had only fused at the bend. There was much fusion of the filaments side by side dorsal to the fold, and the lateral surface sketched showed no ciliated discs, and, for the most part, lateral and latero-frontal cilia were absent, indicating that fusion with the neighbouring filament had begun. As is well shown by the example in Figure 3, B, fusion and degeneration of the two inner arms of the fold take place, and pigment—no doubt liberated from degenerating cells—is generally found collected into granular masses of considerable size. Transverse sections show varying degrees of fusion in different parts, and at different levels of the same fold. In some places four lamellæ are distinct, in others three, the two inner ones having fused. In one fold sectioned the middle one of the three lamellæ was seen to be formed by the fusion of two lamellæ, that is the two inner arms of the fold, as clearly shown by the presence of two series of chitinous supports, mostly somewhat contorted (see Fig. 4, A, p. 495). In another fold sectioned, however, though four lamellæ were present in places, yet where only three were present, the chitinous supports could not be clearly distinguishable into two sets ; this perhaps may be due to the obliquity of the folding. In one example sectioned, where the apparent fold was only about 1·6 mm. deep, the middle lamella of the three present was clearly single—as shown by the distinct single set of poorly developed chitinous supports—and was the ascending lamella (Fig. 4, B). Complete fusion side by side of all the filaments in the middle lamella had not taken place, a few small ciliated spaces remaining. This case would not seem to be explicable by folding alone, but possibly also by differential growth.

Some gills which appeared in surface view to have undergone folding, showed when the filaments were examined in side view, an appearance as in Figure 5 (p. 496). The ascending filaments were only about a third the length of the descending, and in consequence the descending filaments appear to have been pulled over. It would seem that the shortness of the ascending lamella was due to injury to, or puckering of, the filaments composing it. The gills of the mussel in which this condition was noted, had, however, very few interlamellar connexions in the abnormal portion ; possibly they had snapped at some time, for there were small masses of subfilamentar tissue.

In gills where folding with concrescence has occurred, the ascending lamella is sometimes considerably shorter, dorso-ventrally, than the descending one; the question therefore arises whether gills in such a condition will be able to effect a ciliary junction with the mantle and the visceral mass (see Orton, **33**, pp. 460, 462 ; Dodgson, **12**, pp. 168, 171, and the present paper, p. 533). If they are unable to do so there would be imperfect division of the pallial cavity into supra- and infra-branchial

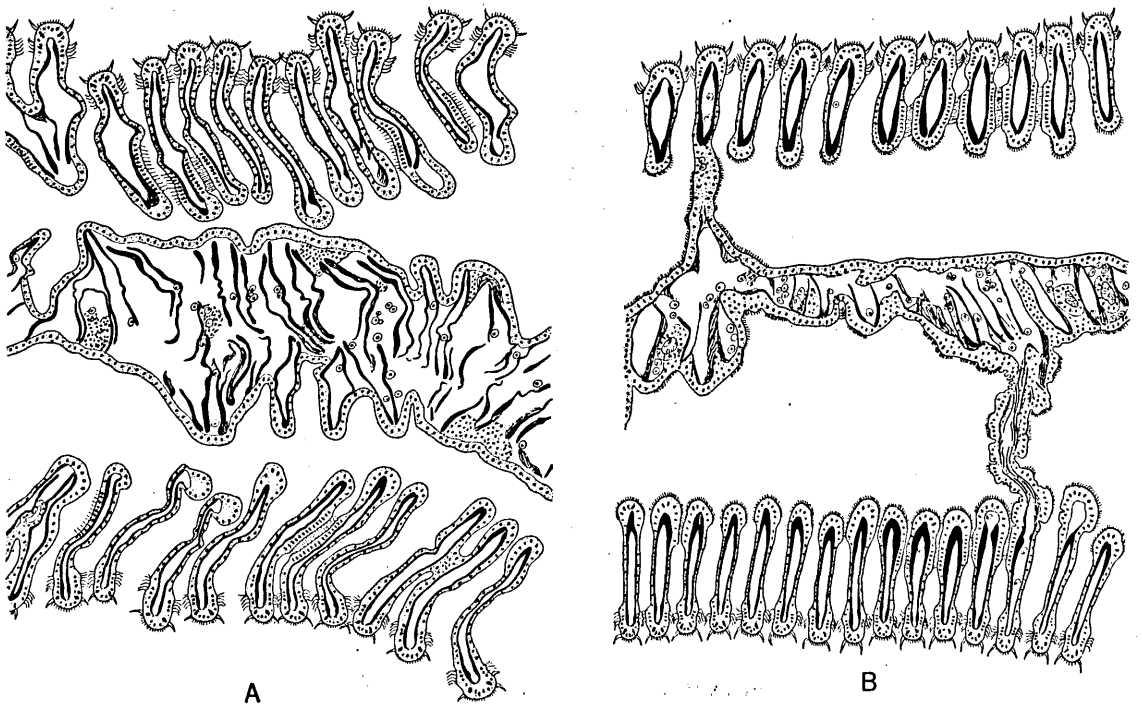

FIG. 4.

A. *M. edulis*. Transverse section through region of a fold—such as shown in Fig. 2—showing three lamellæ, the middle one formed by the fusion of the two inner arms of the fold, the two sets of chitinous supports being clearly discernible in places. The material, fixed in formalin, was badly preserved, but sufficiently to show the chitinous supports. The distribution of the nuclei and cilia is represented diagrammatically: the abfrontal cilia and the numerous gland cells, present especially in the epithelium of the middle lamella, have been omitted. Iron hæmatoxylin and acid fuchsin. $\times 93\frac{1}{3}$.

B. Transverse section through folded region of a gill (fold only ca. 1·6 mm. deep) in which the middle lamella, as shown by the single series of chitinous supports, is single. Complete fusion laterally of all the filaments in the middle lamella had not occurred, a few small ciliated spaces remaining. The difference in width—from frontal to abfrontal surface—of the filaments in the two outer lamellæ is due to the section being slightly oblique. The distribution of the nuclei and cilia is represented diagrammatically. Bouin's fixative; Mann's methyl-blue-eosin. $\times 93\frac{1}{3}$.

chambers; the exhalent current would, in all probability, cease or diminish in strength, and the feeding mechanism would be most probably deranged (see Dodgson, **12**, p. 171). In some mussels with abnormally short ascending lamellæ it has been noticed that such short lamellæ seem

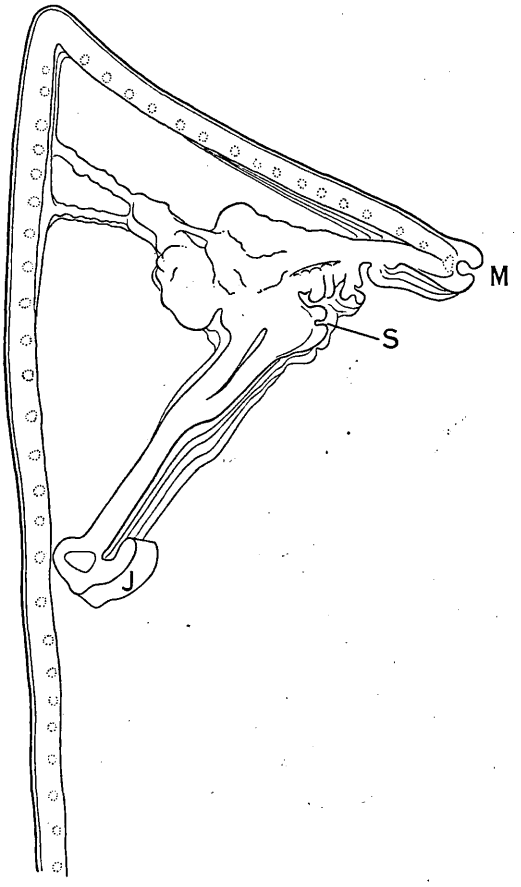

FIG. 5.—Lateral view of a small group of filaments from the gill of a mussel from East Bank, Fal Estuary, November 23, 1927, which showed an apparent fold in surface view. M, main ventral food groove; S, secondary food groove; J, junction area of interlocking cilia on outer surface of dorsal food groove. From preserved material. × ca. 12½.

to be turned out almost at right angles, whence it is possible that the dorsal free edge of the gill, by pulling the gill over towards the side of junction, is able to touch the mantle or the visceral mass. In a few mussels with gills in this condition, a well-defined ridge in the mantle has been noticed (as in Fig. 6, B and C, p. 497), which may help to enable the

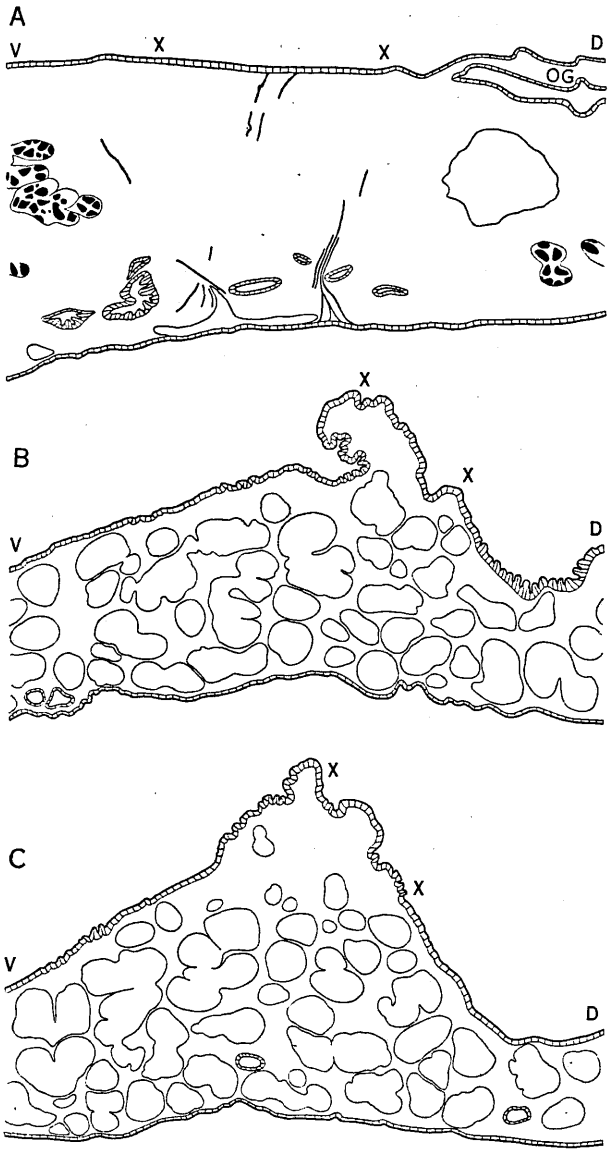

FIG. 6.

A. Transverse section of mantle of normal Mytilus, passing through the zone of interlocking cilia, X to X. OG, plicate organ; D and V, Dorsal and Ventral.

B and C. Transverse sections through different regions of a ridge present in mantle of a Mytilus, in which the gills of that side were extremely short, dorso-ventrally. X–X marks the position of the zone of interlocking cilia on the dorsal slope of the ridge.

D and V, Dorsal and Ventral.

A–C. × ca. 27½.

outer gills to effect a ciliary junction with the mantle. The interlocking cilia (see p. 533) are present on the dorsalward slope of the ridge. Such a ridge tends to become lower some time after the mussel is opened, and also on preservation, perhaps indicating that it is partly due to turgescence.

A marked ridge in the mantle (Fig. 6, B and C) is also generally found in mussels with a gill, or gills, almost entirely absent for a short distance, as may occur through injury, in some instances by whelk-tingles. It would appear to be an effort of the mantle to effect a ciliary junction with the rudimentary or missing part of the gill. A ridge in one instance was noticed to be strongly pigmented.

Gills in which folding has taken place, occasionally have short secondary food grooves along the bend, at what is now the free edge of the gill. It is perhaps only when the filaments are split or injured at the bend that a new food groove arises in this position.

Mussels with folded gills were often in poor condition: the folding, involving considerable reduction of the gill surface and pumping power, as well as frequently disorganising the main food grooves, must necessarily reduce the quantity of food passing to the mouth. In cases, however, where the gill is folded over neatly, as in Figure 1 (p. 491), beyond causing a certain reduction in the area of the catching surface, the food paths would not seem to be greatly disorganised, as particles on the descending filaments pass round the bend and into the main food groove—though it now runs across the surface of the gill—and are carried along it towards the mouth.

Figure 7 (p. 499) shows to what an extent the normal food currents of a gill may be disorganised by irregular folding with concrescence. All four gills of this mussel were in a similar condition. When the gills were supplied with carmine particles it was evident that there was no continuous ciliary current at, or near, the ventral free edge of the gill, or in any position on the gill. Particles collected in small masses, either because of the meeting of ciliary currents, or because of the abrupt termination of short irregular food grooves. No doubt when these reached a certain size they would spill over, and coming under the influence of other currents, might in some cases travel a little further towards the mouth. As all the gills were short there was no likelihood that particles dropping from one or other of the left or right gills would be caught up by the other one of that side. In spite of the apparent impossibility of food in any quantity being able to reach the mouth, the mussel in this particular instance was in fair condition. This perhaps may be regarded as an indication that the changes in gill structure were rapid.

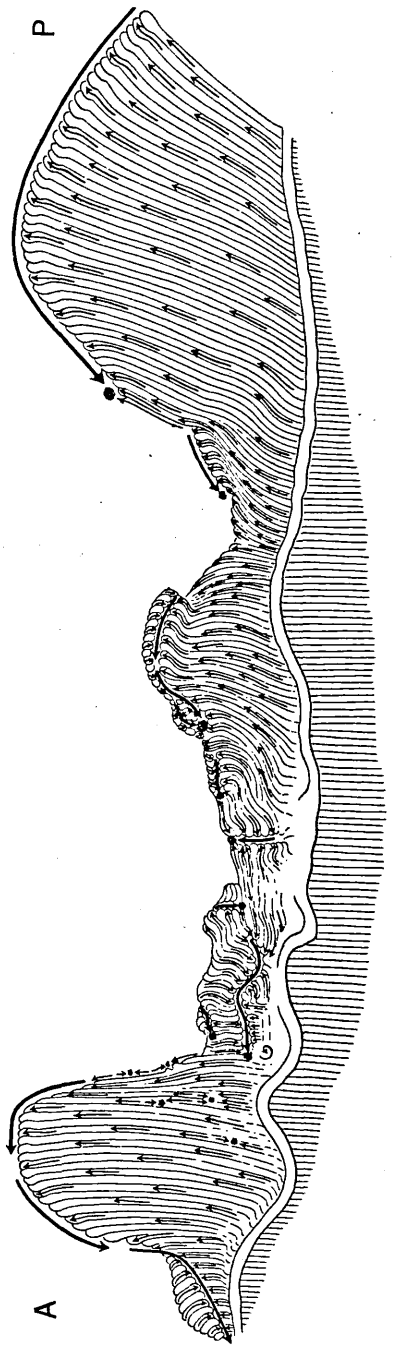

FIG. 7.—Sketch of living gill from a mussel from North Bank, Fal Estuary, 1930, showing disorganisation of food currents by what is, presumably, irregular folding of the gill with fusion. All four gills of this mussel were in a similar state. The direction of the currents along food grooves is indicated by heavy arrows; the direction of the currents caused by the frontal cilia on the filaments by fine arrows. The currents were investigated only by means of powdered carmine on the surface of the gill. A certain amount of reversal of ciliary current appeared to have occurred as indicated. Towards the anterior end of the gill reversal occurred on filaments without secondary grooves: some fusion of filaments laterally had taken place in this region. In two places the dorsal food groove on the ascending lamella was missing. The ascending lamella was considerably shorter than the descending lamella. A, anterior; P, posterior end of gill. The outline of the gill was drawn by camera lucida, but the details were filled in freehand. × ca. 4½.

(*b*) Fusion of the Gill Filaments side by side.

Fusion and crumpling of the filaments, which was greatly developed among the mussels from the Fal Estuary, was very rarely found among mussels—other than those infected with Pinnotheres—from other localities: exceedingly few examples were detected among those from the Estuaries of the Hamoaze and from the Teign Estuary.

This condition varies greatly in extent from the fusion of two or more filaments side by side, to extensive areas of fusion scattered irregularly over the greater part of the lamella.

Some fusion is generally found where slight crumpling or puckering of the gill occurs, as in Figure 8, A (p. 501), and is probably due to crowding of the filaments. In the case of crumpling, the filaments are not only crowded together, but there is also a tendency for them to be forced on to their sides, and, as the lateral faces are of greater width than the frontal, this increases the crowding. In some instances small areas of fusion may be accompanied by a tiny food groove as in Figure 8, B.

Slight fusion of filaments has also been noticed, in some individuals, near the dorsal food groove on the ascending lamella (Fig. 8, C), and is again probably due to the same direct cause, namely crowding, occasioned by slight shortening, antero-posteriorly, of the dorsal free edge of the gill. In the example sketched, seven filaments are fused, but at the food groove the composite filament is not noticeably wider than the normal filaments (see also Rice, **41**, pp. 74, 78).

In some few cases the dorsal food groove on the ascending lamella was seen to be noticeably shortened antero-posteriorly—due apparently in the case sectioned to the presence of cysts*—so that the ascending lamella was thrown into folds parallel to the long axes of the filaments, the folds decreasing in depth ventrally; while the descending lamella was hardly affected, the folds being exceedingly slight and not sufficient to cause fusion of the filaments. Transverse sections showed much fusion of the filaments composing the deep folds of the ascending lamella (Fig. 9, p. 502); the fusion was, however, almost entirely restricted to the abfrontal ends of the filaments and would have been practically invisible in surface view.

Fusion, according to Rice, does not normally occur in filamentous gills, even where folding is extreme, as in Pecten, and he says that its absence "may be easily explained on the ground of the looser structure of the gill (as compared with the folded lamellar gills of certain Eulamellibranchs†) and the possibility of a displacement of the filaments, with consequent

* The cyst sectioned was lined with ciliated epithelium: the contained body had a roughly concentric structure, but was evidently degenerating and could not be identified.

† The interpolation is mine.

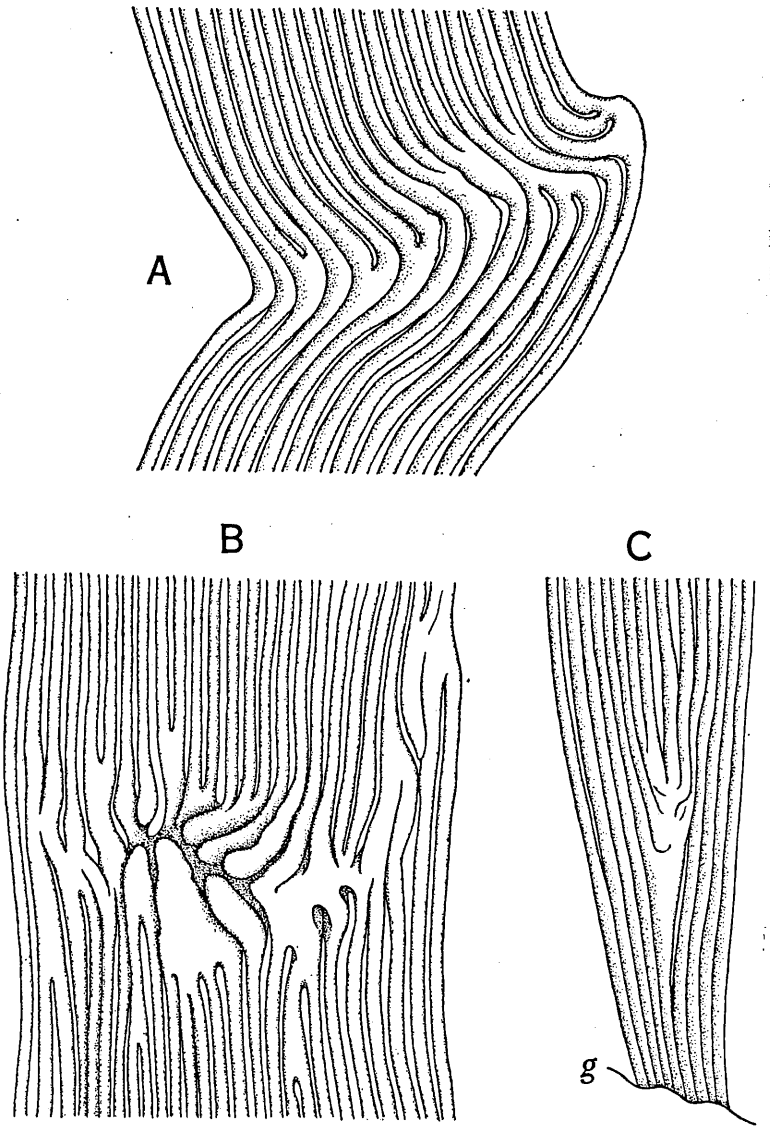

FIG. 8.—Sketches showing fusion of gill filaments on the gills of a mussel from Trelissick Reach, Fal River, November 1, 1927. From preserved material. × ca. 41½.

A. Fusion of gill filaments where crowding had occurred, owing to the filaments being bent out of their true direction. This is an enlargement of a small area, just posterior to the secondary gill or fold, on the right inner gill sketched in Fig. 1, p. 920, Part I (2).

B. Fusion of gill filaments, together with a tiny secondary food groove. From right outer gill. (Anterior is on the left.)

C. Fusion of seven filaments near the dorsal food groove on the ascending lamella, right inner gill. g, ventral edge of dorsal food groove.

relief of pressure " (**41**, p. 78). Its presence in Mytilus gills, which have been thrown into folds, is therefore of interest.

A section such as that of Figure 9 has a superficial resemblance to those of *Avicula argentea* (**43**, Fig. 16, p. 212) and *Margaritifera vulgaris* (**24**, Figs. 7, 12, Pl. 27), but in these two forms fusion of the actual filaments

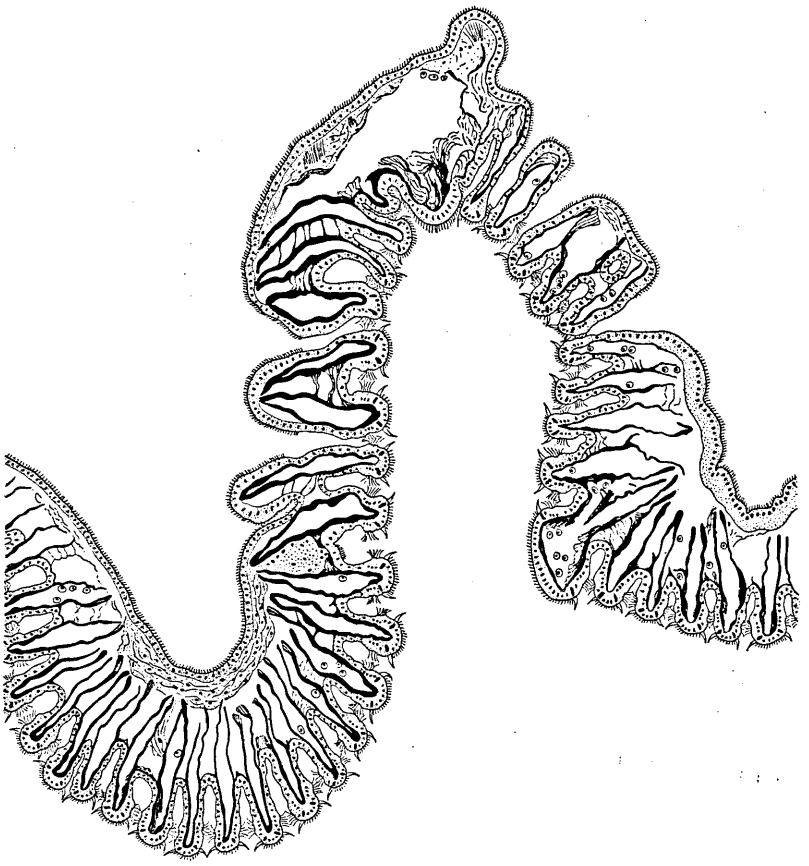

FIG. 9.—Transverse section through dorso-ventral folds in an ascending lamella, near the dorsal food groove, of a mussel from North Bank, Fal Estuary, 1930. The distribution of the cilia and nuclei is represented diagrammatically. The extensive area of ciliation on the abfrontal surface of the lamella, is, however, noteworthy. Bouin's fixative; Mann's methyl-blue-eosin. × ca. 93½.

does not occur; there is a tendency for the filaments to form interlamellar extensions, particularly in the region of the ciliated discs, which by their fusion form interfilamentar junctions; this is clearly seen from Herdman's Figure 6, Plate 27 (**24**).

The foregoing examples of fusion would appear to be due to crowding,

consequent on the puckering and folding of the lamellæ—whatever may be the cause of the latter—but it is more difficult to suggest a cause for the extensive areas of fusion involving irregularly the greater part of a lamella.

A crumpled or puckered appearance of the entire surface of the lamellæ of some gills has been noticed—sometimes restricted to one lamella of a

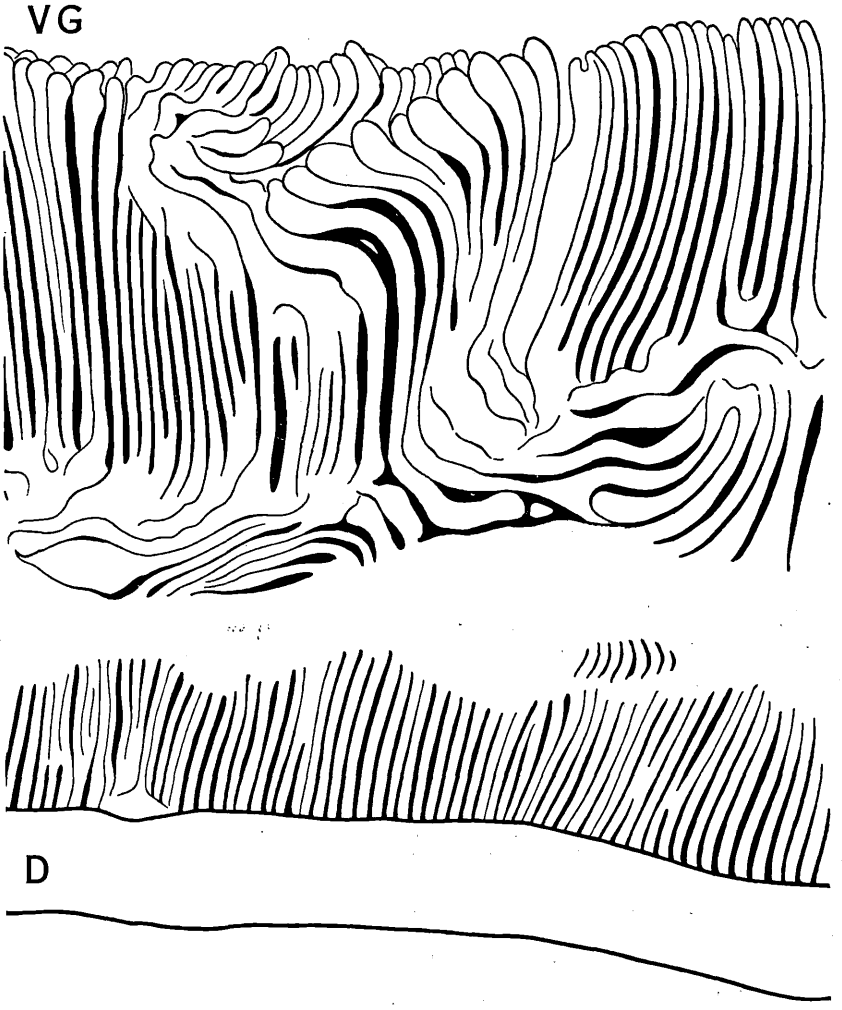

FIG. 10.—Sketch of part of ascending lamella of a gill, showing contortion and fusion of the filaments; in some places the filaments are almost at right angles to their normal direction. The ascending lamella was considerably shorter, dorso-ventrally, than the descending lamella. VG, ventral edge of gill; D, dorsal food groove. From a mussel from Mylor Bank, Fal Estuary, November 22, 1927; preserved material. × ca. 24⅓.

FIG. 11.—Sketch of part of ascending lamella of a gill, showing considerable areas of fusion of the filaments. The living gill showed much brown pigment, collected in masses. VG, ventral edge of gill. From a mussel from near the junction of the Tamar and Tavy (Weir Point), November 3, 1927: preserved material. × ca. 24⅓.

gill and that most usually the ascending lamella—which remains when the gill is placed in water, and this condition may possibly be the forerunner of cases of extensive fusion, where the filaments, when distinguishable, appear to have undergone a kind of puckering, some running almost at right-angles to their normal direction (Fig. 10, p. 503).

In other instances, however, the fused areas have an approximately flat surface (Fig. 11, p. 504), which has the appearance of being due to the fusion side by side of undisturbed filaments, and it is questionable whether this may not have occurred in certain circumstances, consequent on the

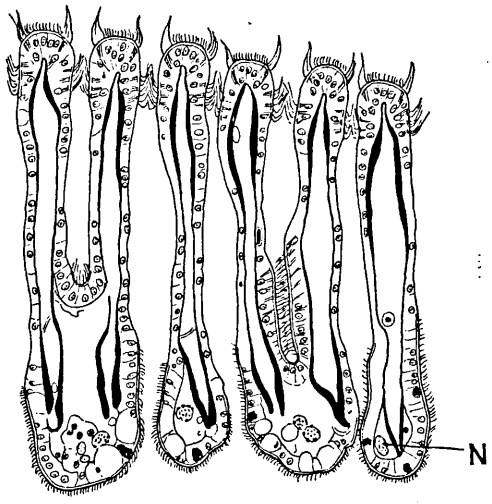

FIG. 12.—Transverse section, single gill lamella, showing fusion of the interlamellar (abfrontal) ends of filaments. N, ? nerve. Bouin's fixative; Mann's methyl-blue-eosin. × 210.

possible swelling of filaments. It is, however, perhaps only a further stage in the process of fusion, masking the irregular surface which follows puckering. The irregular disposition of the chitinous supports, as seen in sections, suggests this possibility, though they have doubtless undergone a certain amount of distortion during embedding and sectioning.

Probable stages in the process of fusion are given in Figures 12 ; 13, A and B ; and 14. Figures 12 and 13, A and B (p. 506), are from a series from one gill of a mussel from the Fal Estuary, 1930 ; Figure 13, A and B, from different levels of the same lamella, and Figure 12 from the opposite lamella. Figure 14 (p. 508) is a section through part of the same lamella as that sketched in surface view in Figure 11 (p. 504), and was from a mussel from near Weir Point (Tamar Estuary). While the ascending lamella showed extensive areas of fusion, the descending one was almost

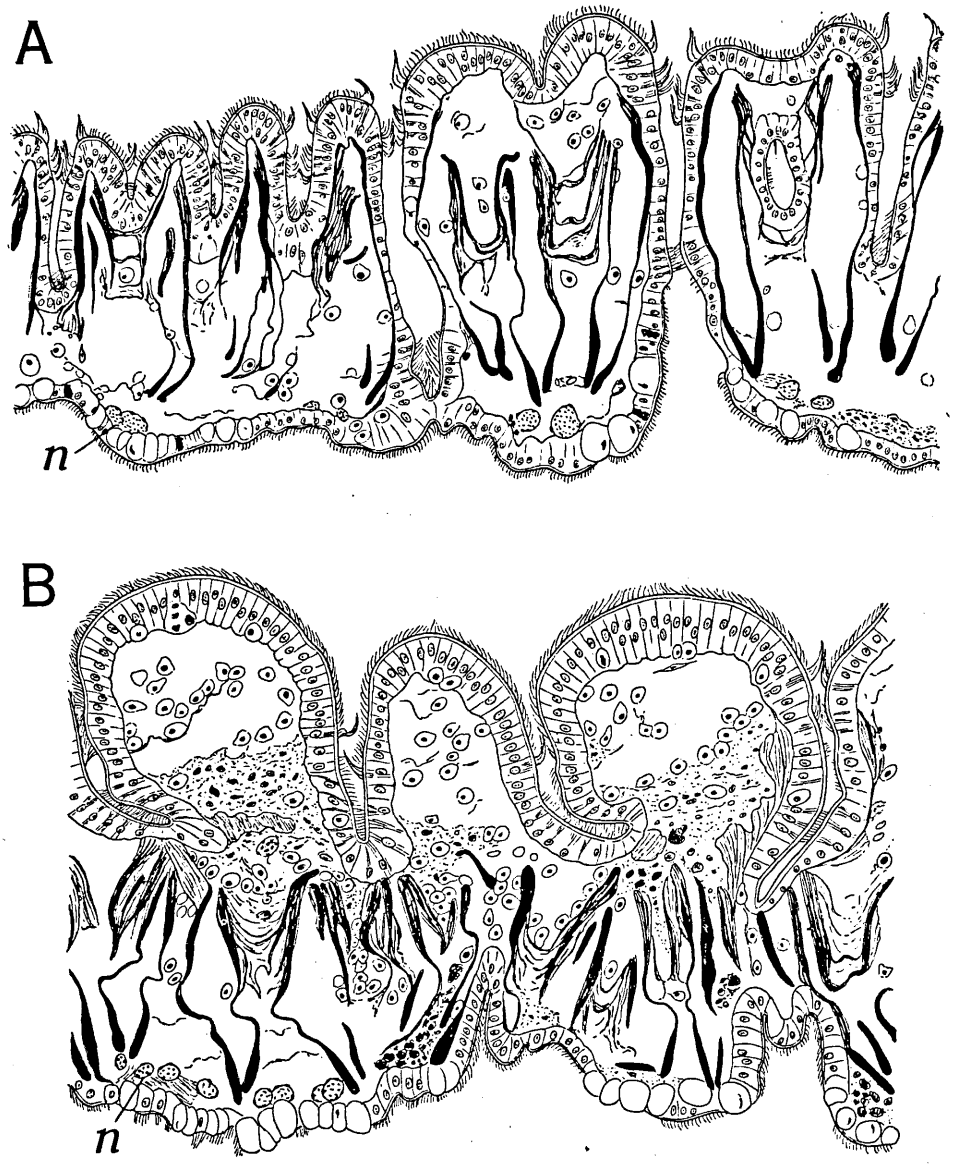

FIG. 13.

A. Transverse section of part of the opposite lamella to that of Fig. 12, showing a further stage in fusion. Towards the centre of the figure three filaments have fused—as shown by the three sets of chitinous supports—though the frontal surface has the appearance of two fused filaments. Between the three sets of chitinous supports are strands or loops of pale staining chitin. The abfrontal epithelium is continuously ciliated, except for the numerous gland cells, which are swollen and pale staining, or darkly staining and granular. n, ? nerve. Bouin's fixative; Mann's methyl-blue-eosin. × 210.

B. Transverse section, single lamella, where fusion is pronounced. Not only has fusion occurred, but also a certain amount of abnormal proliferation of the frontal surface of the lamella in the form of broad ridges and bosses. Ciliated discs persist in some of the furrows, and also latero-frontal and in some instances the lateral cilia. The frontal ends of the chitinous supports are abnormally developed, the additional chitin being pale staining. Gland cells are numerous in the abfrontal epithelium. n, ? nerve. Bouin's fixative; iron hæmatoxylin and acid fuchsin. × 210.

normal, very little fusion occurring: this restriction of fusion to one lamella while the opposite one is almost normal is a rather common feature.

The ridges and bosses caused by irregular proliferation of the frontal epithelium, as in Figure 13, B, may possibly in turn fuse to give a surface resembling that of Figure 14. This is perhaps indicated by the two enclosed spaces—one showing the remains of ciliated discs—and the deep furrow shown in that figure.

While the fused epithelial surfaces doubtless degenerate and are removed by the action of phagocytes, the chitinous supports of the filaments would appear to be very resistant. They are, therefore, in the majority of cases, clear and reliable indicators of the number of filaments which have fused to form a certain stretch of fused lamella, and would seem to offer definite evidence that it is fusion which has occurred.

It may be noted in Figure 13, A, that the central portion of the section, which from the frontal surface would appear to have been formed by the fusion of two filaments, is in reality formed by the fusion of three, as shown by the chitinous supports. In this part of the section the gradual retreat of the spaces, or the smoothing out of the furrows, separating the three filaments, is clearly shown by the successive positions of the strands or loops of pale staining chitin.

The great depth of the cells of the frontal epithelium as shown in Figure 13, A and B, especially in Figure 13, B, may be noted; it will be referred to again under the following section.

Areas of fusion are often visible at a glance owing to their heavy pigmentation, the pigment frequently occurring in dark brown or orange masses of considerable size. Mytilus gills are normally somewhat pigmented, especially along the four main food grooves at the free ventral edges of the gills. The colour is generally yellow or pale orange, though in young normal mussels from Padstow the gills were tinted, more or less entirely, a bluish purple. Following fusion, and the degeneration of a certain amount of tissue, the pigment granules are doubtless liberated and collect in masses (cf. the pigment, which following the transformation of tissue previous to regeneration in *Tubularia mesembryanthemum*, is found lying in a ball within the digestive tract of the newly formed hydranth (**30**, pp. 59, 268).

The ciliation of some areas of fusion was investigated by means of powdered carmine. The ciliary current mostly goes ventrally towards the free edge of the gill, though not always directly ventrally; it may pass somewhat diagonally across the area of fusion. In other cases investigated there were small areas of reversal—judged entirely by movement of carmine particles—and sometimes a swirl of current. Such variations

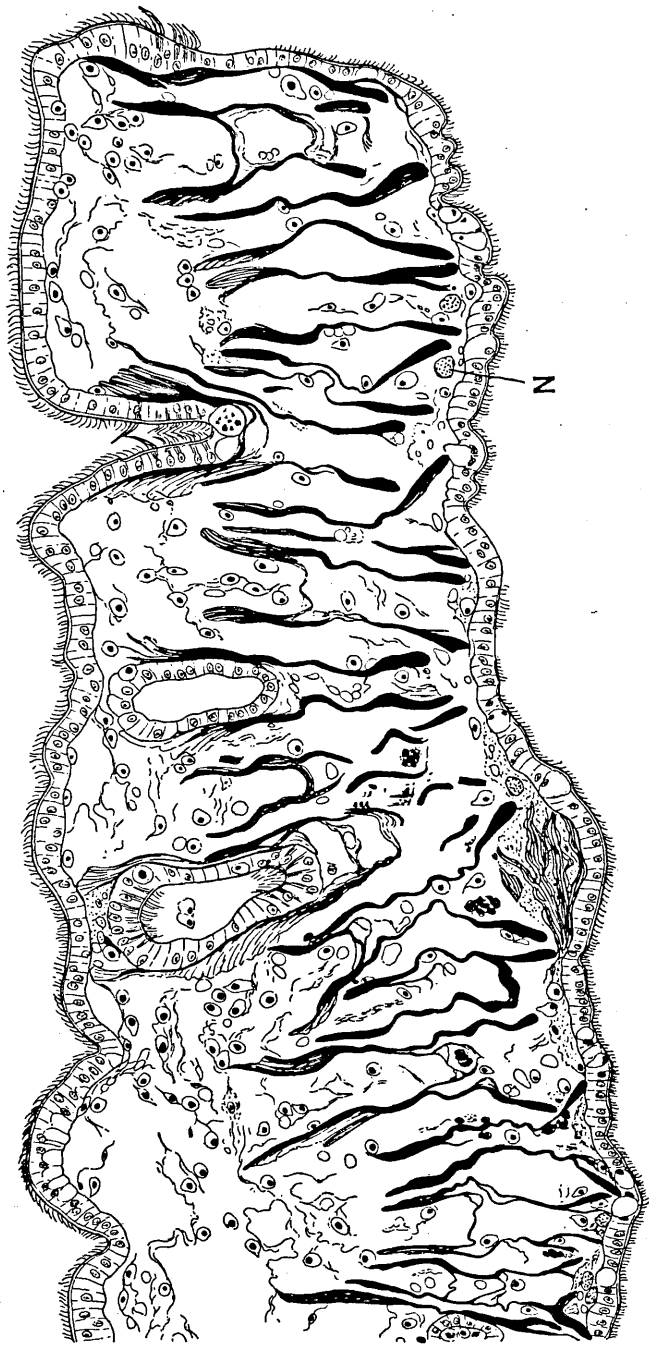

FIG. 14.—Transverse section, ascending lamella, showing extensive fusion of the filaments (17 filaments in the part sketched). This is from the lamella, part of which is shown in surface view in Fig. 11. The frontal surface is approximately flat except for a deep furrow towards the right side of the section: in the furrow latero-frontal and lateral cilia are still discernible. Two enclosed spaces, due to incomplete fusion of the filaments, are present; ciliated discs persist in one of these. The frontal half of the chitinous supports have become enlarged by the addition of layers of pale staining chitin. A certain number of gland cells are present among the ciliated cells of the abfrontal epithelium. Small masses of granular pigment occur. N, ? nerve. Bouin's fixative; iron hæmatoxylin and acid fuchsin. × 210.

may possibly depend on whether the fused filaments were straight, askew, or crumpled.

(*c*) Enlargement of the Gill Filaments.

The enlargement of the gill filaments was a rare occurrence: the majority of such examples—five—came from the estuary at Teignmouth, and one from the Fal Estuary in 1930. (Enlargement of an occasional filament or tiny group of filaments may be found on a gill beneath a pea-crab.) The most striking example was a mussel from Teignmouth

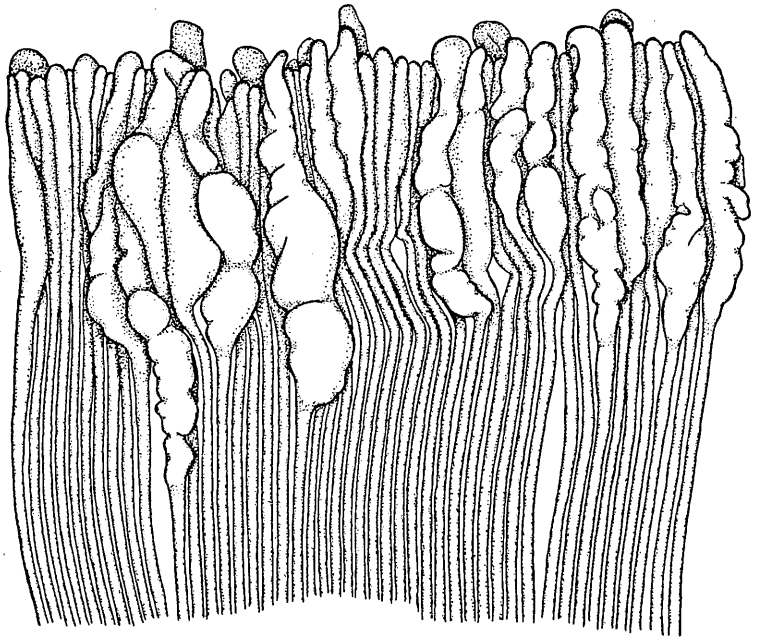

Fig. 15.—Surface view of a small region of an ascending lamella to show enlargement of the filaments in a zone 2·0 to 3·0 mm. wide at the ventral edge of the gill. The main food groove has an irregular appearance owing to the extension ventrally of some of the filaments. From a mussel from Teignmouth, August 21, 1928; preserved material. × ca. 24⅓.

(August 21st, 1928) which showed enlargement of the filaments, generally in small groups, in a zone about 2·0 to 3·0 mm. wide along both sides (descending and ascending lamellæ) of the free ventral edges of all four gills. The enlarged filaments had an irregularly swollen appearance, being pitted in some places with small pockets, and tended to overlie laterally the normal filaments, where these occurred (Fig. 15). While the width across the frontal surface of a normal filament is about 0·05 mm., in an enlarged filament it may reach 0·3 mm. or more. Fusion of filaments laterally, however, was of somewhat rare occurrence and where

it had taken place was restricted to the fusion of the abfrontal ends of the filaments. A single filament in side view is shown in Figure 16, A (p. 510). Out-growth of the lobes of the ventral food grooves had occurred giving an irregular appearance to the ventral edges of the gills (Fig. 15), which appeared otherwise to be straight and uninjured.

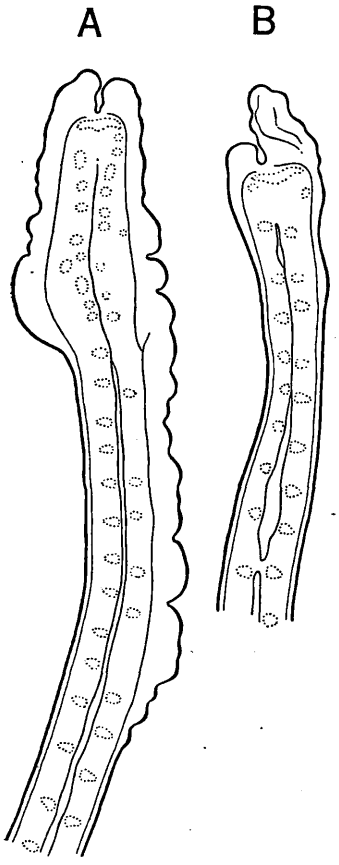

FIG. 16.—Lateral views of two filaments which have suffered enlargement of the frontal surface. B, shows extension of one side of the main ventral food groove. The fine inner line indicates the position of the lateral cilia. From preserved material. × ca. 18¼.

A mussel from the same locality on August 16th, 1928, had the gills in a similar condition, but the enlargement was restricted to a narrower zone (1·0 to 2·0 mm.) at the ventral edges.

The mussels, most unfortunately, were preserved whole in formalin, so that the fixation was poor, but transverse sections of one (Teignmouth, August 21st, 1928) showed certain points fairly clearly (Fig. 17, p. 511). The enlargement of the filament was confined mainly to the frontal face, for the position of the conspicuous lateral and latero-frontal rows of cilia was little changed; proliferation of the ciliated frontal epithelium appeared to have occurred, resulting in a much swollen frontal face with a corresponding enlargement of the internal canal (cf. the apical filaments of the two Eulamellibranchs *Pinna virgata* (**43**, Fig. 17, p. 214) and *Lima inflata* (**43**, Fig. 18, p. 216)). In the section sketched in Figure 17 there appears to be some interlamellar extension of the swollen filament, but this was not evident in all. Transverse sections of the enlarged gill filaments of this mussel showed a great irregular development of the frontal ends of the chitinous supports. While the chitinous supports of normal filaments stain quite darkly, this extra development of chitin is pale staining. Mucus cells were unusually well developed among the ciliated cells of the frontal epithelium; these were seen not only in sections (see Fig. 17) but in single filaments, stained with borax carmine and picro-nigrosin, and mounted whole.

Another mussel, also from Teignmouth (July 10th, 1928), showed slight irregular growth in the occasional extension of a filament beyond the free ventral edge of the gill (Fig. 16, B, p. 510) and in rare isolated groups of

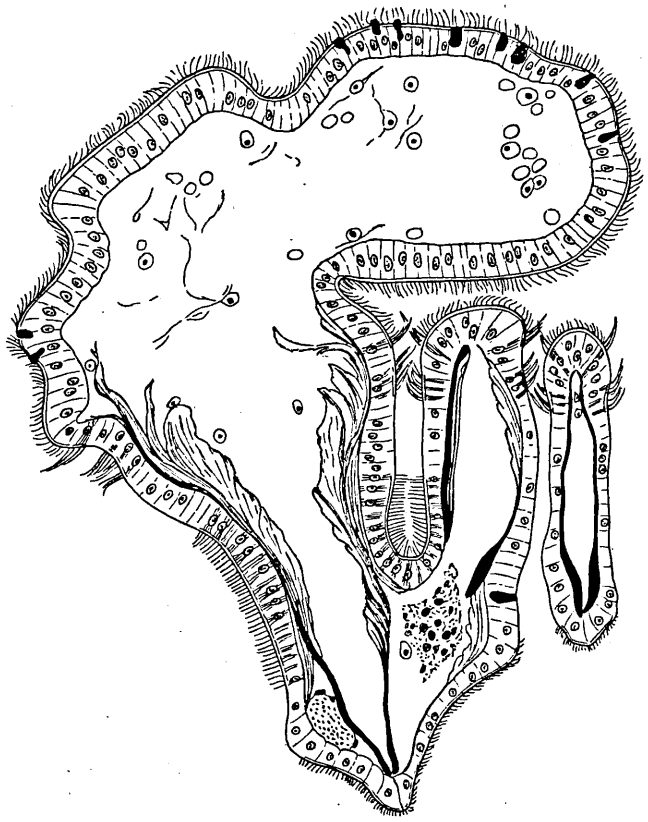

FIG. 17.—Transverse section of filaments from the gill of a mussel from Teignmouth (the same individual from which Fig. 15 was taken), showing one much enlarged filament. As shown by the position of the lateral and latero-frontal cilia, the increased size is largely, or almost entirely, due to the great increase of the frontal surface. This filament has also extended in an interlamellar direction and has partly fused with an adjacent filament, which is only slightly enlarged: a mass of granular pigment is present at the junction of the two filaments. Especially striking is the development of the chitinous support of the enlarged filament; as indicated by the light shading this additional chitin is pale staining. A normal filament is shown on the right. Gland cells are present among the ciliated cells of the frontal epithelium. Formalin; Borax carmine and picro-nigrosin. × 210.

three or four filaments on the surface of the lamellæ as in Figure 18, A (p. 512). Very occasionally a mussel may be opened, in which, following a tear, the torn ends of the filaments have swollen or proliferated in an

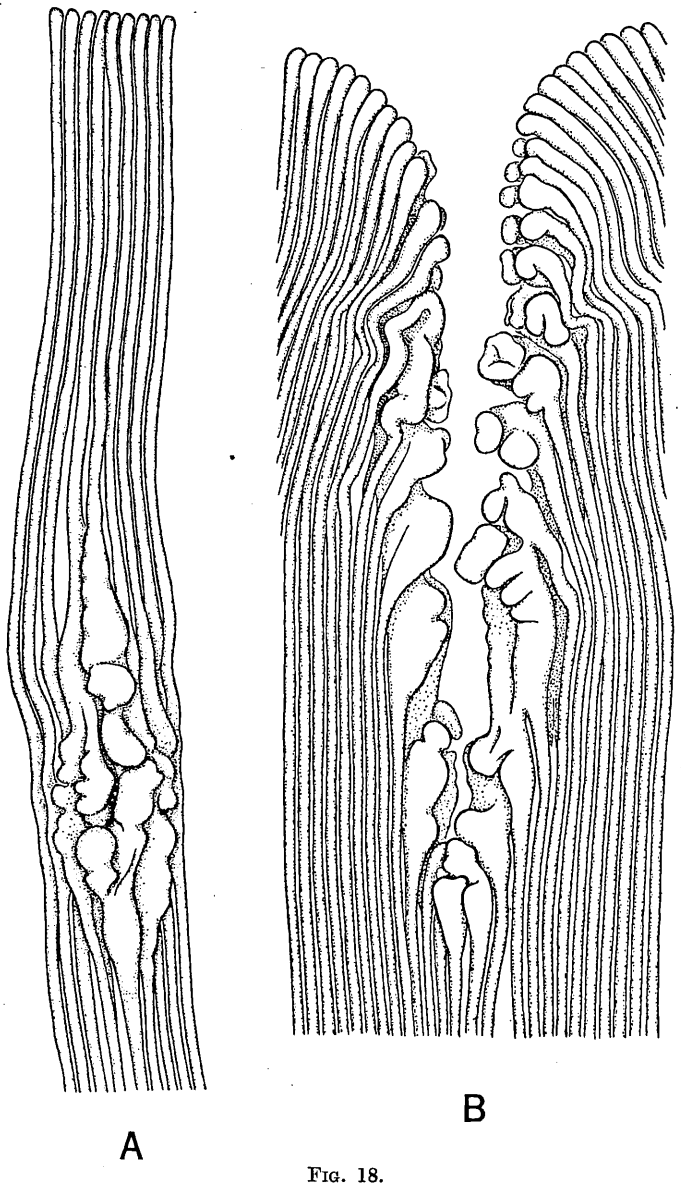

FIG. 18.

A. Sketch showing a small area of enlargement of filaments—three filaments are chiefly concerned—on the surface of a gill of a mussel from Teignmouth, July 10, 1928.

B. Enlargement of the ends of filaments, presumably following a tear, with the formation of a new but irregular food groove. From the same gill as A.

A–B. From preserved material. × ca. 24½.

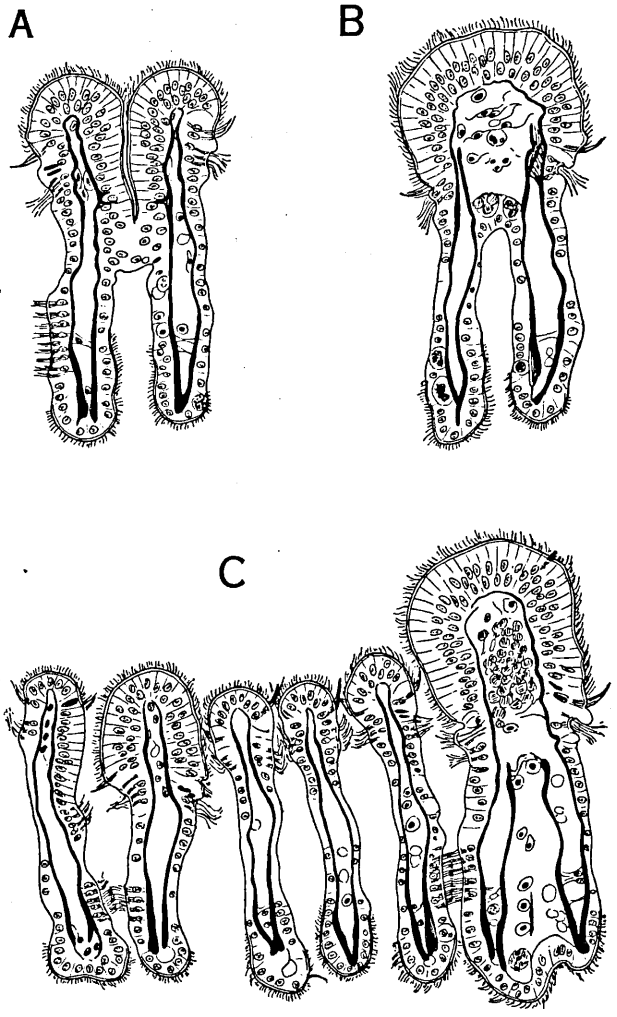

FIG. 19.—Transverse sections (from the same series as that of Fig. 20) showing filaments with abnormally deep cells towards the frontal face; one filament shows deep cells on one side only. To the right of C two fused filaments show a similar condition of the cells. A and B are sections of these same two filaments at a higher—more dorsal—level: in A the fusion is beginning, in B the frontal halves of the two filaments have fused, while in C the fusion is complete. In C a mass of granular pigment is present within the two fused filaments. From a mussel from North Bank, Fal Estuary, 1930. Bouin's fixative; Borax carmine and picro-nigrosin. × 210.

irregular manner while forming a new food groove, as had occurred on the gill of this mussel (Fig. 18, B).

Among the mussels received from the Fal Estuary in March, 1930, a single individual showed enlargement of the filaments. The ventral free edges of the gills were somewhat irregular in places, as though shallow pieces had been removed by injury, and the swollen extensions of the

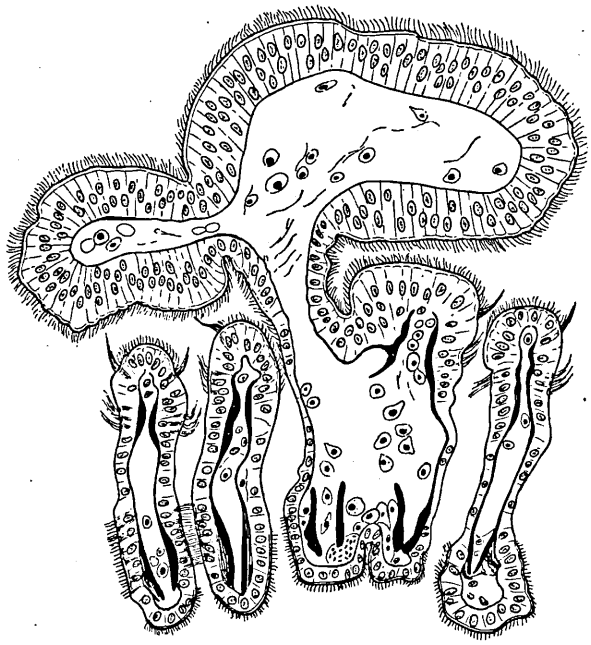

FIG. 20.—Transverse section of five filaments from the gill of a mussel from North Bank, Fal Estuary, 1930, showing a filament with greatly increased frontal surface and great depth of cells, fused with a filament on the right in which the frontal cells are also of great depth. There is no increase in the development of the chitinous supports (cf. Fig. 17). The separate filament on the right shows increased depth of the frontal cells of one side. (From the same series as that of Fig. 19.) Bouin's fixative; Borax carmine and picro-nigrosin. × 210.

ventral ends of occasional filaments increased the irregular appearance. The scattered groups of swollen filaments were mostly found near the ventral margins of the gills, but rarely the swelling was continued to almost half the width of the gill; the swellings had a much pitted appearance. Some of the lamellæ, however, also showed many of the filaments slightly widened, but otherwise normal. In transverse sections of such filaments it was seen that the widening was due to the unusually great depth of the cells towards the frontal part of the filament (Fig. 19, p. 513) (cf. the condition of the frontal epithelium near the ventral food

grove of normal filaments). Filaments were observed with the cells of one side of normal depth, while those of the opposite side were much deeper. Figure 19, A, B and C (right-hand part of section), which are sections through the same two filaments at different levels, show three stages in the gradual fusion of two filaments with enlarged frontal cells. Transverse sections of much enlarged gill filaments showed in this case, as in those from Teignmouth, that it was mostly proliferation of the frontal cells that had produced the swelling (Fig. 20, p. 514) : these cells were of abnormal depth, in some instances almost as deep again as those of the enlarged filaments of the Teignmouth mussels of August 21st, 1928 (cf. Figs. 17 and 20). There was no increased production of chitin, as in the Teignmouth example sectioned.

The enlargement of the gill filaments in the cases given was due no doubt to increased growth of the frontal epithelium dependent on some factor in the environment, e.g. decrease in salinity with consequent increased endosmosis. The abnormally great depth of the epithelial cells of the gill filaments of some mussels (as in Figs. 19 ; 20) is strongly suggestive of growth acceleration.

In the cases cited the enlargement was mostly of the frontal surface of the filaments, and little interlamellar extension was seen ; that it may occur, however, in such a situation in Mytilus was shown by the swollen out-growths in connexion with the interlamellar junctions in the gill of a mussel from the Fal Estuary.

The cilia on the swollen frontal surfaces beat normally and in general in a ventral direction, as shown by the movement of carmine particles.

(*d*) Concrescence of the Two Gills of One Side.

A Mytilus from Teignmouth (July 10th, 1928) showed a curious condition of the gills of the right side. Anteriorly, for about 7·0 mm., the two gills appeared to be fused side by side, and, since the outer one was somewhat shorter than the inner, the two ventral food grooves were at different levels ; immediately behind for about 7·0 mm. the two gills were fairly distinct : throughout this anterior region the gill filaments showed much crumpling. The gills then appeared to have fused again, so that in the middle region for about 18·0 mm. there was one " gill " only, but here it appeared to be formed of two lamellæ only —they could be clearly separated to within 3 mm. of the ventral edge, where they were connected by interlamellar junctions—and as both were provided with a dorsal food groove, they were presumably ascending lamellæ ; the gill was entirely free from the body. At this part the gill was about 7 mm. deep. While the gill filaments of the outer lamella appeared from surface view to be normal, those of the inner

lamella were in places bent somewhat out of the true dorso-ventral direction (i.e. crumpled), with some slight fusion side by side. For the remaining posterior 20·0 mm. the gills were normal and about 11·0 mm. deep. The shell had suffered no injury, and the inner surface of the valve was perfectly smooth.

A Mytilus from North Bank, Fal Estuary (March, 1930), had the gills of the left side, for about 5·0 mm. in the middle region, exceeding narrow (ca. 1·0 to 4·0 mm. deep), fused together, and entirely free from the body. So far as could be judged, the two ascending lamellæ (see **39**, Fig. 209, p. 229) alone were present in the fused portion as there was a dorsal food groove on both lamellæ. From the gill ridge hung short ends (ca. 1·0 mm. long) of the filaments of the two descending lamellæ. The left valve was occupied by a large blister, and though no hole had been bored through the shell in the region of shortness of the gill (Cliona borings were present in the umbo region), yet this condition was possibly due to injury, for the short ends of the descending filaments appeared to have been cut across. The case previously described may possibly have arisen from a condition such as this, as it is now known that regeneration of the gill may occur (see following note in this Journal, p. 551).

Peck (**37**, p. 50) gives an instance of abnormal concrescence in the gills of Anodonta. "In this case a torn portion of the inner gill-plate of the left side beyond the posterior edge of the root of the foot had become intimately adherent by concrescence to the inner surface of the inner gill-plate of the right side of the animal."

GENERAL CONDITION OF MYTILUS FROM THE VARIOUS LOCALITIES INVESTIGATED.

Fal Estuary.*

The mussels obtained from the Fal Estuary in 1927 (1648 examined from October 26th to November 25th) were mostly of small or medium size, ranging, however, from about 4·0 to 10·0 cm. in length, with but few of the large size, and were on the whole in rather poor condition, though the condition varied somewhat in different parts of the Estuary (see Table I). Not only were many of them poorly fished, but a certain number (6·6%) had large blisters and flat areas of wrinkled brown skin on the inner surface of the valves (Fig. 21, p. 519). Some of the blisters were so large that they covered the greater part of the valve and in certain cases projected into the cavity of the opposite one. The covering of such blisters varied greatly: in some it was a soft dark brown skin, in some a

* A chart of the Fal Estuary may be found in **36**, p. 3.

TABLE I.

CONDITION OF *Mytilus edulis* FROM VARIOUS LOCALITIES IN THE FAL ESTUARY.

Locality in Fal Estuary.	Date.	Number of mussels.	Number of mussels with Pinnotheres.	Number of mussels with Abnormal Gills.	Number of mussels with blisters in valves.	Remarks.
	1927					
Position not definitely known.	Oct. 26	250	17 (6·8%)	Numerous, but number not known.	9 (3·6%)	On the whole in rather poor condition. 4·0–9·8 cm. in length.
Position not definitely known.	Oct. 28	295	13 (4·4%)	59 (20%)	19 (6·44%)	On the whole in rather poor condition.
East Bank.	Nov. 2	279	9 (3·22%)	88 (31·54%)	23 (8·24%)	On the whole in poor condition.
Trelissick Reach.	Nov. 2	102	3 (2·94%)	19 (18·62%)	0	On the whole in good condition. Mostly about 5 or 6 cm. in length.
Turnaware Bar.	Nov. 10	9	0	2 (22·2%)	0	
Mylor Bank.	Nov. 23	195	13 (6·66%)	90 (46·15%) (*a*) 67 (*b*) 20 (*c*) 3	17 (8·72%)	Medium condition. 5·5–9·0 cm. long.
East Bank.	Nov. 24	254	10 (3·94%)	121 (47·64%) (*a*) 91 (*b*) 30 (*c*) 0	27 (10·63%)	Medium condition. 4·6–9·2 cm. long.
Parson's Bank.	Nov. 25	264	6 (2·27%)	97 (36·74%) (*a*) 74 (*b*) 23 (*c*) 0	14 (5·30%)	Well fished on the whole. Of rather larger size than those from East Bank.
	1930					
North Bank, between Mylor Pt. and St. Just Pt.	March 7	181	19 (10·5%)	72* (44·44%) (*a*) 22 (*b*) 44 (*c*) 6	26 (5 inhabited by Pinnotheres) (14·36%)	On the whole in fairly good condition. 5·4–12·4 cm. long.

(*a*) = Folding over of free ventral edge of the gill.
(*b*) = Fusion of filaments side by side.
(*c*) = Other abnormalities, including secondary grooves and folds, and simple narrowness of the gill.
* Out of total of 162 free from Pinnotheres.

layer of easily broken shell material, while in others it was so thick that it was difficult to pierce. The contents of those blisters examined, were in some instances almost clear liquid, in others mud, sometimes evil smelling. A certain number of the blisters were no doubt caused by the presence of *Polydora hoplura*,* which badly infested the shells. Cliona had attacked a number of the shells—generally the thicker part towards the umbo—and in a few instances apparently caused blisters.

FIG. 21.—Photographs of a selection of *Mytilus edulis* from the Estuaries of the Fal and Teign, showing blisters on the inner surface of the valves. The mantle has been entirely removed from the valves, except in E, where a triangular area of very thin mantle has been left on the blister. Various reductions.

A. Valve with round blister, which projects (about 8·0 mm.) into the opposite valve, in the posterior region, just ventral to the posterior adductor muscle. In opening the mussel the blister, which is of fairly thin shell, was cut: the dark line on the photograph, due to the cut, is on a level with the edge of the valve. Mussel 6·3 cm. long.

B. Valve with a blister of fairly thin shell material, entirely filling the anterior part of the valve in the mouth region. Mussel 7·5 cm. long.

C. Valve with blisters of fairly thin shell material almost entirely covering the surface. Antero-ventrally one of the blisters, though of shell material, has a wrinkled surface. The depth of the largest blister, measured at the spot where a small piece of the roof has been removed (small black area in photo), is about 11·5 mm. Mussel 9·2 cm. long.

D. Valve with a hard blister, convoluted in form, extending the length of the shell. Mussel 6·0 cm. long.

E. Valve with a large blister, occupying the greater portion, and projecting for about 8 mm. into the opposite valve. The shelly covering is extremely thin and in places has flaked off, exposing the brown skin beneath. The posterior adductor muscle has, to a certain extent, been encroached on by the blister. Towards the anterior and dorsal part of the shell there is a small flat area of dark brown skin. Mussel 7·1 cm. long.

F. Valve with a large smooth blister occupying much of the deeper portion, and reducing the depth of the valve in this region to about 4·0 to 6·0 mm. The blister, in this case, is covered by the shining nacreous layer and appears to be of considerable thickness, while in most other cases the shelly covering, which is somewhat thin, is of a greyish colour with a dull to rather dull surface. Mussel 7·7 cm. long.

G. Valve with almost the entire surface covered by an irregular low blister of dark brown skin. The shining spots on the surface of the blister would appear to be small areas of shell deposit. Posteriorly the blister has been removed from a round area exposing a worm aperture. Mussel 8·0 cm. long.

H. Valve with almost the entire surface covered with blisters, the covering of which is chiefly wrinkled brown skin; in places, however, the lower part of the wall is of very thin shell material. An L-shaped blister in the ventral and anterior part of the valve has had most of its roof removed. Mussel 7·1 cm. long.

I. A solid growth of shell material—judging by the weight—on the inner surface of the valve of a mussel from Teignmouth: it projects about 2·0 mm. beyond the level of the edge of the valve. The surface of the growth is of a dull dark grey colour and finely corrugated. Mussel 7·0 cm. long.

J. Occupying the middle and posterior part of the valve is a rather low irregular blister of hard shell material, with a ridged surface posteriorly. Towards the ventral edge of the valve is a blister of hard shell—except for a narrow irregular line along which it can be pierced by a needle—on a small base: it is about 9·0 mm. deep. Partly merged with the shadow cast by the latter is a small area of wrinkled dark brown skin. Mussel 8·0 cm. long.

* Identified by Mr. D. P. Wilson.

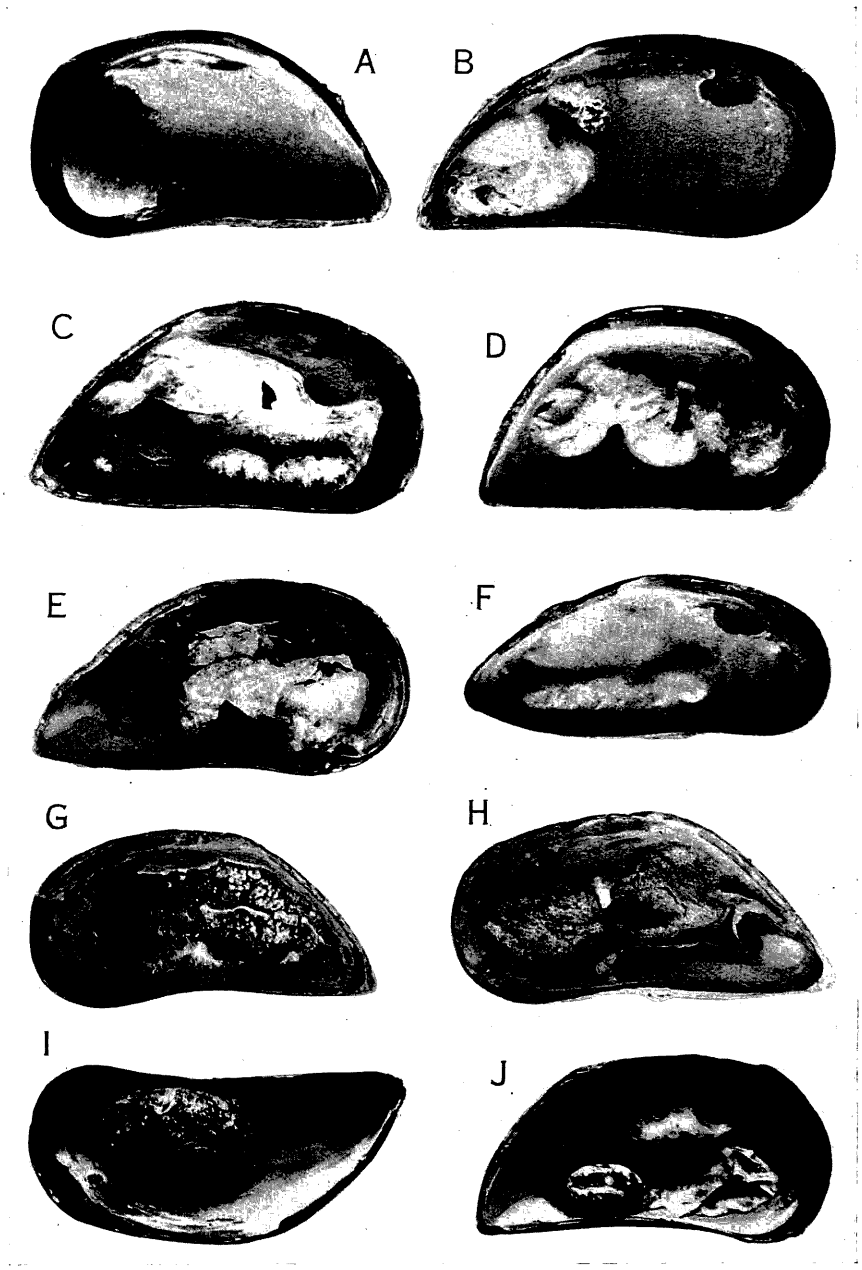

FIG. 21.

Many of the mussels attacked by Polydora showed—on the inner surface of the valves—raised but entirely closed in, tubular passages (see **28**, Fig. III, p. 41) covered with shell deposit of such a thickness that they could only be broken into with bone forceps; in others, however, the covering was much thinner and in a few cases the tube of the worm projected through the thickness of the mantle into the mantle cavity, the apertures of the tube being entirely internal. A somewhat similar state of affairs has been described by Whitelegge in oysters of the coast of New South Wales attacked by *Polydora ciliata* (**47**, p. 48).

The presence of Polydora in a good percentage of the Fal Estuary mussels no doubt contributed to their poor condition. The abnormal condition of the gills, in individuals in which this took the form of folding, with reduction of the gill surface and disorganisation of the food grooves, no doubt also had an adverse effect on the general condition of the mussels.

In a certain number of the mussels there had been incomplete spawning, with irregular retention of the genital products in small masses projecting from the mantle surface. A peculiarity that was noticed in two specimens, was the presence of a horny, dark-coloured, ball in the byssus pit, while a third had a swollen mass, composed of many tiny, translucent balls, in the same position. It might be noted that among the batches of October 26th and 28th, a few mussels arrived with the mantle much swollen out with an accumulation of water between it and the face of the valve.

As it was desirable to know whether the abnormal conditions of the gills persisted, a further batch of mussels was obtained from the Fal Estuary on March 7th, 1930. These were examined with special reference to the state of the gills. Though the general impression gained was that the gills were not so badly abnormal as in those of 1927, yet the percentage with abnormal gills was quite high, namely, 44·4%. This may perhaps be explained by the fact that these mussels were examined especially for the state of the gills, while the previous batches obtained from the Estuary in 1927 were examined primarily for Pinnotheres: in a rapid inspection small areas of fusion of the filaments would be overlooked. In the March 1930 sample, mussels containing Pinnotheres of a size likely to cause injury have been omitted from the percentage with affected gills given above. While the percentage of mussels with abnormal gills is high, it is composed mostly of those with some degree of fusion of the filaments; 22 only—out of a total of 72 with abnormal gills—had the ventral edge of the gill folded over, and in these the folding was not generally as extensive as in those of 1927.

The mussels of the 1930 batch varied in length between 5·4 and 12·4 cm., very few being over 9·0 cm. long. They were on the whole in fairly good condition, though a certain number, including those with highly abnormal

gills—with the surface much reduced and food grooves disorganised—were in poor condition.

Blisters were present in 26 mussels out of a total of 181 (14·36%). In some specimens they occurred in both valves, varying in number from one to three in each. The blisters were broken open and the contents examined : they mostly contained liquid with a varying quantity of mud ; in an exceptional case a piece of the mantle appeared to have been included. Worms were found in nine of the blisters, and in a further six the mud was in the form of fæces, indicating the previous presence of worms. Those found in seven of the blisters were one or more individuals of *Dodecaceria concharum*,* associated in one instance with three or four individuals of *Polydora ciliata*, while in two of the blisters Polydora was present alone. Some few shells were noticed with borings of *Cliona celata* in the thicker part of the shell near the umbo. Old borings of whelk-tingles were seen in some of the shells (about nine ; in two cases, one in each valve) ; they had been covered by shell deposit or skin, and in a few instances had given rise to large blisters. Very rarely blisters so formed were occupied by Dodecaceria or coated with *Cliona celata*,† these forms, no doubt, following the whelk-tingle. In three cases it was noticed that the outer gill of one side was extremely narrow or almost missing near the position of a former Gastropod boring ; the whelk-tingle, no doubt, had partly eaten the gill before being disturbed.

Estuaries of the Hamoaze, near Weir Point.

Mussels from this locality—1291 were examined between October 8th, 1927, and February 17th, 1928—were of varying size, from about 4·0 cm. to 12·0 cm. long ; the batches examined were fairly well fished, though the condition varied somewhat. A number had the shells covered with Halichondria. A certain amount of infection with Polydora occurred : in three cases it was noticed that the tube of the worm passed through the mantle so that the openings were entirely internal ; two of these contained *P. hoplura*, while nothing was found in the third. Mytilus with abnormal gills, other than those inhabited by Pinnotheres, were of rare occurrence.

Estuary of the Yealm.

The samples obtained from the Yealm Estuary—296 were examined between October 10th, 1927, and August 3rd, 1928—were composed of a good percentage of large specimens (about 7·0 to 12·0 cm. long), but the shape of the shell was very different from that of the Padstow mussels, which were also of large size, being of greater breadth in relation to the height. They were generally well fished, but the flesh inclined to be

* Identified by Mr. D. P. Wilson. † Identified by Mr. M. Burton.

yellowish. Very few mussels were noticed with abnormal gills, other than those infected with Pinnotheres, and the percentage of infected mussels was high.

Estuary of the Teign.

The mussels from the Teign Estuary—9262 were examined between December 6th, 1927, and February 26th, 1929—were mostly of small or medium size and on the whole rather poorly fished, though the condition varied somewhat with the different batches, roughly of about 1000 each ; those on January 4th, July 10th, July 19th, and August 21st, 1928, being in fairly good condition. Many were infested with Polydora, the inner surface of the valves showing raised, but covered in, tubular passages of the worms (see **28**, Fig. 111, p. 41). A small number had blisters in the valves ; one had a peculiar, large growth of shell in one valve, which, judging by the weight, was solid (Fig. 21, I, p. 519).

Two specimens, out of a total of 9262 mussels, were seen to be infested with the sporocysts and cercariæ (Bucephalus) of Gasterostomum.

About a dozen cases were noted of the presence of a horny ball in the byssus pit.

Mussels with abnormal gills were of exceptional occurrence, and in most of those noticed the abnormality consisted in enlargement of the gill filaments in certain areas.

It is of interest to note that Patella taken from mussels from this locality are a high shelled form (see also Report of the Council, Journ. Mar. Biol. Assoc., Vol. XVI (N.S.), p. 993, 1930).

The Estuary of the Camel, near St. Issey Cliff, Padstow.

The mussels from the Estuary at Padstow—10,866 were examined between November 8th, 1927, and August 9th, 1929—were fine specimens with smooth, clean shells, high and not very broad. The batches, of about 1000 each, contained a majority of medium and large specimens up to about 13·5 cm. in length. Throughout the period during which mussels were obtained, they were on the whole consistently well fished, with light-coloured flesh.

Blisters, in the valves of the Padstow mussels, were rare ; infection with Polydora was slight, and it was only exceptionally that the worm was found in small heaps of mud just inside the valves at the posterior end.

Infection by a species of Trematode (probably a new species*) occurred in about 235 out of the total of 10,866 mussels examined (2·16%), and seven cases were noted of infection by the sporocysts and cercariæ of Gasterostomum.

* The Trematode is being investigated at Leeds University.

Exceedingly few specimens—other than those infected by Pinnotheres or the Trematode—showed any abnormalities of the gills.

The Promenade Pier, Plymouth.

Two small batches only were examined from the Promenade Pier, one in December, 1927, of 232 mussels, and one in September, 1928, of 108 mussels, a total of 340 mussels. They were of small size : those of the former date were poorly fished, those of the latter date were well fished. A good number had the gills with jagged ventral edges, and three or so had the gills absent, or much reduced in length (dorso-ventrally), for a short distance, with a ridge in the mantle in this region. These have not been considered as abnormalities, as they were most probably due to injury by animals. A single Pinnotheres was found in each batch of mussels.

DISCUSSION.

The abnormalities of the gills of Mytilus, which have been described would appear to be correlated with some factor or combination of factors in the environment, and in the very great majority of cases not to be due to mechanical injury.

Mussels in estuarine, and especially in high estuarine situations, are subject to very fluctuating environmental conditions ; great salinity variations are known to occur, the quantity of detritus carried by the water would vary greatly, and possibly also the mineral constituents of the water and of the silt on the beds, temperature and other factors. Certainly the Fal Estuary mussels would appear to have been, and perhaps are still, subject to the influence of some adverse factor or factors which have upset the physiological processes, resulting in a high percentage of mussels with badly abnormal gills ; but without experimental work it is useless to attempt to attribute the abnormality of these mussels to any one factor. It is curious that mussels from other estuaries (see section, p. 516) were so little affected, and it would appear that conditions in the Fal Estuary differ markedly in some respect.

The various banks in the Fal Estuary* from which mussels were obtained are " mainly muddy, with, in places, top dressings of small shells which vary in amount in different parts " ; but the North Bank and southern part of the Mylor and East Banks, however, have an admixture of calcareous algal gravel, forming " a bottom of medium nature from a slightly muddy gravel, to a slightly gravelly mud " (see Orton, **36**, p. 73).

From the work of Orton (**35**, **36**) on the Fal Estuary oyster beds, it is known that the soil of the beds is rich in certain metals, and some of these

* A chart of the Fal Estuary may be found in **36**, p. 3.

may just possibly have an adverse effect on mussels. The soil on some of the beds, especially the Mylor Bank, contains an appreciable amount of copper (**36**, pp. 67, 70 ; **35**, p. 156), and it is noteworthy that Orton records that there was a distinct variation in the absorption of copper by oysters in March and May, 1921, and November, 1924. He suggests that this difference may mean " either that the copper in the bottom soil on Mylor Bank is becoming covered over, or is to some way losing its power to affect the oysters, or that oysters absorb copper differently at different seasons of the year " (**36**, pp. 67). Oysters apparently " can carry an unbelievable amount of copper in their tissues and still remain healthy in the sense that they are capable of reproduction " (**35**, p. 146). No mussels, however, from the Fal Estuary, or indeed from any other locality, have been noticed with any trace of greenness due to copper absorption, and it is possible that mussels are affected in a different way from oysters by the presence of copper, for Dodgson (**12**, p. 232) apparently found that copper salts had a deleterious effect on mussels, though this was probably in standing water.

Arsenic in somewhat large amounts—arsenic mines occur on the tributaries of the Fal—is also present in the silt on the banks (**35**, pp. 150, 153, 156, 159, 171). Its effect on mussels is unknown, but it may be noted that arsenic, as well as copper, mines were worked at one time also on the River Tamar, below Calstock—though they have been abandoned for some years—and mussels with abnormal gills are exceedingly rare from the beds near Weir Point, at the junction of the Tamar and Tavy.

Zinc occurs in appreciable amounts ; judging by the quantity present in oysters it would appear to be greatest in the locality of Restronguet Creek (**35**, p. 147). Zinc is apparently very toxic to mussels, at least, in standing water, for Dodgson (**12**, p. 140) found that it was impossible to use galvanised wire netting in cleansing experiments because " zinc was deleterious to the mussels, even to the extent of killing them." Under natural conditions, however, the toxicity of zinc to marine animals is probably very slight (see Orton, **35**, p. 147).

In an analysis of samples of soil from beds in the Fal Estuary, 100 to 1600 parts of arsenic, 16 to 240 parts of copper, 21 to 160 parts of zinc, and 20 to 40 parts of tin per million were found simultaneously (see Orton, **35**, p. 159).

The most comprehensive account of the physiology of the mussel is to be found in the section on " The Physiology of the Mussel with special reference to purification " in Dodgson's " Report on Mussel Purification " (**12**). He observed the conditions under which mussels will function normally, and one is impressed with their hardiness and tolerance to widely differing conditions. Their behaviour with regard to much silt in the water (**12**, p. 175), strength of tidal currents (p. 191), variations in

temperature (pp. 194, 198), and in salinity (pp. 208, 209), and lack of oxygen (p. 221) is dealt with in his work. The fact that mussels may exist for as long as 40 days under anærobic conditions, whilst ciliary action may persist for at least 25 days (**12**, p. 221), is especially interesting in view of conditions—such as temporary silting up of mud on the beds, sudden decrease in salinity, etc.—which might exist on the beds causing mussels to remain closed for long periods, with a possible adverse effect on the gills. According to Gray (**21**, p. 79), however, in closed mussels (removed from sea-water) ciliary movement would most probably be inhibited in two or three hours, owing to the concentration of CO_2 in the shell water, and thus the oxygen requirements of the animal would be reduced.

That mussels are tolerant of wide variations in salinity, and may even survive in fresh water, if the dilution of the sea-water be gradual, was shown as long ago as 1816 by Beudant (see Fredericq, **20**, p. 27), but it is well known that heavy mortality may be caused among mussels (**18**, p. 241)—and oysters (**36**, p. 69 ; **8**, p. 17)—in certain situations in estuaries by excessive freshness of the water due to exceptionally heavy rainfall. It is perhaps possible that sudden variations in salinity of an order not sufficient to cause death of the mussel, might yet adversely affect the gills. In spite of the great range of tolerance of the mussel, Flattely and Walton (**19**, p. 81) consider that there is undoubtedly a mean optimum salinity, and it is when exposed to this that the animal is capable of reaching its full development.

The Fal Estuary mussels were on the whole in poor condition, but it is impossible to say whether this was originally the cause or the effect of the abnormal conditions of the gills. As previously mentioned (p. 516), the mussels were badly infested with Polydora and to a less extent with Dodecaceria and Cliona, which in some cases had apparently caused the formation of large blisters in the valves, with general weakening of the mussels ; in some instances the mantle being nothing more than a thin, transparent skin. In this connection it is noteworthy that Daniel (**11**, p. 154) found, in comparing mussels deprived of food with mussels under normal conditions, that they had lost the power to control the water content of the tissue and that " In proportion to the total weight, the loss of water from the tissues of the mussels deprived of food is greater than that which occurs in the control mussels " (**11**, p. 158).

The factor or factors acting on the Fal Estuary mussels have apparently resulted in some cases in a tendency for the gill to collapse, the middle region—the part least supported—folding over longitudinally. Once folding had occurred, fusion of the folded over portion with the surface of the lamella beneath it would appear almost inevitably to follow. In other instances crumpling or puckering had arisen, most probably resulting in the crowding together of the filaments in certain areas, which, when

it became marked, would cause fusion of the filaments. It is curious that in gills which showed numerous areas of fusion it was frequently only one lamella of a gill which was affected, and that most usually the ascending lamella.

As is well known, concrescence is a common phenomenon among the Lamellibranchs, and various authors have given examples of variation—within the same species—in the concresence of gills with the visceral mass, with the mantle and between themselves (see Pelseneer, **38**, pp. 214, 215 ; Odhner, **32**, pp. 45, 48, 50, 53, 55, 60, 64; and Jackson, **25**, p. 326 footnote).

In certain Eulamellibranchs—such as *Cardium edule*, *Chama pellucida*, *Batissa tenebrosa*, *Psammobia vespertina*, *Donax serra*, etc.—where there is folding of the gill, Rice (**41**, p. 77) has described fusion of the gill filaments as a mechanical correlative of the folding of the lamellæ with consequent crowding of the filaments in certain regions ; in this way explaining the presence of a greater number in the upper (dorsal) part of a fold than in the lower (ventral). Ridewood (**43**, p. 159) questioned whether the numerical discrepancy was not due to filamentar branching in the upper parts rather than to fusion in the lower parts of a fold. While perhaps fusion would seem more fully to satisfy the conditions, it is not apparent from Rice's sections through the gill of *Cardium edule* (**41**, Figs. 4–8, p. 79), whether it is fusion or branching. In the case of Mytilus the persistence of the separate chitinous supports, after fusion, would seem clearly to indicate that it is a case of fusion, and not of splitting or branching.

Rice (**41**, p. 78) found that in the Filibranchs—where the gill filaments are only loosely connected by ciliated discs—fusion of gill filaments side by side does not normally occur, even where the folding is extreme, the connexion being sufficiently loose to allow a considerable amount of play. In the light of Rice's findings, the widespread occurrence, among the Fal Estuary mussels, of varying degrees of fusion is of especial interest.

The enlargement of the gill filaments noted in five mussels from Teignmouth and one from North Bank, Fal Estuary, would appear to be due to some factor which has accelerated growth ; the great depth of the cells in some parts is especially suggestive of this. In connexion with the abnormal growth of gill filaments in Mytilus, it is noteworthy that Ridewood (**43**, p. 174) in discussing the variation in extent of the interlamellar extensions of certain Lamellibranchs says, " Like so many features of gill structure this proneness of the filaments to extension in an interlamellar direction is of little, if any, systematic value. It is possibly related to the conditions under which the animal is living, and is the outcome of a permanently altered metabolism of the tissues of the gills. Perhaps it indicates abundant nutrition, or may be ascribable to increased temperature or diminished salinity of the water, or to the depth below the surface

at which the animal lives. Since, however, there is abundant subfilamentar tissue in *Unio pictorum* and *Psammobia pallida*, but little in *Unio ambiguus* and *Psammobia ferroensis*, one hesitates to frame generalisations."

One would imagine that Mytilus would not be prone to indulge in an abnormal growth of gill tissue, for Ridewood (**43**, p. 174) notes that "It is a significant fact that interlamellar junctions having the form of rods occur only in those genera with feeble development of subfilamentar tissue, viz. certain Filibranchia and Submytilacea."

That gill filaments may swell and retain the size after fixation was shown in one case, which is of interest in comparison with the enlarged gill filaments previously described (see p. 509). A Padstow mussel containing a Pinnotheres had shortness (dorso-ventrally) of the gill beneath the crab, and also six or so small groups of enlarged filaments on the face of the gill in this region. This gill was cut out and placed in a finger-bowl of the sea-water in general circulation in the tanks. After three days there was noticeable extension of the ends of some of the filaments along the ventral food groove, as well as swelling of certain of them in a narrow zone along the ventral margin. The cut ends of the filaments, where the gill had been detached from the body, also showed much enlargement. Compared with the swellings seen on the gill when the mussel was first opened, this secondary swelling appeared rather transparent, as though distended with water. The two conspicuous lines of ciliation—the lateral and latero-frontal lines of cilia—were more or less in their normal position in relation to one another, so that it appeared to be chiefly the sides of the filaments that had been blown out. Transverse sections through the swollen filaments are sketched in Fig. 22 (p. 528), and it will be seen that they have a very different appearance from those of Figures 17 (p. 511) and 20 (p. 514). This particular gill, beyond having the filaments somewhat roughly divided in attempting to separate them for examination, was otherwise treated in the same manner as numerous gills which did not undergo swelling. It might be noted that the chitinous supports were poorly developed, and that some few of the filaments were crowded with phagocytes. Later an unsuccessful attempt was made, by pulling filaments somewhat roughly apart, to induce swelling in other gills, when cut out of the mussel and placed in finger-bowls of sea-water. (The salinity of the sea-water in circulation (ca. $36^{\circ}/_{\circ\circ}$–$37^{\circ}/_{\circ\circ}$) is higher than that of normal sea-water (ca. $35^{\circ}/_{\circ\circ}$).)

Drew's (**14**) suggestion, that the intrafilamentar septum (in Pecten) is a brace to keep the filaments from swelling laterally owing to pressure of the blood, and in this way becoming circular and obstructing the flow of water between the filaments (see **10**, p. 44), is especially interesting in view of the swelling of the filaments of this gill. It may be noted that

difference of opinion exists as to the nature of the intrafilamentar septum ; various authors, including Ridewood (**43**, pp. 166, 168), holding it to be composed of chitin, while Kellog (**26**, p. 421) believes it to be endothelium (in *Pecten irradians*). Dakin (**10**, p. 43) found in *P. maximus* that it appeared to stain quite differently from the chitinous skeleton, appearing almost as if it were cellular, while nuclei, which were not adhering blood corpuscles, were seen in it. Setna (**45**, p. 376) states that in Pecten (three species), material fixed in Bouin and stained with Dobell's

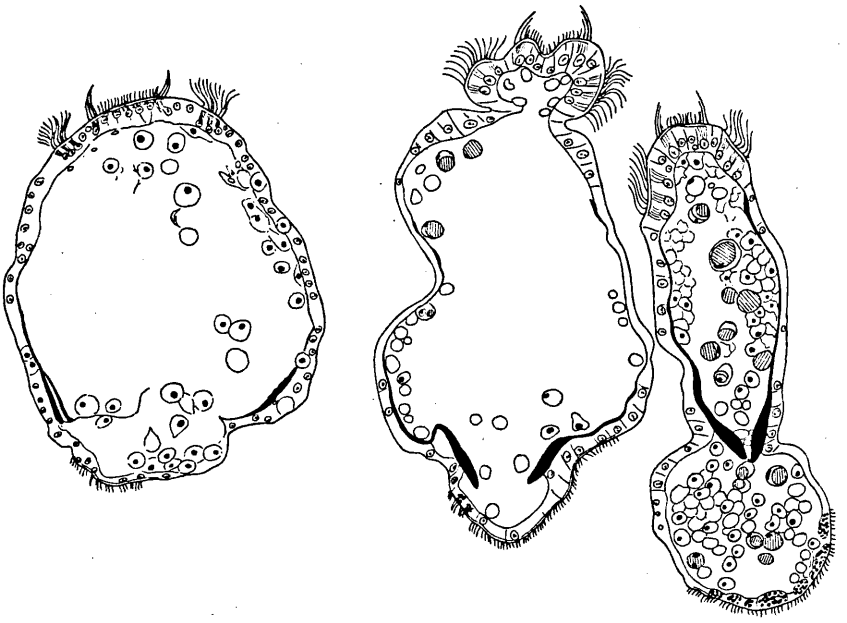

FIG. 22.—Transverse section of filaments from gill which showed increase in size of some of the filaments, after the gill had been cut from the mussel and left three days in a finger bowl of sea-water. The slight development of the chitinous supports and the numerous phagocytes in the filament on the right may be noted. The two filaments on the right are from a different part of the series. Bouin's fixative, Delafield's hæmatoxylin and eosin. × 210.

methyl-blue-eosin, while the chitin stains blue, the endothelial lining, as well as the intrafilamentar septum, stains red. This difference in colour staining between the chitinous supports and the intrafilamentar septum is also seen in *M. edulis* and *Modiolus modiolus* with Mann's methyl-blue-eosin and Mallory's Triple stain, after Bouin and Bouin-Dubosq fixation, but the difference is not so apparent with other stains such as borax carmine followed by picro-nigrosin (used by Ridewood). It is perhaps possible that the intrafilamentar septum may be composed of delicate muscle fibres.

That gill filaments may be increased in size to an alarming extent without rupturing was demonstrated by the active sporocysts of a species of Trematode within the lumen of the filaments of some few mussels from Padstow, causing the temporary enlargement of the filaments as they wormed their way along (Fig. 23). The Trematode possibly spreads

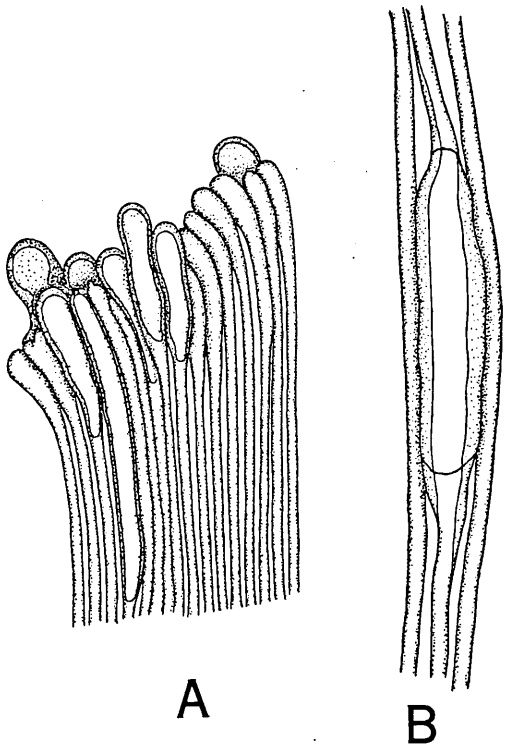

FIG. 23.—Sketches of living gill with sporocysts of a Trematode within the gill filaments. The main ventral food groove in A has an irregular appearance, due to the active sporocysts attempting to push forward. From both A and B it may be seen that the gill filaments recover their normal size after the passing of the Trematode. A, ca. 24⅓; B, ca. 76⅓.

through the mussel by way of the blood vessels ; in some instances they are seen crowded in the pallial vessels, causing them to assume a deep orange colour against the creamy white of the mantle ; the colour of the sporocysts varies, however, from cream to orange in different mussels. In badly infested mussels, the plicate canals (*organes godronnés*) of Sabatier, **44**) are packed with them, as are the mantle and parts of the visceral mass. The dorsal food grooves on the ascending lamellæ are

occasionally crowded with the active sporocysts and cercariæ of this Trematode, but on few occasions have they been seen actually within the gill filaments, though they have at times been noticed pushing their way along the interfilamentar spaces, in which case they may have actually burst through the gill epithelium, or may possibly have been individuals liberated in opening the mussel. When inside the filaments the active sporocysts would seem to tend to work their way towards the ventral free edge of the gill, where they cause extension of the lobes of the main food groove, giving the ventral edge of the gill an irregular appearance (Fig. 23, A, p. 529); and towards the dorsal food groove on the ascending

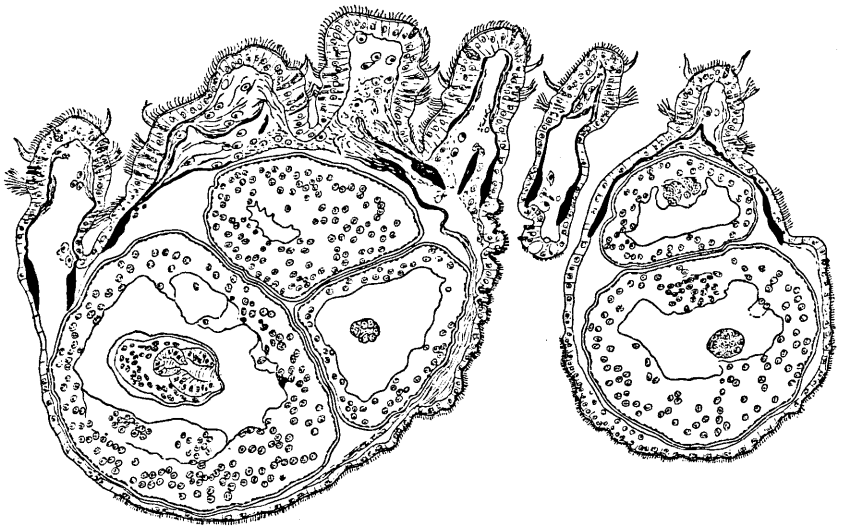

FIG. 24.—Transverse section of part of single lamella of a gill, near the dorsal food groove, showing great enlargement of the interlamellar (abfrontal) ends of the gill filaments owing to the presence of the sporocysts of a Trematode. In the filament on the right, two sporocysts are present side by side: on the left the enlargement of the gill filaments has apparently caused fusion. A cercaria is seen within one of the sporocysts. Bouin's fixative, Delafield hæmatoxylin and eosin. × 140.

lamella. The parasites can be seen to cause such great distension of the filaments that it is surprising they do not burst through the epithelium; it is manifest that the filaments are highly elastic as these resume the normal size after the passage of the parasite. The presence of the sporocysts gives to the filaments containing them an appearance somewhat similar to that described previously (p. 509, and Fig. 15); but the swelling is smooth and also the lines of latero-frontal cilia can be seen running across the swelling (Fig. 23, B), showing that the frontal epithelium experiences no more stretching—possibly less—than the rest of the epithelium. The extreme enlargement of the filaments is strikingly shown

in transverse sections, such as Figure 24, where there are two sporocysts side by side in the same filament. The enlargement of the area of ciliated abfrontal epithelium may be noted. This section also shows that fusion of the filaments may presumably be caused where swollen filaments are forced against each other. One would imagine that fusion from this cause is only likely to occur in areas where the active sporocysts tend to congregate for some time, e.g. near the ventral and dorsal edges of the gills. As mussels infected with the Trematode came from Padstow, where exceedingly little abnormality of the gills occurred among the mussels—apart from those infected with either Pinnotheres or the Trematode—the fusion in this case may be fairly safely attributed to the presence of the Trematode. Figure 25 shows

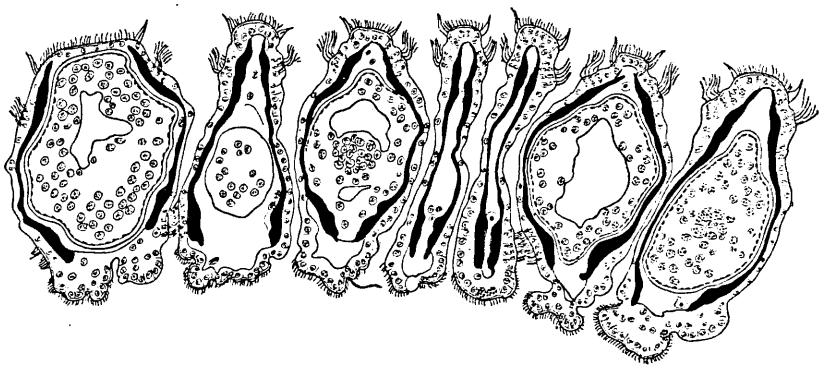

FIG. 25.—Transverse section of part of a single lamella of a gill, to show the crowding of filaments caused by the presence of sporocysts of a Trematode in five out of the seven gill filaments drawn. Bouin's fixative, Mann's methyl-blue-eosin. × ca. 171.

the crowding which resulted when five out of seven filaments, in the same lamella, each contained a small sporocyst.

The various abnormalities described would appear to support Rice's contention that "the lamellibranch gill is an extremely plastic organ, and one very liable to adaptive modification" (**42**, p. 76).

SUMMARY.

In the examination of a total of about twenty-four thousand mussels from various localities in Devon and Cornwall—estuaries of the Fal, Hamoaze, Yealm, Teign and Camel, and the Promenade Pier, Plymouth—it has been observed that those from various parts of the Fal Estuary included a high percentage of specimens with the gills in an abnormal condition, whereas such abnormalities were rare or absent in other

localities. The abnormalities are described from living and preserved material and consisted in the following types :

(*a*) Folding over of the free ventral edge of the gill, with concrescence.

Various stages in the degree of fusion have been observed, from slight fusion at the bend of the fold, to complete fusion of the folded over portion with the lamella beneath. Fusion and degeneration of the two inner arms of the fold, follows folding. The effect is noted of the reduction of gill surface, pumping power, and the disorganisation of the food grooves, consequent on folding, on the general condition of the mussel.

(*b*) Fusion of the gill filaments side by side.

This condition varied greatly in extent, from the fusion of two or more filaments side by side, to extensive areas of fusion scattered irregularly over the greater part of a lamella. Fusion was found to be confined almost entirely to one lamella, generally the ascending, the opposite one being little affected. It is suggested that fusion is due to crowding of the filaments, whatever may be the cause of the latter. The persistence of separate chitinous supports in the fused area, is considered as evidence that fusion has occurred, and not splitting or branching of the filaments.

(*c*) Enlargement of the gill filaments.

This rare form of abnormality was found in five mussels from the Teignmouth Estuary, and in one from the Fal Estuary. The enlargement of the filaments was mostly confined to a narrow zone at the free ventral edge of the gill, and appeared to be due to proliferation of the ciliated frontal epithelium, with a corresponding enlargement of the internal canal. In the mussel from the Fal Estuary the frontal cells of some of the gill filaments were of abnormally great depth : in the case of the gill sectioned from a Teignmouth mussel, great development of the frontal ends of the chitinous supports had occurred. It is suggested that the enlargement of the gill filaments may be due to some factor which has accelerated growth.

(*d*) Concrescence of the two gills of one side.

In two specimens of Mytilus it was noted that on one side, for a short distance in the middle region, one " gill " only was present, formed apparently of two ascending lamellæ and free from the body.

Brief notes are given of the general condition of Mytilus from the various localities investigated. The presence of blisters, in some instances of large size, in the valves of about 7% of the mussels from the Fal Estuary, and of a small number from the Teignmouth Estuary, is noted.

It is suggested that the abnormalities of the gills are correlated with some factor or combination of factors in the environment, information regarding which may be obtainable from further experimental observations.

METHOD OF DIVISION OF THE MANTLE CAVITY IN NORMAL INDIVIDUALS.

It is well known that in certain Lamellibranchs the division of the mantle cavity by the gills into supra- and infra-branchial chambers is not a morphological one, the union of the gills with the mantle, with the visceral mass, and with each other being a ciliary one. (See **39**, p. 228.) The actual method of connexion, however, has been described in but few forms. Herdman (**24**) described and figured it for *Margaritifera vulgaris*, living and well-preserved specimens of which showed apparent continuity of the walls of the supra-branchial chamber, slight pressure being needed for the separation of parts, when the ciliary nature of the junction was revealed. It might be noted that he remarks that in some, if not all, specimens, there was also some slight organic connexion between the two inner gills.

Ridewood described in *Anomia aculeata**—in which descending lamellæ alone are developed—the adhesion of the lower edges of the outer gills with the mantle, and the mutual adhesion of the lower edges of the two inner gills by means of patches of interlocking cilia (**43**, p. 194, and Fig. 8); while similar ciliary junctions have been described by Orton in Nucula (**33**, pp. 462, 463, 468, and Fig. 18) and in *Solenomya togata* (**34**, pp. 39, 41, 42, and Fig. 11), by means of which there is a complete division of the mantle cavity into supra- and infra-branchial chambers.

Dodgson (**12**, p. 171) gives diagrammatic representations of the boundaries of the supra- and infra-branchial chambers in *M. edulis* in three transverse planes.

In living Mytilus the normal ciliary junction between the gills and the mantle, and between the gills and the visceral mass, may be seen in individuals in which the posterior adductor muscle has been cut, if the two valves are separated only sufficiently for the line of junction to be seen. (The animal should be left to recover from shock.) It was found that the junction with the mantle was more likely to occur if the mantle—with the exception of the edge—were separated from the surface of the valve (this may be done by inserting the handle of a scalpel from the anterior end and carefully separating the mantle from the shell), so that it billows out somewhat, in this way compensating, in some degree, for the separation of the valves.

* Now *Heteranomia squamula*, see Winckworth, Proc. Malac. Soc., Vol. xv., pp. 32–4, 1922.

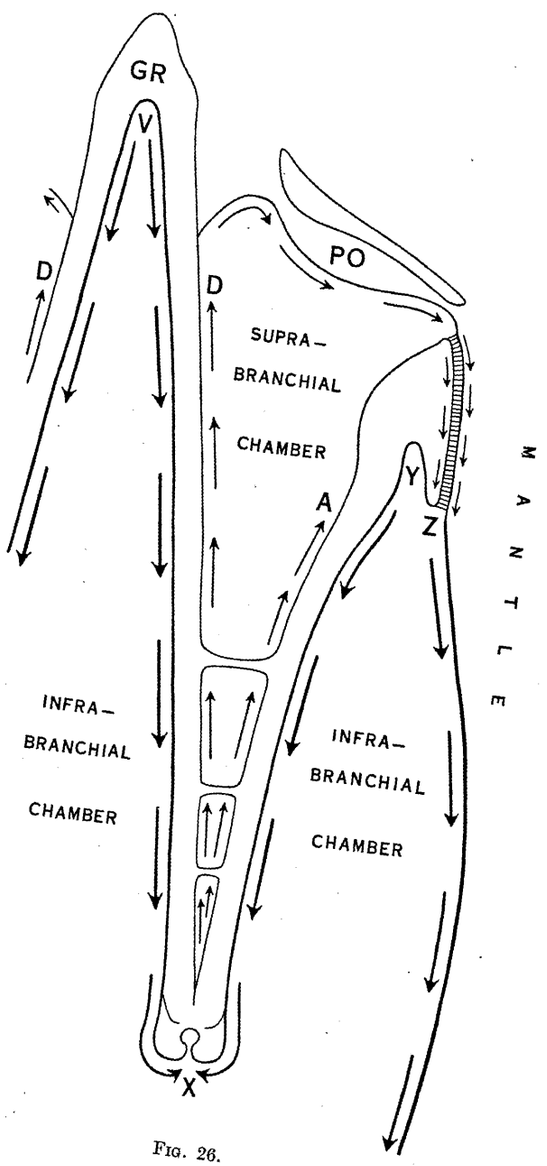
GR
V
D
D
PO
SUPRA–
BRANCHIAL
CHAMBER
A
Y
Z
MANTLE
INFRA–
BRANCHIAL
CHAMBER
INFRA–
BRANCHIAL
CHAMBER
X

FIG. 26.

In two individuals, in which the outer surface of the dorsal food groove of the ascending lamella of both outer gills made almost complete junction with the mantle, it was noted that gentle pressure on the gill caused slight raising of the mantle, which in one instance was very thin. In opened mussels the ciliary junction of gill and visceral mass was only seen for short stretches, owing to the visceral mass being damaged in opening.

The line of ciliary junction of the gill with the mantle in Mytilus is just ventral to the outer ends of the external plicate canals (Fig. 26), and investigation of the surface of the mantle in this region, by means of starch grains stained with iodine, showed that there is a narrow longitudinal zone, roughly about 1·0 mm. wide, over which the movement of particles is extremely slow, to the unaided eye and even with a lens the movement being almost indistinguishable ; particles, however, do move and tend to accumulate at the ventral edge of the zone, which by this means is shown to have a sharply marked ventral boundary. This boundary is usually visible in the living animal, owing to the lesser pigmentation of the zone in comparison with the rest of the mantle. Sections show that normally this region is not a ridge (see Fig. 6, A, p. 497) and may perhaps in specimens with well-developed gonad be slightly sunk. (It was found advisable to fix the mussel in the shell, in this way serious contraction of the mantle being prevented.) As food particles accumulate along the ventral boundary of the zone they get pushed into a narrow anteriorly directed ciliary current which runs just ventral to it (Fig. 26, z), and from which they tend to be drawn into the ventrally directed ciliary currents over

FIG. 26.—*Mytilus edulis*. Diagrammatic representation of one outer division of the supra-branchial chamber, showing the ciliary junction between the outer surface of the dorsal food groove, Y, and the mantle ; and also the currents set up by the cilia on the walls of the chamber. The ciliary currents on the abfrontal surface of the filaments are shown as being directly dorsal, but actually they are somewhat posterior in direction (see Fig. 27). The ciliary currents on the frontal face of the filament and on the mantle are indicated by heavy arrows. The short arrows alongside the junction area, denote currents which occur over the interlocking cilia when the upturned edge of the gill is not adhering to the mantle.

GR, Gill ridge. PO, Plicate organ on roof of supra-branchial chamber.

A and D. Mark the position of posteriorly directed ciliary currents across the abfrontal surface of the ascending and descending lamella respectively, in the region where the ends of the filaments become fused together.

V. Marks the position of the anteriorly directed ciliary current between the bases of contiguous gills. The strength of this current appears to vary in different individuals, which may possibly explain why Kellog (**27**, p. 653) was unable to find it, though it has been observed by Orton (**33**, p. 460).

X. Marks the position of the anteriorly directed ciliary current along the main ventral food groove.

Y. Marks the position of the anteriorly directed ciliary current along the dorsal food groove on the ascending lamella.

Z. Marks the position of the narrow anteriorly directed ciliary current on the mantle. When the dorsal edge of the gill is touching the mantle, Y and Z form one anteriorly directed current.

the mantle region (see Orton, **33**, Fig. 11, p. 459, and Kellog, **27**, Fig. 18, p. 652); this, of course, only occurring when the gill is not adhering to the mantle. It is difficult to observe the appearance of the cilia clothing this tract in the living Mytilus, except in individuals in which the mantle is exceptionally thin, but in *Modiolus modiolus* where the mantle is normally very thin—not being invaded by the gonad in this species—a piece may be cut out and folded, so that the cilia are seen in side view. They closely resemble in appearance those of the ciliated discs on the lateral faces of the gill filaments, with which they agree in their interlocking function. In the living animal, as well as in sections, they have a stiff, regular appearance, as though they do not move far from the vertical during their beat, and can be easily distinguished from those on the mantle dorsal and ventral to them.

The position of the corresponding tracts of interlocking cilia on the visceral mass, may also be demonstrated by the use of starch grains stained with iodine, a longitudinal zone over which particles move extremely slowly, being visible beyond the inner ends of the internal plicate canals.

An examination of the outer face of the dorsal food groove on the ascending lamella of living Mytilus and Modiolus shows that this surface is clothed with cilia of the same appearance as those of the specialised tract on the mantle. A rather slow, somewhat irregular movement of particles occurs over this surface in a dorso-ventral direction, particles being drawn into the anteriorly directed current along the groove (Fig. 26, Y), from which there is a tendency for them eventually to pass on to the frontal face of the gill filaments. This, again, only occurs when the gill is not adhering to the mantle.

Sections show that the ciliated cells of the outer face of the dorsal food groove of the gill, and of the specialised tract on the mantle, have a marked border (see also Herdman, **24**, p. 227), formed by the basal granules.

The slow current over these surfaces may perhaps be sufficient to keep them clean, when the gill is not touching the mantle, and may transfer particles from the supra- to the infra-branchial chamber. When the gill is closely interlocked with the mantle or with the visceral mass, however, it is unlikely that any particles would be able to penetrate the barrier of interlaced cilia.

When the gill is interlocked with the mantle, the anteriorly directed current on the mantle forms, with that along the dorsal groove of the gill (Fig. 26, Z and Y), a single anteriorly directed current. In this condition the current is more clearly defined, and there seems to be less tendency for particles to be drawn from the dorsal groove on to the frontal faces of the filaments, probably because the groove may be more widely open when gill edge and mantle are interlocked. The animal is able to alter the form

of the food groove considerably, and in specimens of Modiolus killed without narcotising, the outer wall of the groove may be reflected, so that the groove is non-existent ; while in Mytilus there is much contraction.

The abfrontal surface of the dorsal groove is abundantly supplied with scattered, very large cilia, and it is possible that they may have a tactile function, giving warning when the ascending lamella falls back on the descending lamella. These large cilia, which may occur singly, or two or three together, beat slowly, passing through 90°, and occasionally less than 90°, though this may be due to abnormal conditions during observation. Similar large cilia are also present among the short cilia on the abfrontal and frontal surfaces of the gill filaments ; and in addition occur among the ciliated cells of the plicate organs, on the surface of the mantle and the body, and on the palps (see also List **29**, p. 110) ; in fact, they probably occur on most external ciliated surfaces. On fixation they separate into their constituent fibres (see also List **29**, p. 110), and in sections, therefore, have the appearance of a tuft of cilia. These large cilia vary considerably in size, as may be seen on examining those on the abfrontal surface of a living gill-filament of Mytilus or Modiolus. In *Modiolus modiolus* they attain a great length, some times reaching 120μ. Gray, in a recent paper (**22**), has analysed the movement of these large cilia on the abfrontal surface of the gill filaments of Mytilus.

Contraction and expansion of the interlamellar junctions, which are first present some short distance ventral to the dorsal groove, along with the muscles of the dorsal groove itself, would most probably be sufficient to pull the gills away from the mantle, from the visceral mass, and from each other, causing temporary separation and approximation such as Dodgson (**12**, p. 170) described between the free dorsal edges of the ascending lamellæ of the inner gills in certain more or less moribund mussels. In this way the supra- and infra-branchial chambers may become continuous. As previously mentioned the dorsal grooves of the gills are provided with muscle-fibres, as seen in sections and shown by the curling up of pieces of dorsal groove cut from the gill.

In animals, which have been opened by cutting the posterior adductor muscle, movement of the gills is observable ; slight in the case of Mytilus (see also Pelseneer in **12**, p. 172), more evident in Modiolus. In the latter, the gills, from a position in which the ventral edges of the two gills of one side are touching, may separate until the angle between the descending lamellæ is 90° or more. Movements of separation and approximation of the gills, may be elicited, at least in Modiolus, by touching the frontal or abfrontal surface of the lamella with a needle. This movement may be compared with the concertina movement of the gills of Pecten, described by Setna (**45**, p. 370), but in Modiolus, while the whole gill is generally involved in the movement, the response is slower and not as certain, and

the movement slower than in Pecten. In Mytilus, the response to the touching of the gills is uncertain and the movement feeble. Such movements of separation and approximation of the gills, however, may also possibly contribute to the application of the dorsal free edges of the gills to the mantle, to the visceral mass, and to each other.

There is little difference in width between the outer surface of the dorsal groove of the gills (about 0·6 to 0·9 mm. wide, varying slightly in different regions and in different individuals) and the longitudinal tract of interlocking cilia on the mantle (about 1·0 mm. wide), so that practically no play of the dorsal free edge of the gill, in a dorso-ventral direction, is allowed for.

Although the junction of the gills with the mantle and the visceral mass in Mytilus and Modiolus would appear to be somewhat easily broken, it is probably of a less temporary nature than in the active Pecten. An opened mussel in which one of the outer gills had made complete junction with the mantle, was kept under observation for three hours, and throughout that time the junction remained unbroken, and was left in that condition when the watching ceased. In fact, observations point to the conclusion that, in mussels which have been opened, once the connection is made it tends to persist while the animal remains healthy, that is up to at least four days. It may be noted that Dodgson (**12**, p. 170) records that in a healthy mussel, under normal conditions, the free edges of the ascending inner lamellæ (in the posterior region) have always been seen to be in close apposition.

During the time the gill is connected with the mantle slight separation and approximation of the descending and ascending lamellæ occur, and, if the mantle has been freed from the shell, these movements may be sufficient to raise the mantle, exceedingly slightly.

In Pecten the temporary nature of the division of the mantle cavity has been observed by Orton (**33**, p. 461), who says "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." It may be noted that preparatory to the clapping of the valves the free posterior ends of the gills swing forward by contraction of the ctenidial muscles (see also **45**) and any connection between the gills and the mantle is broken.

Currents on the walls of the supra-branchial chamber.—In the supra-branchial chamber of Mytilus the main water current is posterior in direction (see Orton, **33**, Fig. 11, p. 459), and most of the surface currents on the walls of the chamber have also a posterior tendency, but have not previously been described.

The plicate canals are found on the roof of the supra-branchial chamber, the width of each division of the chamber being roughly the length of these organs. The external surfaces of the canals are highly ciliated,

rapid currents passing over them, in the main, in a dorso-ventral direction (see Fig. 26). These canals, to which Sabatier gave the name of *organes godronnés* (**44**, p. 56), have a respiratory function.

In Mytilus the cilia on the abfrontal faces of the filaments beat chiefly in a dorsal direction, but actually obliquely across the filaments, so that particles pass across the abfrontal surfaces of the lamellæ in a direction

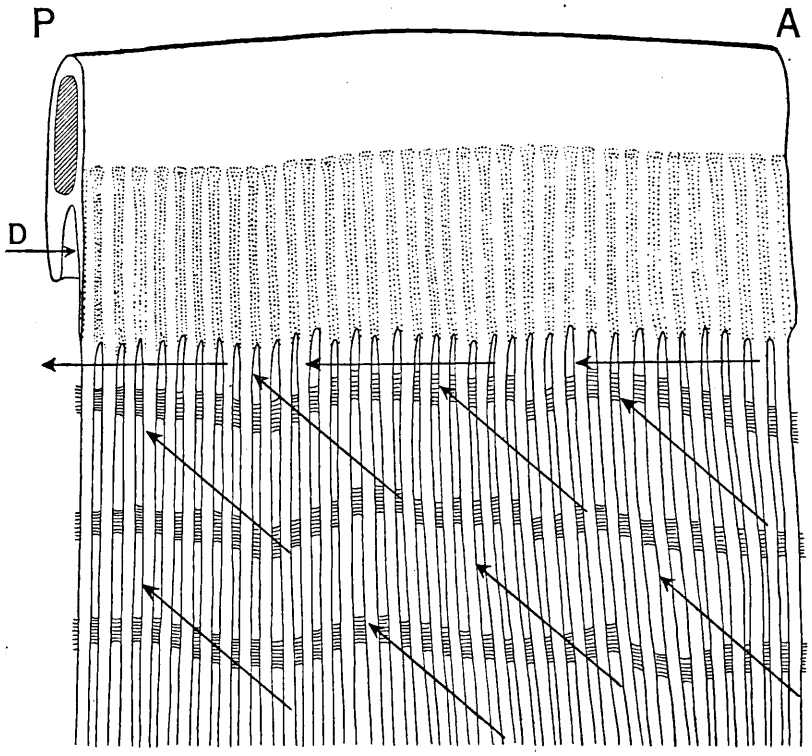

FIG. 27.—Mytilus. View of the abfrontal surface of an ascending lamella in the region of the dorsal food groove, to show the ciliary currents.

A and P. Anterior and posterior.

D. Arrow showing the direction of the current along the dorsal food groove. The narrow stippled areas indicate the chitinous supports in the region where the ends of the filaments are fused together. × ca. 41½.

which is anterior-ventral to posterior-dorsal (Fig. 27). Across the dorsal ends of the gill filaments—in the region where they become fused together—of both descending and ascending lamellæ, the cilia maintain a posteriorly directed current (Figs. 26, D and A; 27). In most of the individuals which were examined the epithelium covering the fused ends of the filaments was either feebly ciliated, or destitute of cilia with the exception of scattered very large cilia (see p. 537), and there

was only occasional slight movement dorsalwards of particles jerked forward by the latter: in such individuals the posterior ciliary current across the base of the filaments was very clear. Very rarely individuals were seen in which the abfrontal cilia were continued on to the epithelium covering the fused ends of the filaments; there was in consequence a ciliary current across this surface, in a postero-dorsal direction, and the purely posteriorly directed ciliary current was not then as clear.

In the few specimens of *Modiolus modiolus* examined, the abfrontal cilia of the gill filaments were very poorly developed or absent, except for large scattered cilia, and the ciliary currents on the abfrontal surfaces of the lamellæ were therefore weak or absent.

The greater part of the material for the work recorded in this paper was obtained during the tenure of a research studentship of Bedford College, University of London. I wish again to express my gratitude to the Director and Council of the Marine Biological Association for allowing me to work at their Laboratory at Plymouth, and to the London University for granting me the use of their table. For the composite photograph of Figure 21 I am indebted to Mr. A. J. Smith. My sincere thanks are due to Prof. J. H. Orton for reading the manuscript, and for helpful criticism and advice.

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Note on Some Abnormalities of Labial Palps and Foot of *Mytilus edulis.*

By

D. Atkins, B.Sc.

With 7 Figures in the Text.

In view of Pelseneer's work on "Les Variations et leur Hérédité chez les Mollusques,"* it seems worth while to record briefly certain observed abnormalities of the labial palps and the foot of *Mytilus edulis*. Among some thousands of specimens examined, however, such conditions were rare, and it is probable that at least some of them arose through injury.

Labial Palps.

The abnormality of the palps most generally met with is evidently the result of natural regeneration, following injury to the tips of the palps. From the injured surface tiny outgrowths arise, usually three in number, two of which appear to have a common base. Figures 1, A–C, shew different degrees of regeneration; two examples have been seen in approximately similar conditions. (The normal tip of the palp may be seen at P in Figure 2.)

Pelseneer (p. 181) records the finding by Sykes of a specimen of *Tellina incarnata* in which the palps were missing, but gives no further examples of variation in palps. However, his Figure 121 (p. 204) of a gill of *Boreochiton marginatus* with trifurcated tip shows a similar state of affairs to that recorded in this note for the palps of *M. edulis*.

Bifurcation of the tip of the palp has been observed in one or two instances.

The right inner palp of a Mytilus from Padstow showed two small accessory palps near the base (Figure 2); these had a common base, only the tips, which pointed in opposite directions, being free. In preservation the tips have become curled, and that of the more proximal secondary palp is hidden beneath that of the more distal one. A second example of this type of accessory palps was noted on the right inner palp of another Mytilus from the same locality, but in this instance they originated about

* P. Pelseneer, Les Variations et leur Hérédité chez les Mollusques. Acad. Roy. Bel. Mém., 2nd sér., Tome V, 1920.

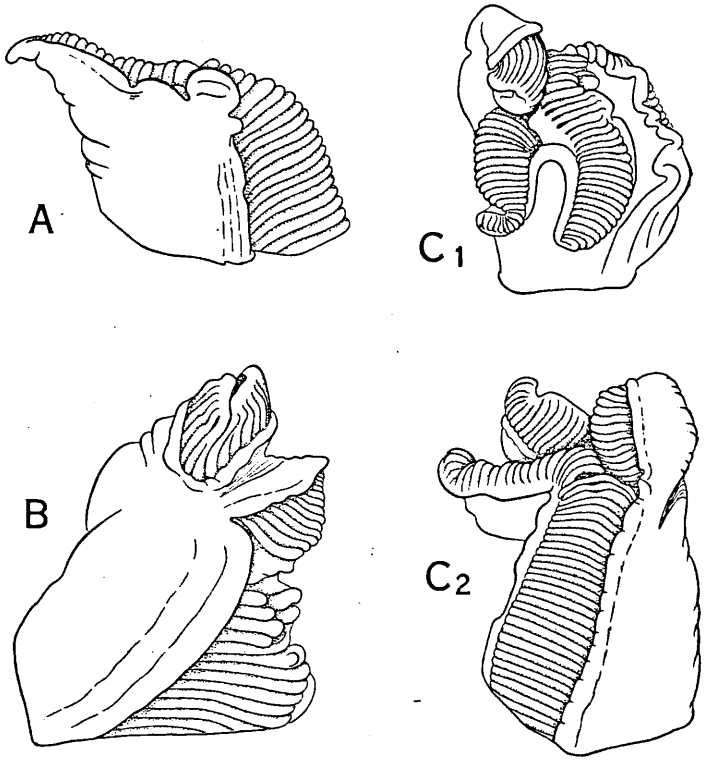

FIG. 1, A–C.—*Mytilus edulis*. Sketches showing stages in the formation of outgrowths from the tips of three palps, A, being the youngest and C, the oldest stage. In C1, the trifurcated tip of the palp has become folded back on to the smooth outer surface during fixation; in C2, it has been forcibly flattened out. × ca. 6¼.

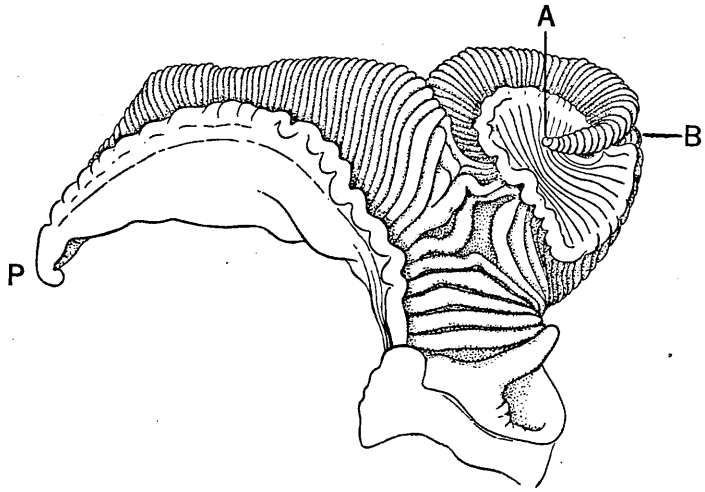

FIG. 2.—*M. edulis*. Sketch of palp with two accessory palps near the base. These have a common base, the tips only being free: that of the more proximal one, B, is hidden beneath the other, A. P, tip of principal palp. × ca. 6¼.

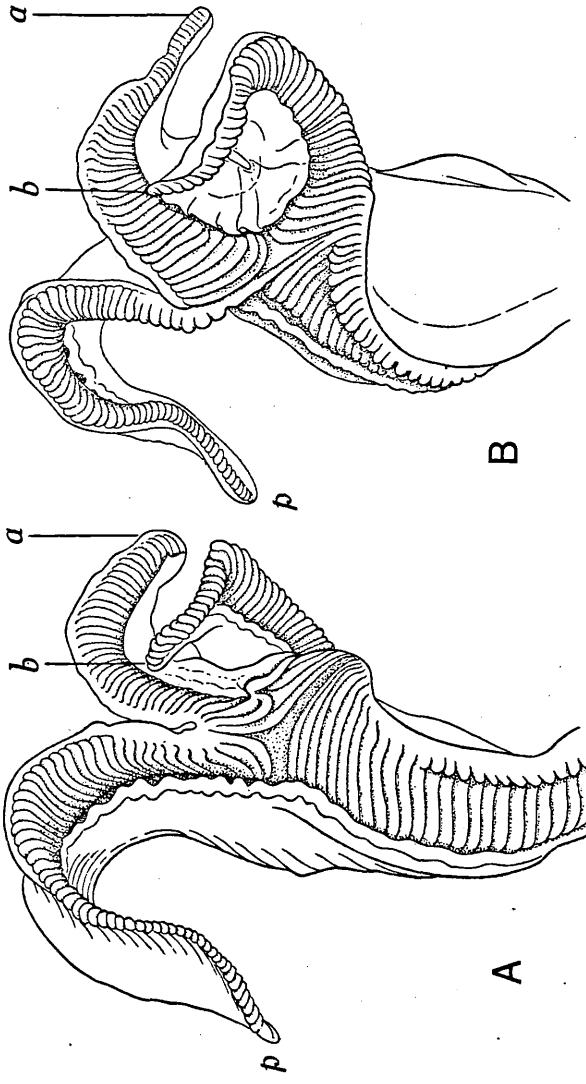

FIG. 3.—*M. edulis*. Different views (A and B) of two accessory palps, *a* and *b*, originating from about midway along the length of the principal palp. *p*, tip of principal palp. × ca. 6¼.

midway along the length of the principal palp, and were more highly developed (Figure 3).

A tiny accessory palp originating from near the base of a left inner palp,

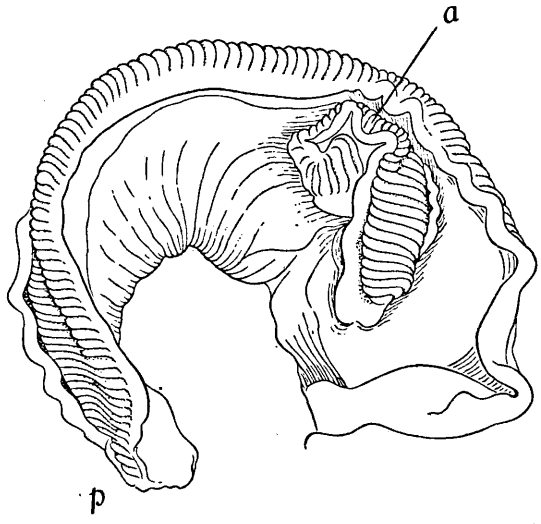

FIG. 4.—*M. edulis*. Palp with a small accessory palp, *a*, near the base on the smooth outer surface. *p*, tip of principal palp. × ca. 6¼.

on its smooth outer surface, is shown in Figure 4. In this instance the difference in size of the principal and secondary palp is marked.

FOOT.

Several different types of foot abnormality have been noted in *M. edulis*. That most generally met with was a small foot-like outgrowth, or rudimentary accessory foot, originating from near the base of the primary foot, the latter showing no injury to its tip. The outgrowth was lateral, but somewhat dorsal in position (see Figure 5), and in three cases was on the right side and in one on the left. The outgrowths varied somewhat in size; that sketched in Figure 5 being the largest seen. These foot-like outgrowths were pigmented a dark brown like the primary foot, but were without a ventral groove or anterior sucker. A single case was noted of a similar tiny outgrowth about midway along the length of the foot and distinctly on the lateral (right) edge. Pelseneer figures (Figure 94 *bis*, p. 133) a somewhat similar outgrowth on the right side of the foot of *Cyclas cornea*, which, however, was spheroidal.

An interesting case of foot abnormality was that sketched in Figure 6, where the accessory foot was ventral in position though slightly lateral, and the ventral groove of the main foot divided, the secondary foot in this instance being provided with a ventral groove.

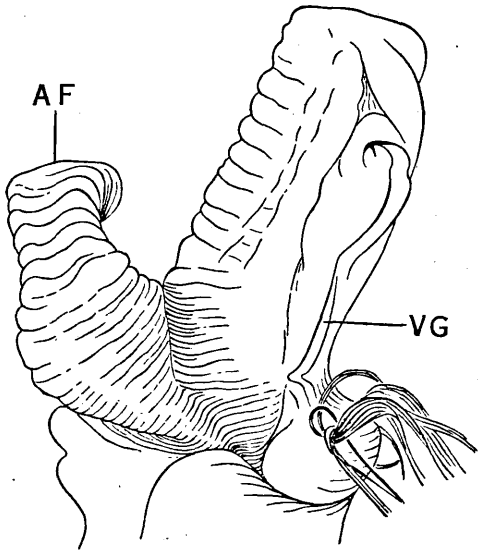

FIG. 5.—*M. edulis*. Foot with a small foot, AF, originating from near the base. VG, ventral groove of primary foot. × ca. 6¼.

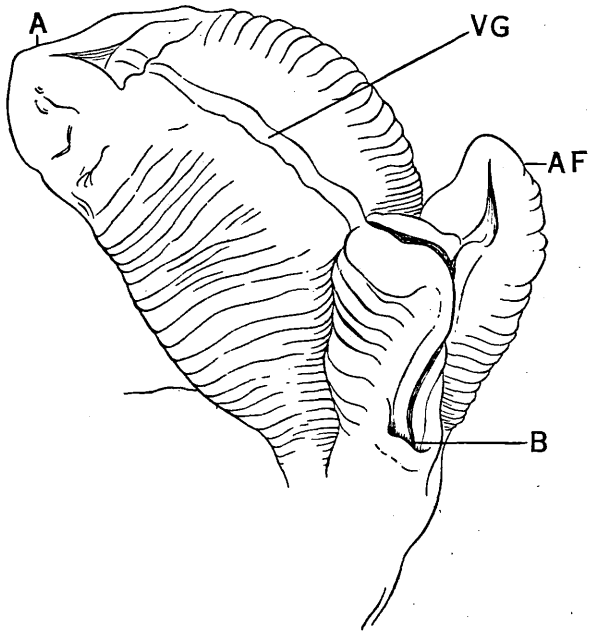

FIG. 6.—*M. edulis*. Foot with an accessory foot, AF, which is ventral in position and is provided with a ventral groove. A, tip, and VG, ventral groove of primary foot; B, byssus pit. × ca. 6¼.

One Mytilus was noted in which the tip of the foot was missing, the foot being obviously injured and discoloured (Figure 7). There was a slight irregular outgrowth from the main foot anteriorly, but what is of especial interest was the presence of tiny foot-like protuberances, one on either side of, and seated on the anterior retractor muscles, that on the left being slightly more anterior in position than that on the right. These

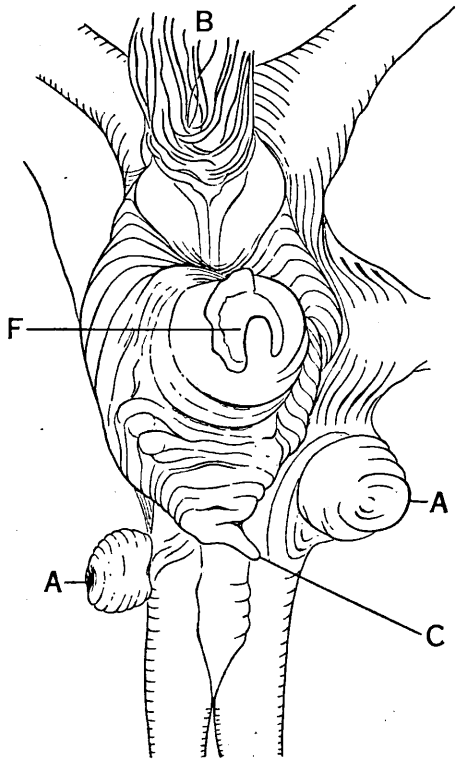

FIG. 7.—Sketch of foot of *M. edulis*, showing the tip missing as a result of injury, and two small foot-like outgrowths, A, A, one on either side of the anterior retractor muscles. F, injured tip of primary foot; C, small outgrowth from primary foot; B, byssus. × ca. 6¼.

were pigmented, but appeared to have no ventral groove. The figure shows them in a much contracted condition. As the foot is protruded from the shell in travelling, and during the spinning of the byssus, it is liable to suffer injury (see also Pelseneer, p. 133), as has evidently occurred in this specimen, but it is doubtful whether the foot-like outgrowths from near the base of the foot are due to this cause.

The position of the foot has been noticed to vary somewhat, in one instance being very anteriorly placed.

9

Note on the Regeneration of the Gill of *Mytilus edulis*.

By

D. Atkins, B.Sc.

With 8 Figures in the Text.

Reprinted from the Journal of the Marine Biological Association of the United Kingdom.
Vol. xvii. No. 2. June, 1931.

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D. Atkins, B.Sc.

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Introduction.

In connexion with work on reversal of the frontal cilia on the gill filaments of *Mytilus edulis* (**1**), it became desirable to know whether the gills were capable of regeneration after injury. With the exception of the peculiar method of growth or regeneration of the incubatory gills in Cyclas, briefly described by Poyarkoff (**11**), which, even if his preliminary observations are confirmed, would hardly appear to be true regeneration,* the only reference that can be found on the subject of regeneration of the gills in Lamellibranchs is that in the paper by Bloomer (**3**) on malformed specimens of *Anodonta cygnea*, where the condition was apparently due to injury: he concluded "that the animal is able to repair even extensive damage to the mantle-lobes, but is not able to make good injuries to the gills" (**3**, p. 138).

As *M. edulis* is not infrequently found having the gills with very jagged ventral edges, and a few specimens even with the gills more or less entirely missing for a short length—in some instances almost certainly attributable to injury by boring whelk-tingles—it was thought that regeneration of gill filaments possibly might not occur in Mytilus. A single specimen experimented on in June, 1929, showed no signs, after 112 days, of regenerating the wedge-shaped pieces cut from the gills, beyond the formation of a food groove at the cut ends (see **1**, p. 960). From further experiments, however, it is evident that regeneration of the gills of *M. edulis* may occur.

EXPERIMENTS.

Mussels with strong shells (ca. 7·0–8·0 cm. long) were chosen for the experiments, so that the shells would not be likely to fracture easily on being forced open. The ease or difficulty with which the valves could be

* "La formation des sacs d'incubation doit gêner considérablement le développement normal du feuillet réfléchi de la lame branchiale interne. En revanche ce feuillet s'accroît d'une façon si singulière que je qualifierai ce cas de régénération de ce feuillet bien que sans doute l'animal n'en perde en réalité aucune portion" (**11**, p. cxxxvi).

forced apart was taken as an indication of the condition of the mussel; those of which the valves could be easily forced apart were rejected.

The shell was first opened slightly with an oyster opener; the pointed and thin side of a wooden wedge inserted; worked further in and slowly twisted, until the mussel was forced open to the greatest width of the wedge (about 1·0 to 1·5 cm.). It was done gradually so as to strain the muscles as little as possible. In spite of care the shell fractured badly in some few instances, and the mussels had to be discarded.

The injuries were made near the posterior end of the gills,* owing to the difficulty of reaching any other part. So far as could be seen, the gills of all the mussels used were normal.

The experimental mussels were placed separately in finger bowls, and the bowls sunk in one of the glass-fronted tanks in the general circulation in the Plymouth Laboratory, the tank used being in the shade.† An average of two to four litres of tow nettings a day were tipped into the tank.

Temperature readings of the water in the experimental tank were not taken, but the highest and lowest morning readings (taken at about 9.30 a.m.) for each month, of water temperatures of a similar tank, three tanks away and on the same side of the building, are as follows:

	Max. °C.	Min. °C.
Dec., 1929	12·1	10·8
Jan., 1930	10·8	9·4
Feb.	9·7	7·1
March	10·3	8·4
April	11·9	9·7
May	13·2	10·7
June	15·4	13·2
July	16·4	14·9
Aug.	16·8	15·0
Sept.	17·2	14·1
Oct. 1–17	15·1	12·6

(These figures have been abstracted from the temperature readings taken daily by Mr. A. J. Smith.)

The experiments were started on November 29th and December 1st, 1929, and in February, two out of the ten experimental mussels were found to have died. Five individuals (A, C, D, F, K in Table I) were opened on July 30th, 1930; of the remaining three, one (E) was found gaping on September 15th, the two survivors (B and J) were opened on October 17th, 1930.

Notes on the experimental mussels are given in Table I.

* For convenience in description the two demibranchs on each side of the body are considered as two gills.

† Coulthard (**6, p. 136**) finds that "Mussels display maximum growth in approximately 50% sunlight, slightly less in darkness, and least in full sunlight."

TABLE I.

EXPERIMENTS ON REGENERATION IN THE GILL OF *MYTILUS EDULIS*.

(All experiments were begun on either Nov. 29th or Dec. 1st, 1929.)

Mussel.	Date of opening in 1930.	Condition on date of opening.	Nature of injury inflicted.	Result.
A.	July 30	A good deal of byssus formed; strongly attached. Mussel rather thin. Gills markedly pigmented.	(*a*) Right inner gill.—Wedge-shaped piece cut out of ventral edge in such a way as to leave some filaments unattached except by ciliated discs.	(*a*) Regeneration both of food groove and filaments occurred (see Fig. 1).
			(*b*) Left inner gill.—Two slanting cuts with scissors from ventral edge of gill in a dorsal and anterior direction, so as to isolate two pieces of gill except for attachment by ciliated discs.	(*b*) Pieces sloughed off: regeneration of food groove and of filaments followed (see Fig. 3).
			(*c*) Left outer gill.—Operation as for left inner gill.	(*c*) Pieces sloughed off: regeneration of food groove and of filaments followed (see Fig. 2).
B.	Oct. 17	Rather poorly fished, but valves fairly stiff to force apart. Gills only slightly pigmented.	(*a*) Right outer gill.—Injured by pulling some of the filaments with forceps.	(*a*) Regeneration of food groove occurred. Injury showed as two long inlets in gill, with some slight abnormality of filaments.
			(*b*) Right inner gill.—Shallow piece cut out of ventral edge.	(*b*) Regeneration of food groove occurred, also some very slight regeneration, with apparent fusion, of filaments.
			(*c*) Left inner gill.—A slanting cut with scissors from ventral edge in a dorsal and anterior direction, so as to isolate a piece of gill except for attachment by ciliated disc.	(*c*) Most of piece sloughed off. Little, if any, regeneration beyond formation of new food groove. At deep end of cut some irregular joining up of cut ends of filaments. Five or so short lengths of filaments separated dorsally from gill by a tiny space, but attached anteriorly and posteriorly.
			(*d*) Left outer gill.—Piece cut out of ventral edge.	(*d*) Regeneration of food groove occurred, also some slight regeneration, with apparent fusion, of filaments (see Fig. 5).

TABLE I—(*continued*).

Mussel.	Date of opening in 1930.	Condition on date of opening.	Nature of injury inflicted.	Result.
C.	July 30	Much byssus formed; strongly attached. Fairly well fished. Gills very slightly pigmented, with practically no intensity of pigment along ventral edges.	All four gills cut obliquely with scalpel, the cuts not reaching the ventral edge. In some cases the gill was supported by the blade of an oyster opener (see p. 557).	No injury apparent when gills examined with microscope. Regeneration of epithelium occurred, and in cases where filaments had been cut through, fusion of cut ends had also taken place.
D.	July 30	Much byssus formed; strongly attached. Mussel in good condition.	As for C.	As for C.
E.	Sept. 15	Valves gaping. Mussel thin.	As for C.	No injury apparent when gills examined with microscope; but a small piece missing from the ventral edge of left inner gill; one of the cuts may have been too near the edge of gill. Regeneration of epithelium had occurred, and in cases where filaments had been cut through, fusion of cut ends had also taken place.
F.	July 30	Much byssus formed; strongly attached. Mussel in good condition. Spawned as female, after being opened and put in finger bowl under circulation.	All four gills cut obliquely with scalpel, the cuts not reaching the ventral edge. In all instances the gill was supported by the blade of an oyster opener (see p. 557).	No injury apparent when gills examined with microscope. Regeneration of epithelium had occurred, and in cases where filaments had been cut through, fusion of cut ends had also taken place.
G.	Feb. 20	Found dead.		
H.		Found dead.		

J.	Oct. 17	Poorly fished, valves easily forced apart. Gills very slightly pigmented.	(*a*) Right inner gill.—A slanting cut with scissors from ventral edge in a dorsal and anterior direction, so as to isolate a piece of gill except for attachment by ciliated discs.	(*a*) Piece sloughed off. Cut made at extreme posterior end of gill, very close to dorsal food groove; as all interlamellar junctions removed, the lamellæ separated, and the cut ventral ends of each have rounded off independently, with irregular edges and *without* formation of food groove.
			(*b*) Right outer gill.—Cut obliquely with scalpel in several places, cuts not reaching the ventral edge. Gill not supported (see p. 557).	(*b*) No sign of injury when gills examined with microscope. Regeneration of epithelium had occurred.
			(*c*) Left inner gill.—As for right outer gill (*b*), but gill supported by blade of oyster opener (see p. 557).	(*c*) No sign of injury when gills examined with microscope. Regeneration of epithelium had occurred, and in cases where filaments had been cut through, fusion of cut ends had also taken place.
			(*d*) Left outer gill.—Large piece cut out of ventral edge.	(*d*) Regeneration of food groove occurred, also some slight regeneration, with apparent fusion, of filaments.
K.	July 30	Valves gaping somewhat; would not close when touched. Mussel in poor condition. Gills rather slightly pigmented, but with a darkly pigmented (brown) ventral edge.	(*a*) Right outer gill.—Large piece cut out of ventral edge.	(*a*) Regeneration of food groove occurred, but no appreciable regeneration of filaments. New food groove was very noticeable as it was almost unpigmented, while that on old part of gill was very darkly pigmented. The gap was somewhat smaller than the piece removed, owing to the inward bending of the filaments at either end.
			(*b*) Right inner gill.—Piece cut out of ventral edge.	(*b*) As for right outer gill.
			(*c*) Left inner gill.—Piece cut out of ventral edge.	(*c*) As for right outer gill.

REGENERATION.

Regeneration of the gill of Mytilus consists of the formation of (*a*) food groove and (*b*) gill filaments. These may be considered separately, as the former may occur without any appreciable regeneration in length of the gill filaments.

(*a*) Food Grove.

A food groove was formed at the cut edge of the gill in all cases, with but one exception, and is apparently always formed, if the cut edges of the filaments of the descending lamella are able to touch and so to fuse with those of the ascending lamella. In the exceptional case (see J, Table I), the cut ends of the descending and ascending filaments had not fused together, but had rounded off independently, the two lamellæ being unconnected in the region of the injury. The ventral edges of the lamellæ were irregular, the filaments having irregularly swollen ends, and no food groove had been formed. There was some fusion of the filaments side by side, towards the ventral edge, and they appeared to be in a somewhat degenerating condition. The cut in this instance was made at the extreme posterior end of the gill where the filaments are either without interlamellar junctions, or there is only one to a filament; such junctions as existed were evidently in the piece of gill which sloughed off following the cut, and there was therefore nothing to prevent the remaining parts of the lamellæ from separating; the non-fusion of their cut ends was apparently due to this cause.

Mussels, which have been found with the ventral edges of the gills in a jagged condition, have been noticed to have continuous, though irregular, ventral food grooves, and offer additional evidence that a groove is practically always formed at the cut edge. An example of regeneration of a food groove following natural injury is sketched in Figure 18, B, of a previous paper on abnormal gills in this journal (**2**, p. 512).

It was found that two secondary folds bearing food grooves were present on the descending lamella of the left outer gill of the experimental Mussel A, as shown in Figure 2: some slight abnormality of the filaments occurred in corresponding positions on the ascending lamella. It is perhaps probable that the injuries done to the gill are accountable for these, though there appeared to be no difference in pigmentation between the secondary folds and the old part of the gill. It will be seen that the secondary groove near the ventral edge of the gill, runs from the main food groove in an anterior and dorsal direction, so that the current along its food groove diverges from that of the main groove instead of joining it, as is more usual in secondary grooves on gills (see **1**). On most of the filaments composing the larger secondary

groove there was no reversal of beat of the frontal cilia, but on a very few it occurred for a short stretch near the secondary groove. There appeared to be no change in direction of the ciliary current on the filaments composing the smaller, and more dorsal secondary groove, but the filaments were not examined singly.

Gills (see C, D, E, F and J, Table I) which had been cut with a scalpel obliquely across the filaments—care being taken not to reach the ventral edge of the gill—in some cases the gill being unsupported, and in others supported by the blade of an oyster opener inserted behind the gill, curiously showed not the slightest sign of injury when examined under the microscope at the end of the experiments. The doubt arose, considering the difficulty of working with mussels with the valves only slightly separated, whether any cut had actually been made. Investigation with an opened mussel showed that if the gill was unsupported the frontal epithelium alone was cut, the chitinous skeleton being sufficiently resistant to prevent cutting of the entire filament. Following the cut, the epithelium peeled off away from it, leaving the chitinous skeleton exposed for a stretch of about 1·0 mm. When the gill was supported by the blade of an oyster opener the result varied. In some instances both lamellæ were cut through; in others only one lamella, though the epithelium of the opposite one was injured; while in others, though the epithelium of both lamellæ was injured, few if any filaments were actually cut through. In all cases the epithelium peeled off for a short distance on either side of the cut or injury. Thus, beyond the cutting of the frontal epithelium, the extent of the injury inflicted with a scalpel is not exactly determinable. However, in the case of the experimental mussels, it is most probable that at least in some instances the filaments were cut through, and there can be no doubt that then the cut ends fused cleanly; where the epithelium alone was cut or injured with consequent peeling off for a short distance, it had regenerated.

This part of the experiment was done in an unsuccessful attempt to cause the formation of secondary food grooves; possibly a tear rather than a clean cut might be more efficacious, but pulling a bent mounted needle, which had been ground to a cutting surface, across the surface of the gill, as was done previously with several mussels, also produced no result. By the latter method the filaments seem to be pulled apart and injured, but not broken.

(*b*) Gill Filaments.

Regeneration of the gill filaments did not invariably occur; in only one (see A, Table I) out of four surviving experimental mussels, was regeneration unmistakable and of some amount (Figs. 1, 2 and 3). In one area on each of the two left gills of this mussel (Figs. 2 and 3) the piece regenerated

was as great or slightly greater in amount than that lost; the maximum length of filament regenerated, 7·3 mm., occurred in a deep narrow area on the left inner gill (Fig. 3), where, however, regeneration was not complete. The rate of regeneration in these gills would appear to have been rather greater than on the right inner gill of the same mussel (Fig. 1), where the greatest length of filament removed was about 5·4 mm., while the greatest length regenerated was about 3·2 mm.; it may be that the shape of the piece severed from the gill has some bearing on this, a narrow deep gap being more rapidly filled in than a broad shallow one.

In two mussels (B and J, Table I) some slight amount of regeneration appeared to have taken place, but it was difficult to distinguish, as owing to the very pale tint of the gills there was no appreciable difference in

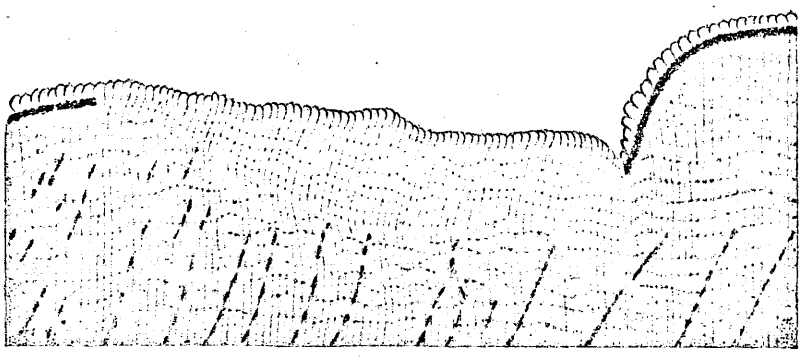

FIG. 1.—Mussel A. Regenerated area on right inner gill; ascending lamella sketched. An attempt has been made to indicate the difference in degree of pigmentation of the old and new parts. The dark line underlying the food groove in the original part of the gill, represents the line of orange or brown pigment normally found in this position; the dark oblique lines represent interlamellar junctions; the dotted wavy horizontal lines, ciliated discs. It will be noticed that a few filaments bordering on the injured area anteriorly, that is at the deepest part of the cut, appear either to have not shared in the growth of the gill, or become reduced in length. (Anterior is on the right.) × ca. $6\frac{1}{4}$.

degree of pigmentation of the old and new regions. It was judged to have occurred partly on a comparison of the size of the pieces removed with the size of the gaps left in the gills at the end of the experiment, and partly on a consideration of the form of the filaments.

At the junction of the old and new part of the gill there is generally a slight bend in the filaments (Fig. 4). In some cases (see Fig. 5) there may be lateral fusion of the cut ends of some of the filaments so that two or three will grow forward as one, and as a result there are fewer in the new part than in the old. The ventral continuation of fused filaments is shown by sections to be single in structure as well as in appearance (Fig. 6, p. 562), as might be expected if this part were due to new growth; if it were due to fusion side by side of existing filaments this would in all probability be

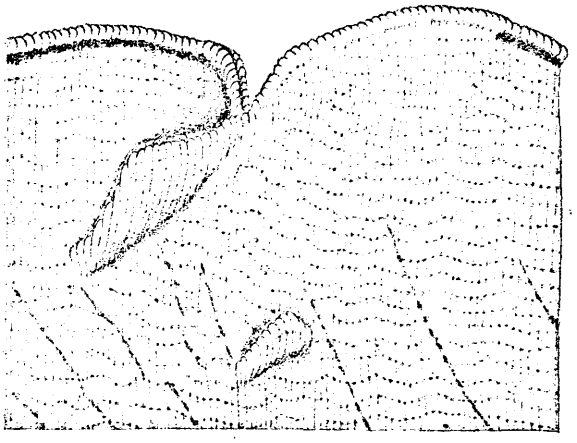

FIG. 2.—Mussel A. Regenerated areas on left outer gill; descending lamella sketched. Two secondary folds with food grooves are shown. (Anterior is on the left.) × ca. 6¼.

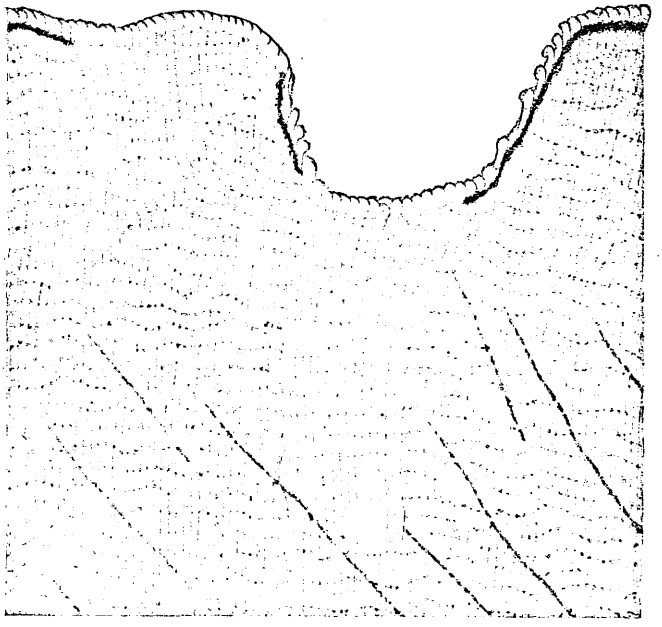

FIG. 3.—Mussel A. Regenerated areas on left inner gill; ascending lamella sketched. (Anterior is on the left.) × ca. 6¼.

apparent in duplication of the chitinous supports in the fused part (see **2**, p. 507). This lateral fusion of the cut ends of certain of the filaments, with forward growth as a single filament, resulted in an irregular number in the descending and ascending lamellæ, and as a consequence, along the ventral edge of the gill instances occurred of the fusion of the ventral ends of two filaments in one lamella, with the ventral end of one in the opposite lamella.

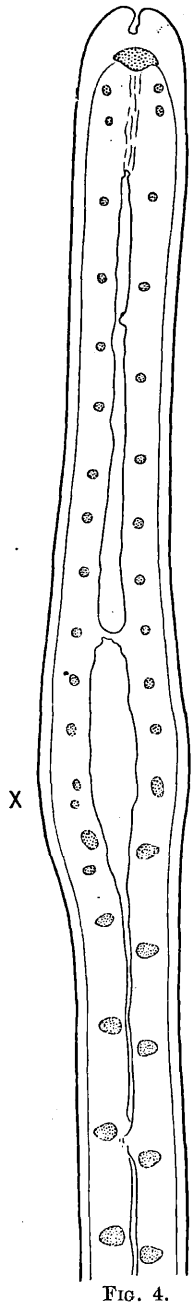

FIG. 4.

But the ease with which slight regeneration can be detected depends largely on the depth of pigmentation of the original part of the gill. The characteristic appearance of the normal gill—when looked at as a whole—with (*a*) the line of orange or brown pigment beneath the main ventral food groove; (*b*) the more opaque, sometimes darker, wavy lines running longitudinally across the surface of the lamella, due to the presence of ciliated discs; and (*c*) the more opaque, and sometimes darker, oblique lines, due to the presence of interlamellar junctions, is shown in the old part of the gill in the sketches in Figures 1, 2 and 3. These three sets of markings on the gill are more clearly visible in some gills than in others, depending largely on the variation in general depth of pigmentation of the gills, which occurs in different individuals. In two mussels (B and J, in Table I) the gills were so pale in tint that even the regenerated food groove showed up very faintly, though under the microscope the difference in pigmentation could be fairly easily seen. In one mussel (A, in Table I), in which an appreciable amount of regeneration had occurred, the regenerated areas were obvious at a glance owing to the difference in intensity of pigmentation between them and the old part of the gill (Figs. 1, 2 and 3). The newly formed parts were practically unpigmented, and the dark line of pigment normally present

FIG. 4.—Side view of filament from a region of regeneration. The junction (at ×) between the old and new parts of the filament is marked by a slight bend: the difference in the size of the ciliated discs in the two regions is noticeable, those in the new part being considerably smaller than those in the old part. One interlamellar junction is present in the new region and also the beginning of a second. Bouin's fixative. × ca. 35½.

running parallel with the free ventral edge of the gill was lacking; the pigment granules seen under the microscope in this position being too few to give any appearance of colour. In the case of the right-inner gill of mussel A (Fig. 1) the oblique dark lines on the old part of the gill, due to the presence of interlamellar junctions, were seen to stop abruptly when reaching the regenerated portion. Under low powers of the microscope, or with a lens, the dark wavy lines caused by the presence of the ciliated discs on the filaments were also seen apparently to stop, or alter in character, against the new tissue in all cases of regeneration of the gills of this mussel (Figs. 1, 2 and 3): in the regenerated region

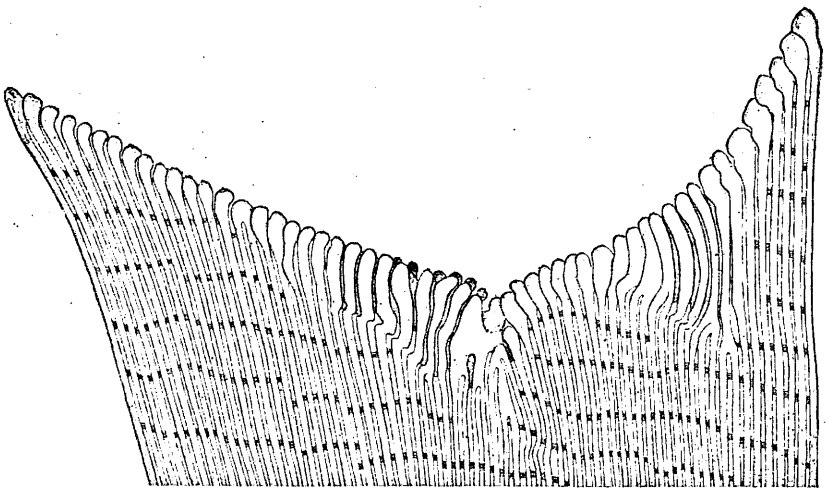

FIG. 5.—Mussel B. Left outer gill, ascending lamella. A small region at the depth of the gap has been sketched, to show the tiny irregular area of regeneration, and the apparent fusion of some of the filaments. In this instance there was no appreciable difference in colour between the old and new parts. (Anterior is on the right.) × ca. 18¼.

these lines, though present, were faint, and difficult to follow. The cause of the difference in intensity of the lines was apparent on examining single gill filaments in side view; in the regenerated part of the gill filament the ciliated discs were on an average about half the size of those in the original part of the filament (see Fig. 4), and were practically destitute of pigment granules. In those instances examined, they also differed in shape, being more or less circular, while those in the old part were somewhat triangular. Single filaments stripped from one part of a gill (preserved in formalin) where regeneration had occurred, showed the mucus cells, which were plentiful on the abfrontal face in the old part, to be absent, or not visible in a total unstained preparation, in the new part. This, however, is probably a point of little importance as the condition of the mucus glands is

likely to vary in different parts of an uninjured filament, and at different times. Microscopic transverse sections through the old and regenerated parts of the gill showed no appreciable difference in the development of the chitinous supports. The difference in pigmentation between the old and

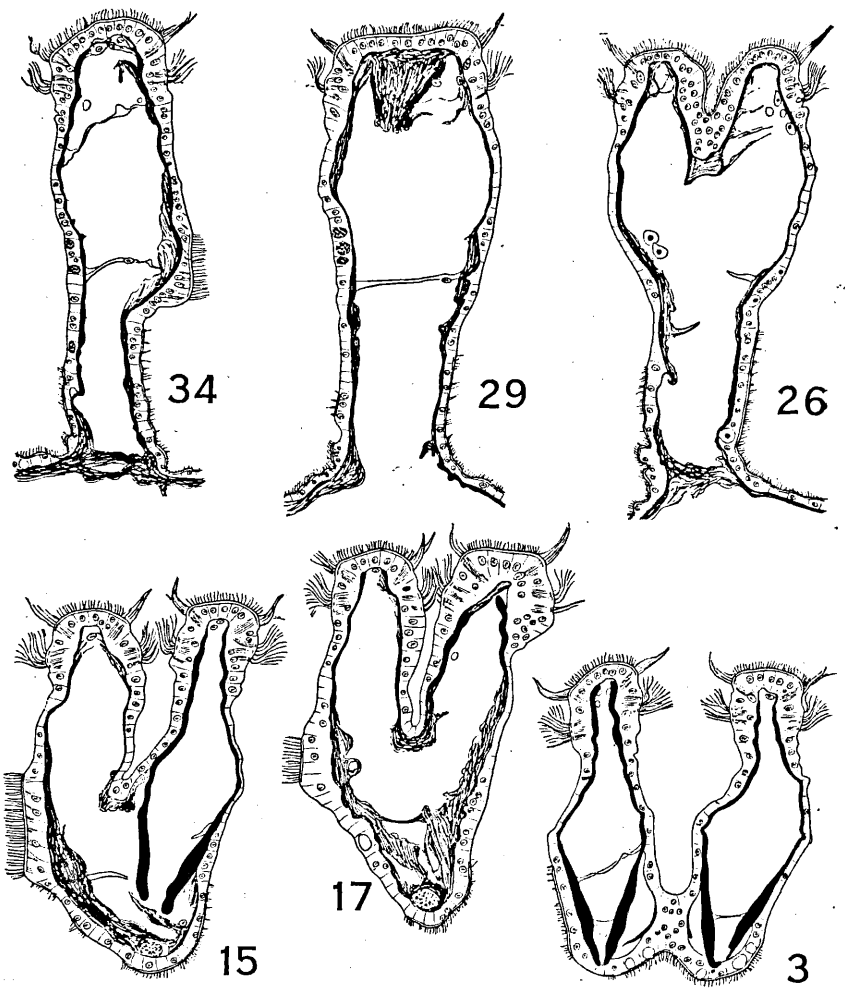

FIG. 6.—Mussel B. Left outer gill, ascending lamella. Transverse sections from a series passing through the junction of the two fused filaments on the extreme right of Fig. 5, to show the change undergone by the chitinous supports and the simple character of the ventral continuation of the filaments. Some slight fusion of the two filaments was evident in the two sections preceding the most dorsal one sketched, namely, 3. The sections are numbered according to their position in the series, so that the number of intervening sections may be known. In the 22nd and following sections (see 26, 29, 34) the filament was connected with several, more posterior, filaments and also with a group in the opposite lamella. The pale staining chitin is indicated by shading. Bouin's fixative; Mallory's Triple Stain. Sections ca. 8μ thick. × 270.

new food grooves was clearly visible in sections passing from one to the other : these were cut a day or two after fixation and the pigment granules had retained much of their original yellow colour.

Interlamellar junctions, to the number of two, have been observed in the regenerated part of some of the few filaments examined singly : they were finer than those in the original part of the filament. In the new part, some at least of the interlamellar junctions appear to be formed by outgrowth from the abfrontal face of one filament (Fig. 7), three cases being noticed of small outgrowths in this position ; two of these, of which note was especially taken, were from the ascending filament and were respectively about 1·2 and 2·59 mm. from the ventral edge of the gill. This is

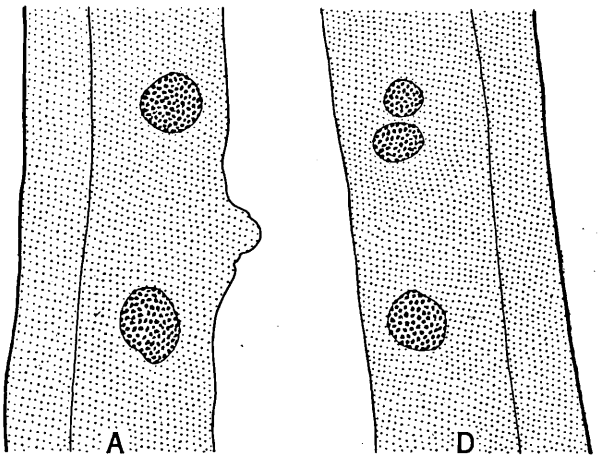

FIG. 7.—Sketch showing origin of interlamellar junction on abfrontal face of ascending part of regenerated filament. The small outgrowth was about 2·59 mm. from the ventral edge of the gill. Bouin's fixative. D and A, descending and ascending filaments respectively. × 140.

of interest in relation to the method of formation of these junctions in the normal development of the gill. According to Rice, they arise through the perforation of a short interlamellar septum, present between the ventral ends of the descending and ascending filaments (see **12**, Fig. 8, p. 73), and such as is found much more fully developed in Modiolus. This he refers to as the Modiolus stage in the development of the filaments of Mytilus.

In the regenerated areas, as shown by sections through the regenerated part of the left outer gill of Mussel B (Fig. 5), much interfilamentar as well as interlamellar connection may occur, in part obliterating the interlamellar space. The condition of the filaments shown in Figure 8 was seen in part of the regenerated area, the particular section sketched being

across some of the normal-looking filaments to the right of the median area of fusion, and between the two most ventral rows of ciliated discs seen in Figure 5. In some parts a similar condition of groups of filaments existed through much of their regenerated length (ca 1·0 mm.).

In a certain number of mussels slanting cuts were made, with scissors, from the ventral edge of the gill in a dorsal and anterior direction, in this way separating a triangular piece from organic connection with the gill, but without removing the piece, which remained connected merely by the

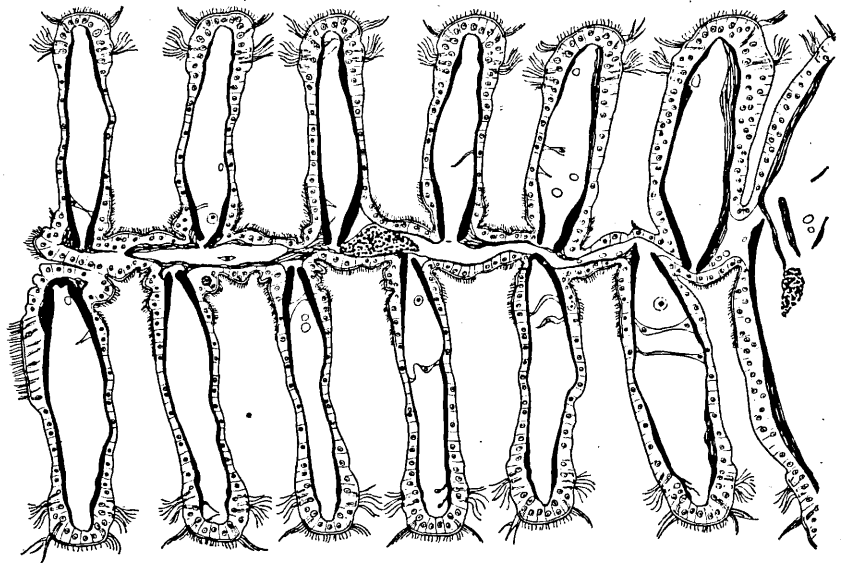

FIG. 8.—Mussel B, left outer gill. Transverse section through part of new area sketched in Fig. 5, showing the filaments in the two lamellæ connected by a median band of tissue. A mass of pigment is present at one place within this median connection. This section is across some of the normal-looking filaments to the right of the median area of fusion, and between the two most ventral rows of ciliated discs, seen in the sketch. Bouin's fixative; Mallory's Triple Stain. Sections ca. 8μ thick. × 200.

ciliated discs on the most anterior and longest length of filament. In the four gills treated in this way (mussels B and J with one gill in each, and mussel A with two gills cut), the pieces had more or less completely degenerated and fallen off. In one instance (left inner gill of B), it appeared that the cut ends of some few disconnected filaments at the depth of the cut (the longest pieces separated) had joined up again, but somewhat irregularly, the ventral ends of two joining the dorsal end of one and vice versa: in this case also, while most of the cut ends of filaments had sloughed off, there were five or so short lengths of filaments separated dorsally from the main part of the gill by a tiny space, but attached anteriorly

and posteriorly; but it is most probable that these filaments were in connexion with each other and the rest of the gill by some organic junctions.

In a previous experiment in June, 1929 (see **1**, p. 961), some organically separated ends of filaments were still connected, after 112 days, with each other and with the main part of the gill merely by their ciliated discs. It, therefore, appears that though such cut pieces of filament may persist for a certain time, after a longer period they are very liable to slough off.

In one mussel (A, in Table I) the two left gills were cut in the manner described above, and regeneration occurred, new tissue partly or entirely filling up the triangular gaps (see Figs. 2, 3).

It may be noted that even after preservation in formalin, or in Bouin's picro-formol for rather more than three months, regenerated areas were recognisable owing to their greater translucence.

DISCUSSION AND SUMMARY.

Experiments have shown that the gill of Mytilus is capable of regeneration, and that this may occur in less than eight months. It may be confined to the formation of a food grove at the cut edge of the gill, without appreciable regeneration in length of the gill filaments. Regeneration of a food groove appears always to occur at the cut edge, if the ends of the descending and ascending filaments are able to touch and so to fuse. On the other hand, regeneration of gill filaments does not seem to occur invariably, and when it does the rate is slow, at least under experimental conditions and in mussels of a length of about 7·0 to 8·0 cm., such as were used for the experiments: it is possible that regeneration would occur more surely and rapidly in young mussels, but owing to the thinness of the shell they would be more difficult to wedge open without fracturing. Coulthard (**6**, p. 136), however, says that "The rate of growth is independent of size in the mussel, being apparently influenced only by the environment." Perhaps the lack of an abundant food supply under the conditions of the experiments should be taken into consideration, though it is well known that in general the amount of food available to an animal has little influence on regeneration (**9**, p. 27). The salinity of the water in general circulation is about 36–37°/$_{oo}$, that is, higher than normal sea-water, which is about 35°/$_{oo}$, and would be considerably higher than the optimum salinity for growth (see Flattely and Walton, **7**, p. 81). This may also possibly have a retarding effect on the initiation of regeneration and the rate.

It is obscure why regeneration does not always occur; so far as could be judged there was no difference in the method of making the cuts, there was little difference in the size and therefore the age of the mussels used,

the cuts were made in approximately the same position on the gill (somewhere between the posterior and middle third of the gill, this position being chosen simply because it was the easiest to reach), and at the end of the experiments—none of which was terminated before the end of eight months—there was little difference in the condition of the various mussels.

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The Loxosomatidae of the Plymouth area, including L. obesum sp. nov.

Quarterly Journal of Microscopical Science
Vol. 75, Part II, June, 1932

Printed in Great Britain

The Loxosomatidae of the Plymouth Area, including L. obesum sp. nov.

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With 24 Text-figures.

CONTENTS.

Introduction.

Four known species of Loxosoma, namely, L. phascolosomatum Vogt, L. crassicauda Salensky, L. singulare Keferstein, and L. claviforme Hincks, have been identified as occurring in the Plymouth area, and a new species L. obesum is described.

Observations were made so far as possible on living material. Text-figures (except Text-figs. 6, B, and 8, A) of living Loxosomas are of individuals narcotized with stovain, and in such individuals the tentacular crown is generally more widely open than is normal. L. crassicauda was the easiest successfully to narcotize, and L. obesum the most difficult. Measurements, unless otherwise stated, are of living narcotized specimens with the tentacles expanded. Total length is measured from the disc of attachment, or the end of the stalk, to the edge of the lophophore, between the bases of the two most dorsal tentacles.[1] The tentacles were not included, so that the measurement should be roughly comparable with that of specimens with closed lophophore.

The only commensal of Loxosoma seen was a species of Licnophora on two individuals of L. crassicauda. About ten specimens were present on each, most of them being on the dorsal surface of the calyx. This Infusorian occurs in numbers on Diplosoma living in the same tanks in the Laboratory as L. crassicauda, and its presence on the Polyzoan was probably accidental.

Loxosoma phascolosomatum Vogt.

This well-known species is found in the Salcombe Estuary growing on the caudal extremity of Phascolosoma vulgare (see also 'Journ. Mar. Biol. Assoc.', vol. vi, N.S., p. 164, 1900), and in addition on Lepton clarkiae and Montacuta bidentata,[2] two tiny Lamellibranchs occurring in

[1] The terms 'dorsal' and 'ventral' are used in accordance with the interpretation of the relations of the body given by Harmer for Pedicellina on p. 261, 'Quart. Journ. Micr. Sci.', vol. xxvii, 1886 (and not for Loxosoma, on p. 264, 'Quart. Journ. Micr. Sci.', vol. xxv, 1885). The mouth is nearer the 'ventral' side, and the anus nearer the 'dorsal' side.

[2] Mysella bidentata in the Plymouth Marine Fauna, 1931.

the burrows of Phascolosoma (pellucidum) elongatum. A short account of this species has already been given by me (**2**), with figures mostly of living specimens.

LOXOSOMA CRASSICAUDA Salensky (Text-figs. 1–3).

Habitat.

In February 1929 specimens of Loxosoma crassicauda Salensky[1] were found growing on the wall of a shallow wooden table-tank, placed under windows facing south in the Plymouth Laboratory. In August of the same year this species was discovered attached to several different kinds of worm-tubes, including Sabella, Branchiomma, and Bispira, and to clean pebbles in a small tank in the Aquarium. It has since been found on the walls of two of the large tanks in the Laboratory. Batches of Loxosomas from the shallow tank were examined about once a month up to February 1930. On September 18, 1929, only four medium-sized individuals (0·75–1·0 mm. long) could be found, though thirty-three had been easily obtained on August 23; by the end of October, however, specimens were again obtainable. Possibly many Loxosomas may have died in the intervening time owing to the high temperature reached by the water in the shallow tank (e.g. on September 11 a temperature of 20–1° C. was recorded).

Although the tubes of Phyllochaetopterus socialis Clap.[2] (probably the original host of L. crassicauda, see **32**) have been examined, so far they have not yielded Loxosomas.

L. crassicauda was first discovered by Salensky (**29**, p. 2) in the spring of 1874 at Naples inhabiting the 'coquilles tuberculeuses' of an annelid which he was unable to identify. Schmidt (**32**, p. 71) in the spring of 1877 found a species on the tubes of Phyllochaetopterus socialis Claparède, which he says completely agreed with Salensky's description and

[1] It has been considered advisable to retain the generic name of Loxosoma for this species, and not to place it in the genus Loxosomella Mort., of which Mortensen (**19**, p. 405) makes it the genotype. In this connexion see Harmer, **12**, p. 6.

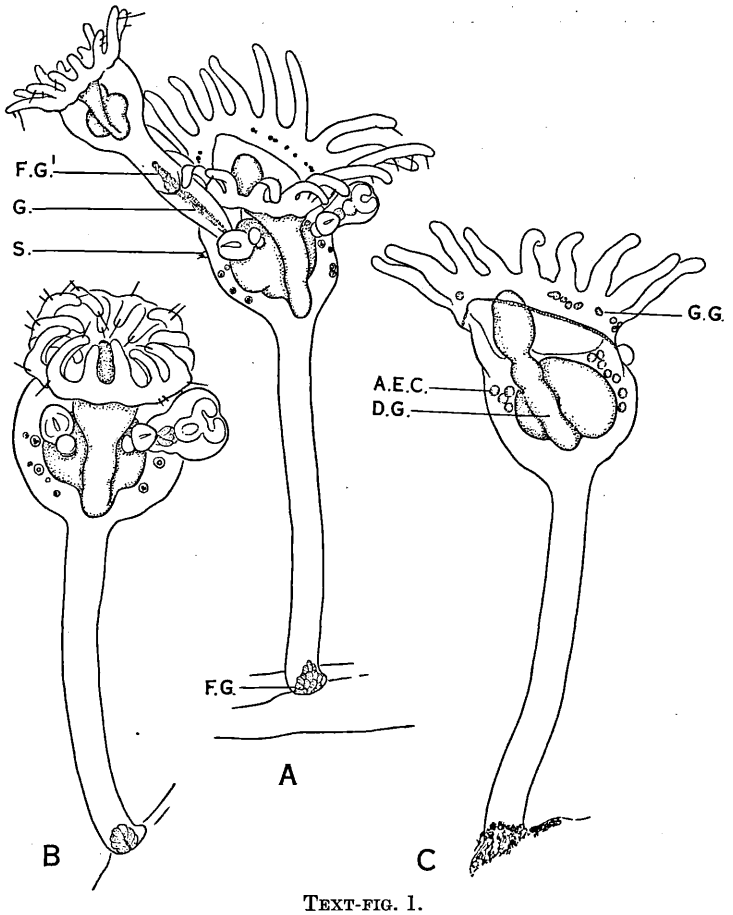
[2] In Plymouth Marine Fauna, 1931, as P. anglica Potts.

figures, except that a foot-gland was present in the adult. This species was later found by Harmer in 1885 (**9,** p. 263) in large numbers attached to the floor of a tank in the Zoological Station at Naples, and since has been doubtfully identified by Kirkpatrick as growing on algae from the Tizard Reef in the China Sea (**17,** p. 23). Sir S. F. Harmer informs me by letter that in 1903 he found very numerous specimens of L. crassicauda on the test of Ciona intestinalis and on the Polyzoan, Zoobotryon pellucidum, growing on the Ciona, in a store-bottle (from Naples) in the Zoological Laboratory at Cambridge.

The record of L. crassicauda at Plymouth would appear to be the first for the British Isles.

Notes on the Morphology.

L. crassicauda at Plymouth may reach a length of 1·87 mm. Measurements of sixty specimens gave an average total length of 1·4 mm., with length of calyx 0·5 mm., and of stalk 0·9 mm.; the average width of the calyx was 0·38 mm. The stalk of adult individuals is between 0·06 to 0·1 mm. wide. L. crassicauda (Text-fig. 1) is a large, transparent species; the calyx is rather broad, the stalk long and slender, the one passing somewhat abruptly into the other. The termination of the stalk is more or less cylindrical; a reduced foot-gland is usually present in the adult. The lophophore is large, the number of tentacles in the adult of the Plymouth form being 15, 16, or 17; usually 16. In the number of tentacles, and the retention of a reduced foot-gland in the majority of adults examined, it differs from those described by Salensky (**29**) and Harmer (**9,** p. 263) of which the number of tentacles is said to be typically 18, though by no means constant, and a foot-gland is said to be absent in the adult. Salensky mentions that of the 18 tentacles 2 are rudimentary (**29,** p. 3), and in his fig. 1, Pl. 12, only 17 are shown. The smaller number of tentacles in the Plymouth specimens would not appear to be an important difference in a species where the number undergoes a progressive increase from that present in the bud on liberation; and, as Schmidt (**32,** p. 72) has recorded, the foot-gland in the



TEXT-FIG. 1.

L. crassicauda. Living individuals. ×57·25. A. Ventral view with lophophore fully expanded. B. Ventral view with lophophore partly closed. C. Sketch showing dorsal surface of animal. Large cells (*A.E.C.*), possibly excretory or accretory in function, are present on either side of the alimentary canal; in this individual they were clear and not granular in appearance. *D.G.*, dorsal groove connecting the apical region of the stomach with the intestine; *F.G.*, foot-gland of adult; *F.G.*^{1}, foot-gland of bud; *G.*, groove of foot-gland; *G.G.*, large granular gland-cells; *S.*, sense-organ. The large transparent vacuolated glands are not visible at this magnification, unless stained intra-vitam with neutral red, and so are not shown in the figure.

adult is indistinct and is often obscured by dirt particles collected round the point of attachment; it generally shows clearly only in stained and mounted specimens. Schmidt says that the gland is of the same nature and size as in the buds, but in the individuals examined it was found to vary in size; in most it was smaller than in the bud, in others it appeared to be breaking down, while in a few it was absent. Actual figures are: out of 81 stained and mounted specimens in which the end of the stalk could be clearly seen, 63 had a distinct gland, in 7 it was tiny, in 5 it was breaking down, and in 6 it was absent. The specimens varied in size from young attached forms 0·8 mm. in length to adults up to 1·87 mm. It is probable that after the bud becomes attached the foot-gland loses its power to secrete and slowly atrophies.

The Plymouth form has the characteristic paired sense-organs of L. crassicauda; their tuft of stiff hairs is about 45μ long. The sense-organs are of a good size in buds only 0·3 mm. in length attached to the parent: they do not appear to be retractile as are those of L. phascolosomatum (**36**, p. 313). Duplication of the sense-organ of one side occurred in an individual, the nerve from the ganglion dividing on approaching the edge of the calyx.

The tactile hairs on the outer, non-ciliated part of the tentacles are particularly long and conspicuous in this species, both in the adult and the bud. In well-developed buds there is usually a stiff sense-hair on either side of the aperture of the foot-gland at the 'heel' of the foot (see Text-fig. 2, B). The pore of the gland opens into the extreme distal end of the groove which traverses the 'sole' of the foot.

Numerous large gland-cells of the two types described by Harmer (**9**, p. 266) occur in two rows parallel to the edge of the vestibule and of the calyx. The opaque granular-looking glands are somewhat pear-shaped, about 15μ to 34μ long, and occur at irregular intervals; the transparent glands, filled with large vacuoles, are considerably larger, and may be 45$\mu \times 27\mu$, with vacuoles up to 13μ in diameter; these occur in a rather regular row slightly dorsal to the former gland-cells. When a slight trace of neutral red is added to the sea-water containing the

Loxosomas, the transparent vacuolated glands, by reason of their end vacuoles taking the stain, show up in a conspicuous row, especially regular in well-developed buds. The small vacuoles near the external aperture of each gland (Harmer, **9,** p. 266, found the glands to open externally) alone take the neutral red, becoming bright, slightly orange red, while those filling the major half of the gland are either tinted extremely faint pink or are colourless. These glands take up the colour rapidly, the granules round the nuclei of the ectoderm cells alone being coloured before them: the colour remains some days after the animals are returned to clear sea-water. The granular gland-cells, on the other hand, only show one or two granules in the centre slightly coloured after twenty-four hours or more. Both types of gland-cell are evidently not mucus glands, as they are unstained by Mayer's muchaematein.

A group of large, rather deep-seated cells about 22μ–27μ in diameter occur in the calyx on either side of the oesophagus (see Text-fig. 1, c). They are generally, though not always, granular in appearance, and in most instances have a definite large granular central mass, or two or three central granules, yellow in colour. The number of these cells varies, but is most commonly four or five on each side, sometimes arranged more or less in linear series, sometimes in a loose cluster; under a high magnification they are seen to be separate from one another in the living animal. Occasionally one or more cells similar in character occur more proximally close to the side-walls of the stomach, but may be separated from the distal group by a considerable space. They appear to increase in number with age; they perhaps have an excretory function, or rather waste products are stored in them. These cells are in the position of Salensky's 'glandules multicellulaires ayant la forme de deux grappes', but ducts have not been distinguished opening to the edge of the calyx as he describes and figures (**29,** pp. 10 and 11, and Pl. 13, fig. 14); it is perhaps possible that he mistook some of the numerous nerves for ducts. He describes them as composed of transparent protoplasm—this may be a phase in their activity—and suggests that they may be 'glandes rénales' (**29,** p. 11). These paired clusters of cells are roughly in the

position of, and somewhat similar in character to, those described by various authors in other species as excretory in character (lophophore and body kidneys of L. saltans (**1,** p. 132), and both groups of excretory organs of L. davenporti (**23,** p. 372) and L. annelidicola (**27,** p. 100)), but they are distinct from the true nephridia studied in L. crassicauda by Harmer (**9,** p. 277), and Stiasny (**34,** p. 192), and of which the wave-like motion of the cilia lining the duct, or perhaps of the flagellum of the flame-cell itself, can be seen. When a trace of neutral red is added to the sea-water, these cells show colour fairly soon; at first it is as a diffuse pink surrounding the yellow granular central mass; later the granular centre takes the colour darkly, becoming dirty, deep, orange red, the original yellow colour no doubt affecting the tone of the red. The colour remains some days after the animals are returned to clean sea-water. When the sea-water is tinted with methylene blue these cells become pale blue, with dark-blue centres, and retain their colour for twelve hours or more. In sections stained with iron haematoxylin and acid fuchsin, after fixation in strong Flemming's fluid without acetic acid, these cells are conspicuous; they show a darkly staining cytoplasmic border, in which is the nucleus, and a granular centre, generally separated by a ring which does not take the stain.

The ectoderm cells of the stalk tend to be arranged in longitudinal rows, especially in young individuals. This is possibly a variable character, for while Salensky (**29,** p. 8) speaks of a longitudinal row of cells, which he took to be glandular, down the dorsal side of the stalk, Harmer (**9,** p. 263) states that there was no regular arrangement of the ectoderm cells in his specimens. Longitudinal muscles only occur in the stalk, but they are sufficiently well developed to allow the animal to throw itself about with irritable violence if touched, the lophophore bending to the base of the stalk.

The alimentary canal is of the normal type. Just proximal to the so-called liver-lobes there is a slight development of the lobes, which Assheton (**1,** p. 129) suggested for L. saltans had a secretory function, in distinction to the 'liver'-lobes, the characters of which he considered indicated active constructive

metabolism. The cells of the 'liver'-lobes in adult L. crassicauda are about 0·025–0·05 mm. deep. The rectum when packed with waste matter is particularly large; after the expulsion of faeces, however, it collapses. Its walls are frequently crowded with large, shining, yellowish spherules and small granules. Assheton considered in the case of L. saltans (**1,** p. 133) that the rectum was in all probability an important part of the excretory system. Sections show some specimens with deep rectal cells, others with shallow cells.

The whole of the alimentary canal is ciliated, as stated by Harmer (**9,** p. 276), but the cells of the lateral diverticula of the stomach may lose their cilia when actively secreting or excreting. Waste matter collected in the dorsal groove of the stomach and in the intestine may be seen revolving, but if the watch-glass containing the animal is jerked, the motion may cease in the intestine for five minutes or more, and then begin again slowly, gradually gathering speed. The stoppage of movement is probably due to muscular contraction causing reduction of the lumen, and so preventing the cilia working efficiently, and not to cessation of beat of the cilia clothing the walls of the intestine. Reversal of the rotation of the mass of food-particles in the intestine and dorsal groove occurs, as described by Cori (**6,** p. 37) in the stomach of Pedicellina. Although the rectum is highly ciliated, no revolving motion of the faeces has been observed in this species: in the rectum of L. claviforme and L. singulare, however, a very slow motion of waste matter has been noticed; that in the intestine revolves rapidly.

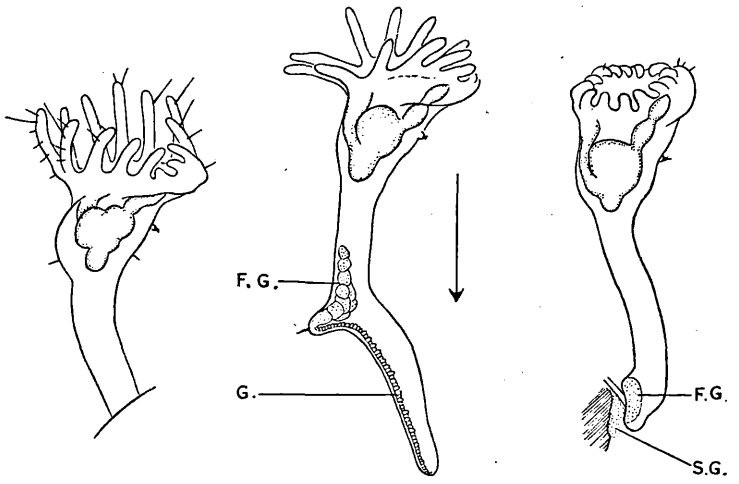
When a slight trace of neutral red is added to the sea-water practically the whole of the cells lining the alimentary canal take the stain, but very slowly, some granules in the rectal cells showing it first. The 'liver'-cells are naturally yellow in colour, and the granules in these become orange with neutral red. The cells of the apex of the stomach contain granules which become almost black red; in the living animal these appear as minute, shining, colourless globules. After an hour or so in sea-water tinted with methylene blue and then removal to clear sea-water, the originally yellow-coloured 'liver'-cells may acquire a distinct green tint. Assheton (**1,** p. 133) found that the

'liver'-cells of L. saltans were hardly affected by methylene blue.

All specimens examined over a period of about eleven months were budding freely; the greatest number of buds seen was four on one side, of which the youngest was a mere ridge, and three on the other as in Text-fig. 1, A; the buds occur near the ventral and distal wall of the stomach (see Text-fig. 1, A and B). They would appear generally to detach themselves from the parent, by violent contortions, bending the 'heel' to the tip of the foot, and the lophophore to the 'heel', when they have attained a length of about 0·65 mm., and possess fourteen tentacles of which four are more or less rudimentary. The two youngest tentacles, which appear as tiny rounded protuberances, occur on either side of the median plane at the distal edge of the lophophore (Text-fig. 2, A). New tentacles are therefore formed either in pairs or alternately—probably alternately in older individuals—in this position, the tentacles increasing in length ventralwards; one occurs on either side of the mouth. It is in the distal median line of the lophophore that the ciliated vestibular groove at the base of the tentacles is interrupted, and particles passing down the tentacles on either side of this point travel in opposite directions round the groove to the mouth. A rudimentary tentacle described by Salensky (**29**, p. 5, and Pl. 12, fig. 1) as occurring near the mouth has not been observed, but all tentacles are not fully extended at the same time. There is, however, considerable variation in length of the tentacles of different adult individuals of approximately the same size, the tentacles generally being shorter in old-looking individuals, with numerous large yellow granular excretory cells (see p. 327), than in transparent ones, with few of these cells. This is variation in length, and not in the state of contraction of the tentacles, as is evident from the difference in the number of groups of lateral cilia, and therefore of lateral cells of the tentacles, in the different specimens. There is a short row of about twelve to fifteen long cilia on each lateral cell, separated from those on adjacent lateral cells by a slight gap, corresponding to the cell-wall.

In the buds the stalk, together with the foot, is slender, and

when fully expanded is very graceful (Text-fig. 2, B). Free buds swim slowly; they move with the calyx hindmost as noted for the free buds of L. nitschei by Roper (**28**, p. 56).



TEXT-FIG. 2.

L. crassicauda. Living buds and young fixed form. ×*ca.* 76·3. A. Bud attached to parent, showing addition of tentacles in the distal region of the lophophore. B. Bud sketched just after liberation from parent. C. The same individual as in B, sketched six days later, showing great reduction in length of the foot, and increase in length of the stalk. It is partly attached to a sponge spicule, and partly to a fragment of vegetable debris. It was already fixed three days after liberation, when it was in much the same condition as in the sketch. *F.G.*, foot-gland; *G.*, groove of foot-gland; *S.G.*, secretion of foot-gland. The arrow indicates the direction of movement of the free bud in swimming.

Buds seem to become attached first—but slightly, for they are easily dislodged—by the extreme tip of the foot. The bud then appears to examine with the pointed heel, which bears one or two tactile hairs, the object it has touched; the 'sole' of the foot meanwhile being well arched. The foot may then

contract strongly, the whole 'sole' of the foot with its open 'duct' or groove being applied to the object. The contracted foot would then seem to be gradually reduced in size; in young individuals the termination of the stalk is more or less cylindrical (Text-fig. 2, c), or, as Schmidt (**32**, p. 72) has described it, like the foot of an elephant.

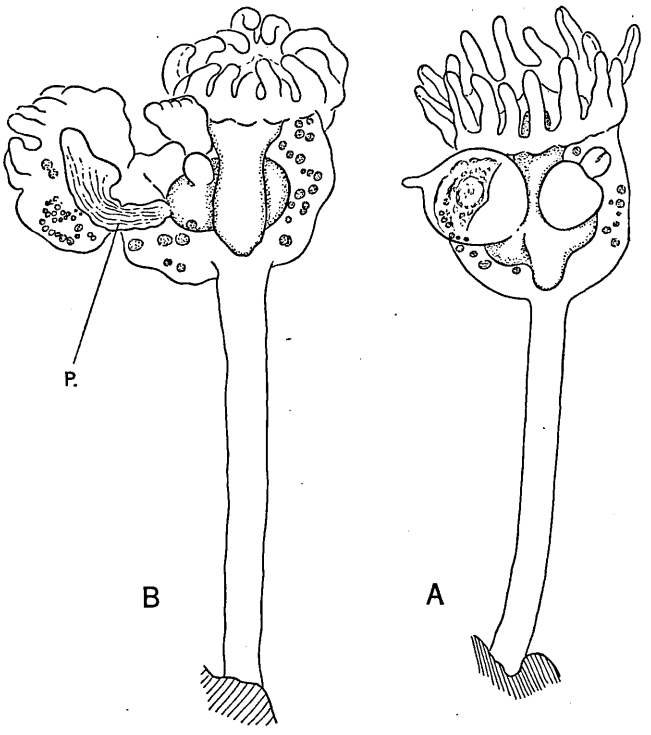
Abnormal Buds.

A few individuals with abnormal buds have been seen. In two or three instances the bud, though of considerable size, was a round mass of undifferentiated cells with a narrow projection at the summit. In the specimen figured (Text-fig. 3, A), however, there appeared to be an extension of the stomach of the parent into the bud of one side. In two specimens the abnormal buds consisted of little more than the lophophore, the vestibule being a slight depression, and without any digestive system. Attached to the parent near the base of one bud was a separate muscular process, which evidently represented the stalk and foot. In one specimen (Text-fig. 3, B) the lophophore of the abnormal bud faced in the opposite direction to that of the parent, and the two halves of the lophophore were unequally developed. This individual also bore normal buds, and a perfectly developed one, on the same side as the abnormal bud, freed itself just before the sketch was made. The second individual bore similar abnormal buds, one on either side, but with the lophophores facing in the same direction as that of the parent. A number of Loxosomas from the small tank in the Aquarium carried well-developed buds, which were slightly abnormal in that the foot was much shorter than usual, and although the groove or 'duct' of the gland was present, the gland itself appeared to be small or absent. These buds grew to a large size while still attached to the parent; apparently owing to the shortness, or lack, of the foot they experienced difficulty in freeing themselves.

Notes on the Life-history.

Batches of individuals, including young and adult forms, from different parts of the south wall of a shallow tank in the

Laboratory, were examined from March 1929 to February 1930. Throughout this time all those in which the sex was determinable were males; in the great majority of these the gonad was tiny,



TEXT-FIG. 3.

L. crassicauda. Living individuals with abnormal buds. ×57·25. A. Ventral view of parent with large round abnormal bud. B. Ventral view of parent, showing dorsal surface of abnormal bud. Two small buds are present on the same side as the abnormal bud. *P.*, muscular process attached near the base of the abnormal bud. Numerous cells, possibly having an excretory function, are present in the calyx.

composed of a small number of clear cells, and the presence or absence of a vesicula seminalis was relied on for the determination of sex. In only a few individuals was sperm seen, and when

present it was generally in one-half of the gonad only, that half being considerably larger than the other. The examination was made for the most part on specimens fixed in formalin, stained with borax carmine, and mounted in alcoholic canada balsam (see Harmer, 'Quart. Journ. Micr. Sci.', vol. 46, p. 264, 1902), and in some instances it was impossible owing to the position of the animals to determine whether or no a vesicula seminalis was present, so that the percentage of males is probably considerably higher than recorded in Table 1 (p. 335). In the living animal it was found almost impossible to be certain of the presence or absence of an empty vesicula seminalis, owing to the prevalence of waste particles in the intestine and rectum. No ova were seen in any of the specimens examined.

These results were so unexpected that a number of individuals from the small tank in the Aquarium were examined on August 19, 1929, for comparison, with the following result: out of nineteen individuals twelve at least were male, that is, about 63 per cent., while the sex of the remainder could not be ascertained; but here again the sex was determined by the presence of a vesicula seminalis, which in all cases was empty. The gonad in all specimens was tiny and no ova were seen.

A possible explanation of these results is that owing perhaps to lack of sufficient food in the unnatural conditions under which the animals were living, the development of the reproductive elements was very slow; the majority of those examined, however, were budding freely, though budding in Loxosoma does not normally seem to retard the development of the gonad, as in other species buds may be found on individuals with well-developed gonad, and even with the vestibule crowded with embryos. The fact that all individuals examined, including those up to 1·87 mm. in length, in which sex was determinable were male, would seem to point to the conclusion that in L. crassicauda individuals are first male; it would hardly seem to be probable that both tanks were colonized by male individuals of a dioecious species. The Loxosomas in both tanks must have been multiplying by budding alone.

It might be noted that the larva of L. crassicauda is at present unknown (see **9**, p. 263).

TABLE I.

Loxosoma crassicauda: Proportion of Recognizable Males in Collections made from a Shallow Tank in the Laboratory during 1929–30.

Date.	*Mar. 23, 1929.*	*May 2, 1929.*	*May 14, 1929.*	*May 28, 1929.*	*June 12, 1929.*	*June 26, 1929.*	*July 24, 1929.*	*Aug. 23, 1929.*	*Sept. 18, 1929.*	*Oct. 29, 1929.*	*Dec. 2, 1929.*	*Feb. 24, 1930.*
Males:												
Number	4	17 (2 with sperm)	8 (2 with sperm)	15 (1 with sperm)	20	15	16	33 (9 with sperm)	0	17 (6 with sperm)	26	10
Per cent.	*40·0*	*54·8*	*34·8*	*75·0*	*83·3*	*68·2*	*61·5*	*100·0*	*0*	*60·7*	*74·3*	*32·3*
Sex indeterminate:												
Number	6	14	15	5	4	7	10	0	4	11	9	21
Per cent.	*60·0*	*45·2*	*65·2*	*25·0*	*16·7*	*31·8*	*38·5*	*0*	*100·0*	*39·3*	*25·7*	*67·7*
Totals	10	31	23	20	24	22	26	33	4	28	35	31

In order to obtain some idea of the rate at which individuals multiplied by budding, two free buds were isolated in finger-bowls. One produced twelve individuals in 85 days; its first bud became free when the parent was 43 days old and 0·9 mm. long. The other produced six individuals in 77 days; its first bud freed itself when the parent was 44 days old and 0·92 mm. long. In the latter instance the first two or three individuals were much worried by masses of bacteria, which enveloped the stalk and part of the body, and had to be removed at intervals. The sea-water in the bowls was changed every few days, but no food was given. The results are therefore unquestionably much lower than they would be under natural conditions.

Loxosoma singulare Keferstein (Text-figs. 4, 5, and 24, c).

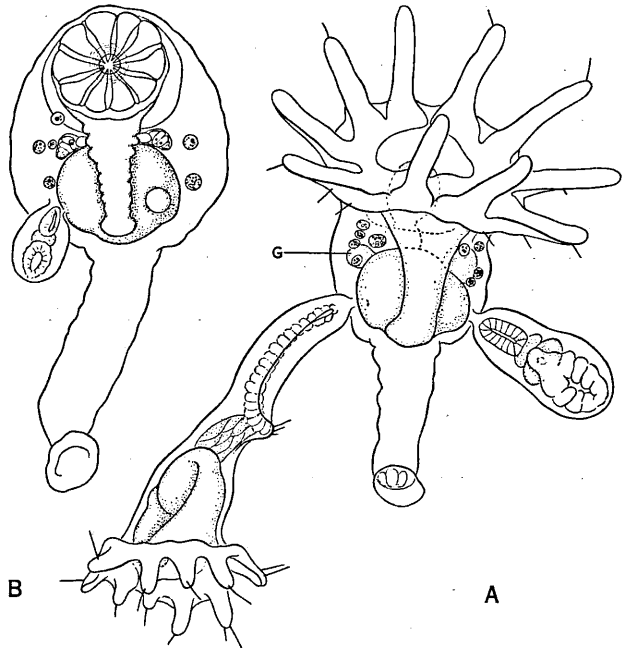
Notes on the Morphology.

A small species of Loxosoma found on the ventral surface of Aphrodite aculeata, and also on the dorsal surface and on the under side of the elytra, is most probably L. singulare (Text-figs. 4–5). In the latter position the Loxosomas lie more or less parallel with the elytron—the stalk near the base being bent almost at right angles—generally with the lophophores facing the elytron, but occasionally facing downwards into the 'respiratory chamber' of the Aphrodite.

This small species on Aphrodite has been identified by Barrois (**3,** p. 9), Hincks (**13,** p. 573), and Harmer (**9,** p. 262), as L. singulare, but there is some doubt as to its identification owing to uncertainty as to the presence, or absence, of a foot-gland in the bud of this species; one is certainly not shown in Claparède's figure (**4,** Pl. 11, fig. 6). Except for the presence of a foot-gland in the bud, the small species found on Aphrodite at Plymouth (Text-fig. 4) agrees in general with the description and beautiful illustrations of that author, its original discoverer, of a species he found on Notomastus (Capitella) rubicundus at St. Waast, Normandy, and which was named L. singulare by Keferstein (**16,** p. 131).

As L. singulare was the first species discovered and

described, it is possible that the presence of a foot-gland in the bud was overlooked; this seems probable as the anatomy of the animal was imperfectly understood; the anal extremity of



TEXT-FIG. 4.

L. singulare. × *ca.* 115·6. A. Ventral view of living female individual with lophophore open. The gonad (*G*) is immature; the ovum on the left side is fairly large, though not opaque. Several large cells, possibly excretory in function, are present on either side of the oesophagus. In this individual the stalk did not end in a disc of attachment, and a vestige of the foot-gland was present. Sense-hairs are present on the 'heel' of the foot of the mature bud. B. Ventral view of mounted female individual with closed lophophore, showing the development of slight wings due to the contraction of the muscles of the calyx. The oesophagus shows ridges of contraction. The gonad contains immature ova in 'pagoda' arrangement. The stalk ends in a disc of attachment.

the intestine was thought to pierce the wall of the pharynx and open outwards in the middle of the mouth, and Claparède

(**5,** p. 29) was doubtful whether the part called by Keferstein (**16**) and himself (**4**) the mouth, might be the anus and vice versa.

Barrois (**3**) in 1877 described the embryology of a Loxosoma from Aphrodite which he identified as L. singulare. His specimens evidently had a foot-gland in the bud (see **3,** p. 10 and Pl. 16, fig. 5), though not in the adult (p. 9). He found this species at St. Waast; it has since been doubtfully identified on the same host by Harmer (**9,** p. 262) at Naples.

Schultz (**33,** pp. 56, 57) in 1895, in his tabulated description of Loxosoma, has for L. singulare under the heading 'Drüse', 0; and then under 'Sonstige Merkmale' 'Der Fuss endigt mit einer Drüse', which is contradictory, unless the latter remark was intended to refer to the buds.

Efforts at Plymouth to obtain this species on its original host, in order to decide the question of identification, have been unsuccessful, the Notomastus dredged from the Rame mud —where Aphrodite carrying this species are taken—being free of the commensals.

L. singulare is described by Claparède (**4,** p. 106) and Keferstein (**16,** p. 131) as having 10 tentacles: Harmer (**9,** p. 262) was somewhat doubtful of his identification of the specimens at Naples, as in the very few he obtained the number appeared to be 12 or 13. Those on Aphrodite at Plymouth, though generally having 10 tentacles may have occasionally 8, 9, 11, or 12, and very rarely 13, depending roughly on the size or age of the individuals. It would appear that in L. singulare, as in perhaps the majority of the Loxosomatidae, the number of tentacles present in the bud on liberation undergoes a slight progressive increase with age; there are very few known species with a constant number of tentacles.

L. singulare is a small species. Claparède gives the length as 0·3 to 0·4 mm.,[1] and Keferstein as 0·4 mm. L. singulare at Plymouth varied between 0·18 and 0·8 mm. in length. Of 72 specimens measured, the average total length was 0·530 mm., with length of calyx 0·305 mm., and of stalk 0·225 mm. The

[1] In (4) Claparède gave the length as 3 to 4 mm., but later (5) corrected it to 0·3 to 0·4 mm.

average calyx width of 54 specimens was 0·179 mm. The width of the stalk varied between 0·03 and 0·08 mm.

The stalk is generally shorter than the calyx, though it varies somewhat in different individuals (an individual 0·7 mm. total length had an exceptionally long stalk 0·45 mm. in length), and ends generally in a disc of attachment (Text-fig. 4, B) (see also Hincks, **13,** vol. i, p. 573; and Harmer, **9,** p. 262), though in some specimens (Text-fig. 4, A) it appears to be absent. Claparède's (**4,** p. 106) description of the stalk and disc is as follows: 'Der Stiel ist farblos und breitet sich in eine rundliche Haftscheibe, durch deren Hülfe der Schmarotzer auf Capitella (Notomastus) festsitzt, aus. Nimmt man die Unterseite der Fussscheibe in Augenschein, so findet man, dass die ganze Sohle mit zahlreichen, 0·014 mm. breiten rundlichen Zellenkernen besetzt ist, die unmittelbar unter der farblosen Cuticula sitzen.' He, however, does not say that the animal was capable of changing its position (as can L. davenporti, **23,** p. 355; and L. saltans, **1,** p. 124), nor does Keferstein (**16**). Keferstein (**16,** p. 131) describes the stalk 'mit dessen fussartiger Ausbreitung er sich auf der äusseren Haut der Annelide befestigt'. In the Plymouth specimens once the animals are attached they do not change their position; they would appear to be attached by a secretion poured out by the foot-gland before this atrophies. In many adults a vestige of the foot-gland is present. Specimens on the ventral surface of Aphrodite are often attached by their discs to the brown-coloured papillae of the worm; when the surface is scraped the latter are broken off at their fine necks, giving to the Loxosoma from this position the appearance of having a very large brown disc of attachment. Longitudinal muscles only are present in the stalk.

The buds occur near the ventral and proximal wall of the stomach, the greatest number seen so far being two on each side. Keferstein apparently saw only one on either side (**16,** p. 132), and Harmer says of his specimens that none possessed more than a single bud, which was provided with a foot-gland, while Hincks (**13,** vol. i, p. 573) found as many as three buds present on a side, on specimens from Laetmonice

filicornis from Shetland. Probably the number of buds present varies, perhaps with the season or with the food supply. Buds may be present on sexually mature individuals of either sex. Budding individuals have been observed in March, April, June, July, September, and October.

True nephridia as described by Harmer for L. crassicauda are present; in addition, large yellowish granular cells, with a possible excretory function, are present in the calyx on either side of the stomach (see also p. 327).

The generative organs are paired, and, so far as is known, the sexes are separate. The number of recognizable ova present in the gonad is small; the ripe ovum is large (*ca.* 0·08–0·09 mm. in diameter) and yolky. A paired shell-gland occurs in connexion with the oviduct (see also Prouho, **27,** p. 105). In females carrying a number of embryos the vestibule is produced into two lobes, one on either side of the rectum (Text-fig. 5, A–B). Harmer (**9,** p. 285) states that Loxocalyx (Loxosoma) leptoclini possesses 'two specialized diverticula of the posterior portion of the vestibule, one on either side of the intestine, which by its projection as a large longitudinal ridge (covered, of course, by ectoderm) into the vestibular cavity gives rise to the two diverticula': in this species, however, the epithelium lining the diverticula is modified for a nutritive purpose. As many as nine or ten embryos may be present simultaneously in the vestibule in L. singulare.

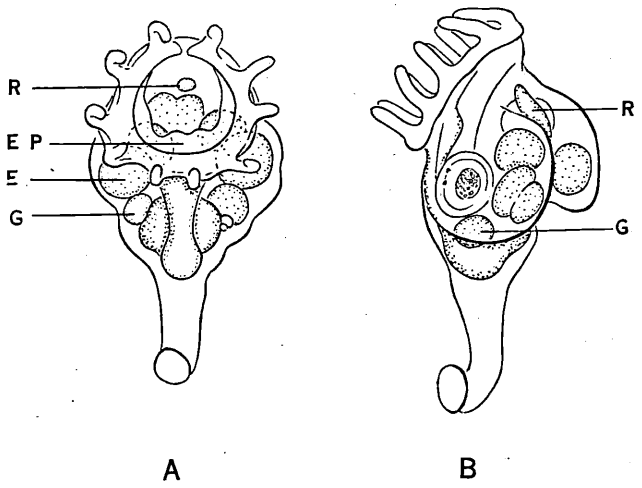
The ripe male gonad is larger than the mature ovary.

The development of the larva has been described by Barrois (**3,** pp. 10–54). It might be noted that the anal cone of the larva of L. singulare bears long cilia, and in addition on either side a stiff tactile hair, although Barrois figures it as being destitute of cilia (**3,** Pl. i, fig. 21). While the eye spots may be 'une couleur carmin' as described by him, in some larvae they have been observed to be a reddish brown. Barrois found embryos in the vestibule during July at St. Waast: at Plymouth they have been seen in the vestibule from April to October; as few specimens have been obtained during the winter months it is impossible to say that breeding does not occur during those months.

Little information has been gathered as to the proportion of the sexes, as this species, though found on a good proportion of Aphrodite, was generally present in very few numbers.

The only records are as follows:

September 1930. (1) On the dorsal surface of an Aphrodite



TEXT-FIG. 5.

L. singulare, sketches of living individuals with embryos in the vestibule. A. Ventral view, lophophore widely open. Five embryos are visible in the vestibule. B. Side view, showing the vestibule produced into two lobes, one on either side of the rectum. Two embryos (unstippled) are almost ready for liberation. *E*, embryo; *EP*, epistome; *G*, gonad; *R*, rectum. ×*ca.* 85·9.

10 L. singulare were obtained, of which 9 were female, and 1 with the gonad too tiny for the sex to be determined. This group, judging from the large bilobed vestibule, with at most one or two embryos (in one instance only an empty envelope), and the small gonad, was probably at the end of a reproductive phase.

On the ventral surface of the same 'host' 2 males only were taken; they were fully mature, the gonad containing sperm.

The females varied between 0·42 and 0·6 mm. in length; the 2 males were 0·38 and 0·53 mm.

(2) On the same date, on the dorsal surface of another Aphrodite, out of the 7 individuals obtained, 5 were female, and 2 had the gonad too small for the sex to be determined. The females had one or two large opaque ova in the gonad, and a well-developed embryo in the vestibule. The females were between 0·44 and 0·64 mm. in length; the individual with indeterminable gonad was 0·40 mm.

October 1930. From the dorsal surface of an Aphrodite 27 L. singulare were taken of which 20 were female, 1 male (with sperm in gonad), and 6 with gonad too small for sex to be determined. Of the females, 13 had a single embryo in the vestibule, 8 in early and 5 in late stages of development, and 1 female had an opaque ovum in the gonad; the remainder had small ova. The females were between 0·42 and 0·8 mm. in length; the male was 0·52 mm. long; those of which the sex could not be determined were between 0·43 mm. and 0·7 mm. The probable explanation of indeterminate gonad in large specimens is that the gonad was spent.

Distribution in the Plymouth Area.

The Aphrodite examined have come chiefly from the Looe and Rame Eddystone Grounds, and in fewer numbers from the Mewstone Grounds; a single individual carrying a considerable number of L. singulare came from Bigbury Bay. L. singulare was present on 56 of the 141 (39·7 per cent.) Aphrodite examined between October 1927 and October 1930, though in most instances in very small numbers. They occur much more frequently on the ventral surface than on the dorsal, but in the latter position usually occur in much greater numbers. When on the dorsal surface they are not restricted in position as is L. obesum (see p. 355), and may occur on the anterior elytra.

Double Specimen.

A double specimen of L. singulare (Text-fig. 24, c, p. 386) was observed in March 1930. It had a common stalk and the bodies united side by side; the two lophophores were

distinct. The oesophagus and rectum of the two individuals were separate, but there was a single bilobed stomach. The specimen was not in good condition when found, and it was impossible to distinguish the nerve ganglion or gonad. No buds were present. This specimen is similar to the third condition of union described by Nickerson (**22**) for double specimens of L. davenporti, except that the single stalk is much broader than normal.

Loxosoma claviforme Hincks (Text-figs. 6–7).

L. claviforme was discovered by Hincks (**13**, vol. i, p. 575) on Hermione hystrix from shallow water, Guernsey. He was somewhat doubtful of the validity of the species as his material had been long preserved in alcohol, and he admits that his diagnosis is very incomplete. The characteristics he gives are as follows: 'Body ovate; tentacles (probably) 10 or 12; peduncle somewhat longer than the body, tapering off gradually downwards, and terminating below in a short, foot-like expansion—the whole figure very regularly clavate when the tentacles are withdrawn; ? pedal-gland; only a single bud observed, placed about half-way down the body.'

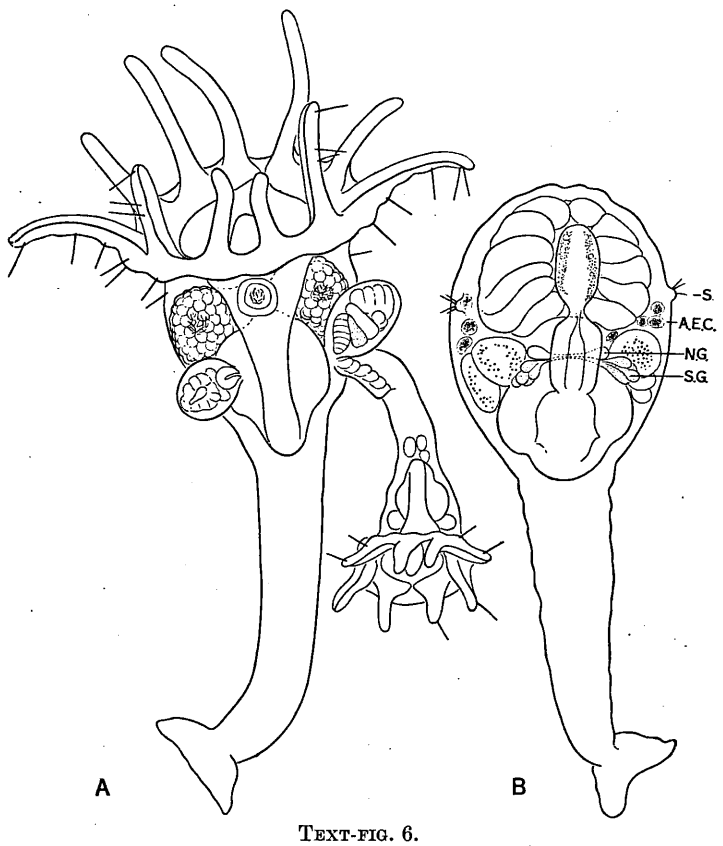
L. claviforme (Text-figs. 6–7) very closely resembles L. singulare (Text-figs. 4 and 5, pp. 337, 341) from Aphrodite aculeata, and Harmer thought it better provisionally to identify with this latter species the few specimens of Loxosoma he found on Hermione hystrix at Naples, until the distinctness of L. claviforme could be more satisfactorily shown (**9**, p. 263). He suggested to me that a renewed examination of these species was desirable, and with this object any specimens of Hermione brought in by S.S. 'Salpa' have been examined. Very few individuals have been obtained so far: two only carried Loxosoma, and one of these had been crushed so badly that the few commensals present were useless for identification purposes; the other had several dozen specimens in perfect condition, and from these it has been possible to work out the characteristics of the species. It is regrettable, however, that more 'colonies' were not obtained, as it is possible there may be some variation in form in different 'colonies'.

Habitat.

The Loxosoma occurred chiefly on the parapodia (Text-fig. 7, A, p. 348), being more numerous anteriorly and posteriorly, while a few were found on the ventral surface. In preserved specimens of Hermione from the Museum at the Laboratory, not only were they found on and between the feet, and practically all over the ventral surface, but also on the dorsal surface, where they were more abundant on the body-wall, beneath the elytra, than on the under-surface of the elytra themselves.

Description.

As previously mentioned, L. claviforme (Text-figs. 6–7) much resembles L. singulare, but differences in size, number of tentacles, position of the budding zone, and above all the presence of paired sense-organs in L. claviforme, clearly distinguish the two species. I have been unable to find sense-organs in L. singulare, though one or two stiff sense-hairs are present in this species in a similar position. The probable evolution of a sense-organ from a sense-cell (see Harmer, **9**, p. 274), makes the distinction between the two difficult when sense-organs are little developed. The sense-organs of L. claviforme are small papillae, bearing a few (3 to 6) stiff tactile hairs, situated one on either side of the calyx (Text-fig. 6, B), but as in L. crassicauda and L. phascolosomatum they are somewhat dorsal in position, and therefore difficult to see unless the animal is in a certain position. The vestibule, in individuals with embryos, becomes produced into two lobes or pouches, one on either side of the rectum, as in L. singulare (see p. 340) and L. leptoclini (**9**), and the sense-organs are on the outer side of these. Possibly their position has some reference to the safeguarding of the embryos while in the vestibule. They are roughly in the same position as those of L. phascolosomatum, but are slightly more distal than those of L. crassicauda, and are not so well developed. It has not been noticed that they are retractile, as are those of L. phascolosomatum. L. claviforme



TEXT-FIG. 6.

L. claviforme. A. Ventral view of living male individual with lophophore open. A small amount of sperm is present in the gonad of either side, and in the vesicula seminalis. The large bud is slightly abnormal in that the foot is short, and a foot-gland is absent, though the groove of the gland is present. B. Dorsal view of living unnarcotized female individual with closed lophophore to show the general clavate shape and the paired sense-organs (*S.*). Small clear globules are present in the ova. Yellow globules and fine granules are present in the cells of the side-walls of the rectum. *A.E.C.*, large yellow granular cells; *N.G.*, nerve ganglion; *S.*, sense-organ; *S.G.*, shell-gland. × *ca.* 115·6.

would seem to resemble Loxosomella antedonis Mort. (**19**), both in the general shape and size, and the position of the

budding zone, but the sense-organs of that species appear to be of a different type.

Stiff tactile hairs are present on the unciliated surfaces of the tentacles and scattered over the calyx (Text-fig. 6, A), as they are perhaps in all, or most, species of Loxosomatidae.

L. claviforme apparently attains a larger size than L. singulare, though size is perhaps rarely a reliable distinguishing character unless numerous specimens have been observed at different times. Living expanded individuals varied between 0·6 mm. and 1·0 mm. in length. Of 23 specimens measured, the average total length was 0·80 mm., with length of calyx 0·37 mm., and of stalk 0·43 mm. The average width of calyx of 22 specimens was 0·23 mm.: the stalk varied between 0·07 and 0·09 mm. in width. As the smallest specimen measured was 0·6 mm. in total length, while buds almost ready for liberation were about 0·32 mm. to 0·34 mm., it is probable that the averages are rather higher than they should be for comparison with those of L. singulare (see p. 338), in which the smallest specimen measured was only 0·18 mm. long.

In L. claviforme the stalk, on the whole, is longer in proportion to the body than in L. singulare; it is rarely shorter than the body, as is usual in L. singulare.

This species was named for its general clavate shape with closed lophophore (see **13**, vol. ii, Pl. 81, figs. 9 a and 10; and also Text-fig. 6, B, of this paper): L. singulare, however, with closed lophophore is sometimes of this shape.

The number of tentacles in the single 'colony' in which counts of these could be made was generally 12; actual figures are as follows: out of 23 specimens, 2 had 13 tentacles, 14 had 12 tentacles, 6 had 11 tentacles, and 1 had 10 tentacles. In L. singulare, on the other hand, the common number is 10; for example, out of 65 individuals, 3 had 11 tentacles, 47 had 10 tentacles, and 15 had 9 tentacles. Specimens of L. singulare with 12 and even with 13 tentacles have been seen, but are rare; there seems a distinct tendency in L. singulare to have a smaller number of tentacles than L. claviforme. Mature attached buds of L. claviforme 0·32 mm. and 0·34 mm. long had 8 tentacles.

Hincks says that the stalk ends in a 'short, foot-like expansion'; in the specimens on Hermione at Plymouth, however, the stalk ended in a small disc of attachment, sometimes perfect in shape, sometimes irregular—this may be Hincks's foot-like expansion—the form possibly depending on the contour of the surface of attachment. The disc, as in L. singulare, is fixed to the 'host' by a substance secreted by the foot-gland before it atrophies, and is not a sucking disc.

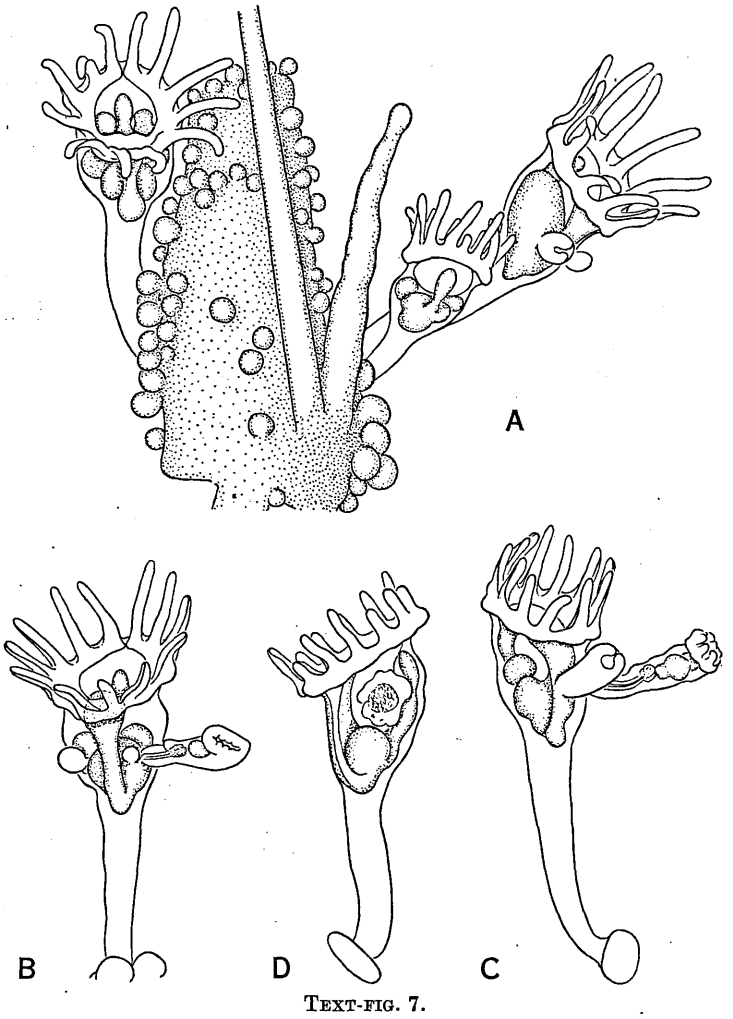
The stalk has longitudinal muscles only.

The budding zone (see Text-figs. 6, A; 7, B), as indicated in Hincks's fig. 9, Pl. 81, is rather more distal than in L. singulare, being in the region of the distal and ventral wall of the stomach. The greatest number of buds seen was two on each side; they are provided with a large foot-gland and groove. A few specimens were seen carrying slightly abnormal buds; the abnormality consisted in shortness of the foot, and absence of a foot-gland, though the groove of the gland was present (see Text-fig. 6, A).

The alimentary canal and generative organs of L. claviforme are similar to those of L. singulare. The cells of the side-walls of the rectum contain large yellow spherules and fine granules. The shell-gland of the female is large (Text-fig. 6, B). In the male the mature gonad is large, and the thick-walled vesicula seminalis is conspicuous (Text-fig. 6, A); a small amount of sperm was seen rotating in the vesicula seminalis of one individual.

A certain number of specimens in August and September carried embryos in the vestibule, the largest number seen being 6; it is possible, however, that the maximum number may be greater. No free larvae were seen.

Of 23 individuals examined for sex, 19 were female (13 with one or more embryos in the vestibule), 2 were male (1 with sperm, the other with a large gonad, though no sperm was visible), and 2 with the gonad too small for the sex to be determined. The females were between 0·64 and 1·0 mm. in length; the 2 males 0·6 mm. and 0·78 mm. long; and the 2 individuals in which sex could not be determined 0·9 mm. and 1·0 mm.



TEXT-FIG. 7.

L. claviforme. Sketches from life. ×57·25. A. Parapodium of Hermione hystrix with attached L. claviforme. Two of the individuals are females, one with embryos in the vestibule, and a large opaque ovum in the right half of the gonad. B. Ventral view of female. One embryo is present in the vestibule. The end of the stalk is surrounded by papillae of the host. C. Side view of female, with buds. D. Side view. One well-developed embryo, showing eye-spots, is present in the vestibule.

True nephridia are present on either side of the oesophagus. As in the other species described in this paper (see pp. 327, 340, 370), some (about six) large granular cells, yellowish in colour, are present on either side of the oesophagus (Text-fig. 6, B). The granules contained in these cells become dark red with neutral red intra-vitam staining.

L. claviforme may be distinguished from L. singulare by: (1) its greater size, with stalk generally longer than the calyx; (2) greater number of tentacles; (3) more distal position of budding zone; and in particular (4) the presence of paired sense-organs.

Loxosoma sp. with Abnormal, Sexually Mature Buds (Text-figs. 8–9).

Description.

A small group of about sixteen interesting Loxosomas was found on the anterior elytra and body-wall of a small Aphrodite aculeata about 9 cm. long, from the Mewstone Grounds in October 1930. While the habitat was that of L. singulare, the specimens appeared to be intermediate between that species and L. claviforme (see Text-fig. 8).

They agreed with L. singulare in:

1. The number of tentacles. Of 14 specimens, apart from abnormal buds, 2 had 11 tentacles, 9 had 10 tentacles, 2 had 9 tentacles, and 1 had 8 tentacles.
2. The absence, or minuteness, of sense-organs.

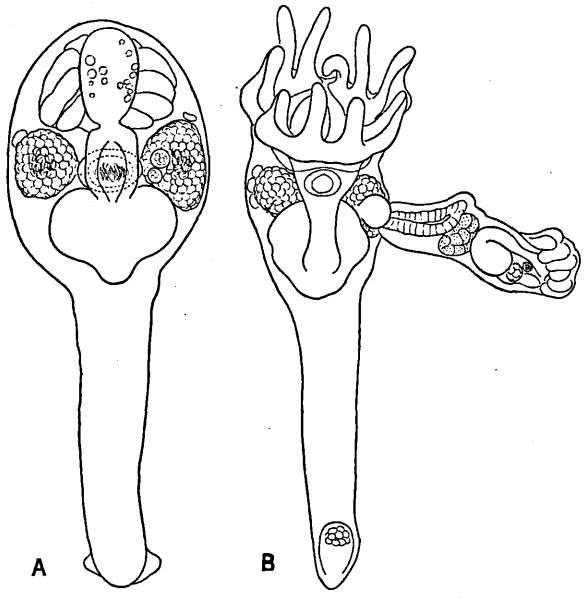
They agreed with L. claviforme in:

1. Size. The length of adults varied from 0·32 mm. to 1·075 mm.; the average length of 16 individuals being 0·69 mm., with length of calyx 0·33 mm., and of stalk 0·36 mm. The average width of the calyx of 12 individuals was 0·20 mm.; the width of the stalk varied between 0·05 and 0·09 mm.
2. The position of the budding zone in the majority of specimens (see Text-figs. 8, B, and 9, A).
3. The shape of the foot: in some individuals it was foot-like, as described by Hincks for L. claviforme.

The shape of the Loxosoma with closed lophophore

(Text-fig. 8, A) is that of L. claviforme, but possibly little importance attaches to this character, as L. singulare also may have this shape on occasion.

Most of the adults of any size were in a dirty condition,

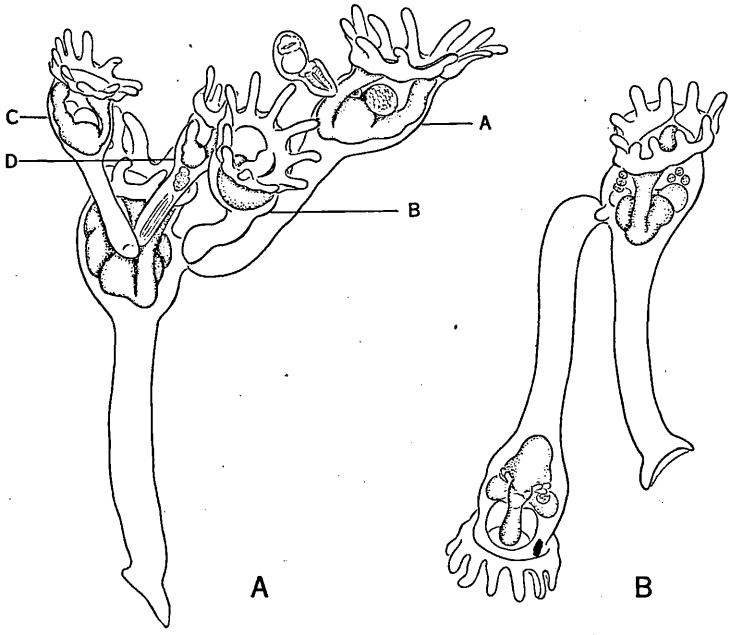


TEXT-FIG. 8.

Loxosoma sp. Living male individuals. ×*ca.* 115·6. A. Dorsal view of solitary adult with closed lophophore, to show the clavate shape. The large gonad contains sperm in both sides; also a small amount of sperm is present in the vesicula seminalis. On the right side two large cells, containing granules, lie dorsal to the testis. This individual had ten tentacles. Specimen unnarcotized. B. Ventral view of an abnormal 'bud', which became separated from the parent on lifting it. A few large cells at the base of the stalk are perhaps a vestige of a foot-gland. The gonad was composed of many small clear cells, but no sperm was present. The large bud, carried by this 'bud', appeared to be normal. By the appearance of the budding zone on the right side a bud had not long freed itself.

and with numerous fine, colourless threads (bacteria ?) attached to them. They had a granular appearance, and this, together with the particles adhering to them, made it difficult to see the inter-

nal organs. A peculiarity of the 'colony' was the number and size of the large granular yellowish cells (excretory cells?, see pp. 327, 340) present in the calyx on either side of the oeso-



TEXT-FIG. 9.

Loxosoma sp. Sketches of living individuals carrying abnormal buds. ×57·25. A. The parent is female, and has ten tentacles; of the 'buds' (*A*) has eleven tentacles and is a male, with vesicula seminalis full of sperm; (*B*) has ten tentacles and is a male; (*C*) has ten tentacles and appeared to be a young female; and (*D*) has eight tentacles and the gonad was too small for the sex to be determined. B. Sketch of a parent carrying an abnormal bud as large as itself. The sex of both parent and 'bud' is female.

phagus; in some individuals as many as fourteen occurred on either side.

Although several specimens had large ova in the gonad, none carried embryos in the vestibule.

A most interesting peculiarity of six of the sixteen specimens (37½ per cent.) was the retention of the buds (Text-fig. 9), so

that in an extreme case the bud was as large as the parent (see Text-fig. 9, B), and in some instances itself bore good-sized buds, which might be normal (Text-fig. 8, B). The abnormality seemed to consist in the absence of a heel to the foot, though a foot-gland and canal were present in at least some buds, and the gland functioned judging by the debris collected round the point of attachment of the abnormal bud to the parent. In normal buds the muscular foot would appear to play an important part in the liberation of the bud from the parent, and the inability of these buds to free themselves, most probably, was due to the abnormality of the foot. As previously mentioned a few specimens of L. claviforme (see Text-fig. 6, A, p. 345) from Hermione hystrix bore abnormal buds in which the foot was short, and though the foot-gland itself was absent, its groove was present.

Sex of the Buds.

The continued attachment of the 'buds' to the parents, resulting in 'buds' with mature gonad, made it possible to obtain some information on the question of the sex of the bud. Vogt (**36,** p. 335) says of L. phascolosomatum '... m'engage à penser que le sexe des bourgeons doit être celui des individus sur lesquels ils ont été produits'. From the few specimens with abnormal buds in this small colony it is evident that though the sex of the bud may be that of the parent, it is by no means always so. The sex, size, and number of tentacles (where these could be determined) of the six individuals and their abnormal buds is given in the table on p. 353.

From the fact that a parent may bear buds of different sex from itself, it seems very probable that in this form at least there may be a change of sex.

In this small colony there was little difference in the proportion of the sexes. Of the sixteen adults examined, eight were female, six were male, one had the gonad too tiny for sex to be determined, and one had one side of the gonad male, though the female shell-gland was present. Females were on the whole of larger size than the males, but the numbers are much too small for the results to be of value. It might be noted that the single

Parent.			Buds.		
	Sex.	*Total length in mm.*	*No. of tentacles.*	*Sex.*	*Total length in mm.*	*No. of tentacles.*
(1)	♀	0·9	?	(*a*) ♂ (see Text-fig. 8, B)	0·6	10
	—	—	—	(*b*) ♂?	0·64	10
(2) ♀ (see Text-fig. 9, A)		1·075	10	(*a*) ♂ (large gonad; vesicula seminalis full of sperm)	0·8	11
	—	—	—	(*b*) ♂ (large testes)	0·55	10
	—	—	—	(*c*) ♀ (young)	0·475	10
	—	—	—	(*d*) sex indeterminate	0·35	8
(3)	♀	0·78	11	(*a*) ♂?	0·35	?
	—	—	—	(*b*) too tiny for sex to be determined	0·36	8
	—	—	—	(*c*) too tiny for sex to be determined	0·34	8
(4) ♀ (fairly large ova)		0·65	10	(*a*) ♂	0·39	10
(5) ♂ (sperm in gonad)		0·65	?	(*a*) ♀ (recognizable ova)	0·46	10
(6) ♀ (see Text-fig. 9, B)		0·86	10	(*a*) ♀	0·86	10

specimen which seemed perhaps intermediate in sex was very near in size to the largest male and the smallest female. Sections of this individual confirmed the presence of a large shell-gland, and of sperm in the gonad of one side. The gonad of the other side could not be distinguished, and its place was occupied by very large granular excretory cells. No vesicula seminalis could be made out. It is perhaps possible that this individual was abnormal rather than intermediate in sex.

There is perhaps some slight possibility that the specimens forming this small 'colony' are hybrids between L. singulare

and L. claviforme. The number of individuals which have indefinitely retained their buds perhaps shows that there is something abnormal in their constitution, though abnormal buds of a similar type, though not sexually mature, have been found in L. claviforme (see p. 347), and among a colony of individuals (those in a small tank in the Aquarium) with all the characteristics of L. crassicauda (see p. 332).

There seems to be no reason why L. claviforme should not be found on Aphrodite, or L. singulare on Hermione.

Loxosoma obesum sp. nov. (Text-figs. 10–24).

Habitat and Distribution.

L. obesum[1] is found on Aphrodite aculeata; living specimens were first obtained during a visit to the Plymouth Laboratory in 1923. This species occurs on the dorsal surface of the worm and on the under-surface of the elytra; on two occasions only a single specimen has been found on the ventral surface, where L. singulare is most frequently taken. The Loxosoma is roughly restricted to the anterior half of each elytron, this being the only part which has a free surface to the space beneath; the posterior half overlaps the anterior half of the elytron behind, and the two surfaces come into close contact during rhythmical movement of the elytra. The Loxosoma inhabits a kind of respiratory chamber, for in Aphrodite the function of respiration is carried out by the thin dorsal body-wall, and a current of water is kept continually moving over it in an antero-posterior direction by the rhythmical movement of the elytra (**7, 8**). The water enters the 'chamber' by percolating through the felt which acts as a strainer, preventing the entry of fine mud; it is forced out of a posterior aperture by the depression of the elytra on to the dorsum, the movement beginning with the anterior pair and passing backwards (see Fordham, **8**). The Loxosoma is therefore well situated in relation to a presumably food-bearing current. In Aphrodite, which have their respiratory surface very thickly

[1] I am indebted to Sir S. F. Harmer for suggesting the name.

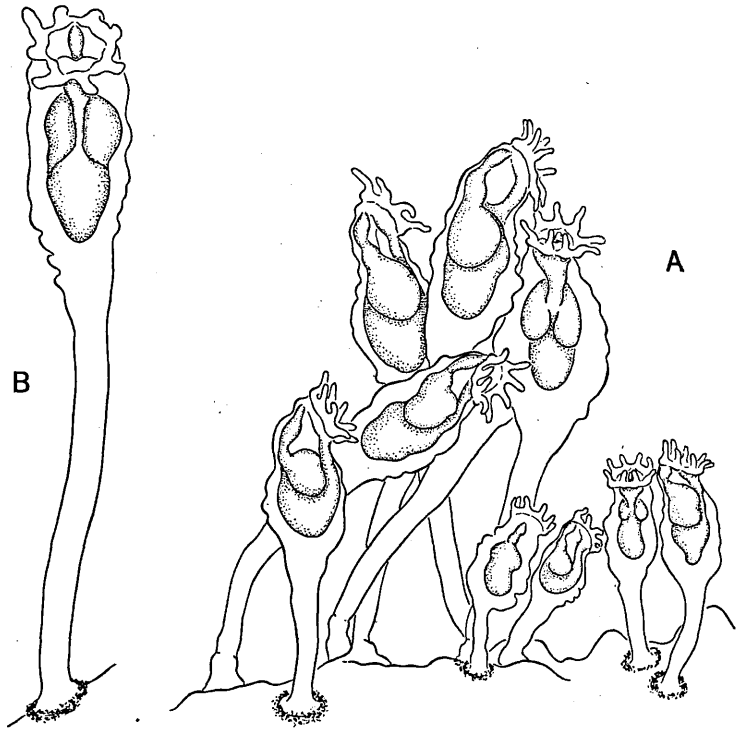
covered with large Loxosomas, it seems possible that they may interfere with respiration. Whether on the elytra, or on the dorsal surface of Aphrodite, the Loxosoma is practically confined to the posterior two-thirds of the worm; L. singulare is not thus restricted in position (see p. 342). In those worms in which great numbers were found, they were absent anteriorly to the seventh pair of elytra. This restriction in position doubtless has a close connexion with the conditions existing beneath the elytra; possibly the current in the anterior third of the 'chamber' is feeble compared with that in the more posterior part, but it is worth noting that it is from the anterior part of the worm that nephridia are absent. The genital products of Aphrodite, together with the coelomic fluid and its contents, pass by way of the nephridiopores into the current beneath the elytra, and may just possibly form an additional source of food for the Loxosomas.

While L. singulare has been found, though mostly in small numbers, on a fair percentage (39·7 per cent.) of Aphrodite examined, L. obesum is rather rare, though when the worm is infected, it is generally heavily. Out of a total of 146 Aphrodite examined between October 1927 and October 1930, only eighteen were infected, that is, 12·3 per cent. Infected worms have been obtained chiefly from the Looe and Rame Eddystone Grounds, though one carrying a few L. obesum came from the Outer Mewstone Grounds.

Description.

L. obesum is a large species; individuals may reach a length of 2·4 mm., while average individuals are rather more than 1·0 mm. in length. Several other large species of Loxosoma are known, but all differ from L. obesum in having a much larger number of tentacles; L. davenporti (**23,** pp. 352 and 374), 0·74–2·4 mm. in length, has 18 to 29 tentacles; L. kerfersteini (**25,** pp. 364, 365, 367), about 1·4 mm. long, has 14 tentacles; L. crassicauda, up to 1·87 mm. long, has 16 to 18 tentacles; L. phascolosomatum (**36**), about 1·8 mm. long (**6,** p. 59), has 12 to 18 tentacles; and L. lanchesteri (**12,** p. 5), up to 1·23 mm. long, has 20 or more tentacles.

In L. obesum (Text-figs. 10–13) the lophophore is small and circular, the small size being especially striking in large individuals. The number of tentacles is very constantly 8, but

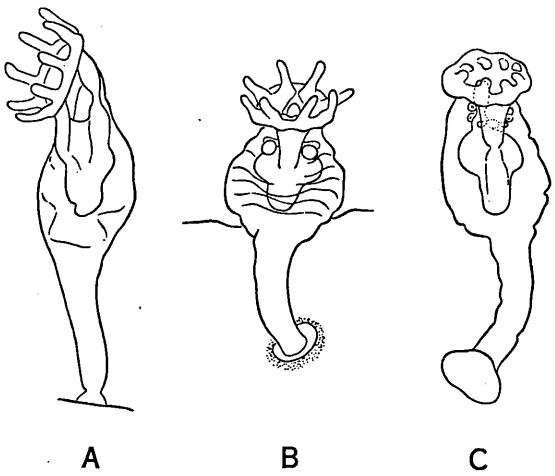


TEXT-FIG. 10.

L. obesum. Living individuals. A. A small group on an elytron of Aphrodite aculeata, showing the general appearance of the type with normal development of the stomach. The gonads were immature, and are not shown. ×41·4. B. An individual of very elongated form from the same elytron as the group sketched in A. ×57·25.

in one infection 2 out of 58 individuals examined had 9 tentacles, while later 1 was seen with 10 tentacles. L. cochlear Schmidt (**31**) and L. pusillum Harmer (**12**, Pl. I, figs. 19 and 20), 2 species which also have 8 tentacles, have a large

lophophore in proportion to the width of the body, as compared with that of L. obesum. The tentacles are short and small. In specimens in which the gonad is immature the calyx narrows considerably just below the lophophore (see Text-fig. 10); proximally it is generally clearly marked off from the stalk, which varies considerably in length (cf. Text-figs. 10 and 13, A),



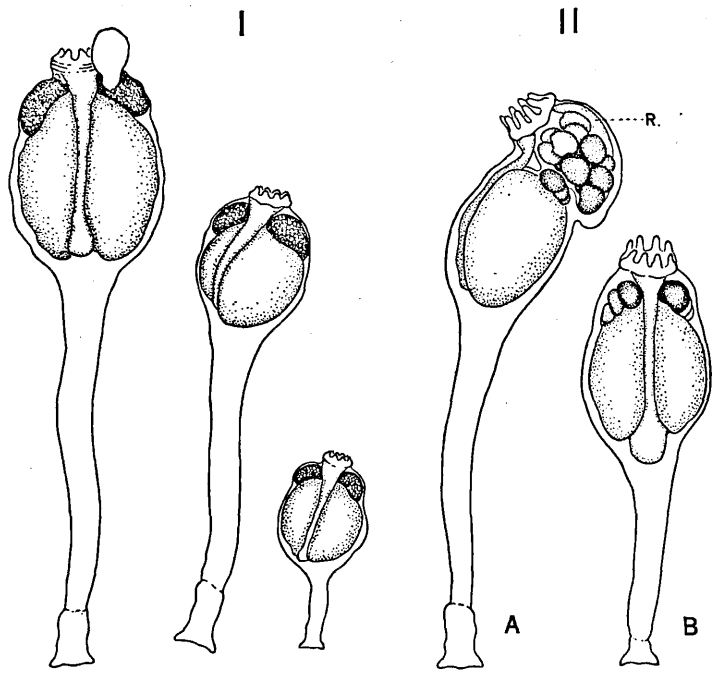
TEXT-FIG. 11.

L. obesum. Small individuals with normal development of the stomach. A. Side view of living specimen with lophophore well expanded and distinctly oblique in position. ×63. B. Ventral view of specimen mounted unstained in glycerine, showing slight development of wings owing to the contraction of the muscles of the calyx. A tiny bud is present on either side. ×57·25. C. Ventral view of living, immature male, with lophophore partly closed. Two large cells, with greenish yellow central granules, are present on either side of the oesophagus. ×63.

and may be anything up to half to two-thirds of the total length. The stalk ends in a disc of attachment (not a sucking disc); in the larger specimens the cuticle of the lower part of the stalk may be thickened and brownish in colour (Text-fig. 12), and there is generally a collection of dirt particles round the base of the stalk. Longitudinal muscles only are present in the stalk.

In the buds a large foot-gland, with its groove, is present; this is preserved as a vestige only in many adults, while it is absent in others.

Variation in Shape of the Calyx.—L. obesum,



TEXT-FIG. 12.

L. obesum. Living individuals with large, swollen, oval-shaped stomachs. I. Three mature males to illustrate the variation in size of mature males. The two largest individuals had the end of the stalk thickened and brownish in colour. The almost terminal position of the tiny lophophore in mature males is well shown in these specimens. ×35·5. II. Mature females. A has an enlarged vestibule containing many embryos. A. ×35·5; B. ×49·1. *R.*, rectum.

with its marked variation in the shape of the calyx in different individuals, is a striking example of the difficulty of defining satisfactorily species of Loxosoma which have no specialized structures, such as sense-organs, cirriform or glandular organs.

In some instances (see Text-figs. 10–13) it is difficult to believe that the animals are of the same species, except for the constant characteristics, the number of tentacles and small size of the lophophore, and the habitat.

L. obesum occurs under two main forms or phases: (1) the one in which the stomach is normally developed for the family (Text-fig. 10); and (2) the other in which the stomach, owing to the exceptional development of the so-called liver-cells, is much enlarged, occupying by far the greater part of the calyx (see Text-figs. 12, 13).

(1) In individuals with the stomach normal in size, the calyx may vary between the broad form (Text-fig. 10, A) and the very narrow and elongated (Text-fig. 10, B), the shape, no doubt, depending to a large extent, if not wholly, on the degree of muscular contraction. (Both figures are of individuals narcotized with stovaine.) Text-fig. 10 A and B, are of individuals in the same 'colony' or infection, but the same animal was not observed actually to change from one form to the other. Text-fig. 11 A–C, are of small individuals of this type. The stomach varies somewhat in shape; it may be distinctly elongated with well-marked lateral lobes, and there may be a large apical region, or it may be almost round, the lateral lobes only indicated by the greater depth of their cells. This variation in shape is evidently due to the great contractility of the animal. The 'liver'-cells are about 0·03 to 0·06 mm. deep in individuals about 1·0 mm. long.

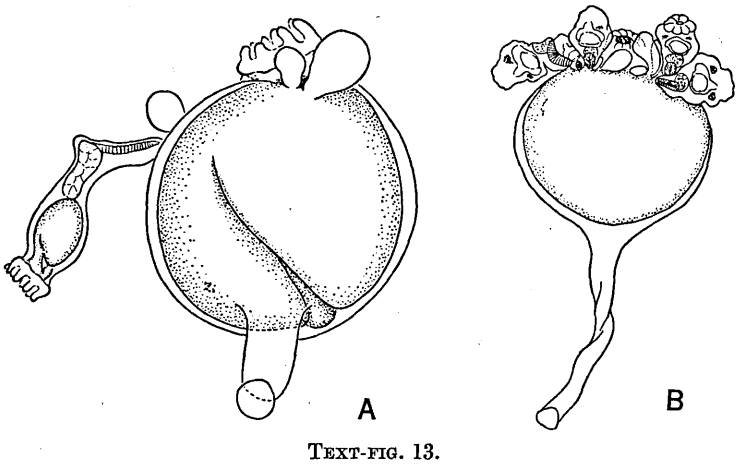
(2) In individuals with much enlarged stomach the calyx may be of two forms:

(*a*) Oval, with the stalk about one-half to two-thirds of the total length (Text-fig. 12). Of ten such individuals, measured with lophophore expanded, the average total length was 1·42 mm., with length of calyx 0·70 mm., and of stalk 0·72 mm.; the average width of the calyx was 0·42 mm., and that of the stalk 0·09 mm.

(*b*) Globular with stalk one-half or less of the total length (Text-fig. 13, A). Measurements of sixteen living individuals, with lophophore more or less closed, gave the following average measurements: total length

0·87 mm., with length of calyx 0·50 mm., and of stalk 0·37 mm.; width of calyx 0·44 mm.

A variation, apparently, of this type, is the form with the calyx much flattened dorso-ventrally, or disc-shaped (Text-fig. 13, B); this is a rare form and has only been seen in individuals of one small 'colony' found on a preserved Aphrodite.



TEXT-FIG. 13.

L. obesum. A. Living individual with large round stomach, and short stalk. Gonad immature, and not shown. ×57·25. B. Individual with large stomach, but the calyx much flattened dorso-ventrally. Five buds are present on either side of the calyx. Preserved material. × *ca.* 41·4.

In 'colonies' individuals with enlarged stomachs are mostly either of one form or the other; it possibly depends on the condition of the stomach.

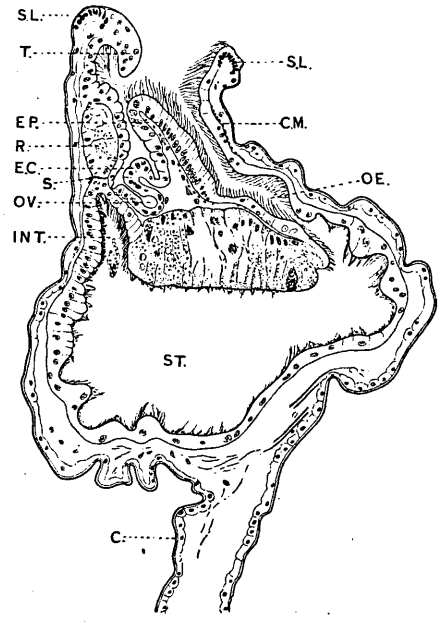
It is characteristic of L. obesum that in the greater number of 'colonies' examined, while most young individuals have the stomach more or less normal, with the so-called liver-cells not unusually developed, the medium and large specimens show an extraordinary development of these cells. They attain a great depth—0·09 mm. or more—and become crowded with granules, while the lobes extend proximally, the apical portion

of the stomach being very small (cf. Text-figs. 12 and 13 with Text-fig. 10). Owing to their extreme development the stomach is much swollen, occupying the greater part of the calyx, and the living animal appears as an opaque white or cream-coloured ball, easily visible to the unaided eye. When the animals are crushed, masses of clear granules of varying size stream out. The granules are on the whole discrete, but a number of oval or pear-shaped collections of granules or globules, 60μ to 80μ long, would appear to be contained in small cells.

The significance of this heaping up of, presumably, reserve products is not understood; it is suggested that it may be connected with the production of sex cells, and, or, with the reproduction of the animal by budding. It is found indiscriminately in males and females. While perhaps the majority of 'colonies' in this condition have been breeding or budding, some have had the gonad immature and with no indication of buds; on the other hand, at least one 'colony' with the stomach in a normal condition had some individuals carrying embryos in the vestibule, though the number carried simultaneously in this instance was very small—one only, with few exceptions, and that well developed; the gonad in the majority of these females contained only small or medium-sized ova. (Some individuals with immature gonad from this 'colony' are shown in Text-fig. 10.) That the great development of the 'liver'-cells is a normal phase in the life-history of L. obesum is evident from the fact that the majority of individuals, which may reach some hundreds or even thousands on each 'host', from 14 out of 20 infected Aphrodite were in this condition. L. obesum with highly developed 'liver'-cells have been found in February (8 out of 9 'colonies' in 1928), March (4 out of 4 'colonies' in 1930), and in September (2 out of 7 'colonies' in 1923).

Alimentary System.—The general form of the alimentary canal may be seen from Text-fig. 14. The oesophagus, which is lined with columnar, highly ciliated cells, showing well-marked ciliary rootlets, opens into the stomach about halfway down on its ventral face (Text-figs. 10 and 11), though the position varies somewhat. In most known species the opening of the oesophagus is nearer the proximal apex of the stomach,

as in L. crassicauda (Text-fig. 1, B, p. 325), L. singulare (Text-fig. 4, p. 337), and L. claviforme (Text-fig. 6, A, p. 345). Along the ventral face of the stomach there is a groove of low ciliated epithelium leading from the oesophagus to the apical region of the stomach, which in turn is continuous with



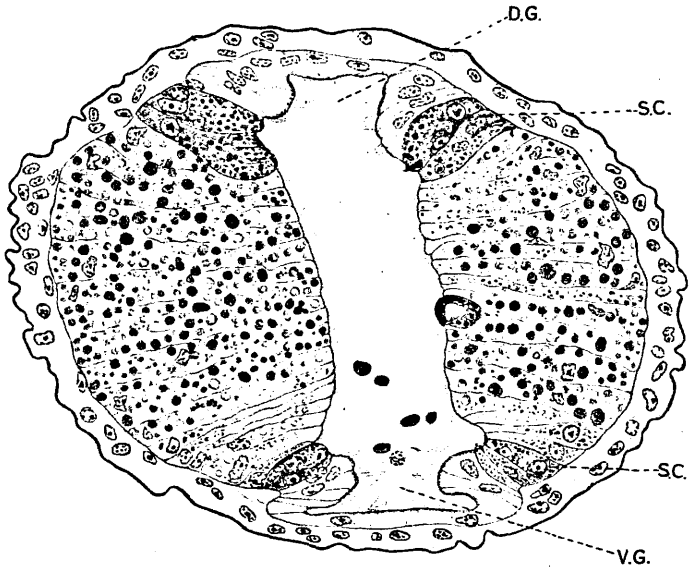
TEXT-FIG. 14.

L. obesum, female. Longitudinal section passing through the oesophagus, stomach, intestine, rectum (surface), and through the ventral and dorsal grooves, connecting the lumen of the oesophagus and intestine, respectively, with the apical region of the stomach. *C.*, cuticle; *C.M.*, circular muscles of oesophagus; *E.C.*, projection on floor of vestibule to which embryos become attached; *EP.*, epistome; *INT.*, intestine; *OE.*, oesophagus; *OV.*, oviduct; *R.*, rectum; *S.*, sphincter between intestine and rectum; *S.L.*, sphincter muscles of lophophore; *ST.*, stomach; *T.*, tentacle. × *ca.* 202·6.

the lumen of the intestine by a dorsal groove lined with a similar type of epithelium (Text-fig. 15). In forms in which the oesophagus opens low down on the ventral face of the stomach only

the dorsal groove is found, as in L. saltans (**1**, p. 128) and in L. crassicauda.

Narrow tracts of secretory cells are present on either side of the ventral and dorsal grooves, intervening between them and the lateral diverticula (Text-fig. 15); and are continuous round the apical region of the stomach, separating the cells of that region from those of the lateral lobes. In some species, notably



TEXT-FIG. 15.

L. obesum. Section transverse to the long axis of the body, passing through the stomach below the level of the entry of the oesophagus, and showing the ventral (*V.G.*), and dorsal (*D.G.*) grooves. On either side of the grooves are narrow tracts of secretory cells (*S.C.*). The 'liver'-cells contain many granules: a single gland-cell is present among the ends of the long 'liver'-cells of one side. The stomach was full of a coagulum which is not shown. Bouin's fixative; iron haematoxylin and acid fuchsin. × *ca.* 430.

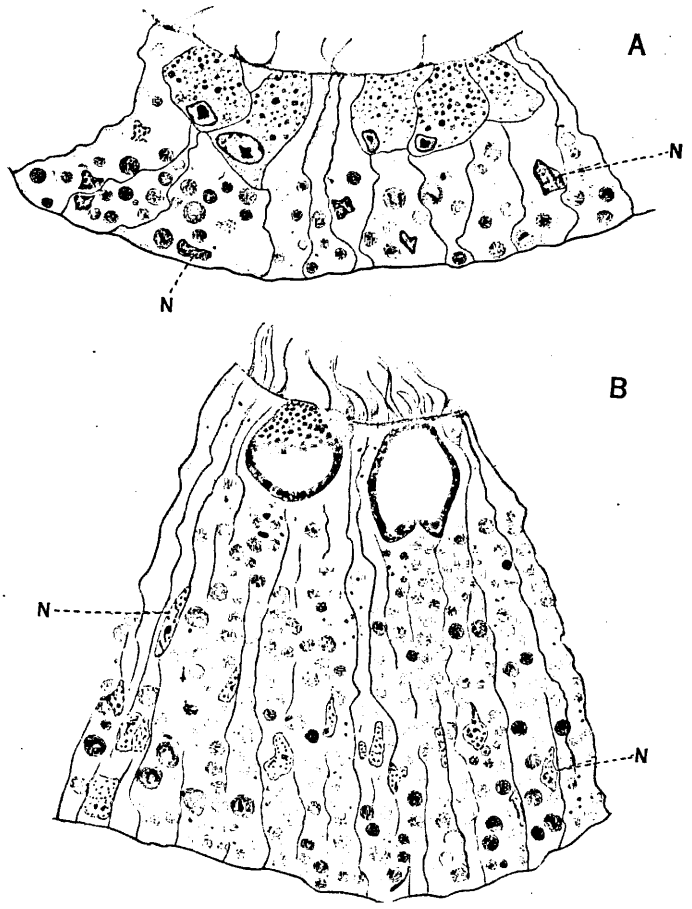
L. loxalina (**1**, p. 121), L. saltans (**1**, p. 129), and L. davenporti (**23**, p. 362) the two semicircular tracts surrounding the apical region appear to be highly developed, forming definite lobes. The appearance of the contents of the cells varies

in different phases of activity. In some cells they may be either finely or coarsely granular, staining with orange G, but not with Heidenhain's iron haematoxylin; in others the granules are larger, and stain darkly with haematoxylin; while in some the staining is so intense that separate granules cannot be distinguished. The contents of these cells appear not to be mucoid in character, as they do not stain with Mayer's mucicarmine or muchaematein. They possibly secrete digestive enzymes. The nuclei are basal, large, round, and with most of the chromatin collected in centrally placed nucleoli.

In L. crassicauda there is a similar disposition of secretory cells, except that the ventral groove is short or absent.

The cells of the lateral lobes of the stomach are lowest where they pass into the tracts of secretory cells (Text-fig. 16, A), but in some parts may reach a great depth, 0·09 mm. or more, although narrow (Text-figs. 16, B; 17). Salensky (**29**, p. 9) gives the depth of the 'liver'-cells of L. tethyae as 0·001 mm.; in this species individuals are about 0·5 mm. long. In L. crassicauda, of which the length of average individuals is about 1·4 mm., they are about 0·025 mm. to 0·05 mm. in length.

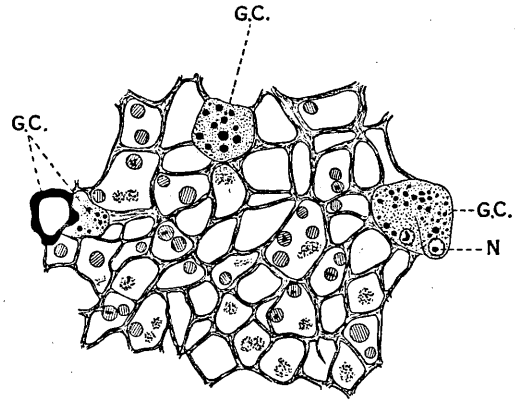
In specimens of L. obesum with the stomach much enlarged the so-called liver-cells are so crowded with coarse spherical inclusions of varying size that the cell-walls and nuclei are difficult to distinguish. The amount of cytoplasm present is extremely small, even when granules are few. The granules stain with varying intensity, most more or less uniformly, but less frequently some occur with a darker staining periphery, while others contain an irregular centre, staining darkly with haematoxylin (see Text-fig. 16). There is some tendency for the granules to collect towards the basal part of the cell. In some individuals very few vacuoles are present in the 'liver'-cells (resting phase?) (Text-fig. 16); in others they are numerous. The contents of these are of at least three kinds. Large vacuoles occur containing rounded masses of the same type of granule as is present free in the cell (V^1, Text-fig. 18). Such masses are seen protruding beyond the free margin of the cells (Text-fig. 19, A), and there is no doubt that they are discharged,



TEXT-FIG. 16.

L. obesum. Longitudinal sections through the epithelium of the lateral diverticula of the stomach. ×735. A. Short cells towards the edge of a diverticulum. Very few granules are present in the cells. Two groups of gland-cells are present, with granules staining with eosin. Bouin's fixative; Delafield's haematoxylin and eosin. B. Long cells, with very few vacuoles (resting-phase?). Two small vacuoles, with minute inclusions, occur near the free edge of the cells, and are probably secretory. The granules stain faintly with orange G, but some have centres staining intensely with iron haematoxylin. Between the ends of the 'liver'-cells are two small groups of gland-cells with granules staining intensely with iron haematoxylin. Bouin's fixative; iron haematoxylin and orange G. *N*, nucleus.

as similar collections of granules occur free in the lumen of the stomach. In this species, as in L. davenporti (**23,** p. 363), excretion is not confined to the rectal cells (see Assheton, **1,** pp. 134–5). Other fairly large vacuoles, which seem to increase in size towards the base of the cells, contain a finely granular material, staining black with iron haematoxylin, which in sections appears as a fine semicircle (V^3, Text-fig. 19, A). Possibly the greater part of the contents has disappeared during the



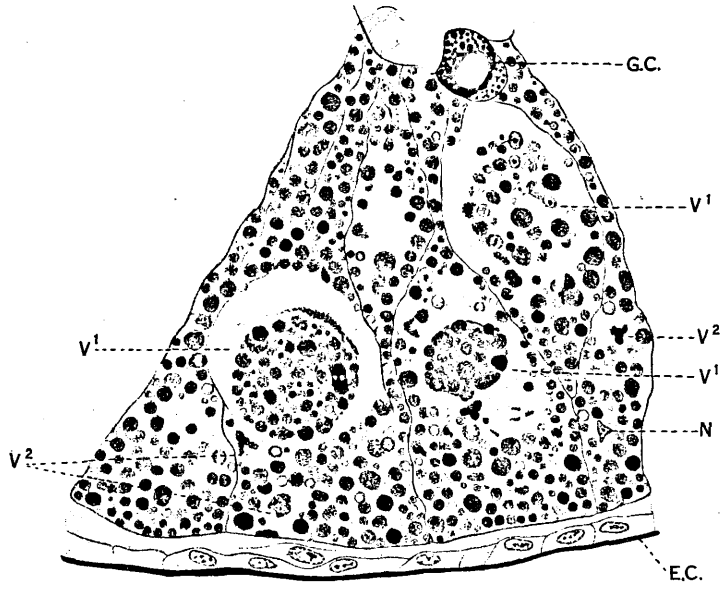
TEXT-FIG. 17.

L. obesum. Transverse section of 'liver'-cells, towards their free ends, passing through three groups of gland-cells (*G.C.*). Within the cells are granules, some with darkly staining centres, and small collections of fine granules staining grey with haematoxylin. *G.C.*, gland-cell; *N*, nucleus of gland-cell. Osmic fixation; iron haematoxylin and eosin. ×735.

process of fixation and dehydration. Individuals which have many of these vacuoles would seem to have few of the first type. Finally, small vacuoles occur containing a small finely granular mass, staining intensely with Heidenhain's iron haematoxylin (V^2, Text-figs. 18, 19, A). These may be seen at the free margin of the cells, and possibly contain secretory granules.

The nuclei are irregular in shape, with a small amount of scattered chromatin. They occur mostly in the basal third of the cells. The cells of the lateral diverticula of L. loxalina and L. saltans (see Assheton, **1,** pp. 121 and 128) are said

to be unciliated, as are also those of L. davenporti (see Nickerson, **23,** p. 362), while those of L. crassicauda (**9** p. 276) are said to be ciliated. In L. obesum the 'liver'-cells appear to occur both in a ciliated and a non-ciliated phase: when the cells are actively excreting, cilia are absent, no doubt



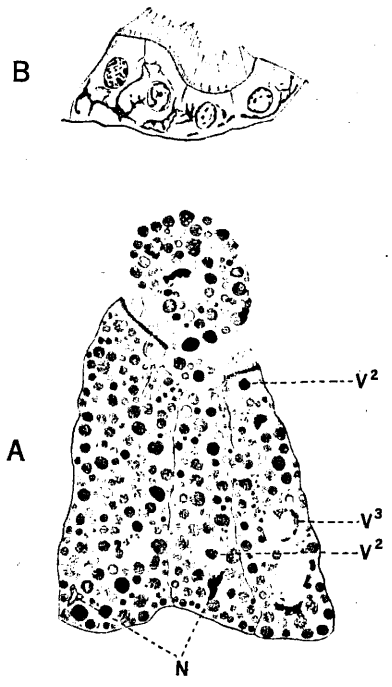
TEXT-FIG. 18.

L. obesum. Longitudinal section through the epithelium of a lateral lobe of the stomach. Two kinds of vacuoles are present: V^1, large vacuole containing large collection of very coarse granules; V^2, vacuole with finely granular contents staining intensely with iron haematoxylin; *G.C.*, gland-cell; *E.C.*, external cuticle of body; *N*, nucleus. Bouin's fixative; iron haematoxylin and acid fuchsin. ×735.

having been shed or absorbed. It is possible that this may occur in the other species mentioned; it does occur in L. crassicauda.

The 'liver'-cells in the only four individuals of L. crassicauda sectioned had a very different appearance from those of L. obesum. Granules were exceedingly few or absent,

but this may be an unusual condition as the animals were living in a tank in the Laboratory, and therefore without abundant food. That granules do occur in the cells is evident from



TEXT-FIG. 19.

L. obesum. ×735. A. Longitudinal section through epithelium of lateral lobe of stomach, to show extrusion of rounded mass of granules. *N*, nucleus; V^2, vacuole containing finely granular mass staining intensely with iron haematoxylin; V^3, vacuole with crescentic arrangement of fine, intensely staining, granules. Bouin's fixative; iron haematoxylin and acid fuchsin. B. Longitudinal section through epithelium of apical region of stomach showing anastomosing strands, which stain intensely with iron haematoxylin. Bouin's fixative; iron haematoxylin and orange G.

Harmer's statement (**9**, p. 276). The cytoplasm was much more abundant than in the corresponding cells of L. obesum. The free ends of many of the cells were rounded, projecting

into the lumen, and it seemed as though they were being set free into the stomach. This is probably a secretory phase. In L. obesum a very few individuals have been observed with somewhat rounded ends to the cells; the cells contained exceedingly few granules, though the cytoplasm was still small in amount. In one L. crassicauda sectioned certain of the 'liver'-cells were dividing transversely, and the free half being shed. Of such parts of cells occurring free in the stomach, some at least contained a nucleus, or degenerating nucleus. An appearance as though parts of cells were being shed has been observed in L. obesum, though here the granules were so numerous that no nucleus was discernible, and it was difficult to distinguish with certainty such a condition from the excretion of large masses of granules.

In L. obesum short gland-cells occur in occasional groups of two or three, between the free ends of the long 'liver'-cells (Text-figs. 15–18). In these the rounded or oval nucleus is basal, and has a large nucleolus. These cells are not mucus-glands, as they are unstained by Mayer's mucicarmine or muchaematein. I have been unable to distinguish any mucus-glands in the alimentary canal of L. obesum, though Assheton (**1**, p. 128) found a few among the cells of the apical region of L. saltans, and mucus is said to be secreted in the stomach of Pedicellina (Cori, **6**, p. 36).

The cells of the conical lower apex of the stomach are low and highly ciliated (Text-fig. 19, B); a similar type of cell lines its ventral and dorsal grooves. In life these cells contain small shining colourless globules; they blacken with Flemming's fluid and are probably fat globules. Assheton suggested for L. saltans that these cells were absorptive (**1**, p. 129). In material fixed in Bouin's picro-formol and stained with Heidenhain's iron haematoxylin, the cells, especially of the apical region and dorsal groove, of some individuals are seen to have anastomosing strands, or fibrils, staining intensely (Text-fig. 19, B), and in some individuals they are so numerous that the cells appear almost full of them.

The intestinal epithelium is densely ciliated, the cilia being thick and fairly short, and staining with iron haematoxylin.

The cytoplasm of these cells is denser than in other parts of the alimentary canal.

The side-walls of the rectum frequently contain large, pale yellow to orange, refringent, excretory spherules and fine granules. So far as could be ascertained the cilia are not restricted to the ventral and dorsal walls as in L. saltans (1, p. 133). In embryo-carrying females the rectum is of great length, stretching across the roof of the enlarged vestibule to open in its normal position (Text-fig. 12, II, A, p. 358).

Excretory System.—A variable number of large excretory or accretory cells (see p. 327), up to twelve or more, are present in the calyx on either side of the oesophagus (Text-fig. 11, c, p. 357). On a trace of neutral red being added to the sea-water, the granules in these cells after a time become dark red: with methylene blue they take a blue tint.

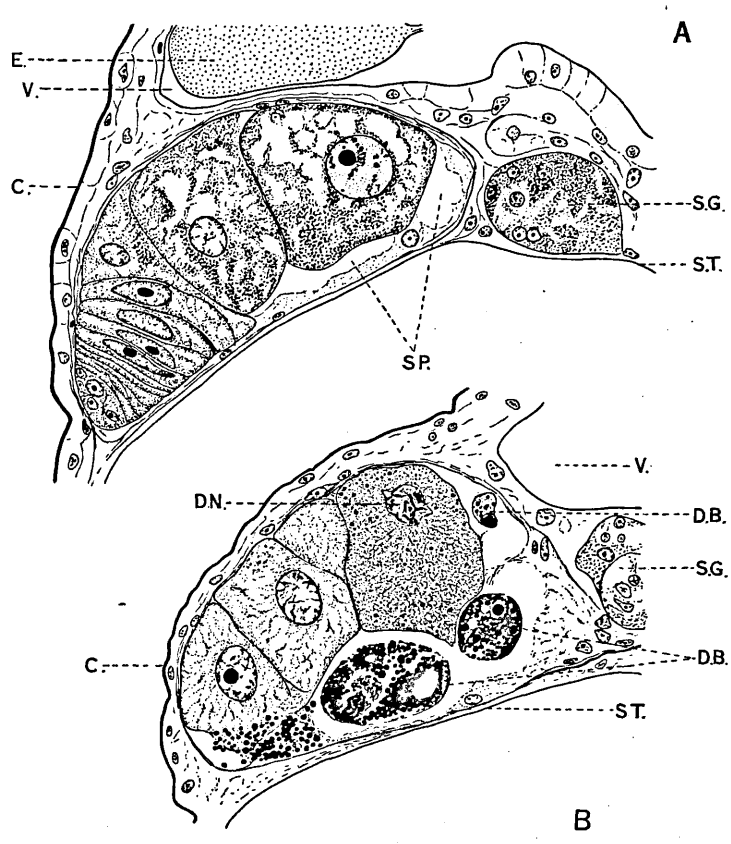
True nephridia were not observed in the living animal, probably owing to the difficulty of observation, but indications of them were seen in sections.

L. obesum has no special organs of sense: a nerve ganglion is present in the usual position, but nerves cannot be traced in the living animal as can be done in L. crassicauda.

Reproductive System.—The sexes, so far as is known at present, are separate, but few sections (about fifty animals) have been examined, and in the living animal degenerating sperm or ova would be difficult to identify. The gonad is paired: the mature testes may reach a large size; the mature ovary is relatively smaller. Spermatozoa when crushed out of the gonad, or vesicula seminalis, are either motionless or undulate slowly. They are thin, with fine tails, and are about 45μ long.

In living individuals in which the calyx has become blown out, as a result of the degeneration of the gelatinous matrix, the muscles can be seen clearly. Owing to the degeneration of the most mature ova rendering it visible, the ovary is seen to be surrounded by a delicate structureless membrane, to which muscle-fibres are attached.

In young females before reproduction is in full swing there appears to be only one well-developed ovum, and several small or tiny developing ova in the gonad. The peculiar flattened



TEXT-FIG. 20.

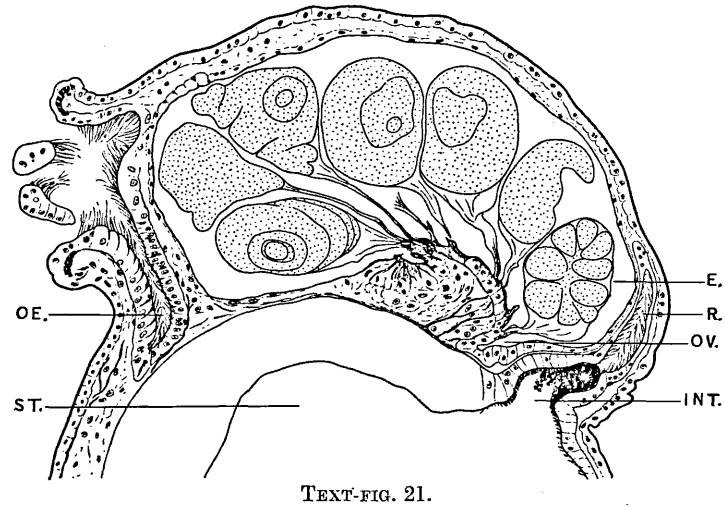
L. obesum. A. Obliquely longitudinal section through ovary, in which two large ova are present; the space (*SP.*) indicates that a ripe ovum has not long been extruded. The flattened and tiered arrangement of the young ova at the lower, blind end of the gonad is noteworthy. Flemming's fluid without acetic acid; iron haematoxylin and acid fuchsin. B. Section through ovary to show presence of degenerating bodies (*D.B.*) composed of globules staining black with iron haematoxylin, as do the yolk globules. Three ova of considerable size are seen in the section; the nucleus (*D.N.*) of the largest is degenerating. Bouin's fixative; iron haematoxylin and acid fuchsin. *C.*, external cuticle of calyx; *E.*, embryo; *S.G.*, shell-gland; *ST.*, outline of stomach; *V.*, vestibule. × 342·5.

and tiered arrangement of the young ova at the lower, blind end of the gonad is shown in Text-fig. 20, A. In individuals reproducing rapidly there may be four to six good-sized ova in each side of the gonad, though the oldest is distinguished by its greater size and greater opacity. When it is considered that the vestibule may contain as many as twenty-four to twenty-six embryos at one time, it is understandable that ova are likely to be approaching ripeness in fairly rapid succession. The ripe ovum is about 0·1 mm. in diameter, heavily yolked and opaque. As noted by Vogt for L. phascolosomatum (**36,** p. 326) an ovum attains ripeness on either side alternately. Rounded bodies have been observed in the ovary of living specimens, which did not appear to be ova; they had a definite dark outline —like that of a bubble—and contained a number of shining globules of varying size. As many as six have been seen in one-half of the gonad, varying from 0·02 mm. to 0·05 mm. in diameter. These were observed in individuals which had been kept in finger-bowls for several days, and it is possible that they were derived from degenerating ova. Similar bodies have been seen in the ovary of living L. claviforme. It may be noted, however, that Harmer (**9,** p. 282) described in L. tethyae the developing ovum devouring curious masses, which he considered play the part of a vitellarium. In two or three of the individuals of L. obesum sectioned, several rounded masses of globules, or granules, staining black—as do the yolk globules—with iron haematoxylin, were present in the ovary (*D.B.*, Text-fig. 20, B). It is probable that these had resulted from degeneration of ova, especially as large ova with degenerating nuclei have been observed (*D.N.*, Text-fig. 20, B).

In connexion with the oviducts is a pair of large pear-shaped glands, which doubtless secrete the delicate vitelline membrane, found surrounding the embryo in the vestibule. Ducts leading from these glands open into the median oviduct near the entry of its two lateral ducts from the gonads.

The embryos, like those of L. phascolosomatum, remain in the vitelline membrane until they are fully formed larvae, and leave the parent on the rupture of the membrane. The embryos are attached to a small projection (present only

in the female) on the floor of the vestibule, between the epistome and the oviduct, by the drawn-out continuations of their envelopes (Text-figs. 21, 22). A similar projection would seem to be present in L. loxalina, from a consideration of Assheton's fig. 5, Pl. 7 (1); a somewhat similar condition is seen in Pedicellina cernua (**6**, p. 26). The envelopes are

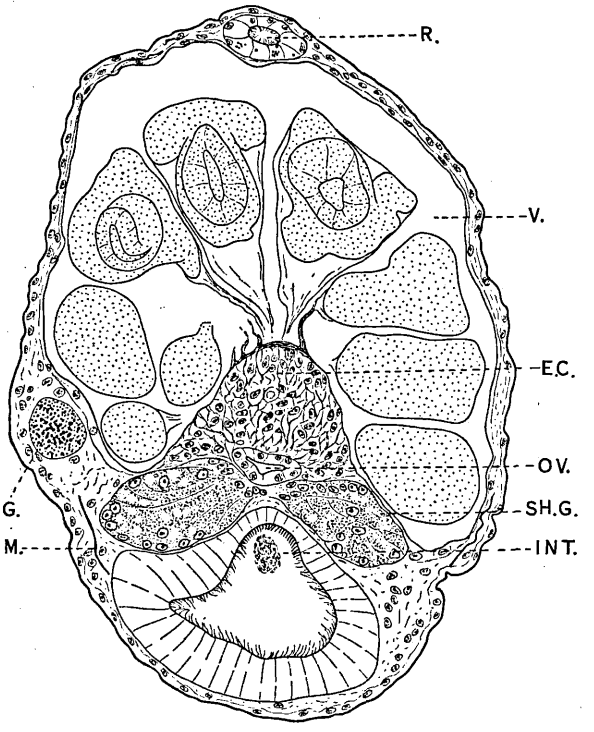


TEXT-FIG. 21.

L. obesum. Longitudinal section through the vestibule of a female, showing the attachment of the embryos by the drawn-out continuation of their envelopes, to a projection on the floor of the vestibule. The youngest embryo (*E.*) is nearest the oviduct (*OV.*). *INT.*, intestine; *OE.*, oesophagus; *R.*, rectum; *ST.*, stomach. Flemming's fluid without acetic acid; iron haematoxylin and acid fuchsin. ×171·4.

sufficiently large for the fully formed larvae to move around in them. Normally a single embryo is contained in each envelope, but on two occasions in different individuals, two embryos, with ciliated ring developed, were enclosed in one vitelline membrane. This perhaps is liable to occur during rapid extrusion of ova into the vestibule. Immature larvae are occasionally forced out of the vestibule by violent contraction of the parent on being disturbed; in such instances they are generally attached together by their stalks in groups of three.

Adult females have the vestibule much enlarged and crowded with embryos (Text-fig. 12, II, A, p. 358), in various stages of development. The number carried simultaneously, which may reach at least twenty-six, appears to be unusually large for the

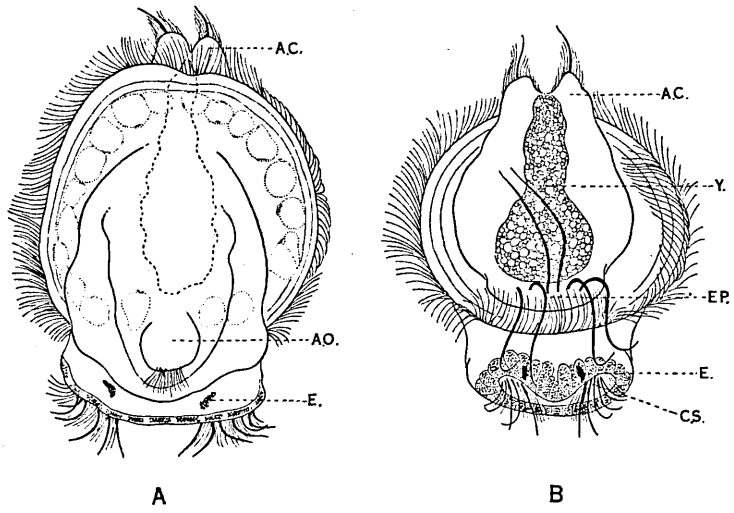


TEXT-FIG. 22.

L. obesum. Oblique section of the vestibule, passing through the embryo-carrier, the oviduct, and the shell-gland. *E.C.*, embryo carrier; *G.*, ovary of one side; *INT.*, intestine; *M.*, muscle-fibres; *OV.*, oviduct; *R.*, rectum; *SH.G.*, shell-gland; *V.*, vestibule. Bouin's fixative; iron haematoxylin and acid fuchsin. ×200.

family, though there is little information as to the maximum number carried in the different species. As many as nine or ten have been seen in the vestibule of a specimen of L. singulare 0·5 mm. long (measured mounted, with lophophore

closed) from the elytra of Aphrodite at Plymouth. This is a large number considering the small size of the species and the size of the ova (about 0·08 mm. to 0·09 mm. in diameter). L. cirriferum (**12**, p. 14), with an average total length of 0·650 mm., carries as many as six or seven embryos simultaneously



TEXT-FIG. 23.

L. obesum. Sketches of living, free-swimming larvae. A. Aboral view; B. oral view. *A.C.*, anal cone; *A.O.*, apical organ; *C.S.*, ciliated sacs of dorsal organ; *E.*, eye-spot; *EP.*, epistome bearing long, stout cilia and covering the mouth; *Y.*, yolk-mass in alimentary canal. ×274.

in the vestibule. In Loxocalyx leptoclini (**9**, p. 288), which has an average total length of about 0·5 mm., the number of embryos in the vestibule 'seldom exceeds about 2 or 3'. The small number is, however, probably correlated with the specialized method of nutrition of the embryos in this species.

Larva.—The larva[1] of L. obesum (Text-fig. 23) resembles

[1] Sir S. F. Harmer has pointed out to me that it also has a striking resemblance in the attitude shown in Text-fig. 23, B, to a figure (Pl. xvi, fig. 14) of the organism which was described by Busch (1851, 'Beobachtungen über Anatomie und Entwickelung einiger wirbellosen Seethiere',

that of L. singulare. The eye-spots are a reddish brown; they are sometimes unequally divided into two. The stiff cilia or sense-hairs of the apical organ ('sucker', 'ciliated disc') are motionless.

The six long stout cilia on the epistome have a slow rate of beat, though the rate varies somewhat; the effective beat is backwards, that is, towards the anal cone. At times they are held motionless, directed backwards. These cilia are compound in structure. The epistome is mobile; it may project over the mouth as in Barrois' figure of L. singulare (**3**, Pl. 1, fig. 21), or may be bent posteriorly.

The floor of the vestibule, including the epistome and anal cone, is ciliated.

The six, or so, stout cilia present among the fine cilia of the ciliated sacs of the dorsal organ also have a slow rate of beat. They do not all beat in the same direction; the inner one of each sac or depression beats roughly across the length of the organ; the two to the outer side of these beat along the length of the organ—the effective stroke being outwards; while the two or three shorter ones at the outer ends of the sacs appear more or less motionless.

The long cilia of the corona beat inwards towards the vestibular cavity; when the corona is in a state of partial contraction the cilia lie motionless directed upwards, as in Barrois' Pl. 1, fig. 13, of L. singulare (**3**). When entirely retracted the corona is reflected to the interior of the vestibular cavity, and the cilia are almost entirely hidden. A larva was observed on one occasion to stop suddenly, while swimming, with the corona fully extended, and the cilia motionless, radiating outwards. While the larva is still within the vitelline membrane, the beat of these cilia is slow, and more or less synchronous over much of the corona, no doubt owing to the constraint of the surrounding membrane. Synchrony of beat is lost in the free-swimming larva; the beat becomes much more rapid, but the rate of beat appears to be under the control of the animal.

p. 132, Pl. xvi, figs. 12–16. Separately published, Berlin) as Cyclopelma longociliatum and later identified by Barrois (**3**, p. 5) as a Loxosoma larva.

The method of progression of the larva varies; at times it swims forward evenly with the dorsal organ, with the eye-spots, foremost, or it may progress by a series of somersaults, while at other times it whirls round and round, keeping more or less in the same spot. Alteration in the method of progression is possibly due to differences in the relative strength of beat of the coronal, and the epistomal cilia. It is possible, also, that changes in the position of the epistome, by causing slight alteration in the general direction of beat of the epistomal cilia, may result in the alteration of the direction of movement of the larva.

Larvae were observed to anchor themselves temporarily, by the oral surface, the coronal cilia beating slowly, while the region with the dorsal organ, protruded to its fullest extent, explored in all directions; when it faced directly upwards, the eye-spots were clearly visible on the floor of the ciliated sacs; in any other position they are visible through the transparent walls of the sacs. While in this position the larva may move slowly forwards by the contraction and expansion of the ciliated corona, which is now elongated and oval in outline, and perhaps helped by clawing movements of the large cilia of the epistome.

Large mucus-glands are present on the floor of the vestibule (as shown by staining with Mayer's mucicarmine and muchaematein), though mucus-glands could not be demonstrated in the adult.

Larvae on one occasion lived at least six or seven days after hatching without alteration in form. It would appear that in this L. obesum resembles L. tethyae, which Harmer (**9**, p. 304) kept alive for eight days after hatching, 'at the end of which time they were still free-swimming, and externally at any rate, showed no obvious indications of buds'. The larvae of L. leptoclini, on the other hand, produced a pair of buds within four days (see Harmer, **9**, p. 300).

Females carrying embryos in the vestibule have been seen in February, March, April, and September: no specimens have been examined during the summer months.

Buds.—The buds are situated on either side of the calyx, just below the lophophore (Text-fig. 13, p. 360). They are found on individuals of both sexes, and on females with the

vestibule crowded with embryos. The number of buds may be large, as many as six on each side, though a smaller number is perhaps more common, many adults having two buds on one side, and one on the other: the number present doubtless depends on general conditions. So far the large number has only been found among large individuals of two small 'colonies' (one taken in February, and the date of the other unknown) in which the gonad was immature or not distinguishable. When a large number of buds is present, there is only a slight difference in size between buds of successive ages (Text-fig. 13, B, p. 360).

Nickerson (**23,** p. 369) says of L. davenporti that there may be as many as six buds a side, but more commonly two, three, or four upon a side. Five or six buds a side have been described for L. kefersteini (**5,** p. 30): L. crassicauda has three or four a side, but the majority of known species appear generally to have a small number of buds.

Buds may reach a length of about 0·55 mm. before they become free. As previously mentioned they possess a large foot-gland and groove.

Individuals reproducing by budding have been observed among infections examined in February, March, April, and September. No specimens were examined during the summer months.

Proportion and Size of the Sexes.

Females have been found very greatly to preponderate over males in infections in which the sex of individuals is easily recognizable, that is, in a population composed mainly of sexually mature, or nearly mature, individuals; but more information is needed, especially of infections in which the gonad of the majority of individuals is immature, though the individuals are large, for among some of these—judging, however, by only one sample—the males may exceed the females in number (see Table II, 2). When the number of males is small, a very high percentage of them is fully mature. Only few infections have been examined in any detail; in three out of the four, females predominated.

TABLE II.

Sex Proportions in Random Collections of Loxosoma obesum from four Aphrodite aculeata.

Date.	♂ No.	♂ %	♀ No.	♀ %	♀ No.	♀ %	♂ *mature.*[1] No.	♂ *mature.*[1] %	♀ *mature.*[1] No.	♀ *mature.*[1] %	*Total.*	*Remarks.*
1. February 7, 1928	0	(0)	90	(100)	0	(0)	0	(0)	8	(8·8)	90	Majority with gonad of median size, but not fully mature. Smallest female with embryos, 1·35 mm. long. Females 0·6–2·1 mm. long.
2. February 20, 1928	77	(48·43)	48	(30·19)	34	(21·38)	37	(48·05)	6	(12·50)	159	Majority of females with small, immature gonad. Smallest female with embryos, 0·96 mm. long. Smallest mature male 0·86 mm. long. Males 0·46–1·9 mm.; females 0·6–1·6 mm.; sex indeterminate 0·4–1·5 mm. long.
3. March 12, 1930	4	(3·45)	110	(94·83)	2	(1·72)	4	(100)	52	(47·27)	116	No measurements made.
4. March 19, 1930 i–iii[2]	21	(17·21)	99	(81·15)	2	(1·64)	21	(100)	48	(48·48)	122	Smallest female with embryos, 0·87 mm. long. Smallest mature male 0·68 mm. Males 0·68–2·2 mm.; females 0·56–2·2 mm.; sex indeterminate 0·6–0·7 mm. long.
iv	17	(6·88)	230	(93·12)	0	(0)	17	(100)	?	(?)	247	Females not measured, and no note made of the number with embryos. Smallest mature male 0·54 mm. long. Males 0·54–1·84 mm. long.

[1] 'Mature', in the male, is determined by the presence of sperm in the gonad or vesicula seminalis; in the female by the presence of an embryo in the vestibule.

[2] i–iv are small groups of Loxosoma taken from different parts of the dorsal surface of the 'host' and examined separately.

Nickerson (**23,** p. 364) and Kowalewsky (**18,** p. 5), for L. davenporti and L. neapolitanum respectively, noted the relative scarcity of males, and Claparède (**5,** p. 30) states that in L. kefersteini from the Gulf of Naples the only individuals showing sexual organs were females, while Vogt (**36,** p. 326) noticed that the tufts or 'colonies' of L. phascolosomatum on Phascolosoma were to a great extent either male or female. A similar condition has been observed for L. phascolosomatum on the shells of Lepton and Mysella in the Salcombe Estuary (**2,** p. 751). The curious state of affairs existing among L. crassicauda in a tank in the Plymouth Laboratory, in which all individuals in which sex was recognizable were in the male condition during the eleven months of observation, is discussed on p. 334.

Some figures of infections are given in Table II; it is probable that males might have been found among the infection of February 7, 1928, if more specimens had been examined. In addition to the data given in Table II, it was observed that of the individuals infecting an Aphrodite on April 20, 1928, there were fewer males than females, and that most of the females had the vestibule crowded with embryos.

When it is taken into account that in heavy infections there may be thousands of individuals on one Aphrodite, the number examined and tabulated (see Table II) is comparatively very small.

It was hoped by measurements of the two sexes to reach some conclusion as to whether the sexes are separate, or whether a change of sex occurs. A belief in the latter occurrence has been expressed by Harmer (**9,** p. 280) and by Nickerson (**23**); the latter writer actually found a specimen with male and female elements in the same gonad, the male state replacing the female.

Nickerson (**23,** p. 367) says that the males he studied (about ten) were of nearly average size, while all exceptionally large individuals, specimens 2·0 mm. or more in length, were without exception females. He suggested—considering this fact in conjunction with specimens in which male elements were replacing female in the gonad—that several periods of sexual activity,

alternately male and female, occurred in the life of a single individual.

Prouho (**27**, p. 107) found in L. annelidicola that the males were larger than the females, though he did not consider he had examined sufficient numbers to establish the law in his species.

Harmer (**12**, p. 15) writing of L. cirriferum says 'Male specimens are usually smaller than females, although I have found a male almost as large as the largest females. I find no evidence of protandry; and eggs may be produced by females which are no larger than the male shown in Text-fig. 13.'

Probably the number of L. obesum examined is too small to prove anything one way or the other. Such measurements as have been made indicate that there is no appreciable difference in size between the sexes; this would be consistent with either a separation of the sexes, or with the occurrence of several periods of sexual activity, alternately male and female, in the life of a single individual.

In a sample[1] from an Aphrodite obtained on March 19, 1930, the average total length of the females was slightly greater than that of the males; the figures were calculated on ninety-one females, thirty-six males, and two individuals in which the gonad was too small for the sex to be determined, and are as follows:

	Female (including 46 with embryos).	*Male.*	*Sex indeterminate.*
	mm.	mm.	mm.
Average total length	1·237	1·165	0·65
Average length of calyx	0·604	0·481	0·38
Average length of stalk	0·633	0·684	0·27
Average width of calyx	0·378 (on 37 females)	0·342 (on 26 males)	

Text-fig. 12 (p. 358) is of individuals from this infection.

[1] This is the same sample, 4, as in Table II, except for 10 individuals which had broken stalks, and 230 females, which were not measured.

In a sample[1] from an Aphrodite obtained on February 20, 1928,[2] the average length of male and female were reversed, the length of the male being slightly greater than that of the female. Actual figures are as follows, calculated on sixty-nine males, forty-two females, and thirty-four individuals in which sex could not be determined (see Table II, p. 379, for the characters of this infection):

	Female (including 4 with embryos).	*Male.*	*Sex indeterminate.*
	mm.	mm.	mm.
Average total length	1·055	1·156	0·950
Average length of calyx	0·571	0·594	0·506
Average length of stalk	0·484	0·562	0·444
Average width of calyx	0·451	0·484	
	(on 48 females)	(on 68 males)	

If these two samples are taken together—a total then of only 274 individuals, of which 133 are female, 105 are male, and the sex of 36 indeterminate—the average total length of male and female is very close, the male being a trace larger than the female.

	Female.	*Male.*
	mm.	mm.
Average total length	1·146	1·160
Average length of calyx	0·587	0·537
Average length of stalk	0·559	0·623

The sample of March 1930 shows a difference in the proportions of the calyx in the two sexes, but in that of February 1928 there is little difference. The difference in the 1930 sample

[1] This is the same sample, 2, as in Table II, with the exception of fourteen individuals with broken stalks.

[2] Measurements of March 19, 1930, were of individuals with the lophophore open, those of February 20, 1930, were of specimens with the lophophore closed, but as in the former instance the tentacles were not included, the measurements are roughly comparable. The Loxosomas of February 20, 1930, were not narcotized, but care was taken that they were uncontracted before measuring.

may probably be explained by the fact that this one included a large number of females with embryos in the vestibule (46 out of 91, 50·55 per cent.), and the enlargement of the vestibule of the embryo-carrying female tends to increase the length of the calyx in proportion to the width. In the February 1928 sample only four of the twenty-four females had embryos in the vestibule.

It might be noted that in the male the large mature gonad tends to displace the ventral part of the lophophore towards the free end, so that the lophophore becomes almost terminal in position (see Text-fig. 12, I, p. 358).

From a consideration of measurements and sex it may perhaps be concluded that the male reaches maturity at a smaller size than does the female. The smallest mature male among the sample from the infection of March 19, 1930, was only 0·54 mm. in total length, while the smallest mature female with one embryo in the vestibule was 0·87 mm. in total length; the presence of sperm in the male, and an embryo in the vestibule of the female being taken as evidence of maturity.

An analysis for sex and size of samples of Loxosoma from two Aphrodite of February 20, 1928, and March 19, 1930, are given in Tables III and IV; these are, except for the omission of individuals with broken stalks, the same samples as in Table II. The figures, inconclusive as they are, are given in some detail, as previous notes on the proportion and size of the sexes in Loxosoma seem to have been based on the examination of very few individuals.

Discussion of Relationships.

There would appear to be no doubt of the specific distinctness of L. obesum. It differs from most, if not all known species with eight, or about eight, tentacles, in the much larger size in attains, in the constancy of the number of its tentacles, and in the small size of its lophophore. Very few species have been described as having practically always eight tentacles; one of these is L. nitschei Vigelius (**35**). This form was originally described from Menipea ternata, Barents Sea, when its height was given as 0·15 mm.; the measurements were made, however, on badly preserved material, and Vigelius's figures and

TABLE III.

Analysis for Sex and Length of a Random Collection[1] of 145 Loxosoma obesum from Different Parts of the Dorsal Surface of one Aphrodite, February 20, 1928.

Length in mm.	*0·25–0·5.*	*0·5–0·75*	*0·75–1·0*	*1·0–1·25.*	*1·25–1·5.*	*1·5–1·75.*	*1·75–2·0.*	*Totals.*
Males, number:								
(*a*) Immature . . .	(1)	(3)	(10)	(9)	(10)	(4)	(1)	
(*b*) Mature (sperm present)	—	—	(7)	(12)	(7)	(4)	(1)	
(*a*) and (*b*) . . .	1	3	17	21	17	8	2	69
Females, number:								
(*a*) Without embryos .	—	(4)	(6)	(25)	(3)	—	—	
(*b*) With embryos . .	—	—	(2)	(1)	—	(1)	—	
(*a*) and (*b*) . . .	—	4	8	26	3	1	—	42
Sex indeterminate, number .	2	5	8	15	4	—	—	34
Totals . . .	3	12	33	62	24	9	2	145

[1] This is the same sample as in Table II, less 8 males (6 mature) and 6 females (2 with embryos) with stalks broken.

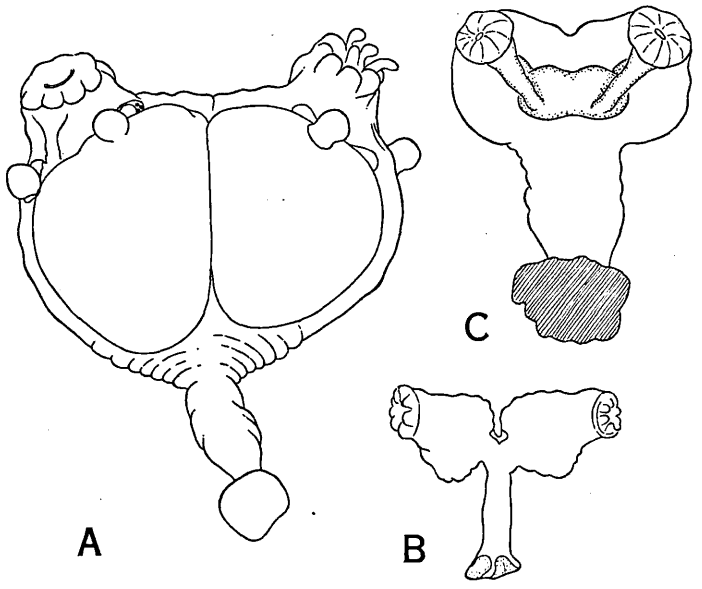
TABLE IV.

Analysis for Sex and Length of a Random Collection[1] of 116 Loxosoma obesum from Different Parts of the Dorsal Surface of one Aphrodite, March 19, 1930.

Length in mm.	*0·5–0·75.*	*0·75–1·0.*	*1·0–1·25.*	*1·25–1·5.*	*1·5–1·75.*	*1·75–2·0.*	*2·0–2·25.*	*Totals.*
Males, number (all with sperm present)	2	4	6	3	2	1	2	20
Females, number:								
(*a*) Without embryos .	(4)	(23)	(17)	(4)	—	—	—	
(*b*) With embryos . .	—	(7)	(10)	(4)	(11)	(5)	(9)	
(*a*) and (*b*) . . .	4	30	27	8	11	5	9	94
Sex indeterminate, number .	2	—	—	—	—	—	—	2
Totals . . .	8	34	33	11	13	6	11	116

[1] This is groups i–iii of sample 4 in Table II, less 1 male and 5 females with stalks broken.

description were necessarily inadequate. It was rediscovered by Roper (**28,** pp. 56, 57), growing in great abundance on algae, hydroids, and polyzoa, &c., in a tank in the Dove Marine Laboratory at Cullercoats, Northumberland, but in her short note little was added to its description. Harmer (**12,** p. 20)



TEXT-FIG. 24.

Double specimens of Loxosoma. A, B. L. obesum (preserved specimens). × *ca.* 76·3. C. L. singulare (living specimen). The end of the stalk is hidden by a collection of debris. × *ca.* 93·3.

mentions that L. nitschei from Cullercoats may reach a total length of 0·59 mm. when fully expanded. From what is known of L. nitschei it is extremely improbable that the Plymouth form can belong to that species. L. obesum is distinguished from L. nitschei by its much greater size and its general form (L. nitschei is said to be short and compact (**35**)). Other species which have eight tentacles are L. murmanica and L. brumpti, from the anterior and posterior ends, respectively, of Phascolion spitzbergense found

in the Kola Fjord, on the Murman coast of the Barents Sea; the former species, however, has the stalk and proximal part of the calyx covered with a thick brown cuticle, and the latter is provided with two prominent sense-(?) organs (**24**). Two species from Malay waters having eight tentacles are L. sluiteri and L. subsessile (**12**, pp. 5, 9, 19); the former is found on Phascolion convestitus and reaches a length of 0·4 mm., the latter occurs on Conescharellina and is only 0·12 mm. in length. Size and form distinguish these two species from L. obesum.

L. obesum differs from all known species of Loxosoma (so far as the life-histories of these are known at present) in the peculiar enlargement of the stomach, which is found in perhaps the majority of individuals.

Double Specimens.

Four double specimens of L. obesum have been seen, which showed two different degrees of union:

1. Two specimens had a common stalk, and the bodies united side by side, with the ventral surfaces facing in the same direction. The two lophophores were distinct; each individual had its own reproductive organs and, in the specimen-carrying buds (Text-fig. 24, A), separate budding zones. The two digestive systems appeared to be separate, though the stomachs were in close contact, causing slight alteration of shape. These double Loxosoma were not sectioned, and in one specimen it was impossible to determine, from the entire preparation, whether the small reproductive organs were male or female, and whether they were all alike. In the second specimen all four reproductive organs were female. The condition of the nervous system could not be determined in one specimen; in the other the nerve ganglions of the two individuals were separate. The lophophores were turned outwards: in the specimen carrying buds the two outer budding zones were on the extreme edge of the calyx, that of the left individual being just on the dorsal surface. These specimens in their degree of

union are very similar to the first one described by Nickerson (**22**).

2. Two specimens showed a lesser degree of union. The stalk was single except for a short distance at the apex, but the bodies were entirely separate. One of these (Text-fig. 24, B) was much smaller than the other. These showed a slightly more advanced degree of union than the second specimen described by Nickerson.

Double Loxosoma have been previously described by Nickerson (**22**) as occurring among normal individuals of L. davenporti, and their origin discussed by him.

The work recorded in this paper and in the following one on 'The Ciliary Feeding Mechanism of the Entoproct Polyzoa, &c.', was carried out at the Marine Biological Association's Plymouth Laboratory, to the Director and Council of which I desire to express my gratitude; part of it was done during the tenure of a research studentship of Bedford College, University of London.

I am greatly indebted to Sir S. F. Harmer, F.R.S., for reading the manuscript, for making valuable suggestions, and for certain references to the literature. My thanks are also due to Dr. E. J. Allen, F.R.S., for reading the manuscript and for the interest he has taken in the work; and to Miss M. A. Sexton for help with the translation of German references.

Summary.

Four known species of Loxosoma, namely, L. phascolosomatum Vogt, L. crassicauda Salensky, L. singulare Keferstein, and L. claviforme Hincks, and a new species L. obesum are found in the Plymouth region, and are described.

L. phascolosomatum is found on Phascolosoma vulgare, and in addition on two molluscs, Lepton clarkiae and Mysella bidentata from the burrows of Phascolosoma (pellucidum) elongatum from the Salcombe Estuary.

L. crassicauda lives in the tanks in the Laboratory. Its average length is 1·4 mm. Between March 1929 and February 1930 males only were found: no ova were seen.

L. singulare.—Occurs on Aphrodite aculeata; it varies between 0·18 and 0·8 mm. in length. In females carrying embryos the vestibule has two diverticula, one on either side of the rectum.

L. claviforme.—It is considered a valid species, and may be distinguished from L. singulare by: (1) its greater size and length of stalk, (2) greater number of tentacles (commonly twelve), (3) position of the budding zone, and (4) the presence of paired sense-organs. Its average length is about 0·8 mm. It occurs on Hermione hystrix.

A small group of Loxosoma, found on Aphrodite aculeata, were intermediate in form between L. singulare and L. claviforme, and were peculiar in retaining a number of their buds. The sex of such buds in several instances differed from that of the parent.

L. obesum sp. nov. is found on the dorsal surface of Aphrodite aculeata. It may reach a length of 2·4 mm.; average individuals are rather more than 1·0 mm. in length. The lophophore is small, and bears almost invariably eight tentacles. Longitudinal muscles only are present in the stalk, which ends in a small disc of attachment. A foot-gland is present in the bud, and is frequently preserved as a vestige in the adult. The buds are near the lophophore, and may be as many as six on either side. The larva resembles that of L. singulare.

Two main forms may be distinguished, differing in shape of the calyx and development of the stomach.

The ovary may contain six well-developed ova on either side, and the vestibule twenty-six embryos.

With one exception, females greatly exceeded males in number, and it is probable that the male becomes sexually mature at a smaller size than does the female.

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DAPHNE ATKINS, B.Sc.

The Ciliary Feeding Mechanism of the Entoproct Polyzoa, and a comparison with that of the Ectoproct Polyzoa

Quarterly Journal of Microscopical Science
Vol. 75, Part III, November, 1932

Printed in Great Britain

The Ciliary Feeding Mechanism of the Entoproct Polyzoa, and a comparison with that of the Ectoproct Polyzoa.

By

Daphne Atkins, B.Sc.

With 12 Text-figures.

Contents.

Introduction.

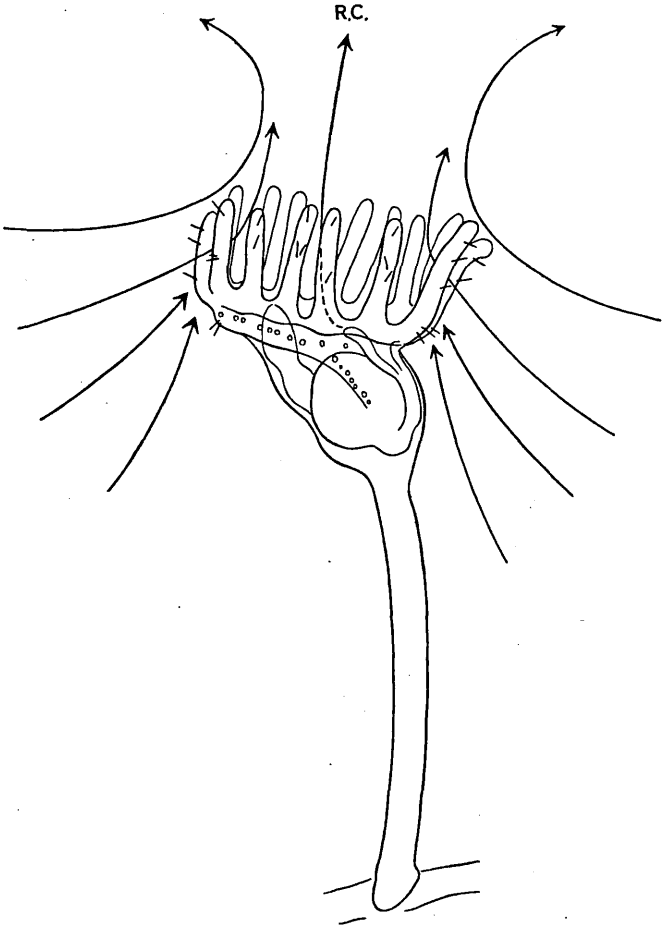
The ciliary feeding mechanism of the Entoproct Polyzoa does not seem to have been worked out in any detail, as has that of the Ectoproct Polyzoa (**4, 5, 18**), although certain references to it occur in the literature of the group (**27, 9**). The following account of the ciliary feeding mechanism of the Entoprocta is based chiefly on an investigation of Loxosoma, though Pedicellina was also observed. L. crassicauda was chosen for the greater part of the work on account of the large size of its lophophore; the method of feeding of the other species of Loxosoma found at Plymouth, namely, L. singulare, L. claviforme, L. phascolosomatum, and L. obesum (**3**), is, however, identical.

The Structure of the Lophophore and of the Tentacles in the Entoprocta.

In Pedicellina, as is well known, the plane of the lophophore is at right angles to the main axis of the stalk and calyx; in Loxosoma the lophophore is set obliquely. In at least some species of Loxosoma, however, the dorsal half of the lophophore is generally bent backwards during feeding, and the lophophore is then practically at right angles to the calyx (Text-fig. 1) (see also Assheton on L. saltans **2**, p. 125, and Pl. 6, fig. 10). The numbers of tentacles springing from the lophophore varies in the different species of Loxosoma, and is generally somewhat variable within the species. The smallest number known to be present is eight, as in L. nitschei (**25**), L. obesum (**3**), &c., and the largest number twenty-nine in L. davenporti (**19**). In Pedicellina cernua the number is fourteen to twenty-four. In Loxosoma and Pedicellina new tentacles arise on either side of the median plane in the mid-distal (dorsal) region of the lophophore.

A narrow platform, or diaphragm, is present at the base of the tentacles; ventrally it is continuous with the large bilobed epistome; dorsally it is interrupted in the middle line where the new tentacles originate (see Text-fig. 5, p. 402). On the diaphragm is a ciliated tract, the vestibular groove, leading to the mouth. The ventral lip is considerably smaller than the epistome, and appears as a ciliated lobe between the bases of the two most ventral tentacles (Text-fig. 5, p. 402).

Normally in Loxosoma and Pedicellina the tentacles are extended, but when the animals are disturbed, or many distasteful particles are present in the water, the tentacles are bent inwards and folded away within the vestibule, while a delicate fold of skin, the velum or tentacular membrane, growing from the edge of the calyx at the bases of the tentacles, is drawn over the retracted tentacles by the contraction of a sphincter muscle present in its circular margin. The opening into the vestibule is thus reduced to a very small orifice. The appearance of L. crassicauda with tentacles withdrawn and lophophore closed is sketched in Text-fig. 2. The sphincter



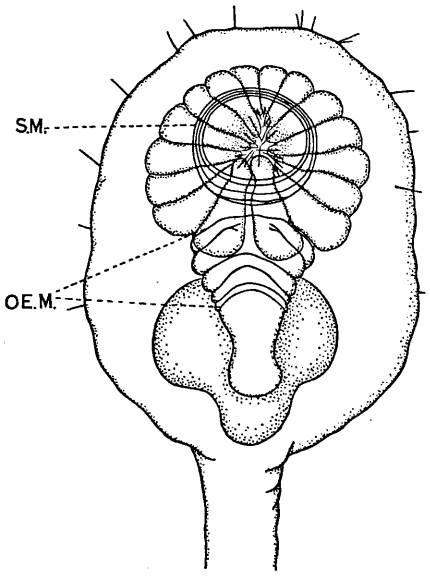
TEXT-FIG. 1.

L. crassicauda. Sketch of a living, unnarcotized animal to show the backward bending of the lophophore during feeding, the direction of the water currents set up by the lateral cilia of the tentacles, and of the rejection current (*R.C.*) caused by the epistomial cilia. ×70.

is not as strongly developed in this species as in some, for instance, L. singulare, and in consequence the opening left into the vestibule is fairly large. Even in individuals killed

unnarcotized, the sphincter contracts little more than is shown in Text-fig. 2. In L. crassicauda the two most ventral tentacles—those on either side of the mouth—fold outside and across the adjacent tentacles.

The tentacles of Loxosoma and Pedicellina are



TEXT-FIG. 2.

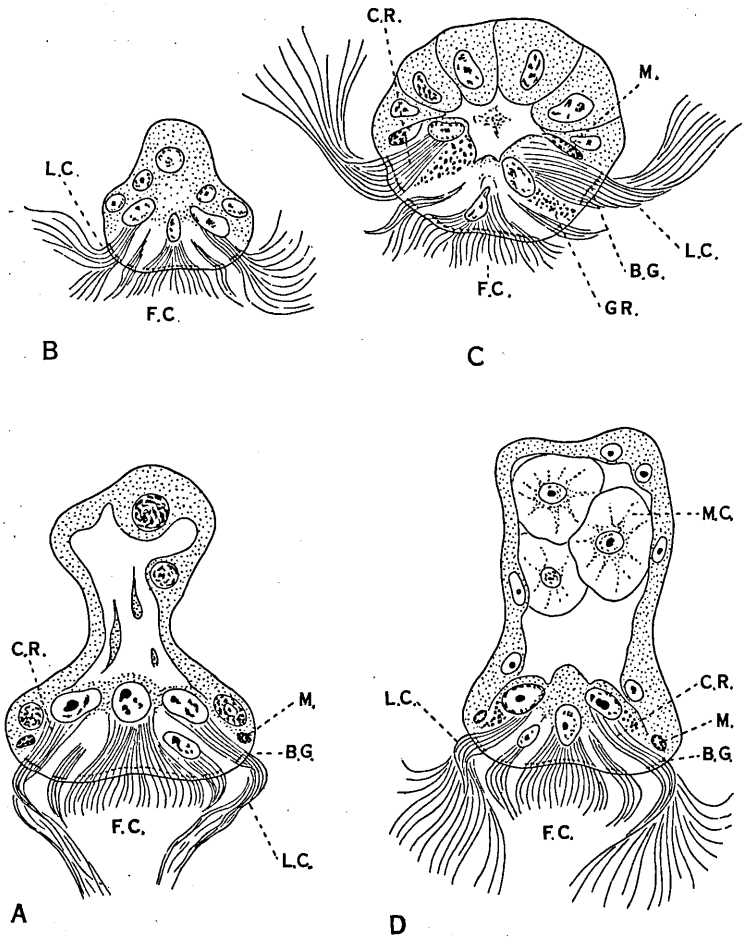
L. crassicauda. Ventral view of living animal with tentacles withdrawn into the vestibule, and lophophore closed. The only muscles shown are the sphincter of the lophophore (*S.M.*) and the muscles constricting the oesophagus (*OE.M.*). Only the alimentary organs are shown. ×140.

supplied with nerves; one nerve enters each tentacle and gives off branches to the sense-cells (Harmer **13,** pp. 271, 273). In L. crassicauda the nerves are visible in the living animal. Muscle-fibres also enter the tentacles, and to these are due the movement of the tentacles during feeding. Independent bending movements of a tentacle—sideways, and inwards and outwards —are observable. To the contraction of these longitudinal muscles, together with the sphincter in the velum, is due the

folding away of the tentacles into the vestibular cavity, when the animal is disturbed. In Loxosoma and Pedicellina there appear to be two longitudinal muscles in each tentacle; these run close to the lateral ciliated cells. The fibres are not easily identified in transverse sections.

The tentacles of Loxosoma are roughly triangular in cross-section, with the base of the triangle facing the lophophoral space (Text-fig. 6, p. 403). In L. obesum the triangle is almost equal-sided (Text-fig. 3, B), in L. crassicauda elongated (Text-fig. 3, A), and in this latter species, especially the two long sides of the triangle, are somewhat concave. This concavity is not due entirely to shrinkage of the tentacles on fixation, for it is seen in the living animal. The tentacles of Pedicellina cernua tend to be roughly rectangular in cross-section (Text-fig. 3, D), except near the tips, where they are triangular.

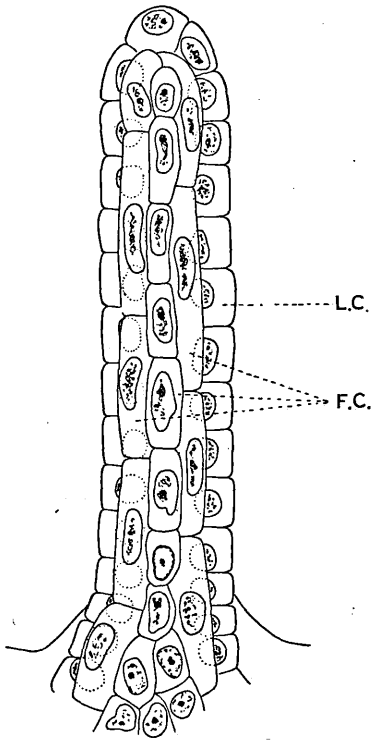
The epithelium of the tentacles consists of three kinds of cells: (1) ciliated cells; (2) non-ciliated cells; and (3) a few scattered sense-cells, bearing one or more stiff tactile hairs, which occur among the unciliated cells. The non-ciliated epithelium is found on the outer and lateral surfaces of the tentacles; there appears to be no regular arrangement of the cells: the nuclei are roundish. The cells on the inner or ciliated surface are in three tracts; a frontal (middle) and two lateral. The appearance in surface view of the ciliated cells of the tentacles of L. crassicauda is shown in Text-fig. 4. The frontal cells forming the middle tract are in three rows, and there is no interlocking of the cells. The middle row is slightly depressed to form a very shallow groove (see Text-fig. 3). The cells are rectangular in surface view, the two outer rows being especially elongated. The nuclei are long and narrow, and generally placed horizontally, but they may be twisted. The nuclei of the frontal cells, especially of those towards the bases of the tentacles, are frequently irregular in shape, as are also those of the cells forming the vestibular groove at the base of the tentacles. The frontal cells bear short cilia, those on the two outer rows being somewhat longer than those on the middle row (Text-fig. 3).



TEXT-FIG. 3.

Transverse sections of the tentacles of Loxosoma and Pedicellina. A. L. crassicauda. B, C. L. obesum. C, section towards the base of a tentacle. D. Pedicellina cernua. *B.G.*, basal granules; *C.R.*, ciliary rootlets; *F.C.*, frontal cilia; *GR.*, granules in lateral ciliated cells; *L.C.*, lateral cilia; *M.*, ? muscle-fibres; *M.C.*, large cells in tentacle of Pedicellina. A and C, fixed in strong Flemming's fluid without acetic acid; B, Bouin's fixative; D, corrosive sublimate: all stained in Heidenhain's iron haematoxylin and acid fuchsin. × *ca.* 1200.

The cells of the lateral series are almost cubical, and have large oval nuclei (Text-fig. 4). They each bear a single row of long cilia. On fixation each cilium separates into its constituent



TEXT-FIG. 4.

Inner surface of a tentacle of L. crassicauda showing the arrangement of the ciliated cells. *F.C.*, the three rows of frontal cells; *L.C.*, lateral cell-row. From an animal fixed in formalin, stained in borax carmine and picro-nigrosin, and mounted entire in alcoholic Canada balsam. ×735.

fibres, and therefore in sections has the appearance of a tuft of fine cilia (Text-fig. 3).

Assheton (**2**, p. 136) described the cells of the ciliated surface of the tentacles of L. saltans as being in three rows, as did Kowalewsky (**15**, p. 3) in L. neapolitanum; Nickerson

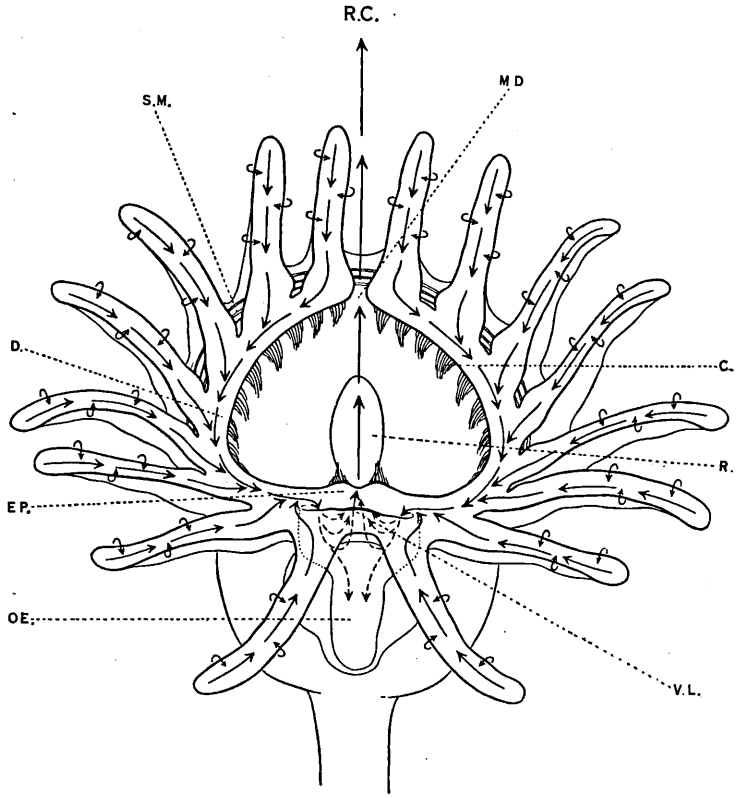
(**19**, p. 354) found no definite arrangement in L. davenporti. Kowalewsky says that the middle row is depressed to form a groove, but that the two lateral rows alone bear cilia; the latter statement is most probably incorrect, for while transverse sections of the tentacles of L. crassicauda and L. obesum show them to be very slightly grooved, the middle tract of cells also is ciliated. In figures of transverse sections of the tentacles of L. saltans (**2**, Pl. 7, fig. 18) and L. davenporti (**19**, Pl. xxxii, figs. 9 and 10) cilia uniform in length are shown over the whole of the inner surface, and it may be noted that a similar uniformity in the length of the cilia is shown by Cori (**9**, Text-fig. 5, p. 9) on the tentacles of Pedicellina cernua. An examination of living specimens of the species of Loxosoma found at Plymouth, and also of Pedicellina cernua, showed that while all the rows of cells on the inner face of the tentacles bear cilia, those of the middle rows are much shorter and finer than those on the two outer rows. An examination of the living tentacle is desirable, as sections do not always show clearly the difference in length of the frontal and lateral cilia. The cilia on the two outer rows of cells are very long, being about 35μ to 45μ long in L. crassicauda, and lash inwards (from the abfrontal to the frontal surface) across the length of the tentacles, except at the tip—occupied by a single cell—where they beat along the length. The short frontal cilia beat along the length of the tentacles and towards the base. In the living L. crassicauda the lateral cilia are seen to be in groups of about twelve to fifteen to a cell, separated by slight intervals corresponding to the cell-walls: the number of cilia may be counted in a cell which has worked out of the epithelium. The metachronal rhythm of these cilia is characteristic, but difficult to describe: viewed from the frontal or abfrontal surface the appearance is of a double row of dots—one of which is very close to the bases of the cilia and is not always visible when the tentacles are viewed from some positions—while, at more or less regular intervals, cilia are extended. The effect of the rows of dots is no doubt due to the bending of the cilia during the stroke. All the cilia arising from a single cell do not beat in the same phase: if, however, the animal has been long

narcotized, and the rate of beat is much reduced, there is a tendency for them to beat more or less in the same phase.

The Ciliary Feeding Mechanism of the Entoprocta.

An undisturbed Loxosoma in the act of collecting food particles has the tentacles well expanded. The degree of expansion of the tentacular crown, however, varies; under natural conditions the tentacles form a shallow funnel (Text-fig. 1), but when under the influence of a narcotic, e.g. stovaine, they may bend outwards so that an almost flat plate is produced, and in extreme instances, the tips of the tentacles may even bend downwards. Text-fig. 5, which is a sketch of a narcotized animal, shows the tentacular crown rather more widely open than it would be under normal conditions. In Pedicellina the tentacles generally seem to be curved slightly towards the lophophoral space, though when the animals are narcotized the tentacular crown may become as widely expanded as that of Loxosoma under similar conditions. While feeding, the calyx, with the lophophore, is turned in different directions. In Loxosoma (L. crassicauda), as previously mentioned, the dorsal half of the lophophore is generally bent backwards, so that it is almost at right angles to the calyx. During expulsion of faeces the backward bending movement of the lophophore is marked.

Water is drawn into the tentacular funnel by the action of the long lateral cilia on the tentacles. The action of these is so energetic that it may be seen to shake the tentacles. The current enters between the outstretched tentacles (see Text-fig. 6), and sets away in front of the animal (see Text-fig. 1, p. 395). When the tentacles are fully expanded the current is therefore roughly from the direction of the attached end of the animal towards the free end: this causes the free-swimming bud to move with the lophophore hindmost. Particles carried in suspension in the water passing between the tentacles are thrown by the lateral cilia on to their inner, or frontal, surface, and passed by the short frontal cilia towards the base, and into the ciliated, vestibular groove, which leads to the mouth (Text-fig. 5). The grooved tract is interrupted in the median dorsal line of the

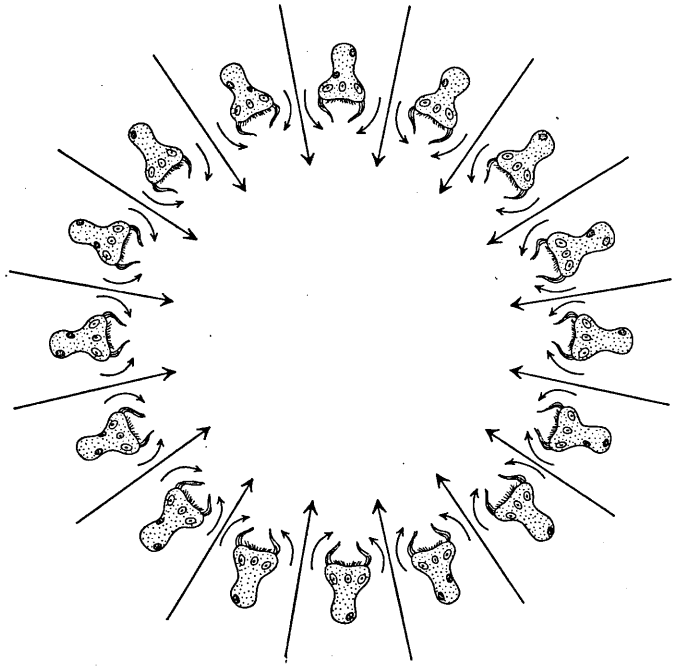


TEXT-FIG. 5.

Sketch of the tentacular crown of L. crassicauda showing the ciliary currents, and the direction of beat of the lateral cilia of the tentacles. Only the cilia (*C.*) arising from the edge of the diaphragm are shown. *D.*, diaphragm carrying ciliated vestibular groove; *EP.*, epistome; *M.D.*, mid-distal (dorsal) region of lophophore; *OE.*, oesophagus; *R.*, rectum; *R.C.*, rejection current set up by the cilia on the epistome; *S.M.*, sphincter muscle in the velum; V.L., ventral lip of mouth. The tiny arrows show the direction of beat of the lateral cilia of the tentacles. × 140.

lophophore, and particles travelling down the tentacles on either side of this point pass in opposite directions towards the mouth. The path followed by particles from the tentacles slopes in the direction of the mouth in passing into the vestibular

groove, except in the case of those from the tentacles on either side of the mouth, which follow a path sloping slightly away from it, and join the collected stream from the tentacles of its side, at the right and left corners of the mouth respectively (Text-fig. 5). During feeding, muscular movements of the



TEXT-FIG. 6.

Transverse section through the tentacular crown of Loxosoma (L. crassicauda) showing the direction of the water currents set up by the lateral cilia of the tentacles. The small arrows show the direction of beat of the lateral cilia. Somewhat diagrammatic. ×231·4.

epistome, mouth region—including that part of the lophophore carrying the two most ventral tentacles—and oesophagus occur.

While feeding with expanded tentacular crown the animal may partly close it with a sudden clutching motion (the movement of the lateral cilia ceasing), and as rapidly extend the tentacles again (the ciliary beat recommencing): or one

tentacle may be flicked inwards, without the others being affected; this appears to occur when a particle—perhaps usually a free-swimming ciliate—strikes the outer surface of a tentacle, where the tactile hairs are found; even the presence of large particles on the inner surface does not appear to call forth this response. Occasionally a single tentacle is bent slowly inwards into the vestibule, and may remain in this position for some minutes, and then be slowly straightened.

L. crassicauda may occasionally add to its diet organisms too large and active to be captured in the usual manner. Small, actively swimming ciliates, which are too powerful swimmers to be carried by the water current of the Loxosoma, at times blunder within the circlet of tentacles and penetrate into the vestibule. The Loxosoma immediately and rapidly approximates the tentacles, bunching them tightly together, and reducing the circumference of the lophophore. The ciliate is thus trapped within the vestibule, and it either accidentally, or helped by the activity of the cilia of the vestibular groove, reaches the mouth and is swallowed. Not till then does the Loxosoma expand its tentacles. One individual was observed to capture six ciliates, at intervals, in this manner, and others were seen behaving in a similar way, with two or three already in the stomach.

Particles may be accepted as food or rejected from one cause or another. When unwanted, unpleasant, or too numerous food particles are carried in the food current the animal may reject them in one of several ways, its behaviour seeming to be rather capricious. In extreme instances it rejects them in a most definite manner, by closing the lophophore and contracting violently. On other occasions the mouth may be closed, but more generally the particles are allowed to enter and are then rejected. In the latter case the upper part of the oesophagus is constricted by circular muscle-fibres (see Text-fig. 2, *OE.M.*), and particles entering the right and left corners of the mouth are carried out again in two converging streams on to the oral surface of the epistome, from which they pass off between the two lobes in a median stream (see Text-fig. 5) to join the main water current setting away in front of the animal. The rejection

current (Text-figs. 1 and 5, *R.C.*) set up by the cilia on the epistome is easily distinguished in animals in which the lateral cilia of the tentacles are more or less motionless, and therefore the main water current almost in abeyance.

If the water were made thick with much powdered carmine or strings of large diatoms, the lophophore was observed, on occasions, to bring about rejection by partly closing—to about the position shown in **3**, Text-fig. 1, B—with most of the long lateral cilia of adjacent tentacles motionless, with their tips interlaced; thus while the main water current was very greatly reduced, the interlaced cilia would act as a filter. The frontal cilia and those of the vestibular groove, continued to beat, and particles already within the lophophoral space were being drawn on to the inner faces of the tentacles, thence into the vestibular groove, and so on to the epistome, continuously.

L. crassicauda was found to feed freely on Nitzschia closterium var. minutissima.[1] When, however, too great a quantity of the culture was added, the animals very soon, perhaps in a minute or two, had swallowed sufficient. They then, though continuing to hold the tentacles expanded, much reduced the supply of diatoms by keeping the lateral, water-current producing, cilia practically motionless wrapped across the inner surfaces of the tentacles. Those towards the bases of the tentacles were generally active, but those on the distal halves were either all motionless, or only an odd group of cilia here and there showed activity. The activity of the lateral cilia was fitful, numerous intermissions occurring, the tentacular crown being suddenly half closed and then slowly opened, these movements coinciding respectively with the stopping and the recommencement of the beat. Occasionally a single tentacle might be curved slowly inwards and downwards to the vestibule. During this time such diatoms as reached and entered the mouth were carried out and expelled from off the epistome. The behaviour described above has also been observed to occur for no apparent reason, in sea-water almost free of organisms, but there is a possibility that it might be due to the methods of observation.

[1] Dr. E. J. Allen, F.R.S., very kindly supplied the culture of diatoms.

A few L. crassicauda, with the stomach full, occasionally reacted to the presence of numerous diatoms (Nitzschia) in the water in a different way: the tips of the tentacles were approximated, the tentacles being bunched together, and the circumference of the lophophore reduced. They might remain like this for several minutes, then slowly expand the tentacles.

At other times when L. crassicauda was observed in water with numerous diatoms, after obtaining sufficient food, they kept the tentacles well expanded, with the lateral cilia especially active, and relied on the rejection current from the epistome to carry off the unwanted diatoms, in the manner previously described (see p. 404).

The Behaviour of the Lateral Cilia on the Tentacles of Loxosoma crassicauda.—While the frontal cilia of the tentacles, and those clothing the vestibular groove at the bases of the tentacles, beat continuously, the lateral cilia of the tentacles of a healthy Loxosoma frequently cease beating, and would appear to be under the nervous control of the animal. Intermission of the ciliary beat of the main water-current producing cilia also occurs in the Ectoproct Polyzoa, both in the fresh-water (see Nitsche on Alcyonella fungosa **21,** p. 27) and in the marine forms (see Borg **5,** p. 248), and in Phoronis (**11,** p. 163). Phoronis hippocrepia at Plymouth, though left undisturbed in their stone during observation, held the lateral cilia more or less motionless, and several attempts made to observe the animals feeding were unsuccessful.

A healthy Loxosoma while feeding frequently clutches all the tentacles inwards, while all the lateral cilia suddenly and simultaneously become motionless, held wrapped across the inner surface of the tentacles in the position of the end of the effective stroke. Such behaviour may occur in response to no perceptible stimulation, or may occur when large particles strike the tentacles, or when the tube of the microscope is gently tapped. If the tube is tapped sharply the animal retracts the tentacles entirely, closing the lophophore. After successive gentle tappings the animal becomes less sensitive, and sharper ones are needed to call forth the reaction.

If the stimulation has been slight the tentacles almost immediately begin to straighten out, and the cilia to start beating. The ciliary beat may begin while the tentacles are still curved, or not until they are practically fully extended.

The recommencement of the beat after a period of quiescence is not simultaneous on all the tentacles, or even on the same tentacle. A wave of activity passing over the cilia may begin at the base of the tentacle and travel rapidly towards the tip; this is perhaps the most usual behaviour. The two sides of a tentacle, however, appear to be independent, for the movement may not begin at the same moment, or travel at the same rate, on both sides. The recommencement of the beat does not invariably take the form of a wave of activity passing from the base to the tip of the tentacle. A slight variation is that the cilia on the first two or three cells of one side at the base may be late in starting. At other times the cilia on two or three cells at the tip may start beating first, followed by those on the basal part of the tentacle, but there is irregularity in the sequence in which the cilia on the different cells become active. During a series of gentle stimulations the cilia of a certain cell of a tentacle of one individual were consistently slow to begin beating after an intermission, and might be several seconds behind those on adjacent cells. It would seem that the cilia arising from a single cell generally become active more or less simultaneously, but it has been observed that the start of beat of the separate cilia may be independent; this is especially seen when the cilia of a cell lag considerably behind those on other cells in becoming active.

As previously mentioned, under certain conditions—for instance when numerous Nitzschia are present in the water and the animal has taken sufficient food—L. crassicauda reduces the water current by holding many of the cilia motionless. A certain number of cilia, however, are active, chiefly those on the basal halves of the tentacles springing from the ventral half of the lophophore. Such groups of cilia as are beating appear to be beating metachronically. The cilia on the distal halves of some of these tentacles may remain motionless, wrapped across the inner surface, during successive periods of

activity and quiescence of the cilia on the basal halves: they may remain motionless for as long as ten minutes, though this is probably unusual.

Although sudden inward bending movements, of all the tentacles together, appear to be invariably accompanied by the stoppage of the beat of the lateral cilia, slow bending movements of a single tentacle, even if the end enters the vestibule, are not so accompanied. The sudden flicking inwards of a single tentacle is unaccompanied by the stoppage of beat of the cilia on the others, or, I believe, on that concerned, though it is difficult to be certain of the latter, as, during the movement, the tentacle passes rapidly out of focus.

In Loxosoma the stoppage of beat of all the lateral cilia on all the tentacles is simultaneous, while the start of the beat of the group of cilia arising from a single cell, and perhaps even of separate cilia, is independent. Carter (**7**, p. 11) has found that in the nudibranch veliger the stoppage of beat of the velar cilia is simultaneous, but that the start of the beat of the separate cilia is independent, and he says, 'this difference between the behaviour at the beginning and end of the intermission suggests that the recommencement of the beat is due rather to the passing away of the impulse which caused the intermission than to a new impulse'. Whether this would be sufficient to explain the behaviour of the lateral cilia of Loxosoma, where a number of the lateral cilia on a tentacle may remain motionless for some minutes, while the remainder on the same tentacle experience successive periods of activity and quiescence, is perhaps doubtful.

In Loxosoma the long cilia on the single cell at the extreme tip of each tentacle, and which beat along its length, are frequently seen motionless, bent slightly in towards the inner surface; in side view they then have the appearance of a single very stout cilium. These cilia appear often to lag some time behind the others in becoming active after an intermission.

When the tentacles are withdrawn into the vestibule and the lophophore is closed (see Text-fig. 2, p. 396), the lateral cilia beat, but rather irregularly owing to the restricted space; intermissions occur, and during these the two rows of cilia are

seen wrapped across the inner surfaces of the tentacles, the tips of those of opposite side interlacing.

Under the influence of stovaine, the cilia beat without intermission, but there is a tendency, if the narcotic be used over a period of half an hour or more, for the ciliated cells to break away. Generally those towards the tips of the tentacles are shed first. Even under normal conditions there appears to be some tendency for the lateral ciliated cells gradually to work out of the epithelium, individuals being observed with cells in the process of being shed. Their place is possibly taken by new cells, and in this way worn-out ciliated epithelium renewed. It might be noted that Carter (**7**, p. 11) describes the breaking free of the cells bearing the velar cilia in unhealthy nudibranch veligers. Cilia on the isolated lateral cells of Loxosoma may continue to beat actively for a short time.

With ether, also, intermissions cease, but it seems that they reappear after a time. Contraction of the muscles, including those of the tentacles and lophophore were observed, both during the time intermissions were inhibited, and when they had returned. This drug, however, was only used two or three times and its action not fully studied. The animals during observation were placed in a solid watch-glass, covered with a sheet of glass, so as to prevent evaporation of the ether.

The occasional intermission of the lateral cilia in healthy individuals, together with the ceaseless beating when under the influence of a narcotic, is suggestive of the behaviour of the velar cilia of the nudibranch veliger under similar conditions (**7**), and it would appear not improbable that they are similarly under the nervous control of the animal. That the tentacles of Loxosoma are supplied with nerves has been demonstrated by Harmer in L. crassicauda (**13**): the nerves, however, were traced to the sense-cells present on the unciliated surface of the tentacles.

In Loxosoma, inhibitory control occurs of cilia concerned with feeding; so far as is known such control is almost restricted to locomotory cilia. According to Fedele, however, the branchial cilia of Doliolum are under the control of the animal (see Gray **12**, p. 125).

A tufted fringe of cilia, 20 to 30μ long, occurs along the free edge of the diaphragm, hanging down into the vestibule, and is continuous across the epistome, a 'tuft' occurring on either lobe (see Text-fig. 5, p. 402). These cilia appear to be frequently motionless, with the exception of the two groups on the lobes of the epistome; on the occasions when they have been observed lashing, they do so irregularly, a few groups (a group to a cell) beating, while the rest are motionless. They seem to be rather less inactive when the lophophore is closed. The beat is at right angles to the edge of the diaphragm, but the direction of the effective stroke was not determined. Their function remains obscure; it is possible that they may prevent particles—straying from the vestibular groove—from falling into the vestibule (particles are not seen within the vestibule of a healthy Loxosoma); or they may effect a circulation of water among embryos in the vestibule. These cilia would appear to belong to the type which is motionless, or only feebly active, except when a stimulus is applied (see Gray **12**, p. 125). The stimulus which would set these cilia moving was not determined; particles passing round the vestibular groove did not necessarily cause them to become active. In a narcotized animal, in which the lateral cilia of the tentacles are beating rapidly and without intermission, the cilia hanging from the edge of the diaphragm are motionless, with the exception of the two groups on the lobes of the epistome, which may show some movement.

There appear to be no glands in connexion with the ciliated tracts on the tentacles, or with the vestibular groove; the large gland-cells which outline the vestibule parallel with the groove in L. crassicauda have been shown by Harmer (**13**) to open to the exterior.

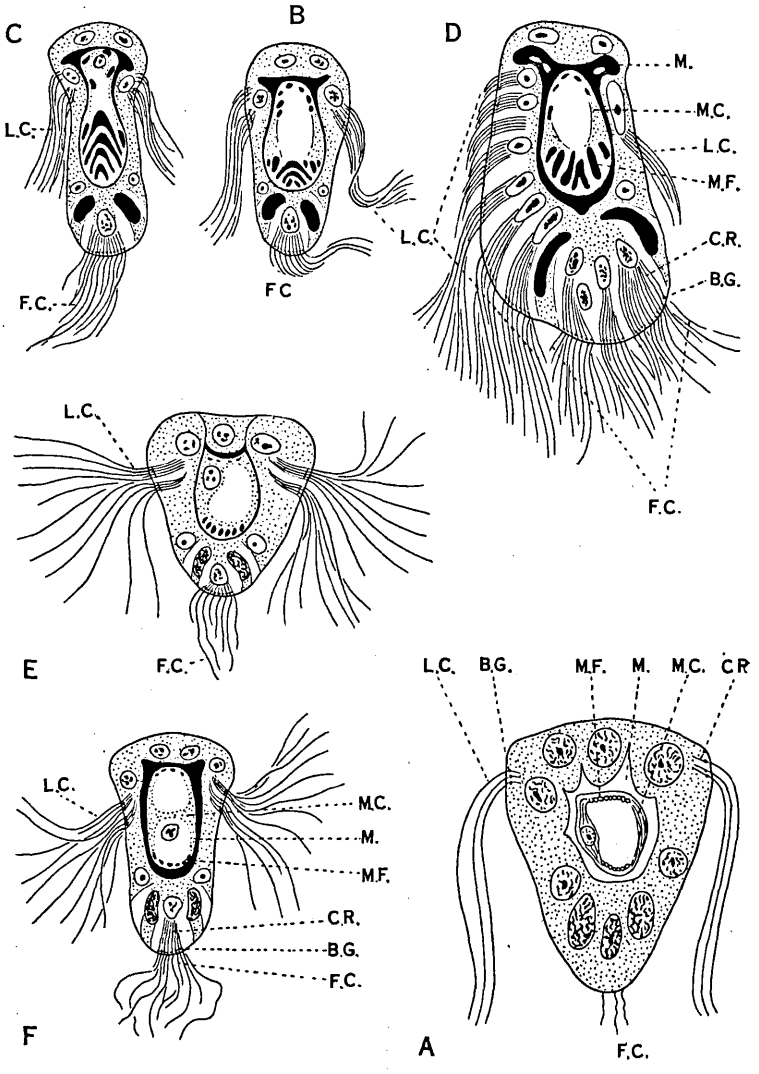
The ciliary feeding mechanism of Pedicellina cernua is essentially the same as that of Loxosoma. The direction of the ciliary currents on the tentacles and along the vestibular groove are shown by Cori (**9**) in his Text-fig. 3, p. 6, though he does not distinguish between the two kinds of cilia on the tentacles. The cilia are differentiated into lateral cilia (see Text-fig. 3, D, p. 398) beating across the length of the tentacles, with the effective beat from the abfrontal to the frontal surface.

and the frontal cilia beating along the length, from the tip towards the base. The metachronal wave of the lateral cilia of Pedicellina is of the same type as that of the lateral cilia of Loxosoma.

A Résumé of Borg's Work on the Ciliary Feeding Mechanism of the Ectoprocta, with a Note on Flustrella hispida.

A preliminary account of the ciliary feeding mechanism of the Ectoproct Polyzoa was published by Borg in 1923 (**4**), and a further one in 1926 (**5**). From his accounts it is evident that the method of feeding in the Ectoprocta is very different from that of the Entoprocta. Borg worked on the Cyclostomata, Crisiella, Crisia, Tubulipora, Berenicea, and Lichenopora, as well as several cheilostomatous and ctenostomatous species (**5**, p. 246): at Plymouth the feeding of Flustrella hispida, one of the Ctenostomata, was especially noticed.

The form of the tentacles in the Ectoprocta, as in Loxosoma, is more or less triangular in cross-section (Text-fig. 7), in some forms (Crisiidae), however, with the apex of the triangle truncated (**5**, p. 216), but while in Loxosoma the base of the triangle faces the lophophoral space, in the Ectoprocta the apex faces the space (cf. Text-figs. 6, p. 403, and 8, B). The outer surfaces of the tentacles are unciliated, but bear a number of very long, stiff, tactile hairs. The lateral cilia (see Text-fig. 7) occur near the abfrontal (outer) face of the tentacles (at either corner of the base of the triangle in cross-section), are long, and beat from the frontal to the abfrontal surface; these are the main water-current producing cilia. From transverse sections it would seem that the lateral cilia occur in a double row on either side of the tentacles. According to Borg these cilia do not beat at right angles to the length of the tentacle, but somewhat obliquely downwards, and the tip of each cilium traces out an elliptical path. They have a marked metachronal wave, which passes up one side of a tentacle and down the other, and runs, therefore, at right angles to the direction of beat of the cilia.



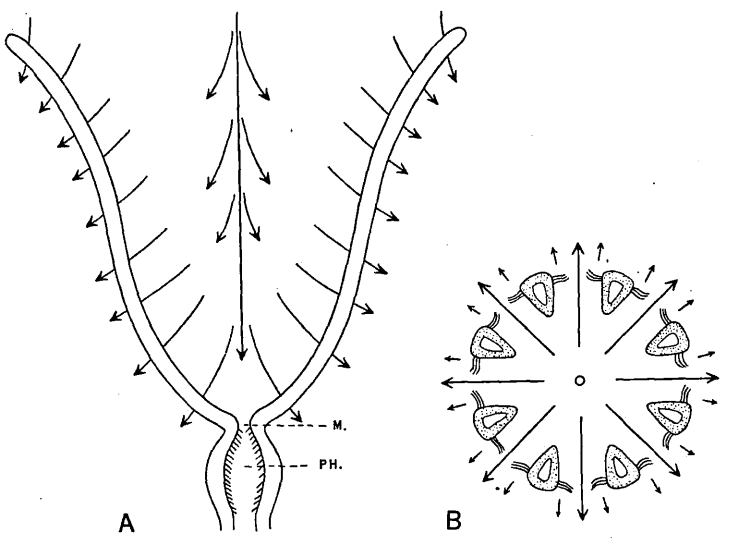
TEXT-FIG. 7.

Transverse sections of the tentacles of Ectoproct Polyzoa. A. Lichenopora fimbriata (Cyclostomata). (After Borg.) × *ca.* 2000. B, C, D. Flustrella hispida (Ctenostomata). B, through distal region of tentacle; C, through basal region of tentacle; D, through base of a tentacle forming part of the rejection tract. × *ca.* 1200. E, F. Electra pilosa (Cheilostomata). E, through distal region of tentacle; F, through basal region of tentacle. × *ca.* 1470. *B.G.*, basal granules; *C.R.*, ciliary rootlets; *F.C.*, frontal cilia; *L.C.*, lateral cilia; *M.*, homogeneous membrane; *M.C.*, mesoderm; *M.F.*, muscle-fibres. B–D, corrosive sublimate; E, F, Bouin's fixative; B–F, iron haematoxylin and acid fuchsin.

The development of the cilia along the frontal face would appear to vary widely in different forms.[1] They may be (*a*) absent, or Borg (**5**, p. 217) states, so feebly developed that he was unable to find them, as in most Cyclostomata; in others (*b*) short and thinly scattered as in the Crisiidae, and in some other forms, for instance, Berenicea patina, Diplosolen obelia, and Lichenopora fimbriata (Text-fig. 7, A) (**5**, p. 216); or (*c*) fairly numerous and long as in Flustrella hispida (Text-fig. 7, B–D) and Alcyonidium (Ctenostomata). Also in Electra pilosa, one of the Cheilostomata, the frontal cilia are fairly long, at least towards the base of the tentacles, though perhaps not very thickly set (Text-fig. 7, E and F). Marcus (see Borg, **5**, p. 248) says of the frontal cilia of Farrella repens that they are immovable and stiff. In the first instance (*a*) a frontal current along the length of the tentacle is obviously absent; in the second instance (*b*), Borg (**5**, p. 248) says he has occasionally seen a particle, which has stuck to one of these cilia, moving slowly along the frontal face towards the mouth, but that these frontal cilia play quite a subordinate part in the nutrition; in (*c*) Flustrella hispida, where the frontal cilia are well developed, they approach the lateral cilia in length and there seems to be little or no movement of particles over them, except perhaps towards the lower part of the tentacular funnel. Here particles may occasionally be seen travelling down them into the mouth. Towards the base of the lophophore, where the tentacles are crowded together, the frontal cilia are especially long, while the laterals appear somewhat reduced in length. The chief function of the frontal cilia—especially of those towards the bases of the tentacles—in Flustrella hispida would appear to be to help produce and direct the main water current towards the mouth.

[1] It is possible that the frontal cilia are longer than they appear in transverse sections. As these cilia beat along the length of the tentacles, it is possible that in preserved material they may lie at an angle to the frontal surface, and in transverse sections would be cut across. The lateral cilia, on the other hand, beating across the length of the tentacles, would be seen at their full length in transverse sections.

In the Ectoprocta the extended tentacles form a funnel with the mouth at the base: in Flustrella hispida the shape of the lophophore is bell-like, the tips of the tentacles being bent outwards. Briefly the method of feeding as observed by Borg (**5**, p. 247) is as follows: a water current is produced by



TEXT-FIG. 8.

A. Diagram showing longitudinal section through tentacular crown, mouth (*M.*), and pharynx (*PH.*), in Cyclostomata. B. Diagram showing section through tentacular crown. The arrows indicate the direction of water currents caused by movements of cilia. (After Borg.)

the lateral cilia of the tentacles, between which it passes outwards (Text-fig. 8) (that is in the opposite direction to the water current in Loxosoma) incidentally carrying with it many food particles. This results in the formation of a current directed straight down the lophophore to the mouth (Text-fig. 8, A). The muscular pharynx acts as a suction-pump which receives the food, and its effect is increased through the strong cilia of the epithelium of the pharynx, which move from above downwards. As Borg points out, the feeding mechanism cannot be regarded as very perfect, many particles escaping with the

water current passing out between the tentacles, and mostly only those in, or near, the median line of the lophophore reaching the mouth. Borg (**5,** p. 248) details the various means by which the animal increases the number of particles brought to the mouth, chief of which are the turning of the tentacular crown in different directions, and the alteration in the direction of the water current by the spreading and the contracting of the tentacles.

The methods resorted to by the Ectoprocta to prevent distasteful particles from reaching the mouth are, according to Borg (**5,** pp. 248, 249):

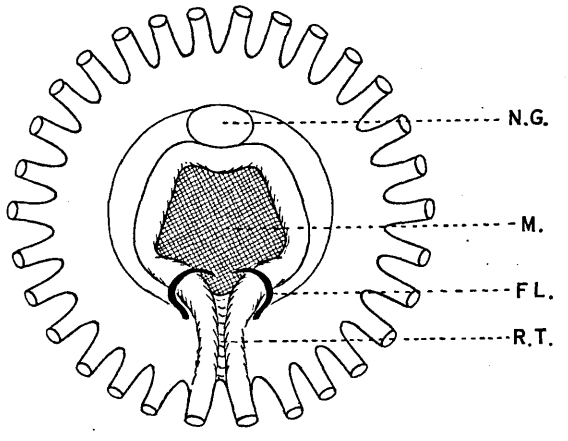
1. Complete or partial retraction of the tentacular crown.
2. Approximation of the tips of the tentacles, thus preventing the formation of the water current towards the mouth, while particles are whirled out between the tentacles.
3. Quick movement towards the median line of a tentacle to free itself from a useless particle, which has adhered to it.

The rejection of useless particles, which have already gained the region of the mouth, is carried out in the following different ways (see Borg, **5,** pp. 249, 250):

1. The mouth remains closed, and particles are then usually carried away by the water streaming out between the bases of the tentacles.
2. 'Particles that have already been swallowed can again be ejected out of the stomodaeum, through a momentary alteration of the direction of movement of the cilia of the pharynx, and a quick opening and closing of the mouth.'
3. Ejected particles, and others too large to pass through the narrow spaces between the proximal parts of the tentacles, often collect in a little heap by the side of the mouth. When this occurs the animal first widens the tentacular crown, and then contracts it with great rapidity; in this way water at first streams in between the tentacles and then is forced out through the opening of the tentacular funnel, carrying with it the heap of particles.

The Method of Rejection of Unwanted Particles in Flustrella hispida.—The method of rejection of un-

wanted particles from the mouth region in Flustrella hispida is more specialized than is that of the forms described by Borg. It was noticed that in Flustrella if the animal does not wish to feed, particles passing into the pharynx travel out again at a certain point ventrally, and, passing between the bases of two tentacles, are carried away in the main current

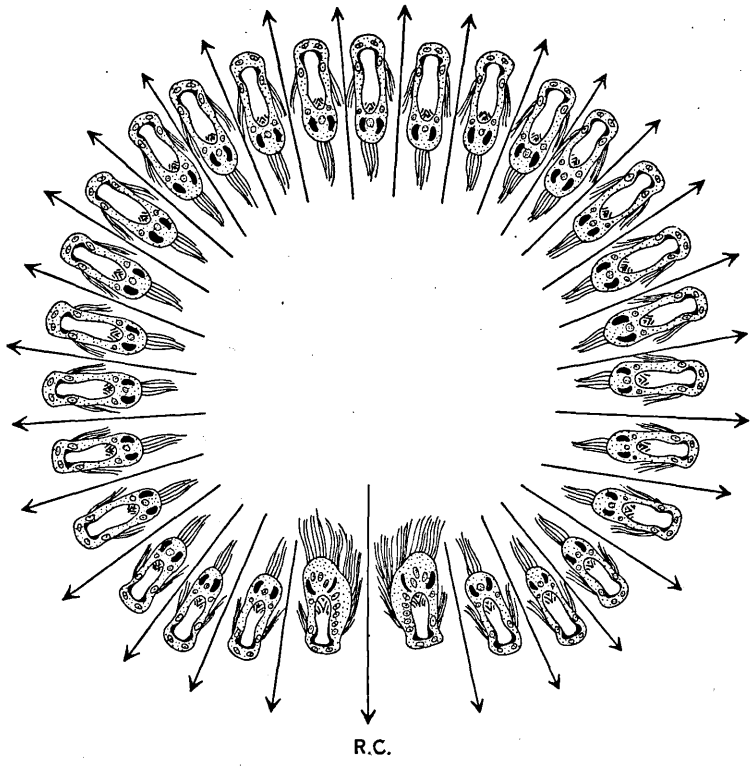


TEXT-FIG. 9.

Surface view of the lophophore of Flustrella hispida. (Slightly modified after Prouho.) *FL.*, flagellum; *M.*, mouth; *N.G.*, nerve ganglion; *R.T.*, ciliated rejection tract. ×225.

setting away from the animal. Closer observation showed that there is a narrow ciliated rejection tract in this region, leading from the mouth outwards between the bases of the two tentacles (Text-fig. 9). These form part of the rejection tract, the cilia for a short distance beating towards the tips. This tract is a continuation of a ventral groove in the pharynx (Text-fig. 12, p. 419) along which the cilia beat outwards towards the mouth. Looking down on an expanded lophophore, this region, with the tentacles on either side of it, can easily be distinguished (Text-fig. 9); its position can be determined in transverse sections through the base of the tentacular crown, owing to the larger size of the bases of the two tentacles forming part of the rejection tract (see Text-fig. 10). On either side of the groove is a large

flagellum (see Prouho, **24**, p. 564), or I am inclined to think a short, almost transverse, row of stout cilia (Text-fig. 11, *FL.*), which beat transversely towards the groove. Their position at the



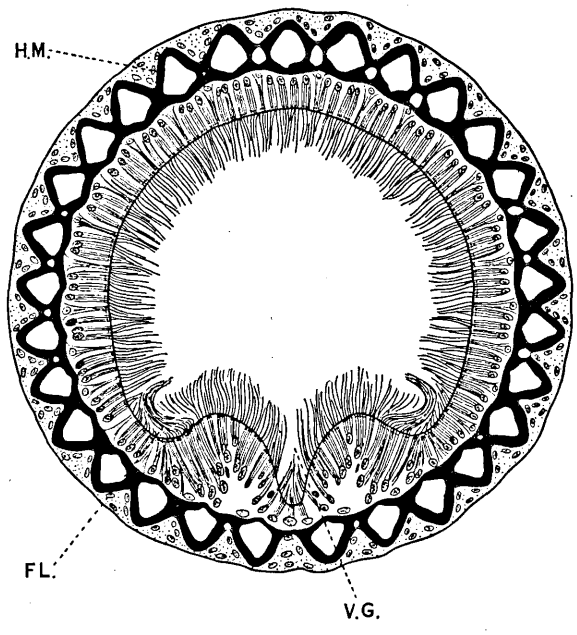
TEXT-FIG. 10.

Flustrella hispida. Transverse section through the tentacular crown (towards the base) showing the direction of the water currents set up by the lateral cilia of the tentacles. *R.C.*, arrow indicating the position and direction of the current carrying particles rejected from the pharynx; the bases of the tentacles on either side form part of the rejection tract. Somewhat diagrammatic. ×430.

end of the beat into the groove is shown in Text-fig. 9: they do not beat continuously, but at irregular intervals.

In Flustrella, therefore, although the cilia clothing the

walls of the pharynx beat mainly in a downward direction, there is a groove in the mid-ventral line (Text-fig. 12) along which the cilia beat upwards, thus the passing of particles, and of water, out of the pharynx is not due to a momentary alteration of the direction of movement of the cilia of the pharynx, such as Borg (**5**, p. 249) found in the species he investigated. It is probable that muscular movement of the walls of the pharynx



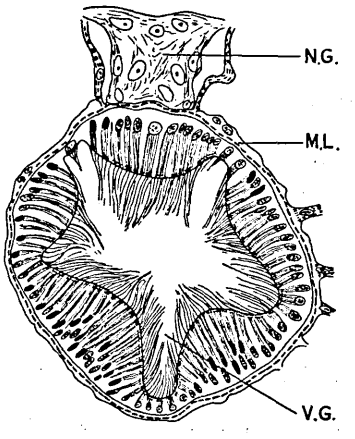
TEXT-FIG. 11.

Flustrella hispida. Transverse section through the lophophore at the level of fusion of the tentacles. *FL.*, flagellum (or short row of stout cilia?); *H.M.*, homogeneous membrane of the tentacles; *V.G.*, ventral groove or rejection tract. Corrosive sublimate; iron haematoxylin and acid fuchsin. Somewhat diagrammatic. × 430.

determine whether particles be brought in contact with the outgoing tract of cilia, for during feeding the walls of the pharynx are in constant movement. Particles accepted as food collect, before being swallowed, in the region where the pharynx passes

into the unciliated oesophagus, but even from here there may be some slight loss of particles, as the ventral ciliated groove is continued for a very short distance among the unciliated epithelium of the oesophagus.

The peculiarity in the form of the buccal region in Flustrella, and an allied genus Pherusa, was noted by Prouho (**24**, p. 564) in 1892, and he says, "La symétrie bilatérale du



TEXT-FIG. 12.

Flustrella hispida. Transverse section through the pharynx at the level of the nerve ganglion. *M.L.*, muscle-layer; *N.G.*, nerve ganglion; *V.G.*, ventral groove or rejection tract. Corrosive sublimate; iron haematoxylin and acid fuchsin. ×430.

lophophore est ici rendue manifeste par cette disposition particulière qui, sans doute, doit être de quelque utilité à l'animal pour le choix ou la préhension de sa nourriture."

DISCUSSION.

From what is known of the structure of the tentacles and their ciliation in the fresh-water Polyzoa, it is probable that the ciliary feeding mechanism of this group is somewhat similar to that of the marine Ectoprocta, though no doubt modified owing to the horseshoe shape of the lophophore in the majority

of forms, and the presence of a large epistome. The lateral cilia in the Phylactolaemata have been described by Allman (**1,** p. 20), as beating towards the tips of the tentacle on one side and towards the base on the other, but he was apparently misled by a marked metachronal wave of the type of the lateral cilia of the marine Ectoprocta, and, as pointed out by Nitsche (**21,** p. 26), in reality the cilia beat across the tentacles (see also Kraepelin, in Borg **5,** p. 245). It is very probable that the effective beat is from the frontal to the abfrontal face as in the marine forms. It might be noted that Gilchrist (**11,** footnote, p. 163) also alludes to the lateral cilia of the tentacles of Polyzoa as beating in opposite directions on each side of the tentacles.

It is of interest that a similar type of metachronal wave, that is one running at right angles to the direction of beat of the cilia, and in opposite directions on opposite sides of a tentacle, filament, or gill-bar, is found for the lateral cilia in widely different groups of animals in which these cilia beat in the same direction, namely, from the frontal to the abfrontal surface, and where their function is that of producing a water current. Groups of animals in which the lateral cilia have a rhythm of this type are: Ectoproct Polyzoa, Phoronis, Lamellibranchs, those Gastropods in which the gills are formed of distinct filaments, and the cilia are differentiated into laterals and frontals (i.e. Gastropods exclusive of Tectibranchs and Nudibranchs), Ascidians and Amphioxus.

It will be evident from the foregoing account that the method of feeding in the Entoproct and Ectoproct Polyzoa is very different; not only are the main water currents in the two groups in opposite directions (cf. Text-figs. 1, p. 395, and 8, p. 414)—illustrated by the fact that in Loxosoma a free bud, or detached small adult, swims with the calyx hindmost, while the opposite occurs in the Ectoprocta—but while ciliary currents (as distinct from water currents)[1] play an important part in the method of feeding in the Entoprocta,

[1] A clear statement of the distinctions between water currents and ciliary currents is given by Graham ('Trans. Roy. Soc. Edin.', vol. lvi, Part III, no. 29, p. 738, 1931).

they may be absent, or little developed, on the tentacles of the Ectoprocta. The difference in the method of feeding is reflected in the size of the particles taken in the two groups, the Entoprocta being restricted on the whole to finer particles than are the Ectoprocta.

The method of feeding in the Entoprocta is rather similar to that of Sabella pavonina as described by Nicol (**20**), though on a simpler plan, and without the specialized sorting mechanism of the worm. In Sabella the beat of the long cilia which maintain the main water current is also from the abfrontal to the frontal surface of the filaments, and they have a metachronal rhythm similar to that of the lateral cilia of Loxosoma. It might be noted, however, that while in Sabella these cilia when at rest have a marked S-form, those of Loxosoma are only slightly curved inwards.

The cilia producing the main water current in Loxosoma and Pedicellina are in the same position in regard to the frontal cilia, that is adjacent to them on either side, as in Sabella pavonina and certain other Cryptocephalous Polychaetes (see Nicol **20**), and incidentally as on the dorsal filaments of Brachiopods (see Orton **23**, p. 293)—though in the latter group the effective beat is in the reverse direction—and have been termed by Nicol latero-frontal cilia. While these cilia are undoubtedly latero-frontal in position, this term is perhaps not altogether advisable as it has been previously applied to, and has come to denote in particular, the slow beating, straining (see Gray[1] **12**, p. 145, and Orton **22**, p. 466)—and not water-current producing—cilia of the Lamellibranch Mollusca. As the long cilia on the tentacles of the Entoprocta agree in their function of producing the main water current—though the effective beat is in the opposite direction—with the lateral cilia on the tentacles of the Ectoproct Polyzoa, and incidentally with those of Phoronis, Lamellibranchs, certain Gastropods, Ascidians, and Amphioxus, they have been termed lateral cilia in this paper.

The ciliary feeding mechanism of the Ectoprocta would

[1] Gray (12, p. 145) also says that 'they appear to keep individual filaments apart, so giving freedom of action to the lateral cilia'.

appear to differ considerably from that of any group so far described in any detail, in that ciliary currents, if not absent, play a subordinate part, while the chief role is played by the water current—set up by the lateral cilia—in conjunction with a suction pump formed by the muscular pharynx.

Due acknowledgements have been made in the previous paper on 'The Loxosomatidae of the Plymouth Area'; in addition I wish to express my sincere thanks to Prof. J. H. Orton for reading the manuscript of this paper.

Summary.

An account is given of the ciliary feeding mechanism of the Entoproct Polyzoa, and of the structure of the lophophore and tentacles. The long lateral cilia cause a current of water to pass inwards between the tentacles, and throw particles on to the short frontal cilia of the inner surface, which carry them to the vestibular groove leading to the mouth.

The behaviour of the lateral cilia of the tentacles of L. crassicauda is described, and it is suggested that they are under the nervous control of the animal.

A résumé of Borg's work on the ciliary feeding mechanism of the Ectoprocta is given, a note on Flustrella hispida being added. It is pointed out that the method of feeding in this group differs widely from that of the Entoprocta.

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Printed in Great Britain by John Johnson at the OXFORD UNIVERSITY PRESS

12

PINNOTHERION VERMIFORME GIARD AND BONNIER, AN ENTONISCID INFECTING PINNOTHERES PISUM.

By D. ATKINS, B.Sc.

[*From the* Proceedings of the Zoological Society of London, 1933.]
[Published June 30th, 1933.]

[*Reprinted from* PROC. ZOOL. SOC. *Part* 2, 1933.]

Pinnotherion vermiforme Giard and Bonnier, an Entoniscid infecting *Pinnotheres pisum*.

By D. ATKINS, B.Sc.* (From the Marine Biological Laboratory, Plymouth.)

(Plates I.–VI.† ; Text-figures 1–14.)

CONTENTS.

INTRODUCTION.

In 1889 Giard and Bonnier (1889, pp. 914–916) gave a short preliminary account, without figures, of a new genus and species of Entoniscidæ, *Pinnotherion vermiforme*, which they found in a *Pinnotheres* inhabiting *Modiolus modiolus* at Wimereux, and in a footnote promised that a full account with figures would follow. This memoir does not appear in the lists of their works in Bull. Sci. France et Belgique, 1909, and would seem never to have been published. In their note the authors appear doubtful of the species of the host, saying only that it was not *P. veterum*; but Bonnier (1900, p. 227) later gave

* Communicated by Dr. E. J. ALLEN, F.R.S., F.Z.S.

† For explanation of the Plates, see p. 362.

it as *P. pisum*, though without adding further details of the parasite. Mercier and Poisson (1929) have since recorded *Pinnotherion vermiforme* infecting *Pinnotheres pisum* at Luc-sur-mer.

Specimens of an Entoniscid, in all probability this species, having been found in the pea-crab, *Pinnotheres pisum*—itself a parasite of *Mytilus edulis*,—it has been thought worth while to add to Giard and Bonnier's description, and to provide figures, especially as little or no work would appear to have been done on the structure of the Entoniscidæ since their time.

The parasite has been found only in *Pinnotheres* infecting *Mytilus* taken from the Estuary of the Camel, near St. Issey Cliff, Padstow, North Cornwall. They have not been sought for intensively elsewhere, but no female *Pinnotherion* were found on external examination of 161 female *Pinnotheres* from the Yealm Estuary, 30 from the Estuary of the Teign, and 68 from the Estuaries of the Hamoaze. In addition thorough examination of 27 large female *Pinnotheres* from the Estuary of the Yealm, Devon, and 17 (16 large and 1 small adult) from the Fal Estuary, Cornwall, gave no result.

In the female *P. pisum*, after the early male-like stage, the carapace is thin and transparent, so that the presence of at least the adult female *Pinnotherion* may be fairly easily detected without the necessity of removing the carapace. Attention was first drawn to the parasite by noting some large opaque white patches in the body of an adult female *Pinnotheres*, which, when punctured with a fine pipette, were found to contain a milky fluid swarming with the well-developed embryos of an Entoniscid Isopod. For some time afterwards *Pinnotheres* were examined externally only, until investigation of a tiny opaque white object lying over the dark red gonad of a female disclosed an adult male *P. vermiforme*. Subsequently *Pinnotheres* were narcotized with chloroform (this was found to affect the parasite little, if at all) and examined fresh, the carapace being lifted off and the internal organs removed and examined. In this way it was discovered that the adult males, and also, though perhaps more rarely, the cryptoniscan larvæ occur free within the thorax and abdomen of the host, and are far from being restricted in their occurrence to the body of the female, as apparently in other genera (G. & B., 1887, p. 225). The male of *P. vermiforme* may therefore exist as an internal parasite. Giard and Bonnier examined some hundreds of *Pinnotheres*, finding one female parasite only, and not noting any males other than those within the brood-chamber of this female. In *P. pisum* the conditions are especially favourable for their detection, for the male *Pinnotherion* is of quite large size for the family, being 1·0–3·5 mm. in length, while the hosts are small. It is possible that the male of other genera of Entoniscidæ will be found to occur free within the body of their hosts.

Numbers of Host and Parasite.

Thorough examination of a total of 473 *P. pisum* from the Camel Estuary, of which 415 were females and 58 males (8 of which were abnormal, see p. 326, and 11 of carapace width 6·0–7·0 mm.), showed 131 to be infected with one or more specimens of *P. vermiforme*, that is, 27·69 per cent. Infection with male parasites alone (26·85 per cent.), however, was much greater than with female parasites, sometimes with males present in addition (0·84 per cent.). Two adult females found among about 850 female *Pinnotheres* before internal examination was begun have not been included in this percentage.

The percentage of female *Pinnotheres* infected was 31·08 per cent. (129 out of 415 examined), the percentage of male *Pinnotheres* infected was 3·45 per cent. (2 out of 58 examined).

Mercier and Poisson found at Luc-sur-mer that 5 per cent. of the total *Pinnotheres* were infected (with female *Pinnotherion*), 9 per cent. of females and 1·5 per cent. of males being infected. They agree with Bonnier (1900, p. 121) that this difference probably results from the predominance of one sex over the other, the male *Pinnotheres* being more rarely found in *Mytilus* than the female. This is no doubt right, but possibly the difference in thickness of the carapace in the two sexes has some influence on the numbers infected in the case of *P. pisum*. While the carapace of the normal male in the middle line is about 0·11–0·24 mm. thick, and the abdomen (dorsal surface) about 0·08–0·17 mm., corresponding figures for the female, after the young male-like stage (see Atkins, 1926), are 0·01–0·02 mm., and the abdomen about the same.

Bonnier (1900, p. 122) notes that infection with Epicarid Isopods appears to be heavier in some years than in others ; *Pinnotheres* have not been examined over a long period, but details of infection in the different months in which they have been examined is as follows :—

Date.	Number of *Pinnotheres* examined.	Number infected.	Percentage infected.
Oct. 11, 1928 ...	103 (95 females, 8 males).	28	27·18
Feb. 27, 1929 ..	186 (159 females ; 27 males, 8 with carapace 6·0–7·0 mm. wide).	49	26·34
June 6, 1929 ...	100 (93 females ; 7 males, including 2 abnormal).	46	46·00
Aug. 9, 1929....	60 (48 females ; 12 males, including 6 abnormal).	4	6·66
May 15, 1930 ..	12 (all females).	2	16·66
Nov. 24, 1931 ..	12 (8 females, 4 males).	2	16·66
Total	473	131	27·69

Proportion of the Sexes.

Actually the disproportion in the sexes is greater than the percentages of infection with male and female parasites (p. 320) show, for several living adult males may be found in one host, together with adult males which have apparently died and been enclosed, in some instances, in a cyst-like structure by the host ; and incidentally cryptoniscan larvæ. The greatest number found together of living adult males is three, of dead males four, and of cryptoniscan larvæ two. In the same host as a large adult female were three living males (one only being near the female, and that on the pleural lamellæ, though outside the enclosing membrane), two dead males, and the moults of two cryptoniscan larvæ. The dead males and the moults were all near the abdomen of the female, though not within the chitinous sheath.

The total number of individuals of *Pinnotherion* (exclusive of some seventeen cryptoniscan larvæ) found since *Pinnotheres* have been examined thoroughly is 172 ; of these 168 were male, namely 97·67 per cent. (142 being active and 26 dead males), while four were females, namely 2·33 per cent. The females were adults with the exception of one taken in October 1928, which was very immature (Pl. II. fig. 4).

Details of the proportion of the sexes of *P. vermiforme* infesting *Pinnotheres* taken from *Mytilus* in different months of the year are given in the table on p. 322.

Proportion of the Sexes in P. vermiforme.

	Oct. 11, 1928.	Feb. 27, 1929.	June 6, 1929.	Aug. 9, 1929.	May 15, 1930.	Nov. 24, 1931.	Total.
Males, living.....	28	56	49	4	2	3	142
Males, dead	4	8	10	1	2	1	26
Total males	32	64	59	5	4	4	168
Per cent.	94·12	98·46	98·33	100·0	100·0	100·0	97·67
Females	2 (one adult; the other very immature).	1 (young adult).	1 (with young embryos).	0	0	0	4
Per cent.	5·88	1·54	1·67	0·0	0·0	0·0	2·33
Cryptoniscan larvæ	(4)	(10)	(2)	(0)	(1)	(0)	(17)
Total (exclusive of larvæ)	34	65	60	5	4	4	172

The occurrence of adult males and of cryptoniscan larvæ free within the body of the host is of considerable interest. Giard and Bonnier (1887, pp. 195, 196), and later Bonnier (1900, pp. 134, 135), record of other species the finding of a certain number of females in the " asticot " stage in this condition, though these were still enclosed within the chitinous membrane formed by the host—as females normally are,—but had lost their connection with the exterior, and they make the suggestion that this most probably occurred during the moulting of the host. Such females, they note, though in the " asticot " stage, attain a large size, but remain sexually immature, and they ascribe this to the severing of external connections. The males found free in *P. pisum* were not surrounded by a chitinous membrane, and it would hardly seem feasible to ascribe the occurrence of so many isolated males to the accidental severing of their connection with the gill-chamber during the moulting of the host.

It appears that the first cryptoniscan larva to attach itself to the wall of the gill-chamber changes into a female, after a transitory period of hermaphroditism, while of later arrivals the first changes into an adult male and the remainder function as males in the cryptoniscan stage (G. & B., 1887). Bonnier (1900, pp. 45, 46) later, however, considered it doubtful whether the sexually mature cryptoniscan larvæ were able to function as males, as he never discovered genital openings. Giard and Bonnier (1887, p. 212) consider that the fate of the cryptoniscan larva (*i. e.*, whether it turns into a female or an adult male) depends on whether its position is favourable or the reverse for obtaining abundant nourishment. Pérez (1924, p. 473), finding a very young female of *Pleurocrypta porcellanæ* in the male's position on a fully mature female carrying embryos, suggests that in the Bopyridæ there may be a possibility that sex is already determined in the larval stage.

In the Entoniscidæ, according to Giard and Bonnier (1887, p. 156), generally one adult male only is present at a time on a female, except in the case of *Priapion* (*Portunion*) *fraissei* (1888, p. 474), where there may be as many as seven. In other species if the single male should disappear they consider (1887, p. 213) that one of the larvæ may take its place, turning into a male. The large number of isolated adult male *Pinnotherion* is remarkable. The mature males are apparently incapable of any further change ; the largest males of *Pinnotherion* found showed the same external and internal structure as the smallest.

The frequency of the males within the body of the host may possibly have some relation to the thinness of the carapace of the crab, entry not being restricted to the gill-chamber, and to be peculiar to the Entoniscid of *Pinnotheres*; but, on the other hand, males have been found, though exceedingly rarely, in the body of the male *P. pisum*, whose carapace is much harder and thicker than that of the female. Out of 58 male *Pinnotheres* examined only two were infected, each with a single male *Pinnotherion*.

Giard and Bonnier (1887, pp. 178, 179) and Bonnier (1900, pp. 119, 120) consider that there is a relation in size between parasite and host, the larvæ attacking young crabs, and that it is usual for Entoniscidæ to infect more frequently young hosts than older individuals, giving as reasons the greater thinness and softness of the carapace in young forms and the greater frequency of the moult. They hold that the parasite enters while the skin is soft and the current through the gill-chamber feeble. It would seem that crabs after a certain age are free from attacks, owing possibly to the thickened branchial membrane proving more resistant to pressure exerted by the larvæ, or possibly the increased strength of the current through the gill-chamber preventing them from attaching themselves in a convenient position ; late infection, however, of *Carcinus mœnas* by *Portunion mœnadis* is not uncommon (G. & B., 1887, pp. 185, 244).

The carapace in the female *P. pisum* being soft and thin (about 0·01–0·02 mm. thick in the middle line of the carapace) it is possible that the parasite is able to enter at any time, as well as at almost any part of the carapace, and is not restricted to the moulting period; possibly also it can enter an adult female, and as moults are less frequent at that age, there would be greater probability of the preservation of the parasite.

The six specimens of female *Pinnotherion* found were in adult female *Pinnotheres* (stages IV.–V., see Atkins, 1926, pp. 476–482) of 10·0 to 13·0 mm. carapace width. Giard and Bonnier (1889, p. 914) mention that their specimen was in a female 15·0 mm. wide. The very immature female found at Padstow was in a female host of 12·0 mm. carapace width, being an exception to the general rule that young parasites are found in young hosts; the thinness of the host's carapace may be responsible for the exception.

Pinnotherion, both male and female, have been found almost entirely in adult *P. pisum* of stages IV. and V. The proportion of adult females examined internally is greater than young forms, but in the young transparent stages, where the gonad is little developed, the parasite, both male and female, might be expected to be visible externally.

Cryptoniscan larvæ have been found in female *Pinnotheres* of 10·0 to 13·0 mm. carapace width. As those larvæ examined were either moults or degenerating specimens, it is impossible to say how long they had persisted in the body of the host; but in at least two cases they were directly under the chitin, between it and the epithelium, and would in all probability be shed when the crab moulted, so that they must have arrived at that position since the previous moult.

Mature male *Pinnotherion* have been found in female *Pinnotheres* of 6·5 to 13·25 mm. carapace width, but the majority were in those of 10·0 to 12·0 mm. All the hosts were of stages IV. and V., that is, adults, even those of small size.

The 58 male *Pinnotheres* examined varied in size between 2·2 mm. and 7·0 mm., and at least eleven were of 6·0 to 7·0 mm. carapace width, while about eight were abnormal, that is, colourless, with thin carapace and scanty hairs. The two infected with male *Pinnotherion* were normal and of 5·0 mm. and 7·0 mm. carapace width.

Effects of *P. vermiforme* on its Host.

According to Giard and Bonnier (1887, p. 179), apart from the action on the genital organ the effects produced by Entoniscids on the organization of their hosts are very variable and inconstant.

Pinnotheres with adult female *P. vermiforme* have been kept in finger-bowls for nine, nineteen, thirty-one, and thirty-five days, the water changed daily, but the crabs left unfed. Under these conditions infected pea-crabs were no less active than uninfected and were in good condition when killed. Tucker (1930, p. 13) found that the Bopyrid *Gyge branchialis* did not materially affect the activity or viability of its host, *Upogebia littoralis*, in aquaria. Giard and Bonnier (1887, pp. 177, 178), however, note the weakening effect of Bopyrids and Entoniscids on the majority of hosts.

The presence of several active mature male *Pinnotherion* (up to three), together with specimens which had died and cryptoniscan larvæ, would appear, as might be expected, to have no appreciable effect on the condition of the gonad of the host—they frequently occur in heavily berried females—and do not prevent moulting, for they have been found in pea-crabs examined after moulting in the laboratory. On the other hand, the presence of the adult female *Pinnotherion* would seem to cause partial to almost complete atrophy of the gonad of the host, as previously noted by Giard and Bonnier

(1889, p. 914). Although the infected females were adults, in one instance there was no sign of the gonad externally (parasite with young embryos); in another a few scattered separate red ova (parasite with empty brood-chamber); and in two others the gonad was a pale reddish-orange trace (in one host parasite with well-developed embryos, and in the other with empty brood-chamber). In these *Pinnotheres* the entire body and even the legs were pale or milky orange in colour (see Pl. I. fig. 1), the colour doubtless being derived from the breaking down of the ova. A young female (see text-fig. 1), probably not yet spawned, was taken from a *Pinnotheres* the ovary of which was about half developed and of medium purple colour; in this instance, although the colour had begun to leave the ova the body of the host so far had not taken on the peculiar orange, or in some instances wine-coloration, which is characteristic of parasitism whether with a female *Pinnotherion*, a Microsporidian, or occasionally with a fungus (see Atkins, 1929, p. 218), which is a drain on the resources of the pea-crab.

The ovary of a *Pinnotheres*, in which a very immature female *Pinnotherion* (see Pl. II. fig. 4) was found, was about three-quarters developed and of dark brick-red colour; it appeared that the parasite had so far had little or no effect on the gonad of the host. Giard and Bonnier (1887, pp. 183, 244) conclude from their observations that, although sterility of the host may be the general rule, there are a certain number of exceptions. *Portunion kossmanni* in *Portumnus* (*Platyonichus*) *latipes* does not necessarily involve sterility or prevent moulting, and Pérez (1923*b*, p. 1935) gives several similar instances in Entoniscidæ and Bopyridæ. Entoniscidæ, which normally produce sterility when adult, may not do so when young, and the host may carry ova (G. & B., 1887, p. 184).

As the French naturalists (G. & B., 1887, pp. 95, 180) have noted for other Entoniscidæ as well as for *P. vermiforme* (1889, pp. 914, 915) the hepato-pancreas (liver) of the host as well as the ovary is much reduced, the parasite occupying practically all the available body-space. According to them the hepato-pancreas is also pale in colour; but the colour of this gland in *P. pisum* varies so widely, from nearly white to yellow and green in uninfected individuals, that it is almost impossible to say definitely that its pale colour in infected specimens is due to the parasite.

Whether the female *Pinnotherion* prevents the moulting of its host is not known, but seems very probable.

Giard and Bonnier (1889, p. 914) say of the single infected specimen of *P. pisum* they found that not only "Cette femelle ne portait pas d'œufs," but "les pattes ovigères étaient légèrement atrophiées." In the six female *Pinnotheres* containing female parasites obtained from Padstow there was no appreciable difference in the pleopods, and as uninfected adults vary somewhat among themselves as to the hairiness of these appendages it would be difficult to determine definitely that the influence of the parasite causes slight atrophy.

Mercier and Poisson (1929, p. 304) concluded from an examination of their specimens that "les femelles ne paraissent pas sensiblement modifiées dans leur morphologie externe par le parasite. . . . Sur un lot de 12 grandes femelles parasitées nous n'en avons observé qu'une seule portant des œufs; ceux-ci étaient peu nombreux."

Reduction of the abdominal appendages of the female host has been recorded for *Inachus scorpio* parazitised by *Sacculina neglecta* (Smith, 1906, pp. 68–69) and for *Upogebia littoralis* parazitised by *Gyge branchialis*. In the latter instance Tucker (1930, p. 43) found that, though considerable variability of the first pair of abdominal appendages was shown by normal animals, yet "Measurements of a series of parasitized females seem to justify the conclusion that the

rate of growth of the appendages is slightly but definitely slowed down by the action of the parasite." There is no question of the parasitized female taking on male-like characters; according to Tucker (1930, p. 97) it is simply a consequence of the demands of the parasite being in some respects more exhausting than those of the ovary. "The failure of certain appendages to develop quite so far or to quite the same size as in normal females is thus a perfectly natural retardation consequent upon the drain on the host's resources caused by the parasite and no more."

At Padstow the infection of *P. pisum* by the female *P. vermiforme* (0·84 per cent.) is not only much slighter than that found by Mercier and Poisson (1929, pp. 303–304) at Luc-sur-mer, where 5 per cent. of the total of *P. pisum* were infected (with female parasites), but at Padstow no male *Pinnotheres* were found infected by female parasites. Mercier and Poisson found that 9 per cent. of females and 1·5 per cent. of male *Pinnotheres* were infected. They note the alteration of the secondary sexual characters of the male *P. pisum* parasitized by the female *Pinnotherion*. The three infected were of large size, 6·5–7·0 mm. in width, and two of them "le facies femelle est accusé par la souplesse de la carapace, la gracilité des appendices et leur faible pilosité." They conclude that "*Pinnotherion vermiforme* est donc susceptible de déterminer chez le mâle du Pinnothère des Moules: du gigantisme, des modifications dans la structure du tégument et dans la conformation de certains appendices. Mais il est à noter que la présence du parasite n'entraîne pas forcément l'apparition synchrone de ces altérations. En effet, pour des causes que nous ignorons, l'un des mâles présente seulement du gigantisme."

It might be noted that *P. pisum* from Padstow and from several localities in Devon and Cornwall evidently normally reach a larger size than those at Luc-sur-mer, and males of 6·0 to 7·0 mm. carapace width are not uncommon, 35 of that size occurring among 273 obtained from Padstow. Of 56 males unsuccessfully examined for *Pinnotherion* 10 were 6·0 to 7·0 mm. carapace width; while 8 of varying size were without the normal male colour-pattern, with thin carapace, slender and only slightly hairy legs, that is, approaching the female facies, a condition such as described by Mercier and Poisson for two of their parasitized males. The occurrence of such abnormal but apparently unparasitized male *P. pisum* is of peculiar interest, and it is hoped to discuss the matter in a later paper.

Relation of the Parasite to the Host.

As is well known from the researches of Fritz Müller (see G. & B., 1887, p. 185) and of Giard and Bonnier the Entoniscidæ, although having the appearance of internal parasites, are actually external, being surrounded by an invagination of the external chitinous covering of the host; these parasites enter from the branchial chamber of the crab. At the point of invagination there is a thickening of the chitinous sheath where it is moulded over the posterior extremity of the abdomen, and in some hosts this may be a dark brown. To this thickened region Giard and Bonnier give the name of "casque" or "calyce chitineux." In *Pinnotherion*, though there is a thickened ring of yellowish chitin at the entrance into the sac (see text-fig. 1, B), it is not as marked as in the genera described by them.

The thickness of the chitinous sheath varies in the different hosts, being especially strong in crabs inhabited by certain species of *Cancrion* (G. & B., 1887, pp. 98, 189, 241), and is also thickened in certain semi-pathological forms of *Portunion mœnadis*. In *Pinnotherion* the sheath is exceedingly fine, almost colourless, or very pale fawn—though in some individuals it may be

distinctly brown in places,—and it was found to be impossible to remove it from the animal, as they were indistinguishable except near the point of entrance. Occasionally a few minute bubbles may be seen between the sheath and the parasite in an individual which has been removed from its host for some little time.

As Giard and Bonnier say (1887, p. 97): "Tous les Entonisciens sont renfermés dans une fine membrane transparente intimement appliquée à la surface extérieure du corps dont elle moule les moindres détails." It is only in sections of *Pinnotherion* that the presence of an enclosing sac or sheath can be distinguished—even then with difficulty in places, as it is so closely applied to the surface. In certain regions, however, the membrane does not follow the contours of the parasite; for instance, the walls of the ventral abdominal canal are not covered (see Pl. IV. figs. 2, 3, 4), and the membrane stretches across the dorsal groove of the thorax (see Pl. V. fig. 2). There are also generally places where there are slight spaces between the two surfaces—not to be confounded with the separation of the chitin of the parasite from its epithelium, as may occur in sections,—and occasionally traces of epithelium may be seen adhering to the outer surface of the sheath; when a parasite is fixed after removal from its host there is a slight difference in the staining reactions of the two membranes with Mallory's triple stain. The adhesion of the sheath to the parasite is in general so intimate that is has been shown in few of the figures of sections.

From sections of *Pinnotherion* it seems extremely doubtful whether—at least in this genus—there is any or a sufficient space between it and the enclosing sheath through which a current of sea-water could pass as shown by Giard and Bonnier in their figure (1887, fig. 25, p. 115). This current, entering through the aperture of invagination, is shown to pass between the sheath and the lamellar pleopods—while these are closed down on the abdomen (see 1887, fig. 21, p. 125),—continue between the sheath and the outer surface of the brood-chamber, and enter the latter through a gap in the hood in front of the cephalogaster. It then passes through the length of the chamber, traverses the ventral abdominal canal—while the pleopods are raised,—and issues by the same aperture as it entered.

If an appreciable space existed between the parasite and the enclosing sheath it seems improbable that it would be moulded so exactly over every detail of the external form. It might be suggested that the close adhesion of the sheath to the parasite seen in sections is due to shrinkage during fixation; this may be possible, but improbable.

It would seem very likely that sea-water entering by the aperture of the sac is forced along the abdominal canal by the depression of the lamellar pleopods on to the abdomen—the movement beginning with the posterior pair,—and so enters the brood-chamber. A reversed movement of the pleopods would force water already in the brood-chamber along the abdominal canal in a posterior direction, to pass out by the aperture in the sac. In life movements of the pleopods are visible.

The currents in the brood-chamber of *Pinnotherion* could not be tested, as after it had been found that there was no appreciable anterior gap in the hood (see p. 330) no further specimens could be obtained*.

* No *Mytilus* were obtained from Padstow between May 15, 1930, and November 24, 1931. On the former date of the 113 received about 14 per cent were infected with *Pinnotheres pisum*, but on the latter the percentage of infection had dropped to 1·4 per cent. (the average percentage infected of the five previous batches of *Mytilus*, obtained between October 11, 1928, and May 15, 1930, had been about 18 per cent.). This great decrease in the numbers of *P. pisum* made the possibility of finding a female *Pinnotherion* too remote to warrant time being spent in opening mussels.

To the pleural lamellæ of the abdomen Giard and Bonnier have ascribed a respiratory function, stating that they were bathed by sea-water (1887, p. 125), but if there be no appreciable space between the surface of these folds and the covering sheath in which a current of sea-water could pass respiratory exchange cannot take place directly between the blood in these expansions and the sea-water. These pleural expansions lie in the hæmocœl of the host, separated from the host's blood by an extremely fine chitinous membrane and its epithelium only; it is tentatively suggested that respiratory exchange occurs between the blood of the parasite and that in the hæmocœl of the host.

In the case of the respiratory (?) folds of the first pair of thoracic appendages respiratory exchange would be effected in the same manner. As these expansions lie in front of the mouth a current of blood probably passes over them as the parasite sucks its host's blood.

The fact that Giard and Bonnier (1887, p. 195) found living females of "asticot" stage, though of abnormal size, with no outlet to the exterior, shows that the animals can exist without being bathed in sea-water.

The pleopods and the oostegites would be bathed in sea-water passing along the abdominal canal and through the brood-chamber, and in their case respiratory exchange would be effected directly between the blood of the parasite and the sea-water.

The Female. (Pls. I.–VI.; text-figs. 1–7.)

The parasite, which may enter from either gill-chamber, stretches from one side of the host to the other (Pl. I. fig. 1), curving beneath the alimentary canal. The body is U-shaped, the head and thorax forming one arm and the abdomen the other (Pl. 1. fig. 2; Pl. II. fig. 3). The thoracic region, which is very short in this species, is prolonged posteriorly by the greatly developed posterior ventral ovarian process. There are no dorsal ovarian processes; of the two ventral ones the posterior, which is cylindrical and extremely long, extends into the abdomen of the host, occasionally reaching the anterior border of the fifth segment. Extension of the body of the parasite into the abdomen of the host occurs in no other known Entoniscid, and in *Pinnotherion* is probably correlated with the fact that in *Pinnotheres* the abdomen is of some thickness, being occupied by the posterior extensions of the ovary. Giard and Bonnier (1889, p. 915) say: "Les muscles de la paroi du corps qui recouvre l'ovaire ont, malgré cette énorme distension, conservé une grande puissance, et les bosses ovariennes sont animées de contractions énergiques. La deuxième surtout présente des mouvements vermiformes, qui lui permettent de se recourber et de s'insinuer, comme nous l'avons dit, dans la queue du Crabe, malgré le reploiement de cette dernière."

A single young female was obtained in October 1928; it was found among the organs of the host after they had been removed, and its position in the body is unknown. It was enclosed, as normally, within a chitinous membrane formed by the host. This female (Pl. II. fig. 4) is in most respects less advanced than the stage of *Portunion mœnadis* described and figured by Giard and Bonnier (1887, pp. 153, 154, and pl. v. fig. 2), in that the curvature of the body is still ventral, the oostegites tiny, the pleural lamellæ distinct and simple, and the pleopods clearly visible. In the loss of all sign of segmentation, however, it is more advanced. The hepato-pancreas was pale yellow; the heart was present in the third abdominal somite, this being the only young stage obtained it was not sectioned.

Giard and Bonnier (1889, p. 914) say of a female *Pinnotherion* with mature embryos: "Mais notre attention fut particulièrement attirée sur une masse d'un gris violacé, visible à travers le tégument dorsal transparent [of *Pinnotheres*] et rappelant l'aspect d'une ponte de *Grapsion cavolinii* Gd." The female from Padstow with embryos well developed (see text-fig. 13, A), but still within the embryonic cuticle, however, showed no violet coloration—in fact, it appeared whitish, due to the presence of a milky fluid in the brood-chamber, which masked the colour of the embryos, of the rich deep yellow gonad, and of the red hepato-pancreas. The absence of the violet colour may have been due to the fact that the embryos were not fully developed. The colour of the females of the Entoniscidæ apparently varies with the age of the ova and embryos (G. & B., 1887, pp. 96, 113). In five out of the six females found the brood-chamber was full of the milky fluid. The exception was a young adult female (see text-fig. 1); in this instance a very little white fluid came from the brood-chamber a short time after fixation, but was not noticeable in the living animal. In dissecting the animal from the host it is almost impossible not to puncture the outer oostegites, when the milky fluid oozes out; in a careless dissection the brood-cavity may be almost free of it by the time the parasite is removed. The origin of this fluid is uncertain; in sections it has much the same appearance as the blood fluid. In places the blood sinuses near the surface are distended with blood (seen in sections), and it seems possible that the milky fluid may be the result of bleeding. Whether it has any function in relation to the embryos is not known. It is surprising that the fluid within the brood-chamber, constantly being renewed by sea-water from outside, yet retains its milky coloration.

Morphology.

The cephalic region seems to be normal for the family; it has not been especially investigated in *Pinnotherion*. An abnormality noted in one individual was inequality in the size of the two lobes of the cephalogaster, the left one being about $1{\cdot}5 \times 1{\cdot}3$ mm. and the right only $1{\cdot}15 \times 1{\cdot}0$ mm. (see text-fig. 1, A).

The Perœopods and the Brood-chamber.

In the adult female the perœopods are rudimentary (Pl. V. fig. 3) except for the oostegites, and have only been recognized in sections, and then but four pairs. They consist of the base and a small lamella which extends almost entirely in an anterior direction.

The first pair of oostegites, which are almost entirely hidden within the brood-chamber, are inserted immediately under the maxillipedes. They are divided into ascendant and recurrent lamellæ only, transverse lamellæ being absent. The ascendant lamellæ are curved over the head and each is folded laterally on itself, the folded margins being deeply lobed, so that small secondary pockets are formed (Pl. II. fig. 3) as in *Cancrion* (G. & B., 1887, p. 241, and pl. iv. fig. 5). The recurrent lamellæ are of great length and considerable width; the full width is not visible in the figure as they are curved inwards, from having surrounded the extremely long posterior ventral ovarian process. They have a somewhat crumpled appearance from being confined within the brood-chamber. The rôle of the first pair of oostegites, according to Giard and Bonnier (1887, pp. 115, 116), is to agitate the water and embryos within the brood-chamber, and to prevent the latter from being compressed.

The brood-chamber is closed in the adult except at the posterior margin. The boundaries of the component oostegites cannot be distinguished in the entire animal, though the distribution of the blood-vessels gives some indication of their relative positions. In sections the overlapping of consecutive oostegites

may be distinguished in places. The hood formed by the second pair of oostegites is deeply lobed, following the contours of the ascendant lamellæ of the first pair, which are lodged within it. In the anterior region of the hood the ventral margins of the oostegites of opposite sides are turned inwards, the outer surfaces of the two being intimately applied, and the combined lamellæ projecting into the chamber as a low fold; posteriorly they simply overlap slightly, as they do dorsally in front of the cephalogaster.

A median artery runs the length of the recurrent lamella, giving off fine branches which join the marginal sinus. The marginal sinus, entering the oostegite at its point of attachment, runs round the entire margin of the recurrent lamella and the greater part of that of the ascendant lamella. At the point of entrance of this sinus into the oostegite an anterior branch is given off which runs in the ascendant lamella a short distance from, and more or less parallel with, its inner margin. A narrow thickened band of chitin accompanies the marginal sinus (see Pl. II. fig. 3 & Pl. III.). Two narrow somewhat thicker bands run on either side of the median artery of the recurrent lamella (see Pl. V. fig. 3) and also of the anterior sinus in the ascendant lamella (Pl. III.). Blood-vessels are present in the outer oostegites; these, however, are not accompanied by bands of chitin.

Giard and Bonnier (1887, pp. 108, 109, 111) describe solid chitinous axes or "nervures" supporting the oostegites, and which are followed by arteries. In *Pinnotherion* no such solid axes occur, though the arteries and sinuses filled with blood, and accompanied in the case of those of the first pair of oostegites by thickened bands of chitin, no doubt act to an appreciable extent as supports, especially in the case of the ascendant lamellæ, where the outer bands of chitin accompanying the vessels near their entry into the lamellæ are especially thick (Pl. III. fig. 3).

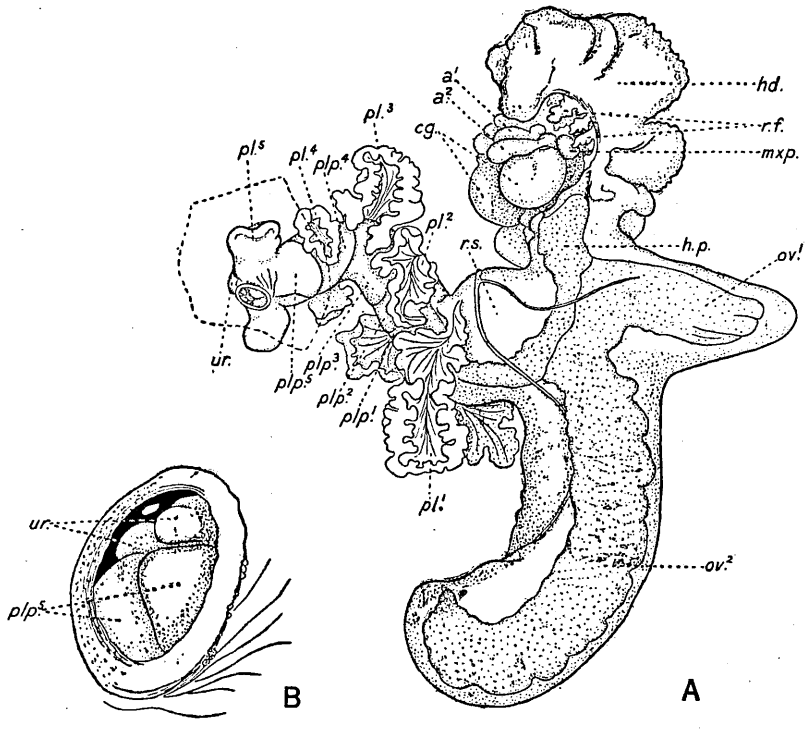
According to Giard and Bonnier (1887, p. 111) in the genera of Entoniscidæ in which the brood-chamber is closed in the adult (e. g., *Grapsion*, *Cancrion*, and *Portunion*) there is a triangular opening—visible in young forms, masked by the "corps spongieux" in adults—between the two oostegites of the second pair (forming the hood) in front of the cephalogaster, by means of which the incubatory cavity is in communication with the exterior—that is by way of a space (see p. 327) said to exist between the parasite and the chitinous sac formed by the host. The borders of the opening are formed by the twisted folds of these two oostegites; simple in the young, they become very complicated in the adult, constituting two "corps caverneux" or "corps spongieux," which come to mingle so intimately as to form a single mass, obstructing the entrance into the brood-chamber. This mass only attains its full development when the animal is adult and about to spawn for the first time. They consider (1887, p. 116) "Le courant pénètre par la partie antérieure, en passant dans les interstices des corps spongieux de la seconde paire de lamelles: grâce à cet appareil, l'eau peut librement entrer débarrassée de toute impureté, et la sortie des embryons est mécaniquement empêchée."

In *Pinnotherion* the formation of the hood and the origin of the "corps spongieux" or respiratory (?) folds differ considerably from the above description. The hood, formed by the second pair of oostegites, is open for a short distance in front of the cephalogaster, leaving a triangular gap such as described by Giard and Bonnier. Through this gap in the hood, however, protrude the ascendant lamellæ, and as their inner edges are united in this region they close the gap (Pl. III. fig. 1). There appears to be a single tiny tortuous passage (persisting only through one or two transverse sections of about 10μ thick) into the brood-chamber, at the extreme anterior extremity of the body

(see Pl. III. fig. 2). It is extremely doubtful whether this is sufficiently large for the entrance of a water current.

In *Pinnotherion* the " corps spongieux " does not arise from the second

Text-figure 1.



Pinnotherion vermiforme, female.

A. Sketch from life of a young adult (which has probably not yet spawned) from the right side. The respiratory (?) folds and the pleural lamellæ have not yet reached their final stage of complexity. The cephalogaster is abnormal in that the two lobes are unequal in size. The thickened ring of chitin surrounding the aperture through which the parasite has entered the host is shown in position over the extremity of the abdomen, and the last two somites are seen through the transparent chitin of the gill-chamber of the host. ×6·3.

B. Chitinous ring over the end of the abdomen of the parasite, enlarged. ×41·4.

a^1., vestige of right antennule; *a.*², vestige of right antenna; *cg.*, cephalogaster; *hd.*, hood-region of the brood-chamber; *h.p.*, hepato-pancreas; *mxp.*, maxillipede; $ov.^1$, $ov.^2$, anterior and posterior ventral processes of the gonad; $pl.^{1-5}$, right pleural lamellæ; $plp.^{1-5}$, pleopods; *r.f.*, respiratory (?) folds; *r.s.*, position of the " receptaculum seminis "; *ur.*, last abdominal somite.

pair of oostegites, but from the first pair of thoracic appendages, as may be seen from Pl. III. figs. 1 & 2. The folds of this organ are given off near the junction of the edges of the ascendant lamellæ of opposite sides; from more

posterior sections (such as in Pl. III. fig. 3) it would appear that, though belonging to the first pair of thoracic appendages, they are possibly not part of the ascendant lamella itself. These folds turn outwards from their point of origin, making an acute angle with the ascendant lamella, and the free edge of the second oostegite fits closely beneath them into this angle. The approximation between the second pair of oostegites and the folds is very close, but fusion does not seem to occur; their distinctness is more evident in some sections than in others. Anteriorly there is some intermingling of the folds of the two sides.

It may be mentioned here that the body labelled " corps spongieux " by Giard and Bonnier (1887) in their fig. 8, pl. vi. and fig. 2, pl. vii. (figures of *Portunion mœnadis*), and considered by them to be a prolongation of the folds surrounding an anterior entrance into the brood-chamber, is almost certainly distinct from those folds (see p. 341).

The folds are comparatively simple in young individuals, and even in young adults (text-fig. 1, A), but become very complicated in fully adult individuals, as do the abdominal pleural lamellæ (*cf.* Pl. I. fig. 2 & text-fig. 1, A). These folds are very similar in their histology to the pleural lamellæ, being thin expansions of vesicular tissue, with many small blood-vessels. It is perhaps possible that they function as accessory respiratory expansions; it is evident that they have not in *Pinnotherion* the function ascribed to them in other genera. The folds each side receive a branch from the anterior lateral artery near its entry into the recurrent lamella.

It is questionable whether the differences in the form of the hood and the origin of the respiratory (?) folds between *Pinnotherion* and the genera described by Giard and Bonnier in their monograph (1887), namely, *Grapsion*, *Cancrion*, and *Portunion*, are really generic differences, or whether they were mistaken in their interpretation. There is certainly an appearance of an opening into the brood-chamber in front of the cephalogaster in the entire *Pinnotherion*, and it was only on sectioning that the apparent gap in the hood was found to be closed by the protruding fused ascendant lamellæ.

If there should prove to be no anterior entrance into the brood-chamber in these three genera, with the possible exception of a minute passage such as is present in *Pinnotherion*, then it would seem improbable that there can be water currents between the body of the parasite and the chitinous sac formed by the host. It is a question well worth reinvestigation if living specimens should be available.

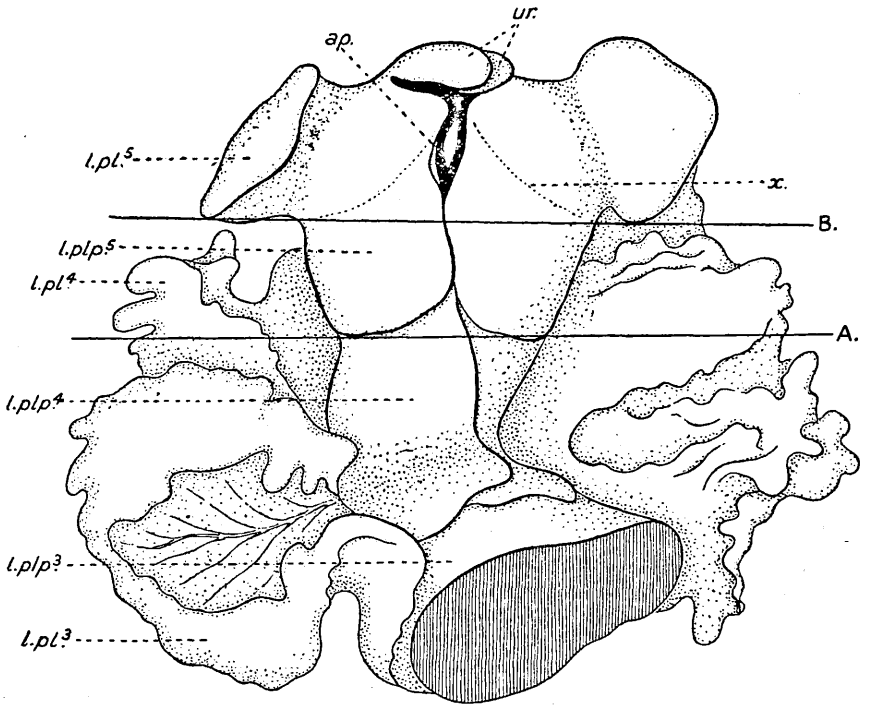
The Pleopods.

The first five somites of the abdomen bear uniramous pleopods and pleural folds; the sixth and last somite is extremely small, deeply divided, and is turned up on to the ventral surface (text-fig. 2). In *Pinnotherion*, unlike apparently *Portunion* and *Grapsion*, which also have lamellar pleopods, the pleopods are uniramous, one ramus, evidently the inner, being absent; yet Giard and Bonnier (1889, p. 915) say of *P. vermiforme*: " Le pléon et ses appendices latéraux et terminaux ressemblent beaucoup aux parties correspondantes des *Grapsion*." It may be noted that the pleopods are also uniramous (the endopodite being absent) in the epicarid and cryptoniscan larvæ of *Pinnotherion*, as is characteristic of these stages in the Entoniscidæ and in certain Bopyridæ.

Each pleopod is produced both anteriorly and posteriorly into a considerable free area with the exception of the first and fifth pairs. In the first pair the free posterior extension is slight, extending only about 140 μ, and therefore

in sections through much of the second somite one pair of pleopods alone are seen (Pl. IV. fig. 1); in the fifth pair it is absent. Extensive overlapping of the pleopods occurs, one lamella of a pair—apparently always the left one—overlaps the opposite one, while each pair overlaps the preceding pair and underlies the following pair. The overlapping is thus from behind forwards (see text-fig. 2), while in *Portunion mœnadis* the opposite apparently occurs (see G. & B., 1887, pl. v. fig. 4). This imbrication is so extensive that a section through the middle of the fourth somite, such as Pl. IV. fig. 3, passes not only

Text-figure 2.



Pinnotherion vermiforme, female. Ventral view of the posterior region of the abdomen. The lines A and B show the position of sections 3 and 5 of Pl. IV.

ap., gap between the fifth pair of pleopods for the passage of the water current; *l.pl.*$^{3-5}$, third to fifth pleural lamellæ of the left side; *l.plp.*$^{3-5}$, third to fifth left pleopods; *ur.*, deeply divided last abdominal somite; *x.*, position of the posterior border of the fourth pair of pleopods. ×24·3.

through the bases of the fourth pair of pleopods, but also the extreme posterior free margins of the third pair and the extreme anterior free margin of the right pleopod of the fifth pair. The overlapping parts of the pleopods fit well down to the bases of the pleural lamellæ (see Pl. IV. fig. 4).

The bases of the pleopods also overlap more or less slightly. In the individual sectioned the bases of the second pair of pleopods overlap those of the first pair for about 130 μ, while the bases of the fifth pair overlap those of the fourth pair for only about 40 μ. A section passing through such a region

shows what appear to be the outer and inner rami of a pair of pleopods (see Pl. IV. fig. 5), whereas actually they are the pleopods of two somites.

The fifth pair of pleopods do not meet in the mid-line posteriorly, a gap being left for the entrance and exit of the water current (see text-fig. 2 and Pl. IV. fig. 6).

Each lamella gradually increases in thickness antero-posteriorly—that is. the underlying part is on the whole thicker than the overlying part (see Pl. IV. fig. 2). They are occupied almost entirely by blood-spaces, and no doubt function as respiratory organs. The chitin lining the ventral surface of the abdomen and the under surface of the pleopods is somewhat thicker than that on the outer surface of the pleopods. A very few short curved spines are present laterally on the ventral surface of the abdominal canal and on the under surface of the pleopods.

In an individual sectioned, which had young embryos in the brood-chamber, the canal under the first, and to some extent under the second, pair of pleopods was obstructed by laminated material which resembled chitin, though its staining reaction with Mallory's triple stain was slightly different from that of the chitin on the outer surface of the body; it stained light blue and greenish blue, and in some parts orange. This material, while preventing the passage of the embryos from the brood-chamber into the abdominal canal, was of so loose a nature that it would be unlikely to obstruct the passage of sea-water. The origin of the material is uncertain, but as its laminæ followed the outline of the first pair of pleopods and were interleaved where the ventral margins of these overlapped it seems possible that it may have been secreted by their under surfaces. Its restricted distribution would seem to suggest this, and to preclude its being shed egg-capsules such as occur in the brood-chamber among young embryos and ova. In a second individual with well-developed embryos there was little of this material, and embryos were present beneath the first one or two pairs of pleopods; these were slightly less advanced in development than those in the brood-chamber.

The pleural lamellæ decrease in size and complexity of folding posteriorly, those of the fifth somite being simple, somewhat triangular expansions (see text-fig. 2 and Pl. IV. fig. 6). The bases of the pleural lamellæ are not as extensive on most somites as those of the pleopods. The bases of the fifth pair of pleopods and pleural folds, however, are nearly co-extensive, and therefore the large free anterior overlapping extensions of the pleopods of this somite may be clearly judged from text-fig. 2. The pleural lamellæ, which are respiratory expansions, are extremely thin, formed of vesicular tissue with many tiny blood-vessels and spaces.

It might be noted that there are apparent inconsistencies in the labelling of the appendages in Giard and Bonnier's (1887) figure 4, pl. v. of *Portunion mœnadis* (the plumose appendages are labelled pleural lamella anteriorly and outer ramus of the pleopod posteriorly). It is of course possible that the more posterior outer rami become highly plumose in the forms described, as perhaps may be gathered from Bonnier (1890, p. 110), who says: "... le parasite, par ses contractions et le mouvement des endopodites de ses pléopodes, aspire l'eau de la cavité branchiale de son hôte et la met en contact avec les masses spongieuses que forment les exopodites des pléopodes et des lames pleurales abdominales et qui ont acquis une complication extraordinaire qui augmente dans des proportions incroyables la surface respiratoire."

A re-examination of the abdominal appendages of *Portunion*, *Cancrion*, and *Grapsion* would seem to be desirable.

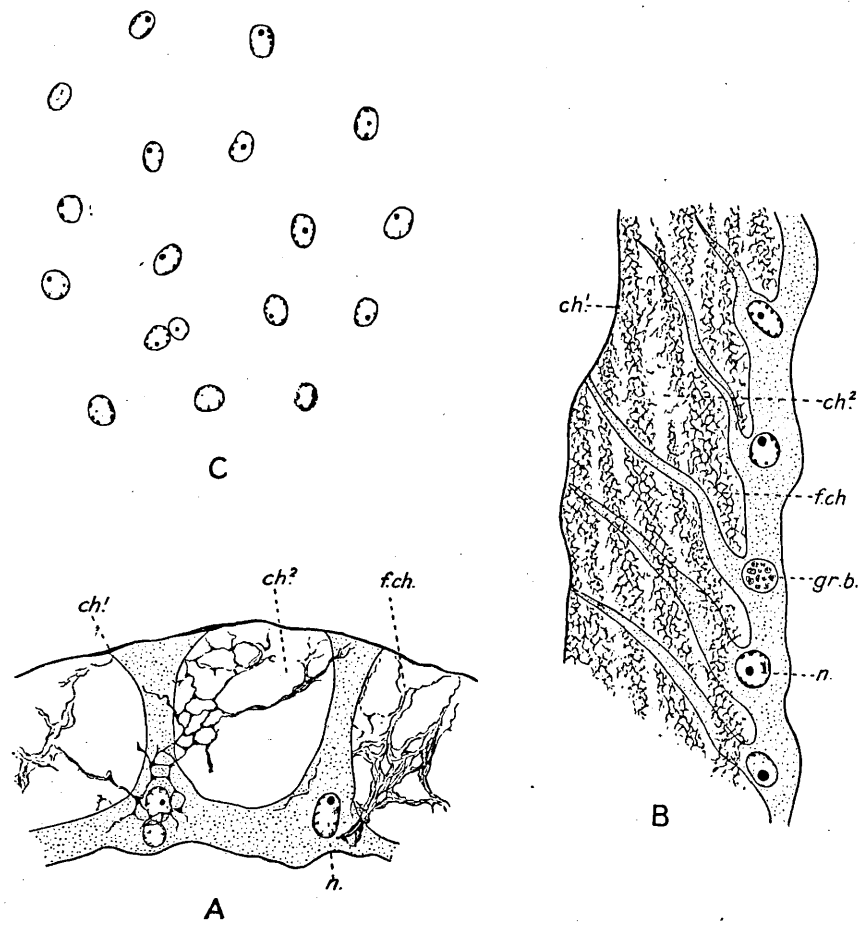
Alimentary System.

In the Entoniscidæ the alimentary canal is highly modified in conjunction with their parasitic blood-sucking habits.

The short œsophagus leads into a bilobed chamber, rhythmically contractile, named by Giard and Bonnier the cephalogaster. This organ is lined with villi, covered with low epithelium. The chitinous lining is fairly thin and consists of a fine darkly staining outer layer and a vacuolated inner layer, which appears to be penetrated by fine cytoplasmic processes. Walz (1882, p. 144) has described the chitin lining the cephalogaster of Bopyridæ as being perforated by very numerous pores, which become evident on treatment with hot caustic potash. Whether the outer darkly staining layer in *Pinnotherion* was perforated could not be determined from sections; specimens were too few to treat with caustic potash. The connective tissue surrounding the cephalogaster and forming the core of the villi is profusely supplied with blood-vessels, branches from which enter the villi. Surrounding the chamber beneath the epithelium is a layer of strong muscle-fibres; in addition radial muscles run between it and the body-wall, being inserted on the cephalogaster between the bases of the villi (see Pl. V. fig. 1). The cephalogaster, in addition to acting as a suction-pump, would seem most probably to have an absorptive function.

Following the cephalogaster is the chitinous organ, provided with a strong dorsal valve, which reduces the lumen to a crescentic slit—in fact, in sections the lumen is generally entirely obliterated (see Pl. V. fig. 1). Strong muscle-fibres surround the organ. In *Portunion*, according to Giard and Bonnier (1887, p. 132), the chitinous lining is of considerable thickness and is clothed with setæ, those of the upper surface interdigitating with those of the lower, and thus forming an effective strainer, preventing the entry of any solid particles taken in with the host's blood. In *Pinnotherion* no setæ could be certainly distinguished; in some sections there was an appearance as of very long setæ lying almost parallel with the surface, but this appearance was most probably due to ridging of the outer cuticula. The chitin lining the organ is of great thickness, especially that clothing the valve, where it may reach a depth of ca. 0·028 mm. The chitin is in two layers; the outer is extremely thin and dark staining, while the inner, which comprises by far the greater thickness of the chitin, has a most peculiar structure. It may be considered perhaps as highly vacuolated, for in one individual fixed in Bouin's picro-formol and stained with Mallory's triple stain (this is a good stain for chitin) this layer was unstained except for scarce, very fine anastomosing fibres (see text-fig. 3, A). In another individual, however, with the same fixative and stain (and also with Heidenhain's iron hæmatoxylin) the fine anastomosing fibres were extremely numerous, forming a very fine network, and were more or less concentrated in laminæ arranged parallel to the surface (text-fig. 3, B), so that with low magnification this layer appeared horizontally striated and fairly darkly stained. This chitinous layer, even in its deepest part, is regularly penetrated by large "cells"; these are somewhat hourglass-shaped in transverse sections of the animal, but, as evident from longitudinal sections, are somewhat flattened from side to side (*cf.* text-fig. 3, A & B). A nucleus, (or more rarely two), is present at the base of each "cell," and sometimes extends a slight way up into the neck. The nuclei have excentric nucleoli. A section parallel to the surface of the epithelium shows the rather regular distribution of the nuclei (text-fig. 3, C), and therefore of the "cells," for the nuclei seem to be confined to the bases of these. The epithelium lining the chitinous organ may perhaps be considered as consisting of tall cells touching only at their bases, which are considerably more expanded than the free ends, while the spaces

Text-figure 3.



Pinnotherion vermiforme, female. Sections of the epithelium of the valve of the chitinous organ.

A. Transverse section. The two " cells " are seen in surface view owing to the thickness of the section. The anastomosing chitinous fibres of the inner chitinous layer are few.

B. Longitudinal section through the epithelium of a second individual. The fibres of the inner chitinous layer are numerous, and are arranged more or less in laminæ.

C. Section passing through the epithelium parallel to the surface of the valve, showing the distribution of the nuclei, and therefore of the " cells."

*ch.*¹, outer layer of chitin; *ch.*², inner layer of chitin; *f.ch.*, fibres of chitin; *gr.b.*, granular body; *n.*, nucleus. The cytoplasm is represented diagrammatically. Bouin's fixative; Mallory's triple stain. × 882.

between the cells are invaded by the inner chitinous layer. It might be noted that this type of epithelium and a variation of it is found covering the external surface of the body (see p. 344). It is very probable that the epithelium

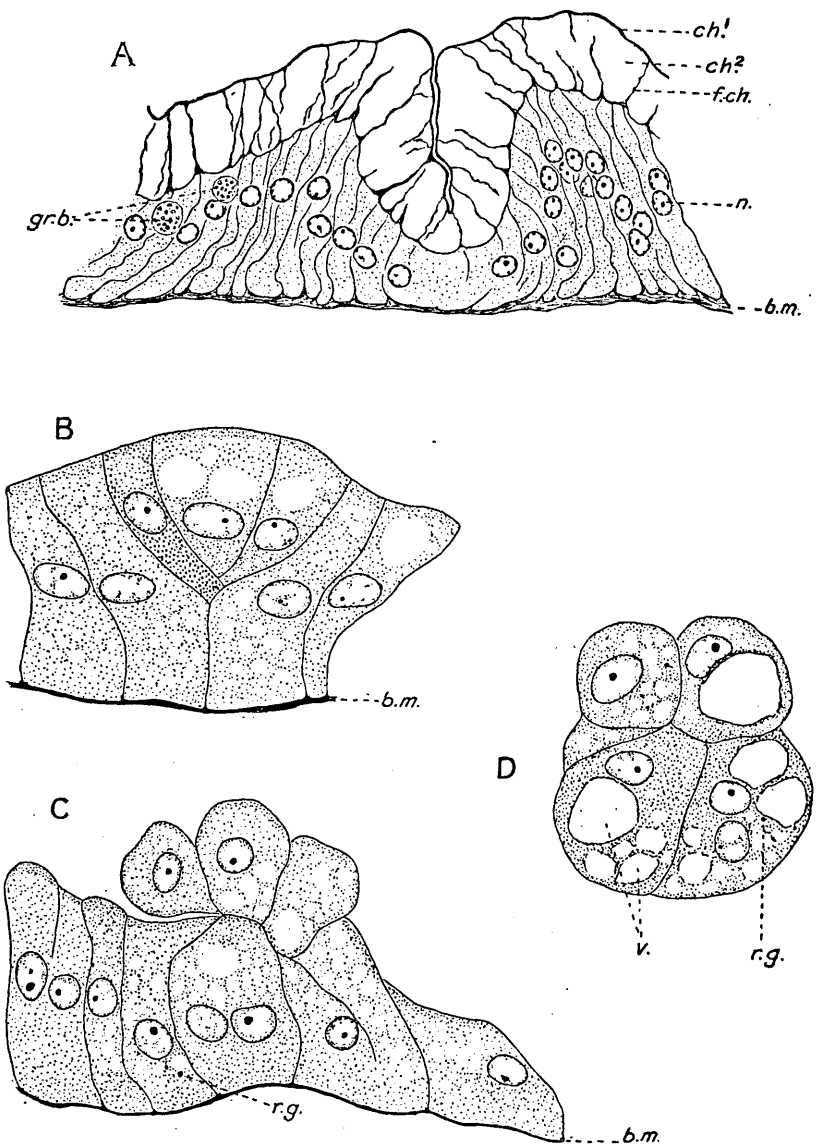
of the chitinous organ is a syncytium; cell boundaries could not be distinguished, but the sections, 10μ or more in thickness, were cut primarily to show the morphology of the animal and not the histology. It has not been possible to determine whether the fine, intensely staining outer layer of chitin is also penetrated by the " cells "; in sections the lumen of the organ is not only obliterated, but the opposed surfaces are crushed against each other, the cuticula being badly contorted. The fine darkly staining chitinous fibres, previously mentioned as being present in the inner layer of the cuticle, stretch from one " cell " to another, and there appears to be either a fine layer of chitin or network of fibres clothing each " cell."

In *Pinnotherion* the chitinous organ would not seem to act as a strainer, but simply as a valve between two strongly contractile organs, namely the cephalogaster and Rathke's organ. In a specimen fixed *in situ* when the host was living, blood-cells, apparently of the host, were present crushed between the two surfaces of the chitinous organ, and small aggregations of similar cells were present at the junction of Rathke's organ and the hepato-pancreas and in the lumen of the hepato-pancreas itself.

Rathke's organ lies in a plane slightly dorsal to the chitinous organ; it contracts alternately with the cephalogaster according to Giard and Bonnier. As would be expected from its behaviour, it is surrounded by a well-developed (clearly striated) muscle-layer (Pl. V. fig. 2). The epithelium, which rests on a well-marked basement-membrane, is thrown into folds, which in the contracted condition, as seen in sections, almost obliterate the lumen. The epithelial cells vary greatly in height (text-fig. 4, A); those in the centre of the folds are tall and very narrow; cell-walls appear to be present, though they may be strong " supportive fibres " (see McMurrich, pp. 87–90). The nuclei are small, round, and occur chiefly in the free outer halves of the cells. The chitinous lining is in two layers, the inner comprising by far the greater part of the thickness, the outer being thin and darkly staining. The inner layer appears to be highly vacuolated, being unstained by Mallory's triple stain, except for darkly staining, chitinous fibres stretching from the epithelium to the outer layer. The surface of the epithelium seems to be pulled out irregularly by these fibres, though whether they contain a cytoplasmic core could not be determined. The chitinous layer, though of some considerable thickness, is only about a third of that of the chitinous organ. In sections, owing to the snapping of the chitinous fibres and consequent separation of the outer layer, the inner layer may appear thicker than it actually is. A somewhat similar type of chitin has been described by Nicholls (pp. 684–686) for the intestine of *Ligia*.

Rathke's organ at its posterior end curves ventrally to lead into the hepato-pancreas (liver of Giard and Bonnier), which extends anteriorly beyond the point of junction as an unpaired cul-de-sac reaching to about the posterior level of the chitinous organ (Pl. V. figs. 2 & 3). Soon after the entry of Rathke's organ the heptao-pancreas divides into two large cæca which extend into the second somite of the abdomen. The epithelium lining the diverticula is raised in places into small folds which project into the lumen. The cells vary in height in different regions. The contents of the cells may be granular, the granules staining either dark blue or reddish in different cells with Mallory's triple stain, or the cytoplasm may be finely vacuolated, or a few large vacuoles may be present. A darkly staining border is found at the free ends of the cells, and closely outlining them is a layer of secretion staining dark blue with this stain. A coagulum staining in the same manner is present in the lumen. The nuclei are large, with distinct nucleoli and little chromatin. The cells occasionally

Text-figure 4.



Pinnotherion vermiforme, female.

A. Transverse section through the epithelium of Rathke's organ.

B–D. Hepato-pancreas. B–C. Transverse sections through the epithelium, showing possible stages in the extrusion of the cells. D. Section through a cluster of hepato-pancreatic cells free in the lumen of the gland.

b.m., basement-membrane; *ch.*¹, outer layer of chitin; *ch.*², inner layer of chitin; *f.ch.*, fibres of chitin; *gr.b.*, granular body; *n.*, nucleus; *r.g.*, red-staining granules; *v.*, vacuole. The cytoplasm is represented diagrammatically. Bouin's fixative; Mallory's triple stain. × 980.

have two nuclei. Hepato-pancreatic cells seem to be shed into the cavity of the organ, either singly or in small clusters (see text-fig. 4, B–D). Such cells when free in the lumen are rounded, highly vacuolated, and each contains one or two nuclei (text-fig. 4, D).

In the living adult animal the hepato-pancreas is reddish in colour, in the young female yellow; the paired cæca contract rhythmically.

The hind-gut fails to unite with the anterior portion of the gut and ends blindly in the second abdominal somite; it is present for a very short distance together with and ventral to the hepato-pancreas (Pl. IV. fig. 1). The hind-gut is therefore of some considerable length in *Pinnotherion*; it is apparently absent in the forms examined by Giard and Bonnier (1887, p. 136). The hind-gut appears to be much branched, for it may be cut several times in the same section, both transverse (see Pl. IV. figs. 2–5) and longitudinal. Its persistence and considerable length perhaps suggests that it may have taken on a secondary function. It might be noted that the hind-gut, though ending blindly, is likewise of some length in the male.

Giard and Bonnier (1887, pp. 133, 134) give a description of the movements of the several parts of the alimentary canal in *Portunion*; this was not verified for *Pinnotherion*, as no living specimens were found after the animal had been sectioned and the structure of the chitinous organ noted.

Circulatory System.

The heart lies in the third abdominal somite. Anteriorly it gives off a median aorta which, on reaching Rathke's organ, deviates to one side, but becomes dorsal again just posterior to the chitinous organ, where it divides into two, a branch passing on either side of the organ. (In *Portunion*, G. & B., 1887, p. 150, it divides at the level of the cephalogaster.) Anterior to the chitinous organ these lateral arteries gradually turn ventralwards, to run for a short distance on either side of the ventral nerve-cord; on reaching the maxillary gland they run on either side of it (each giving off a branch to a maxillipede), and finally enter the recurrent lamellæ to run as median vessels through their length. Each lateral artery just before entering the recurrent lamella gives off (1) a fine artery which continues anteriorly to the outer side of the maxillary gland, and (2) an artery to the respiratory (?) folds.

Near the division of the median aorta paired branches are given off to the two divisions of the cephalogaster, and anteriorly this organ receives yet other branches. The outer oostegites receive arteries from the median aorta, as do the various organs of the body. The distribution of these has not been traced in detail.

A median ventral abdominal sinus is present; two great sinuses run along the thorax at the bases of the oostegites. The distribution of the other sinuses has not been followed with the exception of those of the first pair of oostegites (see p. 330).

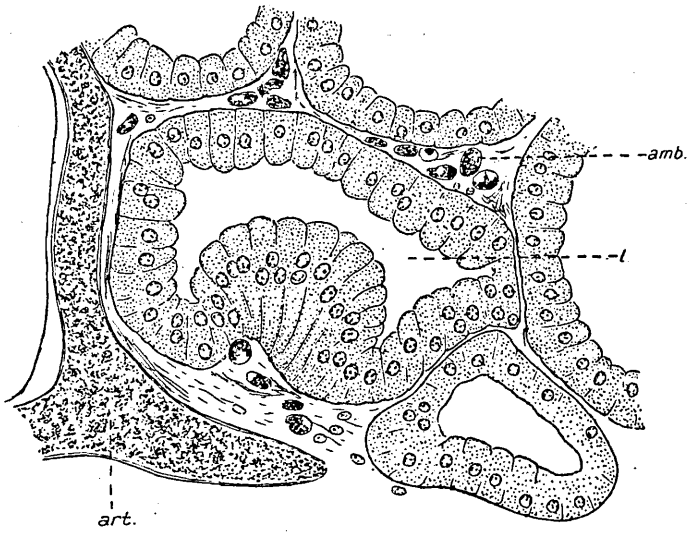
With Mallory's triple stain the blood stains very diversely in different regions, and may be blue, purple, and various shades of red and orange.

Excretory System.

Paired structures, which are possibly vestigial antennal glands, are present in the anterior region at the base of the antennæ. They consist of closely packed lobules, which are mostly a solid mass of cells, though in some places there appears to be a vestige of the lumen. The cells are small, with small nuclei. Much of the gland lies just below the surface of the chitin, but no aperture could be found. This is possibly the gland referred to by Fraisse (1878 *b*, p. 401) as a skin-gland in *Entoniscus*.

A very large gland, which is most probably the fused maxillary glands, stretches from about the level of the antennules anteriorly to slightly beyond the anterior level of the hepato-pancreas posteriorly, lying ventral to the gut and to the nerve-cord where that is present. It opens by paired ducts on the outer surface a short distance in front of the maxillipedes (see Pl. VI. fig. 1): maxillæ are not recognizable. The ducts are at first narrow, but each expands into a small chamber before passing into the gland proper, which near the entrance of the ducts is paired, but soon becomes single, giving off numerous branches. It extends anteriorly for a short distance beyond the level of the external openings of the ducts; Giard and Bonnier's figure 2 (sp.) plate vii. (1887) shows the position of the anterior region of the gland well. The epithelium of the ducts is narrow and the shape of the cells somewhat irregular. The transition from the epithelium of the ducts to that of the gland proper is dis-

Text-figure 5.



Pinnotherion vermiforme, female. Transverse section through tubules of the maxillary gland.

amb., amœbocyte; *art.*, arteriole; *l.*, lumen of tubule of maxillary gland. Bouin's fixative; Mallory's triple stain. ×513·7.

tinct and abrupt. The epithelium lining the numerous tubules is glandular, with strongly staining cytoplasm. The cells, with rounded ends projecting into the lumen (text-fig. 5), appear to be excreting, or secreting, some substance which is for the most part finely granular. No end-sac could be certainly distinguished.

No maxillary glands could be distinguished in the male, possibly owing to its small size and the imperfect fixation.

In the Bopyridæ (see also Rogenhofer, 1908) the maxillary glands are relatively small and simple and the two glands are widely separated. Very large maxillary glands lying below the anterior portion of the stomach and almost meeting in the middle line have been described in *Phreatoicus* (Barnard, 1927, p. 145), a free-living Isopod.

As mentioned previously, the fused maxillary glands would seem to be the body labelled " corps spongieux " by Giard and Bonnier in their figures of *Portunion mœnadis* (1887, pl. vi. fig. 8, & pl. vii. fig. 2), and considered by them to be a continuation of the folds surrounding an anterior entrance into the brood-chamber. Fraisse (1878 *b*, p. 401) evidently recognized its glandular nature in *Entoniscus*, and suggested that it was a cement- or shell-gland, or possibly a salivary gland. He said that it consisted of a great number of much contorted tubes, lined with rather large epithelial cells. He evidently suggested that it was a shell-gland, owing to his mistaking the " fat-body," which extends into the head region, for the ovary. Both Kossmann and Giard and Bonnier strongly criticize Fraisse's interpretation of the structure of this body. Kossmann (1881, p. 166) says : " Ich halte diese vermeintliche Drüse nur für die im Querschnitte solchergestalt zum Ausdrucke kommende starke Faltung und Kräuselung der Brutblätter und das vermeintliche Drüsenepithel für die äussere Epidermis derselben." The French authors (1887, p. 146) entirely agree with this view. Judging by the structure of this organ in *Pinnotherion* Fraisse was correct in interpreting it as a gland in *Entoniscus*.

The so-called fat-body (see Pl. IV. fig. 1, and Pls. V. & VI.) is found accompanying the alimentary canal throughout the greater part of its length, stretching from the head-region to just beyond the posterior level of the hepato-pancreas in the second abdominal somite. It is absent from the more posterior abdominal somites, not being found round the blindly ending hind-gut. It seems probable that, to a certain extent, excretory products are got rid of by being stored in this body, but in the two females sectioned the cells were by no means as heavily loaded as in the males.

Reproductive System.

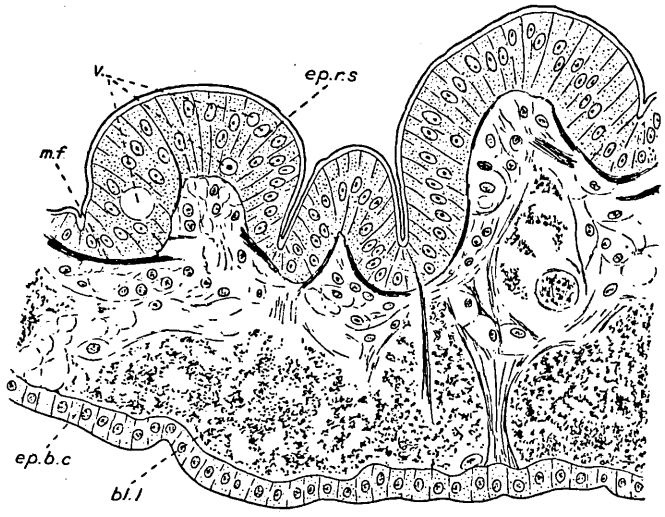
The general form of the ovary may be seen from the figures (Pl. I. fig. 2; Pl. II. fig. 3). There are no dorsal ovarian processes ; of the two ventral the posterior is of great length and penetrates into the abdomen of the host. The finer details of the structure of the ovary have not been investigated. The oviducts are paired; their walls are composed of deep narrow cells, with nuclei about midway. These cells probably secrete the egg-cases ; in one specimen sectioned in which an ovum was present in the oviduct of one side a secretion was being poured out by the cells.

In the Entoniscidæ, with the exception of *Entoniscus porcellanæ*, the embryos in the brood-chamber are all of the same age (see G. & B., 1887, pp. 162, 163, 233). In the two females of *Pinnotherion* sectioned, however, although the embryos were of about the same stage, in the one with young embryos there were, in addition, a number of unsegmented ova, and an ovum was present in the oviduct of one side. It is possible that spawning had been interrupted by the dredging or the journey from Padstow. The number of embryos and ova present was much smaller than in a second female with well-developed embryos.

In *Pinnotherion* there is a large median dorsal organ situated in the angle between the thorax and the abdomen (see text-fig. 1, A) which functions as a receptaculum seminis. The last pair of recognizable peræopods are posterior to it. It would appear to be formed by the modification of the proximal part of the last pair or the last two pairs of oostegites. A groove runs down the dorsal surface of the body ; it is formed by the curving towards each other of the basal part of the oostegites of opposite sides, and the dorsal surface of the body, much reduced, forms the base of the groove. Under the cephalogaster the groove is widely open, but the chitinous wall of the tube containing the

parasite stretches across the opening, so that a canal is formed (see Pl. V. fig. 2). Posteriorly the dorsally curved oostegites approach each other very closely though they do not fuse, and a closed groove results (see Pl. V. fig. 3). This groove leads down into the "receptaculum seminis"—indeed, the latter might be considered as a modification of the part of the oostegites forming the walls of the groove in the posterior region of the thorax. In the anterior and middle part of the "receptaculum seminis" intimate approximation of the oostegites of the two sides occurs, so that it is closed (Pl. VI. figs. 2 & 3). Posteriorly they are slightly separated (Pl. VI. fig. 4), and, as will be seen later, it is probable that the male is able to enter the sperm receptacle here. Paired, somewhat tortuous passages lead from the "receptaculum seminis" into the brood-

Text-figure 6.



Pinnotherion vermiforme, female. Transverse section through the wall of the "receptaculum seminis." The fine structure of the chitin is not shown.

bl.l., blood lacuna; *ep.b.c.*, brood-chamber epithelium; *ep.r.s.*, epithelium lining the cavity of the "receptaculum seminis"; *m.f.*, muscle-fibres; *v.*, vacuole. Bouin's fixative; Heidenhain's iron hæmatoxylin and acid fuchsin. ×513·7.

chamber, opening slightly anterior and dorsal to the apertures of the oviducts (see Pl. VI. figs. 2 & 3).

As will be seen from the figures the "receptaculum seminis" is a space enclosed between the proximal portions of the oostegites of opposite sides, while the brood-chamber is enclosed between the oostegites and the body. Embryos are not found within the "receptaculum seminis."

The wall of the sperm receptacle is deeply folded (see text-fig. 6); the inner surface of these folds is formed of a deep glandular epithelium covered by an appreciable layer of chitin, penetrated, as is characteristic of the chitin of *Pinnotherion*, by protoplasmic or cell processes. The outer surface of the folds has a covering of low epithelium—this is the epithelium clothing the inner surface of the brood-chamber. Between the inner and outer layers of epithelium is a layer of vesicular tissue, with many blood-sinuses. Underlying the inner

epithelium is a layer of muscle-fibres; muscle-fibres also traverse the wall of the "receptaculum seminis" from the inner to the outer epithelium.

In the two females sectioned, one of which had young embryos and unsegmented ova in the brood-chamber and the other well advanced embryos, there was little sperm in the "receptaculum seminis," and most of it was in the passages leading to near the female apertures. In both females there was a small quantity of fibrous chitinous material present in which sperm was embedded. The origin of this material is uncertain; it may possibly be deposited with the sperm by the male.

Traces of sperm have been found along the dorsal groove of the thorax as far forward as the anterior level of the maxillipedes, and have also been observed in the abdominal canal as far back as the second pair of pleopods, being present in the latter position among laminated chitinous material. The traces of sperm in the dorsal groove of the thorax had possibly been squeezed out of the sperm receptacle by the action of the muscles in its walls, for it has been seen that it is continuous with the groove. That in the abdominal canal was possibly deposited by the male as it passed along, as sperm seems to be very easily ejected from a mature male. In one of the females sectioned a body which appeared to be the peræopod of a male (*perp.m.*) was present within the folds of the posterior part of the sperm receptacle (see Pl. VI. fig. 4), while a male which was seen crawling over the pleural lamellæ of this female had the sixth peræopod of the right side missing. The male may have escaped from the female owing to tearing during dissection; the wall of the sperm receptacle itself was uninjured. It would appear probable that the male, which has no copulatory organs, is able to enter the "receptaculum seminis" to deposit sperm, the sperm receptacle, which is roughly about $1{\cdot}6 \times 1{\cdot}2$ mm. in diameter, being of sufficient size to allow of its entry. The greater thickness of the chitin on the inner than on the outer surface of the wall, and on the inner than the outer surface of the pleopods, may be correlated with the passage of the male, the thick chitin preventing tearing by its strong claws.

Males have not been seen within the brood-chamber of the female, though Giard and Bonnier found them in this position, as in other Entoniscidæ. In a form such as *P. vermiforme*, with a specialized chamber for the storage of sperm, it would seem unlikely that the male would normally enter the brood-chamber.

The "receptaculum seminis" was described by Giard and Bonnier (1889, p. 915) in *Pinnotherion* as follows:—"Les organes situés dans le voisinage de l'ouverture génitale, et désignés sous le nom de *réceptacles séminaux*, ont une forme presque ovoïde, et leur surface offre quatre à cinq lobes disposés comme des côtes d'un melon." The two halves of the organ were apparently taken for separate organs: the appearance as of the lobes of a melon is due no doubt to the deep folding of the walls. They doubtless had not at that time examined the organ by sectioning.

In several Entoniscidæ Giard and Bonnier have described and figured the position of small organs which they finally considered to be vesiculæ seminales. They say (1887, p. 146): "Immédiatement derrière l'ovaire, sur les côtés du septième anneau thoracique et un peu vers le haut, se trouvent, comme nous l'avons vu deux petits tubercules géminés, sphériques et d'un blanc mat. . . . Sur les animaux adultes, mais dont la ponte n'est pas encore effectuée, le contenu des vésicles latérales est formé par des corpuscules agiles qui ne diffèrent en rien des spermatozoïdes obtenus par la dilacération du mâle." They open by ducts on the seventh somite, while the oviducts open on the fifth (see G. &. B., 1887, p. 148). Giard and Bonnier at first considered these

to be receptacula semines, but later say (p. 147): "Nous croyons maintenant plus exact de les considérer comme des vésicules séminales en rapport avec des glandes testiculaires qui ne fonctionneraient plus que chez l'*Entoniscus* encore jeune, c'est-à-dire avant la ponte."

The chamber for the storage of sperm in *Pinnotherion* functions as a receptaculum seminis, and is not a vesicula seminalis. Its size, in comparison with that of the animal, is considerably greater than that of the vesiculæ seminales figured by Giard and Bonnier (1887, pl. iv. figs. 3, 4, & 5) for *Portunion mœnadis*, *Grapsion cavolinii*, and *Cancrion miser*, though those of *Entoniscus mülleri* (1887, pl. iv. fig. 6) and *E. porcellanæ* (1887, fig. 28, p. 233) more nearly approach its proportions.

In the two embryo-carrying females sectioned no indication of vesiculæ seminales was detected: a young female, more or less in the "asticot" stage, when cleared, unstained, in cedarwood oil, showed no sign of such organs; but sections would be needed to settle the point.

In no Entoniscid, other than Pinnotherion, do the French naturalists describe a "receptaculum seminis," unless it be in *Priapion* (*Portunion*) *fraissei* (1888, p. 475), where from their description it may perhaps be gathered that it is present in addition to vesiculæ seminales. They state: "Sur les bords latéraux du cinquième somite thoracique, entre les deux bosses ventrales, se trouvent les overtures génitales entourées d'une paire de petites glandes mamelonnées, blanchâtres et semblables par la forme et la couleur aux vésicules séminales qui se trouvent sur le dernier segment du thorax. Ces dernières, situées symétriquement de part et d'autre du corps, sont bien développées et au nombre de *trois* de chaque côté."

So far an opportunity has not occurred of examining those forms in which Giard and Bonnier investigated vesiculæ seminales by means of sections.

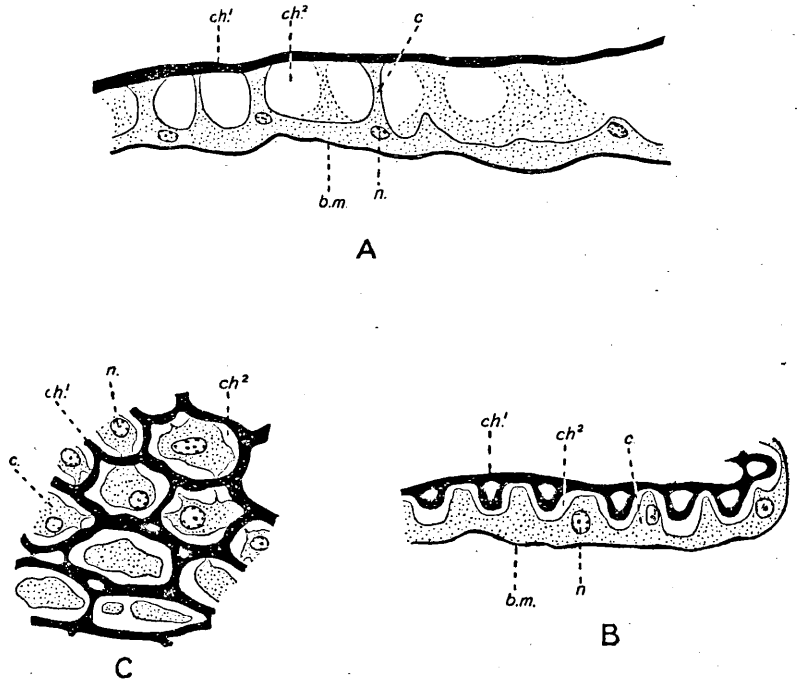
Integument and Connective Tissue.

The chitin lining the surface of the body is for the most part very thin except in certain regions, as, for instance, the dorsal groove of the thorax, the ventral abdominal canal, the under surface of the lamellar pleopods, and in places where muscle-fibres are attached. The external epithelium is of a peculiar character (see text-fig. 7); the cells forming it appear to be distinct from their neighbours except at the base. In a few places, however, the separation of the cells is slight or absent and the epithelium is normal in appearance. Supported as it were on the free ends of the cells is a darkly staining homogeneous layer of chitin (text-fig. 7, A), which varies in thickness in different regions. Between the cells if chitin is present it would seem to be almost unstainable. This type of epithelium and chitin is very similar to that of the chitinous organ though not nearly as deep. In certain regions there is a variation of this type. The minute pits left between the free ends of the cells are filled in by an invasion of the darkly staining chitin (see text-fig. 7, B, C), which has a ribbed appearance in places where it has become separated from the epithelium, while the latter appears spiky. There is a narrow unstained region between the epithelium and the darkly staining chitin; this may be a space due to slight separation of the epithelium and chitin during sectioning, or may represent the almost unstaining layer as found in the first type. In sections through the epithelium parallel to the surface and passing through the distal region of the cells these appear distinct from one another (text-fig. 7, C). A similar appearance has been described by McMurrich (1897, pp. 90–92) for the epithelium lining the "mid-gut" of certain terrestrial Isopods. On parts of the ventral surface of the abdomen the cells would appear

to be arranged in regular series, the thickened chitin between the cells running in parallel rows, with very few cross ridges.

It is possible that this form of the external epithelium and chitin allows for growth without moulting, which does not seem to occur in the Entoniscidæ owing to the impossibility of getting rid of the shed cuticle once they have penetrated the body-cavity of the host (see G & B., 1887, p. 129 ; Bonnier, 1900, p. 104). In the Bopyridæ, on the other hand, moulting is known to occur, being observed by Caroli in *Bopyrus* and *Gyge* (Caroli, 1927, 1929).

Text-figure 7.



Pinnotherion vermiforme, female. Sections to show the structure of the external epithelium.

A. Transverse section of the epithelium on the latero-ventral surface of the thorax (about position of base of peræopods).

B. Transverse section of the epithelium between the two lobes of the cephalogaster, showing the thickening of the darkly staining outer layer of chitin between the " cells."

C. Section parallel to the surface of epithelium such as shown in B.

b.m., basement-membrane ; *ch.*¹, outer darkly staining chitinous layer ; *ch.*², inner unstained chitinous layer ; *c.*, " cell " ; *n.*, nucleus. Bouin's fixative ; Mallory's triple stain. ×1102·5.

The external chitin is generally without setæ except on the abdomen, where a very few curved spines are present laterally along the ventral canal, and on the under surfaces of the pleopods. These spines stain bright red with Mallory's triple stain, while the chitinous layer stains blue ; they are brittle, as they are seen broken across. They contain a cytoplasmic core. It might be noted that

the minute spines on the outer edge of the tip of the mandibles stain bright orange-red with Mallory's triple stain.

The tissue surrounding the organs is highly vesicular. Giard and Bonnier (1887, p. 150) describe it as " le tissu conjonctif aux mailles lâches." Amœbocytes occur in it and it contains numerous blood-spaces.

The Male. (Text-figs. 8–12.)

The adult male of *Pinnotherion vermiforme* (text-fig. 8) occurs free in the thorax and abdomen of the host (see p. 320)—a position not previously described for males of the Entoniscidæ, which, according to Giard and Bonnier, are found only on the female,—and has not been taken from the brood-chamber of the female, though found by them in that position (G. & B., 1889, p. 915). As previously mentioned (p. 343), evidence points to the conclusion that the male is able to enter the " receptaculum seminis " of the female in order to deposit sperm. Males have been taken crawling over the pleural lamellæ of the female, though actually separated from them by the chitinous membrane formed by the host.

When removed from the host and placed in sea-water the parasite lives for two or three days only.

The male is normally somewhat curved ventrally, and when disturbed curls up until the head touches the tip of the abdomen; when preserved unnarcotized it is always strongly curved. Efforts to narcotize the animals so that they could be fixed extended in order to facilitate sectioning were unsuccessful, alcohol, stovain, and isotonic magnesium chloride being tried without result.

Difficulty was experienced in fixing the animals owing to the thickness of the chitin and their tendency when placed in certain fixatives to burst across the dorsal region of the thorax, the internal organs streaming out. Bouin's fluid, and especially Dobell's alcoholic modification, caused rapid and extensive bursting. Strong Flemming's fluid without acetic acid, though not causing this trouble, gave extremely poor fixation. The most satisfactory results were obtained by using sublimate-formol (Carleton, 1926, pp. 37–38), but even so fixation was not perfect.

As is usual in the Epicaridea the male is very small in comparison with the female, though it is of a good size for those of the Entoniscidæ, namely, 1·0–3·5 mm. in length; of known species only those of *Priapion* (*Portunion*) *fraissei* G. & B. (G. & B., 1888, p. 476) attain a greater length. Of the two males found by Giard and Bonnier (1889, p. 915) one was 2·0 mm. long and the other only about a third of that length.

The males of *Pinnotherion vermiforme* obtained and measured at different times fall in the following size groups :—

							Totals.
Length in mm.....	1·0—1·5	1·5—2·0	2·0—2·5	2·5—3·0	3·4	3·5	
Oct. 11, 1928	4	8	7	2	..	..	21
Feb. 27, 1929	11	22	15		..	2	50
June 6, 1929.....	6	18	14	10	1	..	49
Aug. 9, 1929.....		1	1	2	..	..	4
May 15, 1930			2		..	..	2
Totals	21	49	39	14	1	2	126

Text-figure 8.

Pinnotherion vermiforme, male. Sketch of living individual, showing the characteristic ventral curvature. ×76·3.

The external chitin is of considerable thickness. In sections it stains uniformly and darkly with Mallory's triple stain ; it appears to be covered by an extremely thin cuticle (seen by staining with Heidenhain's iron hæmatoxylin and acid fuchsin). In small living individuals the chitin is nearly colourless, but in larger specimens it is frequently pale pinkish fawn, with tiny regularly

arranged darker areas (probably corresponding to the cells of the epidermis), especially noticeable on the thoracic somites and the first abdominal; in such large individuals the chitinous membrane between the somites is nearly colourless, the difference between it and the chitin being very apparent. Numerous minute papillæ are present on the surface of the somites.

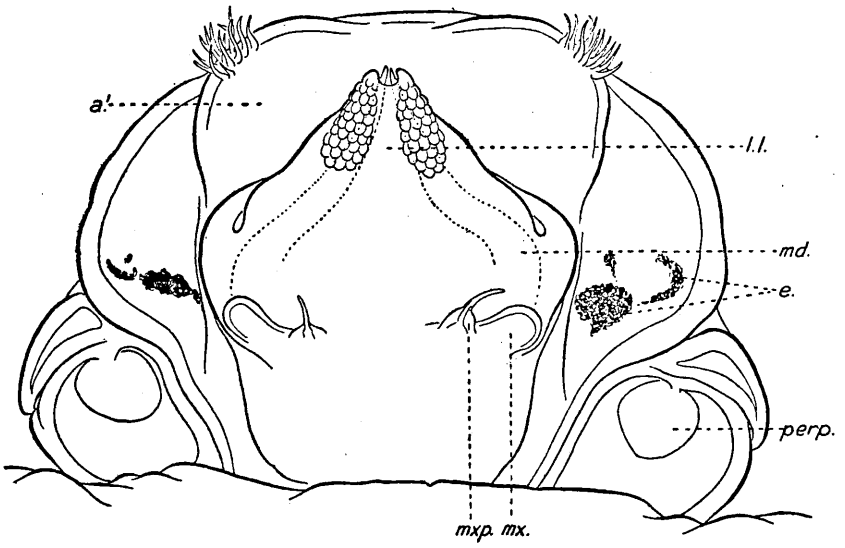
Dark brown, almost black chromatophores, sometimes with a little yellow, are sparingly present in certain of the somites; in connection with at least some of these are bodies showing white by reflected light. The chromatophores are less numerous in the adult than in the cryptoniscan larva, and are more irregular in arrangement and not nearly as diffuse. The eyes appear to be similar in structure to the chromatophores; they are of the same dark brown pigment, but seem to be without the white substance; they have no crystalline lenses.

The hepato-pancreas gives colour to the animal; it varies from pale yellow, through deep yellow to beautiful dark orange in different individuals. When the gland is orange-coloured the whole animal has a pink tint to the unaided eye.

Morphology.

The thorax* is formed of six distinct somites, namely the third to the eighth, the second (bearing the first pair of peræopods), in addition to the first, being

Text-figure 9.



Pinnotherion vermiforme, male. Ventral surface of the head-region of a mature specimen about 3·5 mm. long.

*a.*¹, antennule; *e.*, eye-spot; *l.l.*, lower lip; *md.*, mandible; *mx.*, maxilla; *mxp.*, maxillipede; *perp.*, position of attachment of the first pair of peræopods. × 228.

fused with the head, only the lateral regions of the somite being distinguishable (text-fig. 9). In having the second (first of Giard and Bonnier and Chopra)

* The male of the Entoniscidæ is considered as having eight thoracic somites, the first of which (carrying the maxillipedes) is always coalesced with the head, as in all Isopods (see Calman, 1909, p. 196); Giard and Bonnier (1887, p. 155), on the other hand, speak of it as having seven thoracic somites.

thoracic somite coalesced with the head the male of *P. vermiforme* agrees with that of *Entoniscus porcellanæ* Müller (G. & B., 1887, p. 234, and fig. 28), and incidentally with *Bopyrella* (Chopra, 1923, pp. 472, 473, and pl. xiv. figs. 5, 6, 12), but differs from most Entoniscidæ and Bopyridæ.

The last thoracic somite is without appendages. This somite, and also the first abdominal, bears in the middle line a large triangular projection ("crochets ventraux médians," G. & B., 1889, p. 915), the posterior being slightly the larger of the two. In the presence of a triangular projection or hook on the last thoracic somite *P. vermiforme* differs from the males of all known Entoniscidæ, the appendage of *Priapion fraissei*, as pointed out by Giard and Bonnier (1889, pp. 915, 916), being of an entirely different nature. The tiny tubercle mentioned by them as being present on the second abdominal somite in the mid-ventral line is minute, and does not appear to be present in all individuals.

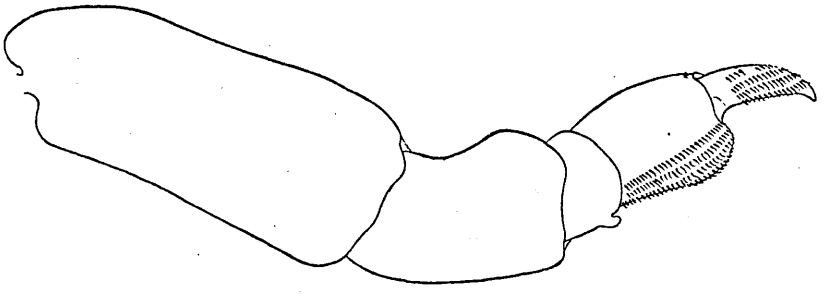
The abdominal somites are without appendages; the last somite (sixth + telson) is bifurcated to form two long hooks, as in *Grapsion*, *Portunion*, and *Priapion*.

Appendages.

The antennules have the form of large bosses bearing fourteen or more short curved setæ (text-fig. 9); antennæ are absent, as in *Cancrion miser* G. & B.

The styliform mandibles, slightly toothed or ridged on the outer edge near the apex, are enclosed in a suctorial "oral cone." Giard and Bonnier (1887, p. 159, and pl. viii. figs. 2 & 12) described and figured maxillulæ as also being present within the suctorial cone in the Entoniscidæ; but this was corrected later by Bonnier (1900, pp. 50, 51). The lower lip is indented and shows

Text-figure 10.



Pinnotherion vermiforme, male. Third peræopod of right side. × 253·3.

two small areas with scale-like markings of the chitin. The muscles of the mandibles are in three sets: (1) strong bands connecting the bases of the mandibles; (2) muscles connecting the base of each mandible with the margin of the second thoracic somite, near the first pair of peræopods (cf. *Priapion fraissei*, where these muscles are attached to the lateral margins of the head-region near the eyes, Giard and Bonnier, 1888, p. 478, and pl. xxxi. fig. 3); (3) converging bands running from the bases of the mandibles to be inserted on the dorsal surface to a small invagination of the external chitin in the middle line. This pit probably marks the position of the anterior border of the fused second thoracic somite, as in *Priapion fraissei* (1888, p. 478, and pl. xxxi. fig. 3),

where this somite is apparently distinct, the muscles are attached to the dorsal surface at the posterior margin of the head-region (*i. e.*, head+first thoracic somite). In the region of the invagination other muscles are inserted which pass back to the posterior border of the fused head and first two thoracic somites.

Maxillulæ are absent; the maxillæ are vestigial, represented by small semi-circular lamellæ immediately in front of the maxillipedes.

The maxillipedes are vestigial, being tiny tubercles bearing a single short seta; they seem to be more reduced in large than in small specimens.

The six pairs of peræopods are all similar, simply increasing in size posteriorly. The fused meropodite-carpopodite segment bears a small tubercle; the under surface of the propodite is provided with several rows of short setæ or spines, as is also that of the hooked dactylopodite (text-fig. 10).

Alimentary System.

The fore-gut is short; in sections the epithelium is raised into longitudinal ridges (text-fig. 11, A), much reducing the lumen; it is most probable that this region is contractile, enabling the male to suck its host's blood.

The gut passes into the hepato-pancreas, which is at first single as in the female, though there seems to be no anterior blind prolongation of the gland; it soon divides into two large cæca (text-fig. 11, B), which extend into the second abdominal somite, rarely into the region of the third, frequently one being slightly longer than the other. Muscles surround the cæca, which are strongly contractile. In the living animal the gland may be yellow or orange in colour. In the region of the testes the hepato-pancreas is depressed and attentuated by their great development.

The hind-gut is very narrow, but can be distinguished in sections. It fails to unite with the anterior portion of the gut, and ends blindly in the second or third abdominal somite.

Circulatory System.

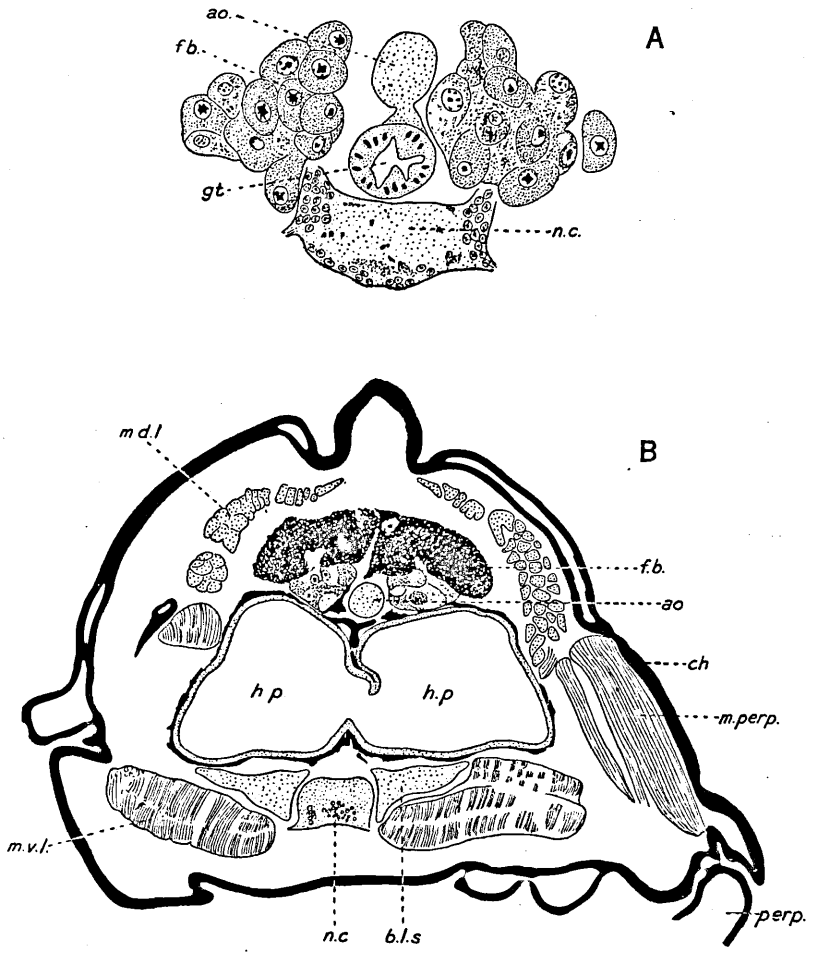
The heart lies in the third abdominal somite, as in the female. Anteriorly it gives off a median aorta. The details of the circulatory system have not been investigated.

Excretory System.

No antennal or maxillary glands could be distinguished in the male, but the fixation of material was not good.

The so-called fat-body (*f.b.*, text-fig. 11) is well developed. It is present in the second thoracic somite and may extend posteriorly as far as the seventh. In the living animal it is clearly visible in somites three to six, appearing white by reflected light and black by transmitted light, no doubt owing to the fact that it is chiefly in this region that the cells are loaded with excretory granules. The "fat-body" is dorsal in position, lying above the hepato-pancreas, and is incompletely divided by the median aorta; where the gonad is present, however, it is found below this, and is here a single narrow strand of cells. The cells of the "fat-body" are very large, with indistinct walls, but where cells occur apart from the main body they are oval or round in form. The nuclei are large and frequently show two or three large, sometimes irregularly star-shaped nucleoli, as well as scattered granules of chromatin. The cytoplasm of those cells not yet containing concretions stains deeply with acid fuchsin. The excretory granules stain intensely with Heidenhain's iron hæmatoxylin, and heavily loaded cells appear as a black mass, with a small lighter area representing

Text-figure 11.



Pinnotherion vermiforme, male.

A. Transverse section showing the relation of the fat-body to the gut, nerve-cord, and the median aorta.

B. Transverse section (somewhat oblique) of the thorax, to show the anatomy.

ao., median aorta; *bl.s.*, blood-sinus; *ch.*, external chitin; *f.b.*, fat-body; *gt.*, gut; *h.p.*, hepato-pancreas; *m.d.l.* and *m.v.l.*, dorsal and ventral longitudinal muscles; *m.perp.*, muscles to peræopod; *n.c.*, nerve-cord; *perp.*, peræopod. The blood in the lacunæ surrounding the hepato-pancreas stains heavily with iron hæmatoxylin, and is shown in black. Sublimate-formol; Heidenhain's iron hæmatoxylin and acid fuchsin. A, ×342·5; B, ×200.

the degenerating nucleus. Cells in this condition occur mainly in the dorsal part of the "fat-body." Cells containing excretory products do not seem to be necessarily more numerous in large individuals than in small, and a male, 1·6 mm. long, had most of the cells of the "fat-body" full of excretory granules.

According to Zenker (see Monod, 1926, p. 198) the "fat-body" has the capacity through its length to differentiate excretory cells. The cells acquiring this function are known as Zenker's glands.

Occasionally small cells of a similar appearance to those of the "fat-body" are seen on either side of and apart from the main body. Very rare isolated cells occur in the abdomen; these are smaller than those of the main mass; they contain fine intensely staining granules.

Reproductive System.

The testes are large and when fully developed depress the hepato-pancreatic cæca and cause them to become attenuated. They extend from about the fifth to the last thoracic somite, sometimes entering the first abdominal. Paired ducts open on the posterior border of the last thoracic somite. On occasion sperm may be seen issuing from the apertures, no doubt owing to the rather violent bending of the animals when removed from the host and worried by placing in a watch-glass for examination. Giard and Bonnier (1889, p. 916) state that the apertures are towards the anterior border of the last thoracic somite; this was probably a slip, as the usual position is on the posterior border.

The Presence of Dead and Degenerating Males within the Body of the Host.

Within the body of the host in addition to living males are also males which have presumably died and which the host has attempted to cover up, for in most instances they are found embedded in a granular mass of tissue. Such dead and degenerating individuals have been found in different regions, sometimes attached to the lobes of the hepato-pancreas (text-fig. 12), sometimes embedded in the gonad in the thorax or abdomen, where they are visible as small yellowish oval or round masses among the red ova. When freed from the surrounding tissue certain of these showed the last four somites of the abdomen bent sharply beneath the much swollen thorax, and sometimes withdrawn partly within it, so that the dead animal appeared as a tiny oval mass (text-fig. 12); it has been observed that animals removed to sea-water begin to swell soon after death. The fact that dark brown or black pigment patches, including the eye-spots, are visible in practically all instances precludes the possibility of these being moults.

As many as four dead mature males have been found in one *Pinnotheres*, and it is possible that in other instances they have been overlooked.

Possibly these males have died in an attempt to moult, as the position of the abdomen of some suggests. In one instance, however, there seemed to be an attempt on the part of the host to surround a living male. The male had worked its way between the carapace and the chitinous membrane forming the roof and outer wall of the gill-chamber in the posterior region, and therefore had little room for movement. It was curved in a semicircle, and the host had partly encircled it with opaque-looking material.

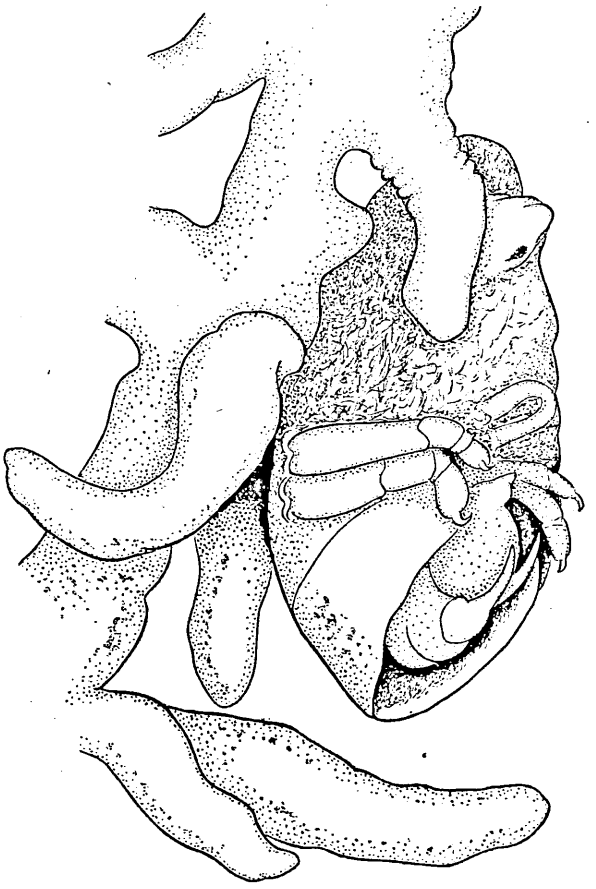
Distribution of Male Pinnotherion *in the Body of the Host.*

The male would seem to occur in no special position in the host. Of 142 living males 85 were found within the thorax, 31 near one or other gill-chamber, and 20 in the abdomen; the position of the remaining 6 was not observed. Assuming that they entered through the wall of the gill-chamber, they must have wandered through the body, though it is possible that those in the abdomen may have entered through the extremely thin chitin of the

ventral surface or the fine chitinous membrane connecting the abdominal somites. I am inclined, however, to believe that in the female *Pinnotheres* after the male-like stage (see Atkins, 1927) the parasite is able to enter at almost any spot on the carapace.

Male *Pinnotherion* have been found lying above the heart of the host,

Text-figure 12.



Pinnotherion vermiforme. Sketch of dead and degenerating male attached to hepato-pancreatic tubules of the host. × 76·3.

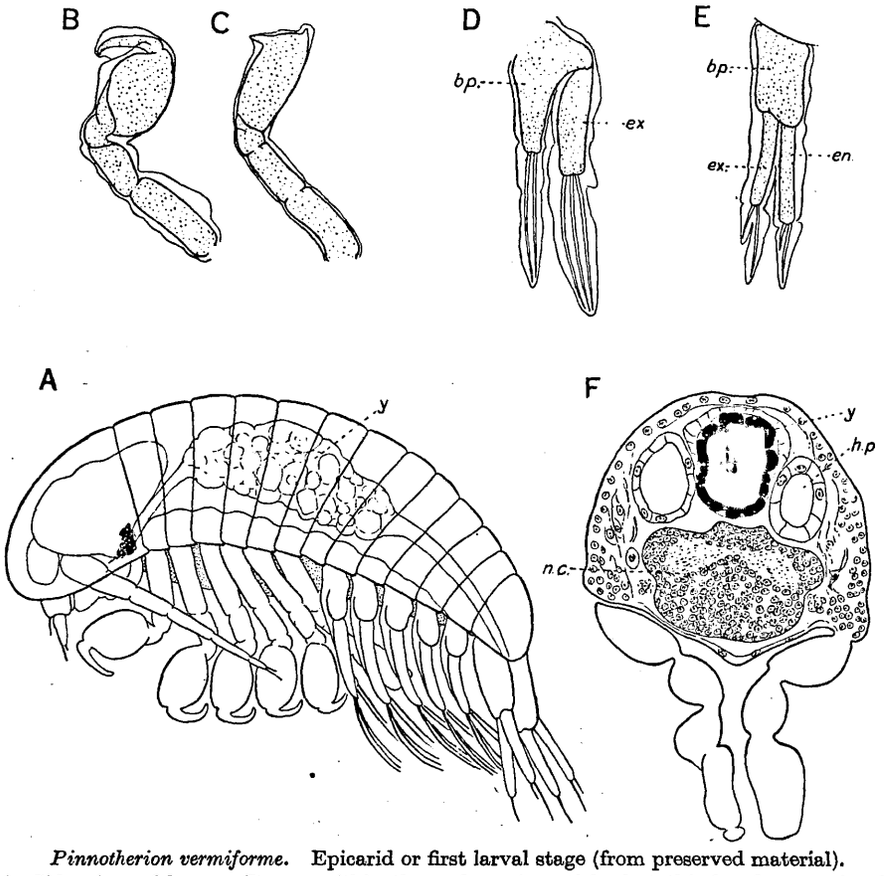
a presumably dangerous position for the latter, the parasite being well provided with claws. One specimen was found actually within a tubule of the hepato-pancreas, and they frequently occur among the gonad.

It might be noted that a fully adult female *Pinnotheres* which was badly infected with a Microsporidian (see Plymouth Marine Fauna, 1931) also contained a male *Pinnotherion*.

THE FIRST LARVAL OR EPICARID STAGE. (Text-fig. 13.)

Two females only have been found with embryos, one in early June and the other in early November. The embryos found within the brood-chamber of the first female were very young, and there were a certain number of unsegmented eggs and empty egg-cases among them. The unsegmented ova were

Text-figure 13.



Pinnotherion vermiforme. Epicarid or first larval stage (from preserved material).

A. Side view of larva. It was within the embryonic cuticle, but this has been omitted for the sake of clearness. ×253·3.

B–E. Appendages of larva of the same brood as A. B. Second peræopod. C. Sixth peræopod. D. Pleopod. E. Uropod. The appendages are shown within the embryonic cuticle. ×342·5.

F. Transverse section of the thorax (near the posterior end of the hepato-pancreas). ×430.

bp., basal segment; *en.*, endopodite; *ex.*, exopodite; *h.p.*, hepato-pancreas; *n.c.*, nerve-cord; *y.*, yolk-mass in the gut.

about 0·12×0·1 mm.; the young embryos were about 0·22 mm. long and about 0·12 mm. deep (dorso-ventrally). These were only slightly more advanced than the stage figured by Giard and Bonnier (1887) in pl. ix. fig. 9 for the embryos of *Portunion mænadis*, and therefore a figure is not given here.

The embryos from the second female were well developed but still within the embryonic cuticle (text-fig. 13, A). They were about 0·28 to 0·3 mm. long (not including the uropods), and about 0·07 to 0·075 mm. broad, and therefore somewhat longer than the corresponding stage of *Portunion mœnadis*, though not as broad. Giard and Bonnier (1887, p. 165) give the size of *P. mœnadis* as 0·19 mm. long and 0·9 mm. broad, the last obviously an error for 0·09 mm. The embryos of *P. vermiforme*, at least while still within the embryonic cuticle, have not the typical Isopod form, but are more or less cylindrical (see text-fig. 13, F).

Giard and Bonnier's (1889, p. 916) description of the coloration of the larva is as follows :—"Il est fortement pigmenté, en brun et en vert, malgré l'obscurité du milieu où il se développe. Ses yeux sont assez gros."

No details can be given of the structure of the antennæ and mouth-parts.

As is usual in the epicarid larva of the Entoniscidæ the sixth pair of peræopods (text-fig. 13, C) differ in form from the first five pairs (text-fig. 13, B), and trail over the pleopods, as is also characteristic of these appendages in the larva of *Portunion* (G. & B., 1887, p. 166). The sixth pair of peræopods of *P. vermiforme* were described as follows :—"La griffe du sixième pereiopode est longue et puissante ; le bâtonnet terminal court et très transparent." This description does not apply to that of the embryo of *P. vermiforme* from Padstow, but the fact that these were not fully developed and were still within the embryonic cuticle may account for the difference. While the "bâtonnet" itself could not be distinguished, there was a small projection of the embryonic cuticle in this position ; the claw, described by Giard and Bonnier as long and powerful, was small, not approaching in size those of the first five pairs of peræopods.

The form of the pleopods and uropods may be seen from text-fig. 13, D & E. The pleopods are uniramous ; the rami of the uropods are nearly equal in length, as in the other species of Entoniscidæ.

The two hepato-pancreatic cæca are present on either side of the yolk remnant (text-fig. 13, F), which is contained within the gut. Giard and Bonnier observed the hepato-pancreas to be very strongly contractile. The hind-gut is continuous with the anterior part of the gut.

The nervous system is highly developed at this stage (see text-fig. 13, F) ; it would appear to have been mistaken by Giard and Bonnier (1889, p. 916) for "les lobules albumino-graisseux," which they described as "présentent une disposition régulièrement métamérique."

The Last Larval or Cryptoniscan Stage. (Text-fig. 14.)

The cryptoniscan larva of *Pinnotherion* has been found in various positions in *Pinnotheres*. They are extremely difficult to find ; many must have been overlooked owing to their minute size and in many instances lack of colour, this most probably in moults. Those discovered were generally just under the carapace of the host, and when it was lifted off were visible as minute opaque specks either on the carapace or on the exposed surface of the body. The fact that in some instances the crab appeared to have partly surrounded them with yellowish structureless material rendered them slightly more visible. It was only possible to distinguish these minute opaque bodies with the unaided eye among living and therefore translucent crab tissue. In two instances a cryptoniscan larva has been found directly under the carapace, between it and the epithelium, with the ventral surface against the chitin. No aperture was visible, but this would be difficult to distinguish, and the larva might possibly have moved from its point of entry.

The distribution in the body of the host of the seventeen larvæ (moults and animals) found, was as follows :—seven just under the carapace in about the centre of the dorsum ; four near or on the wall of the heart ; three near the abdomen of two female *Pinnotherion* ; two near the gill-chamber ; and one attached to the gonad. Of the three near the pleural lamellæ of the two adult female *Pinnotherion* two were close together and were probably moults*, the other was a larva, but in both instances they were not within the chitinous invagination containing the female, but external to it and partly covered by material laid down by the host. In only two females—both containing embryos—have they been sought within the brood-chamber, and in both instances unsuccessfully.

The cryptoniscan larva of *P. vermiforme* is about 0·4 to 0·58 mm. in length † and about 0·15 to 0·18 mm. in breadth. It possesses an irregular double row of large, dark brown, diffuse chromatophores down the dorsum (see text-fig. 14, A), those forming the eyes being especially large. These chromatophores are present also in the mature male, but in fewer numbers and in more compact form. The pigment appears to be very resistant ; it has resisted soaking in 70 per cent. alcohol and also in 10 per cent. formalin for more than a year. Prolonged soaking, of several months, in 2 per cent. acid alcohol, however, removed most of it.

The cryptoniscan larva of *Portunion kossmanni*, which is 0·3 mm. long and 0·1 mm. broad, is described as being entirely white (G. & B., 1887, p. 171).

According to Bonnier (1900, p. 36) the cryptoniscan larva of the Entoniscidæ is distinguished from that of the Bopyridæ (including Giard and Bonnier's families Bopyridæ and Phryxidæ) by the following characters :—

1. The antennule is longer.
2. The antenna has only seven segments (Giard and Bonnier, 1887, p. 171, give six segments), of which the last three form a very short flagellum.
3. The peræopods are all similar.
4. The pleopods lack an endopodite (as certain cryptoniscan larvæ of the Bopyridæ).
5. The exopodite of the uropod is shorter than the endopodite.

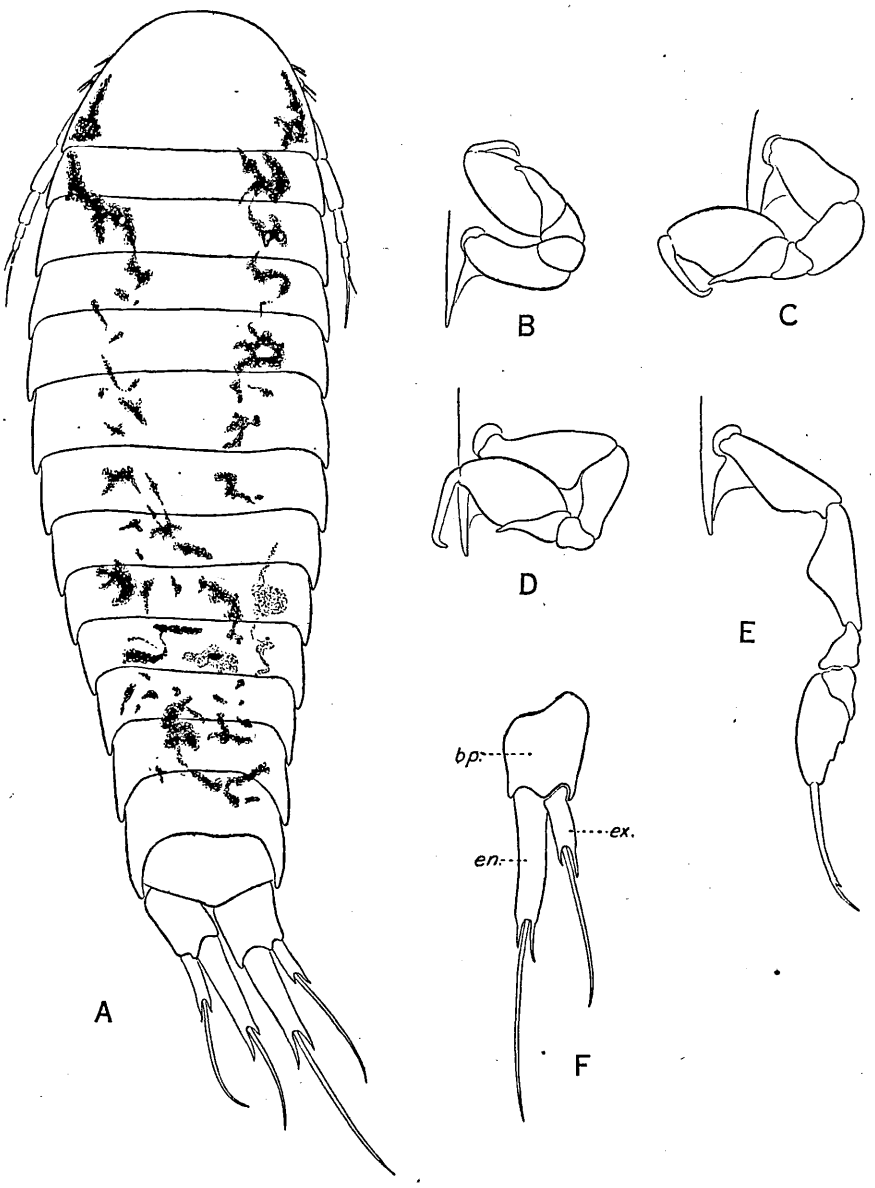
These characters, however, were based on the two forms that alone were known at that time, and of these one only could be referred to its species, namely, the cryptoniscan larva of *Portunion kossmanni* discovered by Giard and Bonnier. The second form was found free in plankton from the Atlantic, north of the Equator, by Hansen (1895, p. 33, pl. iv. figs. 4–4*f*).

Although about seventeen cryptoniscan larvæ of *P. vermiforme* have been found, they were either moults or dead, and in most instances degenerating, specimens, at least partially covered up by the host, and it was found to be almost impossible to free them entirely from the covering tissue without badly damaging them. Some specimens, especially on their ventral surface, were covered by small masses of yellowish structureless material, more or less entirely hiding the appendages. From the different specimens certain of the characters have been made out, though with considerable difficulty and some doubt, and it would appear that the larva has the distinguishing characters enumerated by Bonnier, with one exception, namely, the form of the peræopods. Of these, the first six pairs are alike, there being simply a slight increase in size from the first to the sixth (see text-fig. 14, B–D). They are stout, with strongly

* Near the two moults were two tiny mature, but dead and degenerating males ; it is possible that these had come from the two moults.

† Measured from the anterior border of the head-segment to the base of the uropods.

Text-figure 14.



Pinnotherion vermiforme. Cryptoniscan or last larval stage (from preserved material).

A. Dorsal view of larva, sketched from a moult, with the chromatophores added from another specimen. ×253·3.

B–F. Appendages. B, C, D, E. First, third, sixth, and seventh peræopods. F. Uropod. *bp.*, basal segment; *en.*, endopodite; *ex.*, exopodite. ×342·5.

hooked dactylopodite, the form of the hook being nearly straight, with the tip bent down almost at right angles. The seventh, however, is considerably more slender and elongated than the first six pairs, and the dactylopodite is nearly twice as long as that of the preceding pair, while the shape of the ischiopodite is somewhat different and the propodite is more slender (see text-fig. 14, E). Both in moults and dead specimens it was characteristic that the first six pairs were nearly always bent back on themselves. In the few specimens in which the form of the peræopods were clearly recognizable the seventh pair, however, was trailed posteriorly over the pleopods (*cf.* the appendages of the epicarid or first larval stage, where the first five pairs are bent back on themselves, while the sixth, and last, pair trails over the pleopods). The shape of the coxal plates of the peræopods could not be made out with certainty, but they did not appear to be toothed as are apparently those of the cryptoniscan larva of *Portunion kossmanni* (G. & B., 1887, pl. viii. figs. 7 & 9).

I am unable to give any details of the form of the antennules or mouth-parts. The antennæ have seven segments, the last three being minute and forming a short flagellum. The pleopods appear to be uniramous, the exopodite and the inner angle of the basal segment bearing four or five long setæ. The form of the uropods is shown in text-fig. 14, F; both endopodite and exopodite appeared to have one long hair only, with one or two short spines at the base of it, as in Hansen's larva (1895, pl. iv. fig. 4 *a*). The outer ramus is shorter than the inner, the difference in length being more marked than in the larva of *Portunion kossmanni* (G. & B., 1887, pl. viii. fig. 7) and in Hansen's larva (1895, pl. iv. fig. 4 *a*).

None of the cryptoniscan larvæ of *Pinnotherion* obtained were in a condition for the sex to be determined.

The work recorded in this paper was carried out at the Marine Biological Association's Plymouth Laboratory, to the Director and Council of which I desire to express my gratitude. I am greatly indebted to Dr. W. T. Calman, F.R.S., and Dr. E. J. Allen, F.R.S., for reading the manuscript.

Summary.

Pinnotherion vermiforme G. & B. infects *Pinnotheres pisum* from the Estuary of the Camel, Padstow, North Cornwall.

The males are not restricted in their occurrence to the body of the female, as apparently they are in other genera of Entoniscidæ, but occur isolated in the host, as do also the cryptoniscan larvæ.

Of the total *Pinnotheres* examined 27·69 per cent. were infected with one or other sex of the parasite. Infection with the male parasite alone was 26·85 per cent., with the female (sometimes with males present in addition) 0·84 per cent.

The proportion of the sexes in *P. vermiforme* was found to be 97·67 per cent. males and 2·33 per cent. females.

The presence of the adult female *P. vermiforme* in the host would seem to cause partial to almost complete atrophy of the gonad. At Padstow they have been found in the female host only, though the male parasite has on two occasions been found in the male host.

The question of the relation of the parasite to its host and the possible manner of respiratory exchange is discussed.

The characteristics of the female *P. vermiforme* are as follows:—

1. The first pair of oostegites are without transverse lamellæ, and the recurrent lamellæ are of unusual length.

2. The gonad is without dorsal processes; of the two ventral the posterior is excessively long and cylindrical, with vermiform movements, and extends into the abdomen of the host.
3. The pleopods are uniramous.
4. The hood-region of the brood-chamber lacks any appreciable opening in front of the cephalogaster.
5. The respiratory(?) folds ("corps spongieux" of Giard and Bonnier) arise from the first pair of thoracic appendages, and not from the second, as apparently in other genera.
6. A large chamber for the storage of sperm is formed by the oostegites (probably the last or last two pairs). No other sperm receptacle is present, at least in the fully adult animal.

It is possible that, on a fuller knowledge of the parts concerned, in the other genera of Entoniscidæ the last four characters may be found not to be peculiar to *Pinnotherion*.

The characteristics of the male *P. vermiforme* are as follows:—

1. The presence of a median process (hook) on the last thoracic somite.
2. The fusion with the head-region of the second, in addition to the first, thoracic somite. The only other genus of Entoniscidæ having this character would seem to be *Entoniscus*.
3. The length is 1·0–3·5 mm.

The epicarid and cryptoniscan larvæ are described so far as the material allowed.

According to Giard and Bonnier (1889, p. 916) the genus *Pinnotherion* is closest to *Grapsion*, though clearly distinguishable. With no knowledge of actual specimens of the other genera of Entoniscidæ I am unable to discuss the relationships of *Pinnotherion*.

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Abbreviations used in the Plates.

a.[1]. Vestige of antennule.
a.[2]. Vestige of antenna.
abd. Abdomen.
a.ex. Thin lateral extension of antenna overlying the oral cone.
a.m.r. Median artery of recurrent lamella.
an. Anus.
ao. Median aorta (displaced laterally in Pl. V.).
a.p. Minute anterior passage into brood-chamber.
art.r.f. Artery of respiratory folds.
b.c. Wall of brood-chamber.
b.oost.[1]. Base of first oostegite.
cg. Cephalogaster.
ch.o. Chitinous organ.
ch.o.v. Dorsal valve of chitinous organ.
d.s. Dorsal surface of thorax.
f.b. Fat-body.
h.g. Hind-gut.
h.p. Hepato-pancreas.
l.ao. Lateral aorta.
l.s. Lateral sinus.
m. Mouth.
md. Mandible.
m.f. Muscle-fibres.
mx.gl. Maxillary gland.
mx.gl.o. External opening of maxillary gland.
mxp. Maxillipede.
n.c. Nerve-cord.
o. Ovum in oviduct.
oost.[1]*a.l.* Ascendant lamella of first oostegite.
oost.[1]*r.l.* Recurrent lamella of first oostegite.
oost.[2]. Second oostegite.
ov. Ovary.
ovd. Oviduct.
perp. Peræopod.
perp.m. Peræopod left behind by male in the "receptaculum seminis."
pl. Pleural lamella.
pl.[2–5]. Second to fifth pleural lamellæ.
plp.[2–5]. Second to fifth pleopods.
r.f. Respiratory folds.
R.o. Rathke's organ.
r.s. "Receptaculum seminis."
r.s.o. Opening of the passage leading from the "receptaculum seminis" to near the oviducal opening.
r.s.p. Passage leading from the "receptaculum seminis" to near the oviducal opening.
s.a.a. Anterior sinus of ascendant lamella.
s.m.a. Marginal sinus of the ascendant lamella.
s.m.r. Marginal sinus of the recurrent lamella.
s.m.v. Median ventral abdominal sinus.
sp. Sperm.

The blood-vessels and lacunæ are stippled, the arteries being shown by double walls. Chitin is shown in black. The chitinous membrane surrounding the parasite is indicated by a continuous line in Pl. IV. figs. 2, 3, 4, 5; Pl. V. figs. 1, 2; Pl. VI. fig. 1.

EXPLANATION OF THE PLATES.

PLATE I.

Fig. 1. Sketch to show the characteristic coloration of adult female *Pinnotheres pisum* parasitized by an adult female *Pinnotherion vermiforme*. The gonad, in process of atrophying, is deep orange in colour, and the entire crab is tinted a paler shade of orange by the colour liberated from the degenerating ova. The parasite having entered from the left gill-chamber the hood-region is in the right half and the abdomen in the left half of the host. The anterior portion of the long postero-ventral process of the gonad is visible in the right posterior region of the crab. Carapace width of *Pinnotheres* 11·5 mm.

2. *Pinnotherion vermiforme*. Colour sketch of living fully adult female from the left side. The deep orange of the gonad is somewhat masked by the milky fluid in the brood-chamber. × ca. 6½.

PLATE II.

Fig. 3. *Pinnotherion vermiforme*. Colour sketch of living fully adult female from the right side, with the outer pairs of oostegites (except the part forming the "receptaculum seminis") removed to reveal the first or inner pair. The respiratory (?) folds have been removed. × ca. 7½.

4. *Pinnotherion vermiforme*. Colour sketch of a living very immature female from the left side. The investing chitinous membrane has not been removed; its outline may be seen round the hood and the oostegites which will later cover the gonad. × ca. 22⅔.

PLATE III.

Pinnotherion vermiforme, female. Transverse sections through the hood-region of the brood-chamber. Somewhat diagrammatic. × ca. 41·4.

Fig. 1. Showing the fused ascendant lamellæ of the first or inner pair of oostegites protruding through the gap in the hood (formed by the second pair of oostegites).

2. Through the entire hood, to show the general form and the arrangement of the oostegites. This section passes through the tiny tortuous anterior passage into the brood-chamber: it is posterior to the section shown in fig. 1, and anterior to that in fig. 3.

3. To show the relation of the respiratory (?) folds to the bases of the first pair of oostegites and to the maxillary gland. Embryos are present within the brood-chamber.

PLATE IV.

Pinnotherion vermiforme, female. Transverse sections through the abdomen. Somewhat diagrammatic. × ca. 34·5.

Fig. 1. Through the second somite. The hind-gut, approaching its blind termination, is small. The bases only of the pleural lamellæ are shown.

2. Through the fourth somite, towards the anterior region of attachment of the fourth pair of pleopods. Within the canal formed by these lie the free posterior extensions of the third pair.

3. Through about the middle of the fourth somite, to show how extensive is the overlapping of the pleopods. Within the canal formed by the fourth pair of pleopods are the posterior extremities of the third pair, while to the outside of the canal is the anterior extremity of the right fifth pleopod. The bases only of the pleural lamellæ are shown. Position of section shown at A in text-fig. 2.

4. Through the posterior region of the fourth somite, showing the overlapping parts of the fifth pair of pleopods fitting closely down to the bases of the fourth pair of pleural lamellæ (bases only shown).

5. Through the junction of the fourth and fifth somites. The appearance as of biramous pleopods is due to the bases of the fourth and fifth pairs of pleopods overlapping for a short distance. Position of section shown at B in text-fig. 2.

6. Through the posterior region of the fifth somite. The chitin of the pleopods has separated from the epithelium.

Plate V.

Pinnotherion vermiforme, female.

Fig. 1. Transverse section through the anterior region of the thorax to show the anatomy. The section passes through the posterior region of the cephalogaster.

2. Transverse section of the thorax, passing through Rathke's organ, and the anterior blind prolongation of the hepato-pancreas.

3. Transverse section through the thorax and brood-chamber, showing the junction of Rathke's organ with the hepato-pancreas. The dorsal surface is much reduced. Somewhat diagrammatic. × ca. 41·4.

Plate VI.

Pinnotherion vermiforme, female.

Fig. 1. Longitudinal section through the anterior region of the thorax, to show the extent of the maxillary gland. The section is considerably oblique; anteriorly it passes through one of the apertures of the maxillary gland, and posteriorly through the ventral nerve-cord (*n.c.*), while it fails to cut Rathke's organ.

Figs. 2–4. Transverse sections (somewhat oblique) of the thorax passing through the "receptaculum seminis." Fig. 2, anterior; fig. 3, middle; and fig. 4, posterior region of "receptaculum seminis." Somewhat diagrammatic. × ca. 33.

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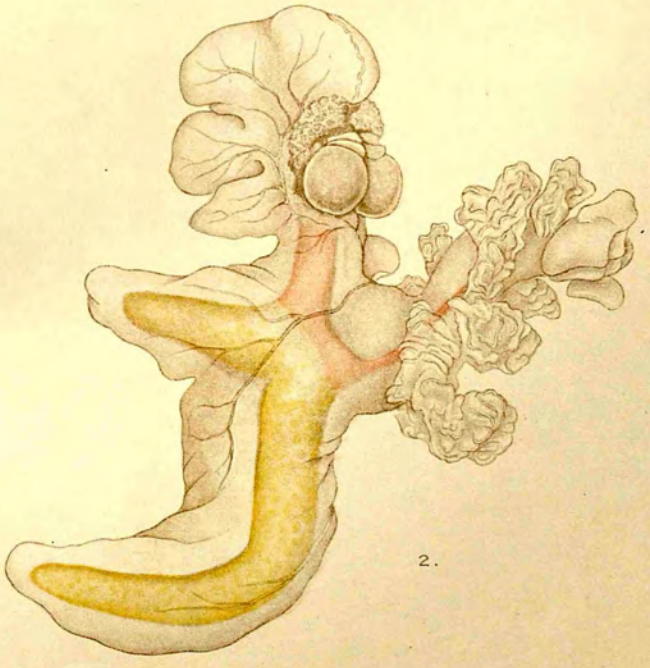

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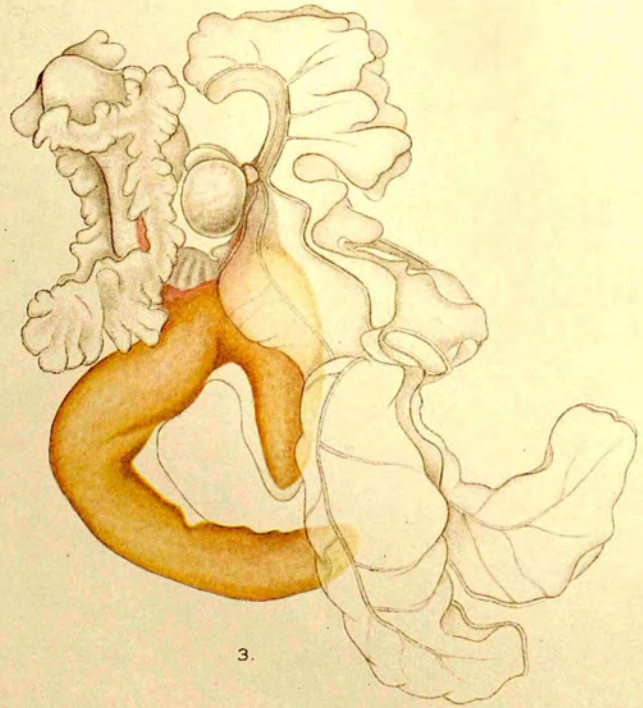
PINNOTHERION VERMIFORME GIARD & BONNIER,
AN ENTONISCID INFECTING *PINNOTHERES PISUM*.



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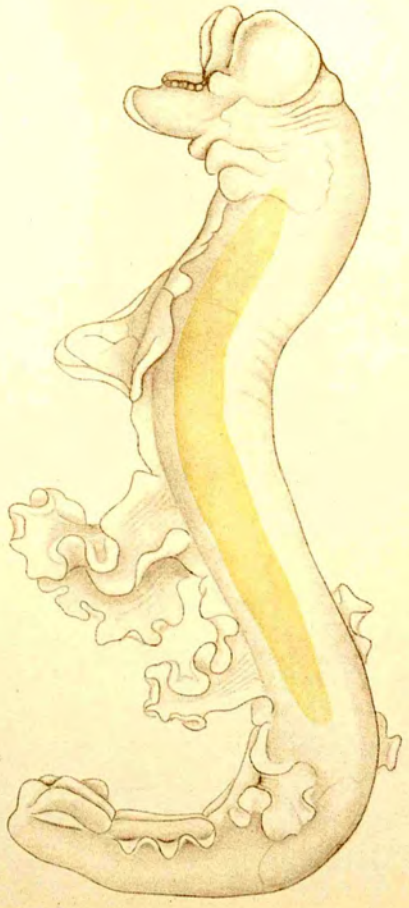

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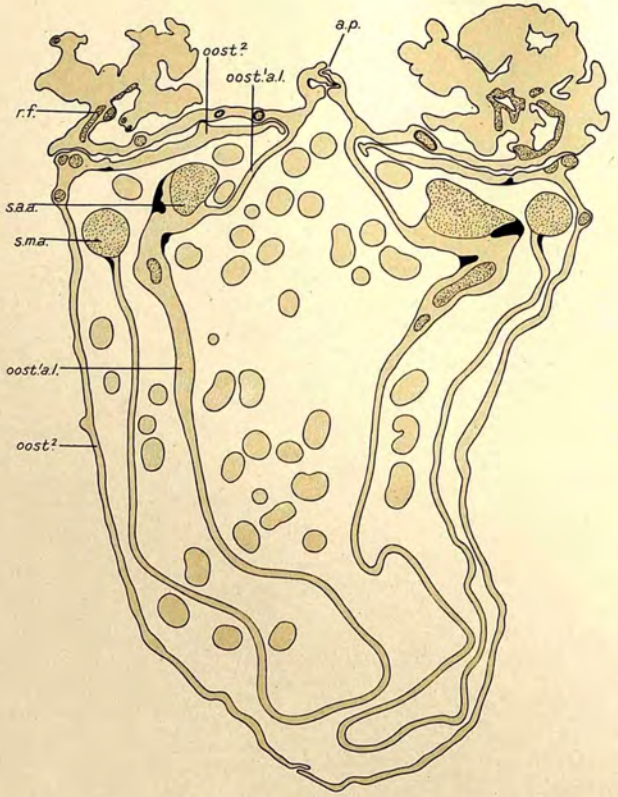

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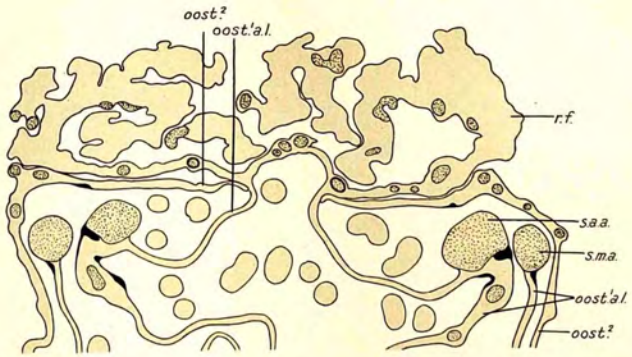

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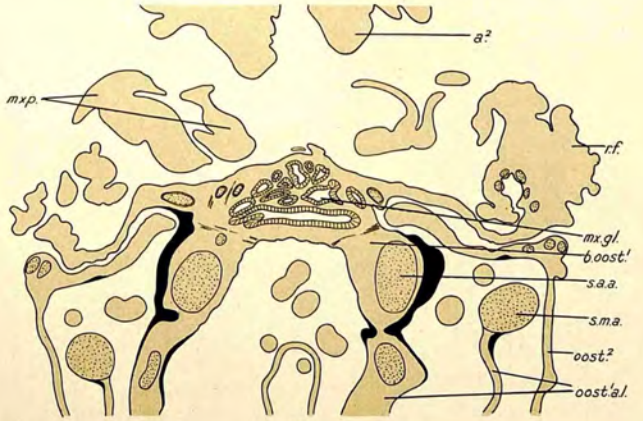

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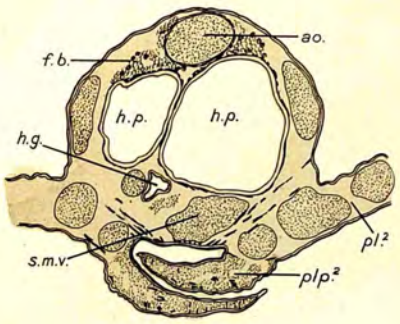

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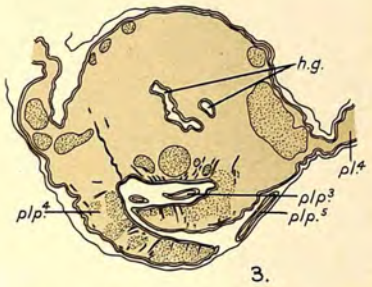

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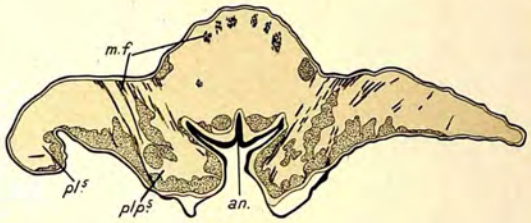

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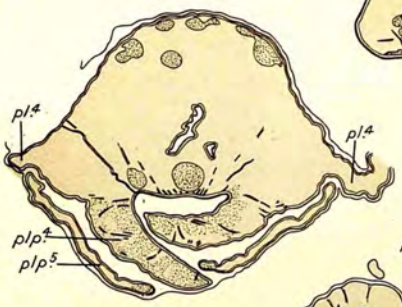

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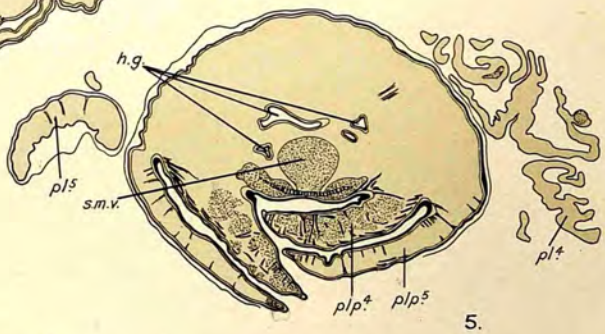

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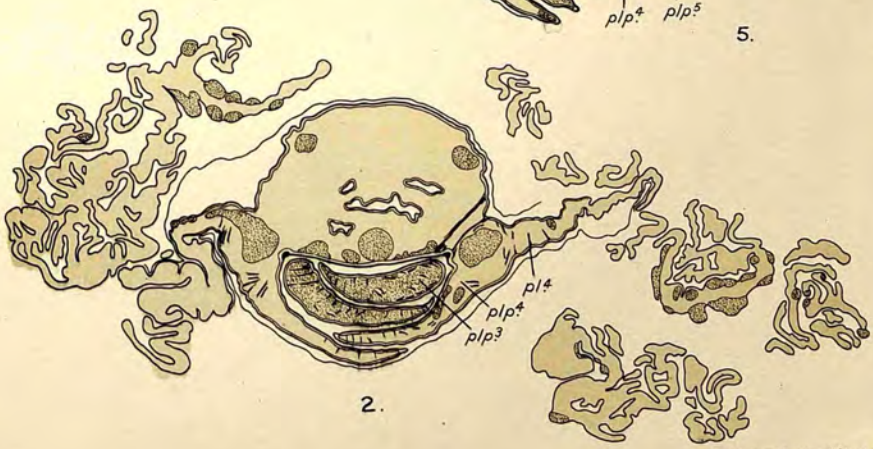

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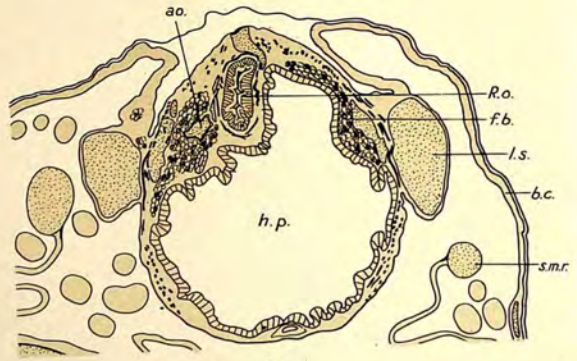

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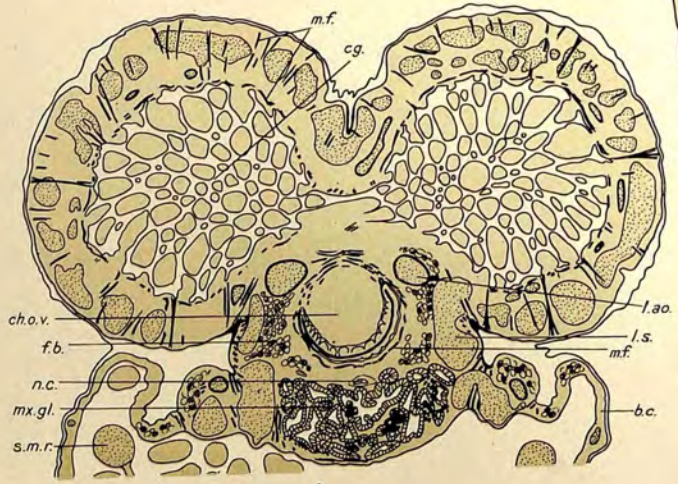

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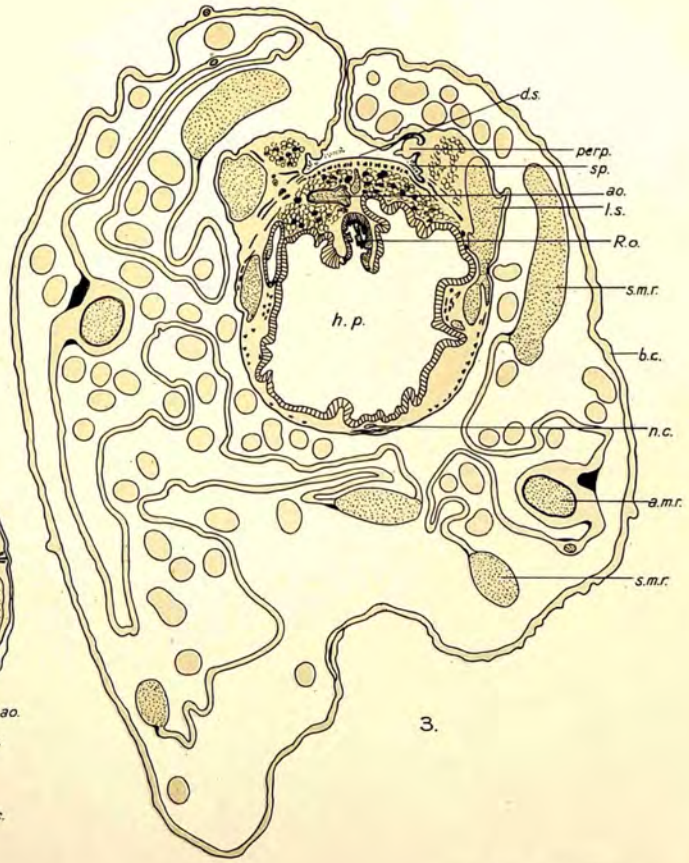

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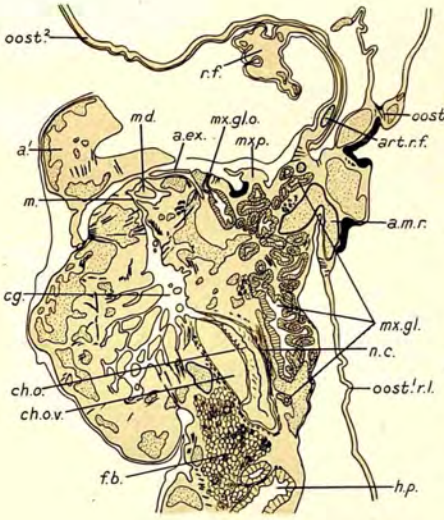

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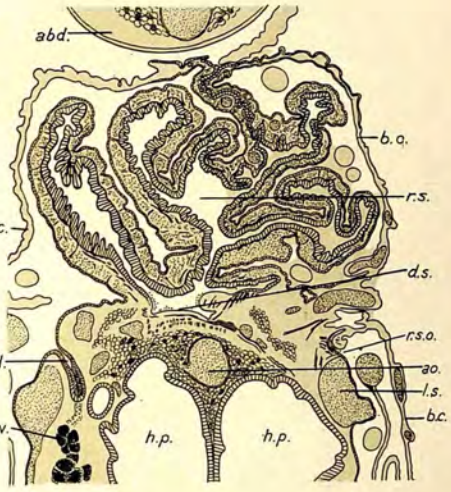

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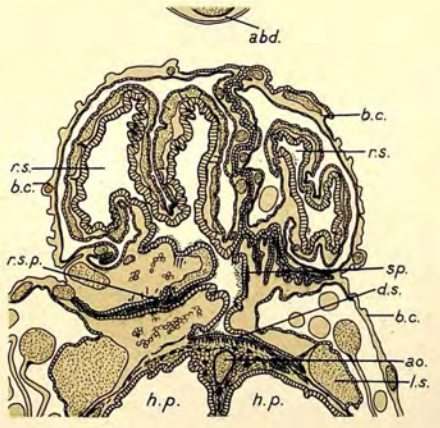

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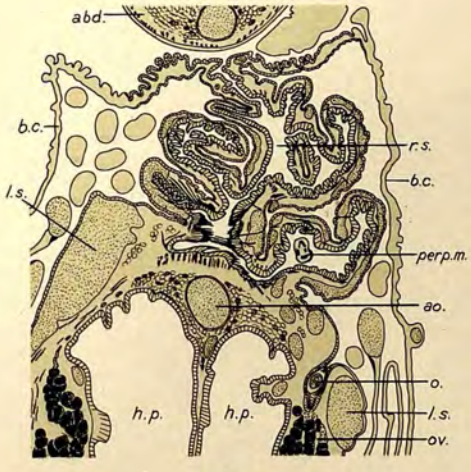

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Rhopalura granosa sp. nov., an Orthonectid Parasite of a Lamellibranch *Heteranomia squamula* L., with a Note on its Swimming Behaviour.

By

D. Atkins, B.Sc.

With 4 Figures in the Text.

Reprinted from the Journal of the Marine Biological Association of the United Kingdom.
Vol. xix. No. 1. August, 1933. Pages 233–252.

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CONTENTS.

INTRODUCTION.

THE Orthonectida, a small group of rare parasites, have attracted considerable interest owing to their doubtful systematic position. In 1868 Keferstein (1868, pl. ii, fig. 8) figured, though he did not describe, a "problematic parasite"* from the digestive tube of *Leptoplana tremellaris*, but it was not until about 1877 that a serious investigation of these forms was undertaken by Giard (1877), who gave to the group the name of Orthonectida. Our knowledge of the organisation and life-history of these parasites, however, is in great part due to the admirable researches of Caullery and his collaborators. The Orthonectida are forms in which the sexual generation is formed asexually from germ cells produced in a parasitic plasmodium.

Some eight species of Rhopalura, and one of Stœcharthrum, are now known.

Rhopalura granosa sp. nov., parasitic in *Heteranomia squamula* L. (=*Anomia aculeata* Müller), in the Plymouth area, is the first Orthonectid

* This species was named *Rhopalura* (*Intoshia*) *leptoplanæ* by Giard (1880, p. 236); it was rediscovered and described by Jourdain (1880)—under the name of *Prothelminthus hessi*—at Saint-Vaast-la-Hougue, and by Caullery and Mesnil (1901 c, pp. 399–400) in the bay of Saint-Martin, under the old fort of Saint-Germain-des-Vaux.

to be described from a Mollusc, members of the group being hitherto known from Annelids, Nemertines, a Planarian, and from an Ophiuroid, *Amphiura squamata*. The only previous record of an Orthonectid for the British Isles would seem to be that by McIntosh in 1873 (p. 129), when he described a curious parasite burrowing in the body wall of *Lincus gesserensis*. The specific name *granosa* has been given on account of the presence of characteristic refringent bodies in the male (see p. 237).

Description of *Rhopalura granosa*.

In *R. granosa* the sexes are separate, and, as in other species of Rhopalura where the male is known, exhibit sexual dimorphism. Sexual dimorphism is so marked in the genus that Giard (1879, 1880) originally referred the two sexes in *R. ophiocomæ* to two genera, Rhopalura and Intoshia.

The Female.

The female (Fig. 1, A and B) is cylindrical, tapering anteriorly and posteriorly, and about 190 to 210μ long, and 60 to 75μ broad, not including the cilia. Individuals, however, vary somewhat in shape, doubtless partly owing to their considerable powers of contraction; a narrow elongated female, ca. 230μ long and 55μ broad, is shown in Fig. 1, B, but this is an extreme form, and rarely seen.

Fig. 1, A and B, of *R. granosa* recall Julin's figures of " femelle aplatie " and " femelle cylindrique " of *R. ophiocomæ* (Julin, 1882, pl. ii, figs. 2 and 1). The type of female shown in Fig. 1, A, is not flattened, however, for there is no appreciable difference observable in the width as it rotates in swimming; the rings are no less clearly marked than in the elongated form (Fig. 1, B). Both forms are found among those issuing naturally from their hosts. Caullery and Mesnil (1901 c, pp. 395–397) think that possibly the cylindrical females of *R. ophiocomæ* are a temporary state, leading to the flattened females: their specimens were apparently taken artificially from the host.

The body of the female *R. granosa*, which is entirely ciliated, shows eight rings, of which the first is the anterior, and the last the posterior terminal cone. The fourth and sixth rings seem to be formed of two rows of cells, while the second, third, fifth and seventh are formed of one row each. The anterior and posterior cones are formed of several rows. Between the rings there is a row of tiny cells, as in the male. The rings are superficial, involving the ectoderm only, the body not being segmented: they are more evident in some individuals than in others. When the animal is swimming forwards the cilia on the anterior cone are directed forwards, and those on the body posterior to it backwards (see Fig. 1, A). When the animal is swimming backwards, however, those on the second ring, as

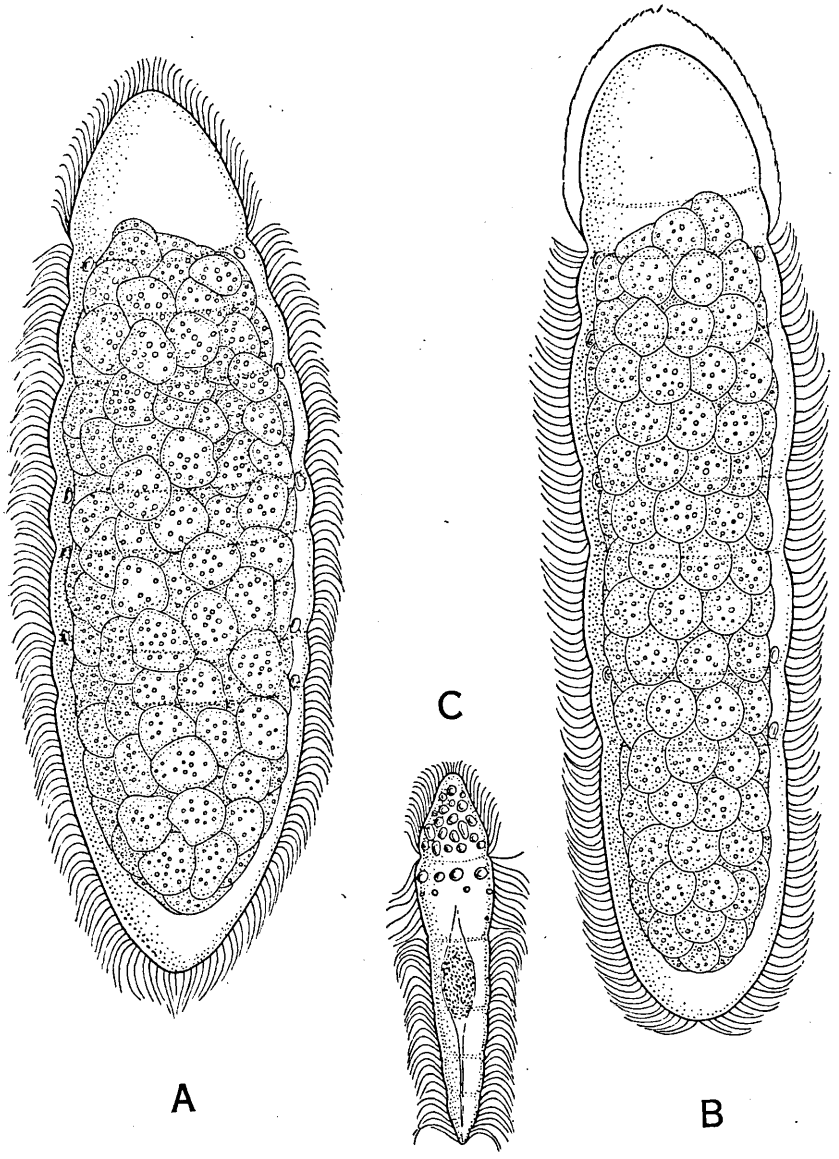

FIG. 1.—*Rhopalura granosa*. Sketches from life of individuals which had issued naturally from the host. The cilia are shown in profile only, although actually the animals are entirely ciliated: they are shown somewhat diagrammatically. × 573½.

A. Female. The cilia are shown as they appear during slow forward movement.

B. Rare, elongated form of the female. The cilia are shown as they appear during reversed swimming. In both forms the asymmetrical anterior extension of the mass of ova is due to the presence of the problematical organ, which is not shown in the figures.

C. Male.

well as those on the anterior cone, become motionless and are applied closely to the surface of the body, the tips being directed anteriorly (see Fig. 1, B, and also p. 247).

The ectoderm cells of the anterior and posterior extremities are deeper than those covering the rest of the body, the depth of the anterior cells being especially noticeable. The latter, in particular, contain a number of granules towards their outer ends, which become red if a trace of neutral red is added to the water. In sections of animals preserved in Bouin's fixative and stained with Heidenhain's iron hæmatoxylin and acid fuchsin the ectoderm cells appear much vacuolated, the vacuolation occurring sometimes at the inner ends, and sometimes at the outer ends of the cells. A problematical organ is present in the anterior cone; narrow prolongations from the organ appear to encircle the cone. It has been suggested by Metschnikoff (1881, p. 285) that this structure may be a remnant of an alimentary canal, and by Caullery and Lavallée (1908 b, p. 465) a nervous ring. A few, one to four, large vacuoles are generally observable in the cells of the anterior cone.

A small number of refringent bodies occur at irregular intervals, in a position between the rings of the body. These become orange with neutral red, and pale blue with methylene blue *intra vitam* staining.

The ova are numerous, very roughly about two hundred. They extend only slightly into the region of the anterior cone. They are about 14μ in diameter, with transparent cytoplasm containing a number of refringent granules, which become red with neutral red used *intra vitam*: it would appear to be these granules which in sections of material preserved in Bouin's fixative stain black with iron hæmatoxylin.

The embryos develop in the body of the parent: they are closely packed, and no movement of the ciliated larvæ is observable, such as occurs in *R. pelseneeri* (M. and C., 1905a, p. 429).

Embryos and ova have been observed, on several occasions, escaping from the parent in the region of the second and third rings. The fact that ova also have been seen to be expelled, points to the conclusion that these occurrences were not normal, but possibly due to unnatural conditions of observation; the position of emergence may, therefore, also be abnormal. A genital pore, such as described by Caullery and Mesnil (1901 c, p. 394) for *R. ophiocomæ*, could not be distinguished, at least in females sectioned while still within the host: no sections were made of those which had emerged.

The Male.

The male (Fig. 1, C) is cylindrical and slender, tapering anteriorly and posteriorly, the broadest region being the second ring. It is 87 to 95μ long and 20μ broad, not including the cilia. The body shows six super-

ficial rings, of which the first is the anterior, and the last the posterior terminal cone. Between the rings is a row of tiny cells, the nuclei of which show clearly in sections. The anterior cone is formed of several rows of ectoderm cells, as is also the second ring.

A characteristic of the male is the presence of large irregular refringent bodies in the cells of the anterior cone, as well as in the first row of cells of the second ring. Occasionally smaller refringent bodies occur in other parts of the second ring. In *R. ophiocomæ*, the only other species in which the males are known to have these curious large refringent bodies in the cells, they are present in the second ring only (Giard,

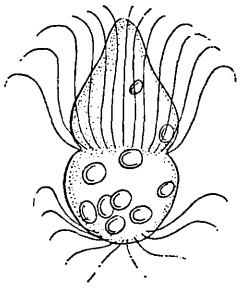

FIG. 2.—*Rhopalura granosa*. Ciliated larva, taken from the body of the parent. × 1470.

FIG. 3.—*Rhopalura granosa*. Fragment of a male producing plasmodium. × 70.

1880, p. 229; Julin, 1882, p. 11). In sections of *R. granosa* preserved in Bouin's fixative these bodies frequently stain lightly with a dark periphery with iron hæmatoxylin and acid fuchsin, but others stain uniformly black. Caullery and Mesnil (1901 c, p. 393) found those of *R. ophiocomæ* disappeared in preparations treated with alcohol and xylol, a vacuole occupying their place. The fixative they used chiefly was a saturated solution of sublimate in sea-water, with the addition of 1% acetic acid.

The male of *R. granosa* is entirely ciliated. The cilia on the anterior cone are rather shorter and denser than those on the rest of the body; they are directed forwards as in the female. Those on the second ring are much less closely set than those on the posterior rings, but appear to be as long. In *R. ophiocomæ*, the species which—of those so far described—seems most closely allied to *R. granosa*, the second ring is said to be unciliated, though Caullery and Mesnil (1901 c, p. 392 footnote) note that

some isolated cells exceptionally bear long cilia. In sections the basal granules of the cilia stain very darkly and clearly with iron hæmatoxylin.

The " testis " is present about the middle of the body. The spermatozoa are flagellated.

The Larva.

The ciliated larva (Fig. 2) forced from the body of the female, by gentle pressure on the coverslip, is somewhat acorn-shaped,* being slightly constricted in the middle region, pointed anteriorly and broadly rounded posteriorly. (The pointed end is apparently anterior, as this is foremost when the larva swims.) It is about 19μ long. Ciliation is restricted to two bands of long cilia ; one in the middle region about the slight constriction, and one posteriorly. Refringent bodies are present in both regions of the larva, but chiefly posteriorly. Cells could not be distinguished in the living state ; larvæ were not sectioned.

The larva of *R. granosa* differs considerably in appearance from those so far described, namely, that of *R. ophiocomæ* (C. and L., 1905, p. 266 ; 1908 b, p. 432, and pl. xv, figs. 43, 44) and *R. pelseneeri* (M. and C., 1905 a, p. 429, and fig. 1), which appear to have no regular arrangement of the cilia, though Caullery and Lavallée (1908 b, p. 432), speaking of the very small size (12–15μ in diameter) and great transparency of the former larva, say : " La disposition des cils mêmes est à peu près impossible à fixer ; ils paraissent longs et peu denses. Ils donnent à ces larves un mouvement rapide, souvent tourbillonnant."

Relationships.

Caullery and Mesnil (1901 c, p. 419) have distinguished three groups in the genus Rhopalura, characterised as follows :—

Cilia limited to narrow rings, *R. pterocirri* St. J. (I).

Cilia entirely (or nearly) covering the body.
- Ova in compact mass. (II).
  - *R. ophiocomæ* Gd.
  - *R. intoshi* Metchn.
- 1 (or 2) linear row of ova. (III)
  - *R. leptoplanæ* Gd.
  - *R. pelseneeri* C. and M.
  - *R. linei* Gd.
  - *R. metchnikovi* C. and M.
  - *R. julini* C. and M.

R. granosa evidently belongs to the second group. It is intermediate in size in both sexes, between *R. intoshi* from *Lineus* (*Nemertes*) *lacteus* and *R. ophiocomæ* from *Amphiura squamata*. In the male it is clearly distinguishable from *R. intoshi* by the presence of large refringent bodies, and from *R. ophiocomæ* by having these bodies in the anterior cone, and the

* Shaped like an acorn in its cup.

first row of cells of the second ring, while in *R. ophiocomæ* they are restricted to the second ring.

The female of *R. granosa* has not been observed to be without cilia on the second ring, as occurs in certain individuals of *R. ophiocomæ* (Giard, 1880, p. 232; Julin, 1882, p. 16; C. and M., 1901 c, p. 393): it has eight rings, while that of *R. intoshi* has nine (Metschnikoff, 1881, p. 284).

The larva differs from that of *R. ophiocomæ* both in the shape and the arrangement of the cilia: the larva of *R. intoshi* is unknown.

The Plasmodia and their Distribution in the Host.

In *Heteranomia squamula* the parasite is found replacing the gonad; it also occurs in the blood lacunæ and vessels in the mantle and the suspensory membranes of the gills, even extending into the dorsal ends of the gill filaments. In one host sectioned, numerous young plasmodia were present in the mantle margin in the posterior region. In heavy infections the parasitic plasmodia, containing the sexual forms of the Orthonectid, entirely replace the gonad of the host, rendering the determination of sex impossible. A fragment of a male containing plasmodium is shown in Fig. 3.

It would appear to be more usual for the males and females to occur in separate hosts, though it is by no means rare for them to be found together (see p. 244); when this occurs one sex generally predominates. Observations were mostly made on living Heteranomia, only two specimens being sectioned. One of the sectioned individuals was parasitised by plasmodia containing males only, many of them being nearly mature. It was well infected, plasmodia occurring in the mantle, visceral mass, suspensory membranes of the gills and dorsal ends of the gill filaments, but much of the gonad remained, sperm being recognisable among degenerating cells in some regions.

The second Heteranomia sectioned was very heavily infected, no gonad being recognisable. The great majority of the plasmodia in this host contained female Rhopalura, but in four separate regions of the visceral mass and mantle, males were present, many being nearly mature, and in at least two of these regions males and females occurred together in the same plasmodium (see Fig. 4). In one region (a), several branches or lobes of a plasmodium contained males, but in a very small portion only were the two sexes present together. In a second region (b), a small island of well-formed males, together with numerous germ cells and groups of germ cells, was present among females, and the males were not segregated in separate lobes of the plasmodium. In a third region (c), a few males were present in a small, almost empty plasmodial lobe, which was rather doubtfully traced into a female plasmodium. The fourth region (d), near

the byssal muscle of the host, was by far the largest. This plasmodium appeared to contain males alone, though its considerable size made the tracing of its many branches difficult.

Where the males and females were present in the same plasmodium, the females yet appeared to contain unsegmented ova, so far as could be ascertained in the crowded condition of these. Caullery and Mesnil (1901 c, pp. 466–467) state that " dans des coupes d'une Amphiura, *qui renfermait des plasmodes des deux sexes* (of *R. ophiocomæ*), plusieurs femelles, à l'intérieur desquelles, au lieu d'ovules, on trouvait des corps plurinucléés ayant tout à fait l'aspect des embryons décrits ci-dessus, mais un peu moins avancés. Nous les interprétons comme tels. Il est parfaitement admissible que, lorsque les deux sexes de Rhopalura existent dans une même Ophiure, les femelles adultes puissent, avant d'arriver au dehors, être fécondées et renfermer des embryons."

It is impossible to be entirely certain that the presence of males and females in the same plasmodium is not due to the disappearance of host tissue dividing two originally separate plasmodia, but it seems not improbable that a plasmodium may produce males and females at different times, the two phases overlapping to some extent. When plasmodia are well established in the host, they ramify greatly, and it is practically impossible to determine their number and limits. The presence of plasmodia with males only in the less heavily infected host sectioned would seem to indicate that, if it should prove to be correct that the two sexes are produced by the same plasmodium at different times, the male phase precedes the female.

It may be noted that curious thread- or rod-like bodies, or regions, of darker staining protoplasm were present in some small portions of female producing plasmodia. Among masses of these occurred a few normal-looking groups of germ cells. The significance of these bodies is obscure ; they may be a normal occurrence, or possibly parasites.

Caullery and Mesnil (1901 c, p. 384 ; C. and L., 1912, p. 159) have described plasmodia which produce one sex only, such as are usually found in *R. ophiocomæ* from *Amphiura squamata*, as " unisexual," and those in which males and females develop side by side in the same plasmodium, as in *R. metchnikovi* from *Spio martinensis* (C. and M., 1901 c, pp. 384, 402), as " hermaphrodite." In *R. intoshi* from *Lineus* (*Nemertes*) *lacteus* an intermediate condition, between that of *R. ophiocomæ* and *R. metchnikovi*, seems to obtain, " male," " female," and " hermaphrodite " plasmodia frequently occurring in the same host (Metschnikoff, 1881, p. 284).

Most known dicœcious species of Rhopalura apparently have " hermaphrodite " plasmodia (*R. leptoplanæ*, C. and M., 1901 c, p. 399, and *R. julini*, C. and M., 1901 c, p. 412, in addition to those already mentioned), *R. ophiocomæ* being the only one with generally " unisexual " plasmodia.

There appears, however, to be considerable variation in the condition of the plasmodia of this species in different localities. Giard (1880, p. 228) and Metschnikoff, 1881, p. 288) found that in *R. ophiocomæ* from *Amphiura squamata* from Wimereux, and from Naples and Spezzia respectively, a

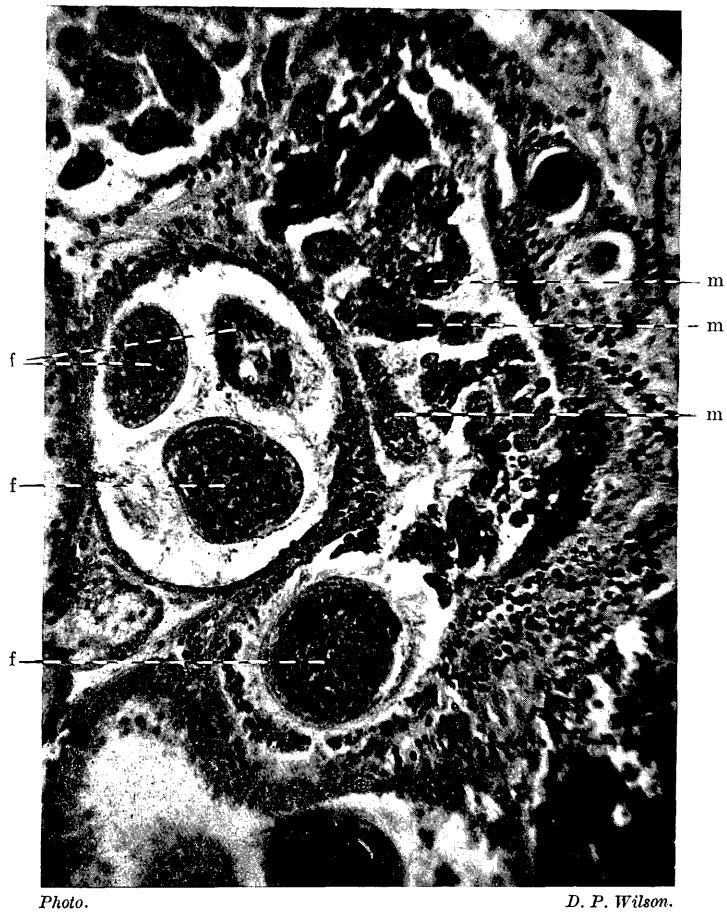

Photo. *D. P. Wilson.*

FIG. 4.—*Rhopalura granosa*. Section of part of a plasmodium containing both males and females. F., female (transverse section); m., male (longitudinal section). Bouin's fixative: Heidenhain's iron hæmatoxylin and acid fuchsin. × ca. 1012.

plasmodium produced Orthonectids of one sex only, males or females, though very occasionally the two sexes might be present in the same host. Julin (1882, p. 8), also working at Wimereux, says: "Je n'ai jamais rencontré dans le même hôte que l'une des deux formes, soit le mâle, soit la

femelle, . . ." Caullery and Mesnil (1901 c, p. 392) found "Dans le cas de la *Rh. ophiocomæ*, chaque plasmode ne renferme que des individus d'un seul sexe, et souvent dans une même Ophiure, tous les plasmodes sont du même sexe," and in a foot-note add : "Dans l'anse Saint-Martin, un tiers environ des Ophiures parasitées renfermait uniquement des femelles, un tiers uniquement des mâles, un tiers à la fois des mâles et des femelles." On the other hand Koehler (1886, p. 609) working at Cette on the same species very frequently found males and females in the same Amphiura, the latter always being less numerous than the males. He rarely found one sex only; in some fifty infected Ophiuroids only two contained males alone. He not only found males and females in the same host, but in the same plasmodium. Working in the same months of the year as Julin, he says (1886, p. 610) that the difference in their results can hardly be due to season, but that "Le genre de vie de ces remarquables parasites n'est donc pas le même à Cette qu'à Vimereux." In 1901 Caullery and Mesnil (p. 392) record that in an exceptional case they found adult males and females, together with developmental stages of both sexes, in the same plasmodium of *R. ophiocomæ*, thus confirming Koehler's observation of 1886.

In *R. ophiocomæ*, where the host is parasitised generally by Orthonectids of a single sex (with the exception of Amphiura at Cette), Caullery and Lavallée (1912, p. 163, foot-note) believe that the infection has mostly arisen from a single larva, and that the rare instances where males and females are present in the same host, have arisen from multiple infection by larvæ of different sexes. They think that one larva may possibly give rise to several amœboid germs, which spread the infection in the host (1912, p. 153).

When mature the males and females leave the host. Those from the gonad of Heteranomia would seem to pass out by way of the renal ducts, for in sections free forms have been recognised in them. The renal ducts opening into the exhalent chamber, the parasite will pass out safely in the exhalent current of the host. The way of escape of those parasites present in the blood-vessels and spaces has not been observed.

The males and females apparently meet outside the host and fertilisation is effected. The mode of fertilisation was not observed in *R. granosa*. It has, however, been studied in *R. ophiocomæ* by Caullery and Lavallée (1908 b, pp. 428–430). They found that on mixing mature males and females artificially taken from the host, "Au bout de 10 à 15 minutes, on observe *très fréquemment* que des mâles sont remorqués, aux flancs des femelles, dans la moitié postérieure de celles-ci, comme s'ils s'étaient accidentellement pris dans le revêtement ciliaire et n'avaient pu s'en dégager. Une femelle remorque parfois deux mâles ; nous en avons même observé, une fois, trois.

Ce phénomène, extrêmement commun dans les premiers temps du mélange, ne se retrouve plus ensuite. Nous avons pu nous convaincre que ces rencontres des mâles et des femelles étaient les circonstances mêmes de la fécondation. Et cependant, la façon dont nagent les deux catégories d'individus n'indique nullement qu'ils se recherchent. On voit les mâles passer très près des femelles sans a'y fixer. Il semble que ce soit purement le hasard qui produise les couples observés. Le contact des deux sexes n'est d'ailleurs jamais très long. Au bout de quelques minutes, les mâles se sont dégagés, les femelles sont de nouveau solitaires. Ce contact n'est jamais non plus intime. Le mâle paraît simplement retenu par sa ciliation à celle de la femelle.

. . . nous avons constaté, d'une façon indiscutable, que les spermatozoïdes sont émis, à ce moment, au dehors. . . .

Caullery et Mesnil (1901, p. 394, pl. x, fig. 2, og.) ont signalé, sur la surface de la femelle, un pore, appelé par eux *pore génital ;* . . . Nous avons lieu de croire que c'est par là que les spermatozoïdes pénètrent."

The embryos develop while in the body of the parent, being liberated as ciliated larvæ. To Caullery and his collaborators is due the discovery that in the Orthonectida the ciliated larvæ carry infection to fresh hosts ; Caullery and Lavallée (1910, 1912) have caused experimental infection of *Amphiura squamata* by *R. ophiocomæ.*

They (C. and L., 1912, p. 140) have discovered that in the life-history of the Orthonectida two generations alternate regularly :—

(1) a sexual generation, constituted in most species of males and females (some species, e.g. *R. pelseneeri*, are hermaphrodite) formed asexually from germ cells produced in the parasitic plasmodium.
(2) a generation produced from the fertilised ova of the preceding generation and carrying infection in the larval state to new hosts, where these larvæ are transformed into plasmodia, which give birth to the sexual generation.

It is puzzling to imagine how minute ciliated larvæ can effect safe settlement in a Lamellibranch. In the Anomiidæ the action of the lateral cilia on the gills is particularly furious, and the inhalent current rapid. One would not expect larvæ of not more than 19μ in length to be sufficiently strong swimmers to resist such a current, though it is possible that their cilia may interlock with those on the gills. If carried to the dorsal groove between the two demibranchs of each side they would in all probability eventually reach the mouth. It is possible, however, that after being thrown against the gills, they may be carried to the free edges of these, and then posteriorly in the rejection current, and dropped on the mantle margin in the posterior region. It may be noted that in one of the two Heteranomia sectioned, numerous young plasmodia were found in the

mantle margin in this region, but the actual path of infection remains obscure.

If a number of Heteranomia from an infected batch be placed in a finger-bowl, numerous specimens of *R. granosa* may be obtained after a time. These will live quite happily in sea-water, whereas those obtained by opening the hosts, being not yet fully mature and ready for their free life, very quickly die. Even the cilia of immature forms frequently break down into droplets. It is remarkable that males, sufficiently mature for the sperm to be active, yet, when artificially liberated from the host die after a very few minutes in sea-water. In well-formed males obtained in this way sperm is frequently seen issuing from about the middle of the body (see also Julin, 1882, pp. 13–14), but this is almost certainly abnormal and not the true method of emission.

If a jet of air be passed through the bowl, the Heteranomia will live for weeks, and a supply of Rhopalura be available. A number of Heteranomia have been kept in this way for some fourteen weeks, though towards the end of that time specimens of Rhopalura were difficult to find, and females with segmented ova rare.

R. ophiocomæ issues from *Amphiura squamata* chiefly in the late afternoon; Caullery and Lavallée (1912, p. 143) suggest that the more or less fixed hour of emergence, providing for the simultaneous emission of the males and females, brings about the meeting of the sexes. No observations were made on the time of emergence of the Orthonectids from Heteranomia.

Number and Distribution of the Hosts Infected.

The infected Heteranomia, with one exception, have been obtained from masses of *Lepralia foliacea*. The Rhopalura was first found on November 25, 1932, infecting Heteranomia taken from a mass of Lepralia turned out of the Plymouth Aquarium, but which had most probably come from off Revelstoke Point or Stoke Point. Ten out of twenty-two (45·4%) of the Lamellibranchs were found to be infected. Of these seven were infected with plasmodia containing females, and three with plasmodia containing males. In an unnoted number of Heteranomia infected with female forms, males were also present. This high percentage of infection, which has so far not been reached in material examined direct from the grounds, may possibly have been artificially induced by favourable conditions in the tanks.

On February 2, 1933, 149 Heteranomia from fragments of Lepralia dredged from off Revelstoke Point were examined. Of these twenty-four (16·1%) were found to be infected; ten with males, ten with females (in one the plasmodia contained only immature forms, which from their size

were probably female), and four with both males and females. When both sexes were present together the males were the more numerous, but as they are so much smaller than the females it does not necessarily follow that the plasmodia producing males occupied more space in the host than those producing females. The hosts varied from 3 to 10 mm. in diameter: that of 3 mm. was parasitised by male-bearing plasmodia.

The following animals, living either attached to, or sheltering in the crevices of the Lepralia obtained on February 2, were examined, but unsuccessfully, for the presence of Orthonectids: ten *Chlamys distorta*, ten *Ophiothrix fragilis*, five *Ophiocomina nigra*, and one *Antedon bifida*.

On February 6, 1933, 165 Heteranomia from fragments of Lepralia trawled from off Revelstoke and Stoke Points were examined. Of these only eleven (6·6%) were infected; four with males, five with females, and two with both males and females. In four the infection was slight. The hosts varied from about 6 to 12 mm. in diameter.

On February 13, 1933, all the Heteranomia of any size from three large pieces of Lepralia trawled from off Stoke Point were examined. Of the ninety obtained fourteen (15·5%) were infected; nine with males, two with females, and three with both males and females. Where the two sexes were present together the males were much more numerous than the females. The hosts varied from about 5 to 14 mm. in diameter.

The Heteranomia obtained on February 2, 6, and 13 were opened and carefully examined at a magnification of about 140, so that it is unlikely that even small numbers of well-developed sexual forms would have been overlooked, though tiny plasmodia most probably would have been.

Thirty-eight Heteranomia from twenty-four *Chlamys opercularis* from the "Corner" Ground off the Mewstone were examined on January 20, 1933: none were found to be infected.

An examination of seventy-three Heteranomia taken from the carapace of a single *Maia squinado* from the Mewstone Ground on March 20, 1933, showed only one to be infected, and that with plasmodia containing males alone.

It is possible that only those Heteranomia which occur in large communities, such as on masses of Lepralia, will be found to be generally infected. The branching colonies of the Polyzoan would also provide shelter from dispersing currents for the Orthonectids emerging from their hosts, thus facilitating the meeting of the males and females. Colonies of *Lepralia foliacea* were dredged and trawled chiefly off Revelstoke and Stoke Points at a depth of from 15 to 22 fathoms.

R. ophiocomæ, a species on which most work has been done, has been found to infect 2·5% to under 10% of *Amphiura squamata* (Giard, 1880, p. 227; Julin, 1882, p. 9; Caullery and Lavallée, 1908 b, p. 425), varying widely in different parts of the same locality (Caullery and Mesnil, 1901 c,

p. 391 ; Koehler, 1886, p. 609), and in different years (Metschnikoff, 1881, pp. 287, 288).

The Swimming Behaviour of *Rhopalura granosa*.

The Orthonectida were so named by Giard from their habit of swimming in a straight line. Giard states (1877, translated 1878, p. 182) : " By the name of Orthonectida I have desired to recall their progression, which is so characteristic that it would of itself suffice for their recognition among the parasites with which they might be confounded."

In *R. granosa* this habit would seem to be very generally confined to animals travelling relatively slowly, as they frequently do on being artificially liberated from the host. It was apparently on individuals of *R. ophiocomæ* and *R. linei* obtained in this way that Giard made his observations. Observations on *R. granosa* have been made on individuals which had issued naturally from the hosts ; mostly on females because of their larger size. The males swim more rapidly than the females, for although there is little difference in the length of the cilia in the two sexes, the males are less than half the size of the females.

The females, when normally active, continually take short flights upwards, often touching the bottom of the watch-glass or finger-bowl only to leave it almost immediately : the males less frequently touch the bottom. They turn in all directions, this apparently being due to bending of the body. It is only when their activity becomes much reduced that they travel largely in contact with the substratum, and then nearly always in a straight line. When swimming at speed these Orthonectids mostly, though not invariably, follow a gently spiral path. They may, on occasion, swim almost perpendicularly upwards, and on reaching the surface film (in a watch-glass of water) swim beneath it for a short distance, before diving downwards again. It is particularly when an animal is swimming perpendicularly upwards that it may be observed to follow a spiral path, for the anterior end of the animal is seen to describe tiny circles. *R. granosa* is symmetrical, with apparently no longitudinal differentiation of cilia, but any slight bending of the body out of a straight line—such as might well occur in an animal capable of muscular contraction—would, owing to the rotation of the animal on its own axis, result in a spiral path being followed.

The cilia on the body do not beat directly backwards, but obliquely, and the animal moves forwards, rotating on its own axis to the left. This is actual, and not apparent rotation due to the appearance of metachronal waves. During backwards swimming the animal rotates to the right.

Caullery and Mesnil (1901 c, p. 402) noted that the males of *R. metchnikovi* while in the plasmodia " montrent une assez grande mobilité ; ils tournent sur leur grand axe à la façon d'une toupie." It is also of interest that they

remark of the male, which is globular, measuring 40μ by 30μ, with the anterior extremity larger than the posterior, "En raison sans doute de sa forme globuleuse, il n'a pas le mouvement en ligne droite, si général dans le groupe et que nous avons constaté, en particulier, pour la femelle. Il est extrêmement mobile et il décrit des sortes de cercles ; il ressemble beaucoup à un Infusoire holotriche." It should be noted that Caullery and his collaborators—in common with previous investigators—in most of their work prior to that recorded in the 1912 paper, apparently used material obtained by opening the hosts.

As in other species of Rhopalura, there is in both sexes clear differentiation of the ciliation of the anterior cone from that of the rest of the body, in that when the animal is swimming forwards the cilia on the anterior cone appear to be directed forwards, while those on the rings posterior to it appear to be directed backwards (see Fig. 1, A). Over both regions, however, the effective beat is backwards, in spite of the difference in appearance. The appearance of the cilia on the anterior cone may be due to a restricted amplitude of beat ; when an animal is swimming slowly and the beat can be seen, they then certainly appear to beat through a small angle. That the effective beat is backwards over the anterior cone may be observed by the movement of particles caused by the action of these cilia in animals artificially liberated before maturity from their host, and in consequence have lost the rest of the cilia while in sea-water (see p. 244). It is of interest that the cilia on the anterior cone resist disintegration considerably longer than those on the rest of the body, and may frequently be seen intact and active, when the others have been shed. These cilia beating alone appear unable to move the animal. It is possible that they have a sensory function in addition to a locomotory one ; their differentiation from those on the rest of the body suggests this.

When the Orthonectids are swimming slowly forwards the appearance of the cilia is as shown in Fig. 1, A and C.

The cilia on the anterior cone, and in addition those on the second ring—though the latter during activity appear to be directed posteriorly with the cilia on the posterior rings—can be suddenly applied so closely to the surface that even at a magnification of 500 they appear as a thick, and but slightly striated cuticle (Fig. 1, B) ; during reversed swimming they were observed always to be motionless. In animals swimming forwards very slowly the cilia on the anterior cone have been observed, on occasions, to be motionless, but it is doubtful whether this occurs under normal conditions.

The cilia on the body posterior to the second ring rarely, if ever, become motionless, but the rate of beat may be much reduced temporarily so that the animal remains almost stationary. Females have been observed to remain for a time practically stationary, but with the body rotating.

This is apparently due to change of direction of beat of the cilia. They have also been seen to stand on end and rotate, being evidently attached posteriorly owing to some viscid property of the cilia in that region.

From observations it seems that the direction of beat of the cilia may be changed, for the Orthonectids are capable of swimming forwards and backwards, though the forward movement is the more usual. Frequently, however, females artificially liberated from their host may continue swimming backwards for the few minutes they live. McIntosh (1873, p. 129), one of the first observers of an Orthonectid, noticed the backward swimming of the parasite he found in *Lineus gesserensis*.

The change in direction of movement from forward to backward swimming is abrupt, the animal giving a sudden dart backwards as the cilia on the anterior cone and second ring are closed down ; during backward swimming these cilia have never been observed to beat, and would, therefore, seem to be incapable of reversing the direction of their beat.

In reversed swimming the cilia posterior to the second ring appear to be directed forwards (see Fig. 1, B)—that is in the opposite direction to that obtaining when the animals are swimming forward. Although it has been impossible to make observations on the movement of individual cilia, the change in direction of swimming would seem to be due to reversal of the effective beat of the cilia.

This power of sudden reversal of direction of movement is probably of value to the animal in rapid retreat from danger. On running into an obstacle, they have been observed frequently to swim in the reversed manner for a certain distance, then to turn round by muscular action, and continue the retreat in the same direction, but with the anterior end foremost. This reaction, however, does not invariably occur, for females at least appear to have a tendency to collect round debris, with the anterior end pushed against it, and the body cilia beating, though not at full speed. They frequently rub backwards and forwards against debris, at the same time contracting and expanding the body, and if the posterior extremity should come in contact, they have been observed to become caught—apparently by some viscid secretion or thread—and unable to free themselves, though the cilia, including those on the anterior cone, beat rapidly. The production of this viscid thread may perhaps be abnormal, due to the unnatural conditions of observation ; a female on one occasion was seen towing a male by such a thread, though at some considerable distance, and on other occasions females have been seen attached to each other posteriorly by a thread and tugging against each other, and so held stationary. It is just possible, however, that the viscid property of the cilia may play some part in the pairing of the males and females.

Males may frequently be observed continually reversing the direction of swimming, at very short intervals of time (a second or less). A

characteristic movement of the male is that of sharply striking the water with the slender posterior region of the body: it is to this that the name Rhopalura refers (see Giard, 1880, p. 231).

I wish to thank the British Association for granting me the use of their table at Plymouth, and the Director and Council of the Marine Biological Association for facilities. For the microphotograph (Fig. 4) I am indebted to Mr. D. P. Wilson.

SUMMARY.

A new species of Orthonectid, *Rhopalura granosa* from *Heteranomia squamula* L., is described. The female is fusiform, and about 190 to 230μ long, and 55 to 75μ broad. The male is also fusiform, but less than half the size of the female, being only 87 to 95μ long and 20μ broad. *R. granosa* is distinguished from all other known species of Rhopalura by the presence in the male of large refringent bodies in the anterior cone, and in the first row of cells of the second ring. The male of *R. ophiocomæ* Giard, a species closely allied to *R. granosa*, has the refringent bodies in the cells of the second ring only.

The infected Heteranomia have been obtained from *Lepralia foliacea* trawled and dredged from off Revelstoke and Stoke Points. In Heteranomia examined direct from the grounds the infection in February, 1933, varied from about 6·6% to 16%, but in a number taken from Lepralia from the Plymouth Aquarium in November, 1932, the percentage of infection was as high as 45·4%.

The parasite is found replacing the gonad of the host; it also occurs in the blood lacunæ and vessels in the mantle, and in the suspensory membranes of the gills, even extending into the dorsal ends of the filaments. In heavy infections the Orthonectid may entirely replace the gonad of the host.

Male and female containing plasmodia usually occur in separate hosts, but it is not uncommon for the two sexes to be found together. From sections it would seem that males and females may on occasion be produced in the same plasmodium.

The swimming behaviour of *R. granosa* is described.

APPENDIX.

Other Organisms Observed in *Heteranomia squamula*.

Few parasites and commensals, other than Rhopalura, were noticed in some four to five hundred Heteranomia examined. Those seen were:—

(1) Rounded masses, *ca.* 60 to 80μ in diameter, of tiny spores in the gonad of two individuals.

(2) A Coccidian in the kidney. The number of Heteranomia infected with this parasite was not noted.

(3) A Rhabdocœle from each of six individuals of the seventy-three taken from the carapace of a single Maia (see p. 245). This Rhabdocœle almost certainly was not *Graffilla gemellipara* Linton, which is common in the mantle cavity and in the gut of *Cardium edule* from the Yealm Estuary and Millbrook. Although the specimens were large they did not contain viviparous young as is characteristic of *G. gemellipara*, and were more opaque than that species: they were broadly rounded anteriorly and pointed posteriorly. In addition to these six specimens another two or three have been seen at different times.

(4) A few larval Trematodes were seen in two or three Heteranomia taken from the Maia mentioned previously.

(5) In a number of Heteranomia a ciliate, possibly a species of Boveria, was present on the mantle.

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Two Parasites of the Common Cockle *Cardium edule*; a Rhabdocoele *Paravortex cardii* Hallez and a Copepod *Paranthessius rostratus* (Canu).

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Reprinted from the Journal of the Marine Biological Association of the United Kingdom.
Vol. xix. No. 2. May, 1934. Pages 669–676.

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CONTENTS.

IN view of the serious mortality reported among *Cardium edule* in the summer of 1933 (Orton) the following account of British parasites of this species may be of interest.

PARAVORTEX CARDII HALLEZ.

Apparently healthy cockles in the Plymouth area are very generally infected with a viviparous Rhabdocœle, *Paravortex cardii* Hallez (Hallez, 1909). In a passing reference to this parasite in a recent paper (Atkins, 1933, p. 250) I incorrectly referred to it as *Graffilla gemellipara* Linton, a species known as a commensal of *Modiolus demissus* at Woods Hole, America (Linton, 1910).* While my paper was still in the press, but too late for correction, I chanced upon Hallez's paper on *Paravortex cardii*, a species of Rhabdocœle parasitic in *Cardium edule* from Le Portel, Boulogne-sur-Mer. Examination of the parasite of cockles from the Plymouth area showed it to be this species, and not *Paravortex* (=*Graffilla*) *gemellipara* (Linton).

The characteristics of *P. cardii* as given by Hallez (1909, pp. 430–1) are as follows: " Vorticide pourvu de deux ovaires, de deux glandes lécithogènes réticulées et anastomosées et de deux testicules globuleux; dépourvu

* Leigh-Sharpe (1933) in a note on the occurrence of a Turbellarian in a *Cardium edule* from Millbrook, Plymouth, also appears to have wrongly identified it as *Graffilla gemellipara*. The animal he figures has the appearance of being somewhat compressed.

de bourse séminale. Orifice génital ventral situé près du pharynx en arrière, à l'extrémité du premier quart du corps. Organe copulateur mâle musculeux, dépourvu de pièces chitineuses et portant deux lobes papillifères. Pharynx doliiforme. Bouche ventrale vers l'extrémité antérieure du corps. Corps cylindrique, à extrémité antérieure plus amincie que le reste du corps, uniformément cilié, blanc légèrement jaunâtre, transparent, dépourvu de rhabdites, très contractile, ordinairement courbé en arc et tournant sur place en décrivant un cercle. Deux yeux noirs réniformes au niveau du pharynx. Longueur maxima, 1 mm. ; largeur, 0·3 à 0·4 mm. Vivipare. Nombreuses coques molles (jusqu'à 40) renfermant chacune un à quatre embryons et disséminées dans le tissu conjonctif. Les coques vides et recroquevillées restent dans le corps de la mère. Vit dans l'estomac du *Cardium edule.*"

The reproductive organs, so far as can be seen in the living animal, are on the plan described and figured by Hallez (1909, Pl. XXVII, Fig. 20). The atrium was rarely distinguished satisfactorily. The general presence of sperm in the female atrium and oviducts and in the vesicula seminalis renders these parts of the generative apparatus clearly visible ; when empty, however, the female atrium and oviducts are distinguishable with difficulty.

Ball in 1916 (p. 455) added to Linton's description of the Rhabdocœle commensal with *Modiolus demissus*, and (p. 459) referred it to the genus Paravortex. He (pp. 459–60) sums up the likenesses and differences of the two species as follows : " Linton's species and *P. cardii* are closely similar both in structure and habits. Both have essentially the same colour and the same shape of body. Both have similar digestive, sensory and glandular organs ; both give birth to living young which develop in capsules within the mother's body ; both show the same peculiar movements when taken from their host and placed in sea-water.

" The two species differ, however, in that the American form attains twice the size of *P. cardii ;* the genital pore is situated farther posteriorly and the ovaries are longer in the latter ;* an atrial canal in *P. cardii* leads from the dorsal part of the atrium backward to the antrum femininum, while in the American species there is no distinct canal but rather the antrum femininum extends backward from the middle of the posterior atrial surface and its opening into the latter is strongly constricted by a sphincter muscle ; the openings of the shell glands in *P. cardii* are distributed along the entire ventral wall of the atrial canal and antrum femininum, while in Linton's species they all open at the anterior end of the antrum just back of the atrium ; the vitello-oviducts

* This is evidently an error for " former," for the genital opening of *P. cardii* is at the end of the first quarter of the body (Hallez, 1909, p. 431) ; that of *P. gemellipara* is at the end of the first third (Ball, 1916, p. 455).

of *P. cardii* are the longer. Linton's species lives as a commensal in the mantle cavity of the ribbed mussel, *Modiolus demissus; P. cardii* is parasitic in the stomach of *Cardium edule.*

"Linton's species resembles *Paravortex scrobicularia* rather than *P. cardii* in the form of the ovaries, i.e., they are elongated in the first two and shorter in *P. cardii.*"

Linton (1910) the discoverer of *P. gemellipara* stated that it was a commensal, but Patterson (1912, pp. 174–5) concluded that it lived chiefly in the kidney. Ball (1916, pp. 462–3), however, failed to find any evidence that it was other than a commensal.

Occasionally specimens of *P. cardii* from Cardium from the Plymouth area are somewhat larger than the maximum length given by Hallez, reaching at least 1·2 mm., but measurements are difficult to make owing to the animals being very contractile, and no really satisfactory narcotic being discovered. Cocain—used by Hallez—was not obtainable; stovain and chloretone were not successful; isotonic magnesium chloride gave fairly good results, but caused shedding of the ectoderm in a short time. The maximum length of *P. gemellipara* is given as 2·0 mm. (Linton, 1910, p. 372).

The greatest number of capsules containing embryos observed by Hallez in a single individual was 40. However, a specimen, about 1·2 mm. long, from a Yealm Estuary Cardium, contained 47 full capsules (20 with embryos with eyes developed), while one from Neille Point had 50 to 60 full capsules, many with embryos with eyes developed. Capsules with more than 2 embryos have not been observed, though some 30 capsule-containing specimens have been examined.

According to Hallez (1909, pp. 438, 446) the adult parasites are always found in the stomach of their host. The embryos escape from the body of the parent and pass into the intestine of the host, where they attain their development in some three or four days (this being the time necessary for the emptying of the gut in cockles deprived of food) and pass out by the exhalent siphon. He believes that copulation takes place normally in the intestine, but perhaps exceptionally during the free-living period. Immediately after copulation there occurs migration into the stomach of another Cardium, where the parasite completes its life history.

Hallez (1909, pp. 438–443) notes that exceptionally the formation of capsules may begin while the Rhabdocœle is in the intestine of the host. While the intestines of few Cardium were examined at Plymouth, it was found that of 14 Paravortex, the largest of which was about 0·9 mm. long, taken from this position from 5 hosts, 7 contained 1 to 10 capsules.

The quantity of sperm in the female atrium and oviducts of young specimens is frequently much less than in large ones with many capsules: it would seem, therefore, that copulation occurs more than once, unless

self-fertilisation takes place as Hallez supposed possible (1909, p. 444). It is of special interest that a Paravortex from a Neille Point cockle was crowded with numerous capsules the contents of which were degenerating. It seems probable that this was due to the ova being unfertilised; the only sperm visible was a minute quantity of immobile sperm in the vesicula seminalis.

Distribution in the Plymouth Area.

Estuaries of the Hamoaze. Infected cockles have been obtained from several localities.

(*a*) Millbrook. Of those procured on October 12th, 1933, the stomachs of the ten examined were all infected with Paravortex; the intestines were not examined. Single individuals were found respectively with: 27 parasites, all small and none carrying embryos; 23 (7 with capsules); 20 (6 with capsules); 14 (12 with capsules); 10 (4 with capsules); 4 (one being large, with many capsules, and 3 tiny); while four individuals contained two each (all with capsules). A peculiarity of this batch was the number of small individuals.

(*b*) St. John's, St. John's Lake. Three small cockles, 11·0 to 18·0 mm. long, gathered on July 27th, 1933, proved to be infected. From one of these thirteen Paravortex were taken, four having 1 to 14 full capsules. Six of them, including one with 4 capsules, were taken from the intestine. The second Cardium yielded nine parasites, 4 carrying 1 to 4 full capsules. Two of them, each with a single capsule, were taken from the intestine. From the third Cardium eight Paravortex were taken, only one having capsules (8); a tiny one came from the intestine.

(*c*) Saint German's on the Lynher River. Twelve out of fourteen cockles (85·7%) obtained on August 25th, 1933, proved to be infected. The stomachs were examined but not the intestines. Five cockles had one Paravortex each—one being also infected with the sporocysts and cercariæ (Bucephalus) of Gasterostomum;—one had 3; one had 4; one had 5; two had 7; and one had 11.

(*d*) Neille Point, near the junction of the Tamar and Tavy. Four out of ten Cardium (40%) examined on August 3rd, 1933, proved to be infected, one large Paravortex being taken from the stomach of each (the intestines were not examined). The number of full capsules present in these individuals was 22, 26, 50 to 60; in one they were too numerous to count.

(*e*) Stonehouse Pool. Twelve out of thirteen cockles (ca. 92%), examined on August 8th, 1933, were infected. The stomachs only were examined: five individuals had 1 parasite each; one had 3; one had 4; two had 5; one had 6; one had 8; and one had 14.

Yealm Estuary. Cardium from this locality are very generally infected;

of five small individuals especially examined in July, 1933, four were parasitised. Details of the infection are as follows : From one cockle, 23 Paravortex were obtained, 3 only being without capsules. The number of full capsules varied from 3 to about 30 in different individuals, 13 having 10 or more. Escaped young were found in the watch glass with these adults. Seven specimens were a millimetre and more in length. From a second Cardium 17 *P. cardii* were taken, 11 having 2 to 16 full capsules. Five individuals were a millimetre and more in length. From a third Cardium 7 parasites were taken, 3 with 1 to 10 full capsules. Two were a millimetre and more long. From a fourth cockle 3 parasites were taken. Of two, about 1·2 mm. long, one had 47 full capsules, the embryos of 20 having eyes already formed, and the other 31 full capsules, 17 containing embryos with eyes formed. The third specimen, about 0·9 mm. long, had 2 capsules with young embryos.

Salcombe Estuary. Parasitised cockles have been obtained from Kingsbridge. Four out of seventeen (ca. 23%) examined from this locality on August 11th, 1933, were infected. The number of *P. cardii* in a host was small, 3 having 2 each and the fourth a single specimen.

From Millbay, near the mouth of the Estuary, 6 cockles, gathered from the surface on September 5, 1933, had no Paravortex. One at least had the interlamellar spaces of the gills swarming with an Ancistrum type of Ciliate.

From these few examples it would seem that infection varies considerably in different localities, being heaviest in cockles from Millbrook, St. John's Lake, St. German's, Stonehouse Pool and the Yealm Estuary. From these five localities 31 out of 41 hosts had more than one parasite, and one had as many as 27. The infection is heavier than Hallez found at Le Portel, for he writes (1909, p. 437) : " Il est à noter que le nombre des Cardium qui n'hébergent qu'un seul individu est très élevé (43 à 52%) et qu'il est relativement rare de trouver plus de quatre parasites dans le même estomac."

P. cardii would seem to have a wide distribution in the British Isles. Nicoll (1906, p. 154 and Pl. IV, Fig. 7) described as a Trematode sporocyst in *C. edule* at St. Andrews, Scotland, a form which is almost certainly this Rhabdocœle. Dr. M. V. Lebour, to whom I am indebted for the reference both to Linton's and to Nicoll's paper, has pointed out to me that she (1904, pp. 83–84) also described as a Trematode sporocyst in *C. edule* from Budle Bay, Northumberland, a form which is no doubt identical with the Rhabdocœle from South Devon and Cornwall. Lebour (1904, pp. 83, 84) found the parasite in about 75% of the cockles examined. Nicoll (1906, p. 154) states : " Rarely were there more than half a dozen in one cockle, and only in about 20% were they entirely absent." Hallez (1909, pp. 435, 436) found at Le Portel, Boulogne-sur-Mer that 141 out

of 300 (47%) *C. edule* examined during August, September, October and November were infected, the number of parasites in a host varying from one to twenty; 43% contained one only. In December about 43% were infected; in February about 46%. He therefore concludes that the winter has no influence on the percentage, which remains very much the same as during the summer and autumn. Analogous results were obtained in the spring. At Dannes-Camiers he found the percentage infected to reach 67%.

Paranthessius rostratus (Canu).

Paranthessius (=*Herrmannella*) *rostratus* (see Canu, 1892, pp. 235–7, Pl. XXIV, Figs 1–13; Monod and Dollfus, 1932, pp. 143–6) has been obtained from the mantle cavity of Cardium from several localities in the Plymouth area. From Neille Point, near the junction of the Tamar and Tavy, the mantle chambers of ten cockles examined on August 3rd, 1933, were aswarm with the copepod. Thirteen cockles from Stonehouse Pool on August 8th, were all infected with Paranthessius, but not heavily. Fourteen Cardium obtained from near Saint German's on the Lynher River, on August 25th, all proved to be heavily infected: females carrying egg-sacs were numerous. Ten cockles examined of those obtained from Millbrook on October 12th were all infected: some of the adults carried egg-sacs.

From Kingsbridge on the Salcombe Estuary seventeen cockles, obtained on August 11th, were all rather heavily infected: many of the copepods carried egg-sacs. On September 5th six cockles from Millbay, near the mouth of the estuary, all proved to be infected: some of the copepods carried egg-sacs.

This copepod was first recorded in the British Isles from *C. edule* from Morecambe Bay, Lancashire, by Fraser (1932). Leigh-Sharpe (1933a, pp. 113–4) has since recorded it from the testis of Cardium from Millbrook, near Plymouth.

Paranthessius is a semi-parasite only (see Canu, 1892) and has been taken in tow-nettings from gulleys on the cockle beds in Morecambe Bay by Fraser (1932).

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On the Ciliary Mechanisms and Interrelationships of Lamellibranchs. Part I. Some New Observations on Sorting Mechanisms in Certain Lamellibranchs

Quarterly Journal of Microscopical Science
Vol. 79, Part II, December, 1936

Printed in Great Britain

On the Ciliary Mechanisms and Interrelationships of Lamellibranchs.

PART I: New Observations on Sorting Mechanisms.

By

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Marine Biological Laboratory, Plymouth.

With Plates 10 and 11, and 43 Text-figures.

CONTENTS.

PREFACE.

THE work recorded in these studies was carried out at the Marine Biological Association's Plymouth Laboratory, to the Director and Council of which I desire to express my gratitude, and was made possible by the kindness of the British Association, London University, and the late Mr. G. Evans in granting me the use of their tables at the Laboratory for various periods.

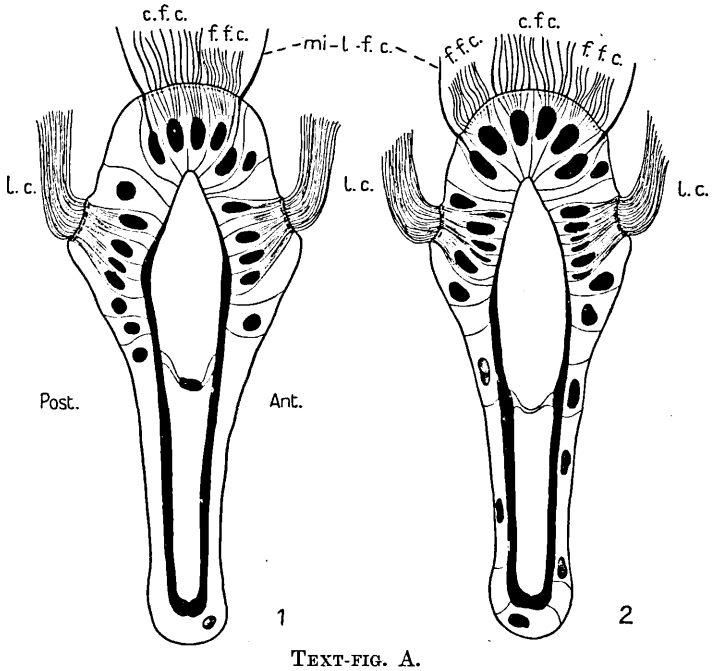
Gifts of material are acknowledged in the separate parts. Mr. R. Winckworth very courteously checked the identification of the many British Lamellibranchs used in the work. My thanks are due to Dr. E. J. Allen, C.B.E., F.R.S., for most kindly reading the typescripts of all these studies. To Professor J. H. Orton I am much indebted for his continued interest in the problems of this research and for helpful criticism of the papers.

I acknowledge with sincere thanks a grant of £20 from the Research and Publication Fund of Bedford College, University of London, toward the cost of publication of Part I.

In the series of studies on Lamellibranchs I have used as much as possible the well-known names, or given the better known synonyms in brackets.

Introduction and Methods.

The interest of the ciliary mechanisms of the various Lamellibranchs described in this paper lies chiefly in the discovery of a new type of sorting mechanism on the gills themselves, that is of neighbouring tracts of frontal cilia (see Text-fig. A) beating in opposite directions on the same gill filament or leaflet, and of which the tract of coarse cilia (*c.f.c.*) in most instances is motionless, or only feebly active, unless stimulated. These tracts function in the sorting of food, but perhaps their chief value will be found to be in removing from the gills the mud or sand with which waters are periodically laden in practically all situations. From observations, it appears that when the coarse cilia (Text-fig. A, *c.f.c.*) of the rejection tracts are fully active, that is when much material is dropped on the gill, they sweep all in the direction in which they are beating—especially if the particles have become connected by mucus—overcoming by their greater strength the action of the fine cilia (Text-fig. A, *f.f.c.*) of the food tracts bearing particles intended for consumption. This does not apply in the same degree to forms such as Nuculana, where the tracts of oppositely beating cilia are at different levels. The two kinds of cilia occur either in two or in three tracts: when in two tracts, the coarse cilia are invariably on the posterior side of the frontal surface; when in



TEXT-FIG. A.

Diagrams of transverse sections of gill filaments to show the arrangement of the tracts of coarse (*c.f.c.*) and fine (*f.f.c.*) frontal cilia. Mucous glands are omitted for the sake of clearness.

1. Shows the arrangement in two tracts, one of fine, short cilia, beating dorsally, on the anterior side of the frontal surface, and one of coarse, long cilia, beating ventrally, on the posterior side. This arrangement of the frontal tracts is found on all the filaments of Heteranomia squamula, Monia squama, and Monia patelliformis, on the ordinary and apical filaments of Pteria hirundo, Ensis siliqua, and Ensis arcuatus, and on the filaments of both lamellae of the inner and the ascending lamella of the outer demibranchs of Cultellus pellucidus.
2. Shows the arrangement in three tracts, a median one of coarse, long cilia, beating ventrally, with on each side a tract of fine, short cilia, beating dorsally. This arrangement occurs in Glycymeris glycymeris, Arca tetragona, and Arca lactea, and on the ordinary and apical filaments of Solen marginatus. In Solen and Ensis large latero-frontal cilia occur, and in this their filaments differ from those depicted in the diagrams. *Ant.*, anterior; *c.f.c.*, coarse, and *f.f.c.*, fine frontal cilia; *l.c.*, lateral cilia; *mi.-l.-f.c.*, fine or micro-latero-frontal cilia; *Post.*, posterior.

three tracts, they are always in the middle, that is on the frontal edge (see Text-fig. A). In these positions they are favourably exposed to the inhalent current which enters chiefly from the posterior end of the shell.

Correlated with the new type of sorting mechanism are in some instances posteriorly beating tracts of cilia on the free edges of the demibranchs, whereas in most Lamellibranchs the tracts beat anteriorly.

Frontal currents in opposite directions on the same gill filament or leaflet have not been previously described, though a difference in the direction of the frontal currents in the grooves and on the crests of the plicate and heterorhabdic gills of Pecten (Kellogg, 1910, pp. 64–6; 1915, pp. 671–2), Ostrea (Yonge, 1926, pp. 324–5), and Lima (Studnitz, 1931, pp. 230–6) is known, and is described also in Pteria, Solen, and Ensis in this paper. Adjoining tracts of frontal cilia beating in opposite directions have been found in a Protobranch, Nuculana minuta, in the flat and homorhabdic Filibranchs, Glycymeris, Arca, Heteranomia, Monia, in the plicate and heterorhabdic Pseudolamellibranchs, Pteria, Pecten, Chlamys, Ostrea, and Eulamellibranchs, Solen, Ensis, and in a flat and homorhabdic Eulamellibranch, Cultellus pellucidus (see also Part II, in the press). It would seem from the results of this work that cilia naturally active only when stimulated are less uncommon than has been thought (Gray, 1928). Recently Lucas (1933) has stated that the cilia of the pharynx of the frog are inactive unless mechanically stimulated.

Adjacent antagonistic ciliary currents are known in a certain number of invertebrates, for instance on the palps of Lamellibranchs (Allen, 1914, 1921; Kellogg, 1915; Nelson, 1923; Yonge, 1926), in the liver diverticula of Helix (Merton, see Gray, 1928) and in the stomodaeum and internal cavities of Ctenophores (Gemmill, 1918), and have been also recorded in two vertebrates (Parker, 1928, 1928*a*, 1930). Where two contiguous tracts of cilia beat in opposite directions the value of having one of the tracts active only on stimulation is apparent; it is possible that this state of affairs will be found elsewhere

than on the gills of Lamellibranchs. In the two vertebrates in which parallel but opposing ciliary currents have been detected the condition is of especial interest. Parker found that in the oviducts of the eastern painted tortoise (Chrysemys picta) and the common pigeon (Columbia livia) there are two sets of cilia beating in opposite directions, the ab-ovarian and the pro-ovarian. In the tortoise the pro-ovarian tract extends from the infundibulum to the intermediate part of the oviduct, but not into the uterus; it is 2 to 3 mm. wide. In the pigeon this tract extends from the infundibulum to the uterus; it is about a fourth the width of the total duct. It would be of interest to know if the tract of ab-ovarian cilia in the oviducts of these animals is in continual activity, or only becomes active on stimulation. The efficiency of the narrow tract of pro-ovarian cilia would presumably be much increased if the ab-ovarian cilia were motionless during the upward passage of sperm.

Gray (1928) has pointed out the necessity of being certain that instances of supposed ciliary reversal are not due to the presence of oppositely beating tracts of cilia; care is all the more needed now that it is known that one of two such contiguous tracts may be active only on mechanical stimulation.

In the observations on the different feeding mechanisms described in the following papers, carmine, powdered animal charcoal, and carborundum powder were used for the detection of currents. The finest carborundum powder (3F) was generally preferred to the first two, owing to the greater security, due to its higher specific gravity, that it was actually in contact with the cilia and moved by them, and not by some superficial water current. Observations on the gills while still attached to the animal, and on the mantle and visceral mass, were made with a Spencer binocular dissecting microscope, magnifying 16 diameters, with daylight as the usual source of illumination; on pieces of demibranch and fragments of lamella with a monocular microscope.

All original figures, except Text-figs. A, 11, 12, 15–20, 29, 33, 40, 41, and Pl. 11, were drawn with the aid of a camera lucida.

SECTION A

The Ciliary Sorting Mechanism of the Gills of Nuculana minuta (Müller) and the Gill Currents of other Protobranchia.

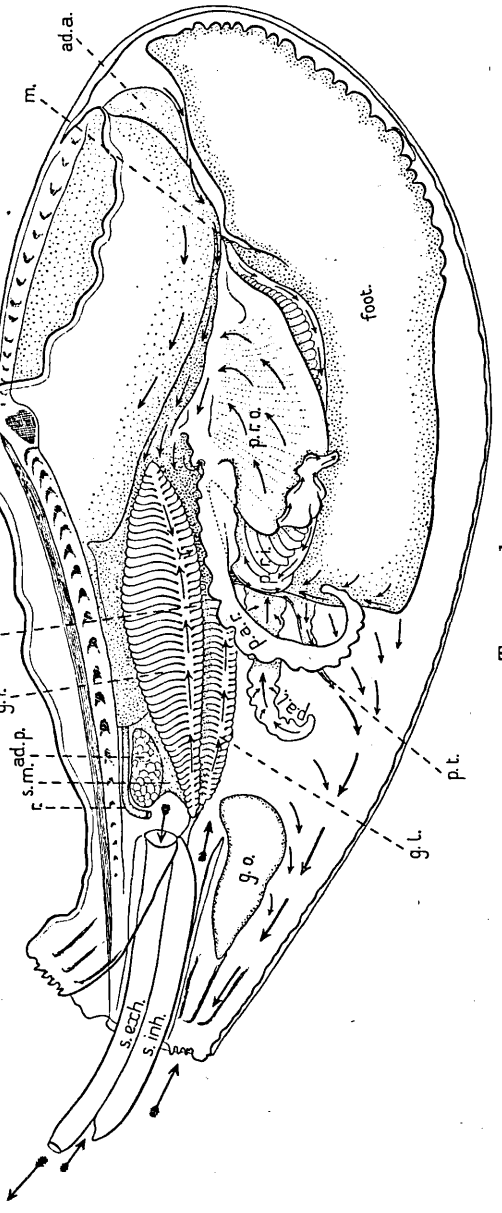
With Text-figures 1–10.

CONTENTS.

INTRODUCTION.

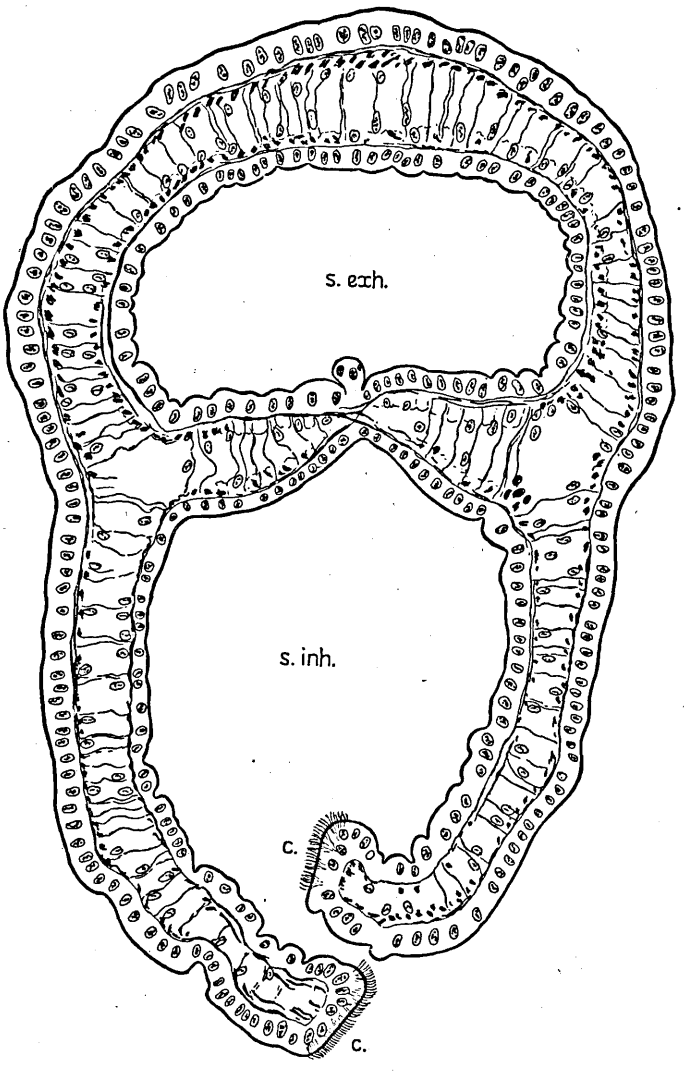
The ciliation of the gill leaflets of Yoldia as described by Kellogg (1892, pp. 414–18) is so peculiar in comparison with that of most Lamellibranchia, that it was considered desirable to examine the closely allied genus Nuculana (= Leda). Living specimens of Nuculana minuta were obtained from the Millport Marine Station. The ciliary currents are difficult to observe owing to the small size of the animals (9 to 12 mm. long): neither Drew (1899) nor Kellogg (1892, 1915) mentioned the size of Yoldia limatula; Morse (1919, p. 149), however, gave the length of the individual he figured as 57 mm.

In Nuculana minuta (Text-fig. 1) the mantle is entirely open ventrally, but posteriorly is produced into two narrow siphons, fused together and capable of extending some little distance (at least 7 mm.) from the shell. The inhalent, which is slightly the wider and shorter, is completely split ventrally (Text-fig. 2) from the base to the bilobed extremity. In life the two edges are generally neatly applied to one another, the junction appearing as a whiter line, but in an animal with the siphons well extended the two halves of the inhalent have been observed very occasionally temporarily to be drawn apart in places. Both in living material and in sections the two ventral edges have been seen to bear short cilia, though the rest of the



TEXT-FIG. 1.

Nuculana minuta (about 12 mm. long) with the right valve removed and the right mantle lobe folded back. The animal has been tilted somewhat dorsally so that both gills are visible. The palp appendages are shown much contracted; the distance between the gills and the dorsal region of the palps is probably due to contraction. The siphons are only partly extended. Arrows indicate the direction of the currents; plain arrows ciliary, and feathered arrows water currents. *ad.a.*, anterior, and *ad.p.*, posterior adductor muscle; *g.l.*, left gill; *g.o.*, glandular organ; *g.r.'*, inner, and *g.r.''*, outer demibranch of right gill; *m.*, position of mouth; *p.a.l.*, left, and *p.a.r.*, right palp appendage; *p.t.*, posterior tip of left outer palp; *p.r.i.*, right inner, and *p.r.o.*, right outer palp; *r.*, rectum; *s.exh.*, exhalent, and *s.inh.*, inhalent siphon; *s.m.*, suspensory membrane of gill.



TEXT-FIG. 2.

Nuculana minuta. Transverse section through the exhalent (*s.exh.*) and incomplete inhalent (*s.inh.*) siphon, showing the position of the cilia (*c.*) which most probably effect a junction between the two edges of the latter siphon. × 360.

surface of the siphons, both internally and externally, is unciliated, and it seems probable that, although in sections the edges were not applied, in life a ciliary junction exists. A weak ciliary junction, such as is frequently dissolved by contraction of the parts on fixation, would explain the differing accounts of the structure of the inhalent siphon in Nuculana; Pelseneer (1891, pp. 168–9; 1911, p. 5) holding that it is closed ventrally, and others (Deshayes, tom. ii, p. 264; Stempell, 1898, p. 350) that it is open. Drew (1899, p. 3) found in Yoldia limatula that 'even in the adult the line of fusion along the ventral side of the inhalent siphon remains distinct, and offers little resistance to splitting'.

The siphons occupy only about the dorsal half of the gaping narrow truncated end of the shell. Ventral to them is the aperture by which the palp appendages usually emerge; though these are sometimes extruded between the valves in the ventral region. The appendages have been seen extended to a length at least equal to that of the shell, the part visible being very narrow. Morse (1919, p. 148) described them as 'thread-like appendages' in Leda (= Nuculana) tenuisulcata (Couthouy), the specimen he figured being 25 mm. long; and remarked 'whether these are thread-like palpi, which seems impossible, or represent a double syphonal tentacle is yet to be determined'.

A siphonal tentacle was not observed in living Nuculana minuta, nor was it identified in sections.

Nuculana would seem to obtain its food (as do Yoldia, Drew, 1899, and Nucula, Drew, 1901; Hirasaka, 1927) chiefly by means of long, extrusible palp appendages, the tips of which wander over the mud; material is conveyed along the highly ciliated grooves of the appendages to the palps and hence to the mouth. The gills in Nuculana minuta are small and that part of them occupied by current-producing and food-conveying cilia very small. Thus although complicated ciliary currents resulting in food-collection have been found on them, these organs play a subsidiary part in feeding. There is no direct connexion between the gills and the palps, and material collected by the gills is removed by the palp appendages and

conveyed to the mouth. Apparently correlated with the scarcity of lateral (current-producing) cilia are pumping movements of the gills, which rhythmically augment the inhalent and exhalent currents.

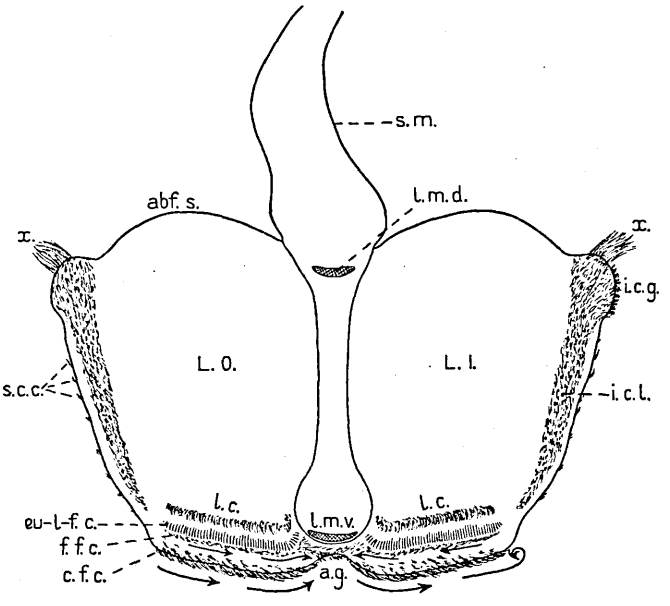
Structure of the Gills.

The small, yellow-tinted gills of Nuculana minuta (Text-fig. 1) are suspended by membranes, and appear to be attached posteriorly, like those of Yoldia (Drew, 1899, p. 12), to the wall that separates the two siphons. It is, however, difficult to be entirely certain of the condition, owing to the small size of the animals and the strong contraction of the siphons on removal of a valve, or on fixation. Pelseneer (1891, pp. 169–70) stated that they are free in Nuculana pella.

About forty to forty-five pairs of leaflets were counted in the gill of a specimen 11·5 mm. long. The shape of individual leaflets no doubt varies, as does the size, in different regions; a pair from about the middle of the gill is shown in Text-fig. 3; the two series, however, are by no means always directly opposite one another. It will be seen from the figure that the frontal surface of the leaflets on opposite sides of the axis are almost in a straight line and form one discontinuous ridge, so that as expressed by Pelseneer (1891, p. 171) and Ridewood (1903, p. 190) 'the leaflets do not hang down'. The part of each leaflet bearing current-producing cilia is very short; shorter than in Nucula and much shorter than in Solenomya (cf. Text-fig. 3 with Text-figs. 9 and 10).

The edges of the gill bend abruptly dorsalward where the current-producing cilia end; the margins of the leaflets are here provided with interlocking cilia (Text-fig. 3, *i.c.l.*) for union with the leaflet in front and behind. The junction is extensive, extending from near the ventral to the dorsal face of the leaflets, which are thus held strongly together. In Yoldia, according to Kellogg (1892, p. 415), the ciliary junctions extend about two-thirds of this distance. In the Nuculanidae, therefore, they are much more extensive than in Nucula (see Text-fig. 9), the leaflets of which easily separate except where they are attached to the axis, and in Solenomya (see Text-fig. 10).

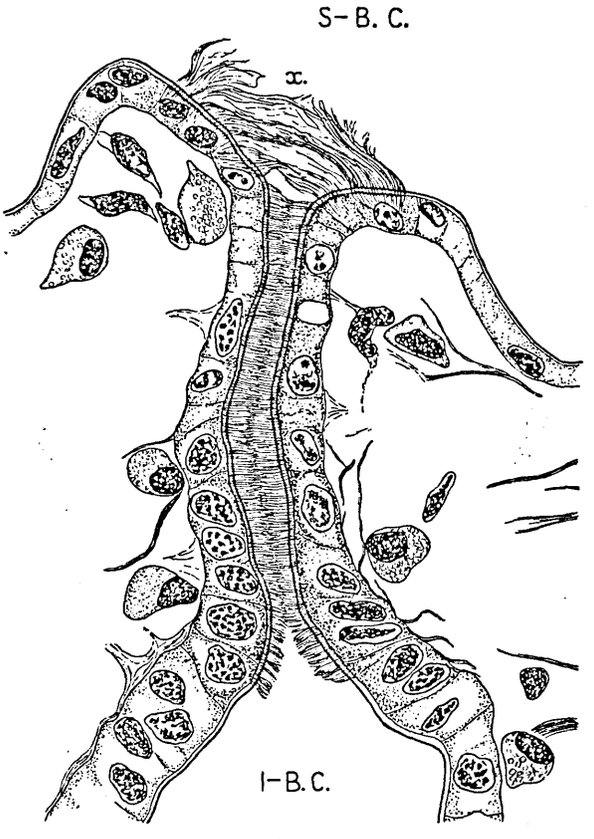
In Nuculana minuta there appears to be no junction between the outer demibranchs and the mantle, sections failing to reveal interlocking cilia, but between the inner demibranchs



TEXT-FIG. 3.

Nuculana minuta. Sketch of a pair of living leaflets from about the middle of a gill to show the ciliation, and the direction of the frontal currents. *abf.s.*, abfrontal surface; *a.g.*, axial food groove; *c.f.c.*, coarse, and *f.f.c.*, fine frontal cilia; *eu.-l.-f.c.*, large latero-frontal cilia; *i.c.g.*, interlocking cilia for union with opposite gill; *i.c.l.*, interlocking cilia for union with next leaflet in the series; *l.c.*, lateral cilia; *l.m.d.*, dorsal, and *l.m.v.*, ventral longitudinal muscle of the gill axis; *L.I.*, inner, and *L.O.*, outer leaflet; *s.c.c.*, scattered ciliation; *s.m.*, suspensory membrane; *x.*, long, fine cilia across the dorsal edge of leaflets. × 70.

of opposite sides there is a strong ciliary junction (see Text-fig. 4) uniting the two gills in a septum across the branchial chamber: anteriorly they are free from the foot. Thus while the two gills are strongly united, they are free both from the mantle and the foot, a state of affairs necessitated by the movements which they perform (see p. 207).



TEXT-FIG. 4.

Nuculana minuta. Section through the ciliary junction between the inner leaflets of the right and left gills. Dorsal of the junction are the long, fine cilia (*x.*) mentioned in the text. The ciliary rootlets of the interlocking cilia were not obvious. *I.-B.C.*, infra-branchial chamber; *S.-B.C.*, supra-branchial chamber. Bouin-Duboscq fixation: Heidenhain's iron-haematoxylin. × 980.

Across the dorsal edge of each leaflet, both outer and inner, of Nuculana minuta is a row of long fine cilia (Text-figs. 3, 4, *x.*): they are about 55μ long, differing much in length from the smaller interlocking cilia (*i.c.l.*, *i.c.g.*), about 5μ long, which effect

the junction between successive pairs of leaflets and between the inner leaflets of the two gills (see Text-figs. 3 and 4). The cilia forming the latter junction occur just ventral to the long cilia, which are thus in the supra-branchial chamber. The function of the long cilia is obscure. Orton (1912, p. 468; see also in this paper Text-fig. 9, *l.c.d.*, *O.c.d.*) referred to similar cilia in Nucula as interlocking cilia, by means of which the division into supra- and infra-branchial chambers was effected. Transverse sections of Nucula radiata Hanley have failed to reveal interlocking of these cilia, or in fact any junction between the gills and the mantle, or between those of opposite sides. Contraction of the branchial muscles on fixation, however, quite probably would cause dissolution of a ciliary junction between the gills, if this were weak; no interlocking cilia were present on the mantle with which those of the outer leaflets could effect a junction. The movements of these cilia are peculiar and not unlike those of interlocking cilia. In a gill of Nucula, the day following excision, trembling of these cilia occurred, with at intervals a sudden bunching together of those in each group. This latter movement coincided with stoppage of the lateral cilia, and was occasionally accompanied by a closing together of the leaflets. On the second day there was little intermission of the lateral cilia or bunching together of the groups of long cilia. In Nuculana trembling movements only of the long cilia were observed. In both Nucula and Nuculana the action of these cilia is not such as to produce a current. It is probable that the long cilia merely rub against the mantle forming a temporary junction, as occurs in a number of Lamellibranchs in which considerable movement of the gills occurs.

Kellogg (1915, pp. 693–4) has described in Yoldia modification of the third and fourth pairs of leaflets from the anterior end of the gill; these plates being without ciliated junctions may become widely separated, and so allow the passage of material directly from the ventral axial groove into the supra-branchial chamber. No such modification of the leaflets appears to exist in Nuculana minuta, but a few anterior pairs are small, as is frequently found both at the anterior and posterior ends of gills, where growth of new leaflets or filaments

takes place. In Nuculana minuta, with one valve removed, particles in the general water current can be observed at times escaping past the latero-frontal cilia and passing between any of the leaflets into the supra-branchial chamber. This may be partly due to the conditions of observation, but it possibly occurs in nature to some slight extent in all Lamellibranchs, indicating some inefficiency in filtering.

The gills of Nuculana are extremely muscular. As in Yoldia there are two longitudinal muscles in the gill axis, one just above the axial groove (Text-fig. 3, *l.m.v.*), and one at the junction of the axis with the suspensory membrane (Text-fig. 3, *l.m.d.*). These are responsible for anterior-posterior contraction of the gills; they appear to be composed of smooth fibres. Running roughly transversely through the suspensory membrane are strong muscle-fibres which entering the leaflets spread through them (Text-fig. 6, *m.f.*), becoming attached to the walls[1] and the chitinous supporting structure. These muscles, which are used in the rhythmical dorsal contraction of the gills, are composed of striated fibres in Nuculana minuta, and doubtless will be found to be so also in Yoldia where they have the same function. Drew (1899, 1901, Text-fig. U, p. 360) has shown these radiating fibres in a figure of a pair of leaflets of Yoldia limatula; this figure is reproduced here as Text-fig. 5.

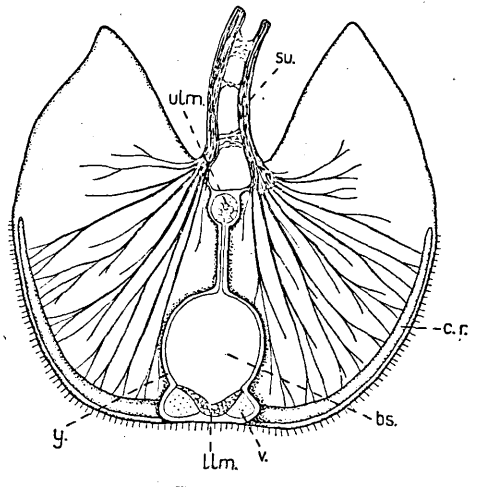
Muscle-fibres cross the very large blood-spaces of the gill leaflets (Text-fig. 6, *t.m.f.*).

Ciliation of the Gill Leaflets and Action of the Cilia.

In the Nuculanidae the lateral cilia are far from the frontal edge of the leaflets, and the frontal cilia extend well round on to the lateral faces (Text-fig. 6). This disposition of the cilia approaches the arrangement in the Gastropod Crepidula (see Orton, 1914, fig. 9, p. 299)—though in this form latero-frontal cilia are absent—and in Trigonia alone among Lamellibranchs (see Part VII in the press). Ridewood (1903, p. 200) stated that in the Arcas 'the lateral cilia are situated at

[1] Whether to the anterior walls only as in Yoldia (Kellogg, 1892) was not determined.

some distance from the frontal edge, and in Arca granosa the frontal cilia extend round so as to cover part of the anterior and posterior faces of the filaments'; but the distance of the lateral cilia from the frontal edge appears to be considerably less than in Nuculanidae and Trigoniidae. In Nuculidae and Solenomyidae the frontal cilia are more or less confined to the frontal

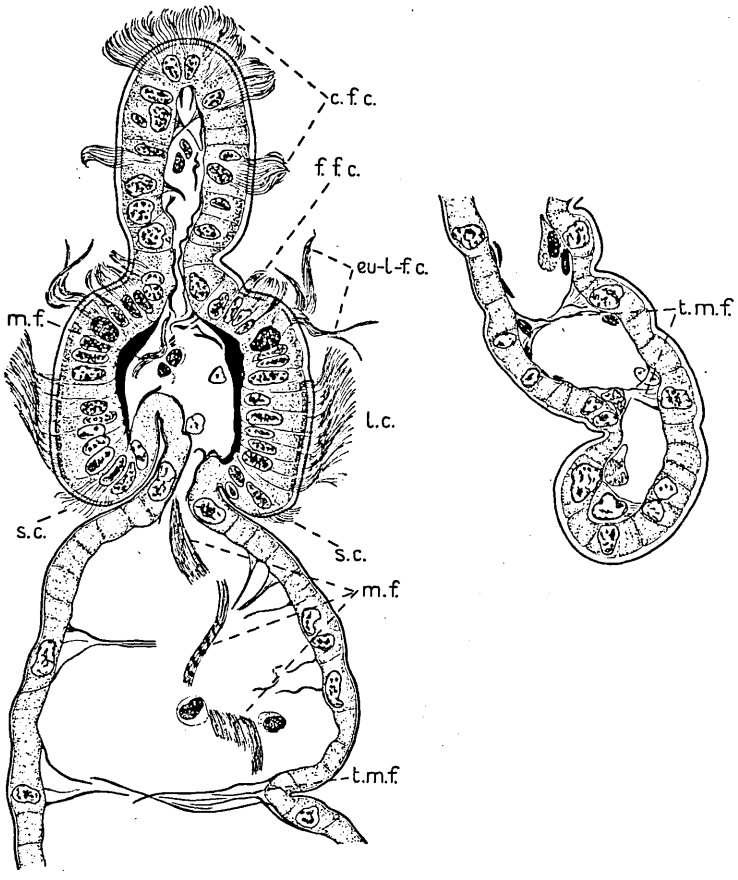


TEXT-FIG. 5.

A pair of plates from a gill of Yoldia limatula. *bs.*, blood-space; *c.r.*, chitinous rod; *l.l.m.*, lower longitudinal muscle; *su.*, suspensory membrane; *u.l.m.*, upper longitudinal muscle; *v.*, cut surface of a chitinous rod; *y.*, cut wall of the gill plate where it bends to join the plate anterior to it. (After Drew, 1901, Text-fig. U, p. 360.)

edges of the leaflets, as in the filaments of most of the higher Lamellibranchs, and the lateral cilia—except for the great width of the tracts—are in the usual position (Text-fig. 7).

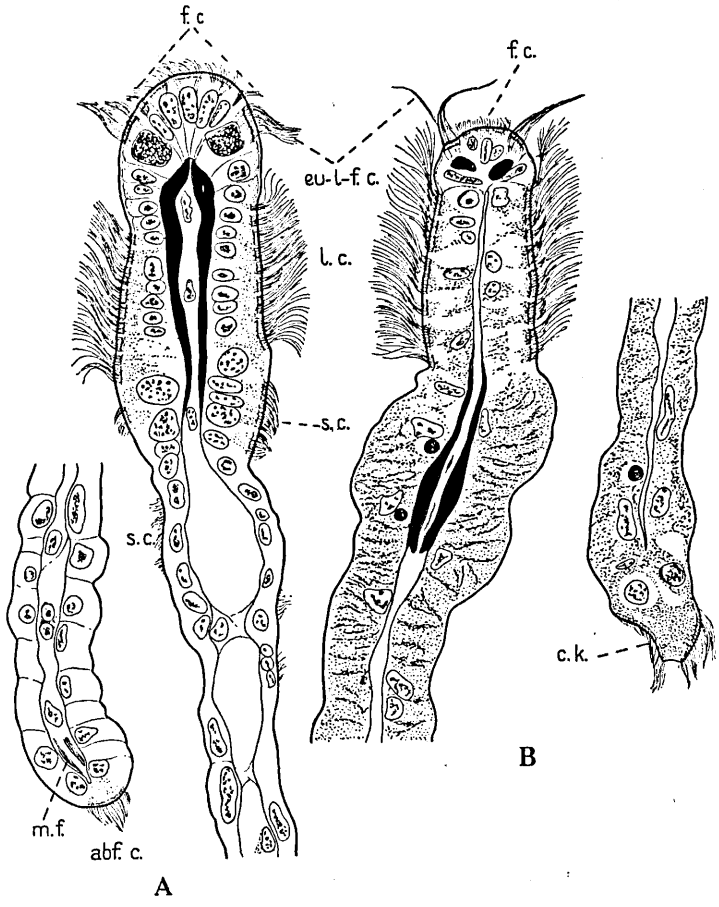
The Frontal Cilia.—These are of two kinds, coarse and long (Text-figs. 3, 6, *c.f.c.*), and fine and short (*f.f.c.*). The fine frontal cilia occur in a tract close to the latero-frontal cilia (*eu.-l.-f.c.*) on both sides of the leaflets, and appear to be in a slight depression; they beat toward the axial groove. These fine cilia, together with the latero-frontal cilia, are possibly Kellogg's (1892, p. 416, and fig. 79, Pl. xci) second lateral row of fine,



TEXT-FIG. 6.

Nuculana minuta. Transverse section of gill leaflet. The whole is not figured because of the great depth (frontal to abfrontal) of the leaflets. The involution of the walls near the lateral ciliated tracts is due to contraction of the muscles. *c.f.c.*, coarse, and *f.f.c.*, fine frontal cilia; *eu.-l.-f.c.*, large latero-frontal cilia; *l.c.*, lateral cilia; *m.f.*, radiating muscle-fibres; *s.c.*, slight ciliation dorsal to the lateral cilia; *t.m.f.*, transverse muscle-fibres. Bouin-Duboscq fixation: Heidenhain's iron haematoxylin. × 735.

short cilia, which he suggested act as strainers: Ridewood (1903, p. 192) doubted their existence.



TEXT-FIG. 7.

Transverse sections of gill leaflets. A. Nucula; B. Solenomya togata. *abf.c.*, abfrontal cilia; *c.k.*, ciliated knob or glandular organ; *f.c.*, frontal cilia; *m.f.*, muscle-fibres: other lettering as in Text-fig. 6. Bouin-Duboscq fixation: Heidenhain's iron haematoxylin. ×735.

Along the frontal surface of the leaflets and extending on to the side faces is a tract of coarse cilia (*c.f.c.*), which laterally tend to become irregular, or to occur in patches (see Text-figs.

3, 6). Those on the lateral faces beat obliquely toward the frontal edge along which particles are conveyed. In Nuculana minuta there is usually a distinct unciliated space between the fine and coarse frontal cilia. The coarse cilia of the frontal edge beat toward the axial groove on the outer leaflets, but toward the inner edge of the gill on the inner leaflets, that is they beat in the same direction on the outer and inner leaflets (see Text-fig. 3). An exception possibly occurs on about the anterior eleven inner leaflets, the coarse cilia beating toward the axial groove.

The Latero-frontal Cilia.—The latero-frontal cilia (Text-figs. 3, 6, *eu.-l.-f.c.*)—actually lateral in position—which are situated on a slight ridge, are well developed, though somewhat irregular in length, the longest being about 30μ. They are not continuous across the axial groove from one leaflet to the opposite one, but are continuous from one leaflet to the succeeding one of the same side. In this Nuculana differs from both Nucula and Solenomya, where these cilia are generally continuous across the axis from one leaflet to the opposite one, as shown by Orton (see Text-figs. 9, 10). In Nucula (Nucula radiata Hanley) an occasional leaflet, however, may have the latero-frontal cilia continuous from it to the succeeding one of the same side; this is generally found to occur on the small ones, possibly not fully developed, at the posterior extremity of the gill. It is important to notice this difference in the arrangement of the latero-frontal cilia in the three families of Protobranchs as it is correlated with the presence and absence of a longitudinal food current along the gill axis. Where the latero-frontal cilia are continuous across the axis, necessarily there can be no longitudinal current (Nucula and Solenomya); where they are not so continuous there is a longitudinal current along the axis of right and left gills (Nuculana, see Text-fig. 1).

The Lateral Cilia (Text-figs. 3, 6, *l.c.*).—The lateral ciliated tract is about six cells wide (see also Part VI, in the press). Dorsal to the definite lateral tracts there is some slight scattered ciliation (Text-fig. 6, *s.c.*) as in Nucula (Text-fig. 7 A, *s.c.*).

On the frontal faces also of the leaflets dorsal to the definite

ciliated tracts there are a few scattered ciliated cells, which appear to produce no definite current (Text-fig. 3, *s.c.c.*).

The Gill Currents.

Briefly the food currents on the gills of Nuculana minuta are as follows. On the frontal surfaces of the leaflets coarse cilia (Text-figs. 3, 6, *c.f.c.*) beat toward the inner edges of the gills: particles collecting here rotate, there being no longitudinal current along the gills in this position. On the sides of the leaflets close to the latero-frontal cilia, fine frontal cilia (Text-figs. 3, 6, *f.f.c.*) beat toward the axial food-groove on both inner and outer leaflets; along this food-groove the current is anterior for most of its length and material is deposited at a certain spot on the inner edge of the gill. This material, and sometimes also that which collects along the whole inner edge, as mentioned above, is removed by the palps and palp appendages and conveyed to the mouth.

The gill mechanism must now be described in detail. The tracts of fine frontal cilia—which are actually on the lateral faces of the leaflets—send particles toward the axial groove on both inner and outer leaflets (Text-fig. 3). Only fine particles seem to be carried by these cilia, such escaping past the coarse frontal cilia.

The coarse frontal cilia beat toward the axial groove on the outer leaflets but toward the inner edge of the gill on the inner ones, with the possible exception of about the eleven anterior on which they may beat toward the groove. Thus on the inner leaflets the fine and coarse cilia beat in opposite direction, while on the outer they beat in the same direction (see Text-fig. 3). Particles carried by the coarse cilia of the outer leaflets may either enter the axial groove and pass along it, or may pass across the groove on to the inner leaflets. Which course is followed perhaps depends on size, very large particles, or masses of particles, stretching across the axial groove and coming under the influence of the coarse cilia of the inner leaflets; or very possibly the groove may be deepened by muscular contraction, the inner and outer leaflets, which project as slight lobes along it, being brought closer together so that particles

can pass directly from the frontal edge of the outer to that of the inner across the groove. If the gill be fed with the finest carborundum powder (3F), while the very finest particles are transported by the fine cilia into the axial groove, the less fine are seen to be carried by the coarse cilia and to collect at the inner ends of the inner leaflets, where cemented by mucus they form a string stretching along the gill. There is no apparent longitudinal current here on either gill, the string merely rotating, but if the amount of material collecting in this position is small and therefore little mucus is secreted, the small rotating masses appear to be thrown occasionally from one leaflet to the next, and very slowly to collect at a point on the gill near the posterior edge of the foot. In Nucula, on the other hand, a distinct longitudinal current along the inner edge is present on the posterior region of the gill, that is from the tip to about the position of the posterior edge of the foot: anterior to this point particles appear to collect at the edges of the leaflets as throughout the gill of Nuculana. There is a difference in the ciliation of the free ends of the leaflets in the two parts of the gill of Nucula.

In Nuculana accumulations of material along the inner edges of the gills either drop on the mantle and are conveyed posteriorly to be ejected on sudden closure of the valves, or are removed by the palp appendages and the smooth posterior or upper margins of the inner palps and transported to the palp surface. Orton (1912, p. 463) observed this action of the palp appendages in Nucula, and Morse (1913, pp. 273–4) in Solenomya velum.

In Nucula, Nuculana, and Solenomya there is no longitudinal current along the outer edges of the gills.

Kellogg (1915, pp. 691–9) apparently observed in Yoldia only frontal currents toward the axial groove, and does not mention observing the collecting of particles along the inner edge of the gill, which is so obvious in Nuculana. From his figure of a transverse section of a leaflet (1892, fig. 79, Pl. xci) it seems probable that tracts of coarse and fine frontal cilia occur in Yoldia, though it does not necessarily follow that the direction of their beat is the same as in Nuculana.

Along the axial groove the rapid current is anterior for the greater length of the gill, that is to about the region of the twelfth[1] pair of leaflets from the anterior end, but in front of this point it is posterior. Particles travelling from both directions are carried on to and along the frontal edge of the inner leaflet of this pair and collect at its inner end (Text-fig. 1). Such collections are removed either by the palp appendage, or by the upper or posterior margin of the inner palp itself, which lies very near the gill.[2]

In Nuculana, as in Yoldia (Kellogg, 1915, fig. 70) and Nucula (Hirasaka, 1927, p. 639), there is no direct connexion between the gills and the palps, in fact in Nuculana the anterior tips of the gills are separated by a distinct interval from the palps (see Text-fig. 1). It is probably owing to the absence of such a direct connexion between gill and palps that in Nuculana on the anterior region of the gill the current along the axial groove is backward.

Nuculana and Yoldia apparently differ in the currents along the anterior portion of the gill. According to Kellogg (1915, p. 694) in Yoldia along the axial groove 'the collections are carried forward, but are halted momentarily about opposite the fifteenth plate by a narrow, backwardly directed tract lying along the bases of the inner plates. Very small amounts seem to pass this point without interference. It is possible that the halt is made here in order to facilitate the transfer of material to the palps, the oral groove of which, at times, lies against this region of the gill. At any rate, if this transfer is not made, the material, after revolving a few times, continues on toward the modified plates', between which he found it passed into the supra-branchial chamber.

The gill currents of Nuculana are more complicated than those of Nucula and Solenomya in which there is no sorting by the frontal cilia. In Nucula (Nucula nucleus (L.) and Nucula radiata Hanley) the frontal cilia are of

[1] It is difficult to determine the exact number owing to the small size of the anterior leaflets.

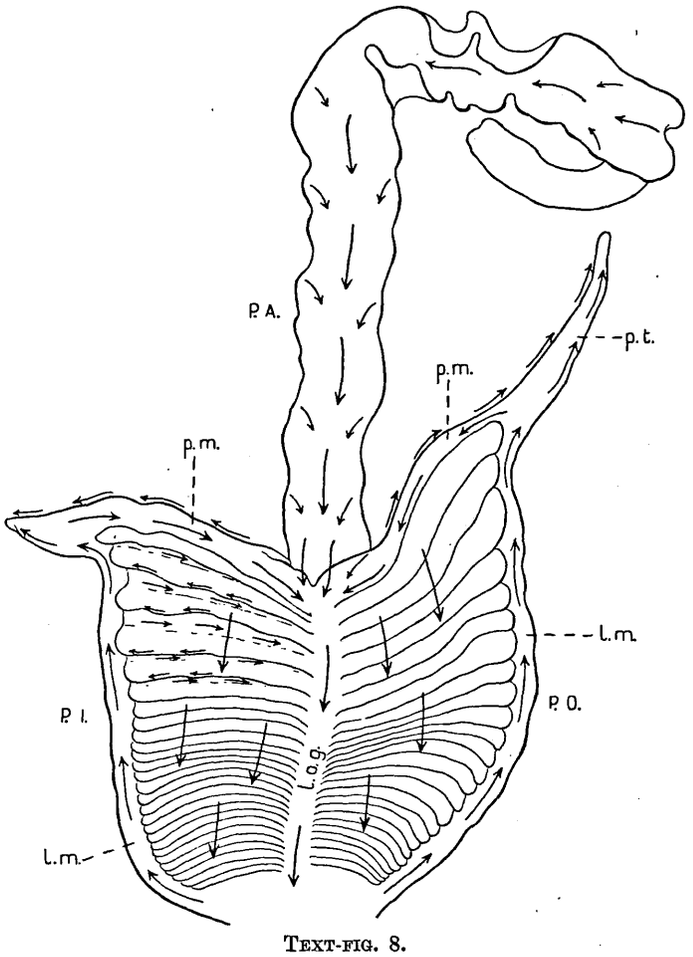
[2] In Text-fig. 1 the upper margins of the palps appear to be some little distance from the gill, but this is due to contraction of the palps and gills.

one kind and all beat in the same direction (as evident from the movement of particles, and observations of the actual direction of beat), that is from the outer edges of the outer leaflets across the axis to the inner edges of the inner leaflets as described by Orton both for Nucula and Solenomya (1912, pp. 467–9; 1913, pp. 40–3). It is difficult to account for Hirasaka's (1927, pp. 639–40) statement that in Nucula 'there are two opposite ciliary currents in each gill surface, a superficial one sweeping towards the margins of the gill, and a deeper interfilamentar current directed towards the central groove or depression. In this central groove and along both the gill margins particles travel rapidly in a forward direction.' The current which he describes as 'sweeping towards the margins of the gill' may possibly be the water current set up by the lateral cilia, which passes obliquely towards the inner and outer margins of the gills in passing between the leaflets. A frontal current toward the axial groove is found only on the outer leaflets, but in an excised gill on which the lateral cilia were motionless and the frontal and latero-frontal cilia alone active, a counter or eddy current between the inner leaflets toward the axial groove has been observed. In Nucula nucleus and Nucula radiata there is no current along the axial groove; the latero-frontal cilia are continuous across the axis (see p. 198) and the surface of the axis between successive pairs of leaflets seems unciliated. Along the gill margins there is a current only along the inner edge in the posterior region.

In Nucula, as in Nuculana, some slight ciliation exists just dorsal to the definite lateral ciliated tracts, which is visible both in sections (see Text-fig. 7 A, *s.c.*) and on the living leaflets. No current, however, could be demonstrated even when the lateral cilia were motionless. This scattered ciliation may possibly be remains of primitive general ciliation of the leaflets as seen on certain Pectinibranch gill filaments.

Palps and Palp Appendages.

The palps in Nuculana, as in Yoldia and Nucula, are large. The posterior extremity of the outer palp of each side is continued into a tongue-like process (Text-fig. 8, *p.t.*) which



TEXT-FIG. 8.

Nuculana minuta. Sketch of the palps and palp appendage of one side. Only the most obvious palp currents are shown. *l.m.*, lower margin of palp; *l.o.g.*, lateral oral groove; *P.A.*, palp appendage; *P.I.*, inner, and *P.O.*, outer palp; *p.m.*, posterior margin of palp; *p.t.*, tongue-like process of outer palp. × ca. 18¼.

leads unwanted particles to the outgoing tract on the mantle (see Text-fig. 1 in which the process of the left outer palp, *p.t.*, is shown well extended). The currents on the ridged surfaces of

the palps pass in at least three directions (see Text-fig. 8); (1) toward the lateral oral groove (*l.o.g.*); (2) less obviously away from the lateral oral groove, and toward the smooth lower margins of the palps (*l.m.*); and (3) transversely across the ridges in an anterior direction.

Along the smooth lower margins (*l.m.*) the current is toward the palp tips and away from the mouth. Along the broad smooth posterior or upper margins (*p.m.*) the current is chiefly toward the lateral oral groove, but on the extreme edge there appears to be a current toward the tips of the palps.

Over the smooth outer surface of both inner and outer palps the current is anterior and dorsal (see Text-fig. 1).

In Nuculana the palp appendage appears to be attached to the outer palp distinctly more dorsally and anteriorly than in Yoldia (cf. Text-fig. 1 with Kellogg's fig. 67, 1915), and presumably in consequence the groove which Kellogg (1915, pp. 693–5; fig. 70) described along the outside of the line of union of the inner and outer palps, and called an extension of the lateral oral groove, is extremely reduced, practically absent. It is merely that the upper or posterior edge of the outer palp is united not with the extreme edge of the inner palp, but just internal to it, so that a narrow free margin extends a very short distance anterior to the point of origin of the palp appendage.[1]

The passage for particles passing from the palp appendage to the palps appears to be considerably wider in Nuculana than in Yoldia, owing to the presence of broad tracts on the posterior margins of the palps (*p.m.*) over which particles pass toward the lateral oral groove (Text-fig. 8, *l.o.g.*).

The palp appendages of Nuculana are very similar to those of Yoldia (Drew, 1899, pp. 10, 11) and Nucula (Hirasaka, 1927, p. 631), the function of which has been so fully described in those forms and in Solenomya (Morse, 1913, pp. 273–4) that nothing needs to be added. The concave surface and both margins are heavily ciliated, the cilia being long and

[1] In Scrobicularia plana a somewhat similar type of union exists anteriorly between the ventral free edge of the inner demibranch and the inner palp, the junction being just internal to the free edge of the palp.

coarse: the convex surface is unciliated. On the excised palps it was noticed that the majority of the cilia on the appendage were frequently almost inactive; when, however, a drop of a rich culture of the diatom Nitzschia was added to the water all became exceedingly active, driving the diatoms toward the palps.

Discussion.

Pelseneer (1891, pp. 273–5) has given reasons for considering that the Nuculidae—in which he then included the genera Leda (= Nuculana) and Yoldia—and the Solenomyidae are the most primitive of the Lamellibranchia, though he allowed that Nuculana is a little more specialized than Nucula for a certain number of points (p. 168). According to Drew (1899, p. 28), however, some of the reasons do not seem to hold good for Yoldia, now included with Nuculana in the family Nuculanidae. Kellogg (1915, p. 691) remarked that 'if this much discussed genus is properly placed among the most archaic of living lamellibranchs, this representative of it certainly possesses the most extraordinarily complex set of ciliary mechanisms observed in the group'. Drew (1899, p. 16) tried experiments to determine, if possible, the part taken by the gills in the collection of food, and though no definite results were reached he did not observe them actively engaged in collecting food. He concluded that 'considering the remarkable activity of the palps as collectors of food, such activity for the gills seems rather unnecessary, and it would also seem that the pumping action of the gills would seriously interfere with their normally performing such a function'. Kellogg (1915, pp. 695–6) commented: 'Drew had not seen the extension of what I have called the lateral oral groove, but I am puzzled to know how the tremendous activity of the gill in collecting and moving forward suspended particles brought to it in the water, could have escaped his notice, the whole process being precisely like the food collection of other lamellibranch gills. The pumping action of the gills does not disturb small collections, and there is no reason for assuming that it would interfere with the transfer of food from gill to palp.'

While Drew underestimated, Kellogg appears to have rather

overrated the importance of the gill as a food collector in Yoldia: both agree as to the importance of the palp appendages in this direction.

It is difficult to believe that the chief function of the gill of Nuculana is that of collecting food. It is not that the various sets of cilia for current producing, food straining, and food conveying are not well developed—in fact they are thoroughly well developed and efficient—but that they are present on such a short stretch of each leaflet (see Text-fig. 3) and that the area for food collecting on the whole gill, which is itself small, is extremely small. The food-collecting surface of the gill is comparatively greater in Nucula, and much greater in Solenomya; in Nucula it was observed that the water current set up by the lateral cilia was considerably stronger than in Nuculana.

In young undamaged specimens of Yoldia with thin shells Drew (1899, pp. 14–15) was able to observe a more or less rhythmical pumping action of the gills. He has described how the gills gradually descend, water passing between the leaflets as they do so. After reaching their greatest ventral depression they remain at rest for a certain period. This resting period is followed by energetic contraction of the suspensory membranes, drawing the gills up dorsally and thus diminishing in size the supra-branchial chamber, and increasing that of the infra-branchial chamber; this results in a vigorous discharge of water through the exhalent siphon and a corresponding inflow through the inhalent siphon. The movements of the gills are accompanied by conspicuous movements of extension of the siphons. He concluded that the currents of water are probably for respiratory purposes and to remove from the mantle chamber dirt and more especially faeces, and suggested moreover that the contraction of the gills might aid in movements of blood as well as of water. Drew pointed out how admirably the gills of Yoldia are fitted for the function of pumping water, for 'in shape they exactly fit the mantle-chamber, in which they form a movable partition. Contact is ensured by the pressure of the blood inside the plates, and by the soft dorsal projections of the plates. These projections must act much like the leather on the plunger

of a suction pump, making good contact when there is pressure from above but not hindering its descent.'

The shells of the specimens of Nuculana minuta were much too opaque to allow of observations on the entire animal, but in those with a valve removed, sudden upward motions of the gills were observed, immediately preceded by the beginning of a slight movement of extension of the siphons. This occurred more or less rhythmically. Movements of the siphons in undamaged Nuculana, similar to those described by Drew (1899) and Brooks (1874) in Yoldia, are very obvious. At intervals they—in particular the exhalent—are rigidly extended and the apertures widely opened. These movements are accompanied by a strong, but short, discharge of water from the exhalent siphon. While the animals were under observation the inhalent current seemed to enter largely by the aperture through which the palp appendages emerge, little entering by the inhalent siphon: this may not be so in their normal habitat. It was mostly through this aperture ventral to the siphons that collections from the mantle (pseudo-faeces) were expelled on sudden closure of the valves. Following the discharge of water, the walls of the exhalent siphon collapse, the ventral wall becoming crescentic inwards, and the aperture appears almost closed. The inhalent siphon remains fairly well extended, with the aperture open.

The interval between the extension of the siphons in three individuals was timed with a stop watch. In one the average length of 53 intervals was $14\frac{1}{2}$ seconds, with a minimum of $7\frac{1}{2}$ and a maximum of $22\frac{1}{2}$ seconds. Following the interval of $7\frac{1}{2}$ seconds the siphons were withdrawn and burrowing movements performed by the foot. In the second animal the average length of 81 intervals was $13\frac{1}{2}$ seconds, with a minimum of 10 and a maximum of 30 seconds. During the timing of this specimen an interval of 1 minute 4 seconds occurred, but this was so unusually long that it is not included in the average. In the third Nuculana the average length of 33 intervals was 12 seconds, with a minimum of $9\frac{1}{2}$ and a maximum of 21 seconds. The siphons were not extended far in this animal.

These observations, necessarily incomplete, tend to prove that

the gills of Nuculana, as those of Yoldia, perform pumping movements. During the sudden dorsal contraction of the gills it is probable that the leaflets are thrown against each other, obliterating the spaces between them, and thus preventing the passage of water. The ciliary junction between the inner demibranchs is very strong, so that the two gills adhere and form a septum across the branchial chamber. Sections of the gill of Nuculana (Nuculana pella) showed the large blood-spaces of the leaflets to be distended with blood, and it seems certain that the gills play a very considerable part in respiration.

From observations on living Nuculana it appeared that though in the intervals between the extension of the siphons the gills function as normal lamellibranch gills, the inhalent current is weak. The pumping action seems undoubtedly a method for increasing the inhalent and exhalent currents in an animal with relatively few lateral, current-producing cilia, thus adding to their efficiency for respiratory purposes and for removing faeces from the supra-branchial chamber. The frontal, food-conveying cilia are no doubt competent to deal with such material as is brought to the gill surface, either by the action of the lateral cilia or by the pumping action of the gills.

In Yoldia and Nuculana, therefore, the strength of the inhalent and exhalent currents is augmented at intervals coinciding with movements of the gills. It is interesting to compare this with the intermittent nature of the inhalent and exhalent currents in the Septibranchs depending on movements of the septum (Yonge, 1928, pp. 239–42). In Nuculana the gills between periods of activity are extended ventrally; in the Cuspidariidae the septum is in its shortest condition during such intervals. Drew's suggestion that the contractions also aid in movements of the blood seems very plausible, and most probably the waves of contraction described by Kellogg (1892, pp. 414–15) as passing along the gill in either direction have the same object.

The muscles responsible for the sudden rhythmical contractions of the gill of Nuculana are composed of striated fibres, furnishing yet one more instance of the correlation of this structure with a continuous series of rapid movements.

The pumping movements which are so marked a function

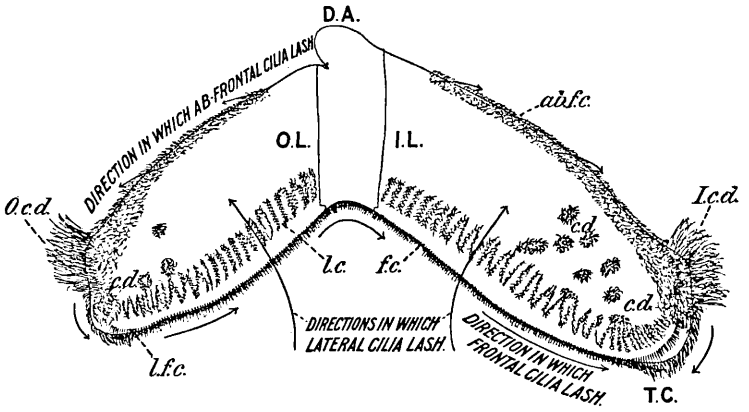
of the gills of the Nuculanidae, are not altogether absent in the Nuculidae: in an individual of Nucula nucleus, with one valve removed, definite, though slight, intermittent dorsal contractions of the suspensory membranes were observed, apart from the slow twisting movements of the free ends of the gills. These sudden movements took place on an average every 16 seconds, but were very irregular, the minimum interval being 5 seconds and the maximum 45 seconds during 49 timings. The irregularity may reasonably be ascribed to the animal having a valve removed. Drew (1901, p. 362) observed slight movements in Nucula delphinodonta. He remarked that 'the opaque character of the shells of adult animals makes it quite impossible to observe the normal movements of the gills. They can be seen to move slightly, however, and it seems probable that the suspensory membranes contract slightly at intervals. Such movements would be useful in causing movements in the contained blood, but they are not sufficient to cause strong currents of water. The shape of the gills is not such as would make them efficient pumping organs.' It may be added that in Nucula nucleus and Nucula radiata junction between the two gills is weak, so that they do not form a strong septum across the branchial chamber, and that they have a considerable free posterior region.

The gill of Nuculana is certainly curious; differentiation of lateral, well developed latero-frontal, and two kinds of frontal cilia is unexpected on a gill of which the surface for food collecting in relation to the total surface of the gill is so very small, and when extremely efficient food collectors, the palp appendages, are present. It seems probable that it has been derived from a form in which the gills were much more important as food collectors. Otherwise it is difficult to account for the elaborate sorting mechanism on a gill of such small size, where the material gathered by the palp appendages would be coarser, and where large palps are present to effect the necessary sorting. It is perhaps possible, however, that the gills are specialized to catch some particular planktonic food.

The frontal currents on the gills of Nuculana are considerably more complicated than on the gills of either Nucula or

Solenomya. Yet it is to be expected that both these latter forms with their greater ciliated gill surface would be proportionately more efficient as regards food collecting.

The leaflets of Nucula and Solenomya are considerably



TEXT-FIG. 9.

Nucula. Anterior view of a living pair of leaflets of the right gill. The leaflets anterior to the pair depicted were cut away. *ab.f.c.*, abfrontal 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 the 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. × ca. 65. (From Orton, 1912, fig. 18, p. 468, by courtesy of the Marine Biol. Assoc. of the United Kingdom.)

narrower from frontal to abfrontal surface than those of Nuculana (Text-figs. 3, 9, 10)—of which the great depth is very striking—and considerably less distensible.

While Nucula, Yoldia, Nuculana, and Solenomya are all burrowers (Drew, 1900, p. 258; 1901, pp. 314–15; Hirasaka, 1927, p. 643), it would seem that Nucula is a generalized type as indicated by much in its structure and embryology (Drew, 1901), and therefore likely to possess the most primitive gill among living Lamellibranchs. It is a gill which is probably an efficient food collector for its size, with food-

collecting cilia occupying all the frontal surface. The frontal cilia are all alike—except for those at the tips of the posterior inner leaflets where there is a longitudinal current—and all beat in the same direction: the frontal currents are thus simpler than in Nuculana and do not effect sorting. The leaflets are fairly narrow from the frontal to the abfrontal surfaces, though deep compared with the filaments of the higher Lamellibranchs. The musculature of the leaflets themselves is mainly restricted to a few strands (Text-fig. 7 A, *m.f.*) running beneath the abfrontal surfaces and causing independent dorsal bending. They are held loosely together by small ciliated disks and are easily separable. The gill of Nucula would seem to be a respiratory and an efficient ancillary feeding organ, the chief one, of course, being the palp appendage. According to Orton (1912, pp. 463–4) it 'presents an early stage in the adaptation of the original respiratory organ to a food-collecting organ'.

Though small, the gills of Nucula are evidently able to create currents sufficient for respiratory purposes and for removing waste matter from the mantle chamber. In Nuculana, a considerably specialized, siphonate, burrowing Protobranch, the lateral cilia of the gills are presumably too few, either primitively, or more probably by reduction, to create a sufficiently strong inhalent current, and their action is augmented by pumping movements of the gills, these being highly muscular, in both axes and leaflets. They not only act as a pumping organ for water, but presumably as a kind of accessory heart; indeed the gills of the Nuculanidae would appear to be somewhat highly modified.

Both Nucula and Nuculana are deposit feeders, bottom detritus with contained organisms being conveyed to the mouth by way of the extensible palp appendages. A distinct tendency is evident among deposit feeders, whether Protobranchs or higher Lamellibranchs (Tellinidae, Semelidae) for the gills to be small and the palps large. In certain small species of Tellina and Abra there is also a distinct tendency for (*a*) the gills to be reduced below a size apparently competent to create a current strong enough to suck detritus up the excessively long inhalent siphon, and for (*b*) a means of increasing the current to be evolved, namely large cirrus-like cilia on the posterior region of

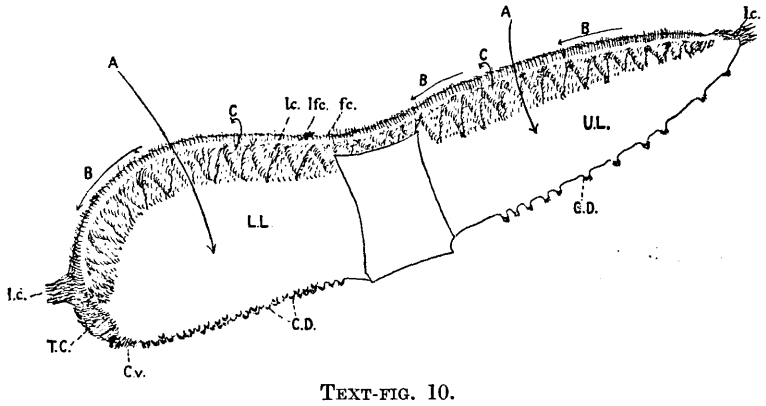
the gills (see Part II, in the press). In Nuculana and Yoldia the small size of the gills, and especially of the ciliated surface, is also possibly, or even probably, due to secondary reduction. In these forms the method devised to increase the strength of the currents, in this case largely for respiratory and cleansing purposes, is by pumping action of the gills. The correlation, however, is not a simple one, for this action is also responsible for movements of blood.

Drew (1901, p. 363) considered it possible that the pumping action of the gills in Yoldia is correlated with the habits of that bivalve (it lives in mud above which it extrudes about the posterior third of the shell during feeding), which 'are such as to render the formation of strong currents of water absolutely necessary, for otherwise the mantle chamber would become clogged with faeces and dirt'. To Nucula, wandering about beneath the surface, he considered strong currents would be a distinct disadvantage. It follows that Solenomya, inhabiting a more or less permanent burrow (Drew, 1900, p. 260; Morse, 1913, p. 263), would also require strong currents, and the large gills might be supposed to have been evolved to that end. There is, however, another possible explanation of the large gills of that genus.

Solenomya possesses considerably larger gills in proportion to the size of the body than does Nucula, with very numerous leaflets—apparently almost destitute of muscle-fibres—and a large ciliated surface. The gills of Solenomya are peculiar in that the outer leaflets are upturned. Morse (1913, pp. 273–5) stated that 'the gills are very bulky, filling nearly half the mantle cavity', and according to him and Ridewood (1903, p. 193) the palps are represented by the palp appendages alone, which are used for transferring food from the gills to the mouth (Morse, 1913). Judging from Morse's figures (figs. 15, 22), the palp appendages are much shorter in Solenomya velum and Solenomya borealis than in Nucula or in Nuculana and Yoldia, and apparently their only function is to remove food from the gills. It is interesting to note that in Capulus hungaricus, a Pectinibranch Gastropod, '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' (Orton, 1912, p. 472). If the palp appendages of Solenomya are not extruded beyond the shell, then this Protobranch is a suspension, and not a deposit feeder, as are the Nuculidae and Nuculanidae.

Thus among the Protobranchia, as among the higher Lamelli-



TEXT-FIG. 10.

Solenomya togata. View of a pair of living leaflets taken from about the middle of the gill to show the directions in which the different sets of cilia lash. 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; *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. × ca. 60. (From Orton, 1913, fig. 10, p. 40, by courtesy of the Mar. Biol. Assoc. of the United Kingdom.)

branchia (exclusive of Septibranchia), two methods of feeding exist, suspension feeding and deposit feeding. In the higher Lamellibranchia suspension feeding is the rule, probably all Filibranchia, Pseudolamellibranchia, and the majority of the Eulamellibranchia feeding in this manner. Deposit feeding is confined, so far as is known at present, to a few families

(Tellinidae, Semelidae, Asaphidae, Hunt, 1925, and perhaps Mysia undata), members of which have exceedingly long, narrow, free, flexible siphons by means of which they suck up bottom detritus and any organisms it may contain. In the higher Lamellibranchs deposit feeding is evidently a secondary specialization. It is perhaps useless to speculate whether deposit or suspension feeding is the more primitive method in the Protobranchia. Morse (1913, p. 275) evidently considered that the reduced condition of the palps in Solenomya is primitive and not secondary; whether this is so the evidence seems too slight to determine. Pelseneer (1891, p. 275) concluded that the Solenomyidae are less primitive than the Nuculidae, in which he included Nuculana and Yoldia.

As a side light on the original respiratory function of the Protobranch gill, it is interesting that in Nuculana, Yoldia (Kellogg, 1915), Nucula (Hirasaka, 1927, p. 639), and apparently in Solenomya (Morse, 1913, pp. 273–5), the gills have no direct connexion with the palps, gill collections being transferred independently by the palps and palp appendages and conveyed to the mouth. In Nucula the longitudinal current along the inner gill margin is present only in the posterior region; in Nuculana particles collect along the inner edge of the gill, but there is no apparent longitudinal current in this position throughout the gill, and along the anterior part of the axial groove the current is away from the mouth.

Hirasaka's (1927, p. 630) statement that 'in Protobranchs there is almost no co-operation between the gill and palp' is undoubtedly incorrect. Though the gills and palps are not directly connected, co-operation between gill and palp or palp appendage has been described in Nucula by Orton (1912) and in Solenomya by Morse (1913), and has been personally observed in Nuculana (see p. 200) and in Nucula. In Nucula material conveyed along the inner edges of both gills collects at a point near the posterior edge of the foot. The significance of this position is its proximity to the posterior edge of the inner palp and to the palp pouch, and material has been actually observed passing from the gill on to the palp, and thence to the lateral oral groove. Anteriorly there is no longitudinal

current on the gill, particles collecting along the inner margin, and from here passing on to the outer surface of the palps along the line of union of the two, and so on to the posterior or convex surface of the palp pouch, over which the current is toward the free edge and on to the concave surface. Such currents may be seen in an animal with one valve removed: on the excised palps the cilia of the pouch tend to be motionless.

Summary.

The structure of the gills of Nuculana minuta is described. Their chief characteristics are: (1) the presence of striated muscle-fibres running transversely through the suspensory membranes and entering and radiating through the gill leaflets. These fibres are concerned in rhythmical dorsal contraction of the gills; (2) the strong ciliary junctions between successive leaflets and between the two gills, so that the gills form a septum across the mantle cavity; (3) the very short region of each leaflet provided with current-producing cilia.

Four sets of cilia are present on the gill leaflets: (1) coarse frontal cilia, beating toward the inner edge of the gill; (2) fine frontal cilia, beating toward the axial groove; (3) large latero-frontal cilia; (4) lateral cilia.

The obvious frontal currents on the gills are toward the inner edges. Material collects here and is either removed by the inner palps and the palp appendages and conveyed to the mouth, or drops on the mantle. Fine particles are transported by the fine frontal cilia to the axial food grooves, along which they are carried to a point level with about the twelfth pair of leaflets from the anterior end. Material from the anterior region of the gill also collects at this point, and the combined collections are removed by the inner palps and the palp appendages and conveyed to the mouth.

The currents of the palps and palp appendages are briefly described.

The behaviour of the gills in pumping water by rhythmical dorsal contraction, as in Yoldia, is discussed.

A comparison is made of the ciliation of the gills, gill currents, and the complex of respiration and feeding in the Protobranchia.

SECTION B

Some New Observations on the Ciliary Feeding Mechanism of Glycymeris glycymeris (L.) and Arca tetragona Poli

With Text-figures 11–20.

CONTENTS.

INTRODUCTION AND HABITS.

The ciliary currents of Glycymeris glycymeris and Arca tetragona are very similar, with but slight variations probably due to the difference in the shape and habits of the two forms.

Arca is elongated, inequilateral, and strongly attached by a byssus, there being a wide opening between the valves ventrally in Arca tetragona Poli, though not in Arca lactea L. Arca creeps by means of the foot when changing its position; a creeping Arca tetragona has been observed to leave a thick trail of mucus.

Glycymeris is equilateral, almost circular and unattached; according to Douvillé (1912, p. 432) it has secondarily taken to a free life. The locomotion of Glycymeris glycymeris, which burrows after the manner of Nucula (Drew, 1900), though much more slowly, has already been described by Vlès (1906), but a few observations may be added. Glycymeris, when laid on one valve on the surface, pulls itself into a vertical position preparatory to locomotion by bending the foot sideways and downwards and thrusting it into the sand. It was noticed that the furrowed surface of the sand resulting

from the first few ineffectual thrusts of the foot was cemented by mucus. This copious secretion of mucus during burrowing, by cementing the sand grains, possibly prevents, at least to some extent, their entry into the mantle chamber.

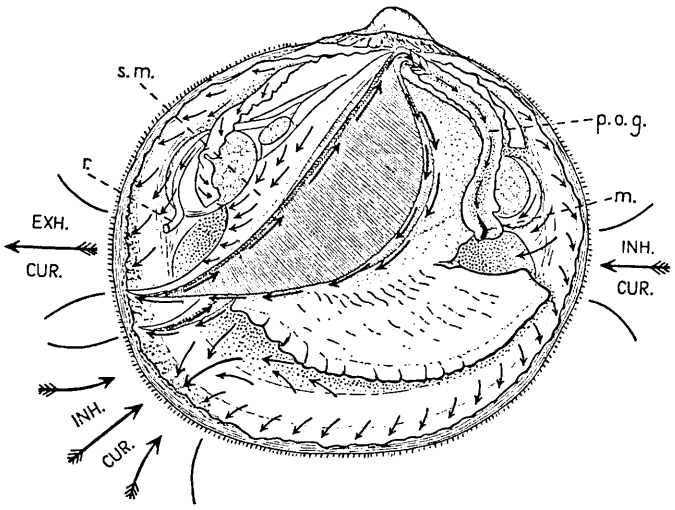
Large specimens (6 cm. and more long) of Glycymeris glycymeris have been kept in the Laboratory under circulation for over five months[1] in bowls with sand and shell gravel 2 to 7 inches deep: shell gravel is the normal habitat of this species. They remained just beneath the surface, and but rarely was the mantle edge visible. When light was excluded by means of a covering black box, they still remained hidden after several weeks. However, it is most probable that in their natural habitat the posterior region of the mantle, forming the inhalent and exhalent apertures, is extended above the surface, for this part is deeply pigmented and provided with eyes (Text-fig. 11). Glycymeris when buried appears to lie indifferently on the right or left valves, and has been found occasionally more or less vertical.

In both Arca and Glycymeris the mantle lobes are free except along the hinge line; they are, however, normally apposed, or fit closely round the foot and byssus in Arca, except in certain regions forming the inhalent and exhalent apertures. The exhalent and main inhalent apertures, separated by a short interval where the mantle edges are in apposition, are situated posteriorly: the inhalent aperture is about twice as large as the exhalent. A secondary inhalent opening is sometimes formed anteriorly, in front of the foot (see Text-figs. 11, 12). On sudden closure of the valves water may be expelled all round the shell, but chiefly anteriorly, at least in Glycymeris which is easier to observe than Arca owing to the absence of a byssus. Glycymeris ploughs through sand and gravel with the anterior end forward, and during the process a strong current is forced at intervals from the mantle chamber anteriorly.

An interesting observation was made on two Glycymeris,

[1] Both Arca and Glycymeris support laboratory conditions well, specimens of both being alive and apparently healthy after 15 months in the tanks, though without soil in which to burrow.

which had been entirely hidden for some time in fine sand, as to the usual regions where currents are emitted. On the surface of the sand were certain dark markings composed of fine silt: the form taken by these was a ring, connected by a semicircular diffuse band with a rounded area, smaller than the

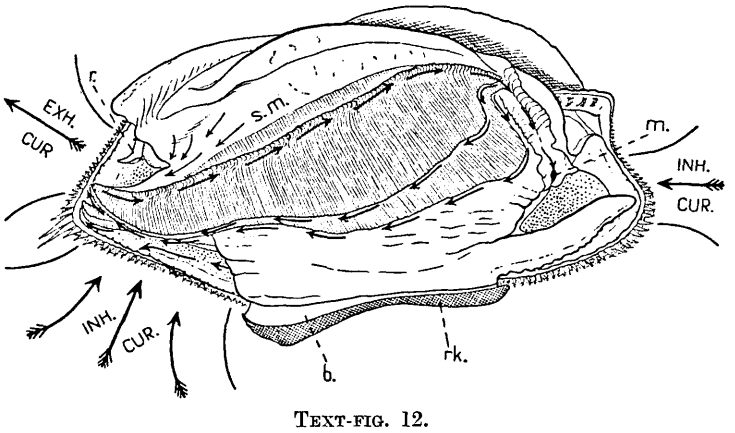


TEXT-FIG. 11.

Glycymeris glycymeris (L.) viewed living from the right side, with the right valve and mantle lobe removed, to show the direction of the longitudinal currents on the gills and the position of the inhalent and exhalent currents. The foot is somewhat retracted dorsally; normally the ventral edge lies against the mantle margin. *EXH.CUR.*, exhalent and *INH.CUR.*, inhalent current; *m.*, mouth; *p.o.g.*, proximal oral groove; *r.*, rectum; *s.m.*, suspensory membrane of gill. Actual size.

ring. On removal of the sand it was found that the ring had been situated over the anterior region of the animal; the rounded area over the exhalent aperture; and the connecting band had corresponded to the curved ventral line of the valves, the animal lying on its side. It would seem that water expelled from the valves forced fine silt upward through the sand until it reached the surface. The steady current from the exhalent aperture produced the dark, rounded area; the occasional but

stronger current expelled anteriorly on sudden closure of the valves produced the ring; while the less distinct connecting band was due to water escaping round the ventral part of the shell. The ring is the first portion of the markings to become visible after an animal has come to rest, and may be well formed in less than 13 hours. This probably indicates that fairly fre-



TEXT-FIG. 12.

Arca tetragona Poli viewed from the right side, with the right valve removed and the mantle lobe folded upward, to show the direction of the longitudinal currents on the gills and the position of the inhalent (*INH.CUR.*) and exhalent (*EXH.CUR.*) currents. The byssus (*b.*) is attached to a layer of rock (*rk.*). *m.*, mouth; *r.*, rectum; *s.m.*, suspensory membrane. × 2.

quent contractions of the valves, to expel unwanted material, take place when the animal first settles down.

In both Arca and Glycymeris during feeding the valves are held slightly apart, the mantle margins protruding some 3 or 4 mm.; the outer surface thus exposed is unciliated. In Arca tetragona, as in Glycymeris glycymeris, the mantle margin is patched with brown posteriorly; eyes are present all round the mantle edge, those anterior to the inhalent aperture being minute and widely and irregularly spaced. In this species the greater part of the mantle, especially posteriorly, is brown or orange: splotches of brown pigment are present on the posterior surface of the foot. In Arca tetragona the

ventral edges of the demibranchs, behind the foot, lie close to the mantle edge, being visible through the inhalent aperture, and the gill filaments are here also patched with brown. Text-fig. 12 shows the gills not fully extended ventrally.

In Glycymeris glycymeris, in addition to the brown pigmentation of the mantle margins posteriorly, there are patches of an opaque white substance, which is found also on the posterior dorsal region of the foot, and on the posterior region of the suspensory membranes of the gills. These are all parts liable to be reached by light in a feeding animal.

Observations of the feeding of an intact animal were mostly made on Glycymeris glycymeris. Glycymeris, Arca, and the Anomiidae (see p. 253) are of those rare forms in which the current along the ventral edges of the demibranchs is posterior in direction, that is away from the mouth (Text-figs. 11 and 12). The posterior tips of the gills extend to the edge of the protruded mantle, some 3 or 4 mm. beyond the shell edge, and particles are either passed directly into the exhalent stream, or first on to the mantle. Large collections of carmine particles travel safely along the ventral edges of the demibranchs, in spite of the absence of a groove; their arrival at the posterior region appears to stimulate the gill tips to bend dorsally.

The valves are occasionally closed rapidly, water being expelled by this means to a distance of 4 to 5 inches by a large Glycymeris. In this way collections of waste material, which have not fallen on the mantle, are removed from the posterior region of the foot and visceral mass.

Adjacent antagonistic frontal currents have been found on all filaments of the gills of Glycymeris and Arca; these effect efficient sorting of particles impinging on the gills. A certain type of material is conveyed dorsally into paths leading to the mouth; other material is transported to the free ventral edges of the demibranchs along which it is carried posteriorly and finally rejected to the exterior.

Structure of the Gills.

In Glycymeris and Arca the gills are eleutherorhabdic or filibranchiate; that of each side is suspended by a deep membrane,

and has a considerable free posterior portion. In the living animal longitudinal muscles are visible across the dorsal ends of the descending filaments. Stimulation of the mantle edge, and also of the extremity of the gill, which bears a cluster of long, stiff, tactile hairs, causes contraction of the adductor muscles and of the gill axes, the latter to about three-quarters of their original length, in both Glycymeris and Arca. Arca appears to be more sensitive to stimulation than Glycymeris, but there is variation in degree of sensitiveness in different individuals.

The osphradium extends to the tip of the gill in both genera, being visible as a pigmented line. The suspensory membrane of Arca tetragona is profusely supplied with mucous glands, both superficial and deep seated, the layer of glands in some regions reaching a depth of more than 300 μ. The form and arrangement of the gland-cells differ considerably from that in the hypobranchial glands of the Protobranchs.

The inner demibranch is rather deeper than the outer in Glycymeris glycymeris, and much deeper anteriorly in Arca tetragona (Text-figs. 11, 12): the ascending lamellae are not as deep as the descending ones. The lamellae are flat and homorhabdic.

The dorsal ends of the ascending filaments are in ciliary connexion with each other, as are also the filaments at the ventral ungrooved edges of the demibranchs, where large elongated ciliated disks occur. Ridewood (1903, p. 200) stated that such disks were absent in Pectunculus (= Glycymeris) glycymeris, but this would seem to be an error. The interfilamentar junctions are ciliated disks. Interlamellar septa are absent, but there are narrow interlamellar extensions of the dorsal ends of the descending filaments. An intrafilamentar septum is present; it is composed of what are probably muscle-fibres, inserted in Arca tetragona on paired prominent thickenings of the chitinous skeleton (Text-fig. 14 B).

Short interlocking cilia are found on the dorsal edges of the ascending lamellae, but the gills appear to be free from adjacent parts; if a ciliary junction occurs, it is a weak one, easily dissolved.

The filaments of Arca tetragona are generally orange coloured, the pigment granules being mostly accumulated in the lateral ciliated cells; some few, however, are present in the frontal cells.

Much of the foregoing account of the structure of the demibranchs is to be found in Ridewood's paper (1903, pp. 199–200).

Ciliation of the Gill Filaments.

The ciliation of the filaments of Glycymeris glycymeris and Arca tetragona is practically identical, and the two forms will be considered together. The few observations that were made on Arca lactea showed that this species also has the same type of filament ciliation.

Frontal Cilia.—The frontal cilia are in three tracts, a median and two outer, in both genera.

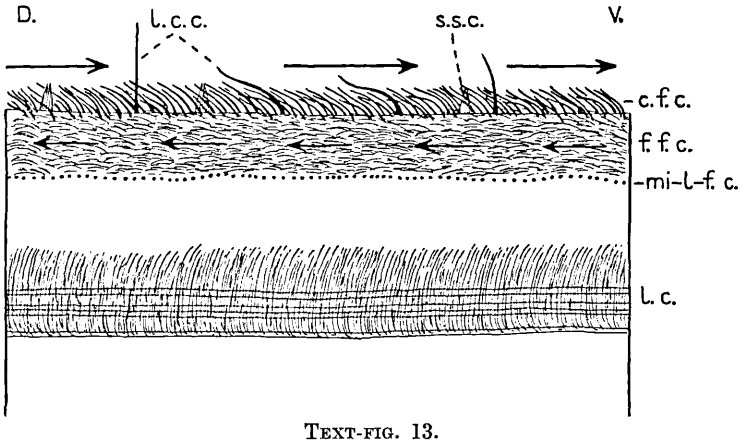
The median tract is of coarse long cilia (Text-figs. 13 and 14, *c.f.c.*), which seem to be more or less motionless unless stimulated. When not actively beating they yet sometimes appear to have a vibratory movement, that is they may move through an exceedingly acute angle. At rest they lie with the tips directed dorsally (Text-fig. 13), their position of rest being at the beginning of the effective stroke, which is toward the free ventral edge of the demibranch. These cilia appear to be rather more sensitive to stimulation in Arca tetragona than in Glycymeris glycymeris, but probably individual variation occurs.

Among the coarse cilia are short, bluntly triangular clusters of stiff hairs (Text-fig. 13, *s.s.c.*), probably tactile in function, which extend little beyond the cilia when these are at rest. There are in addition occasional long stout cilia, or cirri (Text-fig. 13, *l.c.c.*)—also possibly tactile—extending well beyond the frontal cilia; they are capable of movement, but beat irregularly.

The outer tracts—about 14μ wide—are of fine cilia (Text-figs. 13 and 14, *f.f.c.*), which appear to be continuously in motion, the effective beat being dorsalward, though slightly obliquely toward the frontal edge of the filament. In the living filaments these cilia extend round on to the lateral surfaces for some little way, but in sections they are more or less truly

frontal in position, owing to considerable contraction occurring on fixation.

A difference in appearance between the median and the outer tracts can be observed in sections in which the cilia are well fixed and stained. The apparent difference in length of the

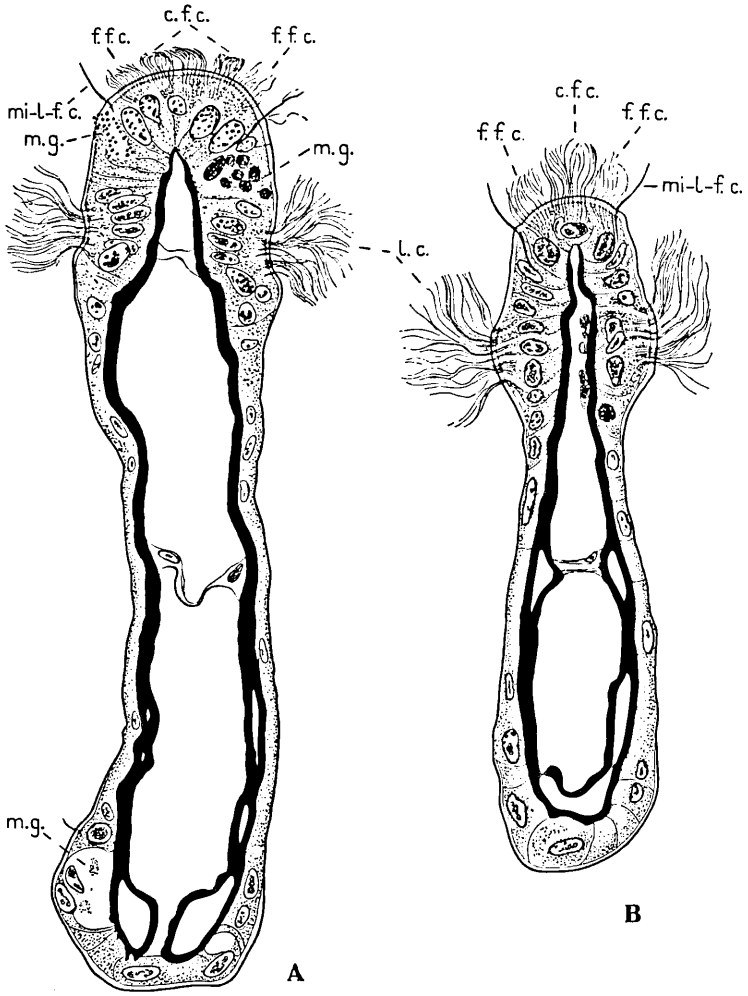


TEXT-FIG. 13.

Glycymeris glycymeris (L.). Side view of a piece of living gill filament to show the various tracts of cilia. The coarse frontal cilia (*c.f.c.*) are shown as they appear when inactive. *f.f.c.*, fine frontal cilia; *l.c.*, lateral cilia, as they appear when motionless; *l.c.c.*, long coarse cilia or cirri; *mi.-l.-f.c.*, fine or micro-latero-frontal cilia appearing in side view as a row of shining dots; *s.s.c.*, triangular cluster of short sense cilia; *D.*, dorsal; *V.*, ventral. The arrows indicate the direction of the effective beat of the two kinds of frontal cilia. $\times 456\frac{2}{3}$.

frontal cilia in the transverse sections of the filaments of Arca tetragona and Glycymeris glycymeris in Text-fig. 14 is largely due to those of Arca being fixed when almost at right angles to the frontal surface, and those of Glycymeris when lying at an acute angle to the surface.

Latero-frontal Cilia.—The latero-frontal cilia are unusually tenuous and short, being only about 14 to 17μ long in both Glycymeris glycymeris and Arca tetragona (Text-fig. 14, *mi.-l.-f.c.*). They are not at all typical in appearance of the latero-frontal cilia such as are found in the great majority



TEXT-FIG. 14.

Transverse sections of the gill filament of: A.—Glycymeris glycymeris (L.); and B.—Arca tetragona Poli. *c.f.c.*, coarse, and *f.f.c.*, fine frontal cilia; *l.c.*, lateral cilia; *mi.-l.-f.c.*, fine or micro-latero-frontal cilia; *m.g.*, mucous gland. Bouin-Duboscq fixation. A. Heidenhain's iron haematoxylin; B. Heidenhain's iron haematoxylin and acid fuchsin. ×735.

of Lamellibranchs. The presence of tenuous, short latero-frontal cilia—distinguished from normal latero-frontals by the term micro-latero-frontal cilia—in the Arcidae, Anomiidae, and most Pseudolamellibranchia (as constituted by Pelseneer, 1911) is described, and the relationship of bivalves possessing them discussed, in a later paper of the series (Part VII, in the press). Their position, which is actually lateral owing to the lateral extension of the frontal cilia, adds to the difficulty of observing and identifying them in living material. In transverse sections, owing to shrinkage on fixation, they are latero-frontal in position. These cilia are more difficult to distinguish in Arca tetragona than in Arca lactea or in Glycymeris glycymeris. In side view of a living filament they appear as a rather regular row of shining dots (Text-fig. 13, *mi.-l.-f.c.*), but in a frontal view, when almost motionless, they appear as a palisade of fine cilia. These cilia are in a single row, and are borne on narrow cells elongated in the direction of length of the filaments. In sections they are difficult to identify, but may be recognized by their darker staining and stouter ciliary rootlets (Text-fig. 14).

Lateral Cilia.—The number of rows of lateral ciliated cells is six, some being extremely narrow (Text-fig. 13).

Abfrontal cilia are generally absent, except for occasional short, bluntly triangular clusters of stiff tactile cilia, similar to those occurring among the frontal cilia.

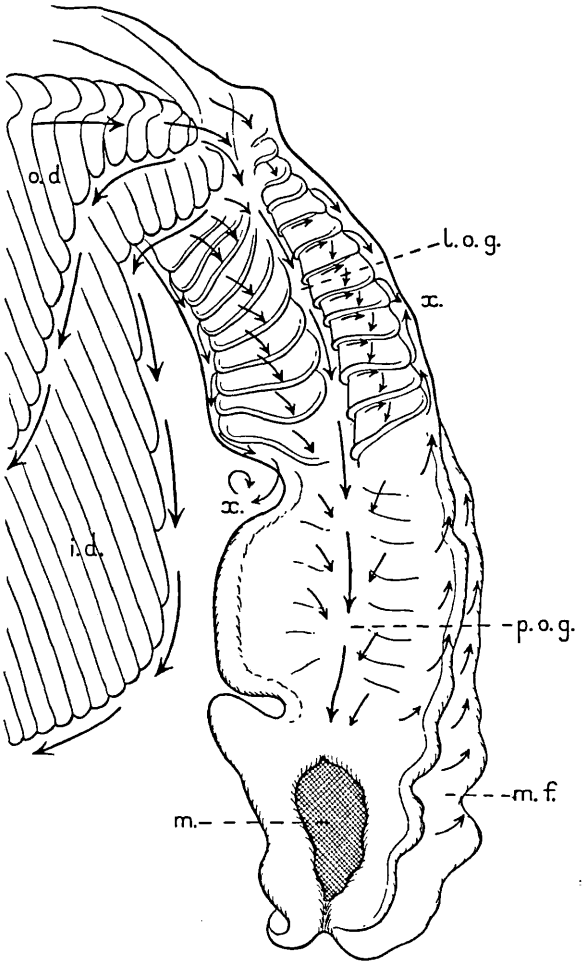
Structure of the Palps.

In both Arca tetragona and Glycymeris glycymeris the palps are small, without a free-pointed extremity, the folded region being no wider than the smooth. In Arca tetragona the folded region of the palp consists of about twelve broad folds (Text-fig. 15): in Glycymeris glycymeris it is greatly reduced, there being no more than one to three folds, while the proximal oral groove (see Kellogg, 1915, p. 629, for the definition of the term) is extremely long. The smooth part of the palps in Glycymeris generally shows slight folds due to muscular contraction. In both species a distal oral groove is almost absent, for the inner demibranch

continues only a slight distance in front of the outer. The great reduction of the folded part of the palps—the chief sorting region in most Lamellibranchs—in the Arcidae is correlated with the efficient sorting mechanism found on the gills themselves (see p. 228).

The smooth part of the outer palps in both genera is produced into a thin flap (Text-fig. 15, *m.f.*), which folds over the inner ones, so that the proximal oral grooves and the mouth are roofed over, and possible loss of food guarded against. The flap, however, is capable of movement and can be withdrawn to expose the grooves.

A similar membrane is found in a number of bivalves with long proximal oral grooves. In the Anomiidae, Solenidae, and Solecurtidae, in which it is thin and transparent, it is found on the outer palps as in the Arcidae; but in Pinna fragilis and also in Atrina rigida (Grave, 1909, p. 417) it projects from the inner palps. In Ostrea edulis, according to Yonge (1926, pp. 297–8), 'the inner and outer palps of the two sides are united to one another in the region of the mouth, which lies in the middle line in the groove formed by the continuation of the grooves between the two sets of palps. The outer palps are united for about a quarter of their length, so that the mouth is entirely enclosed.' In Lima no smooth region of the palps is visible, the inner palps being united to the outer, so that the proximal oral grooves of the two sides and the mouth are entirely hidden; hence Pelseneer (1906) considered that Lima has two mouths. This seems to occur also in Amussium pleuronectes, while in Pecten and Chlamys interdigitating of the highly frilled edges of the 'lips' accomplishes the protection of the proximal oral grooves and the mouth. Lima, Pecten, and Chlamys, and in all probability Amussium, are swimming bivalves producing strong water currents during swimming movements, while in the burrowing forms, Glycymeris, Solenidae (Drew, 1907, pp. 133–5), Solecurtidae, and Pinnidae (Grave, 1909, p. 414) a strong current is forced from the shell anteriorly during burrowing; in all these forms the water current might be expected to dislodge food travelling along the proximal oral grooves if these were not



TEXT-FIG. 15.

Arca tetragona Poli. Sketch of the living palps of one side. *i.d.*, inner, and *o.d.*, outer demibranch; *l.o.g.*, lateral oral groove; *p.o.g.*, proximal oral groove; *m.*, mouth; *m.f.*, membranous flap which roofs over the proximal oral groove and the mouth, but is here shown folded outwards; *x.*, point at which material is rejected.

covered. In the fixed bivalves, Ostrea, Heteranomia, and Monia, it is possible that food material might be dislodged from uncovered proximal oral grooves on clapping of the valves.

The Sorting Mechanism of the Gills.

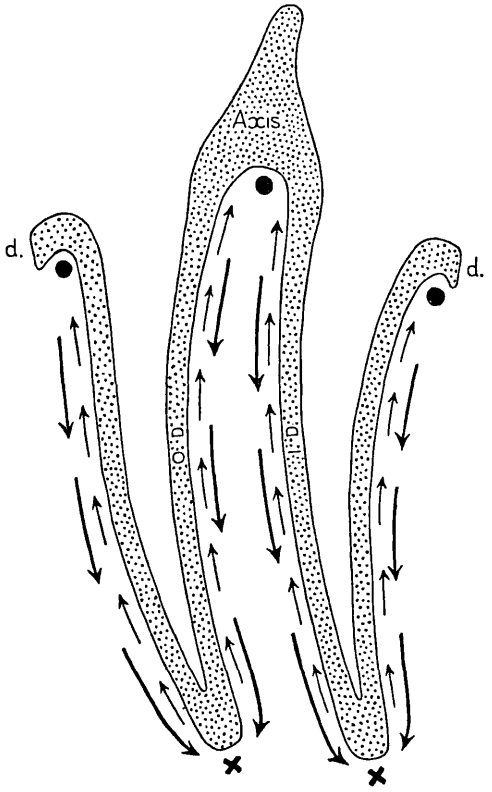
In Glycymeris and Arca there is an efficient sorting mechanism on the gills themselves, correlated with the small size of the palps. Briefly this mechanism results in material which will ultimately reach the palps travelling dorsally along the filaments into orally directed currents, while material to be rejected travels ventrally along the filaments into posteriorly directed currents (Text-fig. 16).

Along the dorsal groove between the bases of the two demibranchs of each side, and along the dorsal edges of all the ascending lamellae, the current is anterior in direction leading to the palps and the mouth. The current along the ventral edges of the demibranchs, on the contrary, is posterior in direction (see Text-figs. 11, 12, and 16), that is, it is a rejection current leading away from the mouth. Such a backwardly directed current in this position is rare in Lamellibranchs, and is known at present only in members of the Arcidae and Anomiidae. It has been previously noted in Arca by Stenta (1903, p. 224) and in Monia machrochisma by Kellogg (1915, p. 666).

On the frontal surfaces of the filaments particles may be transported either dorsally or ventrally on the same filament, and even at the same time (Text-fig. 16). This is not due to reversal of the effective beat of the cilia, but to different tracts of frontal cilia. As previously mentioned, there are three of these on each filament; a median tract of coarse cilia—fully active only when stimulated—with the effective beat toward the free ventral edge of the demibranch and its rejection current; and an outer tract on each side of fine, continuously active, food-conveying cilia, with the effective beat dorsalward into paths leading toward the mouth.

Observations, both on gills while still attached to the animal and on pieces of demibranch, showed that as a general rule heavy particles, such as fine carborundum (3F), travel ventrally

to be rejected, while light particles, such as carmine and animal charcoal, travel dorsally and are conveyed to the palps. From



TEXT-FIG. 16.

Diagrammatic transverse section showing the form of the gill and the direction of the frontal and longitudinal currents in the Arcidae. ● indicates the position of oralward longitudinal currents; X that of posteriorly directed longitudinal currents; arrows show the direction of frontal currents, ventralward currents being due to coarse cilia and dorsalward currents to fine cilia. *I.D.*, inner, and *O.D.*, outer demibranch; *d.*, dorsal edge of ascending lamella.

this it would seem that heavy particles stimulate the coarse cilia to activity, which the light ones fail to do. But conditions during such observations were unnatural in that the gills were

laid horizontally, and particles were therefore particularly subject to the influence of gravity, while under natural conditions the animals may be at any angle to the horizontal. It is difficult then to account for the normal stimulation of the coarse cilia, but it seems possible that heavy particles are flung against the gill, by the water current produced by the lateral cilia, with a greater momentum than are the light particles, thus stimulating to action the median tract. The heaviest particles entering the mantle chamber will of course drop out of the inhalent current, owing to the influence of gravity, as its path widens, but possibly there may be a further sorting of particles before the gills are actually reached, in that, of those remaining in suspension, the heavy may lag behind the light ones in the final acceleration of the current as it approaches its motive source, the lateral cilia. If this occurs, most of the light ones may reach the outer tracts of frontal cilia, and most of the heavy particles come under the influence of the median tract.

That the direction in which a particle will travel is not dependent on its size, as such, has been proved by the use of particles of the same size but of different weights. Thus when particles of carborundum and animal charcoal were used of a size such that they passed through fine silk net of a mesh of 100 strands to the inch, but not through that of 180 to the inch, the greater part of the carborundum travelled ventrally and the animal charcoal dorsally. The quantities dropped on the lamella were, as near as possible, equal in the two cases. Carborundum is very roughly about $3\frac{1}{5}$ times as heavy as animal charcoal. Though particles of the same size are used, one has to judge largely by sight, for even when they are dropped sparsely on the lamellae, mucus tends to cement them in small collections.

A clear-cut difference in the direction in which the two types of particles travel cannot always be obtained; this may possibly be due to varying degrees of sensitiveness on the part of the animal. Animal charcoal on some occasions had a distinct tendency to travel ventrally, particles of the size given above either evidently acquiring the minimum momentum to cause stimulation of the coarse cilia, or mucous production being

excessive for some reason. When immediately after the failure of charcoal to travel dorsally, powdered carmine was used, this was carried dorsally without hesitation. Carborundum is roughly about $4\frac{3}{5}$ times as heavy as carmine.

In experiments with carborundum and carmine, the passage in one direction was more complete in the case of carmine, fewer particles out of each small quantity dropped on the lamella passing ventrally than of carborundum dorsally. Carmine particles, if dropped sparsely enough, are transported dorsally, even from near the ventral margin of the demibranchs; if dropped practically on the ventral edge, they, of course, are carried along it posteriorly. When material is dropped copiously on the lamellae it not only acts directly in the stimulation of the coarse cilia, but probably indirectly in calling forth an excessive production of mucus, strings of mucus and embedded particles becoming entangled with the cilia and tending to cause their activity.

Over the dorsal region of the lamellae there is a distinct tendency for all particles, even of carborundum, to pass dorsally into orally directed currents. Dorsalward movement of particles over the dorsal region of the lamella is found also in many Lamellibranchs in which the frontal cilia over the rest of the lamella beat ventrally: this is indicated in Wallengren's figure of Mytilus (1905, figs. F and G) and in Orton's diagram of the general mode of feeding in Lamellibranchs (1912, fig. 14).

Reversal of the direction in which particles are travelling has been observed, and is somewhat difficult to account for. On one occasion when small quantities of powdered carmine were fed to the gill of Arca tetragona they travelled dorsally, the particles during their passage becoming cemented by mucus and arriving in the dorsal region as a string which stretched across the filaments. This string was then seen to travel back along the path it had come. The string was not always in a straight line as it travelled, either because the coarse frontal cilia were not active on all the filaments concerned, or because it had become caught up, and on such filaments lagged behind. It tended to straighten out as it moved onward. This suggests the possibility that the tug of mucous strings caught

up on motionless cilia may stimulate them to activity, and cause material to be transported in the opposite direction to which it previously had been moving. The formation of the strings of particles and mucus only occurred for a short time after the observations started. After a while possibly the mucous cells become temporarily emptied of their contents, or the gill becomes less irritable, and therefore less mucus is poured out. When little mucus is secreted the carmine particles remain practically discrete, and being light are transported dorsally as usual.

Certain observations given below indicate that the stimulation of the coarse cilia is local, though it has been impossible to determine whether the cilia themselves are directly stimulated, or through the medium of the short, triangular clusters of sense cilia which occur amongst them (p. 222). From the fact that these sense cilia are so short that their tips are only visible when the coarse cilia are at rest, it seems possible that they function in the stimulation of these, but on the other hand they may be concerned with the general sensitiveness of the gills, or may even be concerned with the outpouring of mucus.

That the stimulation of the coarse cilia is local may be inferred from the fact that when a small quantity of charcoal is dropped near the ventral margin of the lamella, and one of carborundum rather more than midway up the lamella, the two travel toward each other; on meeting both are carried ventrally. This incidentally indicates the greater strength of the beat of the coarse than of the fine cilia.

Actual observations (without a coverslip, at a magnification of 500) of the behaviour of the coarse cilia when a particle, or collection of particles, is being transported ventrally, showed that they were active for a variable but rather short distance in front of and behind the moving mass. This may also be seen when material becomes hung up on the lamella.

Very small particles may be seen in surface view of the lamella, at a magnification of 500, to travel dorsally along the sides of the frontal surface of the filaments, that is they travel along the tracts where the fine, continuously active cilia are found. Larger, though still light, particles are carried more or less along the middle of the frontal surface, coming in contact with the

fine cilia of both side tracts, which drive them dorsally; they are apparently light enough not to stimulate the coarse cilia to action. It was in this way evidently that a piece of filter paper, 1 mm. square, was transported—though slowly—dorsally, as was observed during a series of experiments. Tinfoil of the same size was carried slowly ventrally, after generally remaining stationary for varying periods. The tinfoil being smooth it is possible that it was necessary for mucus to collect on it, so that the cilia had something to work against, before movement was possible.

It is probable that while the tracts of cilia beating in opposite directions are used in the sorting of food particles, the coarse cilia are chiefly valuable at such times as the water entering the mantle chamber is laden with sand and mud; this no doubt occurs in Glycymeris during burrowing.

There appears to be little difference in the maximum rate at which suitable particles are transported by the two types of frontal cilia. The minimum time in which powdered carmine was transported dorsally by the fine frontal cilia over a distance of 11·5 mm. was 25 seconds in eight consecutive trials, with a maximum time of 32 seconds and an average of 29 seconds. The variation in the rate is largely, if not entirely, due to the catching up of particles on the lamella, owing to the secretion of mucus.

With the coarse frontal cilia the rate of transportation ventrally of fine carborundum was more rapid when it was dropped fairly thickly and evenly in patches of about 2 mm. across than when sparsely scattered. In the former case the time taken to travel 11·5 mm. was 25 to 27 seconds in four consecutive trials: in the latter the minimum time for seven consecutive trials was 30 seconds, with a maximum of 45 seconds and an average of 37 seconds. It is evident that the coarse cilia were more uniformly and consistently stimulated by the larger quantity of material.

When sand grains between $1{\cdot}3 \times 0{\cdot}8$ and $0{\cdot}3 \times 0{\cdot}3$ mm. were used in small quantities, the rate was somewhat slower than for carborundum, namely in five consecutive trials a minimum time of 35 seconds, with a maximum of 42 seconds and an average

of 37·5 seconds for 11·5 mm. When on three occasions the lamella was well covered with these sand grains—that is with a layer some grains deep—all were cleared from the lamella (up to ca. 12 mm. deep) in 43 to 52 seconds.

Powdered carmine is therefore transported by the fine cilia rather less rapidly than a copious supply of carborundum by the coarse ones. Fine sand impinging on the gill in bulk is removed in less than 1 minute.

The Palp Currents.

In Arca tetragona (see Text-fig. 15) the current diagonally across the folds is oral in direction; in the grooves it is outward, leading into a current, along the smooth border, which ends in a vortex near the anterior limit of this part (Text-fig. 15, *x*.). In the normal position of the palps such collections are removed by way of the rejection tracts of the gills and mantle.

Over the greater surface of the smooth region of the palps particles pass into the proximal oral groove (*p.o.g.*), in which there is an orally directed current. On the thickened outer edges, however, and on the membranous flap (*m.f.*) roofing over the groove, the current is outward and backward. Particles transported by these currents join the collections (at *x*.), previously mentioned, near the junction of the folded and smooth regions of the palps.

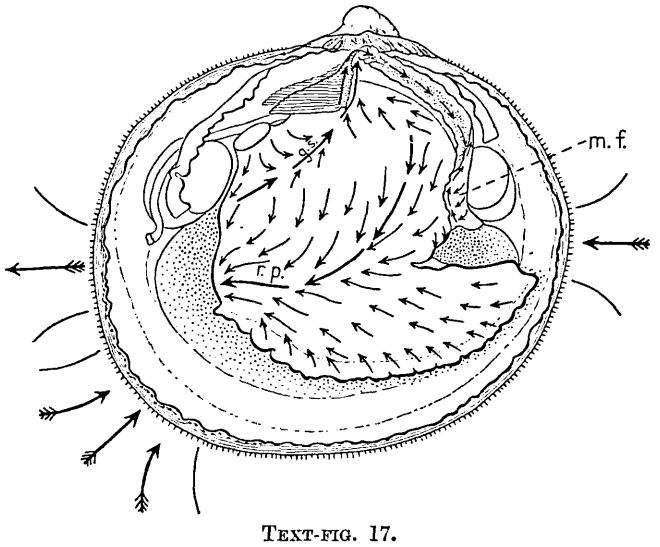
The palp currents of Glycymeris glycymeris are similar to those of Arca tetragona except for the great reduction of the folded region of the palps.

Ciliation of the Visceral Mass and the Mantle.

The Visceral Mass.—The ciliary currents of the visceral mass of Glycymeris glycymeris are shown in Text-fig. 17, those of Arca tetragona in Text-fig. 18. On the dorsal region there is a distinct ciliated tract[1] (*g.s.*) running anteriorly and dorsally, forming with that along the dorsal edge of the

[1] Definite tracts on the mantle and visceral mass are uniformly ciliated, whereas over the rest of the surface the ciliation is scattered, ciliated cells being separated by unciliated ones, though the movement of particles is often very noticeable.

ascending lamella of the inner demibranch—when it is touching the visceral mass—a single current, which at the extreme anterior end passes between the palps. Large particles, however, which fail to enter between the palps, or are rejected by them, will be carried posteriorly along the ventral margin of the inner



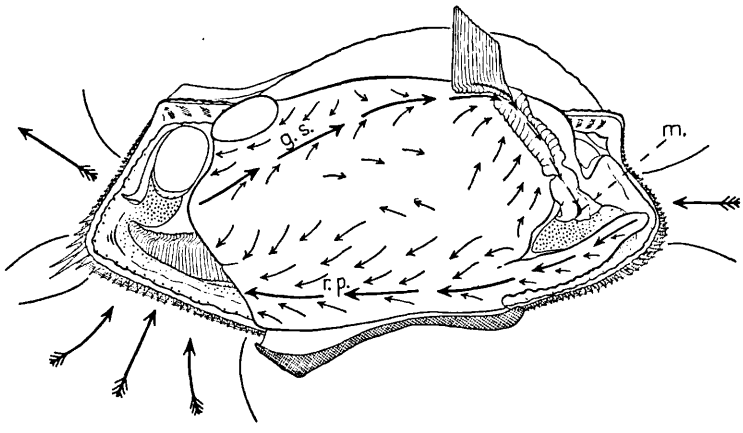
TEXT-FIG. 17.

Glycymeris glycymeris (L.) viewed living from the right side to show the currents on the visceral mass and the foot. The oral end of the proximal oral groove and the mouth is shown roofed over by the membraneous flap (*m.f.*). The foot is somewhat retracted dorsally; normally the ventral edge lies against the mantle margin. *g.s.*, ciliated path on the visceral mass, forming one stream with that along the dorsal edge of the ascending lamella of the inner demibranch; *r.p.*, rejection path. Actual size.

demibranch, the anterior edge of which lies close against the palps. In an opened Arca the anterior tongue-like portion of the foot has been seen bent dorsally, with the tip near the palps and strings of material passing on to it. If this normally occurs it is perhaps possible that collections are sometimes removed by the pedal currents directly from the palps.

In about the region of the junction of the foot with the visceral mass, there is a second distinct ciliated path running

in the opposite direction to the first and ending on the posterior edge of the foot; this is a rejection path (Text-figs. 17, 18, *r.p.*). Particles collecting here either fall on the mantle, or pass on to the gills, or are shot from between the valves on their sudden rapid closure. In Text-figs. 11 and 17 of Glycymeris the foot is shown considerably retracted dorsally. In a feeding animal the ventral edge of the foot lies against the mantle

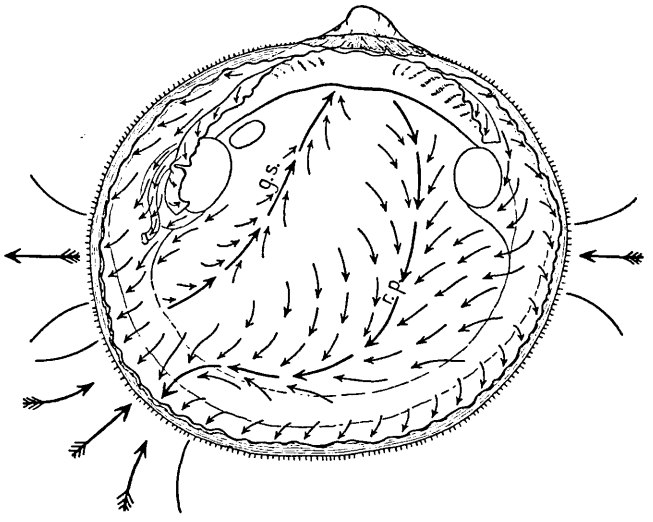


TEXT-FIG. 18.

Arca tetragona Poli viewed living from the right side to show the currents on the visceral mass and the foot. *g.s.*, ciliated path on the visceral mass, forming one stream with that along the dorsal edge of the ascending lamella of the inner demibranch; *m.*, mouth; *r.p.*, rejection path. ×2.

margin, the small posterior projection, near which the ciliated path ends, reaching to the mantle edge, and particles fall from it directly to the exterior. This ciliated path receives tributary streams from the greater area of the visceral mass and foot; those from the foot appear to be very slow, but the rate probably depends on the state of contraction of the foot and on the amount of mucus secreted. Although they are difficult to demonstrate just after opening the animal, after a night under circulation they can be clearly seen. The impeding of the action of the pedal cilia by contraction and mucus may be responsible for Kellogg's (1915, p. 655) general statement that the foot is

not ciliated in any full-grown bivalve. There is a copious secretion of mucus by the foot in both Glycymeris glycymeris and Arca tetragona. In both species there is a small area of the visceral mass where ciliary currents could not be demonstrated. It is overlaid by the gills, which would remove any particles falling on it.



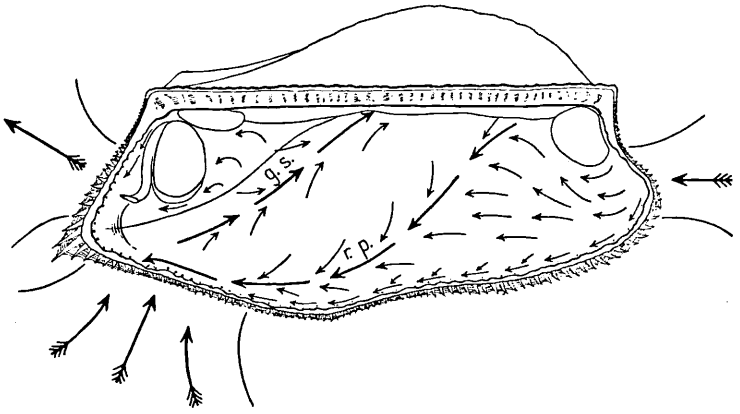
TEXT-FIG. 19.

Glycymeris glycymeris (L.), showing the mantle currents. *g.s.*, ciliated path on the mantle, forming one stream with that along the dorsal edge of the ascending lamella of the outer demibranch; *r.p.*, rejection path. Actual size.

Over the outer surface of the posterior adductor muscle and the rectum currents pass posteriorly into the exhalent current.

The Mantle.—Heavy particles, falling out of the inhalent current, as its path widens, are collected into a recurrent stream on the mantle (Text-figs. 19 and 20, *r.p.*), which ends on the mantle edge in the region of the main, or posterior, inhalent aperture, at which point waste material collects. The mass falls over the edge of the shell as it is added to from behind; rarely under experimental conditions is it expelled by the sudden closure of the valves, for collections on the mantle edge, even

when composed of coarse carborundum, do not appear generally to stimulate clapping of the valves. Waste material (or pseudo-faeces) passes over the mantle margin against the inhalent current: the secretion of mucus probably keeps particles in close contact with the cilia, and prevents their removal by this current. To demonstrate the recurrent tract clearly in the entire animal



TEXT-FIG. 20.

Arca tetragona Poli, showing the mantle currents. *g.s.*, ciliated path on the mantle, forming one stream with that along the dorsal edge of the ascending lamella of the outer demibranch; *r.p.*, rejection path. ×2.

it is necessary to use coarse carborundum, very little of which reaches the gills, practically all falling on the mantle.

On the posterior and dorsal region of the mantle there is a ciliated tract running anteriorly and dorsally, forming with that along the dorsal edge of the ascending lamella of the outer demibranch—when it is touching the mantle—a single current, which at the extreme anterior end passes between the palps. This current (Text-figs. 19, 20, *g.s.*) corresponds to the similar one on the visceral mass. It receives tributary currents from a small area on each side of it. Particles which fail to pass between the palps, or are rejected by them, are removed either by the recurrent tract on the mantle or by that at the ventral edge of the demibranch.

Along the ventral mantle margin of Arca tetragona there is a backward current leading into the main recurrent path; this is probably correlated with the fixed mode of life (see Stenta, 1901), for it is absent in Glycymeris glycymeris, where particles on the mantle margin are carried to the edge throughout its extent.

Summary.

The gills of Glycymeris glycymeris and Arca tetragona are eleutherorhabdic or filibranchiate and the lamellae flat and homorhabdic. The latero-frontal cilia of the filaments are unusually tenuous and short, and are termed micro-latero-frontal cilia. The frontal cilia are arranged in three tracts: a median tract of coarse cilia, with the effective beat ventralward and fully active only when stimulated; and two outer tracts of fine, continuously beating, food-conveying cilia with the effective beat dorsalward.

On the frontal surface of the filaments particles are carried either ventrally or dorsally according to whether they are of a type and a quantity to cause or not to cause stimulation of the coarse cilia. Some observations are given on the nature of the stimulus causing activity of these cilia. The currents along the ventral edges of the demibranchs are, unlike those in most Lamellibranchs, directed away from the mouth; those between the bases of contiguous demibranchs of each side of the body and along the dorsal edges of all the ascending lamellae are toward the mouth.

Correlated with the effective ciliary sorting mechanism on the gills is the small size of the palps.

The ciliary currents of the visceral mass and the mantle of the two species are described.

SECTION C

The Ciliary Feeding Mechanism of some members of the Anomiidae, Heteranomia squamula (L.), Monia squama (Gmelin), and M. patelliformis (L.); with a Note on the Hypobranchial Gland of the genus Monia.

With Plates 10, 11, and Text-figures 21–31.

CONTENTS.

INTRODUCTION.

Kellogg in 1915 (pp. 663–6) briefly described the extraordinary ciliary mechanism of the gills of Monia machrochisma Deshayes with the frontal currents over all lamellae—except for a narrow dorsal zone on each—toward the free edges of the demibranchs, along which material was carried posteriorly, away from the mouth. He found that over a very narrow dorsal zone only of each lamella was material carried to the base and forward to the palps, and was thus forced to conclude that 'apparently the narrow strips at the bases of the lamellae collect sufficient food'. This ciliary mechanism being unlike that known in any other bivalve it was considered of interest to observe additional members of the family. Heteranomia squamula (L.) (= Anomia aculeata Müller, see Winckworth, 1922, p. 33), Monia squama (Gmelin), and Monia patelli-

formis (L.) have been examined: Anomia ephippium[1] could not be obtained at Plymouth, but there is little reason to suppose that it will differ materially from Monia in its method of feeding.

The specimens of Heteranomia squamula examined varied between 8 and 14 mm. in length, those of Monia squama between 1·25 and 4·2 cm., and those of Monia patelliformis between 2·7 and 3·2 cm.

Anomia, Heteranomia, and Monia are much flattened bivalves permanently fixed by means of a byssus passing through a large sinus in the flat right or lower valve: the left or upper valve is concave, the degree of concavity varying in different individuals. The body has suffered considerable rotation and torsion, the anterior half being asymmetrical. In so far as this has affected the food-collecting organs the proximal oral groove of the right side is considerably longer than that of the left, while the right gill is shorter than the left one, and is bent slightly antero-ventrally to meet its fellow, the two continuing backwards side by side in a wide curve.

The gills are suspended by membranes, which are free for about the posterior third.

In Anomia and Monia the demibranchs consist of both descending and ascending lamellae, but in Heteranomia descending lamellae alone are present, and because of this Ridewood (1903, pp. 193–5) placed the latter with Dimya in the sub-order Dimyacea.

The figures of Heteranomia and Monia squama (Pls. 10 and 11) show that the depth of a single lamella of Heteranomia is relatively greater than the combined depth of the descending and ascending lamellae of a demibranch of Monia (the demibranchs of Monia squama and Monia patelliformis are about the same depth).

[1] No specimens of Anomia ephippium were obtained during the course of these investigations (March 1931–December 1934). The record in the Plymouth Marine Fauna (M.B.A., 1931, p. 237), probably includes Monia squama, Monia patelliformis, and Heteranomia squamula, as well as Anomia ephippium, but large specimens of the latter species were never, I am informed, very frequent.

The method of division of the supra- from the infra-branchial chamber varies in the three genera. In Heteranomia there is strong ciliary junction between the lower edges of the two inner demibranchs, and between the edges of the outer and the mantle. In Monia there seems to be no appreciable junction; interlocking cilia are present on the dorsal edges of the ascending lamellae, and where the inner demibranchs are concerned these probably effect a weak union between them, while those of the outer demibranchs merely rub against the mantle, on which no interlocking cilia could be distinguished either in the living animal or in sections. In Anomia the same condition as in Monia is found for the outer demibranchs, except that the dorsal ends of the filaments are themselves united organically in series and are reflected ventrally; the dorsal ends of the ascending filaments of the inner demibranchs, however, are not only organically united in series, but the dorsal edges of the lamellae are united inter se (see Ridewood, 1903, p. 197; Bourne, 1907, p. 263).

The mantle is provided with a velum which is generally held more or less perpendicular to it, the edges of the right and left vela touching, except in certain places functioning as inhalent and exhalent apertures (see fig. 2, Pl. 11). Water can doubtless be drawn into the mantle chamber at any point anterior to the gill tips if the vela are drawn apart, but the usual place of entry would seem to be in the position indicated by the arrows in Pl. 11.

In Heteranomia the margins of the right and left vela are fused from the hinge line to the dorsal border of the exhalent aperture (Pl. 10, *v.f.*). The uniting mantle membrane thus formed is excessively thin and delicate, easily rupturing—as it frequently does during the removal of the right valve.

The edge of the velum and the tentacles are extremely sensitive to stimulation in both Monia and Heteranomia, a gentle touch causing contraction of the mantle, of the branchial axes, and of the adductor and byssal muscles. The gills themselves are much less sensitive to stimulation. Striated fibres are found in the adductor and byssal muscles, and, at least in Heteranomia, in the gill axes.

In Heteranomia and in both species of Monia radial muscles are evident traversing the mantle, the most obvious strands running into the velum near the position of the series of longest tentacles, which occur at more or less regular intervals. These are responsible for contraction of the mantle from the shell edge.

From observations given in this paper it seems that members of the Anomiidae subsist largely on such particles as are brought by the main water current directly to the broad dorsal food grooves of the gills with their oralward currents. On the lamellae the movement of particles is toward the free ventral edges of the demibranchs along which the current is away from the mouth.

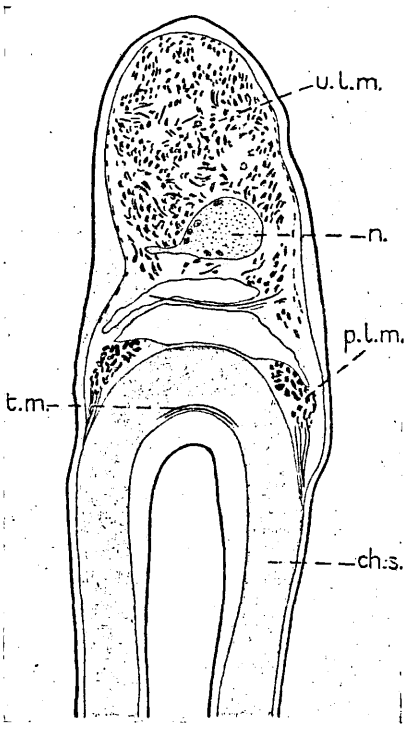
Structure of the Gills and Palps.

(*a*) Heteranomia squamula.

The gill is suspended by a membrane, which contains well-developed longitudinal muscles (Text-fig. 21) responsible for strong contraction of the gill on stimulation of the mantle edge. Throughout the length of the gill axis run widely separated paired longitudinal muscles (*p.l.m.*). The free posterior third of the suspensory membrane is mostly occupied by an unpaired longitudinal, retractor muscle (*u.l.m.*)—accompanied by a large nerve (*n.*)—which becomes inserted on the shell. The fibres of the unpaired longitudinal muscle and the dorsal fibres of the paired ones are finely striated. There is but slight development of transverse muscle-fibres (*t.m.*) above the dorsal groove between the two demibranchs of the gill; fibres from the ventral strands of the paired longitudinal muscles are inserted on the abfrontal surfaces of the dorsal ends of the chitinous supporting structure. By their action these two sets of fibres probably cause separation and approximation of the two demibranchs.

The demibranchs, of which the outer are slightly deeper than the inner, consist of descending lamellae only: the filaments are without interfilamentar junctions except for the ciliated disks connecting them in series at their ventral ends (Text-fig. 22), and the connecting webs at their dorsal ends (Text-fig. 24, *c.w.*).

The lower ends of the filaments of the outer demibranchs are connected with the mantle by interlocking cilia, and those of the inner demibranchs are united with each other for the most

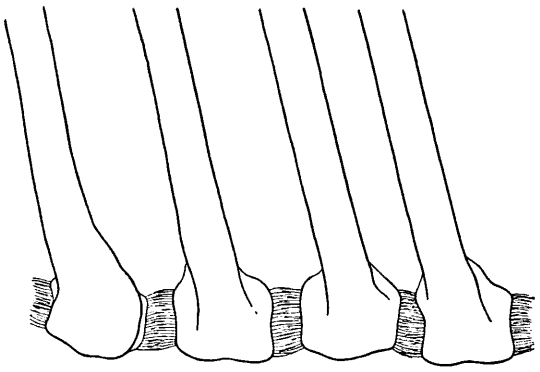


TEXT-FIG. 21.

Heteranomia squamula. Transverse section of the free posterior region of the suspensory membrane of the gill. *ch.s.*, chitinous supporting structure; *n.*, nerve; *p.l.m.*, paired longitudinal ctenidial muscles with striated fibres dorsally and non-striated fibres ventrally; *t.m.*, transverse muscle-fibres; *u.l.m.*, unpaired longitudinal ctenidial muscle. × 166⅔.

part, but the few anterior filaments to the intervening visceral mass, by the same means. The anterior filaments of the right inner demibranch—except for the first few—are very long, thus their ventral ends are enabled to meet those of the left inner

demibranch behind the base of the foot (see Pl. 10). This great depth of the anterior filaments of the right inner demibranch is also found in Anomia ephippium (Sassi, 1905, Pl. 1, fig. 1) and in Anomia (Aenigma) aenigmatica (Bourne, 1907, p. 265, Pl. 15, fig. 1), but not in Monia, the demibranch in the latter genus gradually increasing in depth and being only slightly deeper than the outer in this region.



TEXT-FIG. 22.

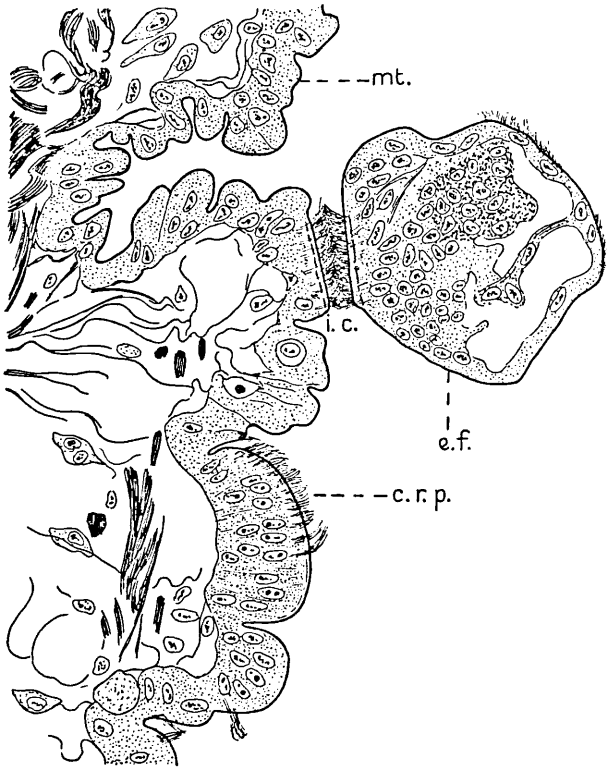
Heteranomia squamula. Frontal view of the ventral ends of four living filaments of an inner demibranch. × 200.

The ciliary connexion is especially strong between the lower edges of the outer demibranchs and the mantle; the ends of filaments occasionally remain connected with the mantle when the demibranch is pulled roughly away; fusion was suspected but sections showed that the junction is entirely ciliary (Text-fig. 23, *i.c.*). It appeared from sections that the band of interlocking cilia on the mantle is situated on a ridge, especially prominent posteriorly. Contraction of the mantle on preservation, however, renders this somewhat uncertain.

Ridewood (1903, pp. 194–5) stated that in the free posterior third of the gill the filaments 'have free rounded ends, without ciliated discs'. This would seem to be an error, for examination of living material showed ciliated interfilamentar junctions on all filaments, even those at the posterior extremity of the gill, and also on all filaments interlocking cilia for junction with

adjacent parts. The demibranchs are firmly attached to the mantle and to each other to the extreme posterior end.

The dorsal ends of the filaments are connected with one another by thin, transparent, interfilamentar junctions or webs



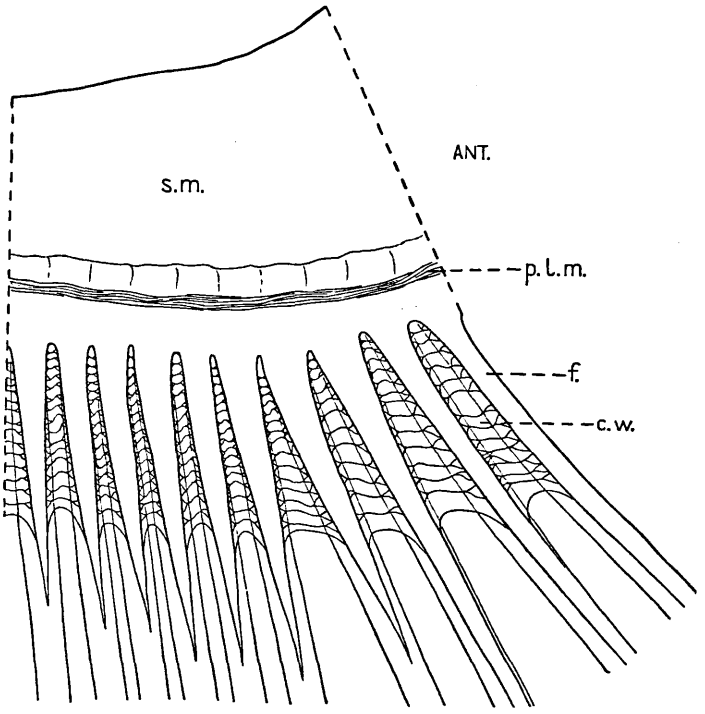
TEXT-FIG. 23.

Heteranomia squamula. Section to show the end of a filament (*e.f.*) adhering to the mantle (*mt.*) by interlocking cilia (*i.c.*), after the demibranch had been pulled roughly away. *c.r.p.*, ciliated rejection path on the mantle. Bouin-Duboscq fixation; Heidenhain's iron haematoxylin and acid fuchsin. × 573⅓.

(Text-fig. 24, *c.w.*), so that the dorsal groove is bounded by entire walls. Running in the webs, between one filament and the next, are exceedingly fine muscle-fibres, which by their

contraction cause the filaments to approach each other in series, thus lessening the interfilamentar spaces.

The Palps.—The palps are of a good size. The smooth region of the outer palps is prolonged into a thin, transparent



TEXT-FIG. 24.

Heteranomia squamula. Suspensory membrane of the gill (*s.m.*) and dorsal ends of the filaments (*f.*) to show the webbed appearance of the latter along the dorsal food groove. *ANT.*, anterior; *c.w.*, connecting web, with fine muscle-fibres; *p.l.m.*, longitudinal (paired) ctenidial muscle. From living material. ×168.

extension which folds over the inner palps, thus enclosing the proximal oral grooves and the mouth. An attempt has been made to show this in Pl. 10 (*m.f.*). The ciliation of the palps was not investigated.

(*b*) Monia squama and Monia patelliformis.

The structure of the gills is very similar in Monia squama and Monia patelliformis, and the two species will be considered together. The suspensory membrane is deep, thin, and delicate; though less muscular than that of Heteranomia, yet the gills are capable of considerable movement. On stimulation of the mantle edge, the gill axes contract strongly antero-posteriorly—the gills being thrown into folds—and the gills, with the ventral edges of the demibranchs touching, bend inwards away from the shell edge. Movements of separation and approximation of the two demibranchs of a side are observable.

An osphradium is clearly visible as a yellow pigmented line on the suspensory membrane of living animals, and runs to the posterior extremity of the gill (Pl. 11, *osph.*).

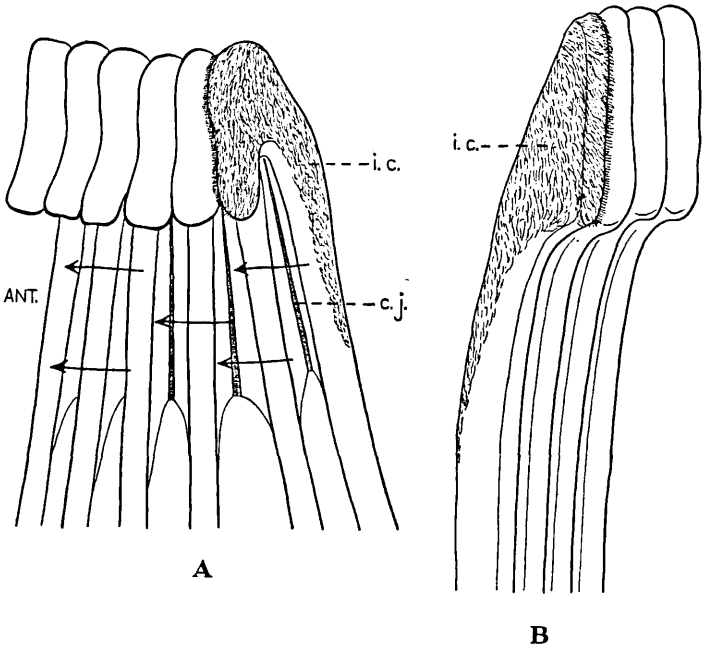
The gills are long, narrow, and curved in a semicircle: the ventral edges are ungrooved. Anteriorly the right inner demibranch is only slightly deeper than the outer and the filaments increase gradually in length, there being no very long anterior filaments as in Heteranomia and Anomia. The ascending lamellae are somewhat narrower than the descending.

The interfilamentar junctions are small, round, ciliated disks. The number of rows has been used as an aid to the identification of the species of Monia by Winckworth (1922, pp. 32–3); it is not, however, entirely constant in the two species, possibly depending to some extent on age. In Monia patelliformis it may be 0 and 1, instead of 1 and 2; and in Monia squama 2 and 2 instead of 2 and 3 or more; that is in addition to the row of ciliated junctions at the ventral edges of the demibranchs.

The dorsal ends of the ascending filaments are strongly held together by very deep ciliated junctions (*c.j.*), giving them a webbed appearance, and forming an imperforate wall for the food grooves in these positions (see Text-fig. 25 A). In both species of Monia the dorsal ends of the ascending filaments of the outer demibranchs (Text-fig. 25 A) differ from those of the inner (Text-fig. 25 B) in that they are bent downward for a short

distance—a condition carried much farther in the genus Anomia. These curved ends are capable of considerable movement, and probably fit closely against the mantle.

A continuous membrane runs across the abfrontal surface of



TEXT-FIG. 25.

Monia patelliformis. A. Dorsal edge of the ascending lamella of the outer demibranch, showing the elongated ciliated junctions and the ventrally curved ends of the filaments. B. Dorsal ends of four filaments of the ascending lamella of the inner demibranch. Arrows indicate the direction of the current along the dorsal food groove. *ANT.*, anterior; *c.j.*, ciliated junction; *i.c.*, interlocking cilia. Living material. × 125.

the dorsal edges of the descending lamellae, so that the food groove between the demibranchs has continuous walls.[1] Contraction of the muscle-fibres in the membrane causes the closing together of the filaments.

[1] Continuous walls to dorsal food grooves are usual in Lamellibranchs.

Interlamellar junctions are absent, except for a low septum at the ventral angle of the demibranchs.

The Palps.—As in Heteranomia the smooth region of the outer palps is prolonged into a transparent membraneous extension (Pl. 11, *m.f.*), which folds over the inner palps enclosing the proximal oral grooves and the mouth. This condition is now known in a number of bivalves (see p. 226). The mouth is sometimes exposed by the separation of the muscular walls of the oral grooves, and the folding back of the membraneous extension. The palp currents were not investigated.

Ciliation of the Gill Filaments of Heteranomia and Monia.

The ciliation of the filaments is very similar in the two genera. The filaments of Monia patelliformis are larger than those of Monia squama, and the ciliation in consequence easier to discern, but there is some increase in size of the filaments with age, as probably occurs in all Lamellibranchs. The filaments of large specimens of Heteranomia squamula (ca. 17 mm. longer diameter) are about the same size as those of Monia patelliformis 27 mm. in diameter.

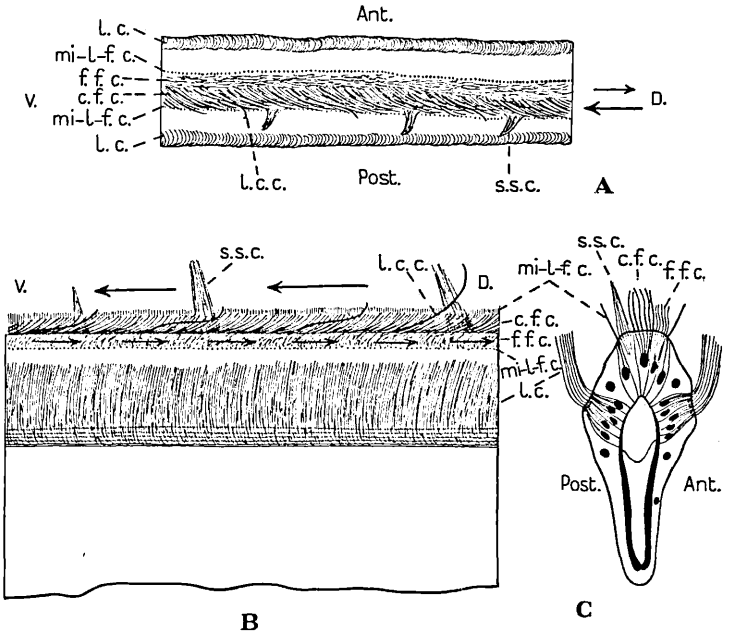
Four sets of cilia are present on the gill filaments: (1) coarse frontal cilia; (2) fine frontal cilia; (3) latero-frontal cilia; and (4) lateral cilia (see Text-fig. 28).

Frontal Cilia.—These are chiefly long and coarse (Text-figs. 26, 27 B and C, 28, *c.f.c.*) much resembling in appearance the coarse frontal cilia of Arca and Glycymeris previously described (p. 222). The effective beat is towards the free edge of the demibranchs. As seen at rest on isolated filaments and pieces of lamella they lie with the tips directed dorsally, that is their position of rest is at the beginning of the effective stroke (see Text-figs. 26 A and B, 27 B).

In addition to the coarse cilia a narrow tract of fine ones with the effective beat dorsalward occurs between them and the micro-latero-frontal cilia on the anterior side of the filament only (Text-fig. 26, 27 A and C, 28, *f.f.c.*): thus in the Anomiidae the frontal cilia are in two tracts. On the outer demibranchs of Heteranomia the fine cilia can be seen on the ends of

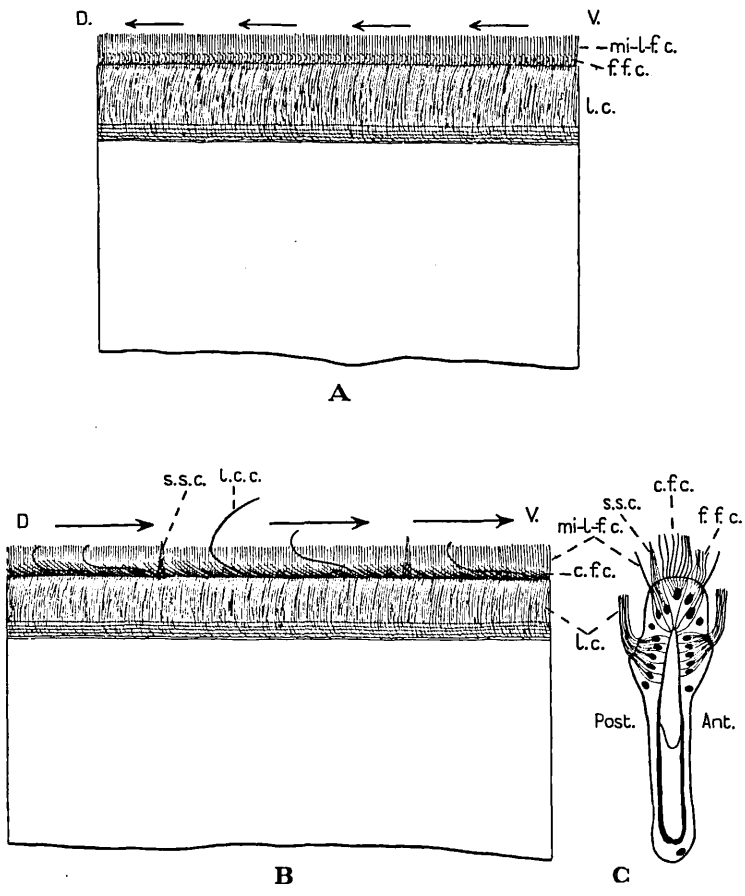
the filaments, for the coarse frontal cilia do not extend to the extreme tips on these demibranchs, which are without a longitudinal current at the free edge.

In Heteranomia large, triangular clusters of probably



TEXT-FIG. 26.

Heteranomia squamula. Sketches to show the various tracts of cilia on the gill filaments. A. Living filament in almost frontal view. The lateral cilia are shown at rest, when they appear as a rounded curb in this view: the micro-latero-frontal cilia appear almost as dots. The sense cilia (*s.s.c.*) are foreshortened. B. Anterior lateral surface of living filament, but the filament tilted slightly so that the coarse frontal cilia are visible. The micro-latero-frontal cilia on the anterior side are indicated by dots for the sake of clearness, though they do not appear as such in this view. From a specimen 14 by 17 mm. In both views the coarse frontal cilia are depicted at rest. C. Diagram of transverse section of a filament. Mucous glands are omitted for clearness. *c.f.c.*, coarse, and *f.f.c.*, fine frontal cilia; *l.c.*, lateral cilia; *l.c.c.*, long, coarse cilia or cirri; *mi.-l.-f.c.*, micro-lateral-frontal cilia; *s.s.c.*, sense cilia; *Ant.*, anterior; *Post.*, posterior; *D.*, dorsal; *V.*, ventral. Arrows show the direction of the effective beat of the frontal cilia. A and B × 430.



TEXT-FIG. 27.

Monia patelliformis. Sketches to show the various tracts of cilia on the gill filaments. A. Anterior lateral surface of living filament. B. Posterior lateral surface of living filament. The coarse frontal cilia are shown at rest. C. Diagram of transverse section of a filament. Mucous glands are omitted for clearness. Lettering as in Text-fig. 26. Arrows show the direction of the effective beat of the frontal cilia. A and B ×430.

tactile cilia (*s.s.c.*) occur isolated between the coarse frontal and the micro-latero-frontal cilia, that is on the posterior side of the filament only (Text-fig. 26). They appear to beat but rarely,

being generally motionless when observed. In addition there are occasional very long and stout cilia, or cirri (*l.c.c.*), which when inactive are practically hidden among the coarse cilia.

In Monia both types of isolated cilia are present (Text-fig. 27 B, *s.s.c.*, *l.c.c.*), but the triangular ones are considerably smaller and less numerous than in Heteranomia squamula. In a large individual of Monia squama (4·2 by 3·7 cm.), however, they were of a good size, though not as large as those of Heteranomia.

Latero-frontal Cilia. These are unusually fine and short; they are micro-latero-frontal cilia (Text-figs. 26, 27, 28, *mi.-l.-f.c.*), as already described in the Arcidae (p. 223). In both Heteranomia and Monia they are about 12μ long.

Lateral Cilia (Text-figs. 26, 27, 28, *l.c.*). The long and very narrow cells bearing the long lateral cilia are in five rows, that nearest the abfrontal surface being especially narrow. The cilia, which have a rapid beat, are somewhat longer in Heteranomia than in Monia.

Abfrontal Cilia are absent. An occasional stout tactile cilium is found on the abfrontal surface of the dorsal edge of the ascending lamellae in Monia. In the large individual of Monia squama mentioned above they reached a length of 44μ.

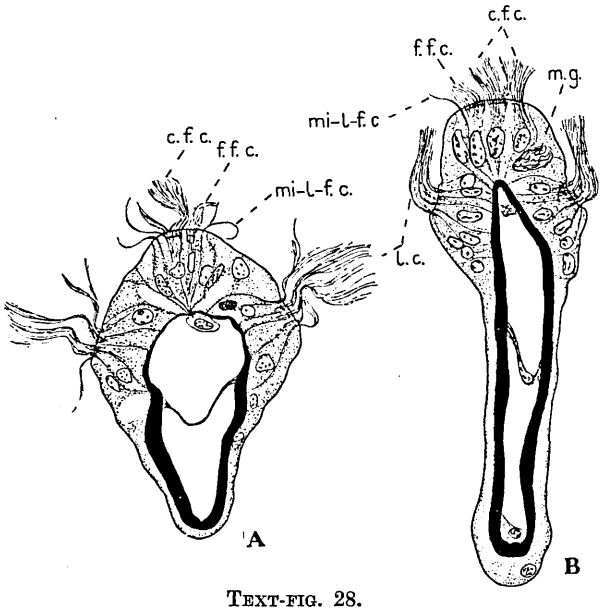
The appearance of the various tracts of cilia in transverse sections of the filaments of Heteranomia and Monia are shown in Text-fig. 28. The coarse and fine frontal cilia are not always distinguishable in sections, as cilia tend to separate into their component fibres on fixation.

The Gill Mechanism of Heteranomia and Monia.

The gill mechanism of the two genera being essentially similar, in spite of the single lamella to a demibranch in Heteranomia, they will be considered together.

The mode of feeding in the Anomiidae has proved difficult to elucidate satisfactorily. It seems, at least under experimental conditions, that the surfaces of the lamellae are concerned chiefly with rejection, the obvious movement of particles on them being toward the free ventral edges of the demibranchs, along which currents convey them away from the mouth and

to the exterior. Fine frontal cilia beating dorsally are present on the filaments, but no appreciable movement of particles due to them has been demonstrated on attached gills and when the lateral cilia were active. It seems as though the Anomiidae subsist largely on material brought by the main water current



TEXT-FIG. 28.

Transverse sections of gill filaments. A. Heteranomia squamula. Bouin-Duboscq fixation; Heidenhain's iron haematoxylin and acid fuchsin. B. Monia squama. Bouin-Duboscq fixation; Ehrlich's acid haematoxylin. The difference in the shape of the blood-space in the two filaments is due to the condition at the time of fixation, and is not a characteristic difference. *m.g.*, mucous gland. Other lettering as in Text-fig. 26. ×735.

directly to the broad dorsal food grooves of the gills and conveyed along them to the mouth. The conspicuous ventral currents on all lamellae, and the posterior direction of the currents along the free ventral edges of the demibranchs was apparently first noted by Kellogg (1915, p. 666) in Monia machrochisma. In the Anomiidae, as in the Arcidae, the ventral edge of the demibranch is a rejection tract.

In Heteranomia a posterior current is found along the adherent ventral edges of the two inner demibranchs, the ends of the filaments bearing coarse cilia which beat posteriorly; but along the ventral edges of the outer demibranchs there is none on the filaments themselves, their ends being without coarse posteriorly beating cilia. (By the absence of these cilia the outer can be easily distinguished from the inner demibranch on excised pieces of gill.) The recurrent path on the mantle (see p. 260) lying just beyond the ventral edge of the outer demibranch serves as a rejection tract for about the anterior two-thirds (see Pl. 10), large particles travelling down the filaments passing into this path. The distance of the path from the edge of the demibranch varies in different individuals, being largely dependent on the shape of the valves (as is well known, Anomia, Monia, and Heteranomia vary rather widely in shape according to the surface of attachment): it is shorter in forms which are longer than deep (see Pl. 10) than in those which are deeper than long. Along the edge of the posterior third of the demibranch there is no appreciable current on the demibranch itself, and the recurrent path of the mantle is at some considerable distance. The fate of unwanted material arriving at the edge in this region is uncertain. A string of mucus and particles stretching along the edge here was observed on one occasion to rotate and travel exceedingly slowly anteriorly until it reached the recurrent path on the mantle, along which it was hurried. Such slow anterior movement is apparently due to the fine cilia, which alone clothe the ends of the filaments of the outer demibranchs. Particles embedded in mucous strings have been seen also to be removed from the edge of the demibranch in this region by the recurrent path on the velum, brought close to it by contraction of the mantle. Whether this reaction of the mantle to the presence of material occurs normally is unknown.

Between the edge of the demibranch and the ciliated path in the posterior region, and anteriorly also in individuals in which the two are some distance apart, some slight erratic movement of particles toward the path occurs, due to groups of cilia.

In the broad groove between the two demibranchs of each side particles travel towards the mouth. In both

Heteranomia and Monia imperforate walls for the groove are formed by a membraneous web (see pp. 246 and 249). In Monia oralward tracts are also found along the dorsal margins of the ascending lamellae of both inner and outer demibranchs, the ends of the filaments being held firmly together by very elongated ciliary junctions (Text-fig. 25, *c.j.*), which also prevent particles escaping between the filaments: as the dorsal edges of the ascending lamellae of the inner demibranchs in all probability touch, even if the ciliary junction is slight, the two currents here will form a single broad tract.

As previously stated two tracts of frontal cilia are present on the filaments, one of coarse cilia beating ventrally, and a narrow one of fine cilia beating dorsally. The coarse cilia beat rapidly and strongly, practically all particles touching the frontal surfaces, particularly those too large to pass between the filaments, being transported by these ventrally into the rejection tracts at the free edges of the demibranchs. This movement of particles is the obvious one on the gills. Collections beyond a certain size passing along the dorsal grooves may even be dragged away by these cilia and carried ventrally.

Mucous glands in the filaments of Heteranomia and Monia appeared to occur mostly on the posterior side of the frontal surface, near the tract of coarse cilia, but in sections of Anomia ephippium from Naples they occurred on both anterior and posterior sides.

Dorsal transportation of particles by the fine frontal cilia has been seen clearly on isolated filaments in side view. On pieces of lamella particles have been observed, though rarely, travelling dorsally over the tracts of fine cilia, but nothing has been seen in the least approaching the general dorsalward movement of small particles that occurs in the Arcidae. On one or two occasions it was found that if the diatom Coscinodiscus excentricus were dropped one by one on an excised piece of gill of Monia patelliformis left undisturbed for over an hour, these were generally transported dorsally even from near the ventral margins of the demibranchs. (Coscinodiscus excentricus though 50 to 90μ in diameter almost floats in sea-water.) The lateral cilia were more or less motion-

less on these occasions. In later attempts with the attached gills of individuals of both species of Monia the diatom was transported ventrally. The Anomiidae are particularly sensitive bivalves and it may be that under experimental conditions the large frontal cilia become active at the slightest stimulation, but that normally diatoms brought in small numbers to the gills are conveyed dorsally. These organisms, however, would have to be too large to pass between the filaments if the lateral cilia were fully active.

The majority of particles sufficiently small to do so pass between the filaments into the supra-branchial chamber when the lateral cilia are active, and so are lost to the animal. The unusually fine form of the latero-frontal cilia would not seem to be entirely responsible for this, for in other bivalves with micro-latero-frontal cilia—even in the Arcidae which also have flat gills—there is no comparable passage of fine particles through the interfilamentar spaces. The filaments are 30 to 40μ apart in Heteranomia, and about 30μ in Monia; the latero-frontal cilia being only about 12μ long thus do not bridge the interfilamentar spaces. In Glycymeris glycymeris also the filaments are 30 to 40μ apart; the latero-frontal cilia are somewhat longer than those of Heteranomia and Monia, being 14 to 17μ, thus more nearly bridging the interfilamentar spaces but leaving an appreciable gap. The spaces between the filaments of both Anomiidae and Arcidae, however, may be lessened by tightening of the ciliary interfilamentar junctions and by contraction of the muscles in the gill axes and in the webs connecting the dorsal ends of the filaments. The beat of the lateral cilia does not appear to be as rapid in Arca and Glycymeris as in Heteranomia and Monia, so far as this could be judged by sight.

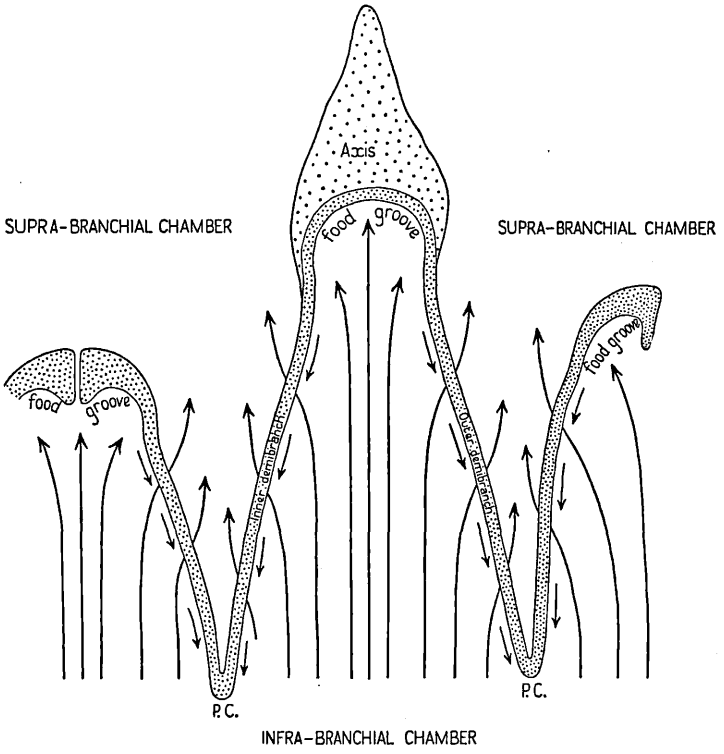
The beat of the lateral, current-producing cilia is particularly strong and rapid in the Anomiidae—Kellogg (1915, p. 666) recorded of Monia machrochisma that 'in no other case has a more furious ciliary action been observed than on the gills and mantle of this form'—and it is probably largely owing to the rapidity of their beat that so many of the particles brought to the gills are swept through into the exhalent chamber. It

is possible that the strength of the inhalent current can be lessened by increasing the size of the inhalent aperture; by approximation of the filaments, which will interfere with the working of the lateral cilia; by stoppage of many of these cilia (intermission is seen on excised pieces of gill, and most probably occurs normally); by closing together of the demibranchs, or some such means, thus allowing the micro-latero-frontal cilia to strain to some extent water passing through the interfilamentar spaces.

In Heteranomia and Monia it can be observed that particles in the main water current travel for some distance almost parallel with the frontal surfaces of the filaments before passing into the interlamellar space, and there for a while follow a path almost parallel with the abfrontal surfaces. Care is therefore needed when examining material under a low-power dissecting microscope to determine whether apparent dorsal movement of particles on the frontal faces of the filaments is due actually to fine frontal cilia, and not movement of particles in the main water current passing almost parallel with the frontal and abfrontal surfaces. The rate of movement of particles transported by the fine frontal cilia is very considerably slower than that of those in the main water current, and this difference in rate allows of distinguishing between the two methods of transportation.

Repeated observations have failed to reveal any appreciable transportation of particles dorsally by the frontal cilia, and ciliary reversal not being observed, it would therefore seem that the Anomiidae collect at least a certain proportion of their food somewhat after the fashion of the Ectoproct Polyzoa (Borg, 1923, pp. 8–9; 1926, pp. 245–50; Atkins, 1932, pp. 411–19), that is they rely largely on what is brought directly to the broad dorsal food grooves of the gills by the main water current (Text-fig. 29). That material does reach the dorsal food grooves in this manner when there is no dorsalward movement of particles along the filaments, can be observed if the gill be fed with carmine particles. Diatoms varying between 10 and 100μ in diameter were found in one section through the stomach of a Heteranomia; the smallest of these might be expected

to pass between the filaments if not brought directly to the food grooves. The feeding method of the Anomiidae in its



TEXT-FIG. 29.

Diagrammatic transverse section of a gill of Monia to show the direction of the water current set up by the lateral cilia, and the direction of the ciliary currents produced by the coarse frontal cilia. Along the dorsal food grooves there are ciliary currents leading to the mouth. *P.C.* indicates the position of posterior currents along the ventral edges of the demibranchs. × ca. 35½. Compare with Ectoproct Polyzoa (Atkins, 1932, fig. 8).

apparent imperfection resembles that of the Ectoproct Polyzoa (Borg, 1926, p. 248).

Ciliary Currents of the Mantle, Visceral Mass, and Foot.

(*a*) Heteranomia squamula.

Mantle.—The ciliary currents of the mantle—apart from one well-defined tract—are difficult to observe. Not only do few individuals recover to any extent from the extensive contraction of the mantle which occurs on removal of a valve, this contraction necessarily interfering with the working of the cilia, but the presence of the large gills creating a strong inhalent current tends to mask the mantle currents: if the gills are removed the mantle contracts so strongly that nothing can be made out. Added to these difficulties is the small size of the animal, about 8 to 17 mm. in diameter. The mantle currents shown in Pl. 10 have been made out from a number of specimens. Owing to the strong current set up by the lateral cilia of the gills carmine particles were found to be of little use for the detection of mantle currents, and the finest carborundum (3F) was chiefly employed.

The lower edges of the outer demibranchs being in connexion with the mantle the area of the mantle in the infra-branchial chamber is narrow, except anteriorly.

One tract on the mantle is clearly defined; it has a yellowish tint and appears thicker than the mantle on each side of it, owing to the depth of its cells and its clothing of coarse cilia. This recurrent path follows the outline of the ventral edge of the outer demibranch for roughly two-thirds of its length (*r.p.l.*), then bends toward the mantle edge, continuing on the inner face of the velum to just dorsal to the posterior tip of the gill, thus ending within the exhalent aperture. Where the tract lies on the velum there is a tendency for particles to pass off the edge and not to travel to the end of the path. Particles collecting on the velum in this region are ejected by sudden closure of the valves. The beginning of the recurrent path on the right side (*r.p.r.*) is seen running parallel with the palps, the mantle margin being folded back to expose it and the palps. As previously mentioned (p. 255) the distance of the recurrent path from the ventral edge of the outer demibranch varies in different indi-

viduals, as does also the point at which the path passes on to the velum: in some it does not do so until nearly opposite the posterior end of the gill. The cilia of this rejection tract can be distinguished at a magnification of 140. Periods of slight and of violent activity are observable, and it seems probable that they are stimulated to activity by the presence of much material.

On the postero-dorsal region of the mantle, currents lead towards the exhalent aperture.

The outer surface of the velum is ciliated and particles travel toward the free edge, except in the postero-dorsal region where fusion of the right and left velar edges occur; here the current is ventralward to the exhalent aperture.

Visceral Mass.—On the anterior region of the visceral mass material falling on the right side is transported to the posteriorly directed current along the edge of the right inner demibranch (see Pl. 10), and on the left side to that along the edge of the left inner demibranch. Over the posterior portion of the visceral mass the ciliary currents are ventral and posterior, particles passing off it into the exhalent current. The outer surface of the rectum (Pl. 10, *r.*) is strongly ciliated, the beat being toward the free end, which bears many long, stiff, sensory cilia and is close to the exhalent aperture.

Foot.—The grooved foot is capable of great contraction and expansion: it is shown in a characteristic position in Pl. 10. An examination both of the living foot and of sections proved that it is uniformly and heavily ciliated, yet when under observation the cilia, in contrast to those on the visceral mass, were generally inactive, whatever the cause, whether clogging by mucus, contraction of the surface, or nervous inhibition. Along the groove the current is toward the base and on to the visceral mass, but from either side of the groove it is toward the ungrooved side and the rejection tract along the inner demibranchs.

Attention may be drawn to a structural difference between Heteranomia and Monia: in Heteranomia the gonad invades the base of the foot; in Monia this does not occur.

(*b*) Monia squama and Monia patelliformis.

Mantle.—The ciliary currents of the mantle, visceral mass,

and foot of the two species of Monia are very similar to each other and to those of Heteranomia squamula. The distinct but narrow recurrent path on the mantle (Pl. 11, *r.p.l.*, *r.p.r.*) ventrally passes on to the velum, the point at which it does so apparently differs somewhat in the two species—though there is some individual variation—being nearly mid-ventral in Monia patelliformis, but anterior to this in Monia squama (Pl. 11). Its position on the velum no doubt affords it some protection from the inhalent current. The path ends near the posterior tip of the gill, where there is a slight bay in the velum, and probably just within the exhalent aperture as in Heteranomia squamula, but as the tips of the gills are freely movable the position of the exhalent aperture is not rigidly fixed. Particles collecting on the velum are expelled by sudden closure of the valves. The beginning of the recurrent path of the right side is seen running parallel with the outer palp in Pl. 11 (*r.p.r.*), the mantle margin being folded back to expose it and the palps.

A recurrent ciliated path leading from the region of the palps along the mantle margin to a point opposite the posterior extremity of the gills is also found in Pinctada vulgaris (Herdman and Hornell, 1904, p. 45, and Pl. vi, figs. 2, 14). In Pecten (Orton, 1912, p. 459 and fig. 13) the ciliated rejection path leads in the opposite direction, from the posterior to the anterior region. This is interesting in view of the possible origin of the Anomiidae from the Pectens (Jackson, 1890, p. 362).

In the postero-ventral region of the mantle particles pass inwards in Monia squama (Pl. 11), but there seems to be some variation in Monia patellifomis, for in two out of the three specimens examined particles travelled outward to the recurrent path.

A broad semicircular tract with little, if any, movement of particles is overlaid by the gills; particles settling on the mantle in this region are probably removed by the currents on the ascending lamellae of the outer demibranchs. Inward from this tract particles travel dorsally and posteriorly on the walls of the supra-branchial chamber. A small area of little or no movement

of particles is also found on the visceral mass where it is overlaid by the ascending lamellae of the inner demibranchs.

On the dorsal half of the mantle in the posterior region a definite ciliated path leads to the exhalent aperture. It is broader and not so straightly defined as the recurrent path. Over the suspensory membrane and 'white folds' of the mantle (see Appendix) currents are posterior toward the exhalent aperture.

On the outer surface of the velum particles are transported toward the free edge.

According to Kellogg (1915, p. 666) in Monia machrochisma 'all material collected or transported by the mantle is brought to a point on the posterior edge, being held in place by the free fold until a large ball is formed. This is thrown out by a sudden contraction of the adductor which closes the valves.' He does not, however, figure definite ciliated paths; such would seem to be absent in the American species, or he had difficulty in investigating them. In Placuna placenta also there is apparently no definite ciliated path (Hornell, 1909, p. 59).

Visceral Mass.—Material falling on that part of the visceral mass surrounding the byssal muscle (Pl. 11, *by.m.*) is carried ventrally into the posteriorly directed currents along the free edges of the demibranchs. Particles collecting on the ventral surface of the byssal muscle are also removed by way of these currents. Along the ventral edge of the visceral mass the cilia beat posteriorly, particles being transported to the ventral surface of the adductor muscle (Pl. 11, *ad.*) and hence to the surface of the rectum (*r.*), off which they pass into the exhalent current. Over the posterior portion of the visceral mass the cilia beat ventrally and posteriorly, particles passing off it into the exhalent current.

Foot.—The foot is highly contractile, being capable of contracting to a small protuberance and expanding to at least half the diameter of the shell, while it varies considerably in thickness, apparently largely owing to the forcible intrusion of blood, for when most fully expanded it is translucent. Sometimes it is seen thrown into one or two coils.

The right, morphologically ventral, side is grooved, but the

groove can be almost obliterated. Currents on the foot lead into the groove, down which particles pass to the base, where they collect in a triangular depression. The normal fate of such collections is uncertain. They have been seen to be squeezed out of the depression, until they came under the influence of currents leading to the rejection tracts on the ventral edges of the demibranchs, and at other times the tip of the foot has been observed to be rubbed over the mass of particles, some particles passing on to the tip whence they again began the journey toward the base, but fell off on the mantle near the recurrent path. It is possible that normally few particles find their way to the base of the foot, falling off the rounded sides on to the mantle as the foot twists and turns.

The foot is in continual restless movement, the tip exploring everywhere within reach, but perhaps chiefly in the antero-dorsal region. On several occasions it has been seen to insinuate itself beneath the membraneous fold over the mouth, though from its usual behaviour it is unlikely that it conveys food to the mouth; more probably it would remove unwanted particles. There seems little doubt but that its chief function is to assist in cleansing the mantle and visceral mass; it may perhaps dislodge adhering particles, and remove such as are too large to be transported by any cilia except those of definite tracts. Several times it has been observed to lift a small lump of carmine, holding it firmly in the spatulate tip by pressure of the margins, then with a quick twisting movement drop it over the recurrent path on the mantle.

Jackson (1890, pp. 356–7) recorded that 'the foot in adult Anomia glabra is a small reduced organ;[1] but in the young it is very large and active. The base of the foot is marked by a deep cleft up to its extreme distal portion and the very young in crawling extends and flattens it against the object of support in a prehensile disc-like fashion, as described in Pecten irradians. After the animal becomes permanently fixed the foot was not observed to extend beyond the margins of the valves; but it was constantly moved within the mantle walls

[1] In Monia it is in this condition very usually for a certain time after the removal of a valve.

in a sinuous manner.' Bourne (1907, p. 261) suggested that in Anomia (Aenigma) aenigmatica 'it seems probable that it can be protruded some distance beyond the shell, and that it is auxiliary to nutrition, minute particles being swept by ciliary action along the groove on its right surface, and thence to the right labial groove'. He, however, having preserved material only, could but guess at the direction of the ciliary currents. Hornell (1909, p. 57), from observations on living Placuna, considered that 'the principal use—if indeed it be not the sole one—the foot here subserves is that of a cleansing organ'. Dakin observed that in Pecten (1909, p. 37) 'it probably is of use for freeing the palps and gills of foreign particles' and that in Spondylus (1928, p. 343) the function of the foot was 'possibly that of cleaning the gills, or as an aid in nutrition'.

Summary.

The structure of the gills and palps of Heteranomia squamula (L.), Monia squama (Gmelin), and Monia patelliformis (L.) are described.

Four sets of cilia are present on the gill filaments of both genera: (1) coarse frontal cilia beating ventrally; (2) fine frontal cilia beating dorsally; (3) micro-latero-frontal cilia; and (4) lateral cilia. On the frontal surface there are in addition isolated triangular clusters of sensory cilia and very long stout cilia or cirri.

The ciliary mechanism of the gills of Heteranomia and Monia is peculiar in that the obvious frontal currents on all lamellae are toward the free edges of the demibranchs, along which material is carried away from the mouth. It would seem that the Anomiidae subsist largely on such material as is brought directly to the broad dorsal food grooves by the main water current, for under experimental conditions but rarely have particles been seen travelling dorsally over the lamellae into these grooves.

The ciliary currents of the mantle, visceral mass, and foot of Heteranomia squamula, Monia squama, and Monia patelliformis are described. A clearly defined recurrent

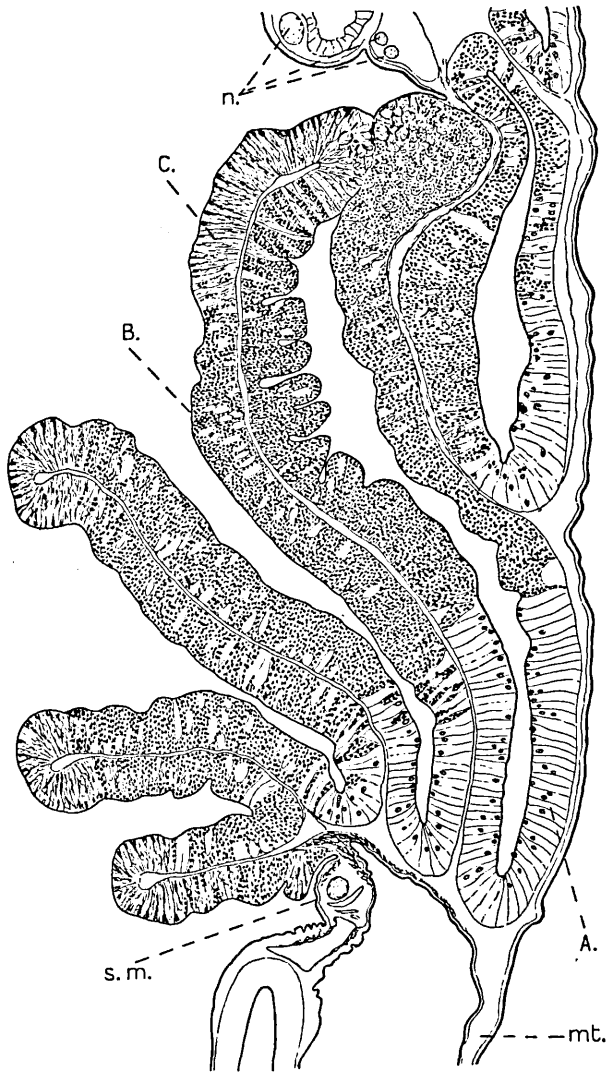
path is present on the mantle in the infra-branchial chamber. In Heteranomia squamula it serves as a rejection tract for much of the outer demibranchs, the ventral edges of which are without a longitudinal current. The foot in both genera assists in cleansing the mantle and visceral mass.

Appendix.

The Hypobranchial Gland of the Genus Monia.

In the genus Monia the mantle just above the line of junction of the suspensory membrane is thrown into large, strongly ciliated folds (Pl. 11, *w.f.*), over which pass rapid currents. Kellogg (1915, p. 665) referred to them in Monia machrochisma as 'white folds' of the mantle, 'perhaps containing extensions of the sexual mass'. In all but one of the specimens of Monia (7 Monia squama and 4 Monia patelliformis) of both sexes examined during March, April, May, June, July, and November, and varying in length from 1·25 to 4·2 cm., these folds were large, thick, and white, and in fact were so obvious that the position of those of the right side could be seen through the thin valve of that side.

Examination of sections and of fresh and stained smears failed to support Kellogg's suggestion that they contained extensions of the gonad, but showed that they are glandular in structure. The following stains were used on sections; Heidenhain's iron haematoxylin counterstained with acid fuchsin, Ehrlich's acid haematoxylin, eosin and light green, muchaematin, and mucicarmine. Most of the secretory cells stain with muchaematin, though in different colours and in varying intensity. They also stain metachromatically with Ehrlich's acid haematoxylin. The very high (up to about 270μ) and large secretory cells appear to be of four main types, and in the specimen of Monia squama sectioned each type appeared to have a definite position with regard to the folds (see Text-fig. 30); but this may not be of general occurrence. At the base of the folds the cells were vacuolated with, or without, a few very large inclusions peripherally (Text-fig. 31 A). The cytoplasm stained but faintly with all the stains employed:



TEXT-FIG. 30.

Monia squama. Transverse section of the hypobranchial gland. A. Region of fold formed of vacuolated cells with a very few large inclusions. B. Region of fold formed of cells containing spore-like bodies. C. Region of fold formed of two kinds of cells intermixed, one containing spindles and the other with ropy contents. *mt.*, mantle; *n.*, nerves; *s.m.*, suspensory membrane of gill. Bouin-Duboscq fixation: Ehrlich's acid haematoxylin. $\times 33\frac{1}{3}$.

the large inclusions stained brownish with muchaematin. The middle regions of the folds were occupied by cells crowded with curious inclusions having the appearance of fusiform spores (Text-fig. 31 B). With iron haematoxylin the centre body of the 'spore' stained heavily, while the remainder was practically unstained. With all the other stains employed the reverse occurred, the centre body staining but faintly, sometimes with a granular appearance, while the rest of the 'spore' took a deep colour; with muchaematin this was deep bright red in small 'spores' and brownish in large ones. The secretory cells at the free ends of the folds were of two kinds intermixed, one containing spindles (Text-fig. 31 c) staining heavily with most stains, and the other having somewhat ropy contents staining light blue with muchaematin. Whether the various cell contents are stages in the formation of a single substance, or are different secretions, was not determined: all in the same cell appear to be of the same type.

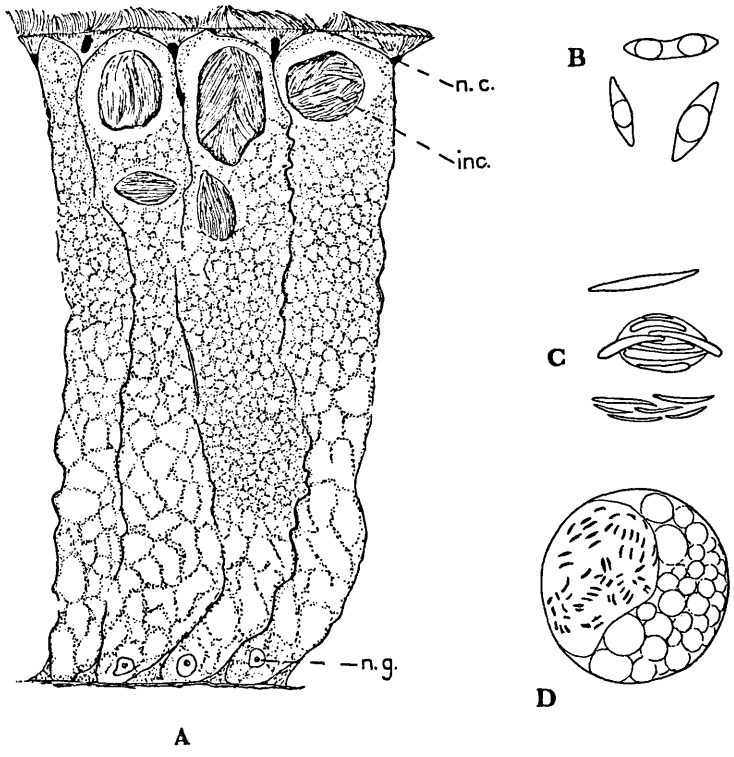
The secretory cells of all types are separated by ciliated cells, which are extremely attenuated but expand peripherally. In the hypobranchial gland of Buccinum the ciliated cells are in contact, forming a continuous ciliated surface, except when the mucous cells are actively secreting (Dakin, 1912, p. 28): this appears to be also the case in Monia (see Text-fig. 31 A). The nuclei of the ciliated cells are peripheral in position (*n.c.*); those of the gland-cells basal (*n.g.*).

Teasing of the fresh folds results in the liberation of isolated 'spores' and spindles, and of packets of these, and also of numbers of the shining centre bodies of the 'spores': in addition some few large bubbles of a vacuolated substance with acicular inclusions are liberated (Text-fig. 31 B–D).

In one of the four specimens of Monia patelliformis which was examined on March 7, 1931, 3·2 cm. long, the folds were small and brownish in colour, the cells no more than 60μ high; spore-like inclusions were rare, the cells mostly containing spindles.

Mechanical irritation of an animal with one valve removed sometimes causes a sudden great outpouring of a white flocculent substance from the folds, which is transported rapidly, by the

long cilia clothing their surface, toward the exhalent aperture. The material when first extruded is not gelatinous, but becomes



TEXT-FIG. 31.

Monia squama. A. Transverse section of cells at base of fold of hypobranchial gland. *n.c.*, nucleus of ciliated cell; *n.g.*, nucleus of gland-cell; *inc.*, inclusion. Bouin-Duboscq fixation: Ehrlich's acid haematoxylin. $\times 456\frac{2}{3}$. B–D. Bodies liberated on teasing fresh gland. B. Spore-like bodies from the middle region of the folds. C. Spindles from the free ends of the folds. D. Large bubble of vacuolated mucus, and tiny acicular bodies. B–D. $\times 573\frac{1}{3}$.

so after a few minutes in sea-water, at the same time losing the white appearance and becoming colourless. In the structureless jelly are innumerable tiny shining bodies, which might be mistaken for sperm. What normally brings about the flow of the

secretion is unknown. It would hardly seem likely to be a cleansing reaction to much sediment in the water, for the secretion is poured into the supra-branchial chamber not far from the exhalent aperture toward which it is rapidly carried, so that it would affect quite a small region of the mantle chamber. Whether or no the secretion is protective, being unpleasant to animals, such as boring Gastropods, likely to feed on Monia, was not investigated.

The 'white folds' of Monia would seem to be homologous with the hypobranchial glands of the Protobranchs, the secretion of which is considered to correspond very closely to mucus (Drew, 1901, pp. 363–4). In none of the Protobranchs examined (Nucula radiata Hanley, Solenomya togata, Nuculana minuta), however, have the contents of the gland been seen to simulate the appearance of fusiform spores. In a Nucula radiata which was sectioned, the irritation caused by the wedging open of the shell, or by the fixative, had resulted in a flow of secretion from the hypobranchial gland, and this was coagulated in the supra-branchial chamber. In the Protobranchs, as in Monia, the function of the hypobranchial gland is unknown, except in Nucula delphinodonta, in which species they are concerned with the formation of the brood-sacs; this, however, is considered by Drew (1901, pp. 364–5) to be most probably a secondary function of these glands.

In two Gastropods, Buccinum (Pectinibranchia) and Haliotis (Aspidobranchia) in which irritation of the animal also causes a sudden copious discharge of mucus from the hypobranchial or mucous gland, it is produced for protection and for the removal of debris from the organs of the pallial cavity (Dakin, 1912, pp. 26–7; Crofts, 1929, p. 34). Crofts (1929, p. 36) mentioned that 'it is useless for hiding purposes, but in copious secretion it may make the surrounding water objectionable to delicate organisms, which might otherwise attempt to feed on the epipodial decorations'.

No hypobranchial glands were seen in Heteranomia. In Anomia ephippium small rounded groups of granular cells, which are probably glandular, and stain brownish with muchaematin, occur in the suspensory membrane of the gills, and in

the fused dorsal edges of the ascending lamellae of the inner and outer demibranchs; but there is no hypobranchial gland resembling that of Monia.

SUMMARY.

In the genus Monia prominent white folds of the mantle dorsal to the suspensory membrane of the gills are of a glandular nature, and are probably homologous with the hypobranchial glands of the Protobranchs.

SECTION D

The Ciliary Sorting Mechanism of the Gills of Pteria hirundo (L.)

With Text-figures 32 and 33.

CONTENTS.

INTRODUCTION.

A young specimen of the rare Pteria hirundo (L.) (=Avicula tarentina) attached to Eunicella verrucosa (Pallas) (=Gorgonia cavolini) was trawled by S.S. 'Salpa' in February 1933, from between Stoke Point and the Mewstone, examined alive and the ciliation of the gill filaments found to be of considerable interest. The specimen was small, only 23 mm. long at the hinge and 12·5 mm. deep, dorso-ventrally.[1] This being an extremely rare form at Plymouth, and other specimens unlikely to be obtained within a reasonable time, such details of the gills and their currents as could be observed are given here, although it would have been preferable to have checked them on other and larger specimens. It was found impossible to discern the mantle currents, as on removal

[1] Forbes and Hanley (1853, vol. ii, p. 253) stated that 'the largest individual we have observed measures nearly 4 inches in length'.

of one valve the mantle contracted back violently almost to the adductor muscle—as also occurs in Pinna—and relaxed but slightly even after 2 days.

The Pteria was lying on the right, less concave valve, attached to the Eunicella by the byssus, which passes through a notch in that valve.

The position of the inhalent and exhalent apertures could not be determined as during the 2 or 3 days it was in the Laboratory the valves were not seen to open to any appreciable extent: they are probably posterior as in Pinna.

The Structure of the Gills.

The gill axes are free posterior to the adductor muscle; there is, however, no deep suspensory membrane as in Pecten, the condition more nearly resembling that in Pinna. Longitudinal muscles are strongly developed; a large nerve is present in the free portion of the axis.

The ascending lamellae are about the same depth as the descending. The dorsal ends of the ascending filaments are in serial organic continuity, as are also the filaments along the ventral edges of the demibranchs. The dorsal edges of the ascending lamellae of the outer demibranchs are united to the mantle by interlocking cilia; those of the ascending lamellae of the inner demibranchs to each other and to the foot by the same means, thus dividing the pallial cavity into supra- and infra-branchial chambers. Division of the pallial cavity by interlocking cilia occurs in other members of the Pteriidae, namely in Pinctada vulgaris (Herdman, 1905, pp. 226–7), Pinctada margaritifera, and Malleus albus (see Part VII, in the press). According to Grobben (1900, pp. 7–9) the same method is found in Isognomon (=Perna), Crenatula, and Vulsella.

The lamellae are broadly plicate and markedly heterorhabdic. According to Ridewood (1903, p. 211) every principal filament has an interlamellar septum, most of them rising one-third or two-fifths the height of the demibranch, though some extend the full height. In the piece of gill sectioned from the young Plymouth specimen all the septa extended the full height of the

demibranch; this may, however, be an immature character. The principal filaments have a widely grooved frontal surface (Text-fig. 32 B) except towards the ventral edge of the demibranch, where they become almost indistinguishable from the ordinary filaments. In preserved material the appearance of the principal filaments varies according to the state of the horizontal muscles. There are about eleven to twelve filaments to the plica in this young specimen, and twelve to fifteen in the adult. In the living uncontracted gills of the Plymouth specimen the plicae were broad and low, the lamellae being only slightly plicate, but on contraction of the gill axes and of the horizontal muscle-fibres of the principal filaments the plicae become deep: they would be likely to appear in this condition in preserved material. The muscles in the gill axes and in the principal filaments are described in Part VIII, in the press.

The interfilamentar connexions are ciliated disks, commonly with no additional organic union, such as is found in Pteria argentea (Ridewood, 1903, pp. 212–13), Pinctada vulgaris (Herdman, 1905, pp. 227–8), and Pinctada margaritifera (see Part VIII). However, organic fusion of an ordinary and principal filament was noticed in sections through the dorsal part of the demibranch of an adult specimen from Naples, but is unusual. The interlocking cilia are borne on short spurs of the inner edge of the filament; they are considerably shorter than in Pecten.

The food groove at the ventral edge of the inner demibranch is well marked, that of the outer demibranch very slightly, as in Malleus. The cilia on the lobes of the food groove (terminal cilia) are long and coarse. The anterior ends of the demibranchs are enclosed by the palps.

Much of the foregoing account of the gills is to be found in Ridewood's paper (1903).

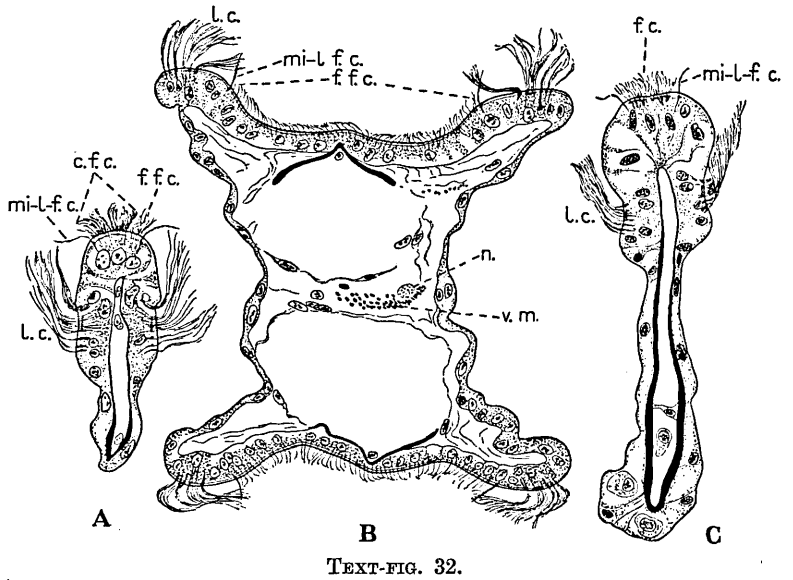
The Ciliation of the Filaments.

The arrangement of the various tracts of cilia on the filaments is shown in Text-fig. 32.

Frontal Cilia.—The frontal cilia on the principal filaments are fine (Text-fig. 32 B, *f.f.c.*), with the effective beat

dorsal in direction. Those on the ordinary filaments are of two kinds arranged in two tracts: on the anterior side of the frontal surface they are fine (Text-fig. 32 A, *f.f.c.*), with the effective beat dorsalward; on the posterior side coarse (*c.f.c.*), with the effective beat ventralward. The latter when at rest lie with the tips directed dorsally as previously described in Arcidae (p. 222) and Anomiidae (p. 250).

No sense cilia could be found on the frontal surface of the



TEXT-FIG. 32.

Pteria hirundo. Transverse sections of gill filaments. A. Ordinary filament of young Plymouth specimen, 23 mm. long at the hinge. B. Two principal filaments and their interlamellar septum, of the same specimen. C. Ordinary filament of adult Naples specimen, 63·5 mm. long at the hinge. The fixation of this specimen was not sufficiently good for the two kinds of frontal cilia to be discernible in sections. *c.f.c.*, coarse, and *f.f.c.*, fine frontal cilia; *f.c.*, frontal cilia; *l.c.*, lateral cilia; *mi.-l.-f.c.*, micro-latero-frontal cilia; *n.*, nerve; *v.m.*, vertical muscle-fibres. Bouin-Duboscq fixation: Heidenhain's iron haematoxylin. A, C. × 735; B, × 562½.

filaments, but such are often difficult to discern, and in all probability will be discovered on further searching.

Latero-frontal Cilia.—These are unusually fine and

short; they are micro-latero-frontal cilia (Text-fig. 32, *mi.-l.-f.c.*) as previously described in Arcidae (p. 223) and Anomiidae (p. 253).

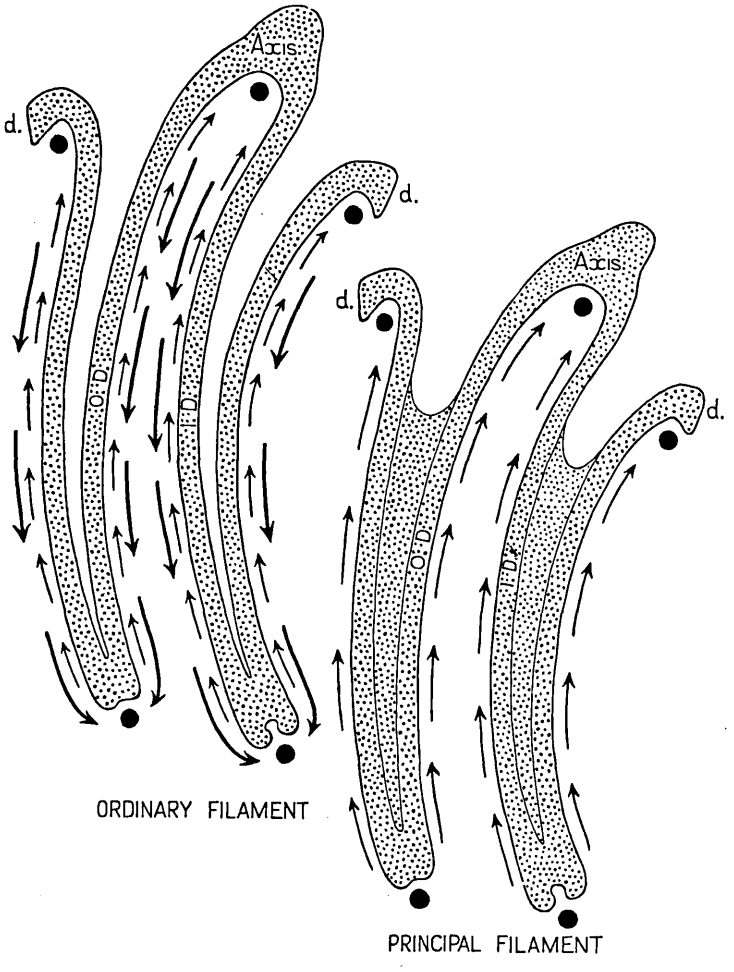
Lateral Cilia.—The lateral cilia (*l.c.*) are borne on five rows of cells. That nearest the frontal surface of the filament is of extremely narrow, elongated cells. It is followed by a row of large, almost square cells. The three succeeding rows are again of narrow elongated cells. A similar arrangement of the lateral cells is found in the allied genus Pinctada, but not in Malleus.

The Sorting Mechanism on the Gills.

The gills of Pteria hirundo are extremely sensitive to stimulation, and not only contract antero-posteriorly, but, owing to vertical muscles in the principal filaments and their interlamellar septa (Text-fig. 32 B, *v.m.*), the demibranchs contract dorso-ventrally, the lamellae becoming strongly crumpled. The dorsal half of a demibranch will remain crumpled after the ventral half has become smooth.

When the gill is flooded with much powdered carmine there is a tendency for it to contract antero-posteriorly, approximating the plicae and hiding the grooves; most of the material therefore falling on the crests, it is carried ventrally into the orally directed currents along the ventral edges of the demibranchs (Text-fig. 33), from which it may be dislodged by twitching of the demibranchs. Such particles as fall into the grooves are carried dorsally, unless they are attached to those on the crests by mucous strings. Dorsally travelling particles join the orally directed currents between the bases of contiguous demibranchs of a gill and along the upper edges of the ascending lamellae. Ventral movement is rapid and there is much jumping of particles as in Pinna, for which occasional long, stout cilia or cirri are probably responsible.

So far the currents appear similar to those already described by various authors in Pecten (Kellogg, 1910, 1915), Lima (Studnitz, 1931), and Ostrea (Yonge, 1926); but if the gill be fed with few carmine particles, under these conditions most of those on the crests, as well as in the grooves, travel dorsally.



TEXT-FIG. 33.

Pteria hirundo. Diagrammatic transverse sections showing the form of the gill and the direction of the frontal currents. ● indicates the position of oralward longitudinal currents. *I.D.*, inner, and *O.D.*, outer demibranch; *d.*, dorsal edge of ascending lamella. Arrows indicate the direction of frontal currents, ventralward currents being due to coarse cilia, and dorsalward currents to fine cilia.

If an ordinary filament be observed at a magnification of about 860 it will be seen that particles travel dorsally over the tract of fine frontal cilia, and ventrally over the tract of coarse cilia. Particles in fact may pass in opposite directions on the same ordinary filament (Text-fig. 33), as in Arca and Glycymeris (see p. 228). In Pteria, therefore, while particles would seem invariably to travel dorsally on the principal filaments (Text-fig. 33), on the ordinary filaments they will travel either ventrally or dorsally according to the quantity and quality received by the gills. Pteria is then a form of exceptional interest from the point of view of ciliary feeding mechanisms, in that in addition to the constant dorsalward currents in the grooves of the plicae, a conspicuous general dorsalward movement of particles takes place on their apices under certain conditions. Such has not been observed in Pecten (see Part II, in the press), Solen, and Ensis (see p. 288), in which tracts of oppositely beating frontal cilia are also present on some or all of the ordinary filaments of their plicate and heterorhabdic gills.

The Mantle.

The mantle of Pteria hirundo is provided with a somewhat narrow velum, the free edge of which bears small tentacles. Tentacles are also present externally at the junction of the velum with the mantle. These tentacles, which are of unequal length, are, unlike those of Pecten, flattened and entirely ciliated, the cilia being short and fine, except toward the tips, where they are long and have sense cilia among them. The velum and also the gills are touched with patches of dark brown. On the inner surface of the velum there is a posteriorly directed current which receives particles from the mantle surface. This is no doubt a rejection current depositing waste material on the mantle edge, but owing to the great contraction of the mantle the posterior limit of the tract could not be determined.

Summary.

The eleutherorhabdic or filibranchiate gills of Pteria hirundo have plicate and heterorhabdic lamellae. The

ciliation of the filaments is chiefly notable for the presence of micro-latero-frontal cilia and for the presence on the ordinary filaments of frontal cilia arranged in two tracts, with the effective beat in opposite directions. So far as could be ascertained from a single small specimen, in the grooves of the plicae the movement of particles is dorsalward; on the crests it is either ventral or dorsal according as to whether the material brought to the gills is such as to stimulate or not to stimulate the coarse, ventrally beating, frontal cilia.

Along the ventral edges of the demibranchs, and between the bases of the two demibranchs of each side of the body, as well as along the dorsal edges of all the ascending lamellae, currents are toward the mouth.

SECTION E

The Ciliary Sorting Mechanisms of the Gills of Solen marginatus Montagu, Ensis siliqua (L.), Ensis arcuatus (Jeffreys), and Cultellus pellucidus (Pennant).

With Text-figures 34–42.

CONTENTS.

SOLEN MARGINATUS, ENSIS SILIQUA, AND ENSIS ARCUATUS.

A difference in the direction of the frontal currents in the grooves and on the crests of Lamellibranchs with plicate and heterorhabdic gills is now known in Pecten (Kellogg, 1910,

1915), Ostrea (Yonge, 1926), Lima (Studnitz, 1931), and Pteria (see p. 275); to these may be added Solen and Ensis.

The Comparative Structure of the Gills in Solen and Ensis.

The appearance of gills and filaments in life may differ considerably from that induced by preservative fluids (see Text-figs. 35, 36), thus living material should be examined whenever this is possible.

The gills in both genera are long and narrow; the gill axes are free for much of their length, that is from a short distance behind the foot. Longitudinal ctenidial muscles are better developed in Ensis than in Solen, but the axes of both are capable of considerable antero-posterior contraction.

The dorsal edges of the ascending lamellae of the outer demibranchs are fused with the mantle in both Solen and Ensis (see also Stenta, 1903, p. 237), a strong junction no doubt being a necessity where the gills are long and the axes free for much of their length. The junction is non-ciliary and of a peculiar cuticular type (see Part IV, in the press); the epithelium of the two opposed surfaces is clearly discernible, even in adults, and it appears that there is strong fusion of the cuticle alone. This had already taken place in a specimen of Ensis siliqua 1·8 cm. long. That the fusion is strong may be demonstrated by inserting a hooked instrument under the filaments of the ascending lamella and attempting to pull it away from the mantle. A similar type of fusion is found between the ventral edges of the mantle lobes anterior to the fourth aperture in Ensis and Cultellus and is described more fully in a later paper (Part IV, in the press). Graham (1931, p. 734) has described the method of junction of the outer demibranch and the mantle as ciliary in Ensis siliqua. It is of course not impossible that the method of union varies in different individuals, or in different regions of the gill, for only a small piece from each of two adults and one young specimen was sectioned, and not the entire gill of any individual. Inability to separate the outer demibranch from the mantle in the living animal is, however, not necessarily

proof of organic union; in Pinna fragilis, for instance, the ciliary junction between the outer demibranch and the mantle is so strong that an attempt to separate the two may result in tearing of the thin mantle before the interlocking cilia give way.

In Ensis the dorsal edges of the ascending lamellae of the inner demibranchs are joined to each other, and to the foot anteriorly, by interlocking cilia. In a young specimen of Ensis arcuatus, about 4 cm. long, there was in addition slight organic union at the ventral edge of the junction in some places. The ciliary junction between the inner demibranchs is easily dissolved; when the two surfaces are separated they come together again after a time (see also Stenta, 1903, p. 237).

In Solen the junction between the dorsal edges of the ascending lamellae of the inner demibranchs is organic for the greater length of the gills, but with the foot and with each other for about 10 mm. behind the foot it is ciliary and easily dissolved. It is curious that the organic junction between the inner demibranchs is of a very different type from that between the outer demibranchs and the mantle. There is no sign of fused epithelial surfaces, or any indication of the fusion that has occurred, not even in the transitional region between the organic and ciliary method of junction. In Cultellus pellucidus the method of division of the supra- from the infra-branchial chamber is largely organic as in Solen marginatus.

The significance of the difference in the method of junction between the inner demibranchs in the Solenidae is obscure. Below are given some points in their structure and habits which may possibly have a bearing on the question.

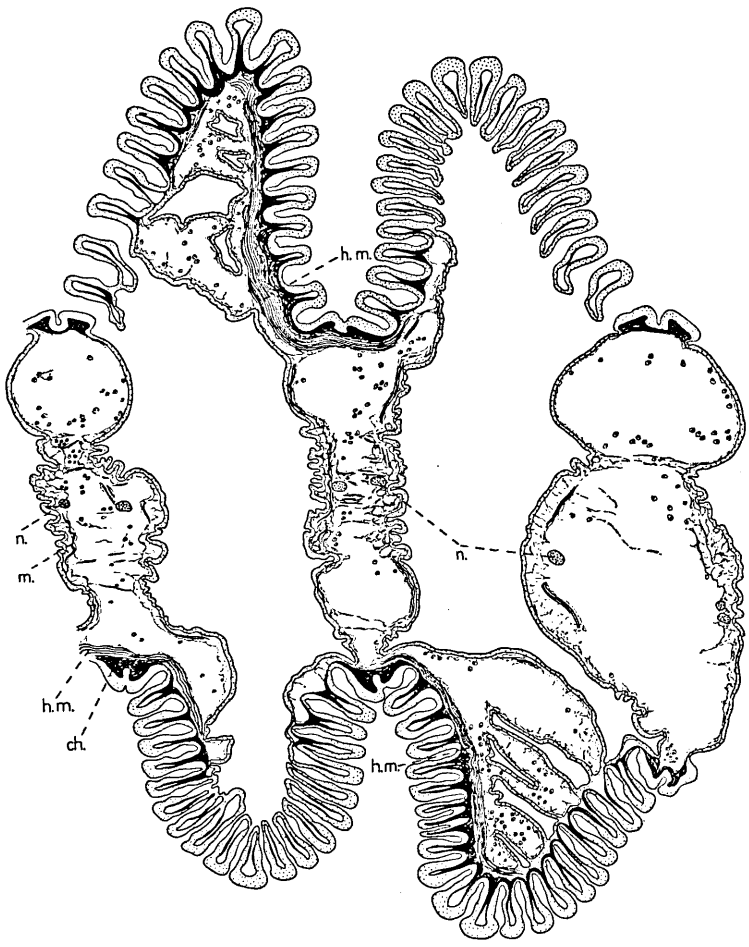
	Inner Demibranch Junction.	*Hinge Teeth.*	*4th Aperture.*	*Siphons.*	*Habitat.*
Ensis	Ciliary	6	Present	Short	Coarse sand.
Cultellus	Organic	6	Present	Short	Silty sand.
Solen	Organic	2	Absent	Long	Fine to medium sand and muddy sand.

Presumably the value of an easily dissolved ciliary junction between the inner demibranchs, as in Ensis, is that it allows

of the throwing together of the supra- and infra-branchial chambers, thus preventing injury to the gills, when a powerful water current is forced out of the pedal aperture during burrowing and swimming movements (Drew, 1907, pp. 133–5). A similarly easily dissolved ciliary junction between the inner demibranchs, while that between the outer and the mantle is strong—though ciliary in this instance—is found in Pinna (Atrina), in which Grave (1909, p. 414) stated that 'the force of the expelled current makes the water fairly boil, washing up quantities of sand and mud from beneath'.

It is possible that Solen and Cultellus, in which the two chambers can be made confluent only round the foot and for a short distance behind it, are not as active, and that the ejected water current is not as relatively strong as in Ensis. In Solen this might be considered as supported by the few hinge teeth guiding the movements of the valves and the long siphons (about 4 inches when extended) allowing it to live at some distance below the surface, but on the other hand Cultellus has short siphons and the same number of teeth as Ensis. Solen and Cultellus are relatively shorter forms than Ensis and it may simply be therefore that they do not need as long an opening between the two chambers.

As is well known, the lamellae of Solen and Ensis are plicate and heterorhabdic (Ridewood, 1903, pp. 254–8). There are about twenty-four to twenty-six filaments to a plica in Solen marginatus (=vagina) and nineteen to twenty-five in Ensis siliqua. The plicae are less deep in Ensis siliqua and in Ensis arcuatus than in Solen marginatus, but not sufficiently to warrant Ridewood's description of 'very feebly plicate'. In living specimens of Ensis seen at Plymouth the plicae were well marked, even when the gill seemed fully expanded, though tending to flatten out at the lower margin of the demibranch; the plicae deepened on fixation (see Text-fig. 34). Ridewood's horizontal section of the demibranch of Ensis siliqua (1903, fig. 47, p. 257) looks much as though it were taken toward the ventral edge, both by the form of the plicae and of the principal filaments and the width (interlamellar) of their septa.



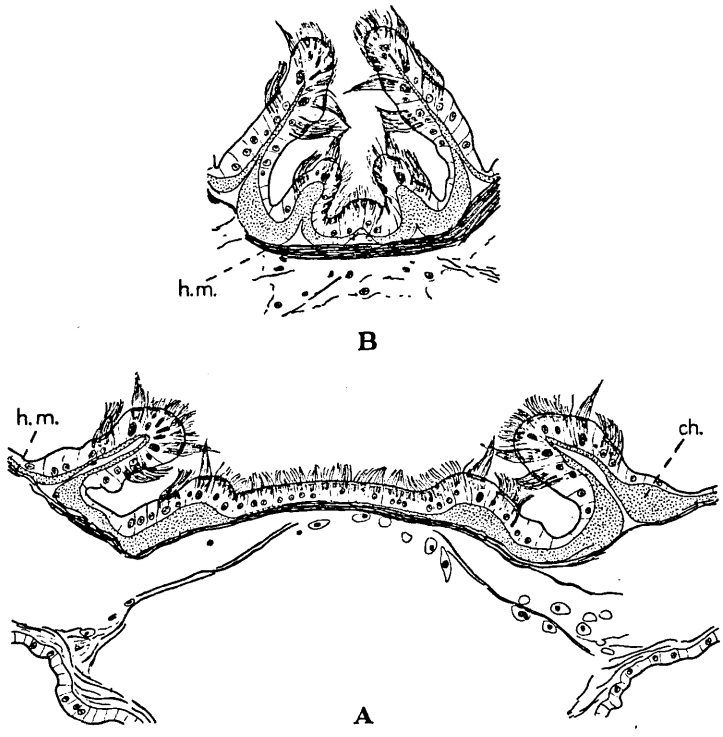
TEXT-FIG. 34.

Ensis siliqua. Horizontal section of part of a demibranch. *ch.*, chitin; *h.m.*, horizontal muscles; *m.*, muscle-fibres; *n.*, vertical nerve. Bouin-Duboscq fixation; Mallory's triple stain. $\times 93\frac{1}{2}$.

The principal filaments of Solen marginatus are broadly grooved (Text-fig. 35 A); they may have, however, a

ridge arising from the centre of a deep groove (Text-fig. 35 B), this being due to the contraction of the horizontal muscles. They have a wider frontal surface than those of Ensis.

Ridewood (1903, p. 257) described those of Ensis siliqua as presenting 'a sharp ridge'; Graham (1931, p. 734) as 'much



TEXT-FIG. 35.

Solen marginatus. Sketches of transverse sections of two principal filaments at the same level of the lamella to show the difference in their shape according to the state of contraction of the horizontal muscles (*h.m.*). The adjacent ordinary filaments are cut obliquely in both sections. *ch.*, chitin; *h.m.*, horizontal muscles. Bouin-Duboscq fixation; Heidenhain's iron haematoxylin and acid fuchsin. × 342½.

flattened'. Toward the lower edge of the demibranch they are almost indistinguishable from the ordinary filaments—as are

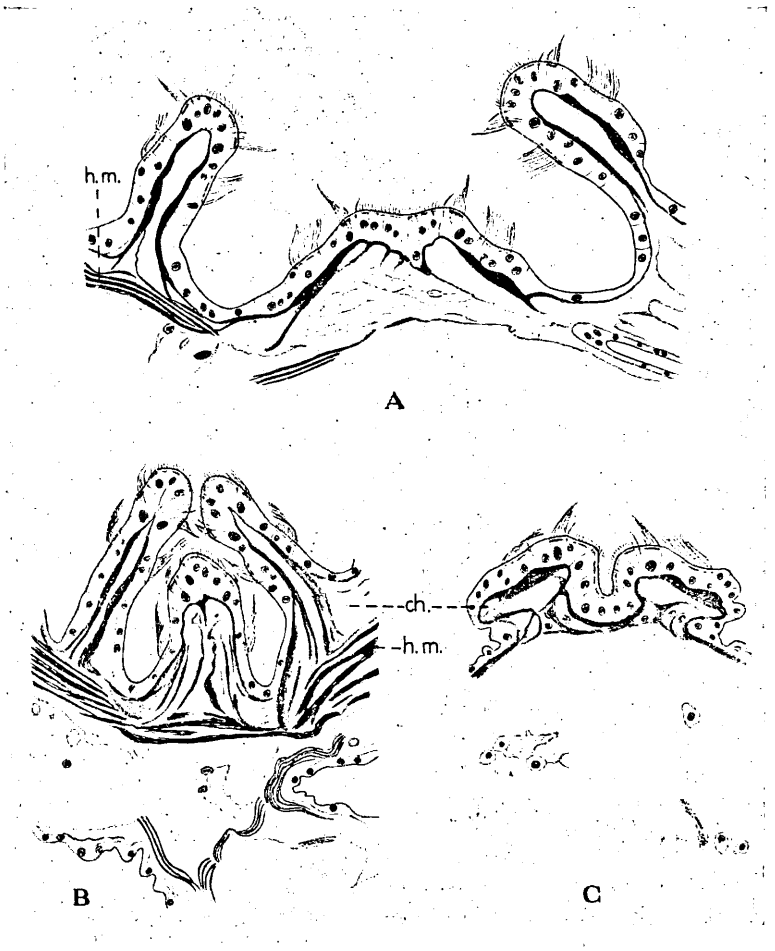
those of Solen—but in the upper parts they are considerably broader as seen in surface view of the living gill. In Text-fig. 36 A the frontal surface of the principal filament though flat is not fully extended. In sections, adjacent principal filaments at the same level may have either broad and flat or sharply ridged frontal surfaces; the difference in appearance being due probably entirely to the state of contraction on fixation of the strong muscle-fibres (*h.m.*) which run in the interfilamentar junctions (see Text-fig. 36). In the contracted state these are liable to cause approximation of the two sides of the filament. In some parts of the lamella the principal filaments may be deeply grooved (Text-fig. 36 c). Ridewood (1903) does not seem to have altogether realized that in preserved material the shape of the frontal surfaces of the principal filaments of various Lamellibranchs is largely dependent on the state of contraction of the horizontal muscles.

In Solen two vertical (dorso-ventral) muscle-bundles, accompanied by nerves, are present in each interlamellar septum. In Ensis the two corresponding nerves are present (Text-fig. 34), but muscle-bundles are absent, though there is some slight development of scattered vertical fibres beneath the epithelium of the interlamellar septa. The demibranchs of Solen are capable of considerable dorso-ventral contraction, not noticeable in Ensis.

The plicae tend to decrease in height toward the lower edges of the demibranchs. In Ensis there is in the living animal a well-marked food groove, with sides of even height, at the ventral edges of both inner and outer demibranchs: in Solen the grooves are shallow.

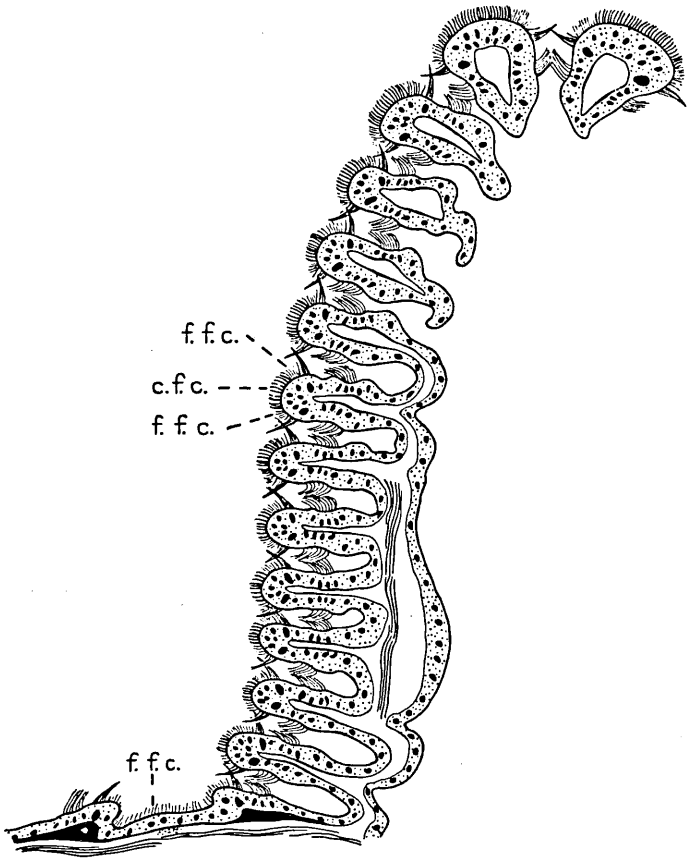
Ciliation of the Gill Filaments.

Direct observation of the appearance and movement of cilia on a Eulamellibranch gill is difficult owing to the filaments being bound together by organic junctions. It is therefore most difficult to separate the filaments for observation in side view. There is, however, a difference in the size of the frontal cilia on different filaments. As there is some variation in the frontal ciliation of the filaments of Solen and Ensis these genera



TEXT-FIG. 36.

Ensis siliqua. Sketches of transverse sections of three principal filaments, showing the difference in their shape according to the state of contraction of the horizontal muscles (*h.m.*). When these are contracted the principal filament is hidden by the adjacent ordinary filaments, as in B. A and B, at the same level of the lamella; C, at a level somewhat ventral to A and B. *ch.*, chitin (both pale and darkly staining); *h.m.*, horizontal muscles. Bouin-Duboscq fixation; A and B, eosin and light green; C, Mallory's triple stain. $\times 342\frac{1}{2}$.



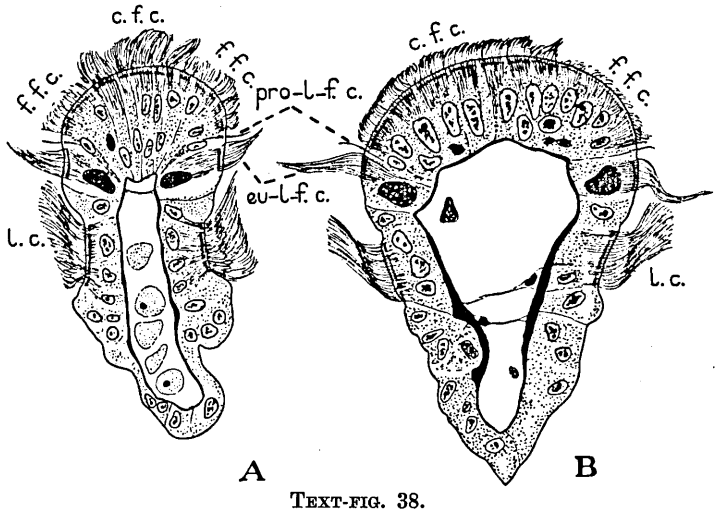
TEXT-FIG. 37.

Solen marginatus. Diagrammatic sketch of half a plica to show the disposition of the tracts of coarse and fine frontal cilia. In this figure and Text-fig. 39, they have been put in mainly from a knowledge of living filaments; the two types are not always discernible in sections. *c.f.c.*, coarse, and *f.f.c.*, fine frontal cilia. × 253⅓.

will be treated separately. Large latero-frontal cilia together with small ones[1] are present in both genera: the lateral cilia are normal.

[1] The presence of these cilia in certain Lamellibranchs is discussed in Part VII, in the press.

Solen.—The frontal cilia of the principal filaments are fine and beat dorsally. Observations of pieces of lamella in surface view at a magnification of about 860 showed all the ordinary filaments to have tracts of coarse and fine frontal cilia, even the apical ones having narrow tracts of fine cilia (Text-fig. 37). In Solen the coarse cilia are in a median tract with the fine ones



TEXT-FIG. 38.

A. Solen marginatus. Transverse section of an ordinary filament, adjacent to the two apical filaments. B. Ensis siliqua. Transverse section of one of two apical filaments. *c.f.c.*, coarse frontal cilia; *eu.-l.-f.c.*, large latero-frontal cilia; *f.f.c*, fine frontal cilia; *l.c.*, lateralcilia; *pro.-l.-f.c.*, small subsidiary latero-frontal cilia. Bouin-Duboscq fixation; Heidenhain's iron haematoxylin and acid fuchsin. $\times 712\frac{1}{2}$.

on each side (Text-fig. 38 A). The effective beat of the fine cilia is dorsalward; that of the coarse ones ventralward. The coarse frontal cilia when at rest have the tips directed dorsally, that is they come to rest at the beginning of the effective stroke, as do those of the Arcidae, Anomiidae, and Pteriidae. It has been observed that when these are motionless a wave or flicker of movement may pass along them and then die out, to be followed after a slight interval by another. Among the coarse cilia are blunt, possibly sensory, cilia, which when beating bend about

the middle of their length almost at right angles. It could not be decided whether movement of these preceded that of the frontal cilia. They appeared to be independent of it, but movement of the coarse frontal cilia did not start within the field of the microscope.

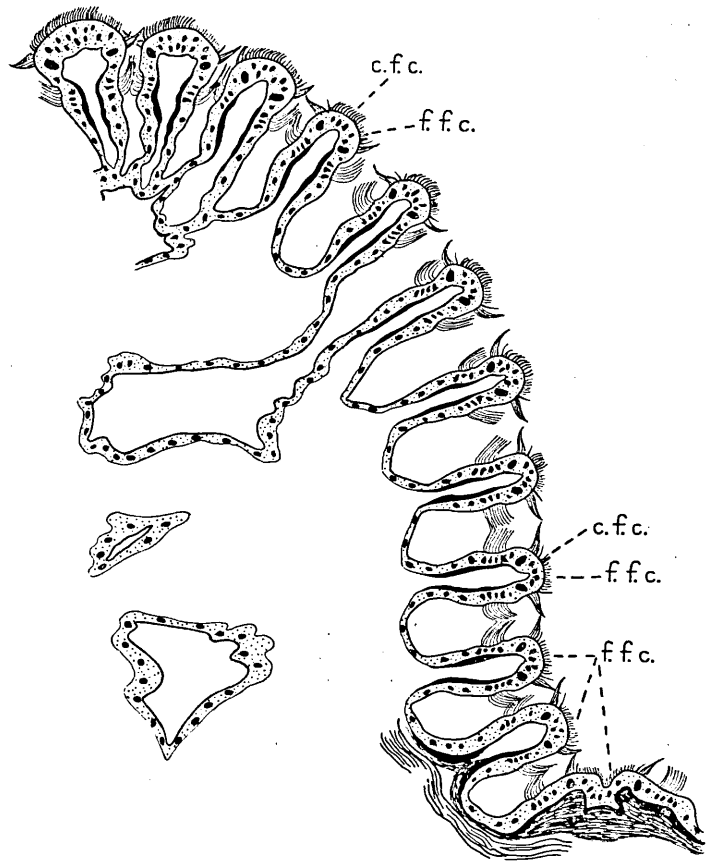
Ensis.—In Ensis siliqua and Ensis arcuatus the frontal cilia on the principal filaments, and in addition on at least the two or three adjacent ordinary filaments on each side, are fine and fairly short, with the effective beat dorsal in direction. It has been observed that on the filaments forming the sides of the plicae two kinds of frontal cilia are present, a tract of coarse long cilia, along the posterior side, with the effective beat ventralward; and one of fine cilia, with the effective beat dorsalward, on the anterior side (Text-fig. 39). It appeared both from the living gill and from sections that while the frontal cilia of the apical filaments are mostly coarse and beat ventrally, there is a tract of fine dorsally beating cilia even on these filaments (see Text-fig. 38 B). A difference in the appearance of the two tracts of cilia can often be seen in sections. The coarse frontal cilia when at rest lie with the tips directed dorsally. It is thought that these cilia may normally be motionless and only become active on stimulation, as they do in Arca, Glycymeris, Pteria, and other forms. This would explain the much less certain movement of fine particles on the apical filaments than of large or many particles. The fine cilia appear to be in continual activity.

Large, thick, blunt cilia occur fairly frequently on the frontal surfaces of the filaments. They are probably responsible for flinging particles off the gill, and in addition are no doubt sensory in function.

Although narrow tracts of fine, dorsally beating frontal cilia occur on the apical filaments of Solen and Ensis, no general dorsal movement of particles along the crests of the plicae has been observed under experimental conditions.

The Sorting Mechanism of the Gills.

Frontal currents are considerably easier to demonstrate in Solen than in Ensis; this is possibly due to the fact that



TEXT-FIG. 39.

Ensis siliqua. Diagrammatic sketch of half a plica to show the disposition of the tracts of coarse and fine frontal cilia. *c.f.c.*, coarse, and *f.f.c.*, fine frontal cilia. $\times 253\frac{1}{3}$.

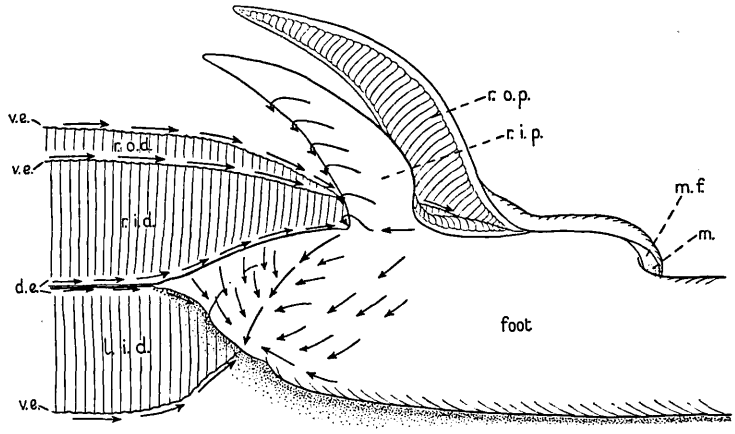
Solen seems to be hardier than Ensis, standing removal from the beds and laboratory conditions better. In Ensis especially it was frequently found on observing an animal directly on, or soon after, opening that the frontal cilia were active only on the few filaments on the apices of the plicae, and that particles lying on the filaments at the bottom of the

open grooves were practically stationary. It was also often almost impossible to demonstrate any ciliary currents, by the movement of particles, in the dorsal grooves between the two demibranchs of each side of the body, or along the dorsal edges of the ascending lamellae. This, however, varied in different individuals and even in different regions of the same individual. Such apparent lack of activity of the great majority of the cilia is apparently due to shock, and is frequently met with in lamellibranch gills, especially of large forms, observed directly on opening—even though they have been in running water for hours or days before opening and not removed from the water during the operation—and it has been found necessary to leave the opened animals under circulation for some hours, preferably over night. This impotence, especially of fine cilia, is no doubt largely due to copious secretion of mucus by the gland cells of the ciliated surfaces following the shock of injury or handling. It has been frequently noticed in some bivalves that after a demibranch, or piece of one, has been removed, the lateral and latero-frontal cilia on it are almost all stationary, while there is little movement of particles on the frontal surfaces, indicating that the frontal cilia are also motionless: this lasts for a short time. It is possible that stoppage of cilia on the still attached gills of an opened animal may occur for a time—from whatever cause. Observations on ciliary currents therefore were mostly made, or at least verified, on animals 12 hours or so after opening. The difficulty of observing currents on a freshly opened animal may possibly explain Graham's (1931, pp. 734–5) statements that in Ensis siliqua 'there is no difference in the direction of the beat of the frontal cilia on principal and ordinary filaments', the frontal currents on all being toward the free ventral edges of the demibranchs, and that 'there is no detectable current along the axes of the ctenidia except at the very anterior end, where they are fused to the base of the foot'.

In both Solen and Ensis orally directed longitudinal currents between the bases of the two demibranchs of each side of the body and along the dorsal edges of all the ascending lamellae—in addition to those along the free ventral edges of the demibranchs—were found to be present throughout the length

of the gill. That between the bases of the two demibranchs of each gill is directly continuous with the oral groove leading to the mouth.

It will be seen from Text-fig. 40 that large particles, or collections of particles bound together by mucus, passing along



TEXT-FIG. 40.

Ensis siliqua. Sketch of the anterior ends of the demibranchs, the palps, and the basal part of the foot, to show the ciliary currents. The outer demibranchs are actually somewhat less deep than the inner, but owing to the position of the animal that of the right side appears deeper. The foot is shown pulled over to the left side. *d.e.*, dorsal edges of the ascending lamellae of the inner demibranchs; *m.f.*, membraneous extension from the outer palp, covering the mouth (*m.*); *l.i.d.*, left inner demibranch; *r.i.d.*, right inner, and *r.o.d.*, right outer demibranch; *r.i.p.*, right inner, and *r.o.p.*, right outer palp; *v.e.*, ventral edge of demibranch. × ca. 1½.

the dorsal edges of the ascending lamellae of the inner demibranchs (*d.e.*) where these are interlocked with the foot, would be very liable to come under the influence of the cilia on adjacent regions of the foot and be carried to a point on its posterior edge. This was no doubt observed by Graham (1931, p. 735), who referred to it as a 'cleansing current'. In the case of the ascending lamellae of the outer demibranchs the strong mantle currents would tend to drag away large particles or collections of particles passing along their dorsal edges.

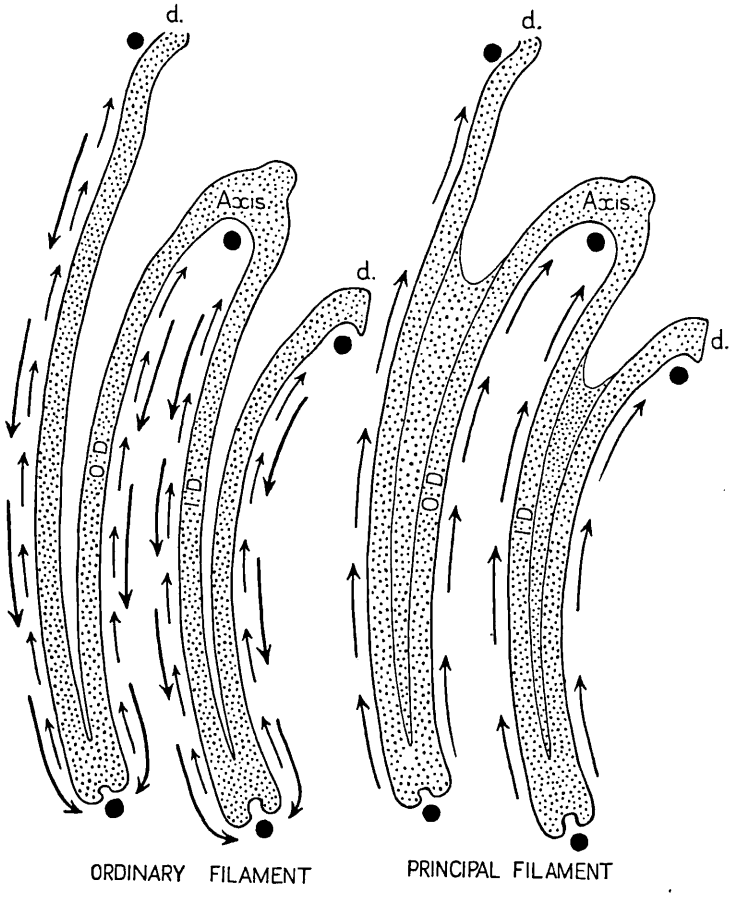
The proximal oral grooves—longer in Ensis than in Solen —and the mouth are roofed over by a membraneous extension from the free edge of the smooth part of the outer palps, as previously described in the Arcidae and Anomiidae (pp. 226, 247). This is no doubt to prevent removal or contamination of accumulations of food particles by the strong currents forced from the anterior end of the shell at various times during burrowing and swimming.

Ciliary Mechanism of the Filaments (Text-fig. 41).

In Solen marginatus, Ensis siliqua, Ensis arcuatus, and the single specimen of Ensis ensis examined, it was found that in general the movement of particles on the plicae was toward the free ventral edges of the demibranchs, but in the grooves between them was dorsal in direction. The dorsalward movement occurred not only on the principal filaments, but on the several adjacent filaments on each side, as in Pecten. On occasions extraordinarily enough the grooves of Ensis could be filled with carborundum powder—fine and coarse—to about a quarter or more of their depth and this would be moved dorsally. If very fine and few particles were dropped on the lamella these moved dorsally on filaments very near to the apices of the plicae.

In Solen movement of particles dorsally over the tracts of fine frontal cilia, and ventrally over the tract of coarse frontal cilia, has been seen on the same filament at a magnification of about 860. But dorsal movement under such conditions is generally seen only when the coarse cilia are almost or entirely inactive. When dorsal movement of particles on those filaments adjacent to the apex of a plica is seen taking place on gills attached to the animal, the coarse frontal cilia are apparently inactive, and the movement is due to the fine ones. The coarse frontal cilia when active overcome, owing to their length and strength, the action of the fine ones, and particles then travel ventrally.

The ventral movement of particles on the filaments at the apex of a plica even on directly opening an animal (see p. 289) is probably explained by the coarseness and strength of beat



TEXT-FIG. 41.

Solen and Ensis. Diagrammatic transverse sections showing the form of the gill and the direction of the frontal currents. ● indicates the position of oralward longitudinal currents. *I.D.*, inner, and *O.D.*, outer demibranch; *d.*, dorsal edge of ascending lamella. Arrows indicate the direction of frontal currents, ventralward currents being due to coarse cilia, and dorsalward currents to fine cilia.

of the frontal cilia on these filaments. Their action is apparently sufficiently strong to overcome the clogging influence of mucus;

it is probable also that these cilia are stimulated to activity, or increased activity, by touching during the operation of opening.

The mechanism for the stimulation of the coarse, ventrally beating, frontal cilia would not seem to be complicated and perhaps not entirely efficient, as evidence the movement of much carborundum dorsally (see p. 292). Professor C. M. Yonge has told me that he has found quantities of sand in the gut of Ensis, and that sand grains occur even in the phagocytes. Injury and abnormality of the gills, due to the presence of sand grains between the lamellae, is not uncommon.

In Solen and Ensis, therefore, as in Pecten, Chlamys, Lima, Pteria, and Ostrea, the dorsalward currents in the grooves between the plicae lead into orally directed longitudinal currents between the bases of the two demibranchs of each side of the body, and along the dorsal edges of all the ascending lamellae. Particles travelling along these paths to the mouth have a much safer passage than those passing along the ventral edges of the demibranchs. Large and therefore unwanted particles are carried along the ventral routes, and if the load be heavy, twitching of the gill may cause it to fall on the mantle, where it will be carried posteriorly and rejected (see Graham, 1931, p. 735).

In the living gill of Solen and Ensis it may be observed that when a good quantity of material is dropped on a lamella a plical groove will be widely open, so that the lamella there is almost flat, while the two adjacent plical crests on each side will be closely approximated, the grooves between them being entirely hidden. This occurs more or less evenly over the entire lamella, and greatly reduces the collecting surface. It has been observed also in Lutraria lutraria (L.) and Thracia villosiuscula (Macgillivray), and in this connexion it is interesting that Ridewood (1903, p. 224) noted in a preserved specimen of Isocardia cor (=humana) that 'the plications of the same lamella were not uniformly spaced, but were arranged in pairs in such a way that one principal filament was in relation with two closely approximated plicae, while the next was situated in a nearly flat portion of the lamella'. Much carborundum causes antero-posterior contraction of the gill and

approximation of the plicae and of the filaments—and in Solen considerable dorso-ventral shortening or crumpling of the demibranchs—so that practically all the plical grooves are hidden and most of the material is carried to the free edges of the demibranchs. The approximation of the filaments interferes with the working of the lateral cilia, and the inhalent current will therefore be reduced in strength.

In the course of the experimental work at least two specimens of Ensis siliqua were seen to behave in the following interesting fashion. When a considerable amount of fine carborundum was dropped on a lamella there was little movement of the particles on the crests and none of those in the grooves, but over a considerable depth of the lamella in the field of vision (with a low-power binocular microscope × ca. 16) stretches or strings of particles were flung clean out of the grooves and above the crests. These strings, probably held together by mucus, fell back into the grooves only to be flung out again. Such concerted movement could not be due to occasional cirri. No opening or closing of the grooves could be certainly detected, though horizontal muscles capable of causing such movements are well developed (see Text-fig. 36). It is possible that sudden slight swaying sideways of the whole demibranch may have caused the particles to be flung out of the grooves. In an Ensis arcuatus less than 3 cm. long, sudden swaying sideways of a demibranch, added to slight closing of the folds, was actually observed to fling particles off the lamella. This is evidently a method of ridding the gills of unwanted material, and may be compared with the similar movements described in Pecten by Kellogg (1915, p. 674) and Setna (1930, p. 370), and in Ostrea by Yonge (1926, p. 325).

A few observations on the beat of the lateral cilia of this small Ensis arcuatus may be added here. One valve was carefully removed and the beat of the cilia observed while the gills were attached to the animal: this was possible owing to the transparency of the shell at this size. The observations were made some hours after removal of the valve, when all the lateral cilia were active, and the metachronal wave regular. Inhibitions, lasting a few seconds, were noticed at more or less regular

intervals. Such inhibition affected simultaneously all the lateral cilia on at least six plicae, and most probably all on the entire lamella, though it was more difficult to be sure of this.

A piece of demibranch was removed from the gill. The lateral cilia on this were at first motionless, but after about 2 hours most of them were beating normally, though there were stretches where they were motionless. On certain of the plicae intermissions did not occur, on others they followed each other rapidly and lasted no more than a second. It would seem that removal of the piece of demibranch—and perhaps its small size—had upset the regularity of the intermissions.

The stoppage of lateral cilia on pieces of demibranch on removal from the animal is general in many Lamellibranchs and was noticed by Lucas (1931, p. 156) in Modiolus modiolus: he also observed intermissions of these cilia both on attached gills and detached filaments. He stated (p. 158): 'it was soon evident that the cilia showed the same variations in their activity when detached from the animal as when attached. The impulse which produces sudden inhibitions apparently is an intrinsic part of gill tissue.'

Douvillé (1907, pp. 100–1) concluded from differences in the character of the hinge that Solen and Ensis are not closely allied, but are examples of similarity of form due to convergence under the influence of a particular environment. If this is so it is extraordinary that a similar type of sorting mechanism on the gills should be found in the two forms, a type which is not found on the plicate and heterorhabdic gills of the allied Solecurtidae,[1] or indeed in any other Eulamellibranchs examined, but only in certain Pseudolamellibranchs.

Cultellus pellucidus (Pennant).

The Structure of the Gills.

The gills of Cultellus pellucidus differ from those of Solen and Ensis in being flat and homorhabdic, and without a groove at the free ventral edge of the outer demibranch.

[1] Graham (1933) has followed d'Orbigny in splitting the Solenidae into two families, Solenidae and Solecurtidae.

The marginal groove of the inner demibranch is shallow. Ghosh's (1920, p. 61) statement that the gills of this species—for which he created a new genus, Subcultellus—are 'similar to those in Solen', that is presumably that they are plicate and heterorhabdic, is evidently due to some misunderstanding of Bloomer's work (1902), on which his diagnosis is based. Mr. H. H. Bloomer has informed me by letter that he considers that the gills of Cultellus pellucidus are flat and homorhabdic. There is thus no question of a second species of Cultellus at Plymouth, as suggested by Graham (1934, pp. 179–80), so far as the character of the gills are concerned.

The dorsal edges of the ascending lamellae of the outer demibranchs are fused with the mantle, the type of fusion being that found in Solen and Ensis (see p. 279). The junction between the dorsal edges of the ascending lamellae of the inner demibranchs inter se is organic, but with the foot is by interlocking cilia. In fact Cultellus pellucidus resembles Solen in the nature of the various junctions between the gills and adjacent parts.

Ciliation of the Filaments.

The frontal cilia on the descending lamella of the outer demibranch are fine and beat dorsally (see Text-fig. 42). Long, stout, tactile cilia occur very rarely on the frontal surface of this lamella, except near the ventral margin.

On both lamellae of the inner demibranch, and on the ascending lamella, together with its narrow supra-axial extension, of the outer demibranch, the frontal cilia are of two kinds, fine and short, and long and coarse. The coarse cilia occur in a tract alongside the latero-frontal cilia on the posterior side of the frontal surface, and on both demibranchs beat toward the free ventral margin. When at rest they lie with the tips directed dorsally, that is their position of rest is at the beginning of the effective stroke. Long, coarse, blunt tactile cilia occur fairly frequently between the latero-frontal cilia and the tract of coarse frontal cilia. The direction of the effective beat of the fine frontal cilia on these lamellae was not actually seen in side view of a filament, or at most glimpsed only once, but it seems

probable from the movement of particles that it is dorsal on all of them.

The Gill Currents.

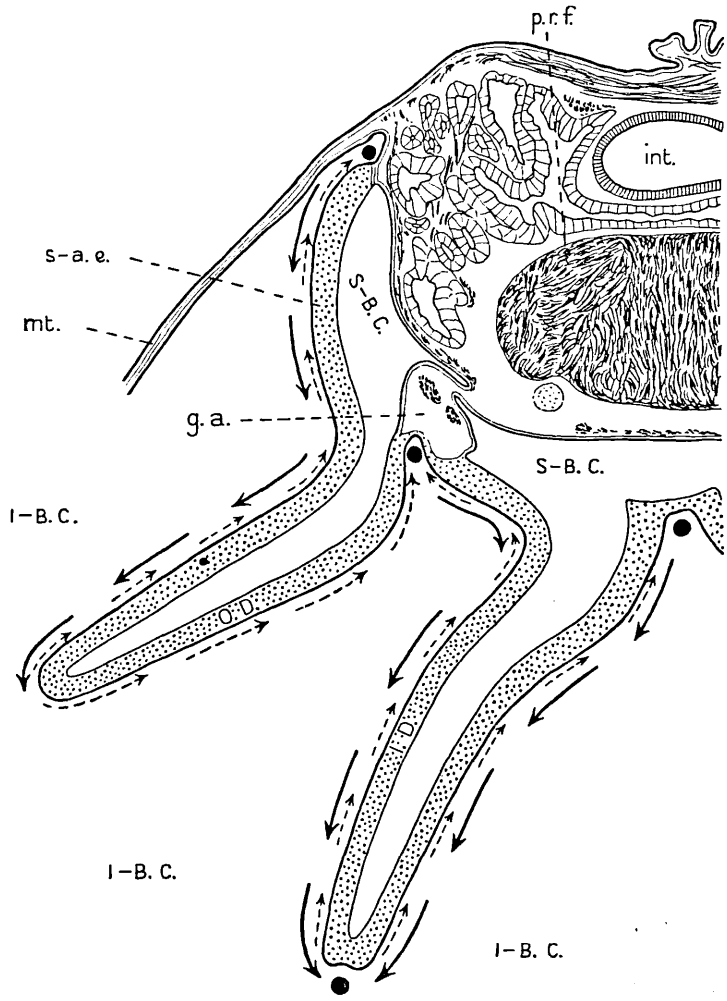
The obvious frontal currents in Cultellus pellucidus are toward the ventral edge on the ascending lamella and dorsalward on the descending lamella of the outer demibranch, and on the inner demibranch toward the ventral edge on both lamellae (Text-fig. 42). This direction of the frontal currents is common among Eulamellibranchs (see Part III, in the press), and is found in Solecurtus scopula (Turton) and Solecurtus chamasolen (da Costa) of the allied family Solecurtidae. Less obvious currents are described later.

With the exception of the descending lamella of the outer demibranch, which is without coarse frontal cilia, the frontal currents are rapid and strong, a thick covering of carborundum being quickly cleared from the lamellae. Cultellus pellucidus is taken from a habitat of silty sand, and no doubt the coarse cilia are an adaptation for removing sand grains from the gills, for specimens have been brought into the Laboratory with much sand in the mantle chamber.

Large particles travelling down the ascending lamella of the outer demibranch pass off at the ventral edge and sometimes on to the deeper inner demibranch; small ones, however, frequently pass round the edge and on to the descending lamella, over which they are transported dorsally into the oralward current between the bases of the two demibranchs of each side of the body. There is no longitudinal current along the free ventral edge of the outer demibranch.

On both lamellae of the inner demibranch many of the large particles appear to pass off at the free edge, only the small ones travelling along the shallow marginal groove toward the mouth. Particles falling from the gills to the mantle are rapidly conveyed into the rejection tracts.

In addition to the oralward tracts between the bases of adjacent demibranchs of a gill, and along the free ventral edge of the inner demibranch, narrow tracts of oralward beating cilia occur along the dorsal edges of the conjoined ascending lamellae of the two inner demibranchs, and between these



TEXT-FIG. 42.

Cultellus pellucidus. Transverse section, somewhat diagrammatic, to show the direction of the frontal currents of the gills. Plain arrows indicate the direction of those caused by coarse frontal cilia; broken arrows those caused by fine frontal cilia. ● position of orally directed longitudinal currents; *I.D.*, inner demibranch; *g.a.*, gill axis with longitudinal muscle-bundles; *int.*, intestine; *mt.*, mantle; *O.D.*, outer demibranch; *p.r.f.*, posterior retractor of foot; *s.-a.e.*, supra-axial extension of ascending lamella of outer demibranch; *I.-B.C.*, infra-, and *S.-B.C.*, supra-branchial chamber. $\times 55\frac{1}{5}$.

lamellae and the foot anteriorly, and also along the dorsal edges of the ascending lamellae of the outer demibranchs (Text-fig. 42, at ●). The passage of particles along these latter tracts appears precarious, at least in the opened animal, all but the finest being dragged from the tracts by the strong cilia of the gill filaments.

While practically all particles reaching the filaments are transported in the directions previously described, yet on the ascending lamella of the outer demibranch, and both lamellae of the inner demibranch, occasionally fine particles—the finest of fine carborundum (3F) and the animal's own red blood corpuscles—were seen travelling for considerable distances dorsalward, the movement occurring along the anterior side of the frontal surfaces, where fine cilia are found; it seems very probable that they were responsible for the movement, though it was not certainly proved.

Summary.

The gills of Solen marginatus, Ensis siliqua, and Ensis arcuatus are synaptorhabdic or eulamellibranchiate, and the lamellae plicate and heterorhabdic. The latero-frontal cilia are large; there are in addition small subsidiary latero-frontal cilia. The frontal cilia on the filaments forming the bottom of the plical grooves are fine and beat dorsally. In the two species of Ensis the frontal cilia on the filaments forming the sides and apices of the plicae are arranged in two tracts with the effective beat in opposite directions; in Solen marginatus in three tracts, a median one of coarse cilia beating ventrally and two outer ones of fine cilia continuously beating dorsally.

In both genera the movement of particles in the plical grooves is dorsalward; on the crests mainly ventralward; on the sides of the plicae ventral or dorsal according apparently to their type and number.

Along the marginal grooves of the demibranchs, between the bases of the two demibranchs of a gill, and along the dorsal edges of all the ascending lamellae, currents are towards the mouth.

The gills of Cultellus pellucidus are synaptorhabdic

or eulamellibranchiate, and the lamellae flat and homorhabdic. The ventral edge of the outer demibranch is ungrooved. On the frontal surfaces of the filaments of both lamellae of the inner and the ascending lamella of the outer demibranch there are, in addition to fine cilia, a tract of long, coarse ones which beat ventrally. The fine frontal cilia, which alone are present on the descending lamella of the outer demibranch, beat dorsally, and, so far as could be ascertained, the tracts of fine cilia on the other three lamellae of the gill also beat dorsally.

The obvious frontal currents are toward the ventral edge on both lamellae of the inner and on the ascending lamella of the outer demibranch, and dorsalward on the descending lamella of the outer demibranch. Along the marginal groove of the inner demibranch, between the bases of the two demibranchs of a gill, and along the dorsal edges of all the ascending lamellae, currents are towards the mouth.

General Summary.

Accounts are given of the ciliary feeding mechanisms in: A, Nuculana minuta (Müller); B, Glycymeris glycymeris (L.), and Arca tetragona Poli; C, Heteranomia squamula (L.), Monia squama (Gmelin), and Monia patelliformis (L.); D, Pteria hirundo (L.); and E, Solen marginatus Montagu, Ensis siliqua (L.), Ensis arcuatus (Jeffreys), and Cultellus pellucidus (Pennant). These Lamellibranchs agree in possessing a certain ciliary sorting mechanism on the gills themselves, namely adjoining tracts of frontal cilia beating in opposite directions on the same gill filament or leaflet. In Pteria, Solen, and Ensis, bivalves with plicate and heterorhabdic lamellae, this occurs on the ordinary and apical filaments only, and is complicated by a difference in the direction of the frontal currents in the plical grooves and on the crests, such as is already known in Pecten, Ostrea, and Lima. In Cultellus it is found on both lamellae of the inner demibranch, but on the ascending lamella only of the outer demibranch. The types of frontal ciliation of the gill filaments dealt with in the papers of Part I are given in Table I.

Tracts of fine frontal cilia, beating continuously, convey particles intended for consumption, while tracts of coarse cilia, fully active only when stimulated, transport material intended to be rejected. In all, except the Protobranch Nuculana, unwanted material is carried to the ventral edges of the demibranchs, which are generally ungrooved or slightly grooved, rarely deeply grooved. In the Arcidae and Anomiidae the current along the edge is posterior in direction, so that such of the unwanted material as does not fall on the mantle is transported directly to the exterior. In Pteria, Solen, Ensis, and Cultellus the marginal current is oralward, but if the load be heavy much falls on the mantle, and is conveyed posteriorly by its recurrent tracts and finally ejected on sudden closure of the valves.

In the Anomiidae the sorting mechanism on the gills was not observed functioning satisfactorily under experimental conditions, in that there was no appreciable transportation of intended food particles dorsally, and it would seem that members of this family feed mainly after the manner of the Ectoproct Polyzoa, that is on particles brought directly to the broad dorsal food grooves by the water current set up by the lateral cilia.

In Nuculana minuta the highly specialized method of sorting on the small gills would seem to have been inherited from a form in which the gills played a considerably greater part in the nutrition of the animal than they do in this Protobranch.

TABLE I.

TYPES OF FRONTAL CILIATION OF GILL FILAMENTS DEALT WITH IN PART I.

A. ADJACENT TRACTS OF OPPOSITELY BEATING COARSE AND FINE FRONTAL CILIA.

On all filaments or leaflets of species with flat and homorhabdic lamellae.

(*a*) In two tracts.

Heteranomia squamula, Monia squama, Monia patelliformis.

(*b*) In three tracts.

Nuculana minuta (inner leaflets), Glycymeris glycymeris, Arca tetragona, Arca lactea.

On ordinary and apical filaments of species with plicate and heterorhabdic lamellae.

(*a*) In two tracts.

Pteria hirundo, Ensis siliqua, Ensis arcuatus.

(*b*) In three tracts.

Solen marginatus.

On all filaments of the inner demibranchs and those of the ascending lamella of the outer demibranchs in species with flat and homorhabdic lamellae.

(*a*) In two tracts.

Cultellus pellucidus.

B. Adjacent Tracts of Coarse and Fine Frontal Cilia beating in the same Direction.

Nuculana minuta (outer leaflets).

C. Fine Frontal Cilia only, with the Effective Beat Dorsalward.

On principal filaments of species with plicate and heterorhabdic lamellae, Pteria hirundo, Solen marginatus, Ensis siliqua, Ensis arcuatus (also on adjacent ordinary filaments).

On all filaments of descending lamella of the outer demibranchs of species with flat and homorhabdic lamellae.

Cultellus pellucidus.

EXPLANATION OF PLATES 10 AND 11.

Abbreviations used in the Plates.

ad., adductor muscle; *b.*, bay in velum; *by.m.*, byssal muscle; *c.m.*, cut edge of right mantle lobe; *EXH.CUR.*, exhalent current; *f.*, foot; *g.a.*, gill axis; *g.l.*, left gill; *g.r.*, right gill; *INH.CUR.*, inhalent current; *m.*, position of mouth; *m.f.*, membraneous fold over mouth and proximal oral grooves; *m.m.*, right mantle margin; *osph.*, osphradium; *p.l.i.*, left inner palp; *p.l.o.*, left outer palp; *p.r.o.*, right outer palp; *r.*, rectum; *r.p.l.*, recurrent path on left mantle; *r.p.r.*, recurrent path on right mantle; *s.m.*, suspensory membrane of the gill; *v.f.*, fused vela; *v.m.*, visceral mass; *w.f.*, white folds of the mantle or hypobranchial gland.

Plate 10.

Fig. 1.—Heteranomia squamula viewed from the right side to show the ciliary currents. The shell valve and much of the mantle and gill of the right side have been removed. The narrow mantle margin (*m.m.*) running parallel with the right outer palp (*p.r.o.*) has been folded back to expose the ciliated path (*r.p.r.*) on the mantle. The main ciliated paths are shown by thick arrows. The velum in the normal position is almost perpendicular to the mantle, but for convenience is shown lying against the shell. The broken arrows just below the gill axis (*g.a.*) indicate the direction of the current in the groove between the two left demibranchs; those in the postero-dorsal region the currents on the visceral mass and left mantle seen through the right mantle. × ca. 12.

Plate 11.

Fig. 2.—Monia squama viewed from the right side to show the ciliary currents. The shell valve, and most of the mantle and gill of the right side have been removed. The narrow mantle margin (*m.m.*) running parallel with the right outer palp (*p.r.o.*) has been folded back to expose the ciliated path (*r.p.r.*) on the mantle. The main ciliated paths are shown by thick arrows. The broken arrows indicate the direction of currents on the visceral mass and left mantle seen through the right mantle. The ciliary currents of Monia patelliformis are very similar, slight differences being indicated in the text. × ca. $3\frac{3}{4}$.

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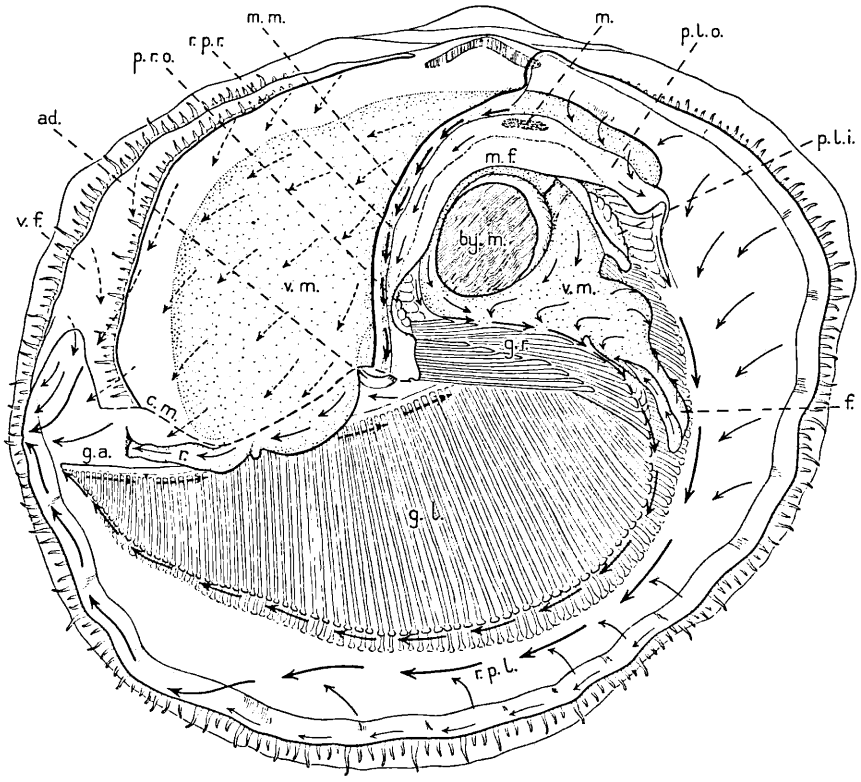

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Fig. 1

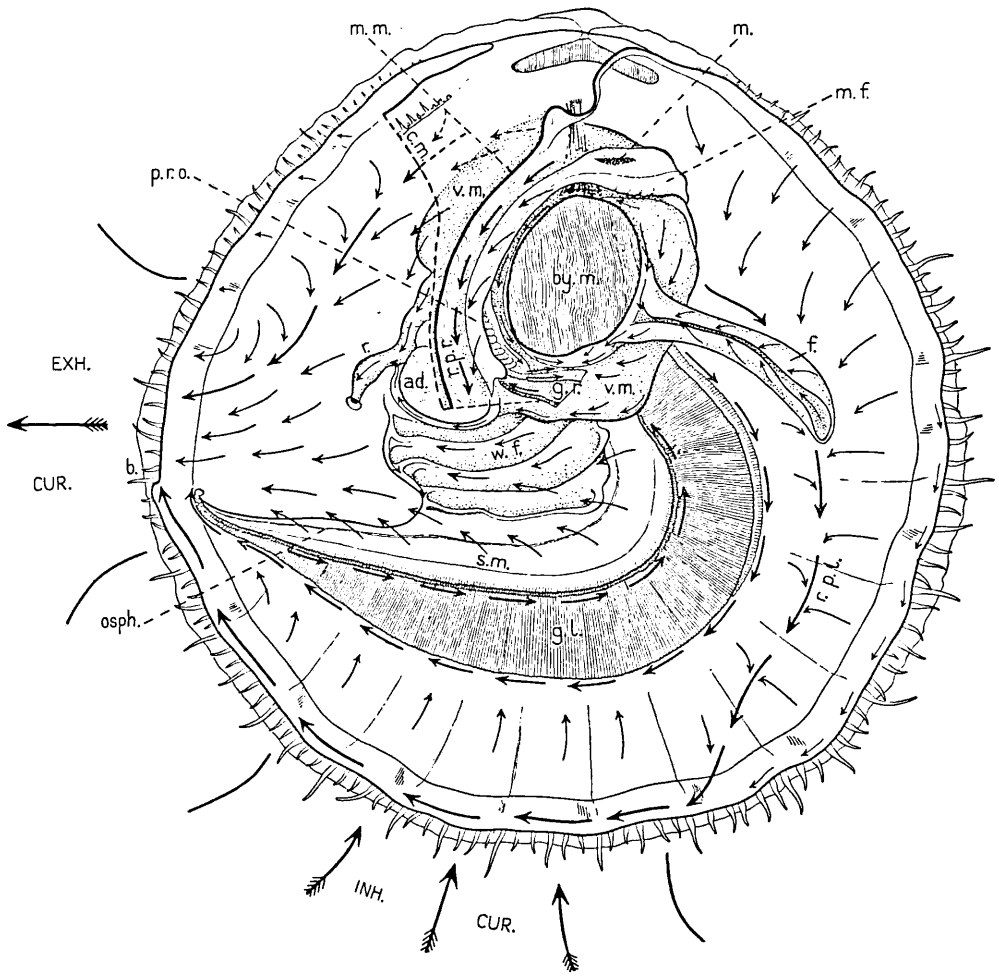

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Fig. 2

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Printed in Great Britain by John Johnson at the Oxford University Press

16

DAPHNE ATKINS, B.Sc.

On the Ciliary Mechanisms and Interrelationships of Lamellibranchs

Part II. Sorting Devices on the Gills

Quarterly Journal of Microscopical Science
Vol. 79, Part III, March, 1937

Printed in Great Britain

On the Ciliary Mechanisms and Interrelationships of Lamellibranchs.

PART II: Sorting Devices on the Gills.

By

Daphne Atkins, B.Sc.

Marine Biological Laboratory, Plymouth.

With 9 Text-figures.

CONTENTS.

INTRODUCTION.

KELLOGG (1915, p. 695) in his paper on the ciliary mechanisms of Lamellibranchs, writing of Yoldia, stated that 'In no other gills that I know of except those of Monia, and Pecten, are there special means of conducting undesirable material to outgoing tracts. In other cases, collections may be of such volume that the marginal groove cannot hold them, and they fall into the mantle chamber of their own weight. It is the function of other gills simply to collect, and pass collections on to the palps[1] on which it is determined whether they shall be continued on to the mouth, or to

[1] The spacing of the words is mine.

an outgoing tract; but here the gill possesses its own outgoing tract, which must inevitably be used unless contact is effected between gill and palp.' Ostrea (Yonge, 1926) and Lima (Studnitz, 1931) have since been added to those bivalves known to possess a sorting mechanism on the gills, and work by the writer on a large number of British Lamellibranchs has shown that the gills themselves in many instances are concerned in sorting to a greater extent than perhaps has been previously realized. In Part I (Atkins, 1936) the sorting mechanisms of the gills of Nuculana, Arca, Glycymeris, Heteranomia, Monia, Pteria, Solen, Ensis, and Cultellus have been treated already in detail; here short accounts of further sorting devices are given. The sorting mechanisms of the gills alone have been investigated, owing to the ground covered and the limited time available. The palps were not examined, nor were accessory sorting structures such as siphon membranes (Kellogg, 1915), and gill shields or curtains (Orton, 1912).

The study of the living gills of many bivalves has shown that a difference in the direction of the frontal currents in the grooves and on the crests of plicate and heterorhabdic gills, as on those of Pecten, is of rare occurrence. Surprisingly rare, for it might be expected to occur generally on plicate gills with wide and grooved principal filaments. Principal filaments are not found in non-plicate gills, and the differentiation of principal from ordinary filaments, may be, to a certain extent, a mechanical consequence of folding, though principal filaments are not found in all deeply plicate gills, for instance not in Mya arenaria and Lutraria elliptica (=Lutraria lutraria) according to Ridewood (1903, p. 251). From the point of view of feeding mechanisms it is the principal filaments with wide, and maybe grooved, frontal surfaces that are of chief interest. In sections the shape of the frontal surface of principal filaments varies quite widely in the same lamella, corresponding largely to the state of contraction of the horizontal muscles.

Plication itself has been considered, and no doubt rightly, a method of increasing the collecting surface of the gills; it will also increase the power of the inhalent current. But having developed plications certain bivalves, especially those with

principal filaments with wide and grooved frontal surfaces, have utilized them as a sorting mechanism. The work of Yonge (1923, 1926) on digestion in Lamellibranchs has clearly demonstrated that the method of digestion is mainly adapted to deal with finely divided food. These particles are collected and in many forms partly sorted by the gills, and still further sorted by the palps. The curious case of the Septibranchs which have changed their method of collecting food, and, having lost the gills, feed on large food masses with consequent change in the formation and function of the stomach to a crushing organ, has been described by Yonge (1928).

An increased gill surface may under certain conditions, such as the presence of much sediment in the water entering, be a distinct disadvantage, for the increased surface will mean a stronger inhalent current bearing unwanted particles to clog the ciliated tracts of the gills, palps, and mantle. Several methods, so far as the gills are concerned, have been evolved to lessen the difficulty.

Utilization of Plicae for Sorting.

(*a*) Pecten Type.

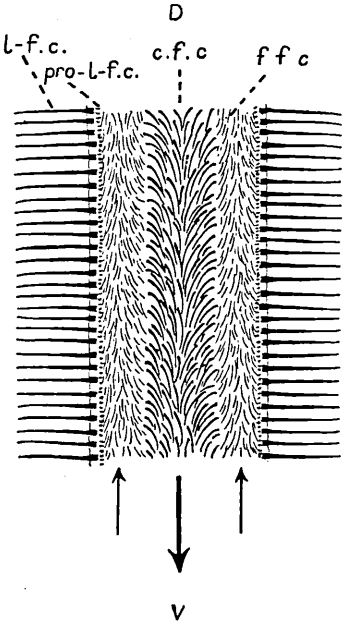
Perhaps the most highly specialized sorting mechanism on plicate gills is the now well-known one in which there is a difference in the direction of the frontal currents in the grooves and on the crests. It is found in Pecten (Kellogg, 1910, pp. 64–7; 1915, pp. 671–5), Ostrea (Yonge, 1926, pp. 322–5), Lima (Studnitz, 1931, pp. 230–3), Pteria hirundo (L.) (Atkins, Part I, 1936, p. 271), and in Solen and Ensis (Atkins, Part I, 1936, p. 278); it will probably be found to occur in Spondylus, and species of Amussium with plicate and heterorhabdic gills, such as Amussium pleuronectes L. (see Atkins, Part V).

In most of these bivalves the dorsal movement of particles is not restricted to the principal filaments, but occurs on the sides of the grooves also, as noted in Pecten irradians and Pecten tenuicostatus by Kellogg (1915, p. 672). In Chlamys opercularis (L.), which has about sixteen

filaments to the plica, the four or five filaments on each side of the principal filament have a current dorsal in direction, while the next two or three have a narrow tract of dorsally beating cilia in addition to the coarse ventrally beating ones. On the one or two apical filaments coarse ventrally beating frontal cilia alone seem to be present. A similar arrangement is found in Chlamys tigerina (Müller). Pteria hirundo, Solen marginatus, Ensis siliqua, and Ensis arcuatus also have tracts of frontal cilia beating in opposite directions on certain of the ordinary and on the apical filaments, as previously described in Part I.

In Ostrea edulis L. the frontal current is wholly dorsalward (except on the ventral ends of the filaments, where coarse terminal cilia beat ventrally) not only on the principal filaments, but frequently also on the filament on each side. Sometimes, however, a narrow median tract of coarse ventrally beating cilia is present on these latter filaments, and often on the lower quarter to a third. These ordinary filaments, which are rather larger than the others, and have thicker chitinous supporting rods, have been called transitional filaments by Kellogg (1892, p. 422). On the rest of the ordinary filaments on which the obvious movement of particles is ventralward, two kinds of frontal cilia occur, a median tract of coarse ventrally beating cilia, flanked on each side by a tract of fine cilia as shown in the sketch of a living filament (Text-fig. 1); a transverse section of a filament is given in Part VII. The fine cilia beat dorsally, as seen by direct observation of their beat, and by the movement of particles. The direction of the beat is less difficult to observe when the cilia are slowing down, for example in a drying preparation. The width of the tracts of fine cilia gradually decreases toward the crests of the plicae, and is very narrow on the filaments forming the apices, where, however, no special differentiation of apical filaments is found. If a small quantity of fine carmine particles—or even the finest particles of 3 F. grade of carborundum—in sea-water is gently pipetted into the water above a piece of demibranch and allowed to drop, or be drawn, gradually on to it, the conveyance of fine particles dorsally can be seen not only on the bottom, but on the sides of the plical

grooves. Even on the crests solitary fine particles can be seen to travel dorsally along the sides of the frontal surfaces of the filaments for considerable distances. The passage of such particles is precarious; frequently they get caught up by the coarse cilia and carried ventrally, for under experimental condi-



TEXT-FIG. 1.

Ostrea edulis. Frontal view of a living ordinary filament (second from principal) to show the tracts of coarse (*c.f.c.*) and fine (*f.f.c.*) frontal cilia. The arrows indicate the direction of their effective beat. *l.-f.c.*, latero-frontal cilia; *pro.-l.-f.c.*, subsidiary latero-frontal cilia; *D.*, dorsal; *V.*, ventral. ×645.

tions at least, the coarse cilia are always active, unless the preparation is drying up. Dorsal movement of particles on the crests is best seen a day or two after excision, when the plicae are well expanded, the filaments well separated, and the gill less irritable than a short time after excision.

In addition to the antagonistic tracts of coarse and fine cilia, there are on the frontal surfaces of the filaments occasional

long cirri, as mentioned by Yonge (1926, p. 324), and also groups of short, blunt cilia and short triangular clusters of cilia; the last two are probably sensory in function.

In Ostrea virginica Gmelin and Ostrea angulata (Lamarck) the frontal current is almost wholly dorsal on the principal and transitional filaments; on these filaments coarse ventrally beating cilia are found only on the ventral ends bordering the marginal grooves. On the remainder of the ordinary filaments the frontal cilia are in three tracts, a median one of coarse ventrally beating cilia, and side tracts of fine dorsally beating cilia. The width of the fine tracts decreases toward the crests and, especially in Ostrea angulata, is exceedingly narrow on the filaments forming the crests of the plicae. In both these species not only have particles been seen to travel dorsally over the tracts of fine cilia, but the direction of the beat has been observed. In pieces of demibranch of Ostrea edulis and Ostrea virginica the plicae expanded well a few hours after excision, but in Ostrea angulata, while they expanded sufficiently to reveal the principal filaments, the ordinary filaments were in close contact—and incidentally the lateral cilia unable to function—after three days. Probably owing to this the dorsal movement of particles over the side tracts of fine cilia was difficult to observe in this species.

The number of filaments to a plica varies rather widely in Ostrea edulis, being eight to seventeen, but generally about twelve to fourteen. So far as can be seen in the living gill, the number is about the same in Ostrea virginica, but generally fifteen to sixteen in Ostrea angulata.

Mucous glands are numerous on the frontal surfaces of the ordinary filaments of the three species of Ostrea, especially on those forming the plical crests, and tend to be in two rows, one on each boundary of the tract of coarse cilia.

The latero-frontal cilia of Ostrea edulis, Ostrea virginica, and Ostrea angulata are only moderately developed, especially as to their size at the base. They vary in length from about 14 to 25μ. It is interesting that these straining cilia should be longest and closest together on the

principal and transitional filaments on which fine food particles are collected, and shortest and farthest apart on the filaments forming the plical crests, which are concerned chiefly with rejection. Frequently they are closer together on the side of the transitional filament next to the principal, than on the side away from it. In Ostrea edulis and Ostrea virginica the distance apart of the latero-frontal cilia varies between about 1·5 to 3·7μ, while on the filaments of the plical crests of Ostrea angulata they are about 6 or 7μ apart. It is possible that there is less dorsalward movement of food particles on the crests of Ostrea angulata than on those of Ostrea edulis and Ostrea virginica, and that with this is correlated the wider spacing of the latero-frontal cilia on the crests of Ostrea angulata.

The ciliation of the filaments has been found to be essentially the same in the three species of Ostrea, Ostrea edulis, Ostrea virginica, and Ostrea angulata.

Judging from the behaviour of the living gills, longitudinal muscles in the gill axes and dorsal edges of the ascending lamellae, and vertical muscles in the interlamellar septa, are better developed in Ostrea angulata than in the other two species.

In Pecten when numerous particles are present in the water they are carried chiefly on the plical crests toward the free edges of the demibranchs; along these they pass orally, but the passage is precarious, especially if the load be heavy. Twitching of the gills may loosen the load, which falling on the mantle will be carried to the margin, to be finally ejected. When few particles are present in the water they travel mostly in the plical grooves, and are carried dorsally into the much safer tracts between the bases of the two demibranchs of each side of the body, and along the dorsal edges of all the ascending lamellae (Kellogg, 1910, 1915). These dorsal channels leading to the mouth are of much importance in this method of sorting. Nelson (1923, p. 167) observed that in the oyster 'A larger proportion of the material brought to the palps by the dorsal groove is accepted than that which arrives via the ventral groove. Observation shows that the larger particles, chiefly sand grains, are consigned mainly to the ventral groove. In

their passage over the gills they evoke a relatively copious secretion of mucus which renders them bulky and consequently less likely to enter between the palps. The majority of food particles, which stimulate a somewhat less secretion of slime while passing over the gills, enter between the palps and are passed toward the mouth. The separation is by no means perfect as some food materials are rejected and much dirt and sand may at times be taken into the stomach.' Yonge (1926, p. 331) found in Ostrea edulis that the smaller particles from the gill axes which pass into the lateral oral groove are not so rigorously sorted as material from the free margins of the gills.

The various movements by which the Pecten gill endeavours to free itself of large or too numerous particles have been carefully described by Setna (1930).

Probably all plicate gills, by means of horizontal muscles, are capable of reducing their surface by approximating the plicae, so that the plicae touch or almost touch, the grooves being hidden. In this way the surface opposed to a heavily laden inhalent current can be almost entirely a rejection one. If the plicae are contracted to such an extent that the filaments touch, the lateral cilia are unable to function, and the inhalent current is in abeyance.

In Pteria, and perhaps to a less extent in Solen, in both of which vertical muscles are well developed in the interlamellar septa, the surface can be further reduced by dorso-ventral contraction of the demibranchs. Such contraction by throwing the filaments against each other will impede, if not prevent, the action of the lateral cilia, and so greatly reduce or stop the inhalent current.

Gills on which the frontal currents are in opposite directions on the crests and in the grooves have certain characters in common: (1) the plicae tend to flatten out in the lower parts of the demibranch; (2) there is little difference between the principal and ordinary filaments at the free margin of the demibranch; (3) though the marginal groove[1] may be sinuous, yet it is of practically the same depth throughout, and has not deeply

[1] The groove at the free ventral edge of the demibranch is termed the marginal groove.

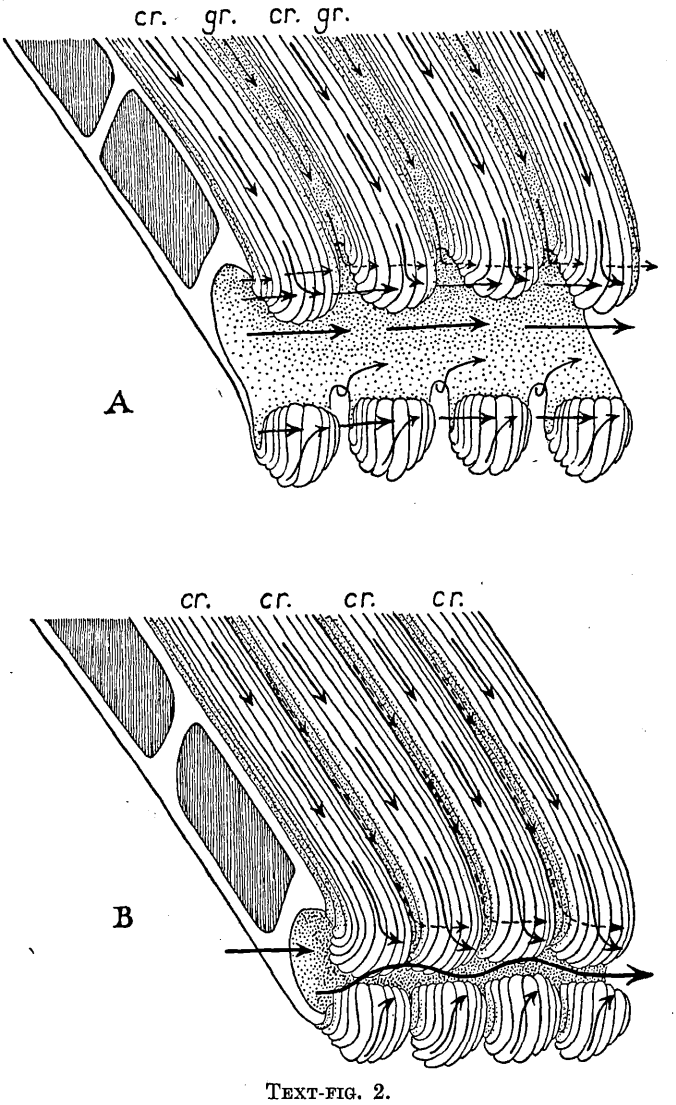
scalloped sides as in Pinna and the Anatinacea. The marginal groove may be extremely shallow, almost absent, as in Pecten, Lima, and the outer demibranch of Pteria hirundo (L.); shallow in Solen marginatus Montagu (=vagina); or fairly deep as in Ostrea, Ensis siliqua (L.), and Ensis arcuatus (Jeffreys), and the inner demibranch of Pteria hirundo.

The foretelling of the direction of the frontal currents from the form of the lamellae is speculative, but probably it will be found that Spondylus and Amussiidae with plicate and heterorhabdic gills should be included with these forms. An examination of Amussiidae with flat gills and of Plicatula should prove interesting, considering the type of sorting found in the Arcidae (see Atkins, Part I, 1936).

Lamellibranchs having the sorting mechanism described, with the exception of Solen and Ensis, are closely allied, being members of Pelseneer's (1911) order Pseudolamellibranchia and Douvillé's (1912, p. 466) Sedentary branch, descended from ancestors characterized by byssal fixation, and with living members characterized by the possession of fine or micro-latero-frontal cilia (see Atkins, Part VII), though in Ostrea they are moderately developed. These bivalves, therefore, may have inherited a similar type of sorting mechanism from a common ancestral group, possibly the Pterineidae. It is curious that Pinna though descended from the Pterineidae, yet—as described in the next section—has a sorting mechanism different from that found in Pteria hirundo. The possession of a sorting mechanism similar to that of Pecten and others by the specialized burrowing forms, Solen and Ensis, and apparently of very different ancestry (see Davies, 1933, p. 325) is most interesting: it seems certain that it has been independently evolved. This type of sorting mechanism was probably evolved in situations where the bivalves were very liable to become silted up; to-day such are occupied by Ostrea, Solen, and Ensis.

(*b*) Pinna Type.

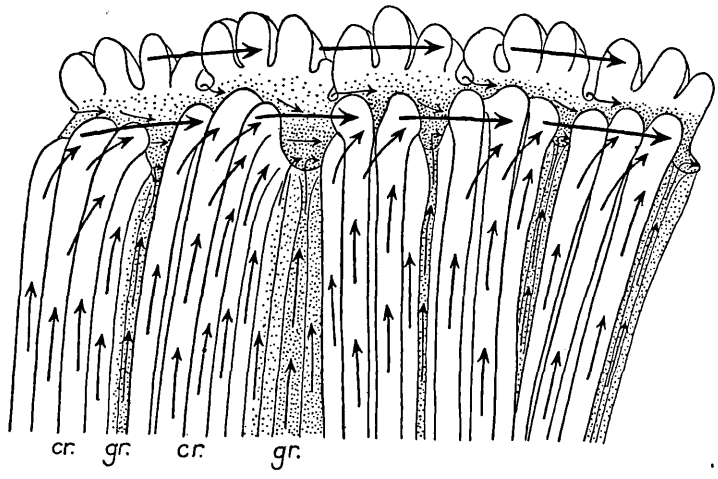
In the second method of sorting the direction of the frontal current in the plical grooves, as on the crests, is toward the free



TEXT-FIG. 2.

Pinna fragilis. Diagrammatic sketches of the ventral margin of a demibranch to show the utilization of the plicae and the marginal groove in sorting. A. Marginal groove open; the plicae expanded revealing the principal filaments. B. Marginal groove closed; the plicae contracted hiding the principal filaments. Broken arrows indicate the direction of deep hidden currents. *cr.*, plical crest; *gr.*, plical groove.

edge of the demibranchs, yet the plicae are utilized in sorting. Such gills are deeply plicate and markedly heterorhabdic. The marginal food groove has deeply scalloped sides, for there is little or no flattening of the plicae at the lower margin of the demibranchs, though a few of the ordinary filaments adjacent to the principal may become fused with it. The walls of the



TEXT-FIG. 3.

Cochlodesma praetenue. Marginal groove shown somewhat open. The large arrows indicate the direction of superficial currents across the lobes of the filaments bordering the marginal groove. *cr.*, plical crest; *gr.*, plical groove. × 84.

groove are thus of uneven height, being high in the region of the crests, and low in the region of the principal filaments (Text-figs. 2, 3). The apical and ordinary filaments forming the crests extend and project considerably over the edge of the marginal groove, while the principal filaments, together with such of the ordinary filaments as have fused with them, only reach the edge of the groove. In other words, the apical and adjacent filaments are somewhat longer than the principal and adjacent filaments; this causes the deeply scalloped appearance of the sides of the food groove of such forms.

The marginal groove is more or less divided into two channels,

one at the depth of the groove lined by fine cilia, and a superficial one lined by long coarse cilia. In the Anatinacea the two channels are separated to a certain extent by long, fine cilia with an anterior streaming appearance.

Fine and few particles only will reach the principal filaments, and the few adjacent ordinary filaments, in the trough of the plical grooves; coarse ones will be eliminated by the narrowness of the interplical spaces. Now it is the principal filaments which lead into the depth of the marginal groove (Text-figs. 2 A, 3), so that particles travelling along these and adjacent filaments alone will reach the deep, safe channel. This channel can be entirely hidden by the drawing together of the opposite lobes of the marginal groove (see Text-fig. 2 B).

Coarse and numerous particles, such as usually travel on the plical crests, either pass directly off the gill, or fall off after being carried a short distance along the edge, or if the load be slight may be carried along it toward the mouth. This is a precarious passage, slight twitching of the gill causing the load to fall on the mantle, whence it is removed to the outside.

In these forms, as in the first group, the gills are highly muscular, and the animal can if stimulated approximate the plicae to such an extent that they touch and the grooves are entirely hidden, so that a much reduced surface, which is entirely concerned with rejection, is exposed to the oncoming current. The gills are also capable of considerable dorso-ventral contraction, especially in Pinna, yet further reducing the surface.

As in the first method there is a difference in the form of the frontal cilia on the filaments in the troughs and on the crests of the plicae, those in the latter position being generally coarser than in the former. But in bivalves which have this second method of sorting, both fine and coarse frontal cilia beat in the same direction. In Lyonsia norwegica (Gmelin), which has thirteen to seventeen filaments to a plica, the three or so apical filaments have a broad middle tract of long, coarse frontal cilia bordered on each filament by tracts of fine, shortish cilia, such as occur on the remaining filaments of the plica. In Pinna fragilis Pennant, which has thirteen to fifteen filaments to a plica, the one to three enlarged apical filaments appear from

sections also to have a middle tract of coarse cilia, as in Lyonsia, but in Pinna it is almost impossible to see the ciliation of the living filaments, owing to the extreme contraction of the gill on the slightest stimulation.

The correlation of fine frontal cilia with food tracts and of coarse ones with chiefly rejection tracts has been found to be of common occurrence on the gills of Lamellibranchs. In plicate gills there is also a distinct tendency for the greater development of mucous glands on the frontal surfaces of the filaments forming the crests, that is on tracts concerned chiefly with rejection, than on those forming the bottom and sides of the grooves, that is on the food tracts. On food tracts, however, mucous glands are by no means absent.

Lamellibranchs with the method of sorting described above are: Pinna fragilis Pennant, Cochlodesma praetenue (Montagu), Lyonsia norwegica (Gmelin), Thracia villosiuscula (Macgillivray), and Thracia distorta (Montagu).

In members of the Anatinacea the inner demibranch is normal, while the outer is upturned and consists of the direct lamella only. In the species of this sub-order mentioned above, the principal filaments of the upturned outer demibranch are continuous with those of the direct (descending) lamella of the inner demibranch, and the plicae of one with those of the other. There is no interruption of the passage of particles across the gill axis.

According to Ridewood (1903, p. 262) the two British species of Pandora, Pandora margaritacea Lamarck (= inaequivalvis) have seven and Pandora pinna (Montagu) (= obtusa) nine filaments to a plica. The plicae therefore are rather shallow, and it is possible that they will be found not to have the same method of sorting as in the forms with deep plicae. A small specimen of Pandora pinna with nine filaments to a plica was examined. The plical grooves were shallow; the broadly rounded crests tended to smooth out at the free edge, the marginal groove having sides of practically even height. It would seem that the method of sorting described in the other Anatinacea does not occur in this species, but further specimens were needed to determine the point.

The habitats of the bivalves are as follows: Pinna fragilis lives almost buried in mud or soft sand, anterior end downwards; Lyonsia norwegica lives in silty sand; Thracia villosiuscula in mud and sand; Thracia distorta in crypts in red conglomerate of the Mewstone Ledge (M.B.A., 1931, pp. 241–52); and Cochlodesma praetenue in clean sand. They therefore live in situations where sediment is liable to be very heavy. In Pinna, as is well known, there is a special waste canal, formed by large folds of the mantle, up which the mud, entering the mantle chamber in large quantities during burrowing, is conveyed for expulsion.

The ancestry of the Pinnidae and the Anatinacea is entirely different (see Douvillé, 1912, p. 466), the former belonging to the Sedentary branch and the latter to the Burrowing branch of Lamellibranchia.

Sorting by the Marginal Groove.

Certain Lamellibranchs having a deep broad groove with sides of even height at the free ventral edges of the demibranchs utilize the groove as a sorting mechanism by opening and closing it. The working of such a groove was especially watched in Solecurtus scopula (Turton) (= candidus); its opening and closing being observed at a high magnification. By the apposition of the walls, the channel of the groove can be entirely roofed over. As in the majority of Lamellibranchs, coarse cirrus-like terminal cilia, beating obliquely anteriorly, are present on the ends of the filaments bordering the groove, while fine frontal cilia, beating directly ventrally into the groove, are relegated to each side of these (see also Wallengren, 1905, I, Pl. ii, fig. 10). At the ends of all filaments, including the apical, fine particles were seen to be carried by the fine frontal cilia into the depth of the groove, whence they have a safe passage to the mouth; while large particles and masses of material were transported precariously anteriorly by the coarse terminal cilia outside the lobes forming the dome of the groove. This material is usually rejected. By the apposition of the sides, too, large masses are prevented from entering the marginal groove, but

even when the groove is fairly wide open such masses of material do not seem generally to enter.

A deep marginal groove functioning in this manner has been observed also in Lutraria lutraria (L.) (= elliptica) and Cardium edule L. The deep marginal grooves of many Lamellibranchs, both of those with plicate and those with flat gills, probably work in this way. Wallengren (1905, II, pp. 17–18) noted the opening and closing of the marginal groove in Mya.

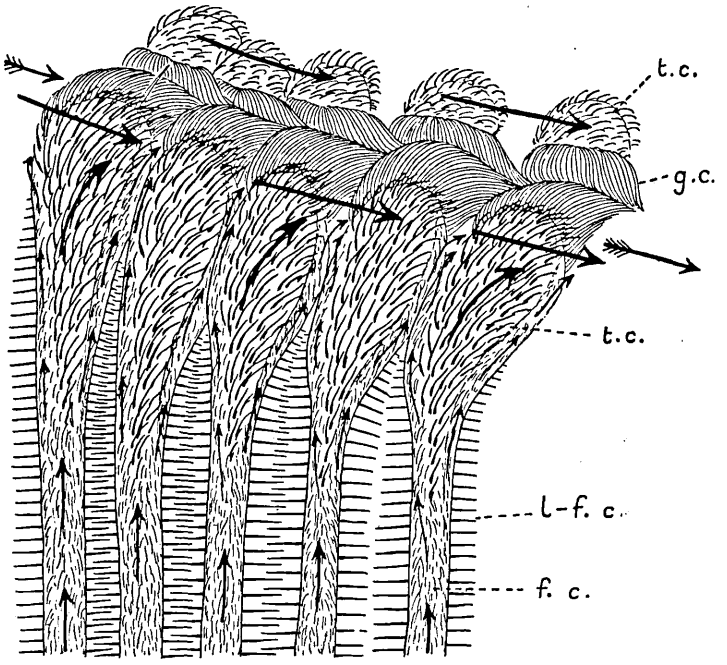
Though the gills of Solecurtus, Cardium, and Lutraria are deeply plicate, and the first two heterorhabdic, the plicae tend to smooth out toward the free margin of the demibranchs, owing to much fusion of the filaments; the marginal groove in consequence is of even depth. In Lutraria a deep groove is found at the ventral edge of both inner and outer demibranchs, but in Solecurtus and Cardium on the inner demibranch only, the outer being ungrooved.

Kellogg (1915, pp. 682–3) observed the opening and closing of the marginal groove in Zirfaea gabbi and Barnea pacifica, two members of the Pholadidea. His interpretation of the mechanism was as follows: 'Apparently the conduct of material over the distance of a foot—as some of it must be carried—in the midst of the rushing stream of the incurrent siphon, would be attended by so much uncertainty in an open groove, that completely covered passages have been developed on the edges of the demibranchs, which assure the delivery of the gill collections to the palps. When material from the lamella reaches the closed groove, its walls part, admit the collection and close over it, if its volume is not too great.'

Guarding Cilia.

A sorting device found on both flat and plicate gills is effected by what may be termed guarding cilia along the marginal grooves of the demibranchs. On each filamentar lobe of the marginal groove, on the side facing the groove, is a transversely set fan-shaped group of long and fairly fine cilia. These cilia beat as a group, with a slow undulating motion, each group behaving more or less as a membrane, and appear to be

only intermittently active—perhaps when touched by particles. The fan-shaped groups of cilia tend to arch over the groove (Text-figs. 4 and 5), the tips of the cilia of one group approaching

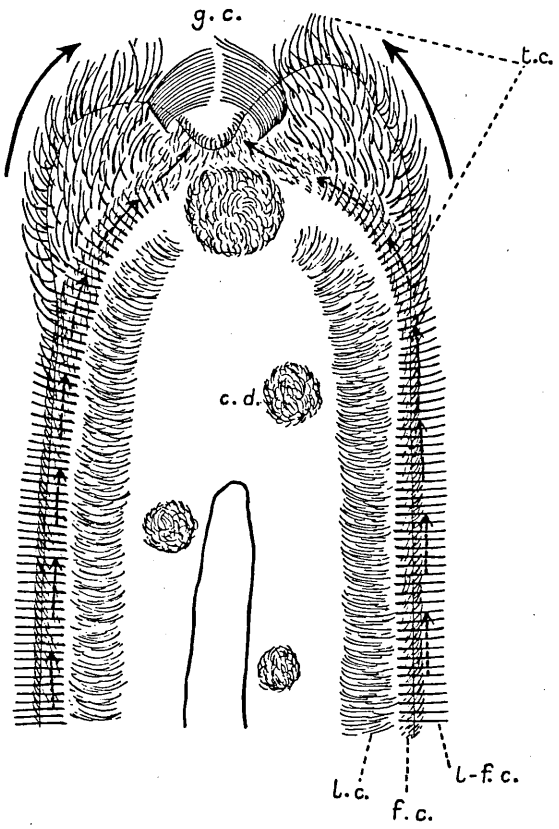


TEXT-FIG. 4.

Musculus (=Modiolaria) marmoratus. Marginal groove with guarding cilia. The small arrows indicate the path taken by fine particles; these pass into the groove by way of the small gap between successive fan-shaped groups of guarding cilia. Coarse particles driven by the coarse cilia on the ventral ends of the filaments (terminal cilia) travel along a superficial channel to the outside of the guarding cilia, as indicated by large arrows. Feathered arrows show the direction of the current within the groove. *f.c.*, frontal cilia; *g.c.*, guarding cilia; *l.-f.c.*, latero-frontal cilia; *t.c.*, terminal frontal cilia. × 300.

those of the opposite one. The position of the cilia relative to the groove varies somewhat in different Lamellibranchs. In some the cilia extend almost at right angles to the lobe, and are

then difficult to discern, as also when they occur well down in a deep groove, as in Solecurtus chamasolen (da Costa)



TEXT-FIG. 5.

Musculus (=Modiolaria) marmoratus. Ventral end of living filament in side view showing the position of the groups of guarding cilia (*g.c.*), with regard to the marginal groove. The small arrows indicate the path taken by fine particles; the large arrows that taken by coarse ones. *c.d.*, ciliated disc; *f.c.*, frontal cilia; *l.-f.c.*, latero-frontal cilia; *l.c.*, lateral cilia; *t.c.*, terminal frontal cilia. ×300.

(=antiquatus). In other bivalves they are set at an acute angle to the lobe, and in some near the tip, and are then clearly visible.

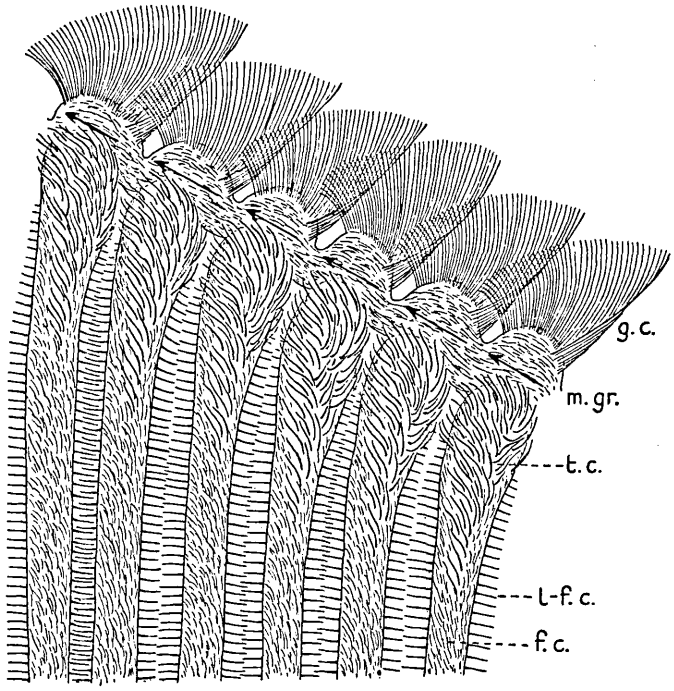
The guarding cilia separate a channel at the depth of the marginal groove, lined by fine cilia, from a superficial channel with coarse, long cilia.

As is well known, stout, cirrus-like cilia are present on the ends of the filaments bordering the marginal groove in the great majority of Lamellibranchs (Text-figs. 4 and 6); these terminal cilia beat obliquely forward. The ordinary fine frontal cilia are continued on each side of the coarse ones to the marginal groove, and beat directly ventrally. Wallengren (1905, I, Pl. ii, fig. 10) has shown this clearly in a figure of the ends of two filaments of Mya. Fine particles travelling down the lamellae are able to enter the deep and safe channel at the bottom of the marginal groove, by passing between adjacent groups of guarding cilia. Coarse particles carried obliquely forward by the coarse cilia either pass off the demibranch edge, or they pass along the superficial and precarious route where a heavy load is liable to fall, or be twitched off, on to the mantle.

Guarding cilia are better developed in some Lamellibranchs than in others. They are well developed in Galeomma turtoni Sowerby; poorly developed in Paphia (=Tapes) pullastra (Montagu). In Entovalva perrieri (Malard) (Text-fig. 6) and Montacuta ferruginosa (Montagu) fan-shaped groups of what are evidently guarding cilia are present on one side only of the marginal groove, that corresponding to the ascending lamella; in these two species they are very long, being about 80μ. In Mysella bidentata (Montagu) also they are present on one side only, but in this form are rather poorly developed. The method of functioning when present on one side alone was not clearly observed, for the three bivalves mentioned above are very small. In Montacuta ferruginosa, however, they were seen almost closed down over the groove, and they possibly can arch over the groove, which in this species is broad, though not deep. These three members of the Montacutidae possess a single demibranch, the inner, on each side of the body.

Wallengren (1905, II, pp. 17, 18, and Pl. i, fig. 4) has described and figured similar fan-shaped groups of cilia in Mya arenaria. According to him in this bivalve these 'fine

bristles', though flexible, are comparatively stiff. He never observed them in active motion, and though the activity of the surrounding cirri caused them to tremble passively, they were



TEXT-FIG. 6.

Entovalva perrieri. The marginal groove of the inner demibranch, with fan-shaped groups of what are apparently guarding cilia present on one side only, that corresponding to the ascending lamella. Sketched from life. *f.c.*, frontal cilia; *g.c.*, guarding cilia; *l.-f.c.*, latero-frontal cilia; *m.gr.*, marginal groove; *t.c.*, terminal frontal cilia. ×300.

always stretched toward each other over the marginal groove. The 'bristles' are necessarily involved in the movements of approximation and separation of the edges of the groove, so that they hide or expose it. He considered that since in Mya the cirri of the marginal groove beat straight forward, the

TABLE I.

Lamellibranchs possessing Guarding Cilia.

Present.	*Habitat.*[1]	*Absent* (in same family).	*Habitat.*
Mytilidae.			
Modiolus adriaticus.	Muddy gravel or sand, 7–40 f. (Jeffreys, ii, p. 117).	Mytilus edulis.	Rocks; shelly sand; gravel; gravelly mud.
Modiolus phaseolinus.	Rocky or hard ground, L.W. to 86 f. Often invests itself in a case of gravelly or shelly fragments (Jeffreys, ii, p. 120).	Modiolus modiolus.	Muddy gravel (Jeffreys, ii, p. 112).
Musculus (= Crenella = Modiolaria) discors.[2]	On roots and fronds of seaweed (Thorson, 1935).		
Musculus (= Modiolaria) marmoratus.	Buried in tests of Tunicates; attached to Cellaria; occasionally in sandy mud outside Plymouth Sound.		
Erycinidae.			
Kellia suborbicularis.	In silt and mud in crevices and inside dead shells.		
Leptonidae.			
Lepton squamosum.	In Gebia burrows in black muddy sand.		
Galeommatidae.			
Galeomma turtoni.	In crypts in red rock of Mewstone Ledge.		
Montacutidae.			
Montacuta ferruginosa.[3]	Associated with Echinocardium cordatum in silty sand.		
Mysella bidentata.[3]	Associated with Ophiocnida brachiata and in Phascolosoma burrows in silty sand, or mud.		
Entovalva perrieri.[3]	Attached to Leptosynapta inhaerens in silty or muddy sand.		
Veneridae.			
Gafrarium minimum.	Gravel, with some mud.	Dosinia exoleta.	Shell gravel; gravelly sand.
Venus verrucosa.	Mixed gravel; fine to medium sand.	Dosinia lupinus.	Fine sand; shell gravel; silty sand.

Venus casina.	Silty sand; muddy gravel.	Venus striatula (= gallina).	Silty and muddy sand; sand; sandy grounds.
Venus ovata.	Silty or muddy sand; sand; shell gravel.		
Venus fasciata.	Shell gravel; muddy or sandy gravel.		
Paphia rhomboides (= virgineus).	Shell gravel; gravelly sand; young specimens occasionally taken from silty soil.	Paphia decussata.	Muddy gravel; fine to medium sand.
Paphia pullastra.	Muddy gravel; fine to medium sand.		
Petricolidae.			
Mysia undata.	Silty black mud.		
Petricola pholadiformis.	Boring in stiff clay, chalk, &c.		
Asaphidae.			
Gari fervensis (= ferroensis).	Fine sand.		
Gari tellinella.	Shell gravel; coarse sand.		
Solecurtidae.			
Solecurtus chamasolen (= antiquatus).	Silty black mud (Rame mud).	Solecurtus scopula (= candidus).	Shell gravel.
Erodonidae.			
Aloidis gibba (= Corbula nucleus).	Silty sand; black mud; muddy gravel.		
Hiatellidae.			
Hiatella arctica.	Boring in limestone; attached to shells, roots of hydroids.		
Hiatella gallicana (= rugosa).	Ditto.		
Pholadidae.			
Pholadidea loscombiana.	Boring in red rock.	Barnea (= Pholas) parva.	Boring in rock.
		Barnea candida.	Boring in rock, hard clay, decayed wood.

[1] The habitats are taken mostly from Mar. Biol. Assoc., Plymouth Marine Fauna, 1931.
[2] Specimens obtained from Millport Marine Station.
[3] Inner demibranch only present; guarding cilia on one side of the marginal groove only, that corresponding to the ascending lamella.

function of the fan-shaped groups of 'bristles' is to hinder small particles, which have entered, from being thrown out again, and in addition to close the entrance to the groove.

Guarding cilia occur in a number of bivalves, both Filibranchs (though not in Arcidae and Anomiidae) and Eulamellibranchs, but have not been found in Pseudolamellibranchs. A list of species which have been found to possess guarding cilia along the marginal groove of one or both demibranchs, with their habitats, so far as these are known, is given in Table I. Species in which these cilia are absent are also given in the table if they belong to a family some members of which possess them. It will be seen that guarding cilia generally occur in bivalves inhabitating soil in which a certain amount of silt or mud is present. In the Solecurtidae the correlation of guarding cilia with a muddy habitat is beautifully clear; Solecurtus chamasolen (da Costa) from silty, black mud possessing them, while Solecurtus scopula (Turton) from shell gravel is without them. In the Veneridae, however, of species taken from similar habitats, some have and some lack these cilia.

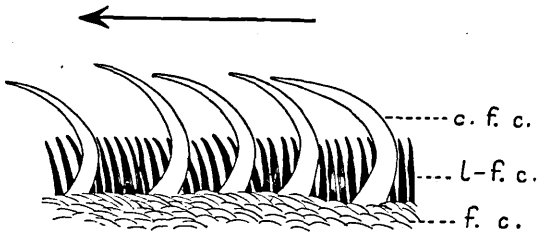
Somewhat similar cilia are present in Lyonsia norwegica, Thracia villosiuscula, and Thracia distorta.

Specialized Large Frontal Cilia.

Unusually large frontal cilia resembling cirri have been found in a few Lamellibranchs with flat lamellae. Such cilia may be suspected in bivalves in which a rapid jumping movement of particles on the gill is observable. Several of the bivalves possessing these cilia inhabit silty sand, and they are no doubt a specialization for removing sand grains from the lamellae. They appear generally to be fully active only on stimulation, and with the position of rest at the beginning of the effective stroke.

This specialization is perhaps carried farthest in Mactra corallina (L.) (=stultorum). The gill is flat and homorhabdic; a wide groove, with a tiny sunk channel along which fine particles travel, is present at the free edge of both inner and outer demibranchs. On the frontal surface of the filaments of

all lamellae, and the supra-axial extension of the outer demibranch, a single row of very long and very stout cilia—much larger than the latero-frontal cilia—occurs close to the latero-frontal cilia along the whole length of the filament on the posterior side (Text-fig. 7). These are fairly close together, though becoming less closely spaced axially. They beat in the same direction as the fine cilia, that is toward the ventral edge on all lamellae, but appear to be fully active only when stimu-



TEXT-FIG. 7.

Mactra corallina. Sketch from life to show the appearance of the frontal cirri (*c.f.c.*), and their size as compared with that of the latero-frontal cilia (*l.-f.c.*), which are almost in side view. The arrow shows the direction of beat of both kinds of frontal cilia. *f.c.*, frontal cilia. ×645.

lated, for instance when much carborundum is dropped on the lamellae. They cause a rapid jumping movement of particles; and would seem to be fitted by their large size for the removal of large particles, such as grains of the sand in which Mactra corallina lives. All but small particles are generally sent off the edges of the demibranchs, the small ones only travelling along the marginal grooves.

Specimens of this species from Bigbury Bay which were placed under circulation over night, when opened at about 3 p.m. the next day, were found to be clogged with much sand. This was removed with difficulty, and the rather frail gills then worked normally. It would appear, therefore, that the gills of Mactra corallina are liable to become clogged with sand grains on disturbance of the sea-bottom.

Similar cilia are present only on the descending lamellae of both demibranchs in Spisula subtruncata (da Costa),

and to a less extent on those of Spisula elliptica (Brown). In Spisula elliptica there appears to be some variation in the distance over which these cilia are found. In two out of five of the specimens examined coarse frontal cilia were practically restricted to the ventral margins of the demibranchs, as in many bivalves, but in the other three on the descending lamella of the outer demibranch they were present over the lower quarter to a third, though widely spaced dorsally. In both species the normal fine frontal cilia on the descending lamella of the outer demibranch beat dorsally over a variable extent of the surface, while the coarse ones—fully active only when stimulated—beat ventrally; thus there are frontal currents in opposite directions on the filaments of this lamella.

Such coarse cilia appear to be generally absent in Spisula solida (L.), except for those usually found on the lobes of the food groove in Lamellibranchs.

In Donax vittatus (da Costa) a single row of very long stout cilia is found on the posterior side of the frontal surface of the filaments over a certain distance from the ventral edge of the demibranchs. The distance apparently varies in different individuals, for in two specimens they were present over the lower quarter to a third of both lamellae of the inner demibranchs and the descending lamella of the outer, while in another two they extended but a short distance from the edge. On all lamellae they beat toward the ventral edge, and therefore on the descending lamella of the outer demibranch the frontal currents are in opposite directions on the same filament, for the fine cilia on that lamella beat dorsally.

Mactra corallina and Spisula subtruncata in which long, coarse cilia are most numerous live in sand and silty sand in coastal waters, Mactra corallina having a preference for shallower water than Spisula subtruncata (Davis, 1925, p. 27; Stephen, 1933); Donax vittatus, in some individuals of which they are present over a quarter to a third of the depth of the demibranchs, inhabits clean sand in the coastal zone; while Spisula elliptica, in which they are variably, but not extensively, present, is found both in silty sand and shell gravel (Ford, 1923, p. 169) in offshore waters;

and Spisula solida, in which they are absent, is generally found mainly in inshore waters in shell gravel and sand, the constituents of which are possibly less liable to be drawn into the mantle chamber when in suspension.

In Abra alba (S. Wood) and Abra nitida (Müller) the inner demibranch is normal; but the outer one is narrow and upturned, and is wanting anterior to the heart, that is for rather more than a third of the length of the inner demibranch. The lamellae are flat. The frontal currents on the upturned outer demibranch are continuous across the axis with those on the descending lamella of the inner demibranch, being ventralward. The frontal cilia on the ascending lamella of the inner demibranch beat toward the free edge, along which is a shallow groove. The movement of particles is rapid, and many seem to pass off the edge of the demibranch. Examination of the filaments shows a median tract of long, stout frontal cilia among the usual fine ones. Little mucus would seem to be secreted on the gills. The stout frontal cilia remove unwanted material, such as sand grains, while the fine ones collect material intended for consumption, but a certain amount of sand is swallowed, for in a specimen of Abra alba the intestine was found to be packed with muddy sand. Both these species are recorded from silty sand (M.B.A., 1931, p. 244).

In Scrobicularia plana (da Costa) (= piperata) a closely allied genus, but from a different habitat, being generally found in stiff mud, though it has been recorded from Salcombe Estuary in gravel (M.B.A., 1931, p. 244), there is no development of coarse frontal cilia, which seem to have been evolved in the Abras to deal with sand grains. It is probable that coarse cilia are not efficient in dealing with particles of mud.

Cultellus pellucidus (Pennant), from a habitat of silty or muddy sand, has rapid frontal currents on the lamellae, with the exception of the descending lamellae of the outer demibranchs. These rapid currents are explained by the presence of a tract of large cilia, between the fine frontal and the laterofrontal cilia, on the posterior side of the frontal surface of each filament of the ascending lamella of the outer, and of both lamellae of the inner demibranch. The ciliary mechanism of

the gills of this species has been described in Part I (Atkins, 1936, p. 296).

The bivalves so far described as possessing coarse or cirrus-like cilia on the gill filaments are all dwellers in sand or silty sand, and afford a clear correlation between adaptative ciliary structures and feeding difficulties incidental to the habitat.

Certain boring bivalves belonging to the Pholadidae and Petricolidae have been examined with interesting results.

Barnea (=Pholas) parva (Pennant), Barnea candida (L.), and Pholadidea loscombiana Turton have flat and homorhabdic lamellae. The gills extend into the base of the conjoined siphons—though to a less extent in Barnea candida than in the other two—and in consequence suffer considerable antero-posterior contraction on the retraction of these, the demibranchs being thrown into uneven folds. This possibly caused Ridewood (1903, p. 259) to describe those of Barnea parva and Barnea candida as having very feebly marked and unequal plicae. In these forms distinct dorso-ventral contraction of the demibranchs occurs, indicating the presence of vertical muscles.

In the two species of Barnea the frontal surfaces of the filaments of all the lamellae have in addition to fine cilia, long, cirrus-like cilia, which, however, tend to space out dorsally. They are rather irregularly disposed, not being in an even row as in Mactra corallina, but are mostly on the posterior side of the filament. The beat is ventral and slightly anterior in direction.

In the allied Pholadidea loscombiana such cirrus-like frontal cilia are absent.

Petricola pholadiformis Lamarck, which according to Pelseneer (1906, p. 270) 'has boring habits as and mimics Pholas (=Barnea) candida' has the ciliation of the filaments and frontal currents very similar to those of that species. Cirrus-like cilia are particularly well developed, being longer, though perhaps not as stout, as those of Mactra corallina. They are in a single tract on the posterior side of the filaments, and on all the lamellae beat ventrally.

The direction of the frontal currents of the four bivalves is given in Part III.

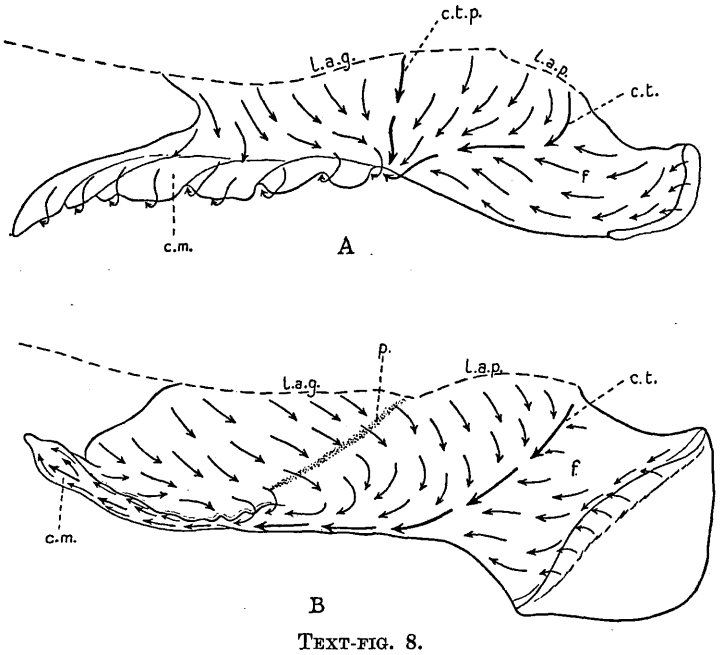
During the activities of rock and wood boring bivalves grains of rock or fragments of wood which the animals produce may be taken into the mantle chamber just as the sand dwellers may take in grains of sand. It is of great interest that similar structures have been evolved on the gills of boring and sand-dwelling forms for expelling coarse particles.

Barnea parva, Barnea candida, and Pholadidea loscombiana are borers, but judging from the ciliation of the gills, the two former are adapted to deal with coarser particles than is Pholadidea, for they have modified coarse frontal cilia, absent in Pholadidea, while it has guarding cilia (see p. 359) along the marginal groove, which are absent in the two species of Barnea. Amemiya and Ohsima (1933, p. 121) found that Barnea (Barnea fragilis) seems to prefer an horizontal surface while other borers, including Pholadidea penita, prefer a much inclined or vertical surface. If the British species of Barnea and Pholadidea have the same preference as the Japanese species it may be that the holes of Barnea are more liable to silt up than are those of Pholadidea. But it must be observed that while Petricola pholadiformis, which has the same habitat as Barnea candida, has similar large cirrus-like frontal cilia, it also has guarding cilia along the deep marginal groove of the inner demibranch, in this agreeing with Pholadidea loscombiana.

Barnea parva, Barnea candida, and Pholadidea loscombiana afford yet another instance in which a more detailed knowledge of the habitats of the three species is needed for a full understanding of modifications which are evidently adaptations to environment.

It may be mentioned here that Barnea candida possesses what Kellogg (1915, pp. 683–7) described in Barnea costata and Barnea pacifica as 'the collecting membrane of the visceral mass'. He considered that mud removal is its function, for 'specimens in which this membrane was found, were taken from waters which frequently were almost thick with silt for many hours at a time, but it was observed that mud was never so abundant as to cause the creatures to withdraw their siphons,

and so prevent its entrance to the mantle chamber'. The condition of the water above Barnea candida is unknown. In this species the membrane was not seen fully expanded,



TEXT-FIG. 8.

Ciliation of 'the collecting membrane of the visceral mass', the visceral mass and the foot of: A. Barnea candida. The thin collecting membrane is in folds and not fully extended. ×*ca.* 6. B. Barnea parva. ×*ca.* 4½. *c.m.*, collecting membrane; *c.t.*, ciliary tract coinciding with anterior edge of the inner palp; *c.t.p.*, that coinciding with the posterior edge of the inner palp; *f.*, foot; *l.a.g.*, line of attachment of the gill; *l.a.p.*, line of attachment of the palp; *p.*, tract along which particles tend to collect temporarily; it probably coincides with the posterior edge of the inner palp.

so it is not known whether it is able to extend into the inhalent siphon, as does that of Barnea costata. The ciliation of the upper surface of the membrane and of the visceral mass and foot differs somewhat from that shown in Barnea costata by Kellogg as a comparison of his fig. 57 (p. 680) and of the

figure of Barnea candida (Text-fig. 8A) given here will show. On the concave under surface the currents are toward the tip as depicted by Kellogg in Barnea costata.

In Barnea parva a 'collecting membrane' is present, but is extremely small and extends little behind the visceral mass (Text-fig. 8B).

In Pholadidea loscombiana there is no 'collecting membrane' and the foot is rudimentary.

Bivalves from two different habitats, sand dwellers and borers, evidently have to contend with the same difficulty, namely the entrance into the mantle chamber of good-sized particles, whether grains of sand or rock, or fragments of wood, and have evolved similar ciliary structures—cirrus-like frontal cilia—to remove the unwanted material.

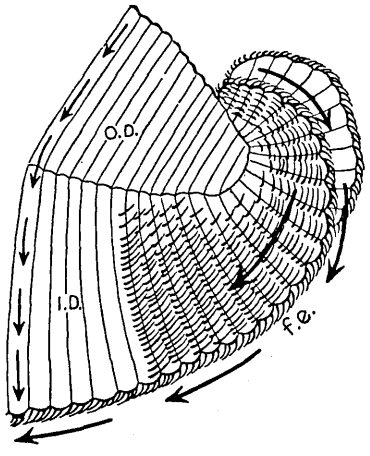
A Method for Increasing the Inhalent Current in certain Bivalves having small Gills and extremely long Siphons.

The specialization of large frontal cilia on the posterior region of the gill, apparently for the purpose of assisting the lateral cilia in the formation of the inhalent current, is found on the small gills of certain bivalves possessing extremely long siphons.

In Abra alba and Abra nitida (Semelidae) the gills are small and strongly made, being rather smaller than the large palps, while the siphons are excessively long. A striking character of the posterior region of the gill is the presence of closely set, large, cirri along the whole frontal surface of about twenty of the posterior filaments of the inner demibranch. The beat, which is rapid and strong, is across the length of the filaments, and creates a strong current away from the inhalent siphon and toward the anterior end of the shell and the palps. The presence of these cilia would seem to be correlated with the excessive length of the siphons, especially the inhalent one, and the small size of the gills. Some additional help in drawing a current of water down the long inhalent siphon doubtless had to be evolved: the siphons themselves are unciliated.

The siphons in Scrobicularia plana (Semelidae), as in

the Abras, are extremely long—the inhalent is stated by Pelseneer (1906, p. 209) to be more than four times as long as the body. There are, however, no large cirri on the posterior region of the gills as in the Abras, though along the ventral margin of the posterior region of the inner demibranch there is a broad band of coarse cilia, or cirri, beating more or less an-



TEXT-FIG. 9.

Abra alba. Diagrammatic sketch of the posterior ends of the (excised) gills to show the position of cirrus-like cilia on the posterior filaments, and the direction of their beat. The acute dorsal curvature of the inner demibranchs is probably due to muscular contraction following excision. *f.e.*, free edge of inner demibranch; *I.D.*, inner and *O.D.*, outer demibranch. ×76⅔.

teriorly, which no doubt help somewhat to increase the inhalent current. Along the rest of the margin they occur in fewer numbers—as is usual on most gills. The gills of Scrobicularia are relatively much larger than those of the Abras, and apparently are capable of drawing a current down the long inhalent siphon, without additional help, other than that of the cirri along the marginal groove described above. In Scrobicularia plana there is a well-developed waste canal, with thin membraneous walls protecting it from the inhalent current. Such a canal has been described in several bivalves by Kellogg (1915).

In two small species of Tellina, Tellina donacina L., and Tellina fabula Gmelin, with gills no larger than the palps, coarse cirri occur over the posterior ends of the gills as in the Abras. In Tellina donacina they are present over the entire frontal surfaces of the posterior forty-five to fifty filaments of the descending lamellae of the inner demibranchs. They have an extremely strong and rapid beat, the effective stroke being obliquely anterior. In Tellina fabula similar cirri are present on about the posterior thirty filaments of the inner demibranchs, and on a few of those of the outer demibranchs.

In Tellina tenuis da Costa, with gills considerably larger than the palps, and Macoma balthica (L.), with fairly small gills about the size of the palps, cirrus-like cilia, beating anteriorly and ventrally, are present on the last few filaments only. Tellina crassa Pennant, with relatively much larger gills than those of Tellina fabula and Tellina donacina, has no such specialization to increase the strength of the inhalent current.

The species of Semelidae and Tellinidae mentioned above, with the exception of Tellina crassa, have gills with flat and homorhabdic lamellae: those of Tellina crassa are gently plicate, but homorhabdic. All are deposit feeders, sucking up bottom detritus and contained organisms by means of their long, free, flexible siphons (Petersen and Jensen, 1911; Blegvad, 1914; Hunt, 1925). Abra alba and Abra nitida are found in mud and silty sand in inshore areas; Scrobicularia plana occurs in stiff mud in the estuaries of the Hamoaze. The habitats of the several species of Tellinidae are as follows: Tellina donacina, coarse sand; Tellina fabula, clean silty sand; Tellina tenuis, clean or almost clean sand; Macoma balthica, muddy sand and gravel; Tellina crassa, shell gravel and coarse sand (M.B.A., 1931; Stephen, 1933). Tellina tenuis and Macoma balthica are littoral species; Tellina donacina, Tellina fabula, and Tellina crassa though occasionally taken between tidemarks usually occur in deeper water.

Why the gills should be relatively small in some of these

deposit feeders and not in others is obscure. There would generally seem, however, to be a connexion between this method of feeding and small gills together with large palps; in the Protobranchs Nucula, Nuculana, and Yoldia, which are also deposit feeders, using their long, extensible palp appendages, the gills are small and the palps large. In certain of the Eulamellibranch deposit feeders it appears as though the gills are retained at a size just sufficient for drawing a current of water down the long inhalent siphon, while the possession of large frontal cilia on the posterior region of the gills, increasing the inhalent current, is definitely correlated with the small size of the gills and the length of the siphons. There seems a tendency for much of the material entering the mantle chamber to be carried directly toward the palps, without being sieved by the gills, but the mode of feeding of these deposit feeders would probably repay further investigation.

Summary.

Some sorting devices on the gills of Lamellibranchs are described. These are:

1. Utilization of plicae for sorting in two ways; the one (*a*) in which the frontal currents are in opposite directions in the grooves and on the crests, and particles intended for consumption are carried in the grooves to the safe dorsal channels, e.g. in Pecten; and the other (*b*) in which the plical grooves open into the safe channel at the bottom of the deep marginal food groove, while the crests lead to a superficial path along the lobes of the marginal groove, e.g. in Pinna.

2. The deep marginal groove of the demibranchs of certain bivalves is able to open and close, thus accepting or rejecting material carried to it by the frontal cilia of the filaments, e.g. Solecurtus scopula.

3. Certain Lamellibranchs have fan-shaped groups of long cilia on the lobes of the marginal groove of the demibranchs, which prevent the entry of large particles or collections of particles, but allow that of small ones, e.g. Musculus marmoratus.

4. In certain bivalves long, stout frontal cilia are found in

addition to the usual short, fine ones. The cirrus-like cilia most probably function in the removal of grains of sand and rock from the gills, e.g. Mactra corallina, Barnea parva.

Small gills and large palps are characteristic of certain deposit feeding bivalves with long free siphons, and the presence of large, cirrus-like cilia on the posterior region of the gills beating obliquely forward, provide additional help to draw the current down the long inhalent siphon.

Certain of the ciliary structures described in this paper are clearly adaptive, correlated with feeding difficulties incidental to the habitat. Fine guarding cilia appear to be frequently correlated with the presence of a certain amount of mud or silt in the soil; they are presumably efficient in dealing with the particles of a muddy soil, but not sufficiently robust when mainly coarse material has to be dealt with. A correlation of cirrus-like cilia with sand dwelling and rock and wood boring habits has been observed.

It will be evident from the observations recorded in this paper that a preliminary sorting of material on the gills before it is passed on to the palps is far from unusual in Lamellibranchs. Further research will most probably add other examples.

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CONTENTS OF No. 315. New Series.

MEMOIRS:

Printed in Great Britain by John Johnson at the Oxford University Press

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DAPHNE ATKINS, B.Sc.

On the Ciliary Mechanisms and Interrelationships of Lamellibranchs

Part III. Types of Lamellibranch Gills and their Food Currents

Quarterly Journal of Microscopical Science
Vol. 79, Part III, March, 1937

Printed in Great Britain

On the Ciliary Mechanisms and Interrelationships of Lamellibranchs.

PART III: Types of Lamellibranch Gills and their Food Currents.

By

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Marine Biological Laboratory, Plymouth.

With 18 Text-figures.

CONTENTS.

INTRODUCTION.

IN the course of work on living gills, those of some ninety odd species of Lamellibranchia, belonging to sixty genera and forty-one families, have been investigated. The great majority were marine, three only, Dreissensia polymorpha (Pallas), Sphaerium corneum (L.), and Anodonta anatina (L.), being from fresh water. Separate accounts of the gills and their currents of all the species would entail much needless repetition, and, except for some forms (Nuculanidae, Arcidae, Anomiidae, Pteriidae, Solenidae, Ostreidae, Pectinidae) which are of special interest and have been dealt with in separate papers (see Atkins, Parts I and II), the majority

can be grouped under more or less clearly defined types. Additional notes on certain of those possessing specialized sorting devices are given in Part II. In the following notes it is quite possible that instances of frontal currents in opposite directions on the same gill filament, as in Barnea candida (L.), Petricola pholadiformis Lamarck, Spisula subtruncata (da Costa), and Spisula elliptica (Brown), have been overlooked and only the obvious currents recorded.

A fact that has emerged from the work is the stability of form and of the direction of the currents on the inner demibranch, and the variability of the outer one.

The inner demibranch has:

1. With apparently few known exceptions, both descending (direct) and ascending (reflected) lamellae, though the depth of the ascending relative to the descending varies. The few exceptions are all found in the Filibranchia. In two of them, Heteranomia squamula (L.), and Dimya argentea (see Ridewood, pp. 193–5), both demibranchs consist of descending lamellae only. Variation of the inner demibranch while the outer consists of both lamellae is found according to Pelseneer (1903, p. 41, Pl. vii, fig. 86; 1906, fig. 207, p. 227, and p. 228) in Adacnarca nitens Pels., a member of the Arcidae, and in Plicatula australis (1911, p. 96, Pl. xii, fig. 11) where the inner demibranch consists of a descending lamella only. Ridewood (1903, p. 208), however, found both demibranchs of Plicatula australis to have descending and ascending lamellae, as did also Watson (1930, p. 26, Pl. v, fig. 3).[1]

2. On the inner demibranch there is always a longitudinal current along the free edge which is oral in direction, except in the Arcidae and Anomiidae where it is aboral in direction (see Part I). There is generally a more or less marked groove at the

[1] Pelseneer (1911, p. 32) suggested that Ridewood had wrongly determined the species, but after the confirmative work of Watson some other explanation of the differing accounts would seem to be necessary. Ciliated disks are present only at the ventral edges of the demibranchs and the upper edges of the ascending lamellae in this species, so that possibly the ascending lamellae are apt to fall down if material is not well preserved.

free edge,[1] but in some bivalves, such as members of the Arcidae, Anomiidae, Pectinacea, Tellinidae, and Semelidae, it is extremely shallow or absent.

3. On the inner demibranch the frontal currents are toward the free edge on both lamellae. However, in Arcidae and Anomiidae, and in Cultellus pellucidus, there is a variation, in that independent or separate dorsal and ventral currents occur on all gill filaments of this demibranch (see Part I); while in certain Pseudolamellibranchia and Solenidae, which have plicate gills, not only does this occur on certain of the ordinary and apical filaments, but in the troughs of the plical grooves the current is entirely dorsalward on both lamellae. In many bivalves for a short distance over the proximal ends of the descending filaments there may be a current axial in direction (e.g. in certain Mactridae, Sphaerium corneum (L.), &c.). This is indicated by Orton (1912, fig. 14, p. 462) in his diagram of the general mode of feeding in Lamellibranchs.

The outer demibranch on the other hand shows considerable variation both in structure and currents. Pelseneer (1911, pp. 95–6) has noted its reduction in length (extends not as far anteriorly as the inner) and in depth (dorso-ventrally) in a number of forms. The chief structural variations are as follows:

1. The outer demibranch may be about the same depth as the inner (e.g. in Mytilus, Galeomma, Pinna, Lima): where such gills are plicate the plications are as deep in the outer as in the inner demibranch. But in most forms it is considerably, though not evenly, narrower (e.g. Sphaerium, Cardium), and, where such gills are plicate, the plications are often less marked than on the inner demibranch, with fewer filaments to a plica.

2. The outer demibranch, with few exceptions, was found to be without a supra-axial extension in the Filibranchia and Pseudolamellibranchia (as constituted by Pelseneer, 1911),

[1] The free edge of the demibranchs may be regarded as normally morphologically ventral, but is by no means topographically ventral in relation to the shell in all bivalves. In those in which the gill axes run obliquely dorso-ventral, the free edges of the demibranchs may be actually almost anterior.

though in some species the ascending lamellae of both demibranchs were as deep, or nearly as deep, as the descending. In Ostrea they may be somewhat deeper than the descending, and this is especially noticeable of the outer demibranch of Ostrea angulata. A supra-axial extension was found in most of those Eulamellibranchs which have an outer demibranch consisting of both lamellae; its degree of development varies greatly, however, from narrow, Lepton squamosum, to deep, with oblique filaments and frequently smooth when the rest of the demibranch is plicate as in certain of the Veneridae; and it may not be present throughout the length of the demibranch. Graham (1934*a*, p. 184) gave as characteristic of the Solenidae the absence of a supra-axial extension to the outer demibranch. In members of this family it appears very narrow in the living animal, but is nevertheless obvious in sections (see Atkins, 1936, Part I, p. 299, fig. 42).

3. The outer demibranch may be upturned and consist of both lamellae, as in the posterior third of the gill of Tellina (see Ridewood, 1903, p. 151). In the Semelidae (= Scrobiculariidae) (Scrobicularia plana, Abra alba, Abra nitida) there also appears to be a recurved portion to the outer demibranch, but it is difficult to judge how far this is due to contraction: Ridewood (1903, p. 235) stated that it is composed of the direct lamella only in Scrobicularia piperata (= Scrobicularia plana). In all these forms the junction of the two lamellae of the outer demibranch is made on a gentle curve, not at an acute angle as between those of the inner demibranch. A much rounded lower edge to the inner demibranch is known only in some Verticordiidae (Anatinacea) (Ridewood, 1903, p. 266).

4. The outer demibranch may be upturned and consist of the direct lamella only, as in the middle third of the gill of Tellina and throughout the gill of the Anatinacea (Ridewood, 1903, p. 151).

Pelseneer (1911, p. 96) considered that dorsal orientation of the outer demibranch is not due to upward bending, but that what remains of this demibranch is nothing but the supra-axial extension in the Anatinacea, and the supra-axial

extension with a mere trifle of the demibranch itself in the Tellinidae.

5. The outer demibranch may consist of the direct lamella only but normal in direction as in Lasaea rubra (Pelseneer, 1889, fig. 2, p. 40). In Heteranomia squamula and Dimya argentea both demibranchs consist of descending lamellae alone.

6. The outer demibranch may be entirely wanting, as in Lucinidae and Montacutidae. In the Teredinidae it is but a vestige (see Ridewood, 1903, p. 260). It is wanting in the anterior third of the gill of Tellina donacina, Tellina fabula, and of Abra. There is some variation in the Tellinidae as to the length (antero-posterior) of the outer demibranch: in Tellina donacina and Tellina fabula it is considerably shorter than the inner, as Ridewood (1903, p. 234) found in Tellina nitida and Tellina (Arcopagia) capsoides, but in Tellina crassa and Tellina tenuis it extends as far forward as the inner, though anteriorly it is very narrow.

It is tempting to connect the variability of form of the outer demibranchs in different Lamellibranchs with their later formation embryologically. Unfortunately there is not a great deal of detailed information on the development of gills. Rice (1908) found in Mytilus edulis—in which the outer and inner demibranchs are very similar—that though the filaments of the outer demibranch do not begin to appear till about twenty filaments of the inner demibranch have been formed, there is a change in the method of formation of the filaments when the spat is about 1·6 mm. in length, and the inner and outer demibranchs then develop pari passu.

Types of Gills and their Ciliation.

In the Lamellibranchia a number of different types of gill structure are found, most of which Ridewood (1903, fig. 2, p. 152) has shown in diagrammatic sections taken transversely to the axes. In the present work the basis of classification is on gill structure and ciliary currents. The various types of gills and their ciliation is as follows, see also Text-fig. 18.

TYPE A (Protobranchia: Text-fig. 1).

In the Protobranchia the gill consists of two rows of leaflets, attached to a branchial axis. The leaflets are dependent, except in the Solenomyidae, in which those of the outer demibranch are upturned.

The frontal currents are from the outer edge of the gill across the axis to the inner edge, along which there is an oralward current, restricted, at least in Nucula, to that part of the gill behind the posterior edge of the foot (Text-fig. 1, I–II). Material collecting at the end of this route may either fall on the mantle and be rejected, or may be removed by the palps and palp appendages and conveyed to the mouth. Material collecting along the inner edge anteriorly, where there is no longitudinal current, is also removed by the palps. There are no currents along the gill axes.

Nuculidae: Nucula nucleus (L.), (2)[1]; Nucula radiata Hanley, (2) (see also Orton, 1912). Orton (1913, pp. 38–40) has described Solenomya togata with similar direction of currents.

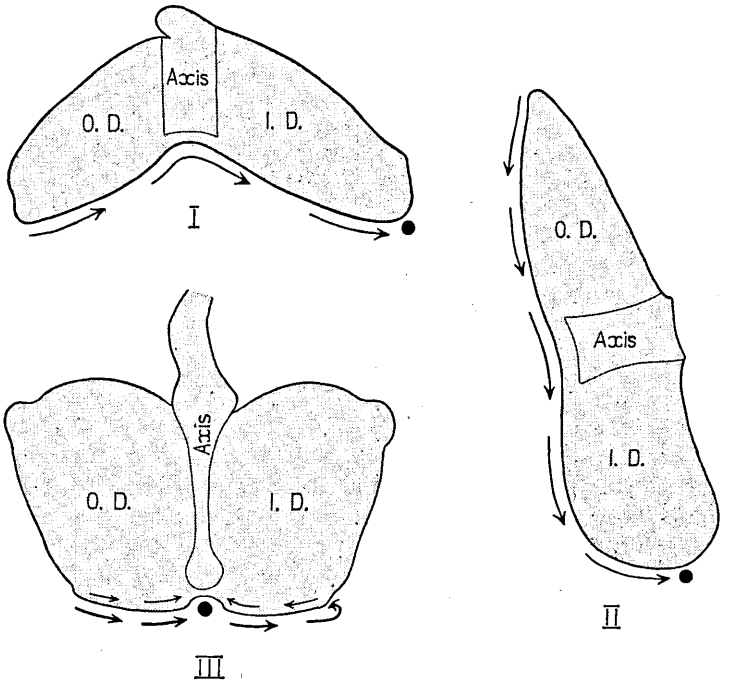
At least one ciliary variation is known:

A (*a*), Text-fig. 1, III.—The frontal currents are rather complicated, being in three tracts on each leaflet. On the frontal edges of the leaflets the current (due to coarse cilia) is as in A, that is from the outer edge of the gill toward the inner edge, but interrupted along the axis by a longitudinal current. Material may either pass across the axial groove, or into it, according apparently to the type of material. There is no current along the inner edges of the gills, and material collecting here either falls on the mantle and is rejected, or is removed by the palps and palp appendages and conveyed to the mouth.

On each side of the frontal surfaces of the leaflets fine frontal cilia beat toward the axial groove on both demibranchs. An oralward current is present in the axial groove to about the twelfth pair of leaflets from the anterior end, but in front of

[1] The numbers in brackets after names of species refer to the number of specimens examined.

this point the current is posterior. Material arriving from both directions is carried along the frontal surface of the twelfth inner leaflet to its inner edge, whence it is removed by the palps and palp appendages and conveyed to the mouth.



LEGENDS FOR TEXT-FIGURES.

In all figures ● indicates the position of oralward longitudinal currents; ⌀ the position of weak or incipient oralward longitudinal currents; ✕ the position of posteriorly directed longitudinal currents. *I.D.*, and *O.D.*, inner and outer demibranchs; *d.*, dorsal edge of ascending lamella. Arrows indicate the direction of frontal currents.

TEXT-FIG. 1.

I. Type A: Nucula. Modified after Orton, 1912.

II. Type A: Solenomya togata. Modified after Orton, 1913.

III. Type A (*a*): Nuculana minuta. Diagrammatic transverse sections showing the form of the gill and the direction of the frontal currents.

Nuculanidae: Nuculana minuta (Müller) from Millport. Full account in Part I (Atkins, 1936).

In Yoldia limatula, according to Kellogg (1915, pp. 691–9), the frontal currents on both demibranchs are toward the axial groove, along the whole length of which the current is oralward, but in addition with a posterior current along the anterior part of it. Frontal currents toward the inner edges of the gills are apparently absent in Yoldia, or Kellogg failed to observe them.

Type B (Filibranchia and Pseudolamellibranchia: Text-figs. 2–5).

In all the Filibranchia and Pseudolamellibranchia examined the outer demibranch differs little from the inner, and is without a supra-axial extension, except in Ostreidae, in which the ascending lamellae of both demibranchs are frequently slightly deeper than the descending. Two main sub-types occur based on structure.

B (1), Text-fig. 2.—The demibranchs consist of both descending and ascending lamellae, and the gill has the form of the letter W, though the outer demibranch may be less deep than the inner. There is a deep groove at the free edge of both inner and outer demibranchs, termed marginal groove (see Rice, 1900, p. 72).

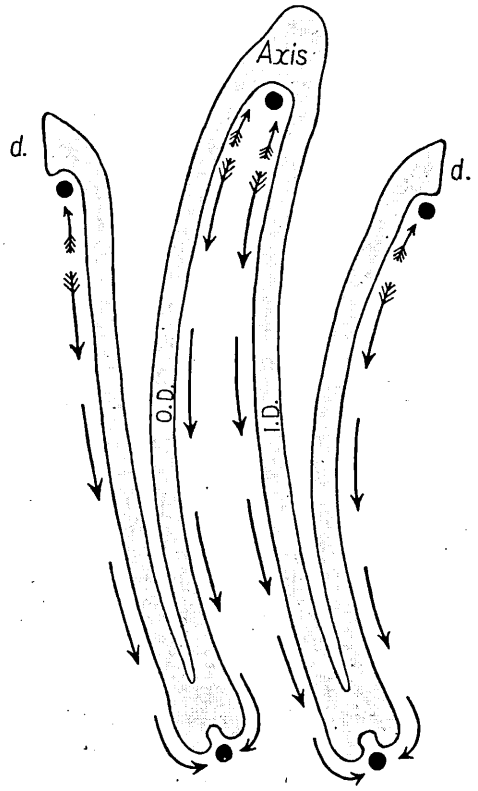
All frontal currents are ventralward, except for narrow zones bordering the dorsal food grooves. Oralward longitudinal currents are found: in the marginal grooves; between the bases of the two demibranchs of each side of the body; and along the dorsal edges of all ascending lamellae.

Mytilidae: Mytilus edulis L., (many); Modiolus modiolus (L.), (6); Modiolus phaseolinus (Philippi), (1); Modiolus adriaticus Lamarck, (2); Musculus (=Modiolaria) marmoratus (Forbes), (2); Musculus (=Crenella) discors (L.) from Millport, (2); gills filibranchiate, flat, and homorhabdic.

Pinnidae: Pinna fragilis Pennant, (3): gills eulamellibranchiate, plicate, and heterorhabdic.

Two ciliary variations of B (1) occur, due to the presence of two kinds of frontal cilia on the filaments.

B (1 *a*), Text-fig. 3.—The gills are filibranchiate, flat, and homorhabdic. The free edges of all demibranchs are ungrooved.

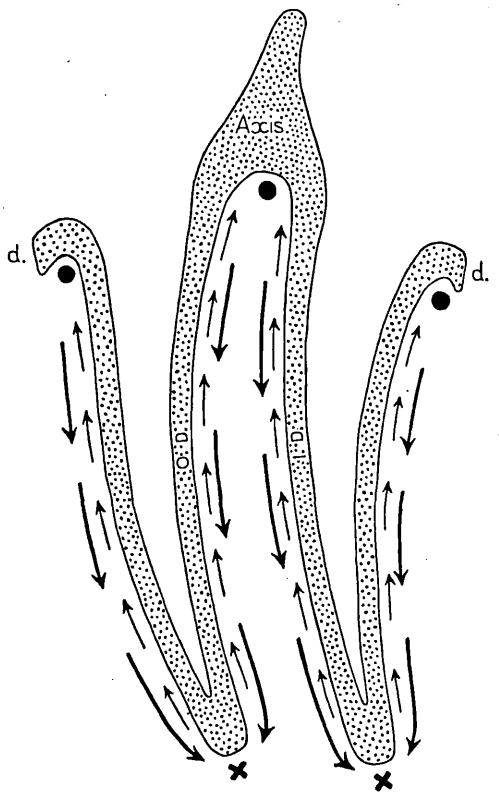


TEXT-FIG. 2.

Type B (1): Mytilidae and Pinnidae. Diagrammatic transverse section showing the form of the gill and the direction of the frontal currents.

Adjacent antagonistic frontal currents occur on all filaments: coarse cilia active only on stimulation, beat ventrally; fine, continuously active, cilia, beat dorsally. These may be in three tracts, a median one of coarse cilia, with one of fine cilia

on each side (Arcidae); or in two tracts, one of coarse cilia on the posterior side of the frontal surface, and one of fine cilia on the anterior side (Anomiidae). Oralward longitudinal currents



TEXT-FIG. 3.

Type B (1 *a*): Arcidae and Anomiidae. Diagrammatic transverse section showing the form of the gill and the direction of the frontal currents.

are found: between the bases of the two demibranchs of each side of the body and along the dorsal edges of all ascending lamellae. Posteriorly directed currents occur along the ungrooved free ventral edges of the demibranchs.

Although tracts of oppositely beating frontal cilia occur in

the Anomiidae, no general dorsal movement of material has been observed under experimental conditions, and the animals would seem to subsist largely on such material as is brought directly to the broad dorsal food grooves by the main water current.

Arcidae: Glycymeris glycymeris (L.), (12); Arca tetragona Poli, (6); Arca lactea L., (2). Detailed account given in Part I (Atkins, 1936).

Anomiidae: Monia squama (Gmelin), (7); Monia patelliformis (L.), (4). Detailed account given in Part I (Atkins, 1936) (for Heteranomia, see p. 387).

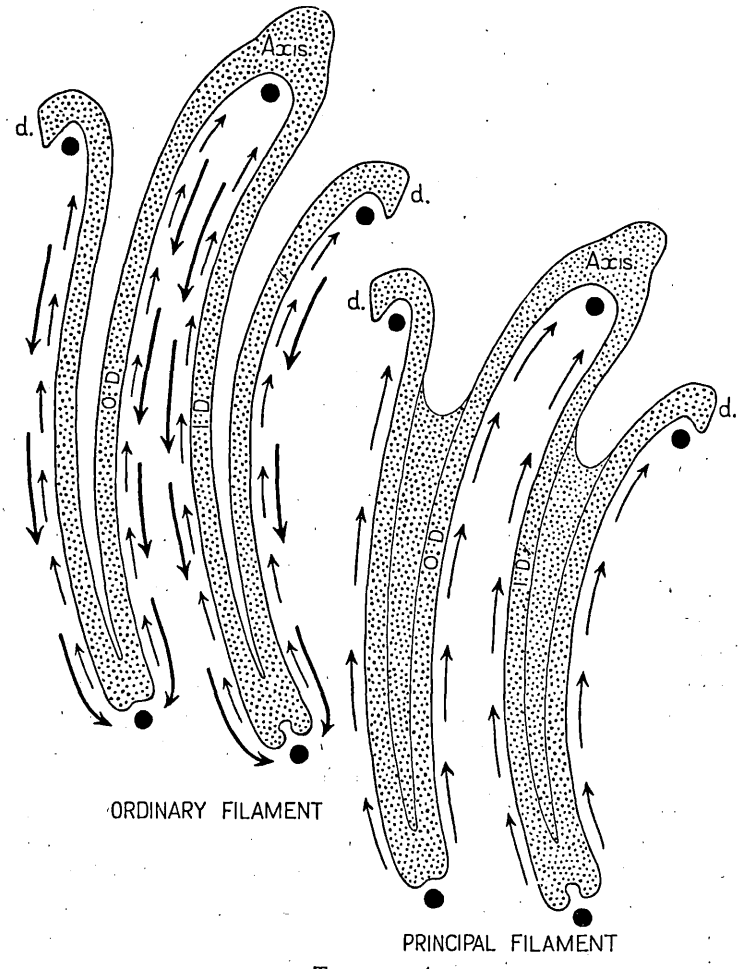
B (1*b*), Text-fig. 4.—The lamellae are plicate and heterorhabdic; the gills may be either filibranchiate or eulamellibranchiate. The free edges of the demibranchs may be grooved (Ostreidae); flattened or slightly grooved (Pectinidae, Limidae); or with the inner grooved and the outer slightly flattened (Pteriidae).

The frontal currents are dorsalward in the plical grooves (i.e. on the principal and adjacent ordinary filaments), and mainly ventralward on the crests (i.e. ordinary and apical filaments). At least in some species (e.g. Pteria hirundo, Chlamys opercularis, Chlamys tigerina, Ostrea edulis, Ostrea virginica, Ostrea angulata), on some, or all, of the ordinary and apical filaments, adjacent antagonistic frontal currents occur; coarse cilia beating ventrally and fine ones dorsally: Lima was not examined for this. As in B (1*a*) these cilia are either in two tracts (e.g. Pteria hirundo), or in three tracts (e.g. Ostrea). Oralward currents are found: along the free ventral edges of the demibranchs; between the bases of the two demibranchs of each side of the body; and along the dorsal edges of all ascending lamellae.

Pteriidae: Pteria hirundo (L.), (1): gills filibranchiate. Full account in Part I (Atkins, 1936).

Pectinidae: Pecten maximus (L.), (3); Chlamys distorta (da Costa), (2); Chlamys tigerina (Müller), (3); Chlamys opercularis (L.), (2): gills filibranchiate.

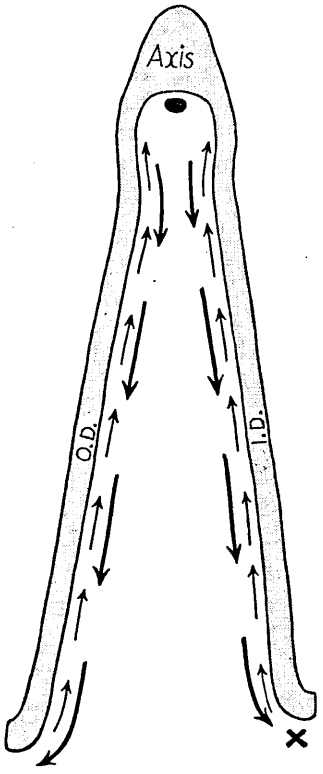
Limidae: Lima hians (Gmelin), (2); Lima loscombi Sowerby, (2); gills eulamellibranchiate (see also Studnitz, 1931).



TEXT-FIG. 4.

Type B (1*b*): Pteria hirundo. Diagrammatic transverse section showing the form of the gill and the direction of the frontal currents. It would represent most Pseudolamellibranchia, except that in Ostrea the ascending lamellae are slightly deeper than the descending.

Ostreidae: Ostrea edulis L., (3); Ostrea virginica Gmelin, (3); Ostrea angulata (Lamarck), (2): gills eulamellibranchiate (see also Yonge, 1926; Nelson, 1923; Atkins, 1937, Part II, p. 342).



TEXT-FIG. 5.

Type B (2): Heteranomia. Diagrammatic transverse section showing the form of the gill and the direction of the frontal currents.

B (2), Text-fig. 5.—The demibranchs consist of descending lamellae only.

The obvious frontal currents (due to coarse cilia) are ventralward on all filaments. A posteriorly directed rejection current

is found along the adherent ventral edges of the two inner demibranchs. A longitudinal current is absent along the ventral edges of the outer demibranchs, the recurrent paths on the mantle serving as rejection tracts for these. Broad oralward longitudinal currents occur between the bases of adjacent demibranchs of each side of the body. Though tracts of fine dorsally beating cilia occur on all filaments, no general dorsalward movement of material has been observed under experimental conditions, and it seems as though the animal subsists largely on material brought directly to the broad dorsal food grooves by the main water current.

It may be considered that this type of gill should have been placed before the W-shaped type, as it is an actual example of the hypothetical type of gill which Pelseneer (1889, p. 43) conceived to be the link between the protobranchiate and filibranchiate types. However, as the frontal currents are complicated, and it is doubtful whether the simplicity of the gill of Heteranomia is primitive—lack of a lamella (Lasaea rubra), and even of a demibranch (Lucinidae, Montacutidae, Teredinidae) is found among Eulamellibranchs—it has been placed second.

Anomiidae: Heteranomia squamula (L.), (12): gill filibranchiate, flat, and homorhabdic. Full account in Part I (Atkins, 1936).

Type C (many Eulamellibranchia: Text-figs. 6–13).

Most of those Eulamellibranchs in which the outer demibranch consists of both lamellae have a more or less distinct supra-axial extension, though it may not be present throughout the length of the demibranch: it is very narrow in some species, e.g. Kellia suborbicularis, Lepton squamosum, and the Pholadidae. In the great majority the outer demibranch is, in varying degree, less deep than the inner. The inner demibranch in some bivalves is almost as deep (dorso-ventrally) as it is long (antero-posteriorly), as in Veneridae and in Sphaerium corneum; in others long and narrow, as in Pholadidae.

Frontal currents on both lamellae of the inner demibranch pass to the free-grooved edge, along which is an oralward current,

as also between the bases of the two demibranchs of each side of the body. In the majority of species longitudinal currents along the dorsal edges of the ascending lamellae of the inner and outer demibranchs were not found (see also Kellogg, 1915), but such are present in Dreissensia polymorpha, Astarte sulcata, and the Solenidae. In Lamellibranchs generally, with some few exceptions (e.g. Mytilidae, Pinna fragilis, Dreissensia polymorpha, Astarte sulcata) longitudinal currents are found along the dorsal edges of the ascending lamellae only when the frontal cilia beat dorsally on these lamellae. This mostly occurs only when the frontal currents are complicated, adjacent antagonistic tracts of cilia being present on the same filament (e.g. Glycymeris, Monia, Cultellus), with, in addition, a difference in the direction of the frontal currents in the grooves and on the crests of certain bivalves having plicate and heterorhabdic gills (e.g. Pecten, Solen).

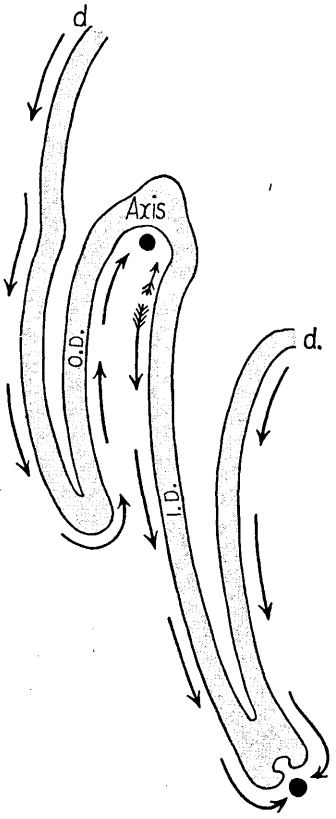
Two main sub-types of C occur based on the absence or presence of a groove at the free edge of the outer demibranch, and correlated differences in the direction of the frontal currents on the descending lamella of that demibranch.

C (1), Text-fig. 6.—In many Eulamellibranchs a groove is present at the free edge of the inner but not of the outer demibranch. The outer demibranch is generally less deep than the inner, especially anteriorly, the most notable exception being Galeomma. The absence of a marginal groove on the outer demibranch of many Lamellibranchs was noted by Rice (1900, p. 72).

There is no interruption of the latero-frontal or lateral cilia at the free edge, the appearance is that of a simple bending of the filaments, with, in some forms, slight flattening of the edge.

The frontal currents on the outer demibranch are ventralward on the ascending lamella, round the bend at the free edge, and dorsalward on the descending lamella, there being no modification of the frontal cilia and no longitudinal current at the free edge. There appears to be a distinct tendency for particles, especially large ones or masses of particles, conveyed by the

frontal cilia of the ascending lamella to pass off the demibranch at the free edge. A proportion of such material is drawn up between the outer and inner demibranchs and on to the de-



TEXT-FIG. 6.

Type C (1): Many Eulamellibranchia. Diagrammatic transverse section showing the form of the gill and the direction of the frontal currents.

scending lamellae of these by the current produced by the lateral cilia.

Oralward longitudinal currents are found: along the marginal groove of the inner demibranch, and between the bases of the

two demibranchs of each side of the body. In Dreissensia polymorpha and Astarte sulcata longitudinal currents are also found along the dorsal edges of all ascending lamellae.

Dreissensiidae: Dreissensia polymorpha (Pallas),[1] (2): lamellae flat and homorhabdic. The inner demibranch hangs somewhat lower than the outer. In Dreissensia polymorpha though the food currents are as described for the type, yet on the descending lamella of the outer demibranch on rare filaments the frontal cilia beat in the opposite direction to the normal, that is they beat ventrally. Particles transported by these cilia, however, pass on to filaments with dorsally beating cilia, either before reaching the free edge, or at the edge.

Astartidae: Astarte sulcata (da Costa), (2): lamellae flat and homorhabdic. In the narrow posterior halves of the gills the junction of the dorsal edges of the ascending lamellae of the inner demibranchs inter se is ciliary, as is also that of the outer demibranchs with the mantle. In the anterior region, however, the junctions appear to be organic. Owing to the easily dissolved nature of the ciliary junction it may be clearly seen that the gill axes are free for a considerable distance posteriorly, being attached again only at the extreme tips.

Thyasiridae: Thyasira flexuosa (Montagu), (2): lamellae flat and homorhabdic. Dark pigment granules present in the sub-filamentar tissue.

Erycinidae: Kellia suborbicularis (Montagu), (2): lamellae flat and homorhabdic. Outer demibranch about half the depth of the inner. For Lasaea rubra see p. 412.

Leptonidae: Lepton squamosum (Montagu), (2): lamellae flat and homorhabdic. Outer demibranch rather less than half the depth of the inner.

Galeommatidae: Galeomma turtoni Sowerby, (2): lamellae flat and homorhabdic. Demibranchs deep: according to Ridewood (1903, p. 228) the outer hangs lower than

[1] I am indebted to Mr. C. Oldham for living specimens of Dreissensia polymorpha, from the Shropshire Union Canal, near Maesbury Marsh, Shropshire.

the inner, but in the two specimens examined at Plymouth there seemed little difference in the depth of the two demibranchs, the outer being perhaps slightly less deep than the inner.

Sphaeriidae: Sphaerium corneum (L.), (2): lamellae flat and homorhabdic. The inner demibranch is almost as deep as long: the outer is about a quarter the depth of the inner. An account of the gill currents, agreeing with the present one, is given by Stenta (1903, p. 225).

Cardiidae: Cardium edule L., (2), (also see Orton, 1912); Cardium ovale Sowerby, (1): lamellae deeply plicate and heterorhabdic. The outer demibranch is only about a quarter the depth of the inner.

Kellogg (1915, p. 667) described Cardium corbis with similar direction of currents and no groove at the free edge of the outer demibranch.

Erodonidae: Aloidis gibba (Olivi) (= Corbula nucleus), (2): lamellae flat and homorhabdic.

Solecurtidae: Solecurtus scopula (Turton) (= candidus), (2); Solecurtus chamasolen (da Costa) (= antiquatus), (2): lamellae plicate and heterorhabdic. The gills extend into the basal conjoined portion of the siphons.

Kellogg (1915, p. 666) stated that in Tagelus californianus 'currents on all gill faces are to the margins and forwards'.

It was observed in a small specimen of Solecurtus scopula $1\frac{1}{10}$ inches long, living in fine sand in the Laboratory, that when well extended the inhalent siphon reached a length of $4\frac{1}{2}$ inches, and the exhalent $3\frac{1}{2}$ inches. The region where the two siphons were conjoined was $1\frac{1}{4}$ inches long. On rapid removal of the animals from the water and rough handling, portions of the siphons distal to the conjoined basal region are frequently thrown off by sudden violent muscular contraction. Fragmentation of the siphons of both Solecurtus scopula and Solecurtus chamasolen is frequently seen when specimens are brought in from S. S. Salpa. If autonomy has recently

occurred the free portions of the siphons will be short. In the contracted state the siphons show annular constrictions, and it is at these places that they are thrown off. From the structure of the moderately long corrugated siphons of Solen marginatus Montagu (= vagina) (Solenidae) it seemed probable that they also are capable of autonomy. Mr. A. J. Smith of the Plymouth Marine Station has informed me that whilst collecting on the sand bank up the River Yealm he saw a medium-sized plaice peck at the siphon of a Solen marginatus, just showing above the sand. The Solen at once burrowed below the surface leaving a section of the siphon on the sand. A few minutes later when the tide went down he dug up the Solen marginatus, thus making sure of its identity: also that he has seen many sections of Solen siphons in dredgings, and some in bowls under circulation.

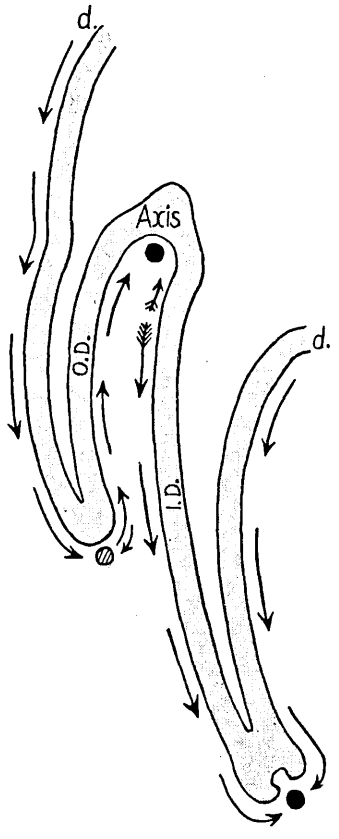
Hiatellidae: Hiatella (= Saxicava) arctica (L.), (2); Hiatella gallicana (Lamarck) (= rugosa), (4): lamellae flat and homorhabdic. The gills are long and narrow; the outer demibranch is about half the depth of the inner; they extend a considerable way into the basal portion of the siphons. The gills are sensitive and contract both antero-posteriorly and dorso-ventrally on stimulation.

Gastrochaenidae: Gastrochaena dubia (Pennant), (1): lamellae flat and homorhabdic. On stimulation the gills contract both antero-posteriorly and dorso-ventrally.

Several ciliary variations of C (1) occur. Two of these, C (1 *a*) and C (1 *b*), show a progressive development of an oralward current along the free edge of the outer demibranch and lead on naturally to C (2); the other two, C (1 *c*) and C (1 *d*), are ciliary variations probably correlated with habitat, and show complications of frontal currents due to the presence of two kinds of frontal cilia on all filaments of certain of the lamellae.

C (1 *a*), Text-fig. 7.—In a few bivalves an incipient oralward current is present along the ungrooved free edge of the outer demibranch. This is due to the presence at the margin of coarse cilia on the posterior half of the frontal surface of each filament (Text-fig. 8). These beat toward the edge and forward, creating

a slight longitudinal current, but frequently sending particles off the demibranch. In fact, in these species there is a slight development of the cirrus-like cilia characteristically found along



TEXT-FIG. 7.

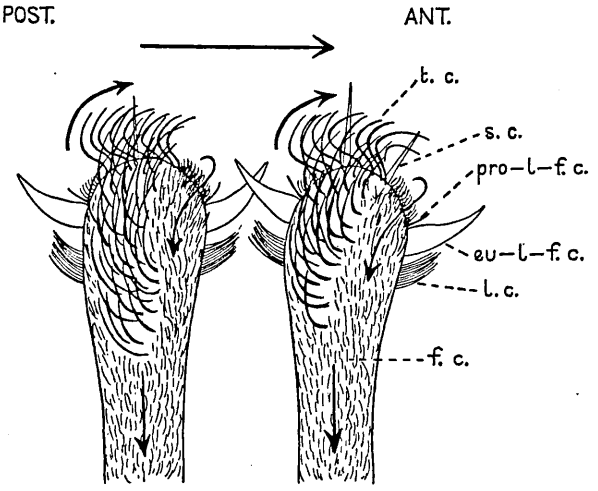
Type C (1*a*): e.g. Pholadidea loscombiana. Diagrammatic transverse section showing the form of the gill and the direction of the frontal currents.

the grooved margins of demibranchs (see Wallengren, 1905, I and II), and which may be called terminal cilia.

On the anterior half of the frontal surface of each filament unmodified frontal cilia are continuous round the bend, and

particles are transported by these from the ascending to the descending lamella.

The terminal cilia are fewer in Pholadidea loscombiana than in the other bivalves of this type: they are somewhat less coarse in Gari tellinella than in Gari fervensis (=ferroensis). In all except Donax vittatus they are confined to the margins of the demibranchs, but in some individuals of that species they are continued dorsally as a single row on the posterior side of the filament for a quarter to a third of the depth of the demibranch. They are also present for a varying distance on the inner demibranch and appear to be a specialization for removing sand grains (see Atkins, Part II). These cilia beat ventrally, and therefore in individuals in which



TEXT-FIG. 8.

Gari fervensis (= ferroensis). Sketch to show the appearance of the living filaments at the free edge of the outer demibranch (descending lamella). The frontal surface is shown in surface view; the large latero-frontal cilia (*eu.-l.-f.c.*) and lateral (*l.c.*) cilia as they appear in optical section. Arrows indicate the direction of beat of the frontal cilia (*f.c.*) and of the coarse terminal cilia (*t.c.*). The latter beat toward the free edge and anteriorly. *Ant.*, anterior; *Post.*, posterior; *pro-l.-f.c.*, pro-latero-frontal cilia; *s.c.*, sensory cilium. $\times 506\frac{1}{4}$.

they extend for a considerable distance on the descending lamella of the outer demibranch the obvious frontal currents over this distance is ventral when they are active, though the fine cilia are beating dorsally from the free edge.

Donacidae: Donax vittatus (da Costa), (4): lamellae flat and homorhabdic.

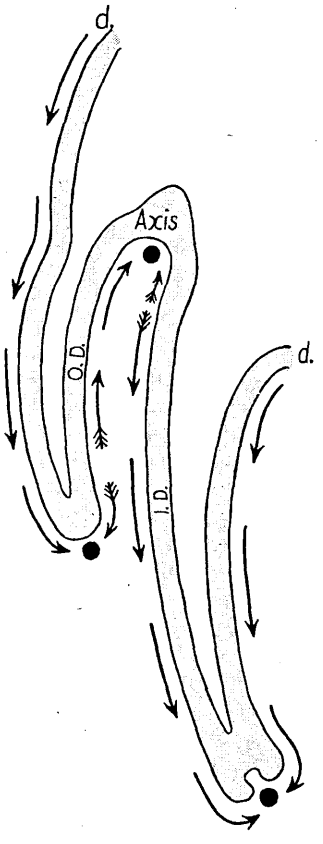
Asaphidae (=Psammobiidae): Gari tellinella (Lamarck), (3); Gari fervensis (Gmelin) (=ferroensis), (3): lamellae broadly plicate and heterorhabdic. Gari tellinella is a deposit feeder, as is also probably Gari fervensis.

Pholadidae: Pholadidea loscombiana Turton, (3): lamellae flat, or slightly plicate, and homorhabdic. The gills are sensitive and contract dorso-ventrally on stimulation. They extend into the siphons, and are here narrow (see p. 407 for Barnea parva, and p. 398 for Barnea candida).

C (1*b*), Text-fig. 9.—The difference between this group and the previous one is in the degree of development of the coarse cilia at the free edge of the outer demibranch. In this group they occupy most of the frontal surface at the demibranch margin. They beat ventrally on both lamellae, and anteriorly, creating a distinct oralward longitudinal current; but even here there is a tendency for particles travelling over the ascending lamella to pass off the demibranch. The terminal cilia extend but a slight distance dorsally from the edge, although the distance varies in different species, e.g. it is greater in Paphia rhomboides than in Gafrarium minimum. Even at the free margin there is an exceedingly narrow tract of fine frontal cilia beating round the bend, but this is overshadowed by the coarse cilia, though to a less extent in Mysia and Gafrarium than in the others.

In Venus verrucosa and Venus casina there appears to be some tendency for grooving of the free edge of the outer demibranch to occur. In one of two Venus verrucosa the free edge was distinctly grooved, though in places a few ungrooved filaments intervened: the longitudinal current was distinct. The frontal current, however, on the descending lamella

was dorsal in direction, except along the free margin for a depth of one or two millimeters, where it was ventralward. Four specimens of Venus casina were examined. In three the



TEXT-FIG. 9.

Type C (1*b*): e.g. Venus fasciata. Diagrammatic transverse section showing the form of the gill and the direction of the frontal currents.

free edge of the outer demibranch was ungrooved, the filaments being merely slightly flattened at the bend. On the descending lamella the frontal currents were dorsal in direction except over

a narrow ventral zone of one or two millimeters over which particles passed ventrally into the longitudinal current along the free edge. In one specimen the free edge of the outer demibranch was distinctly grooved and on some filaments a ventralward current was present for a considerable distance from the free edge.

Veneridae: Dosinia exoleta (L.), (3): lamellae broadly plicate, with little differentiation of principal filaments. In one specimen particles were seen clearly to pass round the free edge of the outer demibranch, while in two others there was a distinct longitudinal current.

Dosinia lupinus (L.) (=Artemis lincta), (3): lamellae broadly plicate. A somewhat weak anterior current along the free edge of the outer demibranch.

Gafrarium (Circe) minimum (Montagu), (2): lamellae of outer demibranch practically flat, those of inner broadly plicate and heterorhabdic.

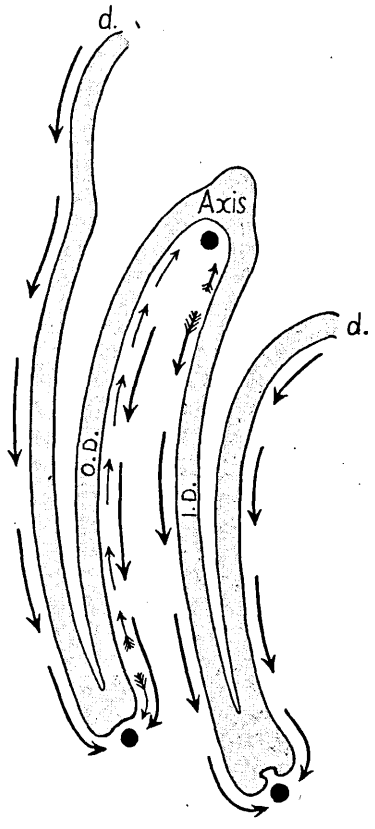
Venus verrucosa L., (2); Venus casina L., (4): lamellae broadly plicate and slightly heterorhabdic. Venus (=Chione) ovata Pennant, (2): lamellae broadly plicate and heterorhabdic. The current along the free edge of the outer demibranch is somewhat slight and particles have been seen to pass round the edge. Venus (=Chione) fasciata (da Costa), (3); Venus (=Chione) striatula (da Costa), (4); lamellae broadly plicate and heterorhabdic.

Paphia rhomboides (Pennant) (=Tapes virgineus), (2): lamellae broadly plicate. For Paphia pullastra and Paphia decussata see p. 405.

Petricolidae: Mysia (=Lucinopsis) undata (Pennant), (4): lamellae broadly plicate. The siphons are free and flexible, and the inhalent very long; this bivalve is probably a deposit feeder. For Petricola pholadiformis see p. 398.

C (1 *c*), Text-fig. 10.—A small group of Eulamellibranchs, Barnea candida (L.), Petricola pholadiformis Lamarck, Spisula subtruncata (da Costa), and Spisula elliptica (Brown), show what are with little doubt

adaptative ciliary structures (see Atkins, Part II), namely, the presence on all or certain of the lamellae of coarse ventrally beating frontal cilia, in addition to the normal frontal cilia.



TEXT-FIG. 10.

Type C (1*c*): e.g. Barnea candida. Diagrammatic transverse section showing the form of the gill and the direction of the frontal currents.

On the descending lamella of the outer demibranch the two kinds of cilia create frontal currents in opposite directions, and so these four species have to be considered separately. In all these forms oralward currents are present between the bases

of the two demibranchs of each side of the body, and along the free edge of both inner and outer demibranchs.

Barnea candida[1] (Pholadidae), (2), has flat and homorhabdic lamellae. The marginal groove of the inner demibranch is shallow, that of the outer extremely shallow, there being little more than a flattening of the edge. In addition to the fine frontal cilia, there is a tract of stout, cirrus-like cilia on the posterior side of the frontal surfaces of the filaments of all lamellae; these beat ventrally. On both lamellae of the inner demibranchs and the ascending one of the outer, the fine frontal cilia also beat ventrally, but on the descending lamella of the outer demibranchs, except for a narrow ventral marginal region, they beat dorsally, that is in the opposite direction to the coarse cilia, as may be seen by direct observations of their beat, and by the movement of particles. The distance from the free edge of the descending lamella of the outer demibranch at which the fine cilia beat in opposite directions varies somewhat on different filaments. When small quantities of fine carborundum (3F) are dropped on this lamella, some particles travel dorsally and some ventrally. Large quantities dropped on the lamella are removed rapidly to the free edge, except over a narrow dorsal region, where large frontal cilia are few or absent, and particles in consequence are conveyed dorsally by the fine frontal cilia.

Petricola pholadiformis[2] (Petricolidae), (2), has broadly plicate, but—so far as can be seen without sections—homorhabdic lamellae. The marginal groove of the inner demibranch is well formed, that of the outer distinct, but shallow: the current along them is oralward. The ciliation of the filaments and the frontal currents on them are similar to those of Barnea candida: the cirri, however, are considerably larger than those of that species.

Spisula subtruncata and Spisula elliptica[3] (Mactridae) have flat and homorhabdic lamellae. In Spisula subtruncata, (3), in addition to the normal frontal cilia a single row of very long and coarse cilia is present on the

[1] For other Pholadidae see p. 396 and p. 407.
[2] For Mysia undata see p. 398.
[3] For other Mactridae see p. 405.

posterior sides of the frontal surfaces of the filaments of the descending lamellae of the outer and inner demibranchs. They are closely placed ventrally, but tend to space out dorsally, being few and far between in the dorsal region. In Spisula elliptica, (5), such cilia generally extend only a short distance from the free edges, though the distance is subject to variation, and in some individuals they extend nearly a quarter to a third the depth on the descending lamella of the outer demibranch, though widely spaced dorsally. In both species the coarse cilia, except for those bordering the margin, appear to be active only when stimulated. On the descending lamella of the inner demibranch the beat of the coarse cilia is in the same direction as that of the fine ones, that is toward the ventral edge.

In Spisula subtruncata the fine cilia on the descending lamella of the outer demibranch beat toward the free edge for a very short distance only: over most of the depth of the lamella they beat dorsally. This is obvious from the direction of movement of particles, and from observations of the direction of beat of the cilia. The relative distances probably vary in different specimens. The row of coarse cilia on the other hand beat ventrally, and when the lamella is flooded with carborundum quickly transport it to the free edge. On the ventral half of the lamella this is the obvious current. Over the dorsal region, where the coarse cilia are few, the movement of particles is almost entirely dorsalward. In Spisula subtruncata there is a good oralward current along the edge of the outer demibranch, but there appears to be some variation in the form of the free edge. In some specimens the filaments were rounded, or but slightly flattened in this position, in others slightly grooved. The flattened and grooved conditions are sometimes found in the same demibranch.

In two out of five specimens of Spisula elliptica the frontal currents and the condition of the free edge of the outer demibranch were similar to those described for Spisula subtruncata. In three, however, the free edge of the outer demibranch was distinctly grooved, and the fine frontal cilia beat ventrally toward it over the lower two-thirds of the descending lamella of this demibranch, the direction of the beat

being seen in side view of the filaments: no dorsal movement of particles over this region of the lamella was observable. The shells of these three animals differed slightly from those of the other two; the connexion of the shell differences with those of the gill, however, may be entirely fortuitous, and Mr. R. Winckworth has courteously identified them all as members of the same species. But it is probable that they are from different habitats. It is to be expected from the relationships of types C (1, 1 *a*, 1 *b*, 1 *c*, and 2) that some species will be found in which a certain amount of variation occurs; in which perhaps a change from ungrooved to grooved condition of the outer demibranch is taking place, with consequent change in direction of beat of the normal fine frontal cilia on the descending lamella of this demibranch (see Atkins, 1930).

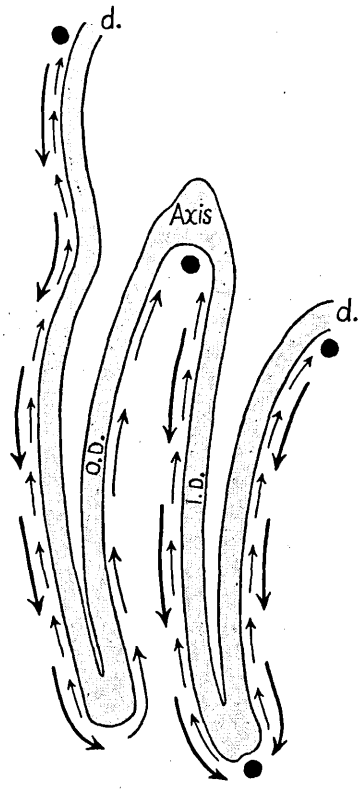
C (1 *d*), Text-fig. 11.—A most interesting ciliary variation of the type C (1) is that found in Cultellus pellucidus, which has flat and homorhabdic gills.

The obvious frontal currents are as in C (1), that is ventralward on both lamellae of the inner demibranch, but ventralward on the ascending and dorsalward on the descending lamella of the outer demibranch, with no longitudinal current at the ungrooved free edge of the latter. On both lamellae of the inner demibranch and also the ascending one of the outer, these currents are due to coarse cilia. On these three lamellae there are in addition tracts of fine frontal cilia, which beat dorsally, judging from the movement of particles. Oralward currents are found not only along the shallow marginal groove of the inner demibranch and between the bases of adjacent demibranchs of each side of the body, but also along the dorsal edges of all ascending lamellae.

Solenidae: Cultellus pellucidus (Pennant), (4). Full account in Part I (Atkins, 1936). For Solen and Ensis see p. 407.

C (2), Text-fig. 12.—In certain Eulamellibranchs a groove is present at the free edge of the outer as well as of the inner demibranch, and distinct oralward currents are present in these grooves. In some species the outer demibranch is only slightly less deep than the inner (Barnea parva), in others consider-

ably less deep (Mya truncata), while in others the depth varies greatly in different regions (Mactra corallina). The marginal groove of both demibranchs is deep in Lutraria

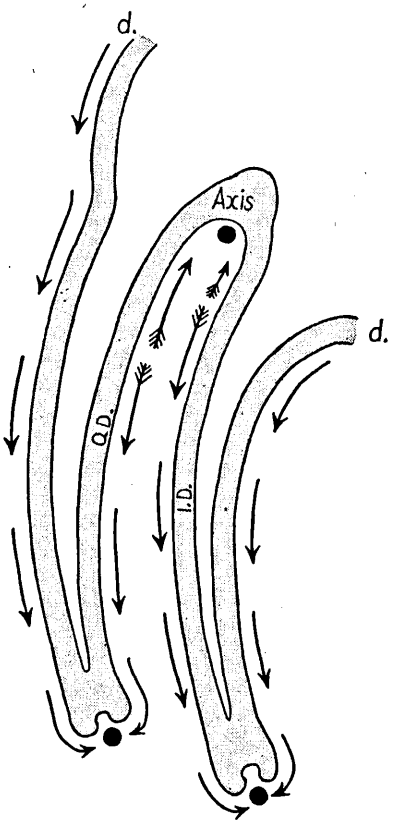


TEXT-FIG. 11.

Type C (1*d*): Cultellus pellucidus. Diagrammatic transverse section showing the form of the gill and the direction of the frontal currents.

lutraria and Mya truncata; moderately deep in Barnea parva, Mactra corallina, and Paphia decussata; rather shallow in Spisula solida; and that of the outer extremely shallow in Paphia pullastra. The groove in some species is not at the exact ventral edge, but slightly on

the inner side, e.g. in Spisula solida and Mya truncata; an orientation probably due to the demibranchs curving inward over the visceral mass.



TEXT-FIG. 12.

Type C (2): e.g. Lutraria lutraria. Diagrammatic transverse section showing the form of the gill and the direction of the frontal currents.

In all these species the frontal currents on all lamellae are toward the free margins of the demibranchs, except over the dorsal region of the descending lamella of the outer demibranch of some forms, where for a certain distance the cilia beat dorsally

into the oralward tract between the two demibranchs of each side of the body. In some (Paphia pullastra, Mya truncata) the current is dorsal for as much as a third to a half the depth of this lamella, but the distance appears to vary in different individuals. In Paphia decussata, with deeply plicate lamellae, the current in the plical grooves of the descending lamella of the outer demibranch passes dorsally over about the upper two-thirds of the lamella, while on the crests it passes ventrally for about the lower two-thirds, so that in the middle third of the lamella currents pass in opposite directions in the grooves and on the crests, but everywhere particles tend to pass from the crests into the grooves.

In Spisula solida the dorsalward current in the dorsal region is present on the descending lamellae of both demibranchs, but over a greater distance on the outer than on the inner. The dividing line between dorsal and ventral currents is not clear cut, but is at different levels on adjacent filaments.

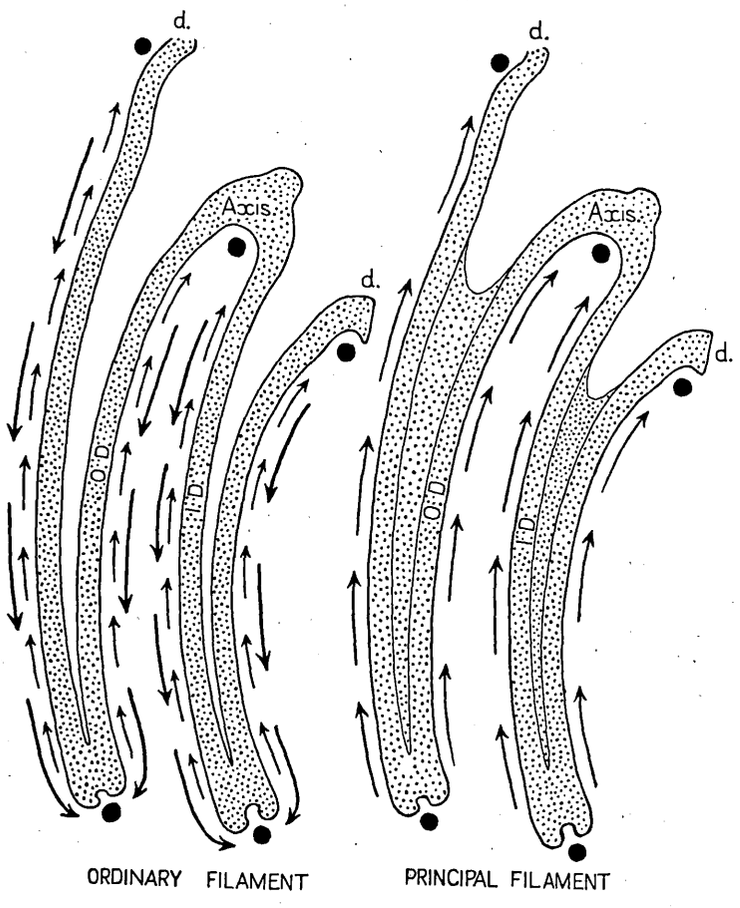
In Mactra corallina and Barnea parva a tract of coarse, cirrus-like cilia is present in addition to the normal fine cilia on the frontal surfaces of the filaments (see Atkins, Part II). There is, however, no difference in the direction of beat of the two kinds of cilia.

Oralward longitudinal currents are found in the marginal grooves, and between the bases of adjacent demibranchs of each side of the body, but were not observed along the dorsal edges of the ascending lamellae.

Veneridae: Paphia (=Tapes) pullastra (Montagu), (4); Paphia decussata (L.), (2): lamellae plicate and heterorhabdic (for other Veneridae see p. 398). Kellogg (1915) found frontal currents to be ventralward on all lamellae of Venus mercenaria (p. 641), Chione fluctifraga (p. 644), Chione succincta (p. 644), Tivela crassatelloidea (p. 644), and Saxidomus giganteus (p. 648).

Mactridae: Mactra corallina (L.) (=Mactra stultorum), (3); Spisula solida (L.), (2): lamellae flat and homorhabdic. Kellogg (1915) described Mactra solidissima (p. 645), Spisula polynyma (p. 647),

and Spisula planulata (p. 648) with similar type of frontal currents (for other Mactridae see p. 400).



TEXT-FIG. 13.

Type C (2*a*): Solen and Ensis. Diagrammatic transverse section showing the form of the gill and the direction of the frontal currents.

Lutrariidae: Lutraria lutraria (L.), (4): lamellae broadly plicate and homorhabdic. Kellogg (1915) described the

same direction of frontal currents for Schizotherus nuttallii, var. capax (p. 632).

Myidae: Mya truncata L., (1): lamellae flat and homorhabdic: the filaments with interlamellar septa are more opaque than those without them, and this tends to give the lamellae a slightly plicate appearance. All frontal currents are ventralward in Mya arenaria (Kellogg, 1915, p. 649; Yonge, 1923, p. 24); and also in Platyodon cancellatus (Kellogg, p. 651).

Pholadidae: Barnea parva (Pennant), (5): lamellae flat and homorhabdic. According to Ridewood (1903, p. 259) there are very feebly marked and unequal plicae.

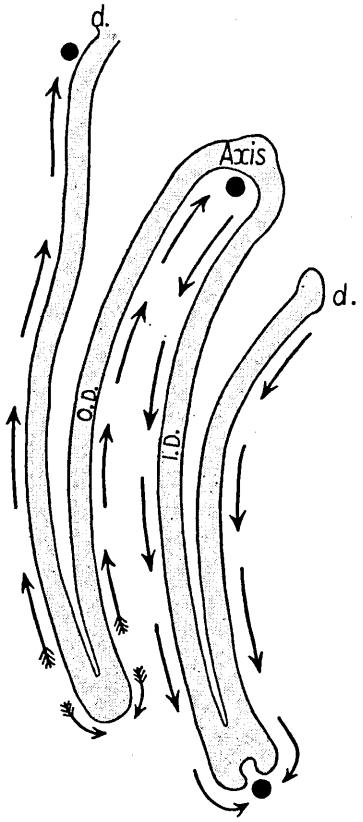
Kellogg (1915) described Pholadidea penita (p. 679), Pholadidea ovoidea (p. 681), Zirfaea gabbi (p. 682), and Barnea pacifica (p. 685) with the same type of frontal currents (see p. 396 for Pholadidea loscombiana, p. 400 for Barnea candida).

C (2*a*), Text-fig. 13.—A complicated ciliary variation of the type C (2) is found in Solenidae with plicate and heterorhabdic gills. The frontal currents on the crests (ordinary and apical filaments) are mainly ventralward, but dorsalward in the grooves between them (principal, and in Ensis adjacent ordinary filaments). On most of the ordinary and apical filaments are adjacent antagonistic currents; coarse cilia beating ventrally and active only on stimulation, and fine cilia beating dorsally and continuously active. Oralward currents are found not only at the free grooved edges of the demibranchs, and between the bases of the two demibranchs of each side of the body, but also along the dorsal edges of all ascending lamellae. This type is similar to that found in a number of Pseudolamellibranchs, B (1*b*) (Text-fig. 4), except for the presence of a supra-axial extension to the outer demibranch. The ciliary mechanisms of the gills of Solen and Ensis have been treated in detail in Part I (Atkins, 1936).

Solenidae: Solen marginatus Montagu (= vagina), (3); Ensis siliqua (L.), (many); Ensis arcuatus (Jeffreys), (many); Ensis ensis (L.), (1). For Cutellus pellucidus see p. 402.

TYPE D (Unionidae: Text-fig. 14).

The outer demibranch of the gill is ungrooved, in this resembling type C (1). The frontal currents, however, differ from those



TEXT-FIG. 14.

Type D: Unionidae. Diagrammatic transverse section showing the form of the gill and the direction of the frontal currents.

described for that type, in fact no marine bivalve has been found with frontal currents similar to those of the fresh-water Unionidae. The gill currents of Anodonta have been investigated by several authors (Stenta, 1903, p. 224; Wallengren,

1905, II, pp. 6–10, figs. A–E; Siebert, 1913; Allen, 1914), most thoroughly by Wallengren; those of Unio by Kellogg (1915, pp. 687–91) and Allen (1914); those of Quadrula and Lampsilis by Allen (1914). Anodonta anatina (L.), (1), was investigated for the present work.

On the inner demibranch the frontal currents are toward the marginal groove on both lamellae: along this groove is an oralward current.

On the outer demibranch the frontal cilia beat dorsally over most of the depth of both lamellae, but for a very short distance at the ventral margin on both lamellae the unmodified frontal cilia beat ventrally, that is toward the free edge (see also Wallengren, 1905, ii, fig. D, p. 8 and p. 9), though slightly anteriorly, and send particles off the demibranch: there are no large terminal cilia at the free edge, and a longitudinal current is absent in this position. Particles travelling up the ascending lamella pass into an oralward current along its dorsal edge; while those travelling up the descending lamella pass into the wide anterior current between the bases of the two demibranchs of each side of the body (see also Wallengren, 1905, ii, figs. A, B, p. 7).

TYPE E (Tellinidae, Semelidae, Anatinacea: Text-fig. 15).

A number of Eulamellibranchs are remarkable in having the outer demibranch upturned, consisting of the direct lamella only in the Anatinacea, but with a recurved lamella in the posterior part of the gill in the Tellinidae (see Ridewood, 1903, pp. 151–3, figs. 1 B–E; 2 H, J) and apparently also in the Semelidae (see p. 378). As previously mentioned Pelseneer (1911, pp. 95–6) considered that it is nothing but the supra-axial extension in the Anatinacea, with a mere trifle of the demibranch itself in the Tellinidae.

On the inner demibranch frontal currents are to the free edge with its oralward current. The free edge of the inner demibranch is either very slightly grooved or else flattened in Tellinidae and Semelidae, which are deposit feeders; and deeply grooved in the Anatinacea, which are most probably suspension feeders.

On the outer demibranch the frontal currents are axial in

direction and continuous across the axis with those of the descending lamella of the inner demibranch, particles being conveyed to the oralward current along the free edge of the latter. In those species in which the outer demibranch possesses a recurved lamella, the current passes around the bend and down the direct lamella (Text-fig. 15, I). In Abra nitida there is an oralward current along the axis in the anterior region of the gill.

Tellinidae: Tellina tenuis da Costa, (2); Tellina fabula Gmelin, (1); Tellina donacina L., (2): lamellae flat and homorhabdic. In Tellina fabula and Tellina donacina the gill is about the size of the palp; in Tellina tenuis the gill is considerably larger than the palp: in all the palps are large.

Macoma balthica (L.), (1): lamellae flat and homorhabdic. Gill about the size of the palp: palps large. Kellogg (1915, p. 661, fig. 33) gave the same direction for the currents of Macoma secta.

Semelidae (= Scrobiculariidae): Abra alba (S. Wood), (2); Abra nitida (Müller), (2): lamellae flat and homorhabdic. Gill about the same size, or rather smaller than, the palp: palps large. Kellogg (1915, p. 660, fig. 32) described similar direction of frontal currents in Semele decisa.

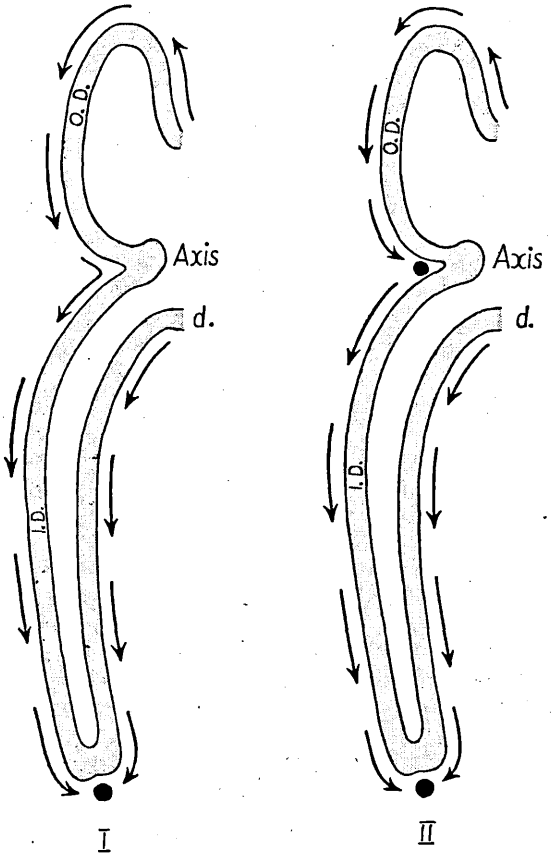
Periplomatidae: Cochlodesma praetenue (Montagu), (1): lamellae deeply plicate and heterorhabdic.

Thraciidae: Thracia villosiuscula (Macgillivray), (2); Thracia distorta (Montagu), (1): lamellae deeply plicate and heterorhabdic.

Lyonsiidae: Lyonsia norwegica (Gmelin), (3): lamellae deeply plicate and heterorhabdic. Kellogg (1915) described the same direction of currents in Mytilimeria nuttallii (p. 656, fig. 22) and Lyonsia saxicola (p. 659, fig. 27).

Pandoridae: Pandora pinna (Montagu), (1): lamellae broadly plicate and heterorhabdic, with nine filaments to a plica. Outer demibranch very narrow.

E (*a*), Text-fig. 15, II.—A variation in the ciliary currents



TEXT-FIG. 15.

I. Type E: Most Tellinidae, Semelidae, and Anatinacea; except that in the Anatinacea the reflected lamella of the outer demibranch is wanting.

II. Type E (*a*): Tellina crassa and Scrobicularia plana. Diagrammatic transverse sections showing the form of the gill and the direction of the frontal currents.

occurs in certain species in that an oralward current is present along the axis, i.e. between the two demibranchs of each side of the body, and particles carried by the frontal cilia of the outer demibranch pass into this. Species with such an axial current

seem generally larger than those without. Except for the dorsal orientation of the outer demibranch, the gill currents are similar to those of the C (1) type.

Tellinidae: Tellina crassa Pennant, (3): lamellae broadly plicate and homorhabdic; inner demibranch large.

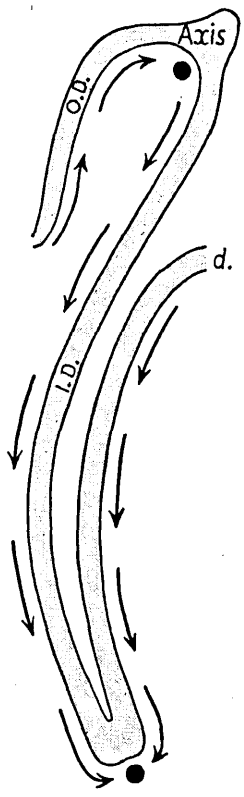
Semelidae (= Scrobiculariidae): Scrobicularia plana (da Costa), (1): lamellae flat and homorhabdic; inner demibranch large. No groove is present at the edge of the inner demibranch, which is but slightly flattened; an anterior current is nevertheless present.

A detailed examination of the feeding mechanism of the deposit-feeding Lamellibranchs, which suck up bottom detritus and contained organisms, by means of their long, free, flexible siphons, would be of interest. While some of these, e.g. Tellina crassa, Tellina tenuis, and Scrobicularia plana, have large gills, others, Tellina fabula, Tellina donacina, Abra alba, Abra nitida, have them considerably reduced, in fact about the same size or rather smaller than the palps. From a somewhat cursory examination of these latter species it seemed as though much of the material entering the mantle chamber by the extremely long inhalent siphon was carried directly toward the large palps (see also Atkins, Part II, pp. 367–370). The correlation of small gills and large palps is also met with in the deposit feeding Protobranchs, Nuculidae, and Nuculanidae, in which the gills are small and the chief feeding organs are the palp appendages, which are extrusible beyond the shell and convey material directly to the large palps (Atkins, 1936, Part I, p. 186).

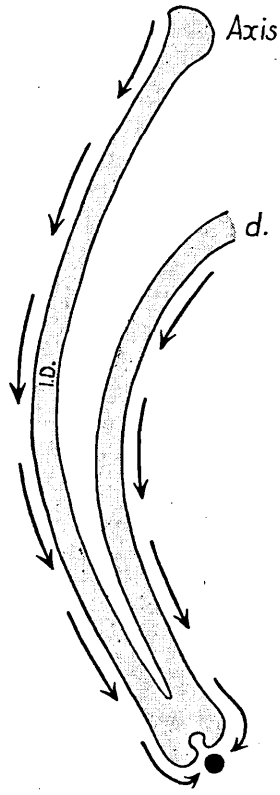
Type F (Lasaea rubra: Text-fig. 16).

The outer demibranch consists of the descending lamella only, but normal in direction. The frontal currents on this lamella are dorsalward into an orally directed current between the two demibranchs of each side of the body. On the inner demibranch the frontal currents are normal in direction, that is they are toward the free edge, with its oralward current, on both lamellae. Lasaea rubra is a minute bivalve and the currents are therefore difficult to discern.

Erycinidae: Lasaea (=Kellia) rubra (Montagu), (2): gills flat and homorhabdic. For Kellia suborbicularis see p. 391.



TEXT-FIG. 16.



TEXT-FIG. 17.

FIG. 16.—Type F: Lasaea rubra. Diagrammatic transverse section showing the form of the gill and the direction of the frontal currents.

FIG. 17.—Type G: Lucinidae, Montacutidae, and Teredinidae. Diagrammatic transverse section showing the form of the gill and the direction of the frontal currents.

TYPE G (Lucinidae, Montacutidae, Teredinidae: Text-fig. 17).

The outer demibranch is entirely wanting in the Lucinidae and Montacutidae, and vestigial in Teredo navalis (see

Ridewood, 1903, p. 260). The formation of the inner demibranch in Teredo is peculiar in that while the direct lamella descends, the reflected lamella passes horizontally inwards (see Ridewood).

The frontal currents of the inner demibranch are normal, passing toward the grooved free edge on both lamellae. The only longitudinal current is an oralward one in the marginal groove.

Lucinidae: Myrtea (=Lucina) spinifera (Montagu), (1), Phacoides (=L.) borealis (L.), (2); lamellae flat and homorhabdic. The single demibranch is deep; in Myrtea spinifera the ascending lamella is only about half the depth of the descending, but in Phacoides borealis it is almost as deep as the descending. The frontal currents appear to be slow. The palps are tiny. In both species the gills are dark brown—except the lobes of the marginal groove—the colour being due to granules in the sub-filamentar tissue, and not in the epithelium of the filaments proper. From a habitat of silty sand.

Montacutidae: Montacuta (=Tellimya) ferruginosa (Montagu), (1): lamellae flat and homorhabdic. The single demibranch is deep; it is sensitive to stimulation. The gill axes run almost dorso-ventrally. The palps are of a good size. Commensal with Echinocardium cordatum in clean or silty sand (Marine Biol. Assoc., 1931, pp. 243, 298).

Mysella (=Montacuta) bidentata (Montagu), (2): lamellae flat and homorhabdic. The ascending lamella is about half the depth of the descending. The palps are large. Found associated with Ophiocnida brachiata, in numbers just below or above the disk, and in Phascolosoma and other burrows in silty sand (Orton, 1923, p. 861; Marine Biol. Assoc., 1931, p. 243).

Entovalva perrieri (Malard), (2): lamellae flat and homorhabdic. Occurring attached to Leptosynapta inhaerens in coarse, loose sand (Marine Biol. Assoc., 1931, pp. 242, 300).

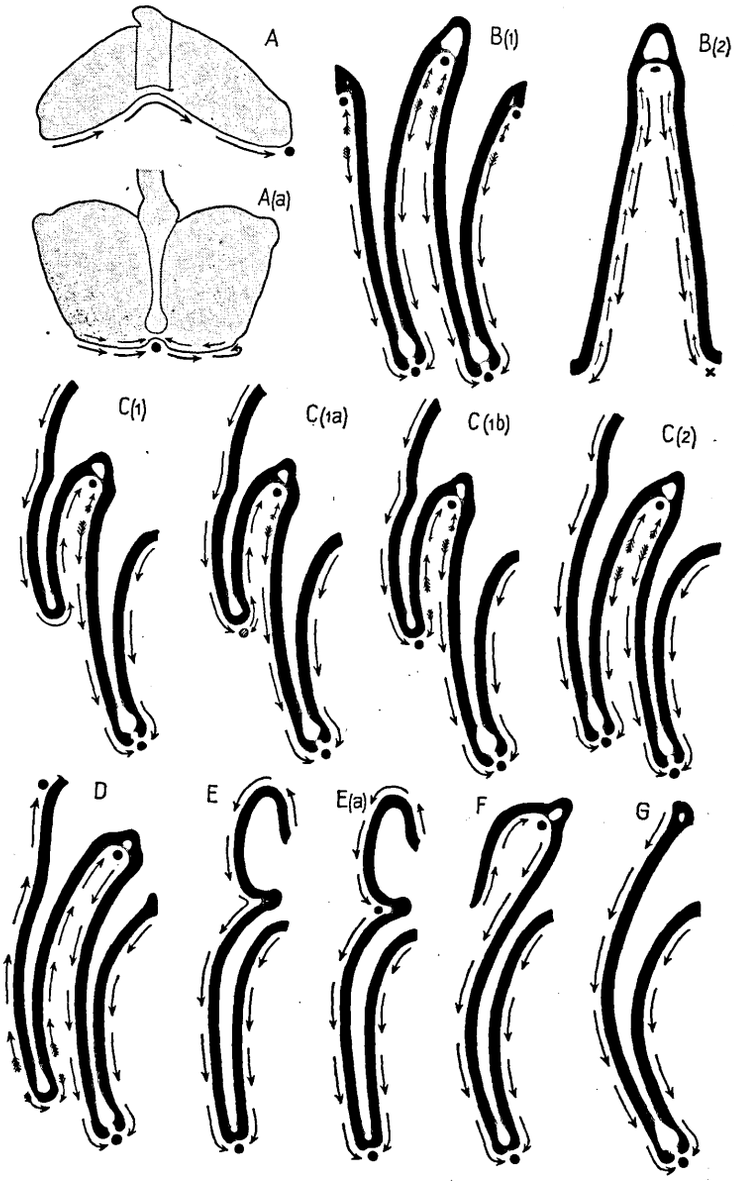
Teredinidae: Teredo navalis L., (1): lamellae flat. For the structure of the gill see Ridewood (1903, p. 260). Bores in wood.

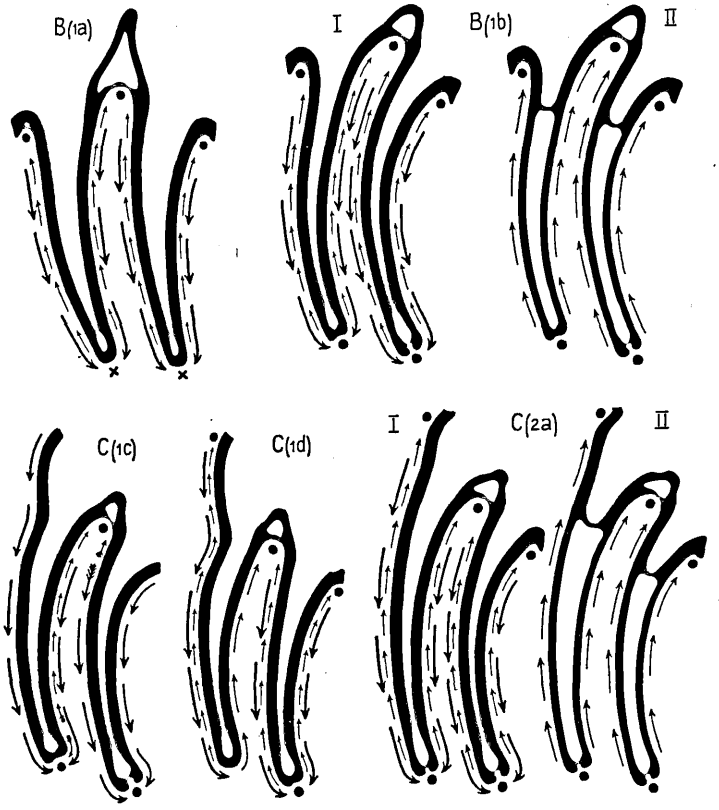
Discussion.

Ridewood (1903, p. 150; fig. 2 D, p. 152) gave the gill W-shaped in transverse section—such as found in most Filibranchia and Pseudolamellibranchia—as occurring in the majority of Lamellibranchia. In most of the British Eulamellibranchs investigated, possessing an outer demibranch consisting of two lamellae, there was a supra-axial extension, slight in some, deep in others, and in the majority the outer demibranch was not only considerably less deep than the inner, but was without a marginal groove.

Kellogg's work on the 'Ciliary Mechanisms of Lamellibranchs' (1915) in which he described those of thirty-two species, apart from the Protobranch Yoldia, gives the impression that it is usual for the frontal currents on both lamellae of both demibranchs to pass toward the free edge, but in many British Eulamellibranchs though the current is toward the free edge on the ascending lamella of the outer demibranch, it is toward the axis on the descending lamella. Where this occurs there is very rarely a marginal groove on the outer demibranch, as found in one specimen each of Venus verrucosa and Venus casina, though there may be a distinct longitudinal current at the free edge. Kellogg (1915) in several American species of Veneridae (Venus mercenaria, p. 641; Chione fluctifraga, p. 644; Chione succincta, p. 644; Tivela crassatelloidea, p. 644; and Saxidomus gigantius, p. 648) found the frontal currents passed to the free edge on all demibranchs; he does not state, however, whether a marginal groove was present on the outer demibranch. Ventral direction of all frontal currents was found in Paphia pullastra and Paphia decussata—though not in Paphia rhomboides—among the eleven British species of Veneridae investigated.

Although some ninety odd species have been examined these belong to a large number of families, so that in many families but one or two species have been seen; the greatest number, eleven, being in the Veneridae. It is therefore not known whether the members of a family usually have the same type


A
A(a)
B(1)
B(2)
C(1)
C(1a)
C(1b)
C(2)
D
E
E(a)
F
G



TEXT-FIG. 18.

Diagrammatic transverse sections of types of Lamellibranch gills with their food currents. The inner demibranch is on the right in all sections.

A. Protobranchia; e.g. Nucula: A (*a*), Nuculana minuta.

B. Filibranchia and Pseudolamellibranchia: B (1), Mytilidae, Pinnidae; B (1*a*), Arcidae, Anomiidae; B (1*b*), most Pseudolamellibranchia: I, ordinary and II, principal filaments; B (2), Heteranomia.

C. Many Eulamellibranchia: C (1), many Eulamellibranchia; C (1*a*), e.g. Pholadidea loscombiana; C (1*b*), e.g. Venus fasciata; C (1*c*), e.g. Barnea candida; C (1*d*), Cultellus pellucidus; C (2), e.g. Lutraria lutraria; C (2*a*), Solen and Ensis: I, ordinary and II, principal filaments.

D. Unionidae.

E. Tellinidae, Semelidae, Anatinacea: E (*a*), Tellina crassa, Scrobicularia plana.

F. Lasaea rubra.

G. Lucinidae, Montacutidae, Teredinidae.

of gill and frontal currents. In nine of the forty-one families different sub-types or types were found within the family. In seven they denote chiefly an increasing efficiency in food conveyance on the outer demibranch, and occasionally some special ciliary mechanism correlated with habitat; in two, Anomiidae and Erycinidae, marked structural differences in the gills. In the Pholadidae three variations were found, namely C (1 *a*), Pholadidea loscombiana; C (1 *c*), Barnea candida; and C (2), Barnea parva (see Text-fig. 18). Two variations were found in each of the following eight families: in Anomiidae, B (1 *a*), Monia squama and Monia patelliformis; and B (2), Heteranomia squamula: in Erycinidae, C (1), Kellia suborbicularis; and F, Lasaea rubra: in Veneridae, C (1 *b*), most species; and C (2), Paphia pullastra and Paphia decussata: in Petricolidae, C (1 *b*), Mysia undata; and C (1 *c*), Petricola pholadiformis: in Mactridae, C (1 *c*), Spisula subtruncata, Spisula elliptica; and C (2), Spisula solida, Mactra corallina: in Solenidae, C (1 *d*), Cultellus pellucidus; and C (2 *a*), Solen marginatus, Ensis siliqua, Ensis arcuatus, Ensis ensis: in Tellinidae, E, Tellina tenuis, Tellina fabula, Tellina donacina, Macoma balthica; and E (*a*), Tellina crassa: in Semelidae, E, Abra alba, Abra nitida; and E (*a*), Scrobicularia plana.

It is an interesting possibility that C (1), C (1 *a*), C (1 *b*), and C (2) form a natural series with increasing efficiency in food conveyance on the outer demibranch (see Text-fig. 18). In the simplest forms, C (1), the frontal currents on the ascending and descending lamellae of that demibranch are continuous, uninterrupted by any longitudinal current at the free edge. Particles are carried into an oralward tract along the gill axes (i.e. between contiguous demibranchs of each side of the body), which is frequently broad, with a strong current. In C (1 *a*) at the free edge there is modification of some of the frontal cilia (terminal cilia), with a slight oralward current. In C (1 *b*) there is a definite oralward current, which, however, has had little effect on the direction of beat of the unmodified frontal cilia.

In one specimen each of Venus verrucosa and Venus casina at the free edge there was a slight groove with a good current, but even this had little affected the direction of beat of the frontal cilia. In C (2) there is a distinct groove with a strong oralward current at the free edge of the outer demibranch, toward which beat the frontal cilia on both descending and ascending lamellae. This last type is rather similar to that found in the Mytilidae and Pinnidae (Type B (1)) except for the general absence of a current along the dorsal edges of the ascending lamellae, the presence in certain species of dorsalward currents over a considerable dorsal region of the descending lamella of the outer demibranch, and the presence of a supra-axial extension. It is found among the higher Eulamellibranch families.

It is generally difficult to see a connexion between the type of gill and frontal currents, and the habitat and mode of life—though it must be confessed that little is known of details of these. Certain bivalves, however, have additional tracts of coarse ventrally beating frontal cilia, which are clearly correlated with habitat (see Atkins, Part II). Such cilia beat in the opposite direction to the normal frontal cilia in some types of gill, and are necessarily included in the present study.

Summary.

Seven main types of Lamellibranch gills and their food currents, together with a number of varieties, have been described. These are shown summarily and comprehensively in the composite diagram in Text-fig. 18.

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CONTENTS OF No. 315. New Series.

MEMOIRS:

Printed in Great Britain by John Johnson at the Oxford University Press

18

DAPHNE ATKINS, B.Sc.

On the Ciliary Mechanisms and Interrelationships of Lamellibranchs

Part IV. Cuticular Fusion, with special reference to the Fourth Aperture in certain Lamellibranchs

Quarterly Journal of Microscopical Science
Vol. 79, Part III, March, 1937

Printed in Great Britain

On the Ciliary Mechanisms and Interrelationships of Lamellibranchs.

PART IV: Cuticular Fusion, with special reference to the Fourth Aperture in certain Lamellibranchs.

By

Daphne Atkins, B.Sc.

Marine Biological Laboratory, Plymouth.

With 11 Text-figures.

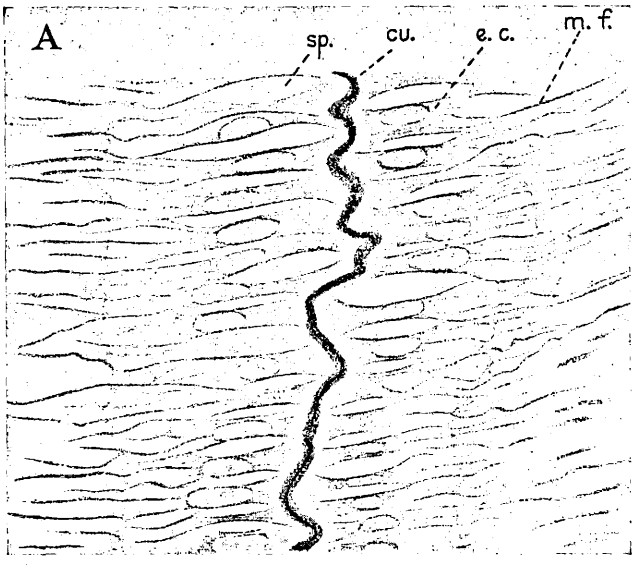
CONTENTS.

INTRODUCTION.

A PECULIAR form of fusion, involving the cuticle only, has been found in a number of Lamellibranchs, but has been chiefly studied in the Solenidae. The positions so far discovered in which this type of fusion occurs are between the dorsal edges of the ascending lamellae of the outer demibranchs and the mantle or the visceral mass in Solen marginatus Montagu (=vagina), Ensis siliqua (L.), Ensis arcuatus (Jeffreys), Cultellus pellucidus (Pennant), Solecurtus scopula (Turton) (=candidus), Lutraria lutraria (L.) (=elliptica), and Tellina tenuis da Costa; between the dorsal edges of the ascending lamellae of the two inner demibranchs in Barnea parva (Pennant); and between the mantle lobes in the region between the pedal and fourth apertures in Ensis siliqua, Ensis arcuatus, and Cultellus pellucidus.

Histological Structure of the Junction.

Material was fixed in Bouin-Duboscq's fluid with the following formula: saturated picric acid in 90 per cent. alcohol, 2 parts; saturated corrosive sublimate (water), 3 parts; 40 per cent. formalin, 1 part; glacial acetic acid, 2 parts. The stains used were Heidenhain's iron haematoxylin counterstained with acid



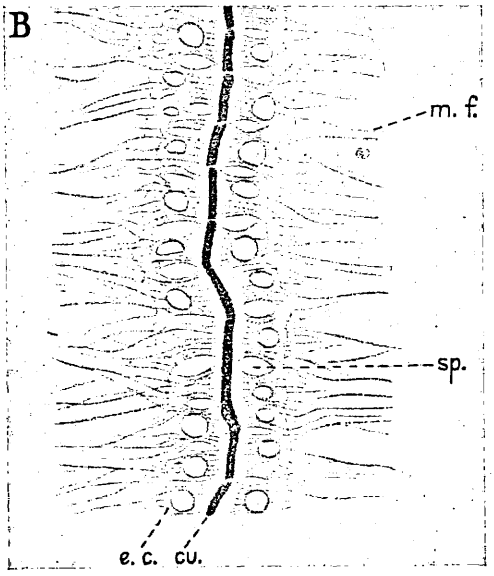
Text-fig. 1 A.

Transverse section showing the method of junction of the mantle lobes in the mid-ventral region between the pedal and fourth apertures. A. Ensis siliqua (adult). ×980.

fuchsin; Mallory's triple stain; and eosin and light green (Gatenby, 1928, p. 432): the latter was preferred as it clearly differentiated the cuticle.

The epithelium of the parts concerned in this cuticular type of junction has generally, in fixed material, a distinctive appearance, the cells being hourglass-shaped owing to the development of spaces between them (Text-figs. 1, 3, 4). It is uncertain, however, to what extent this may be due to shrinkage on fixation:

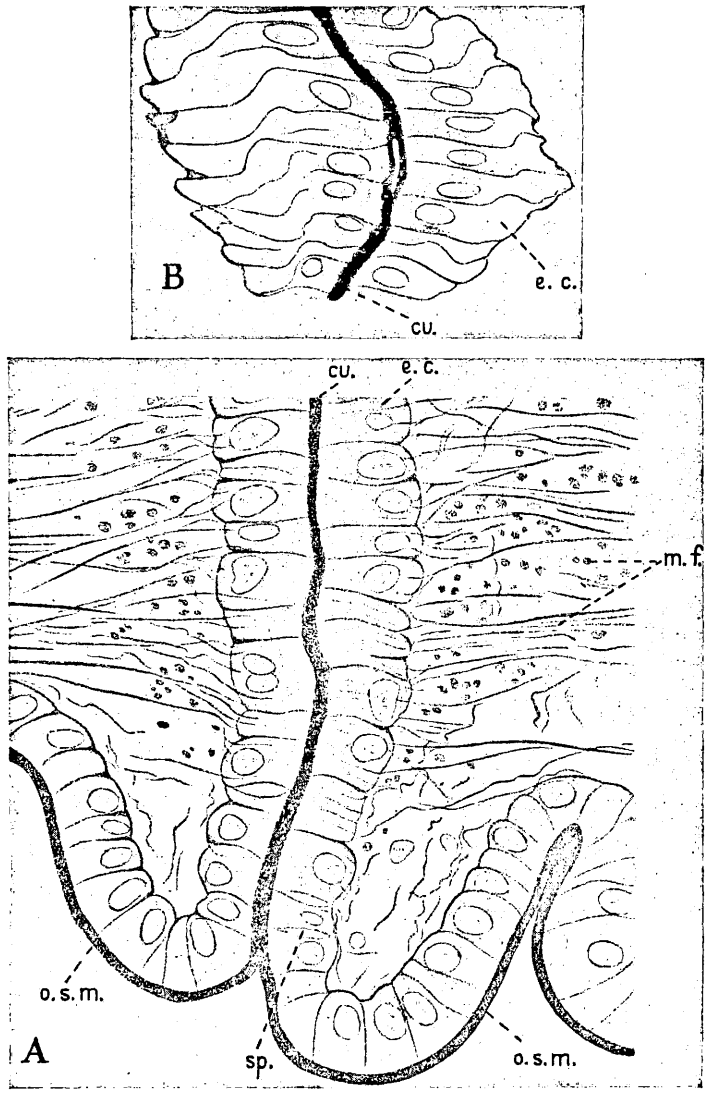
intercellular spaces were rare in the specimen of Cultellus pellucidus sectioned (Text-fig. 2A). Extremely fine muscle-fibrils penetrate the cells, giving to them an appearance rather similar to that of ciliated cells in which the ciliary rootlets are clearly visible (cf. Text-figs. 1 and 11): ciliated epithelia sometimes also show intercellular spaces.



TEXT-FIG. 1 B.

B. Ensis arcuatus (young specimen, 4 cm. long). *cu.*, cuticle: showing a dark median line in (A); *e.c.*, hourglass-shaped epithelial cell; *m.f.*, muscle-fibres; *sp.*, space between the cells. Eosin and light green. ×980.

The cells appear to increase in height with age, for in an Ensis siliqua, 1·8 cm. long, the cells of the epithelium concerned in the junction of the mantle lobes between the pedal and fourth aperture were 5 to 6μ high; in an Ensis arcuatus, 4 cm. long, they were 7 to 10μ high (see Text-fig. 1B); and in an adult Ensis siliqua, about 16 cm. long, they were 18 to 30μ high (see Text-fig. 1A). The combined layers of cuticle



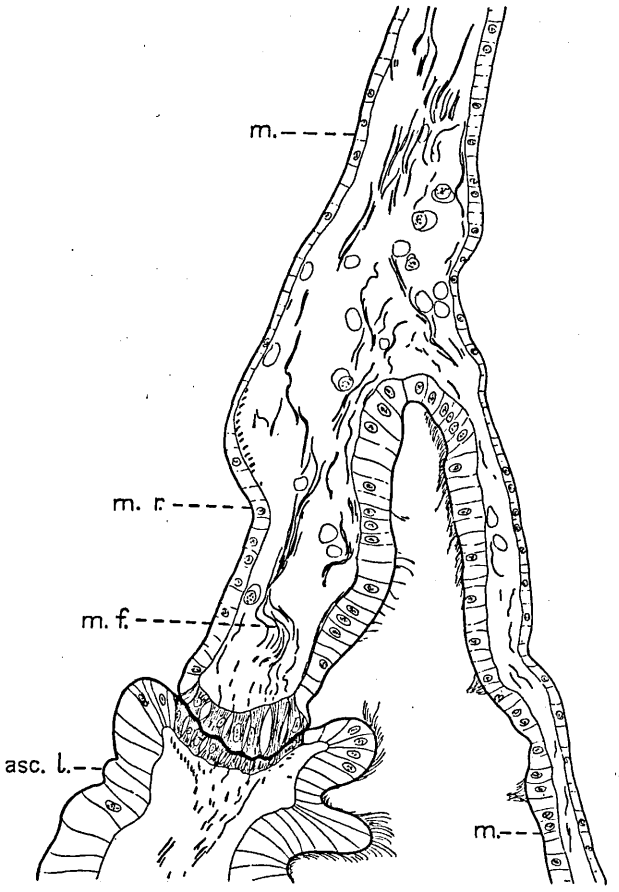
TEXT-FIG. 2.

Cultellus pellucidus. Transverse sections of the junction of the mantle lobes in the mid-ventral region between the pedal and fourth apertures. A. About 216 μ anterior to the fourth aperture. B. Showing breaking down of the cells; about 60 μ in front of the fourth aperture. *cu.*, cuticle; *e.c.*, epithelial cell; *m.f.*, muscle-fibres; *o.s.m.*, outer surface of mantle; *sp.*, space between cells. Eosin and light green. $\times$ 980.

also increase in thickness with age. This latter specimen had been in the laboratory four days, and the mantle had begun to rupture, so it is possible that the stretched appearance of the cells may be due to some extent to the fact that they had suffered tension owing to the gaping of the valves, and did not recover in the piece removed for fixing. However, in the junction between the dorsal edge of the ascending lamella of the outer demibranch and the mantle (Text-figs. 3, 4) in Ensis arcuatus (4 cm. long) the epithelial cells were rather higher than those of the junction between the mantle lobes in the same specimen, though in the former position they would suffer relatively less stress. It is noteworthy that the mantle is produced into a ridge of varying height along the line of attachment of the demibranchs (Text-fig. 3): a similar ridge is found in Solen marginatus.

In an adult Solen marginatus the cells of the epithelium concerned in the union between the outer demibranchs and the mantle were high and the fibrils running through them especially clear: this was also found in the same position in Solecurtus scopula. The epithelial cells of the junction between the two inner demibranchs in Barnea parva were tall and slender and the cuticle clearly visible. In Tellina tenuis though the junction between the upturned outer demibranchs and the visceral mass is of the cuticular type, at least in the posterior region, yet the cells are small, have not the distinctive hourglass-shape, and the cuticle between the two parts is extremely thin and difficult to distinguish.

The chief interest of this type of junction lies in the cuticle of the two opposed surfaces which appear to have undergone fusion, the sinuosity of the cuticle of one side being faithfully followed by that of the opposite side (Text-figs. 1, 2, 4). A small cavity between the two layers in the material of Ensis siliqua sectioned was probably pathological, for it contained some amorphous material. In some instances a darker median line was visible in the cuticle between the two opposed epithelial layers, when stained with eosin and light green. This was observed in the junction of the mantle lobes between the pedal and fourth apertures in an adult Ensis siliqua (Text-fig. 1 A)



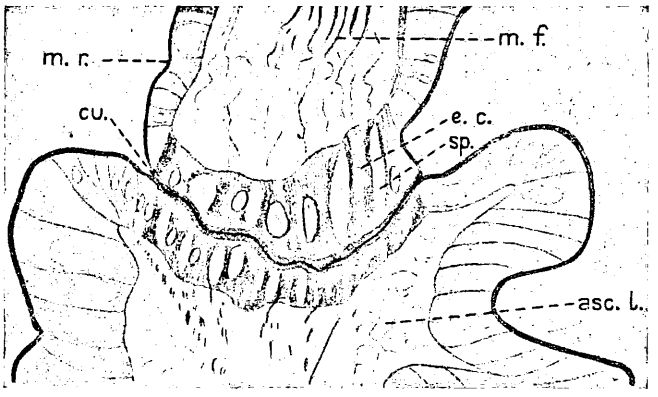
TEXT-FIG. 3.

Ensis arcuatus (4 cm. long). Section showing the attachment of the dorsal edge of the ascending lamella of the outer demibranch to the ridge of the mantle. *asc.l.*, ascending lamella; *m.*, mantle; *m.f.*, muscle-fibres; *m.r.*, mantle ridge. Eosin and light green. ×450.

and in the union of the outer demibranchs and the mantle in an Ensis arcuatus 4 cm. long (Text-fig. 4): curiously enough it was not visible in the junction between the mantle lobes in this small specimen, the appearance being as indicated

in Text-fig. 1 B, the median region of the cuticle staining less heavily than that on each side. A tendency for the cuticle to be faintly striated, with striae at right angles to the fused surface, and to separate in blocks corresponding to the cells is also evident.

From the examination of sections, and from observations on living animals which will be given later, it is evident that the



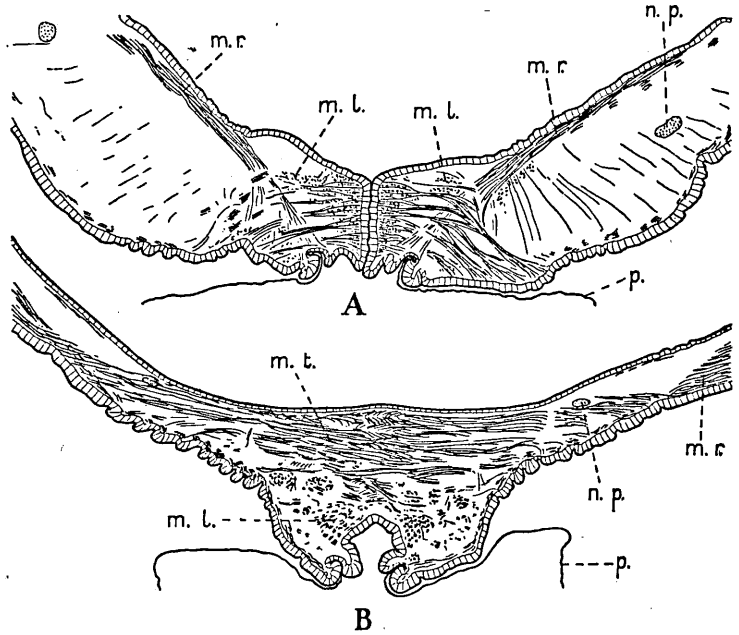
TEXT-FIG. 4.

Ensis arcuatus. Enlarged sketch of the junction of the dorsal edge of the ascending lamella of the outer demibranch and the mantle shown in Text-fig. 3. *asc.l.*, ascending lamella; *cu.*, cuticle, showing a dark median line; *e.c.*, epithelial cell; *m.f.*, muscle-fibres; *m.r.*, mantle ridge; *sp.*, space between cells. Eosin and light green. ×980.

cuticular type of junction does not separate normally; when separation does occur it is due to accident or to tissue deterioration on the approach of death of the animal. Rupture seems to be usually due to breaking down of the cells (Text-fig. 2 B) and not to separation of the two cuticular layers. Rupture of the junction between the outer demibranchs and the mantle, or the visceral mass, and between the two inner demibranchs has not been observed, only of that between the mantle lobes in Ensis and Cultellus on unhealthy gaping of the valves, when the mantle in the ventral region would be liable to suffer considerable strain. In Ensis siliqua the ascending lamella

of the outer demibranch could not be separated from the mantle by pulling the demibranch.

The difference in the form of the junction between the mantle lobes, and in the arrangement of the pallial muscles, in Cultel-



TEXT-FIG. 5.

Cultellus pellucidus. Transverse sections of the ventral region of the mantle to show the general appearance: A. About 200 μ anterior to the fourth aperture. B. About 150 μ posterior to the aperture (ciliated grooves are not present in sections close to the aperture). *m.l.*, longitudinal muscles; *m.r.*, radial muscles; *m.t.*, transverse muscles; *n.p.*, pallial nerve; *p.*, periostracum. Eosin and light green. ×70.

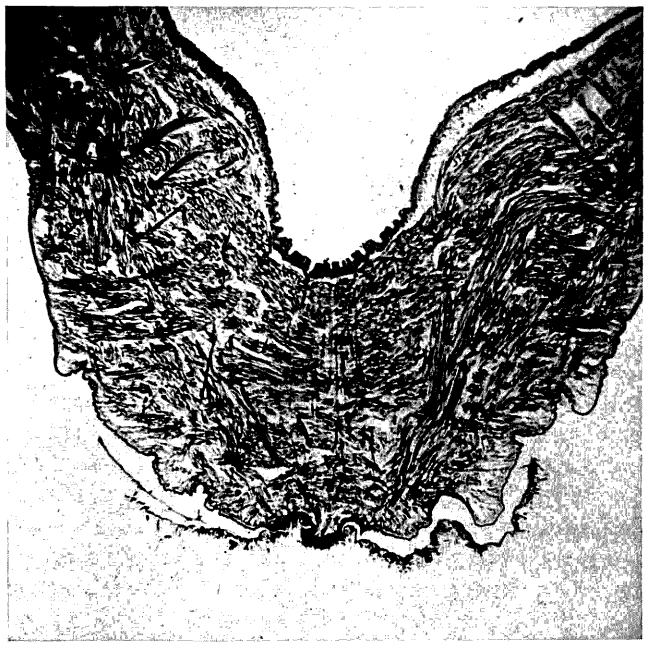
lus pellucidus in the mid-ventral line in front of, and behind, the fourth aperture is evident from Text-fig. 5; A being a section about 200μ anterior and B one about 150μ posterior to it. Anteriorly the junction is cuticular, the epithelium of the two opposed surfaces being clearly visible, and the muscles of the one lobe not penetrating into the other; while posteriorly

fusion is complete, no trace of fused epithelial surfaces being discernible, and muscles crossing the ventral region from one side to the other. A similar state of affairs is found in Ensis siliqua and Ensis arcuatus. Rupture of the mantle occurs only anterior to the fourth aperture where fusion is of the cuticular type, and not posterior to it where tissue fusion is complete. The weakness of the cuticular type of fusion would seem to lie not in the actual fusion of the cuticle, but in the arrangement of the muscles (contrast Text-fig. 5 A and B).

In Solen marginatus, in which a fourth aperture is absent, the mantle lobes being united along the entire ventral surface, the fusion (Text-fig. 6) is throughout of the type found posterior to the fourth aperture in Ensis and Cultellus, that is, it is true tissue fusion. In this bivalve rupturing of the mantle in the mid-ventral line apparently does not occur when the animal becomes feeble and the valves gape, for specimens died with it still intact, but separating from the inner surface of the valves.

Two Lamellibranchs with the fourth aperture near the posterior end of the animal, just below the inhalent siphon, have been examined, namely Lutraria lutraria and Thracia villosiuscula (Macgillivray). Both these species die with gaping valves, without rupture of the mantle in the mid-ventral line. In a Lutraria lutraria, 9 cm. long, the position of fusion of the mantle lobes was clearly visible in transverse sections of the ventral region taken about 10 mm. in front of the fourth aperture (Text-fig. 7). Contraction and contortion of the mantle in this region occurred to such an extent on fixation that the epithelium along the line of junction was thrown into complicated folds, and the cuticle could not be followed as a continuous line: Text-fig. 8 gives some idea of the appearance. In a small specimen less than 2 cm. long, the epithelial cells and their nuclei were somewhat easier to distinguish and the cuticle was clearly visible for short distances. The fusion of the mantle lobes between the fourth and pedal apertures in Lutraria lutraria seems to have proceeded much further, and is evidently much stronger, than in Ensis and Cultellus. It appears that fine muscle-fibres from one

mantle lobe cross the junction into the opposite lobe, but it is impossible to be certain of this owing to the folding previously mentioned. In living Lutraria the position of the line of junction is visible as a double white line, stretching from the fourth to the pedal aperture.



TEXT-FIG. 6.

Solen marginatus. Photograph of transverse section of the ventral region of the mantle about 10 mm. posterior to the pedal aperture. Heidenhain's iron haematoxylin and acid fuchsin. × *ca.* 37½.

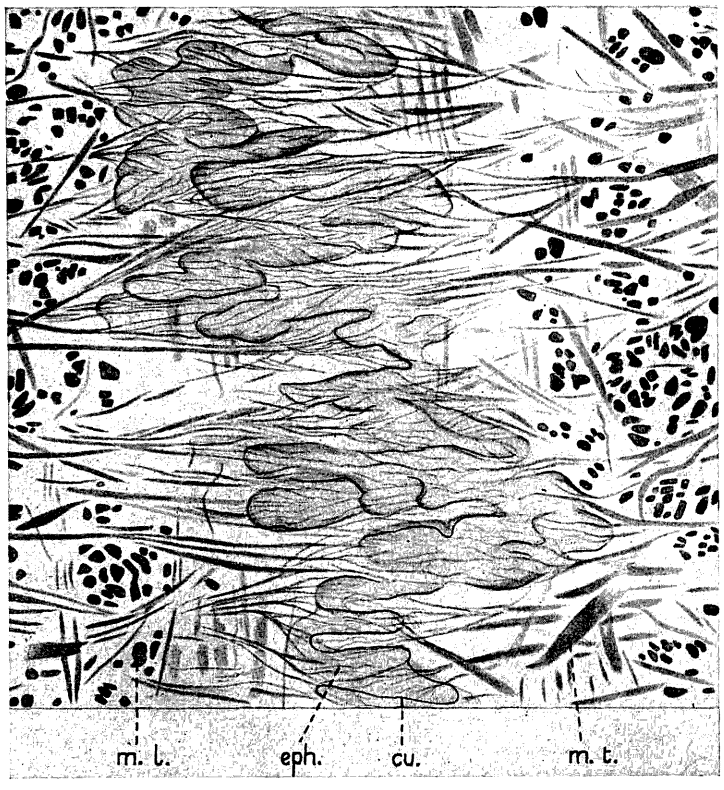
In Thracia villosiuscula true tissue fusion of the mantle lobes is complete, transverse sections of the ventral region of the mantle just anterior to the fourth aperture of a specimen 23 mm. long showing no trace of fused epithelial surfaces (Text-fig. 9).

It is curious that in Cultellus pellucidus and Solen

TEXT-FIG. 7.

Lutraria lutraria (9 cm. long). Photograph of transverse section of the ventral region of the mantle about 10 mm. anterior to the fourth aperture to show the line of fusion of the mantle lobes. Eosin and light green. × *ca.* 127½.

marginatus in which the union of the dorsal edges of the ascending lamellae of the outer demibranchs and the mantle is by cuticular fusion, yet where organic fusion occurs between

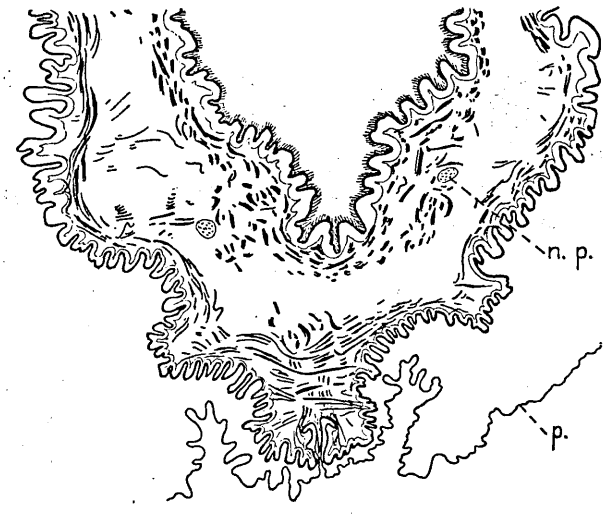


TEXT-FIG. 8.

Lutraria lutraria. Part of the section photographed in Text-fig. 7 drawn enlarged to show the form of the junction. *cu.*, cuticle; *eph.*, epithelium; *m.l.*, longitudinal muscles; *m.t.*, transverse muscles. Eosin and light green. × 450.

the two inner demibranchs, that is from just posterior to the foot to the end of the gills, the fusion is complete with no indication of where it has occurred. All trace is absent even in the region where the organic junction is giving place to the

ciliary union which obtains between the two inner demibranchs for a short distance behind the foot (for about 10 mm. in an adult Solen marginatus) and between them and the foot. A section through the transition region in Solen marginatus is shown in Text-fig. 10. The bridge joining the two inner demi-



TEXT-FIG. 9.

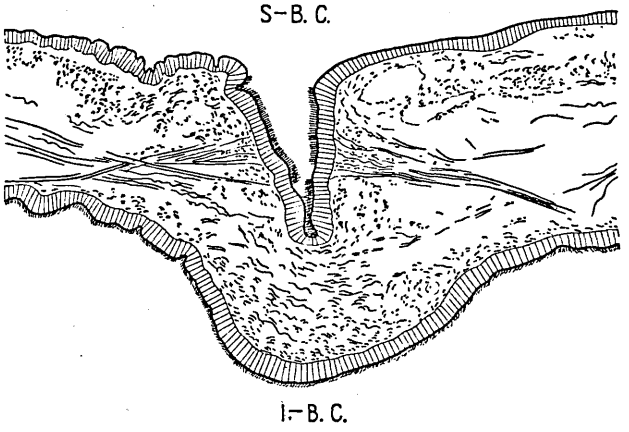
Thracia villosiuscula (23 mm. long). Transverse section of the ventral region of the mantle just anterior to the fourth aperture. *n.p.*, pallial nerve; *p.*, periostracum. Heidenhain's iron haematoxylin. ×93⅓.

branchs is narrow in Cultellus pellucidus, and it is apparently because of this that Eschrich (1931, pp. 573–4) found it easy to pull them apart.

The union between the inner demibranchs and the foot, and inter se, is normally entirely ciliary in Ensis siliqua and Ensis arcuatus, but a small specimen of the latter species showed on sectioning slight local organic fusion, which was true tissue fusion, and not mere fusion of the cuticle (Text-fig. 11).

From the state of affairs found between the inner demibranchs of Solen marginatus, Cultellus pellucidus, and the small specimen of Ensis arcuatus there is no indication

that cuticular fusion is preceded in development by ciliary junction. It is probable that when the cuticular layers of the surfaces in contact are first secreted and probably in a semi-liquid or gelatinous state, strong permanent fusion or adhesion of the two layers takes place; a study of development of these bivalves would probably settle the question.

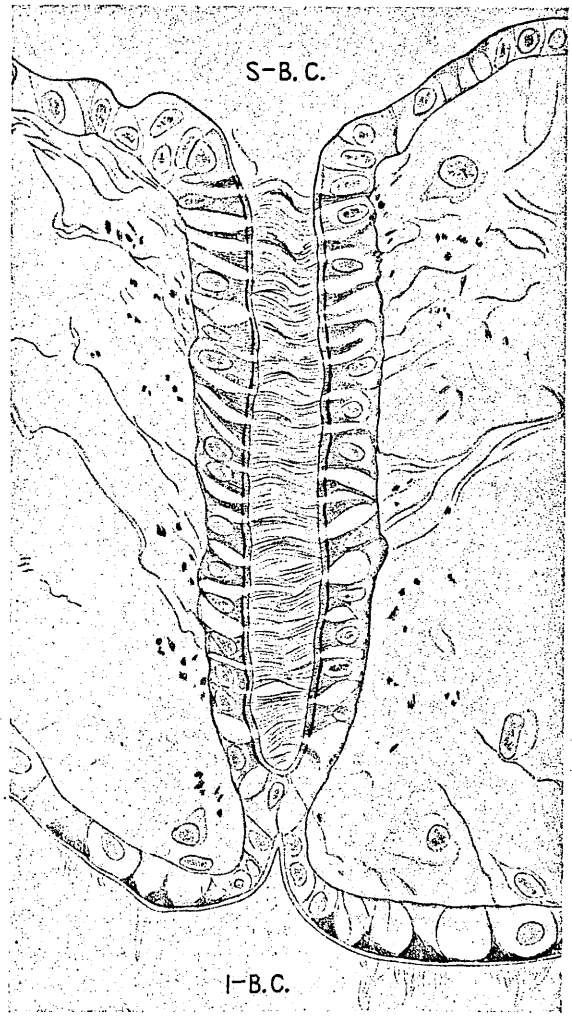


TEXT-FIG. 10.

Solen marginatus (adult). Section through the junction of the dorsal edges of the ascending lamellae of the inner demibranchs in the region where ciliary junction is passing into organic junction. *I.-B.C.*, infra- and *S.-B.C.*, supra-branchial chamber. Eosin and light green. ×70.

CUTICULAR FUSION IN RELATION TO THE FOURTH APERTURE IN CERTAIN LAMELLIBRANCHS.

Perhaps the most interesting occurrence of cuticular fusion is in those Solenidae which possess a fourth aperture, where the mantle lobes fuse between this and the pedal aperture. Certain references to the form of the union of the mantle lobes in this region in Cultellus pellucidus occur in the literature. Eschrich (1931, pp. 539–40) stated: 'Wenn wir von dem bereits erwähnten Spritzloch ausgehen, so ist der Mantel von hier aus nach vorn unverwachsen. Die Ränder legen sich aber, einen hermetischen Verschluss bildend, dicht



TEXT-FIG. 11.

Ensis arcuatus (4 cm. long). Section through the ciliary junction of the dorsal edges of the ascending lamellae of the inner demibranchs. Slight organic union is present ventrally, but this is local and unusual. *I.-B.C.*, infra- and *S.-B.C.*, supra-branchial chamber. Eosin and light green. ×980.

aneinander. Vielleicht ist auch hier eine Verklebung der Kutikularschichten eingetreten.' And according to Graham (1934, p. 176) in this same species: 'Between the anterior end of this aperture (i.e. the fourth) and the anterior end of the bivalve itself is a region where the amount of fusion of the edges of the mantle folds is variable: occasionally specimens are encountered in which this region gapes widely, but normally the edges are closely adpressed; it will be noted that this is mere contiguity: there is no real tissue connexion. The fourth aperture is therefore continuous with the rest of the pedal gape.'

According to Stenta (1903, p. 237) in Ensis siliqua between the fourth and pedal aperture 'sind die Mantelränder jederseits frei und stehen in loser Berührung miteinander'.

From Haas's (1934, pp. 605–8) discussion of the form of the union described by Eschrich (1931) in Cultellus pellucidus in relation to rupture along the mid-ventral line in this region in the Solenidae, and to the different conceptions of the structure of the inhalent siphon in Leda (= Nuculana)[1] (Deshayes, 1857; Pelseneer, 1891, p. 168; 1911, p. 5; Stempell, 1898, p. 350), it is evident that he considered that the adhesion of the cuticular layers is of such a nature that the junction may be easily dissolved without injury to the tissues, in fact he remarked that in the Solenidae 'das Reissen der scheinbaren Bauchnaht ist eben nichts weiter als die Loslösung beider verklebter Mantelrandlappen voneinander'. It would seem from sections of Cultellus pellucidus and Ensis siliqua that this rarely, if ever, occurs, but that the tearing is through the epithelial cells (see Text-fig. 2B), sometimes close to the cuticle which is then left adhering entirely to the epithelium of the opposite mantle lobe. The fusion of the cuticular layers is of such a nature that it apparently can withstand a greater stress than the cell-walls. In fact the separation of the mantle lobes in those Solenidae with a fourth mantle opening is not a reversible process; if it should by some accident

[1] It has been shown in Part I (Atkins, 1936) that in Nuculana (= Leda) minuta the junction of the two halves of the inhalent siphon in the mid-ventral line is a ciliary one, and not of the cuticular type.

occur in a healthy animal under normal conditions, it must be considered as an injury and as such needing repair.

A number of observations have been made on the condition of the mantle between the fourth and pedal apertures in Ensis siliqua and Ensis arcuatus. In these species the fourth aperture which is always present and bordered with tentacles—those of opposite sides interdigitating when the aperture is closed—is roughly 8 to 10 mm. long, in specimens about 18 cm. long.

On April 11, 1933, forty-four specimens of the two species of Ensis (siliqua and arcuatus), which had been gathered that afternoon from the Salcombe Estuary, South Devon, were received in the evening at the laboratory. Of this number nine showed an additional opening between the pedal and fourth apertures: it was found that in most of these the foot had been entirely or partly torn out in removing the animals from the sand. In five of these the fourth aperture was of normal extent (i.e. throughout its length it was bordered with tentacles), but the pedal aperture was enlarged along the ventral surface for distances between 2·5 and 8 cm. This was probably due to the end of the foot thrust in the sand not being in line with the length of the shell as the animal was pulled from the ground and thus tearing through the mantle lobes. In two, a split in the mantle occurred between the fourth and pedal apertures, but confluent with neither. In two, the fourth and pedal apertures were confluent, the valves gaping badly in one of these. The thirty-five Ensis with the fourth aperture normal were placed in bowls under circulation; after four days fourteen only retained it in this condition. Of twenty-five of the original number only six retained it in this condition after six days.

On June 8, 1933, twelve Ensis (siliqua and arcuatus) were collected from Drake's Island in Plymouth Sound: they were mostly small, the largest being about 12 cm. long. The mantle between the fourth and pedal apertures was entire in all specimens. They were placed in bowls under circulation and in eight days all had suffered rupture of the mantle in this region.

On October 20 of the same year a large number of Ensis (siliqua and arcuatus) were received from Salcombe Estuary. Seventy with the fourth aperture normal in size were

placed in bowls under circulation. After seven days about twenty-eight retained it in this condition; these were mostly small specimens, but three (13, 14, and 15 cm. long) were especially heavy looking and brown in colour.

The Ensis obtained in October were more active than those of April and June, and perhaps owing to the cooler weather withstood laboratory conditions rather better than the two previous batches. The highest air temperature recorded in the laboratory during the week beginning April 11 was 66·8° F.; during that beginning June 8 was 73·6° F.; and during that beginning October 20 was 62·8° F.

From the foregoing observations it would seem to be evident that in normal healthy Ensis the fourth aperture is small, and entirely bordered by tentacles; if it is enlarged beyond the region of these, then this is abnormal.

The mid-ventral region of the mantle between the fourth and pedal apertures is a weak place in the Solenidae, as becomes evident when the animals are removed from their natural habitat. Ensis, unless provided with sand in which to burrow, does not live well in captivity, in fact it becomes unhealthy, and may even die, in a very few days; death appears to be hastened by rupturing of the mantle. Solen marginatus, which lacks a fourth aperture and the weak line in the mid-ventral region, when deprived of sand in which to burrow lives considerably longer than does Ensis. After a week or more the valves may gape slightly, but the mantle does not rupture and the animal lives on, though obviously unhealthy.

The ease with which the mantle splits in the mid-ventral line between the pedal and fourth apertures on unhealthy gaping of the valves is no doubt responsible for statements as to the variation in the presence and extent of the fourth aperture in the Solenidae (Bloomer, 1902, p. 133; 1903, p. 44; Graham, 1931, p. 726).

It seems possible that bivalves living more or less permanently buried in sand, mud, &c., rely to a certain extent on the pressure of the surrounding soil to keep the valves from gaping, and in consequence the adductor muscles, and those across the ventral region of the mantle where the margins are united, are not

sufficiently strong to prevent gaping of the valves on enfeeblement of the animals: the position also of the adductor muscles close to the hinge is one in which they are less efficient than they would be nearer the margins of the valves; burrowing bivalves, living in a sheltered position, have no need of tightly closing the shell (Douvillé, 1907, p. 97). It is difficult otherwise to account for their withstanding laboratory conditions far better if provided with sand, &c., in which to burrow. Under such conditions a small Ensis arcuatus, 4·5 cm. long, lived forty weeks; three small Solecurtus scopula (=candidus), 3·3 cm., 3·5 cm., and 2·8 cm. long, eight, fourteen, and fifteen weeks respectively; a small Solecurtus chamasolen (=antiquatus) 2·9 cm. long, twenty-two weeks; and two small Lutraria lutraria, 5 cm. and 3·5 cm. long, thirty-seven and forty-five weeks. Solecurtus, like Ensis, when unprovided with sand supports laboratory conditions badly; Lutraria though somewhat more hardy does not live long. A Mya truncata, on the other hand, has lived in the laboratory for sixty weeks, although unburied, and was apparently healthy when killed. Cultellus pellucidus is especially delicate; frequently a good proportion of those dredged by S.S. Salpa, on arrival at the laboratory, have the mantle between the fourth and pedal apertures ruptured to a varying extent. The ease with which the mantle splits in this position in Cultellus pellucidus has been previously noted by Bloomer (1902, p. 133; 1903, p. 44). The specimen from which Text-fig. 2 was drawn was fixed directly on arrival, and though the mantle appeared intact, deterioration had already set in in some places, as evidenced by the stretching and breaking down of the cells (Text-fig. 2B).

These burrowing bivalves under laboratory conditions, and unprovided with sand in which to hide, soon become 'hockley' (see Orton, 1934, p. 101, for definition of term); the adductor muscles lose tone, and—owing to the elasticity of the ligament—the valves tend to gape, and in Ensis and Cultellus pellucidus the mantle splits along the line of weakness.[1]

[1] In moribund specimens of Ensis the foot is occasionally found inserted into the infra-branchial chamber, the anterior end pointing backwards.

The shell differences which Graham (1931, p. 726) found to be correlated with variation in extent of the fourth aperture in Ensis siliqua might perhaps be better stated in terms of strength of the shell ligament. In 'shells of lighter build' the ligament is possibly less strong than in those of 'more robust construction' and therefore in the former rupturing does not occur so readily—and the fourth aperture will tend to be distinct.

Morse (1913, p. 270) has described in Solenomya velum, a burrowing Protobranch, rupturing of the mantle in the mid-ventral line between the pedal and the single posterior exhalent aperture (there is no fourth aperture in this genus), as the animal becomes enfeebled. He stated that 'There is a median suture in this ventral membrane and in one rupture the suture became dislocated, showing there was a strain upon it. In another case a small rupture appeared on each side of the median suture. That this membrane limits the expansion of the valves is shown by cutting the membrane, when the valves immediately open wider in much the same way as when the adductors are severed in other lamellibranchs.' From Drew's figure (1900, fig. 10, p. 264) of a transverse section of the ventral margins of the mantle and cuticle of Solenomya velum it appears that the fusion of the two lobes is complete and not of the cuticular type: sections of Solenomya togata also failed to reveal any trace of a line of fusion, but fixation was not good. The rupturing which Morse described is evidently due to the thinness of the mantle in the ventral region, and the strength and arrangement of the pallial muscles.

Origin of the Fourth Aperture. As to the origin of the fourth aperture in the Solenidae, Bloomer (1903, pp. 44–5) held that 'From a morphological point of view, it is reasonable to infer that a portion of the pedal aperture first became specialized by developing a tentacular fringe; then this fringe extended posteriorly, and the pallial walls coalesced, separating the fourth from the pedal aperture, and finally the fourth aperture gradually proceeded farther posteriorly, until it attained a position favourable for the function it originated for', which in Ensis siliqua and Ensis ensis he considered to be that of 'an accessory food-providing organ, and

an exhalent orifice for ejecting water or foreign matter, though the latter function is probably a secondary one'. This view of its origin he based chiefly on the fact that in Ceratosolen (= Pharus) legumen (L.)—which has no fourth aperture—'the dorsal and ventral surfaces of the pedal aperture carry a tentacular fringe, and extend farther posteriorly' than in Solen vagina (= marginatus), which also has no fourth aperture; and that in Cultellus pellucidus the fourth aperture is situated more anteriorly (at about the posterior end of the first quarter of the animal) than in Ensis ensis and Ensis siliqua, where it is about the centre of the ventral surface. He held that Solen marginatus is a more primitive form than Ceratosolen legumen; Ceratosolen legumen than Cultellus pellucidus; and Cultellus pellucidus than Ensis siliqua or Ensis ensis. While this view of its origin may be right, it must be observed that the presence of tentacles on the mantle margin is perhaps the rule in Lamellibranchs—in the closely allied family Solecurtidae they are found in Solecurtus scopula on the external surface of the mantle edge throughout its extent (see Graham, 1934, p. 180)—and that their absence round the pedal aperture in the Solenidae might on the contrary be considered as due to specialization of the mantle margins in this region to form the muscular pedal flaps or valves. It seems simpler to imagine that an originally large pedal opening was gradually reduced by fusion of the mantle lobes—as the foot increased in length and came to be protruded from the anterior end of the shell—leaving a small aperture posteriorly, functioning normally as an additional inhalent aperture, and, on sudden closure of the valves, for the ejection of unwanted material.

The fourth aperture in Lutraria and Thracia appears to have originated at an earlier period than in the Solenidae (see also Bloomer, 1903, p. 45), judging from the condition of the mantle in the mid-ventral line between this aperture and the pedal (see p. 431); and in Thracia before Lutraria. In Lutraria it has been found that under experimental conditions at least the aperture seems to be generally closed, but on occasions the entrance of particles has been observed, as

indeed must happen through any open aperture leading into the inhalent chamber of any bivalve, if the lateral cilia of the gills are active. Its chief use, however, appears to be, as Bloomer (1903) observed, for the sudden ejection of unwanted material.

In Lutraria and the Anatinacea the fourth aperture is situated just below the inhalent siphon (Bloomer, 1903; Pelseneer, 1890; 1911, pp. 74–5), and according to Kellogg's figures of Mytilimeria nuttallii Conrad and Lyonsia saxicola Baird (1915, figs. 22, 26, 27, 28) the bay in the mantle, in which material brought by the mantle currents collects, is just posterior to it. It is perhaps easier for material to be expelled by way of the fourth aperture than by the inhalent siphon. In the Protobranch Nuculana minuta (see Atkins, 1936, Part I) it was observed that the mantle collections were expelled just ventral to the inhalent siphon, rather than by way of the siphon itself. In Lutraria and Thracia the fourth aperture is closer to the inhalent siphon than apparently in Mytilimeria nuttallii and Lyonsia saxicola.

Summary.

A form of fusion involving only the cuticle has been found in certain Lamellibranchs between the outer demibranchs and the mantle or the visceral mass; between the two inner demibranchs; and, in forms possessing a fourth aperture, between the mantle lobes in the mid-ventral line between this and the pedal aperture. The histological structure of the junction is described, and is especially considered in relation to the condition of the fourth aperture in the Solenidae.

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CONTENTS OF No. 315. New Series.

MEMOIRS:

Printed in Great Britain by John Johnson at the Oxford University Press

19

DAPHNE ATKINS, B.Sc.

On the Ciliary Mechanisms and Interrelationships of Lamellibranchs

Part V. Note on the Gills of Amussium pleuronectes

Quarterly Journal of Microscopical Science
Vol. 80, Part III, May, 1938

Printed in Great Britain

On the Ciliary Mechanisms and Interrelationships of Lamellibranchs.

PART V: Note on the Gills of Amussium pleuronectes.

By

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With 2 Text-figures.

CONTENTS.

INTRODUCTION.

Two specimens of Amussium pleuronectes L. from the Orissa Coast, Bay of Bengal, were obtained from the Indian Museum, Calcutta, through the courtesy of Dr. B. Prashad. This species was found to resemble Pecten (including Chlamys), not only in the general anatomy, but very closely in the structure of the gills. The specimens had been preserved in alcohol for museum purposes, and though the fixation was quite adequate for work on gill structure, it was too imperfect to show histology and ciliation with any exactitude.

Amussium pleuronectes, which lies on the right valve, as does Pecten, is evidently an active swimmer, for the adductor muscle is composed largely of striated fibres, there being only a narrow strip of smooth fibres about 3 mm. wide where the entire muscle is about 18 mm. wide. The proportion of the adductor occupied by striated fibres is even greater than in Pecten and Chlamys.

THE GILLS AND PALPS.

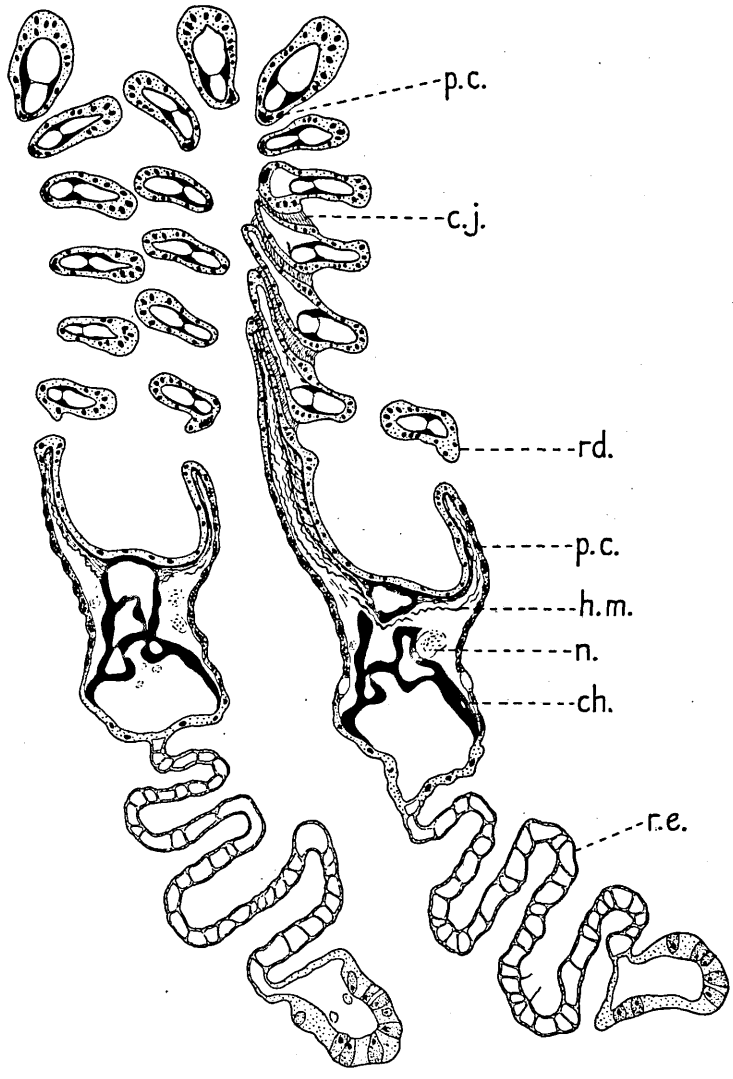
The disposition and structure of the gills of Amussium pleuronectes closely resemble those of Pecten and

Chlamys. Each gill is suspended by a membrane and has a considerable free posterior portion. The arrangement of the ctenidial muscles differs slightly from that in Pecten. The paired longitudinal muscles of the gill axes include striated fibres, as do those of several species of Pectinidae (Janssens, 1893; Dakin, 1909; Setna, 1930). Such striated muscle-fibres are found in organs performing a series of comparatively sudden movements, and it is most probable that the gill axes in Amussium pleuronectes, as in Pecten, are capable of rapid contraction, and that this occurs preparatory to the clapping of the valves in swimming.

The inner demibranch is rather deeper than the outer: the ascending lamellae are rather more than two-thirds the height of the descending. The lamellae are highly plicate and heterorhabdic (Text-fig. 1). The upper edges of the ascending lamellae are free from adjacent parts of the body. The upper ends of the ascending filaments are united in series by interlocking cilia to a depth of about a millimetre. At the lower edge of the demibranch adjacent filaments are connected by ciliated disks. The connexion between the filaments is by interlocking cilia borne on long spurs, those of the principal filaments being especially long. At the greatest depth of the demibranch there are about twenty spurs on the descending filament and fifteen on the ascending. Chitin extends into the spurs both of the principal and ordinary filaments. Horizontal muscles (*h.m.*, Text-figs. 1, 2) are well developed in the principal filaments, the arrangement closely resembling that in Pecten; it is extremely probable that Amussium pleuronectes can also flap the sides of these filaments (see Text-figs. 1 and 2).

The interlamellar junctions have the form of low septa extending about two-fifths of the height of the principal filaments. An interlamellar extension, or respiratory expansion (*r.e.*, Text-fig. 1), occurs on about the upper third of the descending principal filament; it appears to be of much the same structure as in Pecten.

An intrafilamentar septum, formed of muscle-fibres, is present in the filaments, and the chitinous lining of the ordinary filaments is thickened under the insertion of the fibres.



TEXT-FIG. 1.

Amussium pleuronectes. Transverse section through the dorsal region of a descending lamella, showing a plica and a half, and two principal filaments with respiratory expansions. *ch.*, chitin; *c.j.*, ciliary junction; *h.m.*, horizontal muscles; *n.*, nerve?; *p.c.*, pigment cells; *rd.*, ridge on filament adjacent to principal filament for interlocking with it; *r.e.*, respiratory expansion. Alcohol fixation; Mallory's triple stain. ×168.

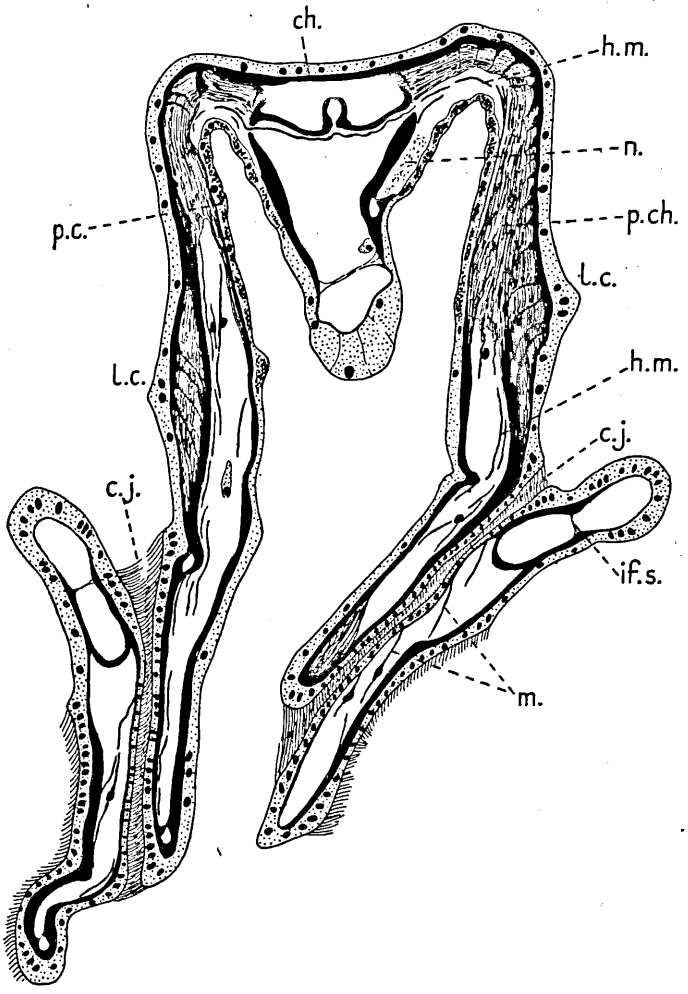
There are eleven to thirteen filaments, but usually twelve, to a plica; the plicae are deep in the upper part of the demibranch but tend to flatten out toward the free margin. The principal filaments are broad, except toward the lower edge of the demibranchs where they become almost indistinguishable from the ordinary filaments in surface view of the lamella. The difference in the form of the principal filament in different parts of the lamella, that is, with the frontal surface concave (Text-fig. 1) and convex (Text-fig. 2) is largely, or entirely, due to the action of the horizontal muscles (*h.m.*). In the upper part of the demibranchs, however, where there is little space for movement of the plicae, the frontal surface of the principal filaments is probably always or generally concave, as in Text-fig. 1. The form of the chitinous skeleton may be seen from Text-figs. 1 and 2.

Setna's (1930, p. 376) words concerning the structure of the principal and adjacent ordinary filaments of Pecten may be repeated here as applying to those of Amussium pleuronectes (see Text-fig. 1), and it is also extremely probable that the interlocking arrangement functions in a similar manner. He wrote: 'the ordinary filaments on either side of the principal filaments possess a ridge appearing in section as a spur turned towards the principal filaments. The principal filaments themselves possess lateral extensions, so that the whole system forms an accessory interlocking arrangement and may be looked upon as an interesting mechanical device by means of which the flapping extensions on the principal filaments fit into the groove formed by the spur. . . ., the principal filaments are extremely active and are responsible for what is described as the "flapping" movement.'[1]

The one or two filaments at the apex of the plica are larger than the rest of the ordinary filaments, except toward the lower region of the demibranch. The six or so filaments forming the plical crests appear to have longer frontal cilia than the others.

The Palps.—In the preserved state the folded surface of

[1] Setna examined Pecten maximus, Chlamys opercularis, and Chlamys tigerina. It has been found that a ridge also occurs on the filaments adjacent to the principal filaments in Chlamys distorta.



TEXT-FIG. 2.

Amussium pleuronectes. Transverse section of a principal and adjacent ordinary filaments (descending lamella) taken near the middle of the demibranch. *ch.*, darkly staining chitin; *c.j.*, ciliary junction; *h.m.*, horizontal muscles; *if.s.*, intrafilamentar septum; *l.c.*, position of lateral cilia; *m.*, muscle-fibres in spur of ordinary filament; *n.*, nerve?; *p.ch.*, pale staining chitin; *p.c.*, pigment cells. Alcohol fixation; Mallory's triple stain. ×456.

the almost rectangular palps is white, and the smooth surface dark brown. The inner and outer lips appear to be fused, or intricately interlaced over the mouth, which is thus hidden.

Discussion.

It was considered of interest to examine any species of Amussiidae as this was a family which in 1888 was placed in the Pectinacea by Pelseneer (pp. 12, 13), was removed by Ridewood in 1903 (pp. 181, 185–6) to the Mytilacea, and was replaced in the Pectinacea by Pelseneer (1906, 1911).

Ridewood based his classification on the form of the gill, which he described as having 'flat lamellae and filaments undifferentiated' in the three species which he examined. These three species, Amussium dalli, Amussium meridionale, and Amussium lucidum are all deep-water forms. Amussium dalli Smith was found in 218 to 1,591 fathoms (Smith, 1885, pp. 308–9; Dall, 1885–6, pp. 209–10); Amussium meridionale Smith in 1,375 to 1,800 fathoms, and Amussium lucidum Jeffreys in 675 to 1,000 fathoms (Smith, 1885, pp. 316, 317). By ill chance he does not seem to have had the opportunity of examining Amussium pleuronectes, a shallow-water form, taken by the Challenger Expedition in 20 to 28 fathoms (Smith, p. 308) and by the Siboga Expedition in 18 to 82 metres (Dautzenberg and Bavay, 1912, p. 35).

Ridewood (1903, pp. 207–8) briefly described the gills of Amussium dalli, Amussium meridionale, and Amussium lucidum as follows: 'In the three species of Amussium examined the upper edges of the ascending lamellae are free from adjacent parts. The upper ends of the ascending filaments are united in series by ciliated discs, as also are the lower ends of the filaments along the ventral edge of the demibranch. There are no ciliated discs besides these two rows. There are no interlamellar junctions of any kind. The ascending lamellae of Amussium dalli reach nearly as high as the descending, but those of Amussium lucidum and Amussium meridionale only extend half-way up

the descending lamellae, or a little higher. An intrafilamentar septum is present, and the chitinous lining is of fairly uniform thickness.'

Pelseneer (1911, pp. 29, 97) who examined Amussium pleuronectes for the Siboga Report makes the general statement that the gills of Amussium are smooth. So that there should be no question of the correct identification of my specimens with plicate and heterorhabdic gills, Mr. R. Winckworth has courteously verified the name attached by the authorities of the Indian Museum.

The position of Amussium pleuronectes in the Pectinacea is supported, not only by the general anatomy, but by the detailed structure of the gills. The condition of the material renders it impossible to make any statement as to the form of the latero-frontal cilia—or indeed of any cilia—but the gill is so similar to that of Pecten that it is most probable that these will be found to be tenuous and small, that is micro-latero-frontal cilia (see Atkins, Part VII).

The Amussiidae then includes species with flat lamellae and at least one with plicate and heterorhabdic lamellae: it would seem unjustifiable to separate them because of this difference in the structure of the gills, placing those with flat lamellae in the Mytilacea and Amussium pleuronectes in the Pectinacea. Curiously enough, though Ridewood (1903, p. 181) stressed the difference between flat and homorhabdic, and plicate and heterorhabdic lamellae in the Eleutherorhabda, yet in the Synaptorhabda he (p. 161) considered that 'The differences presented by Solen and its immediate allies show that the plication of the lamellae and the differentiation of principal filaments are of not more than specific, or at most subgeneric, value'. In the Pectinidae also two types of gills occur; though most species have plicate and heterorhabdic lamellae, one at least, Pecten groenlandicus, has homorhabdic lamellae (Haren-Noman, 1881–2, pp. 28–30.

Dakin (1928*a*, pp. 358–9) has already expressed the opinion that the method of classification by the structure of the gill alone undoubtedly led Ridewood astray in the case of Amussium, and he suggested that 'both on the ground of general

anatomy, as well as on the evidence from a study of the eye, Amussium be brought back to the Pectinidae'.

It is of interest that the three species from deep water should have simple, flat gills, with ciliated interfilamentar junctions restricted to the free lower edge of the demibranch and the upper ends of the ascending filaments. Plication increases the food-collecting surface of the gills, and it might have been expected that deep-water Amussiidae, living where phytoplankton is likely to be extremely scarce, would exhibit such plication. Actually they have flat gills, while the shallow-water species, Amussium pleuronectes, living where phytoplankton is probably comparatively rich, has highly plicate gills with markedly differentiated principal filaments. It may be that the simplicity of the gills of the deep-water species is to be explained by backwardness or retrogression:[1] the temperature at great depths would involve a low rate of metabolism. According to Dall (1885–6, p. 210) Amussium dalli is without palps; so it is possible that it takes in all particles that come to the gills, unless sorting occurs on the filaments as in certain bivalves (see Atkins, 1936, Part I).

Correlated with the difference in the structure of the gills of the deep-water species and Amussium pleuronectes there must be a considerable difference in the frontal currents on the filaments. In Amussium pleuronectes in all probability the gill currents will be found to be similar, if not identical, with those of species of Pecten and Chlamys with plicate and heterorhabdic gills; the deep-water species having simple, flat gills necessarily cannot have the same type. If the examination of the living gills of these forms was feasible it would be of extreme interest, and might very possibly reveal currents in opposite directions on the same gill filament as in the Arcidae, and on certain of the ordinary filaments of Pecten, Chlamys, and others (see Atkins, 1936, 1937).

[1] In the genus Donax Rice (1897, see Ridewood, 1903, p. 162) regarded the simplicity of the flat forms as secondary, and derived by retrogression from the plicate condition.

SUMMARY.

The gills of Amussium pleuronectes L., a species from shallow water, were examined and the lamellae found to be plicate and heterorhabdic, thus differing in structure from those of the deep-water species, Amussium dalli, Amussium meridionale, and Amussium lucidum, which Ridewood found to have flat and homorhabdic lamellae. The gills of Amussium pleuronectes closely agree with those of the Pectinidae also possessing plicate and heterorhabdic lamellae.

Ridewood's classification of the Amussiidae with the Mytilacea cannot be upheld; the position of this family is with the Pectinacea as in Pelseneer's classifications of 1888, 1906, and 1911.

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DAPHNE ATKINS, B.Sc.

On the Ciliary Mechanisms and Interrelationships of Lamellibranchs

Part VI. The Pattern of the Lateral Ciliated Cells of the Gill Filaments of the Lamellibranchia

Quarterly Journal of Microscopical Science
Vol. 80, Part III, May, 1938

Printed in Great Britain

On the Ciliary Mechanisms and Interrelationship of Lamellibranchs.

PART VI: The Pattern of the Lateral Ciliated Cells of the Gill Filaments of the Lamellibranchia.

By

Daphne Atkins, B.Sc.

Marine Biological Laboratory, Plymouth.

With 6 Text-figures.

CONTENTS

INTRODUCTION.

THE lateral ciliated cells of the gills of Lamellibranchs are arranged in a definite manner, which appears to be constant at least for the species. Though there may be considerable variation in the length of the cells in different parts of the same filament (see Text-fig. 5 G), yet the arrangement, or pattern, is the same. In some instances the same general pattern is characteristic of a genus, and even of a family or larger group. The cells from which the lateral cilia arise are rhomboidal, frequently almost rectangular, at the surface, and elongated in the direction of length of the filaments; in some species, however, there is little difference between the length and breadth of certain of the cells, as in Pteria hirundo (Text-fig. 2 F), Phacoides (= Lucina) borealis (Text-fig. 4 B), and Macoma balthica (Text-fig. 5 A), and practically no difference in Teredo navalis (Text-fig. 4 A). In some

patterns the transverse cell-walls of the several rows are more or less in line; in others they are distinctly irregular.

Engelmann in 1880 gave figures of the arrangement of these cells in Anodonta, Cyclas, and Ostrea. He records (p. 513) that 'Form und Grösse der Seitenzellen sind weder bei den verschiedenen Arten, noch auch bei den verschiedenen Zellreihen derselben Art die gleichen': he, however, apparently examined few bivalves. This author (1880, pp. 513–14) was perhaps the first to observe the arrangement of the basal granules of the cilia in oblique rows, which he stated were orientated obliquely at an angle of 45° across the surface of the cell in Anodonta, Unio, Cyclas, Mytilus, and Ostrea. According to Saguchi (1917, p. 221) the rows are transverse to the length of the cell in Anodonta; while Lucas (1932*a*, p. 271) found the angle of inclination to average 35° in Modiolus demissus.

Oblique arrangement of the basal granules of the cilia was observed in the lateral cells of all the species of Lamellibranchs examined, but the exact angle was not determined and the rows therefore are not shown in the figures. The granules stain well with Heidenhain's iron haematoxylin, and indicate the shape and arrangement of the cells clearly in sections parallel to the surface. Slight obliquity of the sections, however, may have resulted in the cells being figured slightly wider or narrower than they actually are. The pattern of the lateral ciliated cells in the majority of the bivalves was determined in this way, and mostly checked either from transverse sections or from the living filaments. The patterns are drawn somewhat diagrammatically in that the cells outlines have been straightened. In all the figures the frontal edge of the lateral ciliated tract is on the right.

The curiously narrow rows of basal granules, which, when present, generally occur on the outer sides (frontal and abfrontal) of the tract (Text-figs. 2, 3), appear to be actually on separate cell rows, at least where they have been checked in the living filaments (e.g. Arca tetragona, Glycymeris glycymeris, Heteranomia squamula, Monia squama, Ostrea, Mytilus edulis). It was found impossible

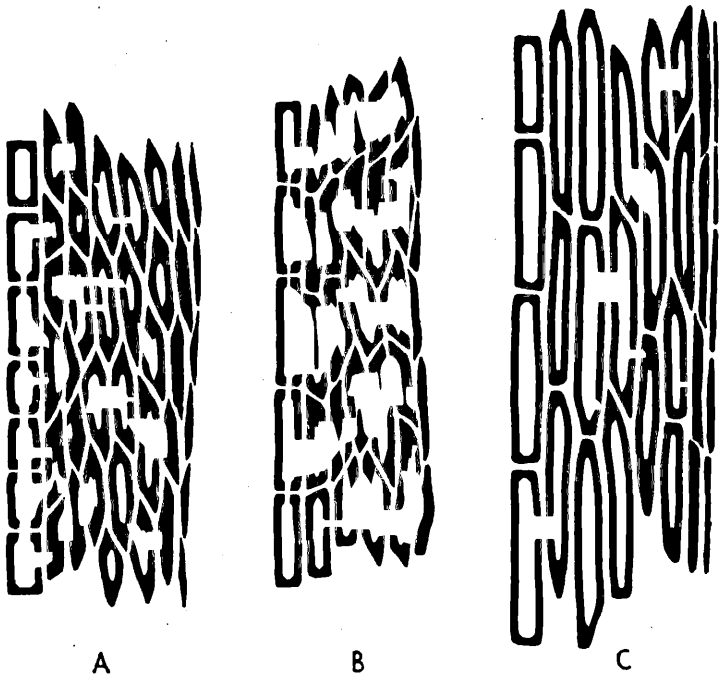
accurately to distinguish breaks in these rows, indicating limits of cells, and in the figures they are shown as continuous lines. The significance of these exceedingly narrow rows of cilia is unknown; it would seem improbable that their chief value can be that of current producers. The lateral cells increase considerably in size basally, as can be seen in transverse sections, and as is indicated by the fact that in figures showing the disposition of the nuclei (Text-figs. 4 A (*a*); 6 A (*a*)) these cover a greater area than the cells at the surface.

The Pattern of the Lateral Ciliated Cells.

I. Protobranchia.

In the Protobranchs, Nucula radiata Hanley (Nuculidae), Nuculana (= Leda) minuta (Müller) (Nuculanidae), and Solenomya togata (Solenomyidae), the lateral ciliated tract is six, seven, or eight cells wide; the ends of the cells being pointed and interdigitating, except those of the outer row on the abfrontal side, which are more or less rectangular and placed end to end (Text-fig. 1). The figure of the lateral cells of Solenomya togata (Text-fig. 1 c) has been composed from two or three sections, but it shows that the cells are longer than in Nucula radiata (Text-fig. 1 A) and Nuculana minuta (Text-fig. 1 B), and that there is not only a tendency for the cells to assume the rectangular shape, but for them to be arranged in definite rows. The somewhat more indefinite, or more primitive, arrangement of the lateral cells would seem to be that occurring in Nucula and Nuculana.

Although tracts of six cells wide are met with among the higher Lamellibranchs they do not attain such a width as in the two Protobranchs Nucula and Solenomya, namely about 26μ in Nucula radiata and about 30μ in Solenomya togata. In Nuculana minuta the tract is about six cells wide, and the total width about 18 to 22μ. The greatest width observed in a higher Lamellibranch was about 19μ in Phacoides (= Lucina) borealis. Measurements mentioned in this note were made on sections, and are therefore probably considerably less than they would be on living tissue.



TEXT-FIG. 1.

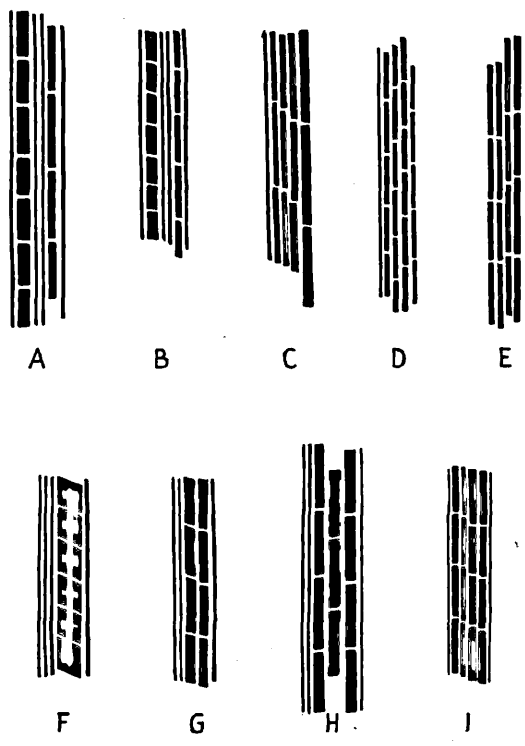
Lateral ciliated cell patterns in Protobranchia. A, Nucula radiata (Nuculidae); B, Nuculana minuta (Nuculanidae); C, Solenomya togata (Solenomyidae). The frontal edge of the tract is on the right of the figure. ×980.

II. HIGHER LAMELLIBRANCHIA.

A. Group Possessing Micro-latero-frontal Cilia.

In the group of Lamellibranchs having micro-latero-frontal cilia (see Atkins, Part VII) the pattern of the lateral ciliated cells is distinctly different in different families and even in different genera, for instance among the Pteriidae.

Arcidae.—In the Arcidae practically the same arrangement of the six cell rows is found in Arca tetragona Poli and Glycymeris glycymeris (L.) (Text-fig. 2 A and B), though the cells are somewhat longer in the former.



TEXT-FIG. 2.

Lateral ciliated cell patterns in the group of Lamellibranchs having micro-latero-frontal cilia. A, Arca tetragona; B, Glycymeris glycymeris (Arcidae); C, Anomia ephippium (Anomiidae); D, Pecten maximus (Pectinidae); E, Lima hians (Limidae); F, Pteria hirundo (Pteriidae); G, Malleus albus (Pteriidae); H, Pinna fragilis (Pinnidae); I, Ostrea edulis (Ostreidae). The frontal edge of the tract is on the right of the figure. It was found impossible accurately to determine the cell limits of the very narrow rows, and these are therefore shown as continuous. ×980.

Anomiidae.—In the Anomiidae a pattern of five-cell rows is common to the three genera, Anomia (Text-fig. 2 c), Heteranomia and Monia, though no doubt slight variations occur in the different genera and species.

Pectinacea.—In Pecten maximus (L.) (Pectinidae)

the narrow lateral ciliated tract, only about 5μ wide, is composed of five rows of cells, the outer on the abfrontal side being exceedingly narrow (Text-fig. 2 D). Five rows of cells also occur in Spondylus gaederopus (Spondylidae). In Lima hians (Gmelin) (Limidae) there appear to be but four rows of narrow cells (Text-fig. 2 E), and the total width little more than 4μ.

Pteriacea.—In the Pteriacea a striking pattern of a row of wide cells with four rows of very narrow ones, one on the frontal side and three on the abfrontal side, is found in Pteria hirundo (L.) (Text-fig. 2 F), Pinctada vulgaris, Pinctada margaritifera (Pteriidae), Isognomon alata (Isognomonidae), and in Vulsella sp. (Vulsellidae), while Malleus albus Lamarck (Pteriidae) has two rows of medium width and three very narrow rows (Text-fig. 2 G). The genus Malleus is not as old as the other genera mentioned, being unknown fossil.

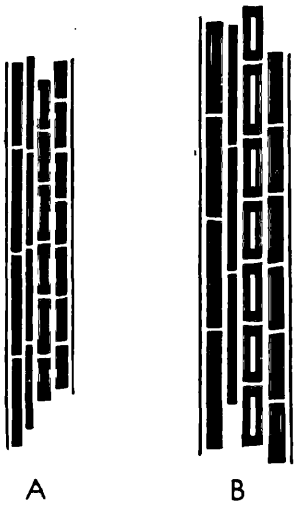
Pinna fragilis Pennant (Pinnidae) has six rows of cells, three of median width and three very narrow (Text-fig. 2 H). In the Ostreidae, Ostrea edulis L. (Text-fig. 2 I), Ostrea virginica Gmelin and Ostrea angulata (Lamarck) have a common pattern of six rows of cells, four of median width and two very narrow, one on the frontal and one on the abfrontal side.

B. Group Possessing Eu-latero-frontal Cilia.

Outside the group of Lamellibranchs with micro-latero-frontal cilia the usual number of rows of lateral ciliated cells appears to be four, except in the Mytilidae (Mytilus edulis L., Modiolus modiolus (L.), Modiolus adriaticus Lamarck, Musculus (= Modiolaria) marmoratus (Forbes)) which have six rows, the two outer being exceedingly narrow (Text-fig. 3). In Musculus marmoratus, so far as can be judged from entire filaments preserved in formalin,[1] the fourth row from the frontal side is very narrow.

[1] In entire unstained filaments of formalin and alcohol preserved material the cell outlines are frequently observable, but in Bouin and Bouin-Duboscq preserved material they are not.

The majority of Eulamellibranchs investigated possess the same type of pattern (see Text-figs. 4, 5) of one row of broad cells, with a row of narrow ones to the frontal side, and two rows of narrow cells to the abfrontal side, of which the outer is sometimes the wider, for instance in Ensis, Solecurtus, Cultellus, Barnea parva, and Hiatella rugosa.

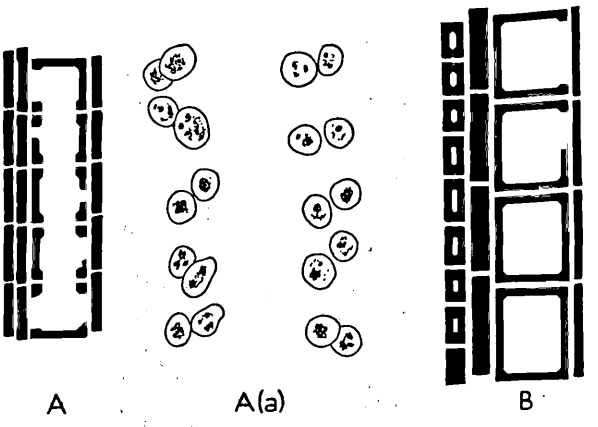


TEXT-FIG. 3.

Lateral ciliated cell pattern in the Mytilidae. A, Mytilus edulis; B, Modiolus modiolus. The frontal edge of the tract is on the right of the figure. It was found impossible accurately to determine the cell limits of the very narrow rows, and these are therefore shown as continuous. ×980.

This general type of arrangement of the lateral ciliated cells was figured for Cyclas (=Sphaerium) cornea by Engelmann (1880, Pl. V, fig. 4) and by Wallengren (1905, fig. E, p. 45) in Mya. Two main variations exist; one in which the cells of the principal row are as wide, or almost as wide, as long (e.g. Teredo navalis, Text-fig. 4 A; Phacoides borealis, Text-fig. 4 B; Macoma balthica, Text-fig. 5 A); and the other in which they are distinctly longer than wide (e.g. Ensis siliqua, Text-fig. 5 F; Solecurtus;

Lutraria lutraria, Text-fig. 5 G; Sphaerium corneum; Tellina tenuis, Tellina crassa, Text-fig. 5 B and C; Aloidis gibba, Text-fig. 5 E; Venus casina, Text-fig. 5 D). No doubt there are specific, as well as generic and family differences in the average width and length of the



TEXT-FIG. 4.

Lateral ciliated cell pattern in two Eulamellibranchs. A, Teredo navalis (Teredinidae); B, Phacoides borealis (Lucinidae); A (*a*), arrangement of nuclei of lateral cells of Teredo navalis. The frontal edge of the tract is on the right of the figure. ×980.

cells of the various rows; and, as previously mentioned, there may be considerable differences in length of the cells in different parts of the same filament. Text-fig. 5 G (*a*), shows lateral ciliated cells from about the middle of an ascending filament of Lutraria lutraria, and Text-fig. 5 G (*b*), from near the dorsal end of the same filament. It is interesting that in the

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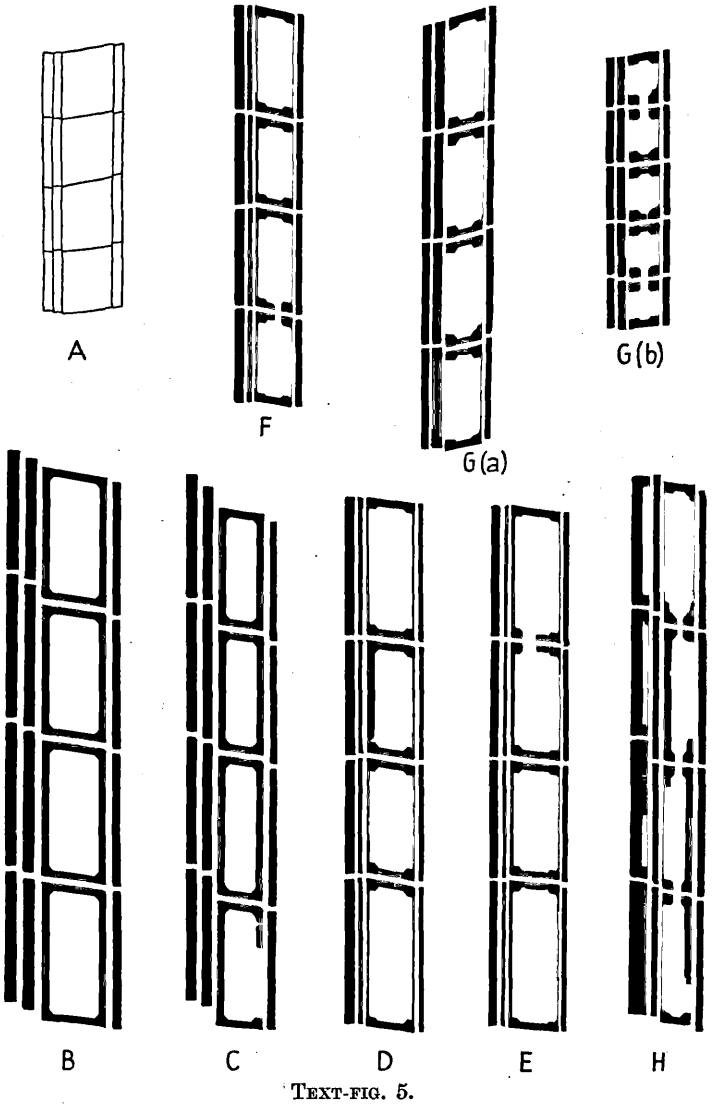
crassa (Tellinidae); D, Venus casina (Veneridae); E, Aloidis gibba (Erodonidae); F, Ensis siliqua (Solenidae); G, Lutraria lutraria (Lutrariidae); G (*a*), from about midway along the ascending filament of the outer demibranch; G (*b*), from near the dorsal end of the same filament; H, Lyonsia norwegica (Lyonsiidae). The frontal edge of the tract is on the right of the figure. The figure of Macoma is drawn from the living filament. A ×573⅓; B–H ×980.



TEXT-FIG. 5.

Lateral ciliated cell pattern in some marine Eulamellibranchs. A, Macoma balthica; B, Tellina tenuis; C, Tellina

Continued on previous page

Tellinidae, Macoma (Text-fig. 5 A) has one variety, and Tellina (Text-fig. 5 B, C) the other.

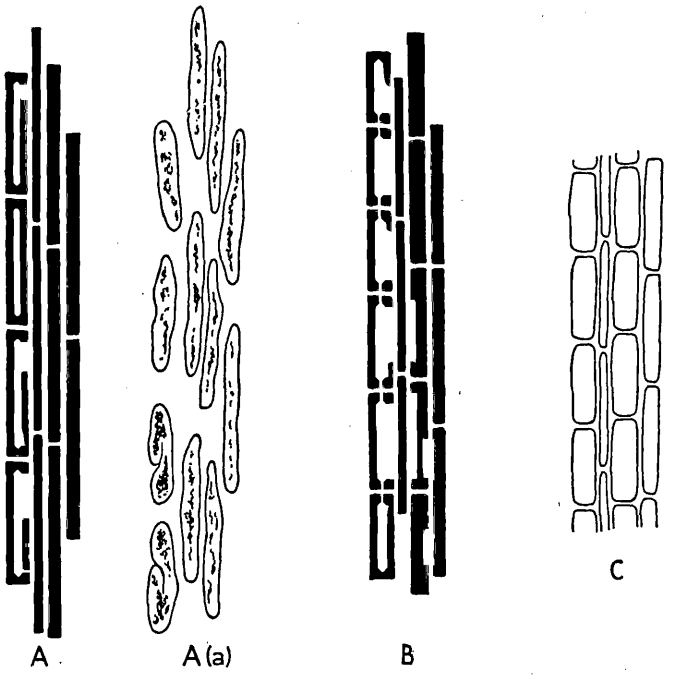
In Lyonsia norwegica the main row of cells is not so noticeably broad as in the majority of the species, while the outer row on the abfrontal side is proportionately broader (Text-fig. 5 H).

Though the number of cell rows is constant the total width of the tract varies much in different bivalves, being especially broad in Phacoides borealis (ca. 19μ) and in Scrobicularia plana (16–18μ). The larger size of the cells of Tellina tenuis in Text-fig. 5 B than of Tellina crassa in Text-fig. 5 C is possibly due to the fact that the specimen of Tellina tenuis from which the gills were taken was a large one, 4·3 cm. long, and that of Tellina crassa a young one only 1 cm. long; there is perhaps an increase in the size of the cells with age.

Bivalves having a lateral ciliated cell pattern of a row of large cells, with one row of narrow ones to the frontal side, and two to the abfrontal side, are the following:

Dreissensiidae: Dreissensia polymorpha (Pallas).
Cyprinidae: Cyprina islandica (L.).
Lucinidae: Phacoides (= Lucina) borealis (L.), (Text-fig. 4 B).
Montacutidae: Mysella bidentata (Montagu).
Erycinidae: Kellia suborbicularis (Montagu).
Sphaeriidae: Sphaerium (= Cyclas) corneum (L.) (see Engelmann, 1880).
Tellinidae: Tellina tenuis da Costa (Text-fig. 5 B): Tellina crassa Pennant (Text-fig. 5, C); Macoma balthica (L.) (Text-fig. 5 A).
Semelidae: Scrobicularia plana (da Costa) (= piperata).
Asaphidae: Gari fervensis (Gmelin) (= ferroensis).
Donacidae: Donax vittatus (da Costa).
Mactridae: Spisula elliptica (Brown).
Lutrariidae: Lutraria lutraria (L.) (= elliptica) (Text-fig. 5 G).
Myidae: Mya (see Wallengren, 1905).

Veneridae: Venus casina L. (Text-fig. 5 D), Venus striatula (da Costa) (= gallina), Paphia decussata (L.).



TEXT-FIG. 6.

Lateral ciliated cell pattern in A, Astarte sulcata (Astartidae); B, Aetheria elliptica (Aetheriidae); C, Anodonta (Unionidae), after Engelmann, 1880. A (*a*), arrangement of nuclei of lateral cells of Astarte sulcata. These are not the actual nuclei of the cells figured in A. The frontal edge of the tract is on the right of the figure. A and B × 980.

Cardiidae: Cardium crassum Gmelin (= norvegicum).

Erodonidae: Aloidis (= Corbula) gibba (Olivi) (Text-fig. 5 E).

Solenidae: Ensis siliqua (L.) (Text-fig. 5 F), Solen marginatus Montagu, Cultellus pellucidus (Pennant).

Solecurtidae: Solecurtus scopula (Turton) (= candidus), Solecurtus chamasolen (da Costa) (= antiquatus).

Hiatellidae: Hiatella gallicana (Lamarck) (= rugosa).

Pholadidae: Barnea parva (Pennant), Xylophaga dorsalis Turton.

Teredinidae: Teredo navalis L. (Text-fig. 4 A).

Lyonsiidae: Lyonsia norwegica (Gmelin) (Text-fig. 5 H)

In Astarte sulcata (Text-fig. 6 A) the four rows of lateral cells form a very different type of pattern from that just described. The narrow cells are extremely long, those of some rows reaching 28μ, with nuclei about 23μ long. It is interesting to contrast these cells and nuclei with those of Teredo navalis (Text-fig. 4 A).

There is not a great deal of difference in the patterns of the lateral ciliated cells of Aetheria elliptica (Aetheriidae) (Text-fig. 6 B) and of Anodonta (Unionidae) (Text-fig. 6 C), two of the Naiadacea. In Anodonta, judging from Engelmann's figure (1880, Pl. V, fig. 2), reproduced in part as Text-fig. 6 C, the second row from the frontal side is somewhat wider than the outer on the abfrontal side, while in Aetheria (Text-fig. 6 B) the reverse obtains. The arrangement of the elongated cells of Aetheria elliptica is surprisingly like that of the marine Astarte sulcata, but is almost certainly due to accidental convergence.

Trigonia margaritacea (Trigoniidae) has four cell rows of more or less the same width, so far as can be determined from alcohol preserved material: the cells are elongated.

Discussion.

It is interesting that in the most primitive order of Lamellibranchs, the Protobranchia, the cells of the lateral ciliated epithelium have for the most part no definite shape or arrangement, their ends being pointed and interdigitating. A single row of elongated, almost rectangular cells placed end to end is present on the abfrontal side of the tract, though in Solenomya togata—in which the gills are larger and more important as food collectors than in Nucula and Nuculana minuta,

which are chiefly deposit feeders—there is a tendency for other cells to assume this shape and arrangement. In the higher Lamellibranchs there is an orderly arrangement of the cells, all being more or less rhomboidal in shape at the surface and arranged end to end in definite rows. Possibly this orderly arrangement of the lateral cells allows of the more efficient working of the ciliary mechanism, than does that of the Protobranchs. It is noteworthy that in all the patterns described some, or all, of the cells are elongated in the direction of the length of the filaments, and still more important in the direction of travel of the metachronal wave.

In the Protobranchs the lateral ciliated tracts are wide, 18 to 22μ in Nuculana minuta, about 26μ in Nucula radiata, and about 30μ in Solenomya togata. Wide tracts are probably primitive, for they have been depicted in transverse sections of the filaments and leaflets of certain Gastropods (Pelseneer, 1891, Pl. XXIII; Woodward, 1901, Pl. 14, fig. 18; Orton, 1912, fig. 5; Crofts, 1929, Text-fig. 10, p. 48). In the higher Lamellibranchs not only are the lateral ciliated cells arranged in an orderly manner, but there is a tendency to reduction in width of the tract, and this is especially evident in the group possessing micro-latero-frontal cilia: in Lima hians the tract is little more than 4μ wide. The greatest width observed in a higher Lamellibranch was about 19μ in the Eulamellibranch Phacoides borealis, while Scrobicularia plana comes very near this with a width of 16 to 18μ.

The variation in the pattern of the lateral ciliated cells in the various families of the group having micro-latero-frontal cilia (see Atkins, Part VII), is in marked contrast with the constancy of the general type of pattern found in the Eulamellibranchs, with the exception of Astarte, Anodonta, and Aetheria. The lateral ciliated tracts in the former group are altogether finer than in the latter, being distinctly narrower and composed of smaller cells—the width of the tract and the size of the component cells does not appear to be primarily dependent on the size of the filament. I do not think that it follows, however, that the inhalent current necessarily is less strong in consequence; in fact the current set up by the lateral cilia in

the Anomiidae seems particularly violent, owing probably to the rapidity of their beat.

The extraordinary constancy of the general pattern found in members of twenty-two families of Eulamellibranchs is curious, and seems to point to their close relationship. Some ciliary structures of the gills are obviously adaptive, being correlated with certain habits and habitats (see Atkins, 1937), but the lateral cilia of the gill filaments are found in all Lamellibranchs and many Gastropods independently of these. Though the lateral cilia are such important members of the ciliary feeding complex, the exact and detailed arrangement of the cells bearing them would seem to have doubtful utility, and where the same pattern is found in different families would seem to indicate their close relationship. The disposition of the lateral ciliated cells is evidently a stable character in Eulamellibranchs, but a variable one in the group of Lamellibranchs with micro-latero-frontal cilia.

Eulamellibranchs with a similar arrangement of the lateral cells, namely a row of large cells, with one row of narrow ones to the frontal side, and two to the abfrontal side, are found both in Douvillé's (1912 *a*, p. 466) 'normal' and 'burrowing' branches. To discover whether the same pattern occurs in all the families of these two lines, or is even common to all the members of a family, will need the examination of many more species; in most families it has been possible to examine only one member.

Summary.

The pattern of the lateral ciliated cells of the gill filaments has been examined in a number of Lamellibranchs and figures given. In the Protobranchia the lateral ciliated cells, except for a row on the abfrontal side, have no definite shape or arrangement; in the higher Lamellibranchs there is an orderly arrangement of the approximately rhomboidal cells in rows. The arrangement of the cells in any species appears to be constant. In the group possessing micro-latero-frontal cilia the variation in the pattern of the lateral ciliated cells in the various families is in marked contrast with the constancy of the general type of pattern found in the majority of the Eulamellibranchs.

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DAPHNE ATKINS, B.Sc.

On the Ciliary Mechanisms and Interrelationships of Lamellibranchs

Part VII. Latero-frontal Cilia of the Gill Filaments and their Phylogenetic Value

Quarterly Journal of Microscopical Science
Vol. 80, Part III, May, 1938

Printed in Great Britain

On the Ciliary Mechanisms and Interrelationships of Lamellibranchs.

PART VII: Latero-frontal Cilia of the Gill Filaments and their Phylogenetic Value.

By

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Marine Biological Laboratory, Plymouth.

With Plate 29, and 12 Text-figures.

CONTENTS.

INTRODUCTION.

THE value of ciliary structures in the classification of the Lamellibranchia must depend largely on a knowledge of their form and of their distribution in the class of animals under consideration, and to some extent of their function. Some ciliary mechanisms, such as tracts of cirrus-like frontal cilia on the gills are obviously adaptive, being correlated with certain habitats and modes of life, namely sand dwelling and rock and wood boring (Atkins, 1937). The presence of fan-shaped groups of long cilia—guarding cilia—along the marginal food grooves of the gills also seems to be adaptive, being correlated with a certain amount of mud or silt in the soil (Atkins, 1937). Such adaptive ciliary structures may have little or no taxonomic value.[1] Those instanced are not restricted to closely related forms, and in a family one member may possess and one lack them.

Certain tracts of cilia[2] forming an essential part of the ciliary

[1] It is not implied that because a character is useful and adaptive it cannot serve in classification, but that among the Lamellibranchia, which appear to be very adaptable, adaptive characters must be used with caution.

[2] The terms frontal, latero-frontal, and lateral, which have been applied to the three tracts of food-collecting cilia on the gill filaments (see Ridewood, 1903, p. 163) are descriptive of the position these cilia occupy in the great majority of Lamellibranchs, but they have come to denote cilia with certain characteristics, especially as to function, and are therefore applied in instances where they are not descriptive of position, at least in preserved material, and in some instances most probably on the living gill. For example, the frontal cilia may extend well round on to the lateral faces of the filaments, and the latero-frontal cilia may be clearly lateral in position as in Nuculana minuta (Text-fig. 8) and Trigonia margaritacea (Text-fig. 1 c).

feeding complex, though independent of habit and habitat, are so universally present on the gills, with little or no modification of their form, that these again are useless in classification. Such are the lateral cilia of the gills, which create the inhalent current, found in all Protobranchia, Filibranchia, Pseudolamellibranchia, Eulamellibranchia, and even on the few filaments forming the branchial sieve in Poromya among Septibranchia, as well as in certain aspidobranch and pectinibranch Gastropods: analogous tracts of cilia occur in several groups of ciliary feeders outside the Mollusca. The mere presence of such cilia therefore has no classificatory value, but the arrangement or pattern of the cells bearing them may be of generic, and family, and possibly of wider, value; for instance, the same type of cell-pattern is characteristic of a large number of eulamellibranch families (Atkins, 1938*a*).

The frontal, food conveying, cilia of the gills are also an essential element in the feeding complex, and too widely present to be of value in classification. Modification of these cilia seems to be largely in relation to habitat (Atkins, 1937). But the modification in which adjacent antagonistic tracts of frontal cilia on the same gill filament occur on all lamellae, is found chiefly in one group of Lamellibranchs, 'the Aviculidae and their allies', but is not entirely restricted to this group—it is found also in the Solenidae (Atkins, 1936)—and is not found in all its members, for instance not in Pinna (Atkins, 1937).

The latero-frontal cilia of the gills form an additional part of the ciliary feeding complex, but, apparently, are not absolutely essential, as are the lateral (current producing) and frontal (food conveying) cilia, for they have been described only in Lamellibranchs, not in Gastropods; nor have analogous cilia been described in ciliary feeders outside the Mollusca. They are straining cilia, preventing the unimpeded passage of particles between the gill filaments to the supra-branchial chamber. They thus contribute to the efficiency of the method of feeding, preventing the escape and wastage of perhaps desirable food particles, but would not seem to be indispensable.

Two chief types of latero-frontal tracts have been found to exist, the one efficient, composed of a row of large, with also

a second row of small latero-frontal cilia, on each side of the frontal surface; the other apparently rather inefficient, composed of one row only of tenuous and small latero-frontal cilia on each side. The types are unconnected with habits or habitats. The distribution of the second type among Lamellibranchs is not irregular, but is distinctive of a particular group. It may seem ridiculous to consider that the composition of a certain tract of gill cilia can be of value in determining genetic affinity, but the fact remains, that without any preconceived ideas, and setting out merely with the intention of spending odd minutes noting what proportion of Lamellibranchs had large latero-frontal cilia, and what proportion had small ones—or, as was at first thought, were without them—it was gradually realized that the occurrence of only small latero-frontal cilia is characteristic of members of a group 'the Aviculidae and their allies' or the 'sedentary' branch of Lamellibranchs established by palaeontologists (Jackson, 1890; Douvillé, 1912*a*) mainly, or entirely, on shell characters. One desideratum of a character for use in determining phylogeny, namely conservatism, seems to be possessed by the latero-frontal ciliated tracts, for, so far as the present work has gone, there appears to be little variation within the two types, and they therefore afford an important and reliable character for purposes of broad classification.

In addition to the acknowledgements already made in Part I of the series, I wish to thank Professor A. Morley Davies for criticizing the present paper from the palaeontological viewpoint, and to renew my thanks to Professor J. H. Orton for most helpful general criticism of this paper in particular. Professor E. S. Goodrich has not only edited it, but has made suggestions for which I am much indebted to him.

Material and Methods.

The great bulk of the material used for this, as for the other papers of the series, was brought in by S. S. Salpa of the Marine Biological Association of Plymouth. Living specimens of Nuculana minuta and Musculus discors were obtained from Millport Marine Station by purchase, as were also living specimens of Petricola pholadiformis from Whit-

stable, and Bouin-Duboscq-preserved specimens of Pteria hirundo, Spondylus gaederopus, Anomia ephippium, Solenomya togata, and Nuculana pella from the Zoological Station of Naples.

My thanks are due to a number of zoologists who have most kindly furnished me with valuable material: to Dr. B. Prashad of the Indian Museum, Calcutta, for alcohol-preserved specimens of Amussium pleuronectes, Pinctada vulgaris, Pinctada margaritifera, Malleus albus, Isognomon isognomon var. canina, and Arca (Scaphula) celox; to Mr. G. C. Robson of the British Museum for fragments of the gills of Trigonia margaritacea, Placuna placenta (?), Vulsella sp., Isognomon alata, Aetheria elliptica, and Mülleria dalli; to Mr. A. G. Lowndes for living specimens of Anodonta anatina and Sphaerium corneum; to Mr. C. Oldham for living Dreissensia polymorpha; to Mr. G. A. Steven for a formalin-preserved specimen of Chlamys vitrea; and to Professor C. M. Yonge for Bouin-preserved specimens of Spondylus sp. from the Great Barrier Reef.

I am indebted to Professor J. H. Orton for the loan of Sir W. A. Herdman's slides of the gills of Pinctada vulgaris and Placuna placenta from Liverpool University, and to Mr. H. H. Bloomer and Mr. G. C. Robson for the loan of slides of the gills of Mutela bourguignati.

The form of the latero-frontal cilia of the gills is discoverable most rapidly and reliably from the examination of living material, and this was done whenever possible. When preserved material only was available, entire filaments were examined unstained in alcohol, or formalin, with a drop or two of glycerine added, and the results obtained verified by the examination of stained sections.

Material was fixed in Bouin-Duboscq's fluid (see Atkins, 1937 *b*, p. 424). Sections were cut 5μ or 6μ thick. The stains chiefly employed were Heidenhain's iron haematoxylin, either alone or counter stained with acid fuchsin, and Mallory's triple stain.

All drawings, except Text-figure 2 c, were made with the aid of a camera lucida.

A. THE LATERO-FRONTAL CILIATED TRACTS OF THE GILL FILAMENTS.

The Occurrence of Large or Eu-latero-frontal Cilia, together with Subsidiary or Pro-latero-frontal Cilia.

It has been known for a number of years that some Lamellibranchs have large latero-frontal cilia (*eu-l-f.c.*, Text-fig. 1), or cilia of the corner cells, on the gills (Peck, 1877; Engelmann, 1880; Janssens, 1893, &c.), though some of the earlier workers did not discern the direction of their effective beat or discover their function. These cilia are large, cirrus-like, and impossible to overlook, and, as described by Orton (1914), have 'the appearance of flexible combs working along the sides of the filaments'. They are present on each side of the tract of frontal cilia and 'stand out from the sides of the filaments, forming a sort of grating between them, and lash relatively slowly across the length and towards the middle of the frontal face of the filament' (Orton, 1912). The latero-frontal cilia are straining cilia, and throw particles on to the frontal face of the filament whence they are transported by the frontal cilia.

The structure and movement of these large cilia have been investigated by numerous workers (Engelmann, 1880; Janssens, 1893; Wallengren, 1905, I; Gray, 1922, 1928; Carter, 1924; Grave and Schmitt, 1925; Bhatia, 1926).

Carter's (1924) account is the most detailed. He investigated

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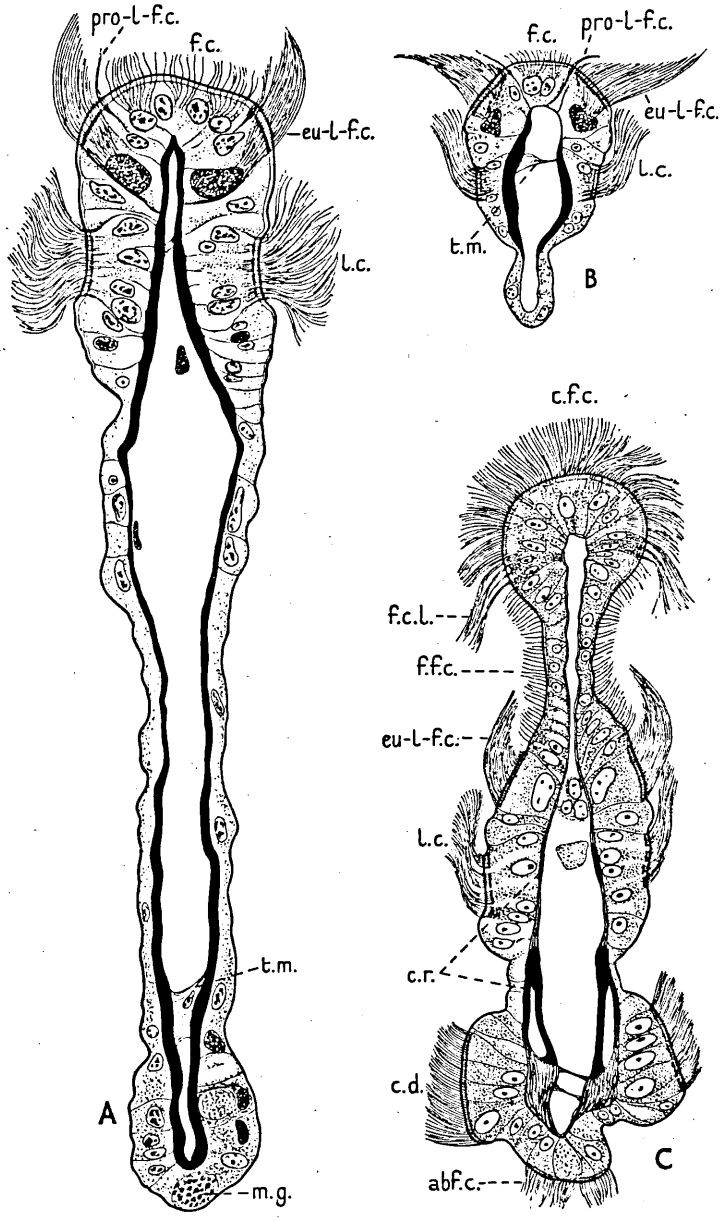
Transverse sections of filaments of marine Lamellibranchs having eu-latero-frontal cilia. A, Modiolus modiolus; B, Kellia suborbicularis; C, Trigonia margaritacea. Fig. 1 C was composed from several sections. *abf.c.*, abfrontal cilia; *c.d.*, ciliated disc; *c.f.c.*, coarse frontal cilia; *c.r.*, calcified rods; *eu-l-f.c.*, eu-latero-frontal cilium; *f.c.*, frontal cilia; *f.c.l.*, long frontal cilia borne on three or four rows of long cells; *f.f.c.*, fine frontal cilia; *l.c.*, lateral cilia; *m.g.*, mucous gland; *pro-l-f.c.*, pro-latero-frontal cilium; *t.m.*, transverse muscle-fibre. The chitinous skeleton is shown in black, except in Trigonia margaritacea where it is shaded and the calcified rods shown in black. A and B Bouin-Duboscq's fixative; C, alcohol fixation; A–C, iron haematoxylin and acid fuchsin. ×735. For this, and other figures of gill filaments, sections have been chosen which were as free as possible of mucous glands, as these interfere with the orderly arrangement of the ciliated cells.



TEXT-FIG. 1.

[*For description see previous page.*]

these large, complex cilia by means of the micro-dissection needle and found that though they appear homogeneous when living, they are composed of a series of triangular plates (10 to 15 in Mytilus galloprovincialis) set one behind the other in the plane of the beat, with the shorter in front (Text-fig. 2 c, a, b, p. 355), that is on the side which is directed forward in the effective stroke (Text-fig. 2 c, c). These plates together form a blade-shaped compound cilium with the flat side of the blade in the plane of the beat (Text-fig. 2 c). When the cilium dies, or on fixation, the plates forming the cilium break up, and there is left a double row of fibres (individual cilia) formed by their edges. Below each fibre lies a basal granule; there is therefore a double row of granules below each latero-frontal cilium.

A ciliary structure of this complexity cannot rightly be called a cilium, but as the term latero-frontal cilium is well established in the literature it is retained here.

Gray (1928, p. 18) has described how the latero-frontal cilium is perfectly straight when at rest and that 'movement occurs by a flexure which begins at the tip and passes down to the base thereby bending the cilium into a hook-shaped structure', while 'during recovery the process is reversed for the cilium straightens from the base to the tip' (Text-fig. 2 c, c.).

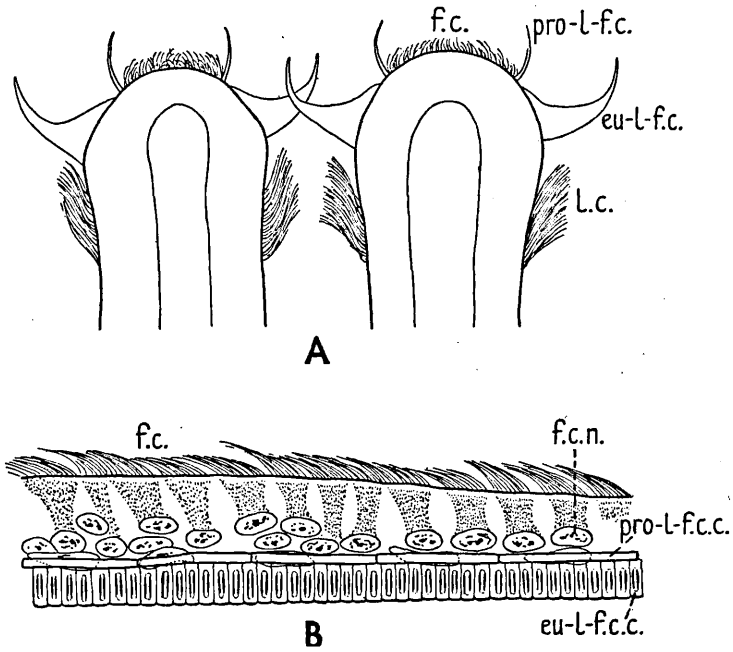
In Lamellibranchs with large latero-frontal cilia there is, in addition, along the frontal side of these, a row of cilia which may be considered either as specialized frontals, or, perhaps more correctly, as a second row of small or subsidiary latero-frontal cilia (*pro-l-f.c.*, Text-figs. 1, 2 A). They are difficult to observe, being over-shadowed by the large ones, but it has been determined that they are in a single row, and that the beat is toward the frontal surface—as is that of the latero-frontal cilia—though somewhat obliquely in the direction of beat of the frontal cilia. They are more closely set than the large cilia, and are borne a number on a cell. The cells which bear them are narrow and elongated in the direction of length of the filament. In Ensis siliqua one cell covers the same length as do about eight large latero-frontal cells (Text-fig. 2 B); in Anodonta as six or seven, and in Cyclas cornea (=Sphaerium corneum) as about ten (see Engelmann, 1880, Pl. V, figs, 2, 4). The number of

these subsidiary latero-frontal cilia to a cell could not be determined, but, as they are more closely set than the large ones, there would be more than eight, six or seven, and ten respectively to a cell, and possibly double or more than these numbers, in Ensis siliqua, Anodonta, and Sphaerium corneum.

The presence of these cilia was first observed in transverse sections of the gill filaments of Modiolus modiolus (Text-fig. 1 A), when the appearance was assumed to be due to slight obliquity of the sections, so that part of a second large latero-frontal cell was cut. The appearance was so consistently present, however, that the correctness of this interpretation seemed highly doubtful. Careful examination of living filaments revealed the presence of a row of cilia, stouter than the frontal cilia, with certain of the characteristics of the latero-frontal cilia. These cilia have been found generally in bivalves with eu-latero-frontal cilia, including Mytilus edulis. They are more clearly discernible in some gills than in others, according largely to the transparency of the gill. For instance they were seen more clearly in the living gill of Kellia suborbicularis than perhaps in any other, except Thyasira flexuosa, though they are not particularly clear in sections of that gill (Text-fig. 1 B). In Lamellibranchs in which the outer demibranch is without a marginal groove, and the filaments are merely bent round, the various ciliary tracts are seen in profile at the bend, and the subsidiary latero-frontal cilia may occasionally be clearly seen. They are extraordinarily clear along the free edge of the outer demibranch of Thyasira flexuosa (Text-fig. 2 A, *pro-l-f.c.*). These cilia are distinguishable from the frontal cilia in successfully stained transverse sections of well-fixed material (fixed in Bouin-Duboscq's fluid: stained Heidenhain's iron haematoxylin) because they are stouter and stain more darkly, and by their darker staining ciliary rootlets. The nuclei of the cells are narrow and elongated in the direction of the length of the filament, and in cross-section appear small. They have no greater affinity for basic dyes than have the oval nuclei of the frontal cells.

So far as I am aware the only reference to these ciliated cells

is in a footnote in Engelmann's paper of 1880 (p. 511)—of which I was ignorant until after their discovery—in which he stated:

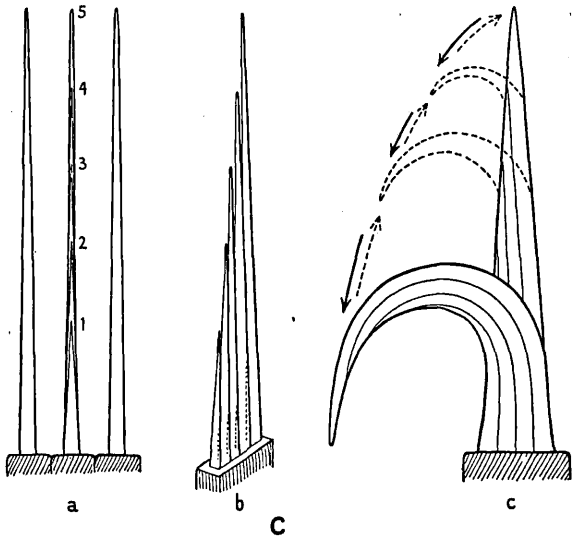


TEXT-FIG. 2 A and B.

A, Thyasira flexuosa. Two living filaments in optical section at the free edge of the outer demibranch, to show the pro-latero-frontal cilia (*pro-l-f.c.*). The frontal cilia (*f.c.*) were beating toward the observer, and therefore are not seen at their full length. *eu-l-f.c.*, eu-latero-frontal cilium. *l.c.*, lateral cilia. ×537½. B, Ensis siliqua. Sketch to show the shape of the pro-latero-frontal cells (*pro-l-f.c.c.*). *eu-l-f.c.c.*, eu-latero-frontal cell; *f.c.*, frontal cilia; *f.c.n.*, nucleus of frontal ciliated cell. The double rows of basal granules of the eu-latero-frontal cilia are shown. Bouin-Duboscq's fixative: iron haematoxylin and acid fuchsin. ×918¾. See p. 355 for Text-fig. 2 C.

'Zwischen den Eckzellen und den gewöhnlichen Flimmerzellen des Rückens ist noch eine, bisher wie es scheint übersehene, Lage sehr schmaler, in der Längsrichtung der Leistchen langgestreckter Flimmerzellen eingeschaltet. Sie mögen Neben-

zellen heissen. Ihr eigenthümlicher Bau stimmt wesentlich mit dem der "Seitenzellen" überein. Speciell ist die Anordung und Einpflanzung der Cilien auf der Oberfläche bei beiden die näm-



C

TEXT-FIG. 2 C.

Diagrams illustrating the structure and movement of the composite eu-latero-frontal cilia, represented as being each composed of five plates only. (*a*) Frontal view of three cilia: plates are indicated in the middle one. (*b*) Oblique view of one cilium. (*c*) Cilium in side view to show the type of movement (after Gray, fig. 12 b, 1928, somewhat modified). The cilium is straight when at rest. The plain arrows indicate the direction of the effective stroke; the broken arrows the direction of the recovery stroke.

liche.' He figured these cells in Anodonta and Cyclas cornea.

No observations on the arrangement of the basal granules of these cells have been made for the present work, but from the living gill the cilia appear to be in a single row, and to resemble the large latero-frontal cilia in this, and the direction of the effective beat, position of rest and type of metachronal wave, rather than the lateral cilia, which they were said to do by

Engelmann. The subsidiary latero-frontal and the lateral cilia do agree, however, in being borne on narrow cells, elongated in the direction of length of the filament. The subsidiary latero-frontal cilia probably act as a second sieve, preventing the escape of small particles between the bases of the eu-latero-frontal cilia.

It is possible that Janssens (1893, p. 66) saw something of these cells in sections, for describing the latero-frontal cells of Anodonta anatina he wrote: 'Sur les coupes, on croit souvent avoir sous les yeux la section de deux rangées de cellules, Fig. 15 en bas, mais c'est une apparence produite par l'obliquité de la section ou d'autres causes.'

Thus many Lamellibranchs may be considered as possessing two rows of latero-frontal cilia on each side of the frontal surface, a row of very large and another of small or subsidiary latero-frontal cilia. The large ones may be termed eu-latero-frontal cilia, and the subsidiary ones pro-latero-frontal cilia.

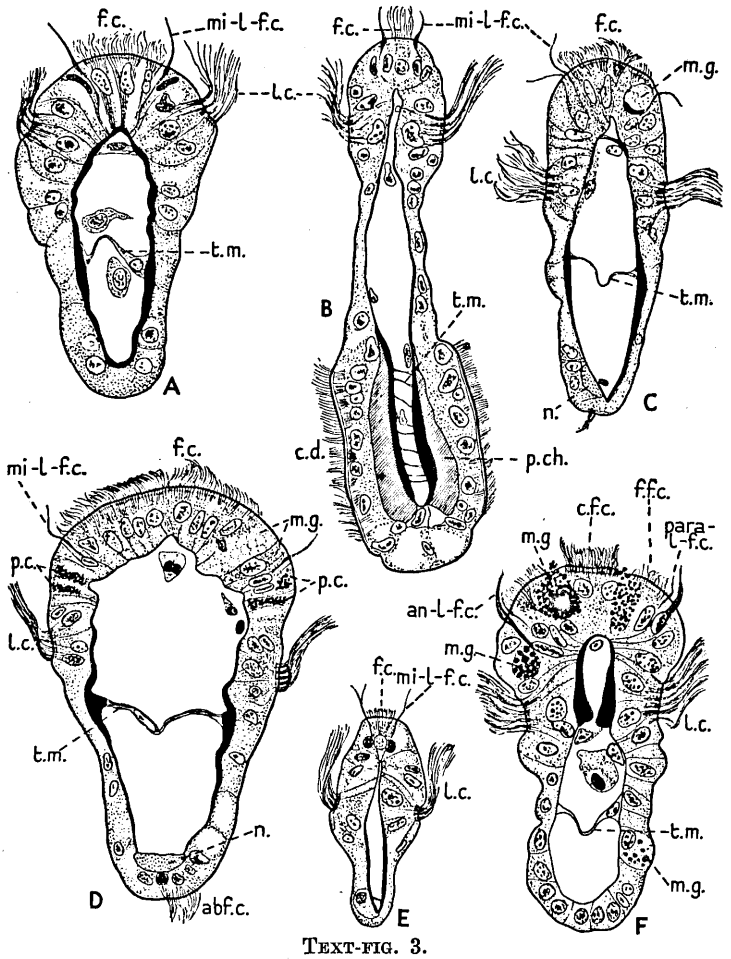
In Nuculana and Nucula the nuclei in a row on the frontal side of the eu-latero-frontal cells are long and narrow—in the direction of length of the leaflets—indicating the presence of a row of long, narrow cells, such as bear the pro-latero-frontal cilia in higher Lamellibranchs, but it is extremely difficult to identify with certainty pro-latero-frontal cilia on the living leaflets of Protobranchs, owing to the thickness of the leaflets. The closeness to one another of the eu-latero-frontal cilia (about 1μ or less apart) and in Nuculana the position of the latero-frontal tracts, well down on the lateral faces of the filaments (see Text-fig. 8, p. 373), add to the difficulty. A renewed and careful attempt at the definite identification of pro-latero-frontal cilia in Nucula nucleus was made in April 1937, and it was finally concluded that there is a regular row of cilia on the frontal side of the eu-latero-frontal cilia, corresponding to the pro-latero-frontal cilia of the higher groups, and that these cilia are most probably pro-latero-frontals. Their position of rest, however, could not be observed, and this was unfortunate, as latero-frontal cilia of whatever kind, and frontal cilia, differ in their attitude when brought to rest, latero-frontal cilia being

straight, while frontal cilia are curved. Pro-latero-frontal cilia have not been labelled in Text-figs. 7 (p. 372) and 8 (p. 373), which are reproductions from Part I (1936), but may be discerned in the sections of Nucula and Nuculana, though not in those of Solenomya of which the fixation was not particularly good. In Nucula a pro-latero-frontal cell covers about the same length as do four or five eu-latero-frontal cells.

The Occurrence of only Small or Micro-latero-frontal Cilia.

Eu-latero-frontal cilia, such as described in the preceding pages, are absent in certain families of Lamellibranchs, which are characterized by the possession of small and tenuous latero-frontal cilia. Small cilia of this kind may be termed micro-latero-frontal cilia (*mi-l-f.c.*, Text-fig. 3 A–E). Such families have been generally considered as lacking latero-frontal cilia, with the exception of the Anomiidae in which they were observed by Orton (1914), though in his paper he does not distinguish between their size in this family and in Mytilus, for instance. In his note-book of 1912—which he kindly allowed me to see—he noted, however, that 'the straining cilia of Anomia aculeata Müller (=Heteranomia squamula (L.)) are extremely fine'.

Latero-frontal cilia have generally been considered absent in the following bivalves: Glycymeris and Arca (Orton, 1914); Pecten (Kellogg, 1892; Janssens, 1893; Dakin, 1909; Orton, 1914; Setna, 1930; Gutsell, 1931); Lima (Studnitz, 1931); Pinna (Atrina) rigida (Grave, 1911) and Pinctada (=Margaritifera) vulgaris (Herdman, 1905). In the work of several of these authors, however, the absence of latero-frontal cilia is inferred, as they are not mentioned, or not shown in the figures, but Janssens—who gave beautiful and detailed figures of the gill structure of a number of Lamellibranchs—definitely stated that 'dans les diverses espèces de Pecten que nous avons eues à l'étude, nous n'avons jamais pu découvrir les cellules des coins', and Gutsell that 'the elongate latero-frontal cilia described for Mytilus, Ostrea, and



TEXT-FIG. 3.

Transverse sections of filaments of Lamellibranchs having micro-latero-frontal cilia, and of Ostrea edulis having anomalous together with para-latero-frontal cilia. A, Arca (Scaphula) celox; B, Malleus albus; C, Pecten maximus (one of the apical filaments); D, Spondylus gaederopus (one of the two apical filaments); E, Lima hians (ordinary filament, third from principal); F, Ostrea edulis (ordinary filament, fifth from prinicpal). *abf.c.*, abfrontal cilia; *an-l-f.c.*, anomalous latero-frontal cilium; *c.d.*, ciliated disc; *c.f.c.*, coarse frontal cilia;

[*For remaining description see opposite.*]

various lamellibranchs have not been found in the scallop (Pecten irradians), nor have I succeeded in demonstrating that the most lateral of the frontal cilia (in a latero-frontal position) function as would typical latero-frontal cilia'.

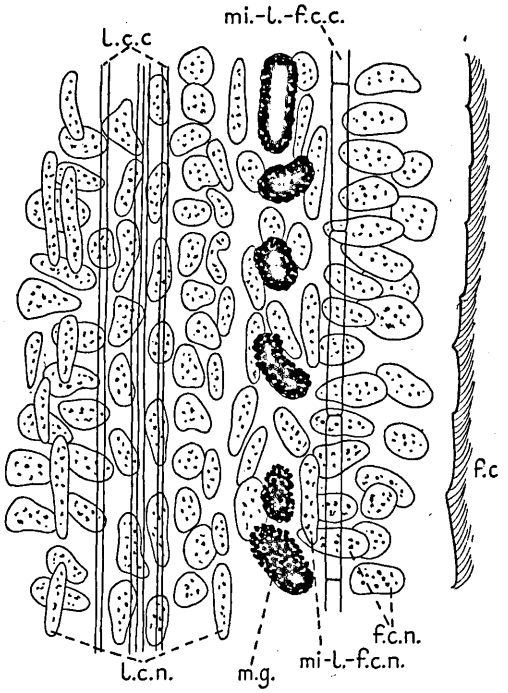
Curiously enough Pelseneer (1891) depicted large latero-frontal cilia in his figures of Anomia ephippium, Pectunculus (=Glycymeris) glycymeris, Arca barbata, Pecten opercularis, and Lima hians, and indeed showed them as large as in a figure of Modiolaria (=Musculus) marmoratus for instance. Hornell (1909) also figured and described large latero-frontal cilia in Placuna placenta. In Sir W. A. Herdman's slides of Placuna I find the latero-frontal cilia to be small as in Anomia (Atkins, 1936). Bourne (1907) did not show or mention latero-frontal cilia or cells in Anomia (Aenigma) aenigmatica.

In the living gill the micro-latero-frontal cilia when more or less motionless appear as a fine palisade viewed from the frontal surface. In Glycymeris glycymeris and Arca tetragona they are about 14 to 17μ long; in Heteranomia and Monia about 12μ long. Measurements of the width and breadth at the base were not made, but the cilia are very slender. In lateral view of the filament they appear as a row of shining dots, no doubt owing to bending during the stroke.

Certain details of the form of the micro-latero-frontal cilia, and the cells bearing them, have been gathered from entire filaments and from sections, which were not, however, cut for this purpose.

In the Arcidae it has been found that the cells (*mi-l-f.c.c.*, Text-fig. 4) bearing the micro-latero-frontal cilia are narrow, elongated in the direction of length of the filament, and with long narrow nuclei (*mi-l-f.c.n.*). In Glycymeris glycy-

f.c., frontal cilia; *f.f.c.*, fine frontal cilia; *l.c.*, lateral cilia; *m.g.*, mucous gland; *mi-l-f.c.*, micro-latero-frontal cilium; *n.*, nerve; *p.c.*, pigment cells; *p.ch.*, pale-staining chitin; *para-l-f.c.*, para-latero-frontal cilium; *t.m.*, transverse muscle-fibre. The chitinous skeleton is shown in black. A, B, alcohol fixation; C–F, Bouin-Duboscq's fixative; A–F, iron haematoxylin and acid fuchsin. ×735. Transverse sections of gill filaments of the Arcidae, Anomiidae, and Pteriidae have already been given (Atkins, 1936).



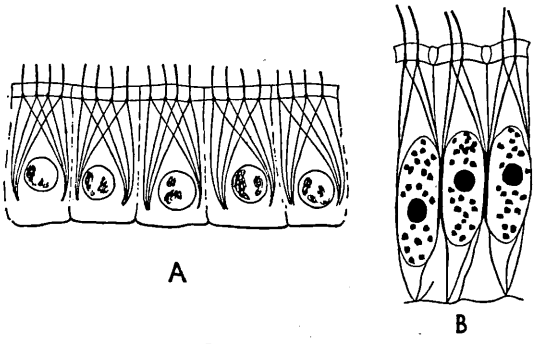
TEXT-FIG. 4.

Glycymeris glycymeris. Lateral surface of part of a filament to show the shape of the micro-latero-frontal cells (*mi-l-f.c.c.*). The lateral ciliated cell rows (*l.c.c.*) are also shown, though individual cells are not indicated. As the lateral ciliated cells are considerably larger basally than peripherally, it will be observed that the rows of nuclei do not lie directly beneath the rows of cells—as these appear at the surface—to which they belong. *f.c.*, frontal cilia; *f.c.n.*, nuclei of frontal ciliated cells; *l.c.n.*, nuclei of lateral ciliated cells; *m.g.*, mucous gland; *mi-l-f.c.n.*, nucleus of micro-latero-frontal cell. Two per cent. osmic acid only. × 980.

meris there are roughly about eighteen cilia to a cell: ciliary rootlets were not seen in longitudinal sections of the filaments in this species, nor in Arca tetragona, but were seen in transverse sections.

In Pecten the number of micro-latero-frontal cilia to a cell could not be determined.

In Pinna fragilis there are four small latero-frontal cilia to a cell (Text-fig. 5 A): these will be termed provisionally micro-latero-frontal cilia, though there is some doubt as to their homology, owing to the possibility of there being a second row of latero-frontal cilia present (see p. 363). Each cilium, or more



TEXT-FIG. 5.

A, Pinna fragilis. Section, nearly sagittal, through the latero-frontal epithelium. Bouin-Duboscq's fixative; iron haematoxylin. ×1,470. B, Mytilus edulis. Sagittal section through the latero-frontal epithelium. Fleming without acetic, iron haematoxylin, counterstained with orange G and silver nitrate. $\frac{1}{12}$ objective and No. 18 (Zeiss) eye-piece. B, after Bhatia, 1926.

probably each of the fibres of the cilium, has two rootlets, or rhizoplasts, which diverge widely from a basal granule to pass on opposite sides of the nucleus. The rootlets of the four cilia cross one another, except the outer ones of the two outer cilia. A similar disposition of the rootlets is found in the cells of eu-latero-frontal cilia, for example in Mytilus, where the two rootlets of the fibres forming the sides of a triangular plate of the large complex cilium pass on opposite sides of the nucleus, the two inner ones crossing each other (Text-fig. 5 B). According to Lucas (1931) the ciliary rootlets extend to the nuclear zone only, and not to the base of the cell, as described by Bhatia (1926). Apparently two of the micro-latero-frontal cilia of Pinna fragilis correspond to a single large complex latero-frontal cilium, of Mytilus for instance. In Pinna fragilis, however, the four cilia of each cell are entirely separate, and not

connected, as are the two fibres forming the sides of a triangular plate of the large complex cilium of the majority of Lamellibranchs. It is not impossible, though I think it unlikely, that each cilium of Pinna may consist of two rows of fibres side by side as in eu-latero-frontal cilia, but so close together that at a magnification of 1,470 diameters two sets of ciliary rootlets could not be distinguished.

The anomalous latero-frontal cilia of Ostrea (see p. 365) could be derived from micro-latero-frontal cilia as seen in Pinna by division of the cell; in such a hypothetical division two sets of basal granules with their rootlets would pass into one cell, and the other two sets of basal granules with their rootlets into the other. The two cilia of each cell might then approach each other and finally their fibres become connected by membranes. Possibly eu-latero-frontal cilia may have arisen either in this way from cilia of the micro-latero-frontal type, or as fully formed eu-latero-frontals.

The intra-cellular fibre system of epithelial cells may serve a function of co-ordination, as suggested by Worley (1934), but it is noteworthy that there is a similar complicated arrangement of the ciliary rootlets of the eu-latero-frontal cilia (e.g. in Mytilus) where the ciliary fibres linked up by these rootlets must beat synchronously—for they form the edges of a triangular element—and of the micro-latero-frontal cilia of Pinna, where the four separate cilia of a cell linked up in a similar manner probably beat metachronously. Unfortunately the beating and metachronism of the latero-frontal cilia of Pinna were not especially noticed owing to the difficulty of observing them in this form. If in Pinna the cilia on individual cells should be found to beat metachronously, then it would seem possible that the arrangement of ciliary rootlets may not be related to the type of unicellular co-ordination. Under the influence of certain drugs the metachronous beating of the cilia of individual epithelial cells may change to synchronous, but this is attributed to the harmful effect of the drugs on the regulatory mechanism, the cilia becoming uncontrolled and usually beating simultaneously due to their mechanical effect upon each other (Worley, 1934).

Although cilia with a structure closely comparable to that of

eu-latero-frontal cilia are known, for instance the velar cilia of the Nudibranch veliger, where each cilium consists of about fifteen plates and there are two, three, four, and sometimes more such complex cilia to a cell (Carter, 1926), and the very long abfrontal cilia or cirri of Mytilus, each consisting of four or five plates in Mytilus galloprovincialis (Carter, 1924), it is not known whether they have a similar arrangement of the ciliary rootlets, or if the arrangement described above is peculiar to cilia with a straining function. Carter (1928) held that a ciliary rootlet is not a definitely differentiated portion of the cytoplasm, and doubted the existence of such fibres in the latero-frontal cells of Mytilus and in those of the velar cells of Nudibranch veligers.

In thin transverse sections of the filaments of Pinna fragilis there is occasionally an appearance as of two latero-frontal cilia on each side of the filament. This may be due to slight obliquity of the sections. In most bivalves an examination of the living gill is the best way in which to settle such a question, but the living gill of Pinna is extremely difficult to deal with owing to its deep plications, organic junctions, and above all, extreme sensitiveness, the slightest stimulation causing it to contract to a contorted mass of filaments. If two rows should prove to be present, then the arrangement of the ciliary rootlets in the latero-frontal cells of Pinna as compared with that in the Ostreidae (see p. 365) is all the more interesting. It is possible, however, that diverging ciliary rootlets from an entire cilium, passing on opposite sides of the nucleus as in Pinna, or from a ciliary fibre of a triangular element as in Mytilus, may be linked up in some way with a special type of behaviour, and so are likely to be found in all cells the cilia of which have this characteristic. It is therefore perhaps not impossible that all types of straining cilia will be found to have diverging rootlets.

In Malleus albus each latero-frontal cilium has a short row of basal granules, rather less than 1μ long, in the plane of the beat; this indicates that the cilia are slightly blade-shaped, that is, they are wider in the plane of the beat than in the plane perpendicular to it. The material from which the sections were

cut had been preserved in alcohol, and probably because of the resulting poor fixation the ciliary rootlets could not be distinguished in longitudinal sections through the latero-frontal epithelium. There appeared to be about four cilia to a cell, but this could not be definitely determined. The width of these cilia at the base—unusual for micro-latero-frontals—suggests that there is just a possibility, as in Pinna fragilis, of two rows of latero-frontal cilia, though a second row was not discernible in sections, and in the state of preservation this was hardly to be expected.

The latero-frontal cilia themselves are less close together in Pinna fragilis and Malleus albus than in Glycymeris and Arca, and are fewer to a cell, and somewhat larger. Owing to the possibility of there being two rows of latero-frontal cilia in Pinna fragilis and Malleus albus details of the structure of the latero-frontal cilia in these two species have been omitted from Table I, p. 370.

Lucas (1931) noted for Mytilus edulis and Amblema costata that in fixed and stained preparations the nucleus of the eu-latero-frontal cells has a stronger affinity for basic dyes than have the nuclei of other cells of the gill. This was found to be so in most of the gills sectioned for the present work, but not invariably. In most bivalves with micro-latero-frontal cells there seems to be little, if any, difference in affinity for basic dyes between the nuclei of these cells and others, but the Indian fresh- and brackish-water form, Arca (Scaphula) celox, is an apparent exception in which the nuclei in cross-section are narrow and stain darkly (Text-fig. 3 A). The micro-latero-frontal cilia in this species of Arca (museum material preserved in alcohol) showed more clearly than in well-fixed material of other forms.

Lamellibranchs with micro-latero-frontal cilia, with the possible exception of Pinna, appear to be without a subsidiary row, such as is present in bivalves with eu- and in those with anomalous latero-frontal cilia.

Micro-latero-frontal cilia have been found to possess certain of the characteristics of eu-latero-frontal cilia, namely:

(1) their arrangement in a single, regular row;

(2) the direction of the effective beat, which is toward the frontal surface;
(3) their position of rest;
(4) the same type of metachronal wave. The metachronal wave was especially noted in the Arcidae, Anomiidae, and Pectinidae.

They differ from them, however, in their (*a*) smaller size, especially in the width and breadth at the base; (*b*) apparently simpler structure, being probably composed of fibres and not of triangular plates; and (*c*) in that more than one is borne on a cell, while there is only a single eu-latero-frontal cilium to a cell.

Micro-latero-frontal cilia agree closely with the pro-latero-frontal cilia of bivalves possessing eu-latero-frontal cilia (see Table I, p. 370): they may be actively straining cilia, or may perhaps act merely as a guard to prevent loss of food particles from the frontal tract.

The Occurrence of Moderate-sized or Anomalous Latero-frontal Cilia, together with Subsidiary or Para-latero-frontal Cilia in one family only, the Ostreidae.

In one family, the Ostreidae, the latero-frontal cilia of the main row are only moderately developed, especially as to their size at the base, and may be termed anomalous latero-frontal cilia (*an-l-f.c.*, Text-fig. 3 F, p. 358). They are however about 14 to 25μ long.

The cells from which these cilia arise are small and bear one cilium each, as may be seen when the cells are becoming dissociated under the influence of the narcotic stovaine. These cilia appear to have the same structure, and the same arrangement of their ciliary rootlets as in Mytilus, but, while being blade-shaped, they are much less wide at the base in the plane of the beat (roughly about $1\frac{1}{4}\mu$), than those of Mytilus galloprovincialis (4–5μ, see Carter, 1924) and other bivalves having eu-latero-frontal cilia (see *eu-l-f.c.*, Text-fig. 1, p. 351, and *an-l-f.c.*, Text-fig. 3 F). The effective beat is in the same direction and the position of rest is the same as that of the

other forms of latero-frontal cilia, and the metachronal wave is of the same type.

The eu-latero-frontal cilia of bivalves are characteristically, closely, and evenly spaced; those of Ensis siliqua for example are about 2μ apart, those of Nucula nucleus about 1μ apart. In Ostrea edulis, Ostrea virginica, and Ostrea angulata it has been found that the length of the anomalous latero-frontal cilia and their distance apart varies on different filaments. They are longest and closest together on the principal and transitional filaments, and shortest and farthest apart on the filaments forming the plical crests. Frequently they are closer together on that side of the transitional filament next to the principal than on the side away from it. In Ostrea edulis and Ostrea virginica the distance apart of these cilia varies between about 1·5 to 3·7μ, while on the filaments of the plical crests of Ostrea angulata they are about 6 or 7μ apart.[1] In the genus Ostrea the frontal currents on the principal and transitional filaments are dorsal in direction, and particles intended for consumption are mainly carried along these. That the latero-frontal cilia, which are straining cilia preventing particles from being swept through to the exhalent chamber, should be longer and closer together on these filaments than on those forming the plical crests, which are concerned chiefly with rejection (Atkins, 1937), is indicative of functional correlation.

While the anomalous latero-frontal cilia of Ostrea are easily seen in fresh material, they are difficult to distinguish in sections

[1] An interesting instance of wider spacing of eu-latero-frontal cilia on one side of a filament than on the other was observed over stretches of the filaments of Petricola pholadiformis, due to the presence of a protozoon 35 to 80μ long, adhering by the whole length of its body parallel to the filament in the region between the lateral and latero-frontal cilia, and suppressing some of the latero-frontal cilia, so that they were about twice as widely spaced as normally; while in some places they were entirely wanting for short stretches. The parasites, which were very numerous, were frequently attached along one side only of a filament, the opposite side where the latero-frontal cilia were normally spaced being free from them. This parasite though allied to the Ciliata appeared, in the stage seen, to be without cilia.

(see also Yonge, 1926): this is no doubt owing to the fact that under the action of fixatives they tend to separate into their constituent fibres, and, as the cilia are only of moderate size, the tufts of fibres are not very noticeable. They were found to retain their form better in sections of material fixed in 2 per cent. osmic acid than in Bouin-Duboscq's fluid.

Subsidiary latero-frontal cilia are present in the Ostreidae, but are very difficult to distinguish even in the living gill. They are possibly somewhat smaller than those of bivalves possessing eu-latero-frontal cilia; however, the gills are rather opaque and the cilia therefore difficult to observe even in a preparation of a single lamella. Apart from the organic junctions, the presence of numerous blood cells in the lacunae of the demibranch tends to make it opaque, especially when these are greenish.

As will be seen from the second half of this paper (p. 383), it is probable that the anomalous latero-frontal cilia of the Ostreidae are not homologous with eu-latero-frontal cilia, and as the homology of the subsidiary latero-frontal cilia of this family with the pro-latero-frontal cilia of forms possessing eu-latero-frontals is doubtful, it is proposed to call them para-latero-frontal cilia. In Text-fig. 1 of Part II (1937), therefore, these cilia should have been labelled *para-l-f.c.* and not *pro-l-f.c.* Para-latero-frontal cilia have been omitted from Table I, p. 370, for, from the little that is known of them, they appear to agree in structure and arrangement with pro- and micro-latero-frontal cilia.

To summarize: anomalous latero-frontal cilia agree with eu-latero-frontal cilia in being borne singly on small cells, of which the greater diameter is at right angles to the length of the filament; in having, so far as is known, a similar structure and a similar arrangement of their ciliary rootlets; and in the direction of the effective beat, position of rest, and type of metachronal wave. They also agree in being accompanied by subsidiary latero-frontal cilia.

They differ from eu-latero-frontal cilia, however, in their smaller size, especially as to the width at the base in the plane of the beat, inconspicuousness in sections, and marked variation in length and spacing on different filaments of the same individual.

Lamellibranchs with Eu-latero-frontal Cilia.

In 1891 Pelseneer depicted large latero-frontal cilia in all thirteen of the lamellibranch gills he figured in his 'Contribution à l'étude des Lamellibranches', including those of five species, Anomia ephippium, Pectunculus (=Glycymeris) glycymeris, Arca barbata, Pecten opercularis, and Lima hians in which large ones are undoubtedly absent. Kellogg (1892) soon after stated that they were absent in Solenomya velum and Pecten irradians—in the first instance almost certainly incorrectly—and expressed the opinion that latero-frontal cilia are 'not so widely found among Lamellibranchs, I believe, as seems to be so generally supposed'. Ridewood (1903), in the course of his extensive work on the gills of Lamellibranchs, found them to occur in the great majority (his remarks on these cilia are based presumably on preserved material only), and this has been borne out in the present work, mostly on living gills. As late as 1930, however, Nicol referred to species possessing latero-frontal cilia—that is eu-latero-frontals—as 'aberrant Lamellibranchs'.

During the course of the present work, large or eu-latero-frontal cilia were found in members of the three families of Protobranchia (they were previously recorded by Orton, 1912, 1914, in Nucula and Solenomya togata); in all the marine families of Eulamellibranchia obtainable at Plymouth, and in the fresh-water families Dreissensiidae, Sphaeriidae, Unionidae, Mutelidae, and Aetheriidae. In the Filibranchia they were found in the Mytilidae and Trigoniidae only. They were absent in all the Pseudolamellibranchia examined. A list of the species of Lamellibranchia found to have eu-latero-frontal cilia is given on p. 374. Pro-latero-frontal cilia are perhaps always present also, though they have not always been recognized owing to difficulties of observation or imperfect preservation of material.

A visual impression is that there is little or no direct correlation between the size of the bivalve, gill, or filament, and that of the eu-latero-frontal cilia. There is no great difference in the size of these cilia in Modiolus modiolus, which may reach

a length of 11 cm. or more, and in Kellia suborbicularis, of which the largest specimen seen was about 1 cm. long. The depth of a filament, from the frontal to the abfrontal surface, of Modiolus modiolus is more than four times that of one of Kellia suborbicularis, while the frontal surface is about three times wider, antero-posteriorly, as shown in Text-fig. 1 A and B (p. 351).

While a certain amount of variation in the size of eu-latero-frontal cilia is found when actual measurements are taken, there is no possibility of confounding them with micro-latero-frontal cilia. (A provisional comparison of the different types of latero-frontal cilia is given in Table I.)

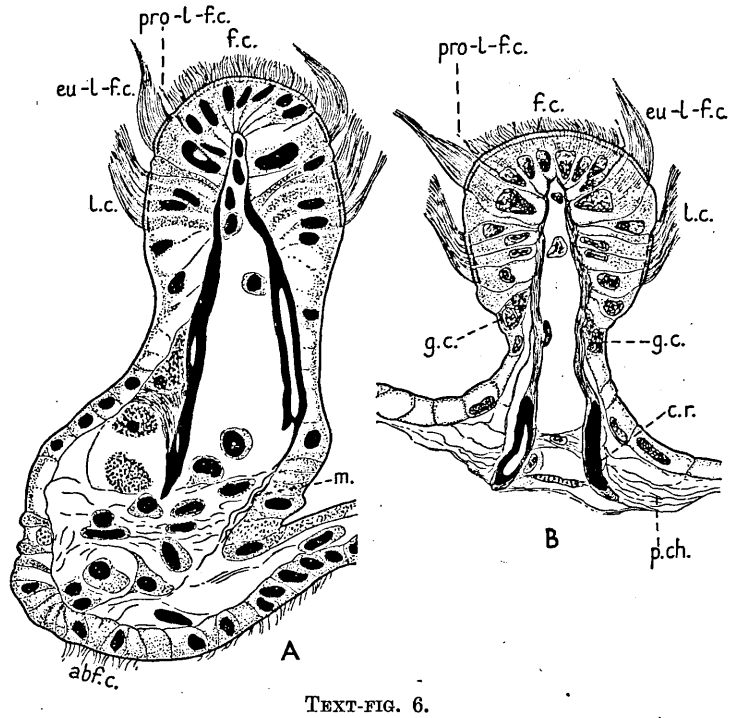
Among fresh-water forms, Lampsilis and Quadrula are stated by Grave and Schmitt (1925) to have latero-frontal cilia which often exceed 15μ in length, and are about 1 to 1½μ in diameter at the base. While this is unusually small for eu-latero-frontal cilia, the size at the base is sufficient to prevent their being confounded with micro-latero-frontal cilia. Measurements were made of these cilia in a few fresh-water forms during the present investigation. Dreissensia polymorpha was found to have eu-latero-frontal cilia about 24μ long, and roughly about 9μ wide at the base in the plane of the beat, measured living. Those of Aetheria elliptica are about 27μ long (measured from preserved entire filaments), though they appear somewhat less than this in transverse section (Text-fig. 6 A), and are about 6 or 7μ wide at the base in the plane of the beat (measured from sections); those of Mutela bourguignati (Text-fig. 6 B), judging from sections, are about 20μ long, and about 6μ wide. Measurements made on sections, however, are unreliable, as apart from the occurrence of shrinkage, the entire length of the cilium may not be cut.

Among marine forms Carter (1924) gave their length in living Mytilus galloprovincialis as about 30μ, and at the base ¾ to 1μ broad in the plane perpendicular to the beat, and 4 to 5μ wide in the plane of the beat. The only measurements I have made of eu-latero-frontal cilia of marine forms were in Gastrochaena dubia, in which these cilia are roughly about 26μ long and 6 to 8μ wide at the base in the plane of the beat

TABLE I. *Provisional Comparison of Types of Latero-frontal Cilia.*

	Eu-latero-frontal Cilia.	*Anomalous latero-frontal Cilia.*	*Micro-latero-frontal Cilia.**	*Pro-latero-frontal Cilia.**
Cells.	Small: longer diameter at right angles to length of filament.	As eu-latero-frontal cilia.	Long, narrow: elongated in the same direction as filament.	As micro-latero-frontal cilia.
Number of cilia to a cell.	1	As eu-latero-frontal cilia.	More than 1: about 18 in Glycymeris glycymeris.	A number to each cell (see p. 352).
Structure of cilium.	Composed of a number of triangular plates (10–15 in Mytilus according to Carter, 1924), bounded by fibres on each side of the cilium. Surface of plates at right angles to plane of beat: plates shorter on side of cilium which is directed forward in effective beat. At the base the cilium is considerably wider in the plane of the beat than at right angles to it, so is characteristically broadly triangular in side view.	Probably as eu-latero-frontal cilia, though they are not as large.	Probably no plates, but each cilium composed of a few fibres, probably placed one behind the other in the plane of the beat, so that the cilium is slightly wider in this plane, than in that at right angles to it.	Probably no plates, but each cilium composed of a few fibres, probably placed one behind the other in the plane of the beat. The difference in the width and breadth at the base is slight.
Basal granules.	Each plate associated with a pair, so that in surface view of the cell there is a double row of basal granules at right angles to the length of the filament.	Probably as eu-latero-frontal cilia.	The arrangement was not observed.	The arrangement was not observed.
Ciliary rootlets.	Two diverge from each basal granule, and pass on opposite sides of the nucleus, there being two pairs to each plate.	Probably as eu-latero-frontal cilia.	The arrangement was not observed.	The arrangement was not observed.
Length of cilium.	About 20–30 μ (Lampsilis and Quadrula often exceed 15 μ).	14–25 μ.	About 12 μ in Heteranomia and Monia: 14–17 μ in Glycymeris and Arca.	About 10 μ in Modiolus modiolus, and 6 μ in Kellia suborbicularis (measured from sections).
Width of cilium at base in the plane of the beat.	About 4–9 μ, excluding those of Lampsilis and Quadrula which are said to be 1–1½ μ in diameter, and of Xylophaga which are about 2 μ wide.	Roughly about 1½ μ, measured from sections.	Not measured, but probably not much greater than at right angles to the plane of the beat.	Not measured, but probably not much greater than at right angles to the plane of the beat.

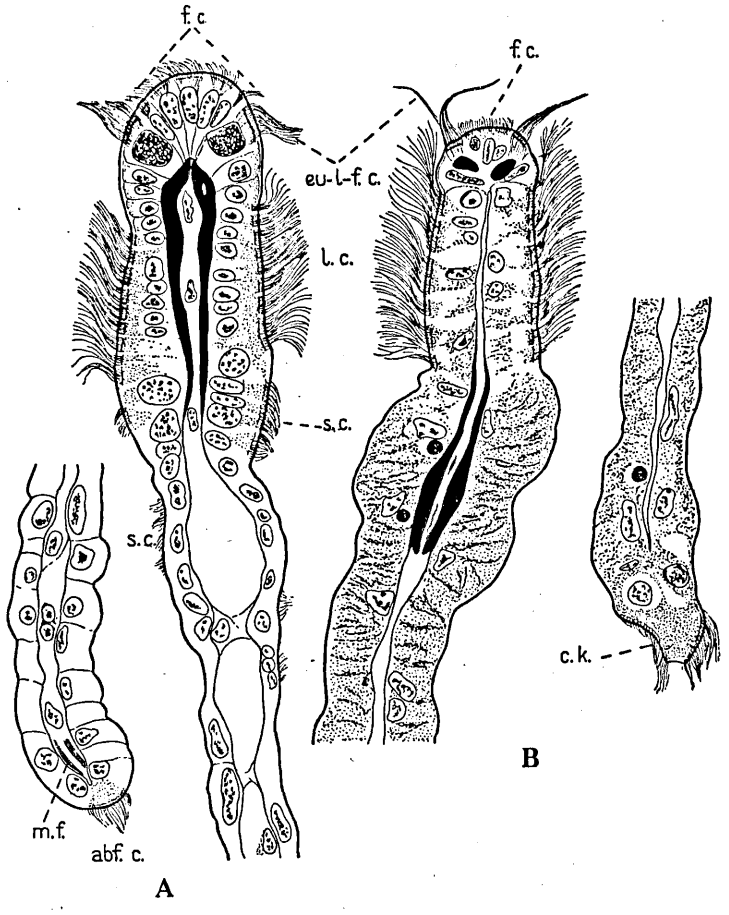
* Para-latero-frontal cilia appear to agree with micro- and pro-latero-frontal cilia in the little that is known of them.



TEXT-FIG. 6.

Transverse sections of the filaments of two fresh-water Lamellibranchs, having eu-latero-frontal cilia. A, Aetheria elliptica; B, Mutela bourguignati (inner demibranch). *abf.c.*, abfrontal cilia; *c.r.*, calcified rod; *eu-l-f.c.*, eu-latero-frontal cilium; *f.c.*, frontal cilia; *g.c.*, gland-cell; *l.c.*, lateral cilia; *m.*, muscle-fibres; *p.ch.*, pale-staining fibrous chitin; *pro-l-f.c.*, pro-latero-frontal cilium (?). The chitinous skeleton is shown in black in Aetheria, but in Mutela it is shaded and the calcified rods shown in black. Alcohol fixation; iron haematoxylin and acid fuchsin. Owing to the condition of fixation pro-latero-frontal cilia could not be identified with certainty. ×735.

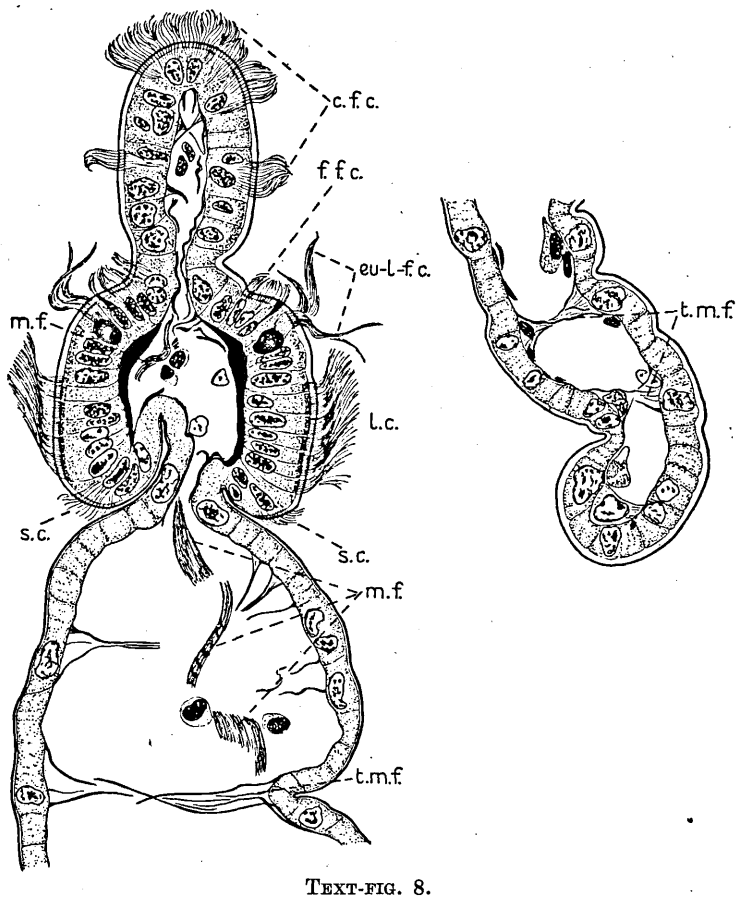
(measured living), and in Xylophaga dorsalis, in which they are roughly 20μ long and only 2μ wide at the base in the plane of the beat (measured from sections). This narrowness of the eu-latero-frontal cilia in Xylophaga is not found in the allied Barnea parva, and seems exceptional among marine forms.



TEXT-FIG. 7.

Transverse sections of the gill leaflets of two Protobranchs. A, Nucula; B, Solenomya togata. *abf.c.*, abfrontal cilia; *c.k.*, ciliated knob, or glandular organ; *eu-l-f.c.*, eu-latero-frontal cilia; *f.c.*, frontal cilia; *l.c.*, lateral cilia; *m.f.*, muscle-fibres; *s.c.*, slight ciliation dorsal to the lateral cilia. Bouin-Duboscq's fixative; iron haematoxylin. ×735.

In the Protobranchia there is a certain amount of variation in the shape of the eu-latero-frontal cilia. In Nucula they are



TEXT-FIG. 8.

Transverse section of a gill leaflet of the Protobranch Nuculana minuta. The whole is not figured because of the great depth (frontal to abfrontal) of the leaflets. The involution of the walls near the lateral ciliated tracts is due to contraction of the muscles. *c.f.c.*, coarse, and *f.f.c.*, fine frontal cilia; *eu-l-f.c.*, eu-latero-frontal cilia; *l.c.*, lateral cilia; *m.f.*, radiating striated muscle-fibres; *s.c.*, slight ciliation dorsal to the lateral cilia; *t.m.f.*, transverse muscle-fibres. Bouin-Duboscq's fixative; iron haematoxylin. ×735.

rather short, but very broadly triangular in side view (Text-fig. 7 A); while in Nuculana minuta (Text-fig. 8) and

Solenomya togata (Text-fig. 7 B) they are longer, but less broadly triangular. In Nuculana minuta they are about 30μ long, and in Nucula nucleus about 20μ long, measured living.

What is especially characteristic of the size of eu-latero-frontal cilia, is not so much the length, which apparently may vary from 15 to 30μ at least, but their breadth at the base in a plane perpendicular to the beat, and more especially their relatively great width in the plane of the beat; this last dimension giving them their distinctively triangular shape in side view.

List of Lamellibranchs found[1] to have Eu-latero-frontal Cilia.

PROTOBRANCHIA.

Solenomyidae: Solenomya togata.[2]
Nuculidae: Nucula nucleus (L.), Nucula radiata Hanley, Nucula nitida Sowerby.
Nuculanidae: Nuculana (=Leda) minuta (Müller), Nuculana pella.[2]

FILIBRANCHIA.

Trigoniidae: Trigonia margaritacea.[2]
Mytilidae: Mytilus edulis L., Modiolus modiolus (L.), Modiolus adriaticus Lamarck, Modiolus phaseolinus (Philippi), Musculus (=Modiolaria) marmoratus (Forbes), Musculus (=Crenella) discors (L.).

EULAMELLIBRANCHIA.

Dreissensiidae: Dreissensia polymorpha (Pallas).
Astartidae: Astarte sulcata (da Costa).
Thyasiridae: Thyasira flexuosa (Montagu).
Lucinidae: Myrtea spinifera (Montagu), Phacoides borealis (L.).
Ungulinidae: Diplodonta rotundata (Montagu).

[1] The list is comprehensive, but does not include the examination of members of all families of Lamellibranchs.

[2] Preserved material only examined.

Erycinidae: Kellia suborbicularis (Montagu), Lasaea rubra (Montagu).
Galeommatidae: Galeomma turtoni Sowerby.
Leptonidae: Lepton squamosum (Montagu).
Montacutidae: Montacuta ferruginosa (Montagu), Mysella bidentata (Montagu), Entovalva perrieri (Malard).
Cyprinidae: Cyprina islandica (L.).[1]
Sphaeriidae: Sphaerium corneum (L.).
Unionidae: Anodonta anatina (L.).
Aetheriidae: Aetheria elliptica,[1] Mülleria daleyi.[1]
Mutelidae; Mutela bourguignati.[1]
Cardiidae: Cardium echinatum L., Cardium ovale Sowerby, Cardium edule L., Cardium crassum Gmelin (=norvegicum).
Veneridae: Dosinia exoleta (L.), Dosinia lupinus (L.), Gafrarium minimum (Montagu), Venus verrucosa L., Venus casina L., Venus ovata Pennant, Venus fasciata (da Costa), Venus striatula (da Costa), Paphia (=Tapes), rhomboides (Pennant), Paphia pullastra (Montagu), Paphia decussata (L.).
Petricolidae: Petricola pholadiformis Lamarck, Mysia undata (Pennant).
Donacidae: Donax vittatus (da Costa).
Tellinidae: Tellina tenuis da Costa, Tellina fabula Gmelin, Tellina donacina L., Tellina crassa Pennant, Macoma balthica (L.).
Semelidae: Scrobicularia plana (da Costa) (=piperata), Abra alba (S. Wood), Abra nitida (Müller).
Asaphidae: Gari fervensis (Gmelin) (=ferroensis), Gari tellinella (Lamarck).
Solenidae: Solen marginatus Montagu (=vagina), Ensis siliqua (L.), Ensis arcuatus (Jeffreys), Ensis ensis (L.), Cultellus pellucidus (Pennant).
Solecurtidae: Solecurtus scopula (Turton) (=candi-

[1] Preserved material only examined.

dus), Solecurtus chamasolen (da Costa) (=antiquatus).
Mactridae: Mactra corallina (L.), Spisula elliptica (Brown), Spisula solida (L.), Spisula subtruncata (da Costa).
Lutrariidae: Lutraria lutraria (L.) (=elliptica).
Myidae: Mya truncata L.
Erodonidae: Aloidis gibba (Olivi) (=Corbula nucleus).
Hiatellidae: Hiatella arctica (L.), Hiatella gallicana (Lamarck) (=rugosa).
Gastrochaenidae: Gastrochaena dubia (Pennant).
Pholadidae: Barnea candida (L.), Barnea parva (Pennant), Pholadidea loscombiana Turton, Xylophaga dorsalis Turton.
Teredinidae: Teredo navalis L.
Periplomatidae: Cochlodesma praetenue (Montagu).
Thraciidae: Thracia villosiuscula (Macgillivray), Thracia distorta (Montagu).
Lyonsiidae: Lyonsia norwegica (Gmelin).
Pandoridae: Pandora pinna (Montagu) (=obtusa).

Lamellibranchs with Micro-latero-frontal Cilia.

In Lamellibranchs in which micro-latero-frontal cilia occur, the frontal cilia frequently extend round on to the lateral faces of the filaments, and, therefore, the micro-latero-frontal cilia are actually lateral in position, thus increasing the difficulty of discerning these tenuous cilia when a filament is viewed from the side. A certain amount of shrinkage, however, occurs on fixation, so that in transverse section they are more or less latero-frontal in position (Text-fig. 3, p. 358).

In successfully stained transverse sections of well-fixed material the micro-latero-frontal cilia themselves can frequently be seen, and nearly always they can be distinguished from the frontal cilia by their more conspicuous basal granules and darker staining ciliary rootlets. But by far the best way to determine their presence is in the living gill. When living material was unobtainable, and where fixation was far from perfect, as in

alcohol-preserved museum specimens, it seemed justifiable to deduce the presence of micro-latero-frontal cilia when eu-latero-frontals were clearly absent. Entire filaments were examined unstained in alcohol, or formalin, with a drop or two of glycerine added, and the results obtained verified by sectioning. In entire filaments the presence of eu-latero-frontal cilia is generally easily determinable, unless the material is in very poor condition. The arrangement and size of the nuclei of the latero-frontal cells was also taken into consideration. When eu-latero-frontal cilia are present the row of large, closely set nuclei is conspicuous, and the absence of such a row was taken as confirmative evidence of the absence of eu-latero-frontal cilia. The nuclei of the micro-latero-frontal cells, which are elongated in the direction of length of the filament, and are widely spaced, are inconspicuous in the entire filament. It is not impossible that the presence of moderate-sized or anomalous latero-frontal cilia, as in Ostrea, might be overlooked, though the presence of a row of small, closely set nuclei, as in that genus, should be evident at least on wide principal filaments.

Micro-latero-frontal cilia are difficult to distinguish even in living gills until one has become accustomed to them, and it is understandable that their presence escaped workers restricted to preserved material. In 1931 on a first examination of Heteranomia squamula (L.) (=Anomia aculeata Müller) latero-frontal cilia were thought to be absent, and it was only in view of Orton's (1914, p. 299) published statement of their presence (his notebook in which they are described as 'extremely fine' had not then been seen, and was not until September 1932), that a careful search was made and they were discovered in a reduced form. The difference in size of the large latero-frontal cilia of many Lamellibranchs and the tenuous ones of Heteranomia was so striking, that it seemed possible that small ones had been overlooked in Pecten, and other species, by workers familiar with them in their fully developed form, and it was decided to examine the bivalves available, with the results given in this paper.

Micro-latero-frontal cilia would seem to be straining cilia, or at least to act as a guard to prevent loss of food particles from

the frontal tract, but their effectiveness as such is presumably less than that of the large ones, and very much less in Heteranomia and Monia (Atkins, 1936).

Micro-latero-frontal cilia have been found in the following families: Arcidae, Anomiidae, Pteriidae, Pectinidae, Spondylidae, Limidae, Pinnidae, and are inferred to be present in the Amussiidae (Atkins, 1938). They are also inferred to be present in the Isognomonidae and Vulsellidae (see p. 376). A list of species is given on p. 379.

The distribution in the Lamellibranchia of species having micro-latero-frontal cilia is of great interest. The form of these cilia does not appear to be correlated with habitat, for bivalves possessing them are adapted to a variety of environments. Some are shallow water forms; others have a wide vertical range. Some live in comparatively clear water; others in situations where sediment is liable to be heavy. A number are attached by a byssus, temporarily (Arca, Pinctada, Malleus, Isognomon, Pinna, and certain Pectinidae and Limidae to rocks and stones; Pteria to Eunicella), or permanently (Anomia, Heteranomia, and Monia); others are cemented to rock (Chlamys distorta, Spondylus, and Plicatula). Among these attached forms Pinna is perhaps alone in being able to burrow by means of a strong water-current (Grave, 1911). Placuna and Glycymeris are unattached. According to Hornell (1909) 'the bottom favoured by Placuna placenta is a fairly stiff or pasty greyish-black mud. On this the shells generally lie prone upon their convex left valves, the hinge region sometimes slightly sunk in the mud, which may lightly cover the dorsal third of the shell.' Glycymeris glycymeris burrows by means of its foot in sand and shell gravel, lying more or less hidden beneath the surface (Atkins, 1936). The two burrowing members of the group do not employ the same methods: the free living, circular valved Glycymeris burrows chiefly by means of its foot, though with the aid of a current expelled from the anterior region of the shell; the byssiferous, triangular shaped Pinna by means of a water-current expelled from the pointed anterior end of the shell (see Grave, 1911); this sharply pointed extremity is no doubt of assistance

in penetrating the mud and soft sand in which the animal lives. Many of the Pectinidae and Limidae, and the Amussiidae are free swimming; Lima hians is nidamentous. Vulsella lives embedded in sponges.

There thus appears to be no correlation between habitat or mode of life and the possession of micro-latero-frontal cilia, but, as will be seen later (p. 383), it is considered that these cilia indicate the genetic relationship of families possessing them.

List of Lamellibranchs found to have Micro-latero-frontal Cilia.

FILIBRANCHIA.

Arcidae: Arca tetragona Poli, Arca lactea L., Arca (Scaphula) celox Benson,[1] Glycymeris glycymeris (L.).

Anomiidae; Anomia ephippium L.,[1] Heteranomia squamula (L.), Monia patelliformis (L.), Monia squama (Gmelin), Placuna placenta.[1]

PSEUDOLAMELLIBRANCHIA.

Pteriidae: Pteria hirundo (L.) (=Avicula tarentina), Pinctada (=Margaritifera=Meleagrina) margaritifera (L.),[1] Pinctada vulgaris (Schumacher),[1] Malleus albus Lamarck[1] (see, however, p. 363).

Vulsellidae: Vulsella sp.[1] (most probably).

Isognomonidae: Isognomon alata[1] (most probably).

Pinnidae: Pinna fragilis Pennant (see, however, p. 361).

Pectinidae: Pecten maximus (L.), Chlamys distorta (da Costa) (=pusio), Chlamys vitrea (Gmelin),[1] Chlamys opercularis (L.), Chlamys tigerina (Müller).

Amussiidae: Amussium pleuronectes L.[1] (most probably).

Spondylidae: Spondylus gaederopus,[1] Spondylus sp.[1] (from Great Barrier Reef).

[1] Preserved material only examined.

Limidae: Lima hians (Gmelin), Lima loscombi Sowerby.

Lamellibranchs with Anomalous Latero-frontal Cilia.

Anomalous latero-frontal cilia, as previously mentioned, have been found in only one family of Lamellibranchs, the Ostreidae, which were placed by Pelseneer (1911) in the Pseudolamellibranchia. The species examined were Ostrea edulis L., Ostrea virginica Gmelin, and Ostrea angulata (Lamarck).

The Arrangement of the Various Ciliary Tracts on the Gill Filaments.

(*a*) In Lamellibranchs with Eu-latero-frontal Cilia.

The common arrangement of the various ciliary tracts of the gill filaments in bivalves with eu-latero-frontal cilia is that shown in transverse sections of Modiolus modiolus, Kellia suborbicularis (Text-fig. 1 A–B, p. 351), Mutela bourguignati and Aetheria elliptica (Text-fig. 6, p. 371). Abfrontal cilia may or may not be present (*abf.c.*, Text-fig. 6).

In two Protobranch families, Nuculidae and Solenomyidae, the arrangement is closely comparable, except that the tracts of lateral cilia are very wide, 26μ[1] in Nucula radiata and 30μ in Solenomya togata (Text-fig. 7 A–B, p. 372). A wide tract of lateral cilia is possibly primitive, for it is found in certain Gastropods, for instance in the Rhipidoglossae, Fissurella graeca L., Trochus cinerarius L. (Pelseneer, 1891), Pleurotomaria beyrichii (Woodward, 1901), and Haliotis tuberculata (Crofts, 1929), and in the Pectinibranch, Crepidula fornicata (Orton, 1912). In Nucula the unciliated tract between the lateral and eu-latero-frontal cilia is of some width; in Solenomya togata it is narrow, and the tips of the lateral cilia extend to the level of the frontal surface (Text-fig. 7 B). Kellogg (1892, Pl. XCI,

[1] Measured from sections parallel with the surface of the cells; in living filaments they are probably wider.

fig. 77) showed the lateral and frontal cilia as continuous in Solenomya, but this was corrected by Orton (1913).

In the Protobranch family Nuculanidae the lateral ciliated tracts, six or seven cells wide (measuring 18 to 22μ in sections of Nuculana minuta), are far from the frontal surface (*l.c.*, Text-fig. 8, p. 373), but owing to the great depth (frontal to abfrontal) of the leaflets, they are yet much closer to it than to the abfrontal surface. Close to the eu-latero-frontal cilia (*eu-l-f.c.*) is a tract of fine frontal cilia (*f.f.c.*): between these and the coarse frontal cilia (*c.f.c.*), the main tract of which is actually more or less on the frontal surface, is an unciliated region. A description of the ciliation of the gill leaflets of Nuculana minuta has already been given (Atkins, 1936).

The arrangement of the ciliated tracts in Trigonia margaritacea (Text-fig. 1 c, p. 351) is unlike that found in any other Filibranch or Eulamellibranch, resembling rather that in the Protobranch Nuculana minuta (Text-fig. 8), though with certain differences. It is not suggested, however, that there is any close relationship between Trigonia and Nuculana, which is a considerably specialized Protobranch (Atkins, 1936). The four rows of lateral cilia (*l.c.*) are far distant from the frontal surface, being in fact slightly nearer the abfrontal than the frontal surface (as in the Gastropod Crepidula (Orton, 1914)). Separated from the lateral cilia by one or two unciliated cells are the large latero-frontal cells, bearing large and long cilia (*eu-l-f.c.*). Both cells and cilia have the characteristic appearance found in numerous Lamellibranchs. Determination of the presence or absence of pro-latero-frontal cilia was impossible owing to poor fixation. The cilia clothing the frontal surface are remarkably long (*c.f.c.*); they are shown in the figure at about their full length, though they are generally cut short in sections. In a latero-frontal position are long cilia (*f.c.l.*), which, judging by their attitude in sections, beat mainly across the length of the filament, though it was impossible to determine the direction of the effective beat. From an examination of the entire filament it was seen that they are borne on three or four rows of long narrow cells, the cells being elongated in the direction of length of the filament. These cilia may

possibly send particles toward the frontal surface (that is if the effective beat should prove to be toward that surface), as do the scattered patches of coarse cilia in Nuculana minuta (Atkins, 1936); or (if the effective beat should prove to be abfrontal in direction) they are perhaps additional current producing, that is functionally lateral, cilia: an examination of living material is the best way to determine this. Between these cilia and the true latero-frontal cilia, the surface of the filament appears to be uniformly ciliated (*f.f.c.*), though it is impossible to be certain of this owing to the imperfect fixation. The cilia are finer, shorter, and not as closely set as those of the frontal surface. By analogy with certain other bivalves, it seems possible that the long, stout cilia of the frontal surface will be found to transport unwanted particles ventrally, while the fine ones, clothing the sides of the filaments between the coarse frontal and the latero-frontal cilia, will be found to convey particles which are destined to be eaten. The frontal currents on the gills of this species are likely to be of much interest.

Ridewood (1903, p. 202) stated that the frontal and lateral cilia of Trigonia lamarki are normal. Unless the arrangement of the ciliated tracts of the gill filaments differs widely in the two species, Trigonia margaritacea and Trigonia lamarki, he evidently included the true latero-frontal cilia (*eu-l-f.c.*, Text-fig. 1 c) with the lateral (*l.c.*), and assumed the long cilia in a latero-frontal position (*f.c.l.*) to be the true latero-frontal cilia. The arrangement of the cilia is so unusual that I have ventured to give a figure, although the material was preserved in alcohol for museum purposes and the fixation is imperfect. Examination of well-preserved material, and above all of the living gill is very desirable.

Pelseneer (1891, Pl. XIII, fig. 43) gave a figure of a transverse section of a filament of Trigonia pectinata in which no lateral cilia are labelled; it is possible that what he has named ciliated discs are the lateral, together with the latero-frontal, cilia. In Trigonia margaritacea, and also in Trigonia lamarki (see Ridewood, 1903), the ciliated discs are close to the interlamellar edge of the filament, and not as shown in Pelseneer's figure.

An interesting feature of the filaments of Trigonia margaritacea (alcohol preservation) is the presence of calcified rods (*c.r.*, Text-fig. 1 c), which were previously thought to occur only in Mülleria and the Unionidae (see p. 394).

In Xylophaga dorsalis the frontal cilia extend well round on to the lateral surfaces of the filaments, and the unciliated space between the latero-frontal and lateral cilia is rather wide. These peculiarities are not found in the allied Barnea parva.

(*b*) In Lamellibranchs with Micro-latero-frontal Cilia.

In these Lamellibranchs the arrangement of the various ciliary tracts appears to be more or less constant (see Text-fig. 3, A–E, p. 358), though the width of the frontal tract may vary, the cilia extending round on to the lateral faces; abfrontal cilia may, or may not, be present.

B. LATERO-FRONTAL CILIA AND PHYLOGENY.

Discussion on the Relationships of the Various Types of Latero-frontal Cilia.

From the work recorded in the foregoing pages it is now known that three variations of the latero-frontal tract of Lamellibranchs exist, namely: (1) eu-latero-frontal cilia, together with pro-latero-frontal cilia; (2) anomalous, together with para-latero-frontal cilia; and (3) micro-latero-frontal cilia. The second variation is known from one family only, the Ostreidae.

It is known that eu-latero-frontal and—though with less certainty—pro-latero-frontal cilia (see p. 356) are present in living Protobranchs, so that it is possible that the latero-frontal tract of the higher Lamellibranchs, with eu- and pro-latero-frontal cilia, may have been inherited from that order, and is not necessarily a new development. The presence of eu-latero-frontal cilia on gills, which, certainly in Nuculana and Nucula, are not used greatly in feeding, points to the antiquity of these cilia in the Protobranchia.

The relationship of the various types of latero-frontal cilia

is speculative whilst so little is known of the structure of the tenuous kinds of latero-frontal cilia (namely, the micro-, pro-, and para-latero-frontal cilia) and their cells: a detailed study of the histology of these was outside the scope of the present work, but a provisional comparison of the structure of the various types of latero-frontal cilia is given in Table I, p. 370. So far as is known the micro- and pro-latero-frontal cilia are closely comparable in structure; they are both of small size, are borne a number on a cell, and the cells and their nuclei are narrow and elongated in the direction of length of the filament. It is probable that these cilia are not composed of triangular plate-like elements, as are the eu-latero-frontal cilia of Mytilus and others, but of a few simple fibres. Whether, however, the micro- and pro-latero-frontal cilia are homologous, or only analogous, is not certain. The possibilities are that micro-latero-frontal cilia (*a*) are homologous with pro-latero-frontal cilia; (*b*) have given rise by specialization to eu- and to anomalous latero-frontal cilia; (*c*) are distinct structures, and so only analogous to pro-latero-frontal cilia; or (*d*) are reduced eu-latero-frontal cilia, though this is unlikely (see p. 387).

The anomalous latero-frontal cilia of the Ostreidae appear to be closely comparable in structure with eu-latero-frontal cilia, though of smaller size. They agree in that a single complex cilium arises from a cell, the cells are small, with the greater diameter at right angles to the length of the filament, and the arrangement of the ciliary rootlets appears to be similar in the two instances. However, it is extremely probable from a consideration of phylogenetic relationships, based on other characters (see p. 409), that the anomalous latero-frontal cilia of the Ostreidae are not homologous with eu-latero-frontal cilia, but that these cilia of similar structure have arisen independently in the Lamellibranchia, and that their similarity is due to convergence: one has not attained the size of the other.

In the Ostreidae not only are there anomalous but also para-latero-frontal cilia. It is therefore necessary to consider the origin of the two rows. One possibility is that micro-latero-frontal cilia, such as are found in other members of the group, have persisted as the para-latero-frontal cilia of the Ostreidae,

the anomalous arising as new structures not derived by modification from any pre-existing cilia. A second possibility is that the anomalous latero-frontal cilia have been derived from micro-latero-frontal cilia, perhaps by the approximation of these in pairs, and the formation of connecting membranes, the para-latero-frontal cilia being new structures, perhaps modified frontals. In this event there would have been progressive specialization of frontal cilia, the outermost of these being modified to form micro-latero-frontal cilia, and these again to form anomalous cilia, while a subsidiary row of latero-frontals (para-latero-frontal cilia) arose by modification of the now outer frontal cilia. An investigation into the composition of the latero-frontal tract in the Pteriacea to determine whether a second row of cilia is actually present in Pinna, and may be in other members of the sub-order, might throw light on the question.

It has already been shown how the anomalous cilia of Ostrea could have been derived from the type of cilia of the main row in Pinna (see p. 362), and if two rows should occur not only in Pinna, but in other members of the Pteriacea, it seems very possible that the anomalous latero-frontal cilia have originated in some such manner.

The appearance of latero-frontal cilia in the Lamellibranchia, whether evolved independently in the different lineages, or as modifications of one ancestral type must be considered. To the lateral and frontal cilia inherited probably from ancestors common to both Gastropods and Lamellibranchs (Pelseneer, 1891) have been added latero-frontal cilia. The latero-frontal tracts, however, are not all of the same type, and the possibilities are either that the variations have been derived from one original type, or that the various branches of Lamellibranchs have independently evolved the same straining device, that is, the same sort of latero-frontal cilia on each independent line of evolution. The evolutionary tendency has been directed in this event toward the attainment of complex cilia composed of triangular plates, namely eu- and anomalous latero-frontal cilia.

Four suggestions may be made: (*a*) The ancestral Lamellibranchs may have had a single row of micro-latero-frontal cilia

on each side of the frontal tract, probably arising by modification of the outer frontal cilia. This constitution of the straining apparatus persisted in most members of a branch represented to-day by the Arcidae, Anomiidae, and Pseudolamellibranchia, but in certain members there was an attempt at the production of a more efficient apparatus by the addition of larger cilia, possibly in Pinna, and certainly in the anomalous cilia of the Ostreidae, the highest, though by no means the most recent, member of the group. In another branch, or branches, the addition of large complex cilia to the original micro-latero-frontal tract took place early, such branch or branches being represented by the Protobranchia, Mytilidae, Trigoniidae, and Eulamellibranchia, in which the straining apparatus consists of a row of pro- (= micro ?) and a row of eu-latero-frontal cilia on each side of the frontal tract. There would thus have been parallel evolution of complex cilia, eu-latero-frontal cilia in one branch or branches, and anomalous in another. As suggested previously, when two rows are present, the micro-latero-frontal cilia may have persisted as para- and pro-latero-frontals (that is, all are homologous), the anomalous and eu-latero-frontal cilia being new structures, not derived from any pre-existing cilia; or the two rows may have arisen by progressive modification of the outer frontal cilia, in which case the eu- and anomalous latero-frontal cilia would have arisen by specialization of micro-latero-frontal cilia.

(*b*) Secondly, the micro-latero-frontal cilia type and the eu-, together with pro-latero-frontal cilia type, may have been independently evolved from forms in which no latero-frontal cilia were present, the micro- and pro-latero-frontals being analogous.

(*c*) Thirdly, the original type of latero-frontal tract may have been eu-, together with pro-latero-frontal cilia, this type persisting in the branch or branches represented by the Protobranchia, Mytilidae, Trigoniidae, and Eulamellibranchia. The loss of eu-latero-frontal cilia would then have to be postulated in the group represented by the Arcidae, Anomiidae, and Pseudolamellibranchia, with a fairly successful attempt at the regaining of complex cilia in the anomalous latero-frontal cilia

of the Ostreidae. This loss and then recovery of complex cilia is unlikely. If this has occurred then the micro- would be homologous with the pro-, but not necessarily with the para-latero-frontal cilia.

(*d*) Fourthly, the original type of tract may have been eu-latero-frontal cilia alone. To these pro-latero-frontal cilia were added in Protobranchia (probably), Mytilidae, Trigoniidae (possibly), and Eulamellibranchia. It would then be necessary to postulate the reduction of eu- to micro-latero-frontal cilia in the Arcidae, Anomiidae, and Pseudolamellibranchia, and either their enlargement to anomalous cilia with the addition of para-latero-frontal cilia in the Ostreidae, or the persistence of micro- as para-, and the addition of anomalous latero-frontal cilia.

Of these four possibilities (*c*) and (*d*) seem the most improbable.

The evolution of straining cilia has apparently occurred only in the Lamellibranchia, no other group of ciliary feeders, so far as is known, having acquired this refinement of the ciliary method of feeding.

Essential ciliated tracts of the food-collecting mechanism of the gills are the lateral, as current producing, and the frontal cilia, for conveying material, these being found in both Gastropods (Streptoneura) and Lamellibranchs: analogous tracts occur in several groups of ciliary feeders outside the Mollusca. The latero-frontal or straining cilia increase the efficiency of the ciliary method of feeding, but apparently are not essential. Latero-frontal cilia have not been described in any Gastropod, so that it may be taken for granted that eu-latero-frontals are absent. The only Gastropods that were examined for micro-latero-frontal cilia were the Pectinibranch Crepidula fornicata and the Rhipidoglossate Aspidobranch Calliostoma zizyphinum, and in these species I was unable to find them: Crepidula is a ciliary feeder (Orton, 1912), while Calliostoma possibly does not consume the material collected by the gills. Though this is very slight evidence indeed, it is perhaps safe to presume that latero-frontal cilia of any kind are absent in Gastropods, and that these ciliary structures have arisen in, and are characteristic of the Lamellibranchia. It is possible

that the appearance of these structures in the Lamellibranchia may be connected in some way with the loss of the radula; it is hoped to go into this in a later paper.

The Taxonomic Value of the Latero-frontal Ciliated Tracts.

Gill structure as a means of classification has been criticized in that it is liable to progressive modification, and thus reliance on it tends to produce 'horizontal' rather than 'vertical' divisions (Douvillé, 1912*a*; Davies, 1933). The composition of the latero-frontal ciliated tracts seems to be a more or less stable character, in fact, except for the Ostreidae, it was found that bivalves (117 species representing 51 families investigated) have one or other of two types, namely: (*a*) eu-, together with pro-latero-frontal cilia; or (*b*) micro-latero-frontal cilia alone. With the exception of the Ostreidae, no bivalve has been found in which the latero-frontal ciliated tracts cannot be easily determined to belong to one or other of these types. This character is therefore not open to the above-mentioned objection. But while the composition of the latero-frontal ciliated tracts may be used to separate a large group with micro-latero-frontal cilia from a much larger group with a row of eu- and a row of pro-latero-frontal cilia on each side of the frontal surface, it is useless, so far as my knowledge goes, for the determination of smaller divisions: this, however, may not prove to be so in the group characterized by the possession of micro-latero-frontal cilia when more is known of the structure of these cilia.

In the following discussion it is claimed, or assumed, that the character of the latero-frontal cilia affords a real clue to the broad affinities of bivalves, and offers a test of existing classifications.

Review of Pelseneer's and Ridewood's Classifications of the Lamellibranchia.

The two classifications of the Lamellibranchia best known to zoologists are perhaps those of Pelseneer (1906) and Ridewood (1903), based largely on gill structure; that of Pelseneer being the more widely accepted. Pelseneer, in 1911, returned

to his older classifications of 1889, 1891, and 1892 retaining the Order Pseudolamellibranchia, including the Aviculacea with the Pinnidae and Ostreidae, and the Pectinacea with the Limidae.

The two classifications are given briefly on p. 390, in relation to, and so far as they affect the present work. The composition of the latero-frontal ciliated tracts in the various families is indicated, so that it may be seen at a glance how the different types are dispersed through the sub-orders and orders of these classifications.

In Ridewood's classification, forms previously considered allied are widely separated, and dissimilar forms associated. He (p. 184), himself, stated that 'It is not claimed that the scheme of classification set forth in the following pages represents the genetic affinities of the forms included; but while disinclined to inflict upon a long-suffering world of zoologists a new classification of the Lamellibranchia in which I myself have no great confidence, I have, for reasons similar to those stated in a previous paper, arrived at the conclusion that, for purposes of ready reference, a key to the species examined based on the particular feature under consideration is not only justifiable, but even useful.'

Examining Ridewood's classification in some detail we find that in the Protobranchia the two families, Nuculidae (in which he included the Nuculanidae) and Solenomyidae, have eu-latero-frontal cilia, most probably also with pro-latero-frontal cilia at least in the Nuculidae (see p. 356).

His order Eleutherorhabda can be shown to be not less than diphyletic, some families possessing eu- together with pro-latero-frontal cilia, and others micro-latero-frontal cilia only. He defined the sub-orders as follows: Dimyacea; gill lamellae flat and homorhabdic, with no ascending filaments: Mytilacea; gill lamellae flat and homorhabdic, with ascending filaments: Pectinacea; gill lamellae plicate and heterorhabdic, with ascending filaments.

In the Dimyacea he placed Dimya argentea and Anomia aculeata (=Heteranomia squamula). Heteranomia has micro-latero-frontal cilia: whatever the form of the latero-frontal cilia of Dimya—which I have not had

Ridewood's and Pelseneer's Classifications of the Lamellibranchia.

Ridewood (1903).

Order 1. Protobranchia. Nuculidae,[2] Solenomyidae.[2]

Order 2. Eleutherorhabda.
Sub-order 1. Dimyacea: Dimya,[5] Anomia aculeata (= Heteranomia squamula).[4]
2. Mytilacea: Anomiidae (excluding Anomia aculeata),[4] Arcidae,[4] Trigoniidae,[1] Mytilidae,[1] Melinidae,[4] Amussiidae.[4]
3. Pectinacea: Spondylidae,[4] Pectinidae,[4] Aviculidae.[4]

Order 3. Synaptorhabda.
Sub-order 1. Ostreacea: Pinnidae,[4] Limidae,[4] Ostreidae.[3]
2. Submytilacea.[1]
3. Tellinacea.[1]
4. Veneracea.[1]
5. Cardiacea.[1]
6. Myacea.[1]
7. Pholadacea.[1]
8. Anatinacea.[1]
9. Poromyacea.[5]

Pelseneer (1906, modified 1911).

Order 1. Protobranchia. Solenomyidae,[2] Nuculidae,[2] Ledidae.[2]

Order 2. Filibranchia.
Sub-order 1. Anomiacea: Anomiidae.[4]
2. Arcacea: Arcidae,[4] Pectunculidae,[4] Philobryidae,[5] Trigoniidae.[1]
3. Mytilacea: Mytilidae.[1]
4. Dimyacea: Dimyidae.[5]

Order. 3. Pseudolamellibranchia.
Sub-order 1. Aviculacea: Aviculidae,[4] Vulsellidae,[4] Pernidae,[4] Pinnidae,[4] Ostreidae.[3]
2. Pectinacea: Pectinidae,[4] Amussiidae,[4] Spondylidae,[4] Limidae.[4]

Order 4. Eulamellibranchia.
Sub-order 1. Submytilacea.[1]
2. Tellinacea.[1]
3. Veneracea.[1]
4. Cardiacea.[1]
5. Chamacea.[5]
6. Myacea.[1]
7. Adesmacea.[1]
8. Anatinacea.[1]

Order 5. Septibranchia.[5]

[1] Eu- together with pro-latero-frontal cilia (but see p. 368). [2] Eu- together with pro-latero-frontal cilia apparently present (see p. 356). [3] Anomalous together with para-latero-frontal cilia. [4] Micro-latero-frontal cilia only. [5] No members examined.

an opportunity of examining—there seems no justification for separating Heteranomia from the rest of the Anomiidae.

Of the six families placed in the Mytilacea, the Anomiidae, Arcidae, and Melinidae have micro-latero-frontal cilia, and their presence is inferred in the Amussiidae owing to the close similarity of the gills of Amussium pleuronectes to those of the Pectinidae in which these cilia occur, although latero-frontal cilia could not be distinguished because of poor preservation (Atkins, 1938).

In his family Melinidae Ridewood placed the genera Melina (=Perna =Isognomon) and Malleus. Of these two genera, micro-latero-frontal cilia have been distinguished in Malleus albus (*mi-l-f.c.*, Text-fig. 3 B) (see, however, p. 363): the gills of Isognomon alata and Isognomon isognomon were not sufficiently well preserved to distinguish micro-latero-frontal cilia, but eu-latero-frontals were almost certainly absent. It might here be observed that Pelseneer in his classification of 1906 placed Malleus in the Aviculidae, but followed Ridewood in assigning Perna (Pernidae) to the Mytilacea: in 1911 he replaced this latter family in the Aviculacea.

In the Amussiidae Ridewood included Plicatula australis, which Pelseneer (1906) placed in the Spondylidae, and Watson (1930) concluded should either be a distinct family in the Pectinacea, or the Pectinidae should be divided into not less than four sub-families—the Amussiinae, Plicatulinae, Pectininae, and Spondylinae. I have been unable to obtain material of Plicatula.

There can be no doubt but that Ridewood was wrong in including the Amussiidae in the Mytilacea even on a consideration of the form of the gill. It has been shown in a previous paper (Atkins, 1938) that the gills of Amussium pleuronectes are plicate and heterorhabdic, and in fact very closely resemble those of certain of the Pectinidae, and unless it is to be separated from members of the family with flat and homorhabdic gills (Amussium dalli, Amussium meridionale, Amussium lucidum), then the natural position of the Amussiidae, from a consideration of general anatomy, is near the Pectinidae in the sub-order Pectinacea.

The Amussiidae are not alone among the Eleutherorhabda in containing some members with flat and homorhabdic, and others with plicate and heterorhabdic gills. In the Pectinidae a species, Pecten groenlandicus, with flat and homorhabdic gills is known (Noman, 1882). In fact in this family there is considerable variation in the structure of the gills (see Text-fig. 12, p. 414). The simplest is Pecten groenlandicus with flat and homorhabdic lamellae, lacking interlamellar septa, and with a single row of ciliated discs, those at the lower edge of the demibranch; most known species appear to have plicate and heterorhabdic lamellae, with interlamellar septa, and with a number of ciliary interfilamentar junctions as in Pecten maximus, Pecten irradians, Chlamys opercularis, Chlamys distorta, Chlamys tigerina, and Chlamys vitrea; the most highly developed would seem to be Pecten tenuicostatus Mighels (= Pecten grandis Solander) in which organic interfilamentar junctions occur, though ciliary ones are present near the free margin of the demibranch (Drew, 1906, 1907*a*). In the Pteriidae, Stempellaria magellanica (see Clasing, 1921) and Malleus albus,[1] have flat and homorhabdic gills, while Pteria and Pinctada have plicate and heterorhabdic gills. In the Vulsellidae, within the same genus, one species Vulsella rugosa, has flat gills, and another, Vulsella lingulata, plicate gills, (see Pelseneer, 1911). It will thus be seen that the difference between flat and plicate gills does not warrant the separation of related species and genera, as Pelseneer recognized in 1911.

Of the sub-order Mytilacea there now remains the Mytilidae and Trigoniidae to be considered. These two families alone of Ridewood's sub-order have eu-latero-frontal cilia, together with pro-latero-frontals in the Mytilidae (the filaments of Trigonia margaritacea were not well enough preserved to make identification of pro-latero-frontals possible) and most probably

[1] There seems some doubt as to the family in which Malleus should be placed. Jackson (1890) considered it as closely allied to Avicula, and provisionally placed Vulsella (Vulsellidae), and Malleus on the same branch from Avicula: Pelseneer (1906, 1911) placed Malleus in the Aviculidae itself.

belong to a distinct phylogenetic group, or groups, from that of the rest of the families in the sub-order. It seems very improbable that there is any close relationship between the Mytilidae and the Trigoniidae, for the ciliation of the filaments is markedly dissimilar (see p. 381; Text-fig. 1, A and C, p. 351). The position of the Trigoniidae will be discussed later (p. 394).

Little need be said of the three families, Spondylidae, Pectinidae, and Aviculidae, placed by Ridewood in the sub-order Pectinacea: all three possess micro-latero-frontal cilia.

Ridewood (1903, p. 181) stated his reasons for the separation of forms previously classed in the Pectinacea and their inclusion in the Mytilacea as follows: 'Of the genera of the Pseudolamellibranchia which it is now proposed to associate with the Filibranchia under the title Eleutherorhabda, some have well-developed principal filaments and plicate lamellae (e.g. Avicula, Meleagrina, Pecten, Spondylus), whereas others have flat lamellae and filaments undifferentiated (e.g. Plicatula, Malleus, Melina, Amussium, and Dimya). So sharply marked off are these first four genera from all the rest of the Eleutherorhabda by reason of their strongly differentiated principal filaments and their plicate lamellae, that it is well to let them constitute a sub-order by themselves.' It is difficult to follow why Ridewood should have ascribed such importance to the difference between flat homorhabdic, and plicate heterorhabdic lamellae in the Eleutherorhabda, while considering (p. 161) that in the Synaptorhabda such a difference was of not more than specific, or at most subgeneric, value; and after drawing attention to the fact that principal filaments are ontogenetically a secondary differentiation, in Pecten for example (p. 162). Pelseneer in 1911 justly criticized Ridewood's use of this character, and also his use of the structure of the interfilamentar junctions, whether ciliary or vascular, to divide the Pseudolamellibranchia among the Eleutherorhabda and Synaptorhabda.

It is necessary to consider Ridewood's sub-order Ostreacea, which he placed in the order Synaptorhabda along with seven sub-orders now known to possess eu- together with pro-latero-frontal

cilia, and the sub-order, Poromyacea, which included bivalves generally classed in a separate order Septibranchia. Of the three families of the sub-order Ostreacea, the Limidae and Pinnidae possess micro-latero-frontal cilia, the Pinnidae possibly with an additional row (see p. 363), while the Ostreidae have anomalous, together with para-latero-frontal cilia. Thus the composition of the latero-frontal tract indicates that the Synaptorhabda, as the Eleutherorhabda, are at least diphyletic, and the Ostreacea should be removed from the Synaptorhabda as Pelseneer contended in 1911.

We have now to see how Pelseneer's classification is affected by a consideration of the composition of the latero-frontal ciliated tracts, and it may be said at once that it is only in the Filibranchia and Pseudolamellibranchia that any change is suggested.

In the Protobranchia the three families Solenomyidae, Nuculidae, and Ledidae (= Nuculanidae) all have eu-latero-frontal cilia, most probably with pro-latero-frontal cilia also, as found in the Nuculidae (see p. 356).

His order Filibranchia, as Ridewood's order Eleutherorhabda, is almost certainly diphyletic, if not triphyletic. The Anomiidae, Arcidae, and Pectunculidae have micro-latero-frontal cilia; the Trigoniidae and Mytilidae eu-latero-frontal cilia, together with pro-latero-frontals certainly in the Mytilidae. Pelseneer (1889, 1891, 1892, 1906) derived the Trigoniidae from the Arcidae and placed the two families together in the sub-order Arcacea. The difference in the composition of the latero-frontal tracts, as well as the arrangement of the various ciliary tracts of the filaments, in the two families, indicate that they belong to distinct phylogenetic groups, though at about the same level of gill and mantle evolution. From a consideration of the different arrangement of the ciliary tracts in the Trigoniidae and Mytilidae it is unlikely, as previously mentioned, that these two families are at all closely related. The position of the Trigoniidae is of much interest, and in this connexion a peculiarity of the filaments of Trigonia margaritacea may be mentioned here; that is, the presence of calcified rods[1] embedded in the chitinous sup-

[1] These were obvious in entire filaments of alcohol-preserved material,

porting structure (*c.r.*) (Text-fig. 1 c, p. 351). The presence of these rods in Trigonia is curious, as, according to Ridewood (1903, p. 168), calcified rods are peculiar to the filaments of the Unionidae and Mülleria. They have been described in Anodonta, Unio, Mülleria, and Monocondylaea: from the appearance of sections of the filaments of Mutela bourguignati (Text-fig. 6 B, p. 371) it is evident that they are also present in that species. Calcified rods are thus characteristic of a number of the Naiadacea: they appear, however, to be absent in Aetheria; Ridewood (p. 230) did not mention them in his description of the gills of Aetheria plumbea, and there is no indication of them in the filaments of Aetheria elliptica. Ridewood may have overlooked their presence in Trigonia lamarki, unless this is a character which varies in related species.

Neumayr (see Douvillé, 1912*a*) concluded from a study of the hinge that the Unionidae and Trigoniidae were closely related. Douvillé (1912*a*, p. 443), however, has pointed out that the similarity between the hinges of Unio and Trigonia is delusive, for the tooth of Trigonia is not originally double as that of the Unios, but is derived by division from a primitively simple tooth. Douvillé, himself, derived the Trigoniidae from the Preheterodonts by way of the Myophoriidae, and considered that they gave rise to no higher forms. Prashad's (1931, p. 48) objection to the association of the Unionidae (or super-family of the Naiadacea) and the Trigoniidae in the same order, Schizodonta, is based on the difference in the structure of the gills in the two families, the former being eulamellibranchiate and the latter filibranchiate. The difference as between the two types of gills seems to me not of great importance in view of the occurrence of both ciliary and organic

owing to their having been fractured at intervals. The two main rods occur toward the interlamellar ends of the filaments and are continuous throughout the length of the filament. Two other, but much smaller, rods are situated beneath the lateral ciliated cells; they appear to be only intermittently present. Material prepared for sectioning was soaked for a short time in weak hydrochloric acid alcohol; the part of the rods remaining after the treatment stains intensely with iron haematoxylin, as indicated in Text-fig. 1 c (p. 351).

interfilamentar junctions in the same individual in Pecten tenuicostatus, of compound ciliary and organic junctions in certain species of Pteriidae, Limidae, and Pinnidae (see p. 406), and of the apparent ease with which extensive interfilamentar and interlamellar junctions are produced in abnormal gills of the filibranchiate species, Mytilus edulis (Atkins, 1930). A greater difficulty is the arrangement of the ciliated tracts of the filaments, for this is likely to be a more stable character, few variations being known (see p. 380). Though the three families of the Naiadacea, the Unionidae, Aetheriidae, and Mutelidae, have eu-latero-frontal cilia as have the Trigoniidae, yet the arrangement of the various tracts of cilia is that common to the Mytilidae and the Eulamellibranchs possessing eu-latero-frontal cilia (Text-figs. 1 A, B, p. 351; 6, p. 371), while the arrangement in Trigonia margaritacea is entirely different (Text-fig. 1 c). Although this would not be an insuperable difficulty in the way of the derivation of the Unionidae from the Trigoniidae, or from a common ancestor, it would seem to indicate that the two families are not closely related, in this agreeing with the conclusion reached by Douvillé. The calcified rods of the two families may quite possibly have been developed independently. It must not be overlooked, however, that there is nearly as great a difference in the arrangement of the ciliary tracts in two families of Protobranchs, the Nuculidae, and Nuculanidae, which at one time were classed as one family, as in the Trigoniidae and Unionidae.

In Pelseneer's order Pseudolamellibranchia are included a number of families with micro-latero-frontal cilia, and one, the Ostreidae, with anomalous together with para-latero-frontal cilia. My material representing the families Vulsellidae and Pernidae (= Isognomonidae) was not sufficiently well preserved to allow of the identification of micro-latero-frontal cilia, but eu-latero-frontals are almost certainly absent; it may perhaps be assumed that the former kind of cilia are present (see p. 376). Micro-latero-frontal cilia were identified in Malleus albus, but there seems some uncertainty as to whether Malleus is a Vulsellid or a Pteriid (see p. 392). The presence of micro-latero-frontal cilia is assumed in the Amussiidae, owing to the

close similarity of the gills of Amussium pleuronectes to those of the Pectinidae (Atkins, 1938).

The families of the Pseudolamellibranchia are closely related, and, as will be seen later, in all probability form with the Arcidae and Anomiidae a monophyletic group.

In his classification of 1906 Pelseneer placed the Aviculidae, Vulsellidae, Amussiidae, Spondylidae, and Pectinidae (and certain extinct families) together in the sub-order Pectinacea. The last three families mentioned are more closely related to one another than they are to the first two, and this he recognized in 1911 in creating a sub-order Aviculacea for the first two families together with the Isognomonidae and Pinnidae, and with the Ostreidae as an offshoot, and placing the last three together with the Limidae in the Pectinacea.

Pelseneer's view of the close relationship of the families of the Pectinacea is borne out by work on the gills. Apart from the common possession of micro-latero-frontal cilia the members of the Amussiidae, Pectinidae, Spondylidae, and Limidae investigated (which were all forms with plicate and heterorhabdic lamellae) agree very closely in the structure of the gills. They have: (1) a suspensory membrane to the gill; (2) a similar arrangement of the muscles of the gill axis; (3) a similar arrangement of the horizontal muscles of the principal filaments; (4) few or no vertical muscles in the lamellae; (5) respiratory expansions on the principal filaments; and (6) chitinous supporting structure of the principal filaments of similar form in all except the Limidae. In the forms with flat and homorhabdic gills, for example Amussium dalli, Amussium lucidum, Amussium meridionale, and Plicatula australis, respiratory expansions are apparently absent.

Pelseneer's order Eulamellibranchia contains only families, which, so far as my work has gone, possess eu- together with pro-latero-frontal cilia. Palaeontologists, however, consider that this order is not a monophyletic one, and Douvillé (1912*a*) has divided it into two groups, a 'normal' and a 'burrowing' branch. The possession of the same type of latero-frontal tract by both groups may be explained by their probable origin, the 'normal' branch from a nuculoid form, and the 'burrowing' branch from

a form of which Solenomya may be considered representative (Davies, 1933): both Nucula and Solenomya have eu-latero-frontal cilia (Text-fig. 7, p. 372), and, as it has been seen (p. 356), Nucula, if not Solenomya, probably has pro-latero-frontal cilia as well. In the phylogenetic division of the Eulamellibranchia the form of the latero-frontal cilia is therefore apparently of no assistance. It is curious that a certain type of pattern of the lateral ciliated cells is common among both 'normal' and 'burrowing' groups of Lamellibranchs (Atkins, 1938*a*). Differences in the detailed arrangement of these cells would seem to be of doubtful utility, and the same pattern occurring in different bivalves might be expected to indicate relationship. This character may repay a fuller investigation than I was able to give to it (1938*a*). It is perhaps possible that the 'normal' and 'burrowing' groups of Lamellibranchs are not as widely separated as suggested by Douvillé's table (1912*a*, p. 466).

Relationship of Lamellibranchs with Micro-latero-frontal Cilia.

Bivalves with micro-latero-frontal cilia, those previously considered as lacking such cilia, are not scattered haphazard through the Lamellibranchia, but are found in families which are more or less closely related (see Text-fig. 9), forming, except for my inclusion of the Arcidae, a group designated 'the Aviculidae and their allies' by Jackson (1890). This is the same group as Douvillé's (1912*a*) 'sedentary' branch, except for his inclusion of the Mytilidae. That a group established by palaeontologists almost entirely on shell characters should be related also by the condition of a certain tract of cilia on the gill filaments is most interesting.

Jackson (1890, p. 362) found the Aviculidae and their allies to be linked in one great group by characters of anatomy and shell structure which connect the several members, and to be characterized 'by possessing prodissoconchs of homogeneous laminar structure, but not prismatic, and with umbos directed posteriorly'.[1] The suc-

[1] Professor A. Morley Davies informs me by letter that '"umbos

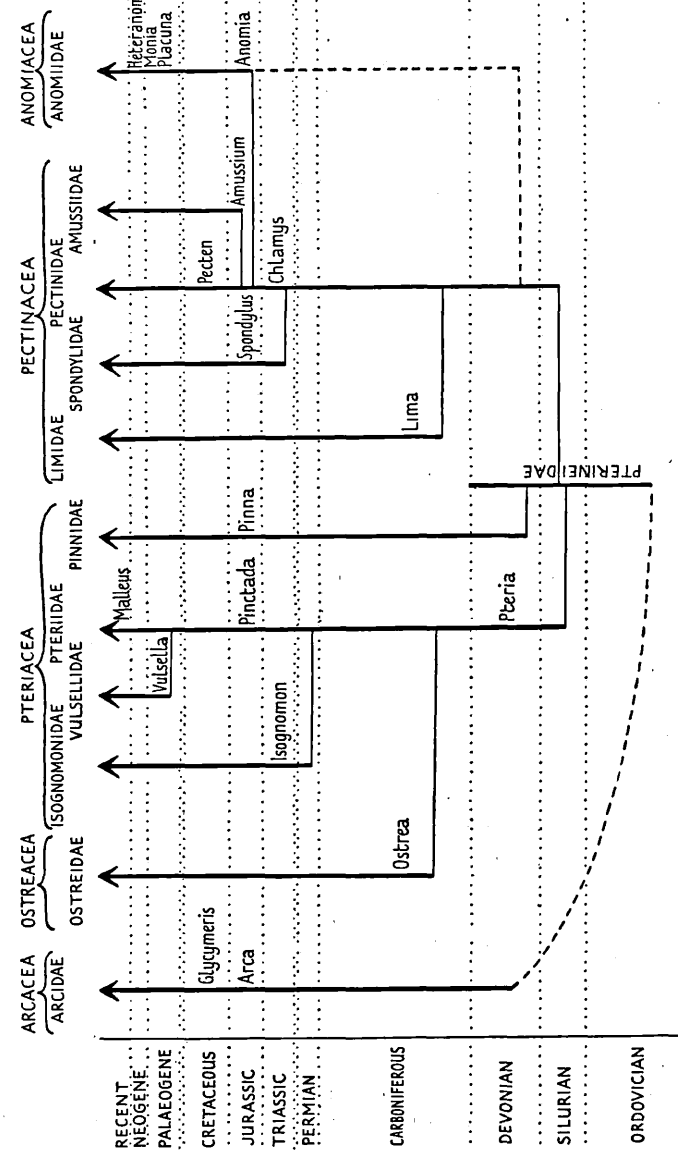
ceeding dissoconch has 'an external layer of prismatic cellular tissue which is more or less developed but exists at least in the early nepionic stages of one valve' (1890, p. 377).

Douvillé (1912*a*, p. 460) characterized his 'sedentary' branch as 'essentiellement byssifères'. He considered that fixation by the byssus has impressed certain characters on the group which tended to persist through various changes in the mode of life. This method of fixation may be accomplished in very different ways according to the length of the byssus. When it is so short that fixation is practically by the foot, as in Arca, it results in an inequilateral shell, the posterior region, where the exhalent and main inhalent apertures are situated, being more developed than the anterior, but with little or no difference in the size of the adductor muscles. As the byssus lengthens pressure is exerted by the foot on the anterior adductor, and as the pressure increases this muscle diminishes in size, as in the Pinnidae, and finally disappears (many forms of the group). The reduction of the anterior adductor is accompanied by that of the anterior region generally.

Byssal fixation and cementation, however, are not confined to the 'sedentary' branch, and in two families at least, the Aetheriidae and Tridacnidae, may be accompanied by the monomyarian condition. According to Yonge (1936), however, in the Tridacnidae this condition was brought about in an entirely different way—by rotation of the mantle and shell round the visceral mass—from that in the 'sedentary' branch. Douvillé, of course, included the Mytilidae, in which byssal fixation has resulted in reduction and disappearance of the anterior adductor muscle in some species, in his 'sedentary' group: the position of the Mytilidae will be discussed later.

The group (Arcidae, Anomiidae, Pteriacea with Pinnidae, Ostreidae, Pectinacea with Limidae) characterized by the possession of micro-latero-frontal cilia would appear in all probability to be a monophyletic one (Text-fig. 9). As previously

directed posteriorly" is not, as it might seem at first sight, an embryonic or juvenile character, but is an effect of later unequal growth. Possibly its general presence in "the Aviculidae and their allies" may be connected with the reduction of the anterior region of the shell'.



TEXT-FIG. 9.

Geological occurrence and phylogenetic inter-relationships of the group of Lamellibranchs characterized by the possession of micro-latero-frontal cilia (only families and genera examined included). Geological occurrence obtained largely from Dall (in Zittel, 1913); phylogenetic relationships largely from Jackson, 1890. (Arcidae is used in a wide sense to include *Glycymeris* and allied genera, and *Paralellodon* and allied genera).

stated, it differs from Jackson's group in the inclusion of the Arcidae, but this ancient family appears from palaeontological evidence to be connected with the Pteriacea, for according to Arkell (1930, pp. 306–7) it can scarcely be doubted that Cypricardites (=Palaearca), which ranges from the Ordovician to the Devonian, and Parallelodon, a genus of Arcidae, were descended from a common stock. Cypricardites was placed in the Arcacea by Dall (in Zittel, Eastman edition, 1913, vol. i reprinted in 1927 and 1937), but Zittel (German edition, 1924, see Arkell) classed it with the Ambonychiidae, a family of the Pteriacea. Douvillé (1912*a*) associated it with the Pterineidae. He held that the ancient forms of the Arcidae approach much more to the Pterineidae than to the Nuculidae, but thought that the Arcidae really constitute a branch parallel to that of the Aviculidae (= Pteriidae), but fixed only by the foot, and in consequence with a much less great reduction of the anterior adductor muscle, and of the anterior portion of the animal generally. In the living genus Limopsis (sometimes classed with the Arcidae, sometimes in a separate family, and which according to Pelseneer (1911, pp. 8, 9) should, with Pectunculus (=Glycymeris), be placed in a family Pectunculidae, apart from the Arcidae), however, the anterior adductor muscle is frequently much reduced, and in an allied family, the Philobryidae, is wanting (Pelseneer, 1906, p. 258).

Palaeontologists differ as to the position of the Mytilidae. This family was included by Douvillé in his 'sedentary' branch, but omitted by Jackson from 'the Aviculidae and their allies'. Douvillé (1912*a*, p. 460) distinguished two great groups in the 'sedentary' branch: (1) the Pterineidae with straight hinge, and amphidetic ligament, at first simple and inserted on a more or less developed area; and (2) the Mytilidae with curved hinge, opisthodetic ligament, remaining marginal, and without an area. Jackson (1890, p. 364), on the other hand, stated that 'The striking differences in the prodissoconch and nepionic stages of the Mytilidae and Aviculidae are sufficient, I think, to separate these groups, and the Mytilidae should be put in a group distinct from the Aviculidae and their allies, which I have shown are all bound together by important features as one

group'. His conclusions are supported by the difference in the composition of the latero-frontal tracts in the Mytilidae and in the Pteriidae and their allies (see pp. 368–380).

Comparing the group with micro-latero-frontal cilia with Pelseneer's classification of 1911 it will be seen that this group corresponds to his order Pseudolamellibranchia (see p. 390) together with the Arcidae and Anomiidae, which last two families he associated with the Mytilidae and Trigoniidae in the Filibranchia. As previously stated, the Arcidae and Anomiidae have a type of latero-frontal tract quite distinct from that of the other two families of the Filibranchia, with which they appear to have no close relationship.

Pelseneer abandoned the order Pseudolamellibranchia in 1906, but in 1911 (p. 119) he stated: 'je suis ramené à mon idée ancienne et première qu'il faut reconstituer un groupe entre les Filibranches et les Eulamellibranches—groupe représentant un stade phylogénétique postérieur au premier et formant une branche, globalement moins spécialisée que le second et orientée dans une autre direction.' He (1911, pp. 120–1) defined it as follows: (1) the gills have ciliary or cellular interfilamentar junctions (or both) and are free or attached to the mantle by ciliary junctions, but (2) the pallial lobes are without suture (whilst all Eulamellibranchs have always non-ciliary and vascular interfilamentar and interlamellar junctions, and always one or several pallial sutures; (3) the auricles inter-communicate; (4) the presence of abdominal sense organs[1] on the posterior adductor muscle; (5) the anterior adductor muscle is wanting; (6) the byssus is normally well developed.

Pelseneer's order Pseudolamellibranchia is not sufficiently inclusive, for the present work indicates that the Arcidae and Anomiidae are related to the families forming that order. Palaeontological evidence for the inclusion of the Arcidae has been briefly given (p. 399); it remains to consider the Anomiidae.

[1] Paired abdominal sense organs are present on, or near, the posterior adductor muscle in the Arcidae, whilst a single organ is present on the right side only in Placuna placenta (Anomiidae), as in Pecten (Willey, 1911, pp. 158–61). Paired abdominal sense organs also occur in the Trigoniidae (Pelseneer, 1906) and in the Mytilidae (Field, 1922).

The present research certainly does not support Pelseneer's (1911, p. 16) contention—in opposition to Jackson, Bernard, Rice, and Stenta—that the affinities of Anomia are with the Filibranchia and especially with the Mytilidae. Although the form of the latero-frontal cilia cannot help in solving the problem of the immediate ancestry of the Anomiidae, whether they are derived from the Pectens, as Jackson supposed, or from some other member of the group, it at least indicates that they are members of 'the Aviculidae and their allies'. Jackson (1890, p. 362) thought it possible that Anomia was derived from the Amussium or Hemipecten group of the Pectens, as these resemble Anomia in having thin nacreous shells. According to Douvillé (1912*a*) the nacreous type of shell precedes the porcelaneous in evolution, and forms derived from porcelaneous types are always porcelaneous; it therefore seems that Anomia, whatever its ancestry may prove to be, must have been derived from forms with nacreous shells. The Anomiidae are known certainly from the Jurassic: there is a record of Anomia in the Devonian, but this occurrence seems doubtful as there is no other record before the Jurassic.

To summarize the various views considered here: Jackson saw in 'the Aviculidae and their allies' a natural group from which the Mytilidae are clearly separated; he did not include the Arcidae. For Douvillé his 'sedentary' branch is 'essentiellement byssifères'. It contains not only the forms included in Jackson's group, but also the Arcidae (which he considered really constitute a branch parallel to that of the Pteriidae) and the Mytilidae. He distinguished two great groups in the 'sedentary' branch, the Pterineidae and the Mytilidae, separated by certain characters of the hinge. For Pelseneer his order Pseudolamellibranchia is a group between the Filibranchia and the Eulamellibranchia, though not ancestral to the latter, its members connected by a number of characters in common. It corresponds to Jackson's group less the Anomiidae, which family Pelseneer contended has affinities, not with the Pseudolamellibranchia, but with the Mytilidae.

The group characterized by the possession of micro-latero-frontal cilia corresponds to Jackson's group of 'the Aviculidae

and their allies' with the addition of the Arcidae; to Douvillé's 'sedentary' branch less the Mytilidae; and to Pelseneer's Pseudolamellibranchia with the addition of the Arcidae and Anomiidae. The sub-orders and families in the group are then (so far as my material goes) as follows:

Arcacea: Arcidae.
Anomiacea: Anomiidae.
Pteriacea: Pteriidae, Isognomonidae, Vulsellidae, Pinnidae.
Pectinacea: Pectinidae, Amussiidae, Spondylidae, Limidae.
Ostreacea: Ostreidae.

The geological occurrence and phylogenetic interrelationships of the group are shown in Text-fig. 9, p. 400.

Discussion on the Origin of the Group Characterized by the Possession of Micro-latero frontal Cilia.

Eu-latero-frontal cilia are present in living representatives of all three existing families of the Protobranchia, together with pro-latero-frontal cilia at least in Nucula. The presence of these large straining cilia on gills which, certainly in Nucula and Nuculana, play only a subsidiary part in feeding, points to the antiquity of eu-latero-frontal cilia, and incidentally suggests that the gills of ancient Protobranchs may perhaps have played a greater part in feeding than do those of most of their modern representatives. This has already been suggested for the Nuculanidae on the evidence of the complicated frontal currents present on the small gills of Nuculana minuta (Atkins, 1936). It may very well be that in the Protobranchia, suspension feeding (as in Solenomya) is more primitive than deposit feeding (as in Nucula and Nuculana).

It has been generally considered that the Nuculidae,[1] or

[1] Schenck (1934) in his paper on 'Classification of Nuculid Pelecypods' though not doubting that the family Nuculidae has Devonian representatives, yet insisted that he had seen no Nucula, sensu stricto, in rocks of Palaeozoic age, the Palaeozoic specimens he had studied not being closely related to the type species of Nucula, s.s.

nuculoid forms, are the stock from which sprang the higher Lamellibranchs (Jackson, 1890; Pelseneer, 1891, 1911; Rice, 1897, &c.), with the exception of Douvillé's 'burrowing' branch, or Desmodonts, of which Davies (1933) suggested Solenomya as representative of the ancestral form. If this be so, and if eu- together with pro-latero-frontal cilia were present in primitive Nuculidae, as they are in their living representatives in the genus Nucula, then it would seem to follow that from the Nuculidae have arisen at least two lines, one in which this type of tract has persisted (Mytilidae, Trigoniidae, Eulamellibranchia) and the other in which eu-latero-frontal cilia have been lost (Arcidae, Anomiidae, Pseudolamellibranchia), excluding the possibility of their reduction. It seems very improbable, however, that such useful structures in the ciliary method of feeding as eu-latero-frontal cilia once possessed would be lost, so long as the method of obtaining food remained the same, and then an attempt made to regain them, as exemplified by the anomalous latero-frontal cilia of the Ostreidae. This is the more unlikely as the mainly deposit feeding Protobranchs, Nucula and Nuculana, have retained eu-latero-frontal cilia, though having no great use for them. The fact that in the second line (with micro-latero-frontal cilia) the most highly developed latero-frontal cilia—the anomalous—are found in the highest family of the group, the Ostreidae, points to the evolution of these structures within the group, and it would seem that the similarity both of structure and function between the anomalous and eu-latero-frontal cilia is due to convergence.

It may thus be conjectured that the remote ancestors of the 'sedentary' branch are to be sought in forms other than the Nuculidae, or any Protobranch family with living representatives, for these all have eu-, if not also pro-, latero-frontal cilia. Judging by the persistence of eu-latero-frontal cilia in the Nuculanidae and Nuculidae on gills which play only a subsidiary part in feeding, as well as by the uniformity of composition of the latero-frontal tract within existing families of Lamellibranchs, it seems improbable that extinct members of the Nuculidae, Nuculanidae, and Solenomyidae differed much from living members in the form of their latero-frontal cilia. But it

may be that some ancient, extinct families of Protobranchs were without eu-latero-frontal cilia, and gave rise not only to forms with such cilia, but also to those with micro-latero-frontal cilia. Douvillé (1912*a*, pp. 443–4) noted that three families of Palaeoconchs, the Cardiolidae, with equivalve shells, the Antipleuridae and Vlastidae, with inequivalve shells, would be perhaps better placed in the 'sedentary' group, but he thought it probable that these are not to be considered as primitive forms (p. 421): it is therefore likely that they are not sufficiently generalized to have given rise to the 'sedentary' branch, and besides they are not known until the Silurian, while the Pterineidae occur in the Ordovician.

Thus, though the 'sedentary' branch of Lamellibranchs can be traced back to the Pterineidae (Ordovician to Carboniferous) yet their origin and relationship with other groups of Lamellibranchs remains obscure. It is an unfortunate truism that the taxonomic value of any character drawn from the soft parts of an animal is greatly restricted in that the position of fossils cannot be tested by such characters.

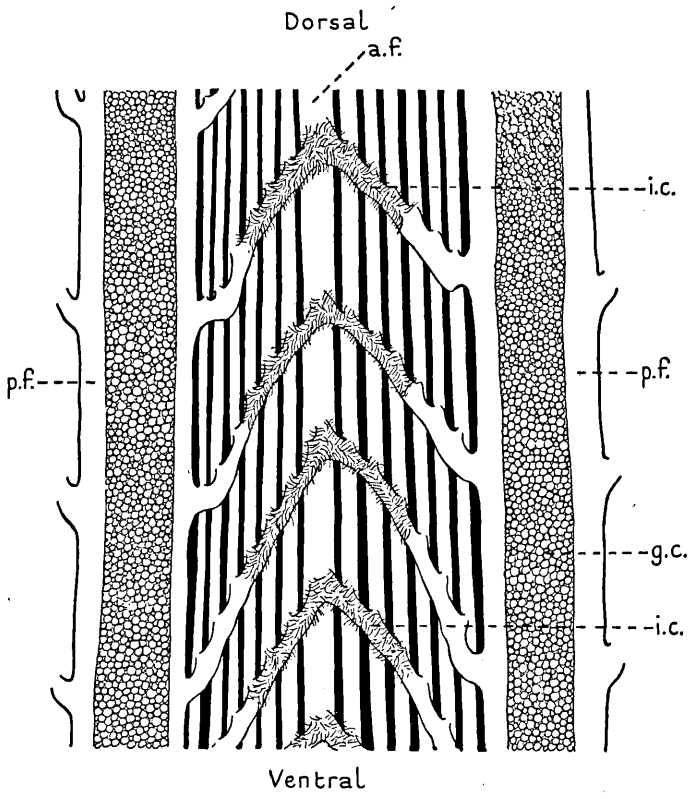
The Evolution of the Eulamellibranchiate or Synaptorhabdic Gill in the Group Characterized by the Possession of Micro-latero-frontal Cilia.

Within the group characterized by the possession of micro-latero-frontal cilia are two families, Pectinidae and Pteriidae, which, though characteristically filibranchiate or eleutherorhabdic, yet contain members with the synaptorhabdic tendency; one of these, the Pectinidae, and the forerunners of the other, the Pterineidae—and probably the Pteriidae themselves—have given rise to forms with eulamellibranchiate or synaptorhabdic gills (see Text-fig. 12, p. 414).

Most known members of the Pectinidae have gills with purely ciliary interfilamentar connexions, but the giant scallop Pecten tenuicostatus Mighels has both organic and ciliary junctions, the latter occurring near the free margins—the youngest parts—of the gills (Drew, 1906, 1907 *a*), where, as will be seen later, in Lima vestiges of ciliated discs are found.

From the Pectinidae in Carboniferous times arose the eulamellibranchiate family Limidae (Jackson, 1890, pp. 388, 391). The gills of Lima hians and Lima loscombi are curiously Pecten-like, the organic interfilamentar junctions having the appearance of spurs—such as are found in Pecten, Spondylus, and Amussium—which have fused. In Lima hians (fig. 1, Pl. 29) and Lima loscombi remains of ciliary junctions persist, being found mostly toward the ventral margins of the demibranchs, but the junctions are mainly organic. Ridewood (1903, p. 217) noted that in Lima inflata obsolete ciliated discs were merely suggested by the regularity of the prismatic epithelium.

An apparently unique use of interlocking cilia is found in the Limidae (Lima hians and Lima loscombi), in which the interfilamentar junctions do not run across the plicae as horizontal septa, as in Pinna and Ostrea, for instance. The interfilamentar junctions occur at regular and rather close intervals; they arise from the side of the principal filament and pass across the abfrontal surface of the ordinary and apical filaments to the next principal filament. The junctions are not directly transverse; they run in a series of V's, the apex of each being directed dorsally, and situated on an apical filament (Text-fig. 10). Long interlocking cilia, with the characteristic rotary movement of such cilia, are present on the intraplical face (i. e. facing the exhalent chamber) of that part of the interfilamentar connexion which extends across the filaments forming the crest of the plica (in Text-fig. 10 the apical and three adjacent filaments on each side). Under normal conditions the two arms of the V interlock (see fig. 1, Pl. 29), and hold the sides of the crests together, so that the plicae are steep-sided. Flattening of the plicae can only take place in that region devoid of interlocking cilia adjacent to the principal filaments, unless the cilia are torn apart, as shown in Text-fig. 10, which probably does not normally occur. Movement of the plicae is mostly a bending sideways of one fold toward the next, so that they partly overlap (see Text-fig. 11): only to a slight extent does widening and smoothing out of the plicae occur. It would seem that these ciliary junctions act in the manner of organic



TEXT-FIG. 10.

Lima hians. Sketch from life of the abfrontal surface of a plica. The plica has been opened out, so that the cilia normally interlocking on opposite limbs of the V-shaped interfilamentar junctions, are shown in a non-interlocking position. (The number of filaments to a plica in Lima hians varies between about 14 and 19.) *a.f.*, apical filament; *g.c.*, gland-cells of abfrontal surface of principal filament; *i.c.*, interlocking cilia; *p.f.*, principal filament. $\times 93\frac{1}{3}$.

intraplical septa—such as occur in Pinna and Ostrea—in preserving the form of the plicae, and this method is a possible precursor of organic union, a step in the tendency to progressive firmness of the gill. The lacunar tissue of an organic horizontal

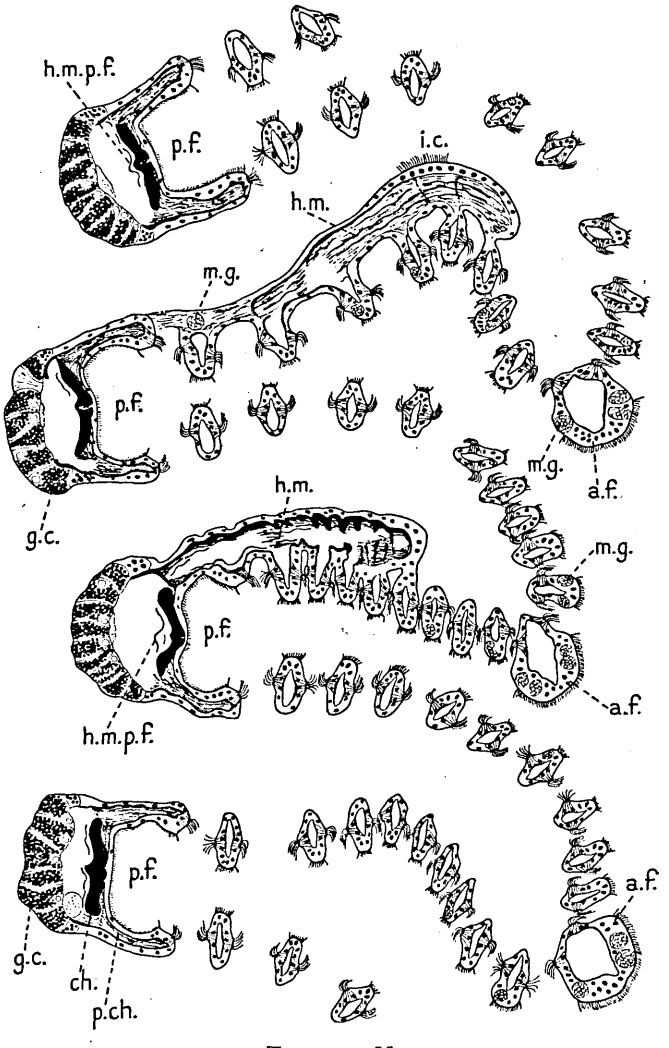
septum probably allows of greater play in increasing and decreasing the depth of the plicae than is possible by the ciliary method, and is without its weakness.

In the Pteriidae there are at least three species which show the synaptorhabdic tendency. In the genus Pteria, Pteria hirundo has ciliary interfilamentar junctions (an instance of a principal and adjacent filament in organic union was observed, but this is unusual, and may have been due to proximity to the base of the gill), but in Pteria argentea the junctions are of a compound nature, the intraplical edges of the spurs that bear the ciliated discs having fused (Ridewood, 1903, pp. 212–13). A similar condition has been described in Pinctada vulgaris (Herdman and Hornell, 1904, p. 60; Herdman, 1905, pp. 227–8), and has been found during the present work in Pinctada margaritifera.

The Pinnidae, which arose in Devonian times, probably from Leptodesma, one of the Pterineidae (Jackson, 1890), has living members in which the gills have extensive organic interfilamentar junctions, they are in fact eulamellibranchiate, yet sections of Pinna fragilis have shown that vestiges of ciliated discs still exist alongside the organic unions (fig. 2, Pl. 29), as in Lima hians and Lima loscombi.

In Pteria hirundo the interfilamentar junctions are entirely ciliary; in Pteria argentea, Pinctada vulgaris, and Pinctada margaritifera they are mainly ciliary with some little organic union; in Pinna fragilis mainly organic with vestiges of ciliary junction. In the Pteriidae and Pinnidae there are therefore species the gills of which form a graded, though not a direct evolutionary, series.

A third eulamellibranchiate or synaptorhabdic family, the Ostreidae, has arisen within the group, but is somewhat apart from the rest—possessing anomalous together with para-latero-frontal cilia—though it obviously should be included on account of its derivation on independent grounds from either the Pteriidae or Pectinidae. Its gills are more highly evolved than those of either of the other two families with eulamellibranchiate gills, Limidae and Pinnidae, not only in the degree of development of the latero-frontal ciliated tract, but in the presence of organic



TEXT-FIG. 11.

Lima hians. Transverse section of three plicae and four principal filaments of a lamella to show the bending sideways of the plicae. *a.f.*, apical filament; *ch.*, darkly staining chitin; *g.c.*, gland-cell

[*For remaining description see opposite.*]

fusion between the dorsal edges of the ascending lamellae of the outer demibranchs and the mantle, and between those of the inner demibranchs inter se; and in the absence of any vestiges of ciliary interfilamentar junctions, such as exist in Lima and Pinna (the first interfilamentar junctions of the gills of the spat of Ostrea virginica (Jackson, 1890, p. 304) and of Ostrea edulis (Yonge, 1926, p. 320) are organic). In the group under consideration the gills of Ostrea are the most definitely eulamellibranchiate in structure.

The immediate ancestors of the Ostreidae are doubtful; it is not known with certainty whether they have arisen from the Pteriidae or the Pectinidae. Jackson (1890, p. 307) thought it probable that Ostrea was derived from the Pteriidae, suggesting that it was descended either directly from Perna (=Isognomon) or a close common ancestor of the two genera, or from Avicula (=Pteria). Ostrea appeared in Carboniferous times, Isognomon is not known until the Trias (Dall in Zittel, 1913, pp. 450, 447), so that Ostrea is unlikely to have descended directly from Isognomon. The Pteriidae are present in the Silurian, Pteria itself in the Devonian; it is possible therefore for Ostrea to be descended either from Pteria, or some other member of the family. Dall (in Zittel, 1913, p. 455) followed Jackson in deriving Ostrea from the Pteriidae; Pelseneer (1911, p. 119) placed it as an offshoot from the Pteriacea: Davies (1933), on the other hand, considered that Ostrea shows by its hinge structure and muscle-plan its general affinity to Pecten. In 1853 Forbes and Hanley (vol. ii, p. 261) placed Lima, Pecten, Ostrea, and Anomia in the Ostreidae.

Gill structure unfortunately does not afford any help in determining the immediate ancestry of the Ostreidae. The gill axes are free for much of their length, but differ from those of

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of abfrontal surface of principal filament; *h.m.*, horizontal muscle-fibres of the interfilamentar junctions; *h.m.p.f.*, horizontal muscle-fibres of the principal filaments; *i.c.*, interlocking cilia on intraplical faces of the interfilamentar junctions; *m.g.*, mucous gland; *p.ch.*, pale-staining chitin; *p.f.*, principal filament. Bouin-Duboscq's fixative; Mallory's triple stain. ×200.

the other two families with eulamellibranchiate gills, Limidae and Pinnidae, in the slight development of the longitudinal muscles. Vertical muscles in the demibranchs of Ostrea edulis are poorly developed: absence or paucity of such muscles is characteristic of the Pectinacea, including the Limidae, while the Pteriidae and Pinnidae usually have such muscles well developed. It is doubtful whether any relationship of the Ostreidae to the Pectinacea can be considered as indicated by the state of development of these muscles, for in Vulsella sp., belonging to the family Vulsellidae of the Pteriacea, vertical muscles are poorly developed, extending only a short distance from the gill axes into the principal filaments. The slight development of vertical fibres in Vulsella may possibly be correlated with the peculiarly sheltered life, embedded in sponges, and in Ostrea with a life of fixation from a very early age. Frontal currents similar to those of Ostrea are found on the gills of both Pecten and Pteria, in fact opposed frontal currents on all lamellae, frequently on the same filament, are common in the group with micro-latero-frontal cilia, the only known exception being Pinna (Atkins, 1936, 1937, 1937*a*).

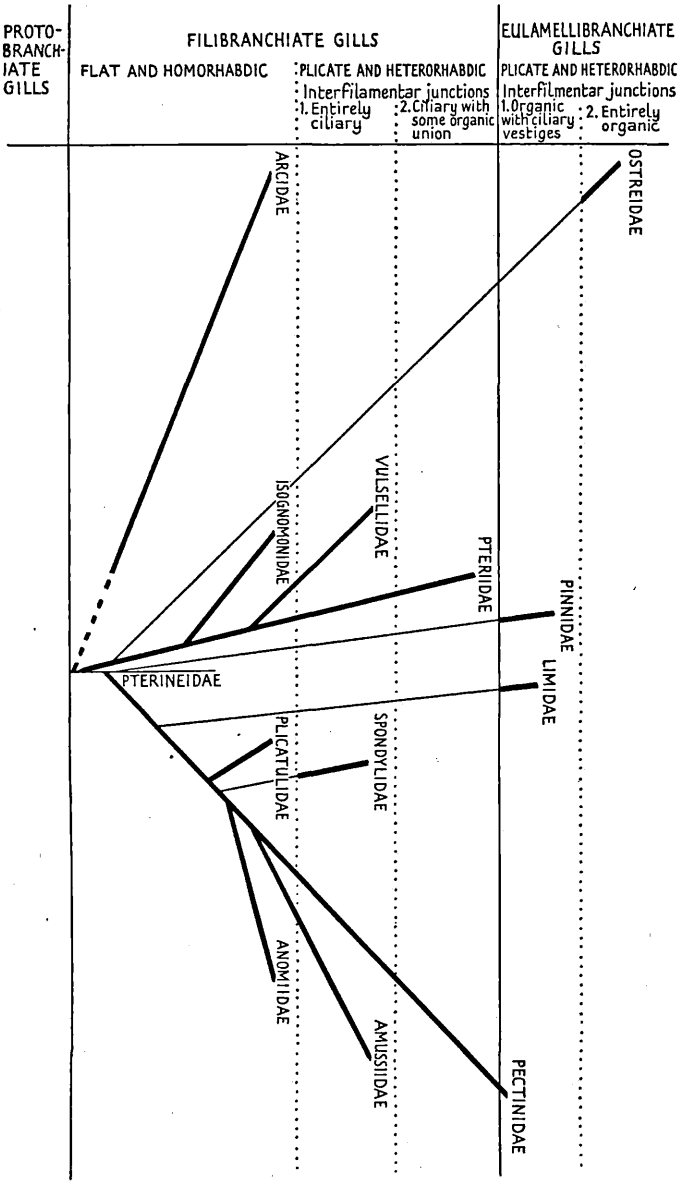
In the group with micro-latero-frontal cilia, eulamellibranchiate gills, so far as is known, are always plicate and heterorhabdic, in contrast to those of the group with eu-latero-frontal cilia, which are frequently flat and homorhabdic. It seems that in the former group the growth of organic junctions has only occurred in gills which had already developed plications, while in the latter group it has occurred also in the flat-gilled stage. Flat homorhabdic and plicate heterorhabdic gills have been separated in Text-fig. 12, but though it seems possible, or probable, that the simpler condition generally precedes the more complex, yet the fact that the two conditions are found not only in the same family, but in the same genus (Pelseneer, 1911), suggests that the step from the one condition to the other is small. In the eulamellibranchiate genus Donax, which contains species with flat, with slightly plicate, and with strongly plicate lamellae, Rice, with what justification I do not know, regarded the simplicity of the flat forms as retrogressive (quoted

by Ridewood, 1903, p. 162): the possibility cannot be excluded that in filibranchiate gills the flat condition may in some instances be secondary.

To sum up, in the group with micro-latero-frontal cilia some families are still in the filibranchiate or eleutherorhabdic stage (Arcidae, Anomiidae, Pectinidae, Amussiidae, Spondylidae, Plicatulidae, Pteriidae, Vulsellidae, Isognomonidae), though showing an early stage in the transition to the eulamellibranchiate or synaptorhabdic condition in the compound junctions of Pteria argentea, Pinctada vulgaris, and Pinctada margaritifera, and considerable organic junction in Pecten tenuicostatus; others have attained the eulamellibranchiate stage (Limidae, Pinnidae, Ostreidae) but certain of them (Lima hians, Lima loscombi, Pinna fragilis) show in vestiges of ciliary junctions, signs of a passage through a filibranchiate stage (see Text-fig. 12).

In the group with micro-latero-frontal cilia there is clear evidence of the passage from the filibranchiate to the eulamellibranchiate condition. In the group with eu-latero-frontal cilia no such evidence has yet been demonstrated, though it is probable that existing Eulamellibranchs had ancestors with filibranchiate gills.

I think it is evident from the foregoing pages that gills at about the same stage of evolution occur in but distantly related groups of Lamellibranchs—that in the different lineages there is the same tendency towards consolidation of the gills—and therefore that the terms Filibranchia and Eulamellibranchia, Eleutherorhabda and Synaptorhabda, should only be used as descriptive of stages in gill evolution, and not logically as the names of orders. Gill structure is essentially a progressive character as already pointed out by Douvillé (1912*a*) and Davies (1933). Pelseneer (1911) held that the evolution of the gill may be considered as symbolizing the phylogenetic evolution of the Lamellibranchia: on this Douvillé (1912*a*, p. 423) commented: 'Les caractères tirés de cet organe sont bien certainement des caractères évolutifs, mais . . . leur valeur phylogénique est très douteuse; les différents rameaux évoluent en effet d'une manière analogue, et ils doivent présenter la même succession



TEXT-FIG. 12.

Diagram showing the condition of gill evolution in the group of Lamellibranchs characterized by the possession of micro-latero-frontal cilia. When families have living members with the gills in a certain stage this is indicated by a thick line.

de caractères; ceux-ci ne peuvent donc permettre de reconstituer les rameaux.'

Common Characters of Lamellibranchs Possessing Micro-latero-frontal Cilia.

Lamellibranchs within the group characterized by the possession of micro-latero-frontal cilia, have, in addition, a number of characters in common as given below. Not all these characters are restricted to members of the group, certain of them, which are probably primitive, occurring for example in those forms noted below which are apparently only distantly related. Three such characters are: (*a*) freedom of the posterior region of the gill axes (as also in aspidobranch Gastropods); (*b*) freedom of the dorsal edges of the ascending lamellae of the gills, or ciliary connexion only inter se and with adjacent parts; and (*c*) the absence of pallial sutures.

The Trigoniidae and Mytilidae, both of which were placed in the same order as the Arcidae and Anomiidae by Pelseneer, have some or all of these characters. In the Trigoniidae all three are found; in fact this family seems to be at about the same level of evolution as the Arcidae as regards gill and mantle freedom, though of different lineage. The Mytilidae, with certain exceptions (Mytilus ovalis, Musculus marmoratus, Septifer bilocularis (Ridewood, 1903)), agree with members of the group in the entirely ciliary method of division between the infra- and supra-branchial chambers, and in the relative freedom of the mantle margins, there being only a narrow pallial suture, but at least in Mytilus edulis and Modiolus modiolus, differ from them in the shortness of the free portion of the gill axis and its reattachment at the extremity.

Certain Eulamellibranchs exhibit some of these characters; in Astarte sulcata is found freedom of the posterior portion of the gill axis, and in the same region ciliary connexion of the gill inter se and with adjacent parts (Atkins, 1937*a*); there is also but one pallial suture. In the Solenidae and Solecurtidae (as represented by Solen marginatus, Ensis siliqua, Ensis arcuatus, Cultellus pellucidus, Solecurtus

scopula, and Solecurtus chamasolen), the gill axes are free for a considerable distance, and this possibly occurs in a number of Lamellibranchs, but masked by the fusion of the dorsal edges of the ascending lamellae with some adjacent parts. In the genus Venus (Venus verrucosa, Venus casina) the gill axes are free for a short distance and then reattached at the extreme tip as in Mytilus edulis.

As mentioned previously these are probably primitive lamellibranch characters, the retention of which has not been restricted to any one group, though certain of them have tended to persist to a greater degree in some groups than in others.

The common characters of the group with micro-latero-frontal cilia are as follows:

1. 'Prodissoconchs of homogeneous laminar structure, but not prismatic, and with umbos directed posteriorly'; the succeeding dissoconch with an external layer of prismatic cellular tissue (Jackson, 1890). In this description Jackson did not include the Arcidae, in different genera of which the umbos in the adult may be directed forwards, inwards, upwards, or backwards (Reinhart, 1935). I have been unable to ascertain whether the remainder of this definition is applicable to the Arcidae.

2. Essentially byssiferous, leading to the greater development of the posterior than the anterior region of the animal (Arcidae), to reduction of the anterior region generally, and especially to reduction (Pinnidae) and disappearance (many forms) of the anterior adductor muscle (Douvillé, 1912*a*). Byssal fixation is not restricted to the group.

3. Considerable free posterior region to the gill axes. In some forms (Malleus, Isognomon, Pteria, Pinna, Ostrea) the gill axes are free for much of their length; in the Arcidae, Anomiidae, and Pectinacea to a less extent. According to Pelseneer (1911, p. 29) in the Pectens the extent of the free posterior portion of the axis varies in different species, being long in those with a stout byssus, and very short in free and swimming forms. In the Ostreidae the dorsal edges of the ascending lamellae of the outer demibranchs are fused with the mantle, and those of the inner demibranchs inter se, so that

the condition of the gill axes is not seen without dissection. In Ostrea also the united dorsal edges of the two inner demibranchs are fused with the visceral mass anteriorly, for a distance varying between about a third and two-thirds of the total length in different species (Ostrea edulis, Ostrea virginica, Ostrea angulata).

In certain members (Arcidae, Anomiidae, Pectinacea) the gill axis is usually borne on a more or less deep suspensory membrane; such a membrane is absent generally in the Pteriacea (Pteria, Malleus, Pinctada, Pinna, Isognomon) and in the Ostreidae.

4. Considerable development of muscles in the gill axes, Ostreidae (Ostrea edulis) excepted. While characteristic of the group, this character is by no means restricted to the group.

5. Method of division of the supra- from the infra-branchial chamber: the division of the mantle chamber is either merely by the touching of the upturned edges of the demibranchs against adjacent parts, or by interlocking cilia, and rarely by organic junction.

It is advisable to discuss this character in some detail. Where the division is brought about merely by the touching of the dorsal edges of the ascending lamellae of the outer demibranchs against the mantle, and by those of the inner demibranchs inter se and against the foot or visceral mass, interlocking cilia are frequently present on the gills, though not on the parts they come in contact with: where the two inner demibranchs are in contact there is probably weak, easily dissolved, ciliary union. According to Bourne (1907) the short stiff cilia on the pallial faces of the velar filaments—that is the long reflected dorsal ends of the ascending filaments—of Anomia (Aenigma) aenigmatica function as ciliated discs, and give a sufficient amount of friction against the mantle—which is without corresponding cilia—to prevent the whole of the ascending lamella from slipping down. Division by mere touching of the gills against adjacent parts is found in the Arcidae (Arca, Glycymeris), Monia (Anomiidae), and Pectinacea. In Anomia ephippium and also in Anomia aenigmatica (Bourne, 1907) this method prevails between the outer demibranchs and

the mantle, but the inner demibranchs are in organic union. In a fragment of gills labelled Placuna placenta(?) from the British Museum, the union of the dorsal edges of the inner ascending lamellae was of a compound nature, being mostly organic, but with an exceedingly short ciliary junction to the ventral side of the organic fusion (fig. 3 A, Pl. 29). This type of junction has been described also in Placuna placenta by Hornell (1909, p. 70), while Ridewood (1903, p. 199) has stated for the same species that the two inner lamellae of the inner demibranchs are not united at their upper edges, the gills in this differing from those of Anomia ephippium, with which they otherwise agree exactly. It is possible that if material is alcohol preserved, the two edges might very easily be torn apart, or perhaps the method varies in different regions; one or other of these suggestions may possibly be the explanation of the conflicting statements.

Retention of the primitive condition of freedom both of the posterior region of the gill axes, and of the upturned edges of the demibranchs from adjacent parts, in the otherwise highly evolved Pectinacea has been possibly dependent on the active habits of many of them; it allows of the supra- and infrabranchial chambers being thrown into one during swimming, thus preventing possible injury to the gills. It is known that preparatory to the clapping of the valves in swimming the extremities of the gills swing forward by contraction of the longitudinal muscles of the gill axes, and this obviously necessitates freedom from connexion of the gills with adjacent parts.

Division of the mantle chamber by ciliary contacts is found in Heteranomia squamula (Anomiidae) (Atkins, 1936), and in the Pteriacea, though not in the Ostreidae. The contradictory statements of various authors as to whether the lamellae are free from, or attached to, adjacent parts in members of the Pteriacea may be explained by the ciliary nature of the junction allowing of fairly easy separation of the opposed surfaces. Grobben in 1900 (pp. 493–5) had already recognized the ciliary nature of the junction in Pteria and Pinctada, and considered it to be universal in the Pteriidae, in which he included Isognomon, Crenatula, and Vulsella, but

his paper seems to have been overlooked by Ridewood (1903) and Herdman and Hornell (1904, 1905). To the forms examined by Grobben may be added Malleus albus. According to Ridewood (p. 206) in this species 'the upper edges of the ascending lamellae are free from adjacent parts', but 'the apex of the ctenidium is fused with the mantle edge'. In a specimen received from the Indian Museum, Calcutta, the dorsal edges of the ascending lamellae of the two inner demibranchs were in ciliary connexion: those of the outer demibranchs were joined to the mantle by the same means, but the left outer demibranch had become partly detached, probably in opening the animal. In the region where the gill axes are free the interlocking was especially strong: sections through the gill and mantle failed to reveal any organic union. On the mantle margin, in the position of the posterior tip of the gill, fragments of lamella remained attached to the mantle after removal of the gill; sections, however, showed that the union was entirely ciliary, and that the tips of the gills are not fused with the mantle margin as Ridewood supposed, unless this occurs in some individuals and not in others.

In certain of the Pteriidae and in the allied family Isognomonidae there is undoubted slight organic fusion, as well as ciliary junction, between the two inner demibranchs. In Pinctada vulgaris while the junction is mostly ciliary, to the ventral side of this there is a narrow organic bridge (Herdman, 1905, p. 227): this is also found in Isognomon alata (fig. 3 B, Pl. 29). A junction of a compound nature has already been described in Placuna placenta (Anomiidae), but in that instance the relative importance of the two kinds of union was reversed (see fig. 3, Pl. 29). In Pteria macroptera a compound ciliary and organic junction is found between the two inner gills, but apparently only for a certain length behind the visceral mass (Pelseneer, 1911, p. 25).

In the Pinnidae the division between the two mantle chambers is generally by ciliary contacts. This was found to be so in unspecified Pinna by Grobben (1900, p. 495) and Stenta (1903, p. 228), in Atrina rigida by Grave (1911, pp. 418–19), and in Pinna fragilis by myself. In the latter species, at least,

there is a marked difference in the strength of the union between the gills themselves in the middle line, and between the gills and the mantle: the former junction is easily dissolved in the living animal, the latter most difficult to separate; indeed it was thought that the union was organic until sections were made. Ridewood (1903, p. 214) stated that in Pinna nobilis the upper edge of the outer ascending lamella is fused with the mantle, though in the four other species he examined (Pinna pectinata (=fragilis), Pinna nigra, Pinna zealandica, Pinna virgata), it was free; it is not impossible that he may have been misled by a strong ciliary junction such as occurs in Pinna fragilis.

The gills being long and the axes free for much of their length in Malleus, Pinna, and others, it is understandable that the junction of the gills with the mantle is necessarily strong. If such gills become separated from the mantle it would probably be difficult for them to regain their position. In Pinna the weakness of the ciliary junction in the middle line will allow the supra- and infra-branchial chambers to be thrown into one—thus preventing injury to the gills—during burrowing, when water is violently expelled from the shell anteriorly.

In Ostrea alone is the division between the two mantle chambers entirely organic. Ostrea, which is in all probability the most highly evolved member of the group, at least as regards the gills, for there are no vestiges of ciliary interfilamentar junctions, has moderate-sized or anomalous latero-frontal cilia: these differ in certain respects from the eu-latero-frontal cilia occurring in bivalves outside the group (see p. 365).

To summarize: division of the mantle chamber is (*a*) by touching of the upturned edges of the demibranchs against adjacent parts in the Arcidae and the Pectinacea, and in Monia among the Anomiidae. While this condition is found between the outer demibranchs and the mantle in Placuna and Anomia, between the two inner demibranchs there is a compound ciliary and organic junction in the former, and an entirely organic junction in the latter. (*b*) By interlocking cilia in Heteranomia squamula (Anomiidae) and the Pteriacea, though there is also some slight organic fusion between the

two inner demibranchs in certain Pteriidae and Isognomonidae. (*c*) By entirely organic junction in the Ostreidae.

Forms with the first method of division of the mantle chamber have each gill, or the united gills, free from adjacent parts: such gills are generally borne on more or less deep suspensory membranes. Forms with the second and third methods of division have the gills more or less firmly attached to adjacent parts: such gills generally lack suspensory membranes (see p. 417).

6. Gills with the outer and inner demibranchs similar, in that there is no supra-axial extension to the outer demibranch, though the ascending lamella of both demibranchs may be as deep as the descending. In the Ostreidae, however, the ascending may be rather deeper than the descending lamellae, and this is especially noticeable in the outer demibranch of Ostrea angulata.

In the unrelated family Mytilidae the outer demibranch is also without a supra-axial extension, and possibly also in the Trigoniidae.

7. In those species of which it has been found possible to obtain living material, namely, members of the Arcidae, Anomiidae, Pectinidae, Limidae, Pteriidae, Pinnidae, and Ostreidae, it has been found that longitudinal currents are present at the free ventral edge of both inner and outer demibranchs (except the outer demibranch of Heteranomia), though these may be posterior in direction as in the Arcidae and Anomiidae. Also characteristic of the group, with the exception of the Pinnidae, is the presence of opposed frontal currents on all lamellae, frequently on the same filament (Atkins, 1936, 1937, 1937*a*). Outside the group this arrangement of frontal currents is found in the Solenidae (Atkins, 1936). In the Mytilidae investigated longitudinal currents are present at the free ventral edges of both demibranchs, but frontal currents are entirely ventralward. The presence of opposed frontal currents on all filaments but of certain lamellae only in Barnea candida, Petricola pholadiformis, Spisula subtruncata, Spisula elliptica, and Cultellus pellucidus has been shown to be a special adaptation (Atkins, 1937, 1937*a*).

8. Absence of pallial sutures. The mantle lobes are charac-

teristically free throughout their extent in the Arcidae, Anomiidae, Pteriidae, Isognomonidae, Amussiidae, Pectinidae, Spondylidae, Plicatulidae[1] (see Watson, 1930, p. 25), and Limidae. The right and left vela are fused for a certain distance from the hinge ventrally in the posterior region in Heteranomia squamula (Atkins, 1936), and anteriorly in certain species of Lima without byssal fixation (e.g. Lima hians). Slight fusion of the opposite mantle lobes in the region of the posterior tips of the gills occurs in the Pinnidae and in the Ostreidae. In Lima hians and Lima loscombi there is no fusion in this position, but the opposite vela are greatly increased in depth locally to form projections, which approach a pointed membraneous process of the postero-ventral region of the visceral mass, and which, even when the valves are widely gaping as usual in these species, make a partial, if not complete division between the exhalent and inhalent currents.

The degree of fusion between the two mantle lobes is probably more an adaptive character correlated with certain habits rather than a progressive one. The retention of the primitive condition of an open mantle in the group with micro-latero-frontal cilia is probably dependent on their being typically surface forms. Surface forms and mobile burrowers have retained a largely open mantle in spite of one or two sutures, though many of these among the Eulamellibranchs, have developed siphons. Such siphons, however, rarely attain more than a moderate length, and are generally partially or entirely united; when the siphons are very long and separate this is an adaptation to deposit feeding, as in the Tellinidae and Semelidae. An extensively closed mantle, mostly though not invariably accompanied by siphons, is found generally among burrowers and borers occupying more or less permanent holes, and perhaps has been developed largely as a means of increasing the strength of the expelled current on sudden closure of the valves, the fused mantle margin being withdrawn into, and thus causing reduction of, the infra-branchial chamber as described by Drew in Solenomya (1900) and Ensis (1907). It may be that such forms

[1] No member of this family was examined, but there is no reason to doubt that it is correctly placed in the Pectinacea.

need to be able to expel especially strong currents to keep their burrows clean and increase the depth: perhaps the arrangement compensates for the tendency of the adductor muscles toward contiguity to the hinge and to reduction in size, with consequent loss of power, evident in at least certain forms living in sheltered positions where there is no need for the shell to be tightly closed.

9. The inner fold of the mantle margin is commonly well developed, especially in swimming members where it forms a deep velum. The velum is deep in the Pectinidae, Amussiidae, Spondylidae, and Limidae; moderately deep in the Anomiidae, Pteriidae, and Ostreidae; narrow in the Isognomonidae; in Plicatula australis it is no more than 'a small ridge scarcely $\frac{1}{4}$ mm. in height' (Watson, 1930, p. 25).

10. The mantle is capable of withdrawing a considerable distance from the shell edge—that is, the retractor muscles of the mantle margin are inserted far from the shell edge—but to a much less extent in the Arcidae.

11. There is a tendency for members to lie on, or be attached by, the right valve.

Forms cemented by the right valve are, Spondylus, Chlamys distorta, and Plicatula australis.

Forms permanently attached by the byssus passing through a sinus in the right valve are, Anomia, Heteranomia, and Monia.

Forms temporarily attached by the byssus with the right side next the surface of attachment are, Isognomon, Malleus, Pteria, Pinctada, and certain Pectinidae.

Unattached forms lying on the right side are the free and swimming Pectinidae and the Amussiidae.

There is a difference of opinion as to the valve on which Placuna placenta (Anomiidae) lies: according to Hornell (1909, p. 46) it is the left convex valve; according to Fischer (1887, p. 933) it is the right. Jackson (1890) refers to Woodward as mentioning that, when young, Placuna has a byssal sinus in the right valve.

Apart from the uncertain case of Placuna, Ostrea seems to be alone in the group in lying on the left valve, which is cemented to the underlying surface. It is doubtful, however,

whether much importance should be attached to the habit of lying on, or being attached by, the right valve (for see Pelseneer, 1911, p. 86). Ostrea is then exceptional in the composition of the latero-frontal ciliated tract; in the method of division of the mantle chamber; in the poor development of the longitudinal muscles of the gill axis; and in making attachment by the left valve.

Some free and some attached forms generally maintain the valves in a vertical position, for example, Lima hians, Lima loscombi, and Arca. When at rest beneath the surface Glycymeris appears to lie indifferently on the right or left valve, and has been found occasionally more or less vertical.

12. The presence of abdominal sense organs on the posterior adductor muscle (see p. 402). The position of these organs, however, appears to be correlated with the absence of siphons, abdominal sense organs occurring in this position in asiphonate forms outside the group with micro-latero-frontal cilia, for example, in the Trigoniidae (Pelseneer, 1906, p. 237) and in the Mytilidae (Field, 1922, p. 175).

13. The auricles intercommunicate; the Anomiidae excepted. Intercommunication of the auricles is also found in most Mytilidae (Pelseneer, 1911, pp. 95, 120).

Suggested Modifications of the Classification of the Lamellibranchia.

I am loath to add further names to the classification of the Lamellibranchia, while unable to divide phylogenetically the great group with eu-latero-frontal cilia, but I am inclined to the opinion that two groups, Macrociliobranchia and Microciliobranchia should be provisionally introduced. In the Macrociliobranchia are placed the Protobranchia, the Filibranchia (emended to include the Mytilacea and Trigoniacea only), the Eulamellibranchia (Pelseneer, 1911), and the Septibranchia. It is very probable, however, that the emended Filibranchia is still diphyletic, as already pointed out (p. 394). The Septibranchia may provisionally be classed as an order of the Macrocilio-

branchia: this seems warranted by their probable origin from the Anatinacea (with eu-latero-frontal cilia). The disappearance of latero-frontal cilia in this order is no doubt to be correlated with the change in the mode of feeding. Small latero-frontal cilia have been noted in Poromya oregonensis by Ridewood (1903, p. 274), but it is probable that these should be regarded as vestiges of eu-latero-frontal cilia, rather than as true micro-latero-frontal cilia.

As previously mentioned (p. 413), the terms Filibranch and Eulamellibranch indicate stages in gill evolution, likely to occur in different lineages, and therefore their permanent retention as names of orders, Filibranchia and Eulamellibranchia, does not seem desirable, but until the Macrociliobranchia can be divided according to genetic affinities they must be retained, though lamellibranchs with filibranchiate and eulamellibranchiate gills occur in the other group, Microciliobranchia.

In the Microciliobranchia the Anomiacea, Pteriacea, Pectinacea, and Ostreacea appear to be more closely related to one another than they do to the Arcacea, but whether this is sufficient to warrant the creation of two orders, the order Pseudolamellibranchia (emended) lapsing, I am unable to determine. In order to introduce as few new names as possible the order Pseudolamellibranchia has been retained in an emended sense, in spite of its unsuitability, leaving the introduction of a new name until such time as the revision of the Macrociliobranchia is undertaken. Pelseneer recognized the Pseudolamellibranchia as a natural group, in spite of filibranchiate and eulamellibranchiate members, but he missed the link that connects them, namely, the characteristic composition of the latero-frontal ciliated tract, and omitted to include the Arcidae and Anomiidae.

The suggested classification of the Lamellibranchia is then as follows:

Class LAMELLIBRANCHIA.

Group I. MACROCILIOBRANCHIA. Latero-frontal tracts of the gill filaments or leaflets consisting of a row of eu-latero-frontal cilia, with also a row of pro-latero-frontal cilia in all or most members.

Order 1. PROTOBRANCHIA (Pelseneer): Nuculidae, Nuculanidae, Solenomyidae.

Order 2. FILIBRANCHIA (emended). Restricted to Filibranchs with latero-frontal tracts of the type described for the group. This order is the order Filibranchia of Pelseneer, less the Anomiacea, the Arcidae, and allied families.

Sub-order 1. MYTILACEA (Pelseneer, 1911). This is the Mytilacea of Pelseneer, 1906, less the Pernidae.

Sub-order 2. TRIGONIACEA. Gill filaments with distinctive arrangement of the ciliary tracts, see p. 381. Trigoniidae.

Order 3. EULAMELLIBRANCHIA (Pelseneer, 1891, 1892, 1911, not 1906).

Order 4. SEPTIBRANCHIA (Pelseneer).

Group II. MICROCILIOBRANCHIA. Latero-frontal tracts of the gill filaments consisting characteristically of a row of micro-latero-frontal cilia.

Order 1. PSEUDOLAMELLIBRANCHIA (emended). This order is the order Pseudolamellibranchia of Pelseneer, 1911, emended to include those Filibranchs (Anomiacea, Arcidae, and allied families) with latero-frontal tracts of the type described for the group.

Sub-order 1. ARCACEA (emended). This sub-order is the Arcacea of Pelseneer less the Trigoniidae and allied families.

Sub-order 2. ANOMIACEA (Pelseneer).

Sub-order 3. PTERIACEA, including the Pinnidae (= Aviculacea of Pelseneer, 1911, less the Ostreidae).

Sub-order 4. PECTINACEA, including the Limidae (Pelseneer, 1911).

Sub-order 5. OSTREACEA. Latero-frontal tract consisting of anomalous together with para-latero-frontal cilia. Ostreidae.

Pelseneer (1911) and Douvillé (1912*a*) have both given diagrams illustrating their conceptions of the phylogeny of the Lamellibranchia as a whole; Jackson (1890) gave only that of the Aviculidae and their allies.

In Pelseneer's diagram there is a single tree with many branches, and the divisions (orders) are horizontal and indicate stages in the evolution of the gills. The Filibranchia are shown

as derived from the Nuculidae; the Pseudolamellibranchia from the common ancestor of the Mytilidae and the Arcidae; the Eulamellibranchia from the Mytilidae by way of the Astartidae; and the Septibranchia from the Anatinacea. Comments on this classification have been made on pp. 394–398.

Douvillé, on the other hand, recognized three divergent branches from the beginning, corresponding to the three principal modes of life of the class, which he held early impressed on the branches certain characters which tended to persist through later secondary modifications. The three branches are:

(1) the 'normal' branch, more or less active and free living, descended from 'formes primitives nacrées normales' by way of forms like Actinodonta;

(2) the 'sedentary' branch affected by byssal fixation, descended from 'formes primitives nacrées fixées' by way of the Pterineidae; the Arcidae being connected with these through Palaearca (=Cypricardites); and

(3) the 'burrowing' branch modified by a protected life in a more or less permanent burrow, descended from 'formes primitives nacrées cavicoles' by way of the Solenopsidae, Protomyidae, and Grammysiidae. His divisions are thus vertical. Davies (1933) has recently given a clear exposition, with diagrams, of Douvillé's scheme of classification and compared it with several other well-known classifications, so that there is no need to enter into it fully here. At present the only modifications of Douvillé's phylogeny that I am able to suggest are two: (*a*) the exclusion of the Mytilidae from the 'sedentary' branch. Though the condition of the latero-frontal tract shows that this family belongs to the Macrociliobranchia, yet it gives no indication of its allies, nor does the pattern of the lateral ciliated cells, which is not of the common type found among the 'normal' and 'burrowing' branches. Dall (in the Eastman edition of Zittel, 1913, p. 462) suggested that the prototypes of the Mytilidae are to be found in the Modiolopsidae: Douvillé placed Modiolopsis in his 'normal' branch (though placing the Mytilidae in the 'sedentary' branch): this perhaps indicates where the allies of the Mytilidae should be sought. And (*b*) that possibly the 'burrowing' branch is not as widely separated from the

'normal' branch as is indicated in his diagram, a conclusion suggested by the character of the latero-frontal tract and the pattern of the lateral ciliated cells. A certain pattern of the lateral cells is common among both 'normal' and 'burrowing' branches, though it is not the only pattern found among these; the Mytilidae, Trigoniidae, Astartidae, Unionidae, and Aetheriidae having patterns different from the common one (Atkins, 1938*a*). I think the work recorded in this paper also shows that Nucula cannot be regarded as broadly ancestral to the 'sedentary' branch.

Summary.

Certain Lamellibranchs have the latero-frontal tract composed of large complex 'cilia', here called eu-latero-frontal cilia, together with subsidiary ones, termed pro-latero-frontal cilia. This type of latero-frontal tract occurs in some or all of the three families of Protobranchs (there is some doubt as to the presence of pro-latero-frontal cilia in all the families), and in the Mytilidae and probably the Trigoniidae (fixation too imperfect for the identification of pro-latero-frontal cilia) among the Filibranchs, and in all the marine families of Eulamellibranchs obtainable at Plymouth, and in the fresh-water families, Dreissensiidae, Sphaeriidae, Unionidae, Mutelidae, and Aetheriidae. A list of the species investigated is given.

Other Lamellibranchs, which were previously considered as lacking latero-frontal cilia, have been found to possess small ones only, difficult of observation, termed micro-latero-frontal cilia. These occur in the Arcidae, Anomiidae, Pteriidae, Pectinidae, Spondylidae, Limidae, Pinnidae, and are inferred to be present in the Amussiidae, Vulsellidae, and Isognomonidae, in which eu-latero-frontal cilia are certainly absent. A list of the species examined is given.

In one family, the Ostreidae, moderate-sized latero-frontal cilia, termed anomalous latero-frontal cilia, together with subsidiary ones, termed para-latero-frontal cilia are present.

In bivalves having eu-latero-frontal cilia the arrangement of

the various ciliary tracts, frontal, latero-frontal, and lateral is fairly constant, notable exceptions being a Protobranch, Nuculana, and a Filibranch, Trigonia. In bivalves having micro-latero-frontal cilia the arrangement of the various tracts seems more or less constant.

The homology of the various types of latero-frontal cilia is discussed. The composition of the latero-frontal ciliated tracts has been found to be a stable character, and, as it is correlated with other characters, has taxonomic value.

It is suggested that the variations in the constitution of the latero-frontal tracts tend to show that Ridewood's (1903) classification does not express genetic affinities, as he himself conceded, nor does Pelseneer's (1911) entirely, and that Pelseneer's order Filibranchia, and Ridewood's orders Eleutherorhabda and Synaptorhabda are not monophyletic.

Families possessing micro-latero-frontal cilia appear to be closely related, and form a group, which, with certain modifications, corresponds to 'the Aviculidae and their allies', or the 'sedentary' branch of Lamellibranchs, previously established by the palaeontologists, Jackson and Douvillé respectively, largely on shell characters. Thus the constitution of the latero-frontal tracts of the gill filaments supports the findings of palaeontologists with regard to this group. Unfortunately neither Jackson nor Douvillé proposed a formal name for the group.

The relationship of forms with micro-latero-frontal cilia, and the evolution within the group of the eulamellibranchiate or synaptorhabdic gill are discussed. One family, the Ostreidae, which must be included on account of its relationship with either the Pteriacea or Pectinacea (based on other evidence) has moderate-sized, or anomalous latero-frontal cilia together with para-latero-frontal cilia. The anomalous latero-frontal cilia differ in certain respects from the large cilia characteristic of the majority of the Lamellibranchia, and are presumed to have arisen independently.

Common characters of the group characterized by the possession of micro-latero-frontal cilia, in addition to the form of the latero-frontal cilia, are: (1) shell characters of the prodissoconch,

Arcidae excepted; (2) byssal fixation; (3) considerable free posterior region to the gill axes; (4) considerable development of muscles in the gill axes, Ostreidae excepted; (5) method of division of the pallial cavity, Ostreidae excepted; (6) gills without a supra-axial extension to the outer demibranch; (7) presence of longitudinal currents at the free ventral edge of both inner and outer demibranchs; and of opposed frontal currents on all lamellae and frequently on the same filament, Pinnidae excepted; (8) absence of pallial sutures, Pinnidae and Ostreidae excepted; (9) inner fold of the mantle margin characteristically well developed, especially in swimming forms; (10) insertion of the retractor muscles of the mantle margin at a considerable distance from the shell edge, Arcidae excepted; (11) tendency for members, except the Ostreidae, to lie on the right valve; (12) abdominal sense organs on the posterior adductor muscle; and (13) intercommunication of the auricles, Anomiidae excepted.

Two groups of the Lamellibranchia are proposed provisionally, namely Group I, Macrociliobranchia, including the orders Protobranchia (Pelseneer), Filibranchia (emended to include only the Mytilacea and Trigoniacea), Eulamellibranchia (Pelseneer, 1911), and Septibranchia (Pelseneer); and Group II, Microciliobranchia, with the order Pseudolamellibranchia, emended to include the sub-orders Arcacea (excluding the Trigoniidae), Anomiacea, Pteriacea, Pectinacea, and Ostreacea. The Macrociliobranchia will need revision, for it is very probable that the Filibranchia (emended), if not the Eulamellibranchia, are still not monophyletic.

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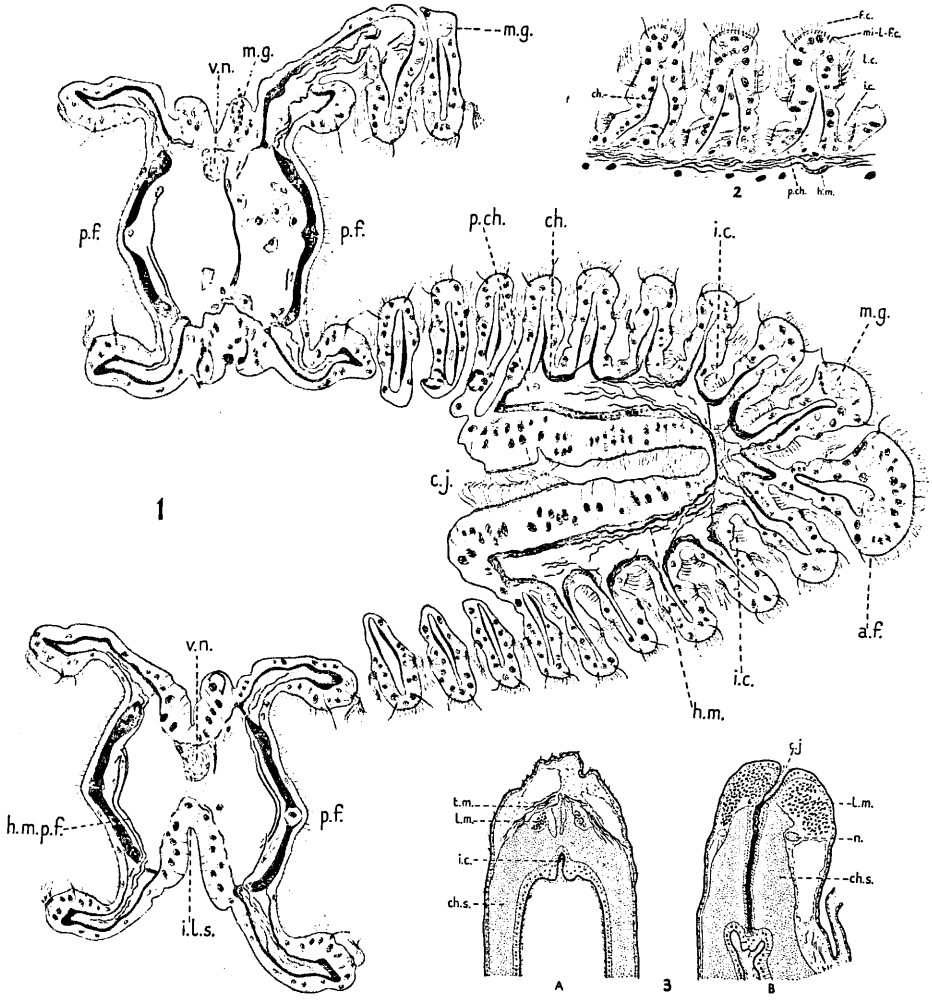
EXPLANATION OF PLATE 29

Fig. 1.—Lima hians. Transverse section of a plica to show vestiges of ciliary interfilamentar junctions (*i.c.*), ciliary junction between two limbs of a plica (*c.j.*), and muscle fibres. *a.f.*, apical filament; *ch.*, darkly staining chitin; *h.m.*, horizontal muscle-fibres of interfilamentar junctions;

h.m.p.f., horizontal muscle-fibres of principal filaments; *i.l.s.*, interlamellar septum; *m.g.*, mucous gland; *p.ch.*, pale-staining chitin; *p.f.*, principal filament; *v.n.*, vertical nerve. Bouin-Duboscq's fixative; iron haematoxylin and acid fuchsin. ×344.

Fig. 2.—Pinna fragilis. Transverse section of three filaments, showing micro-latero-frontal cilia (*mi-l-f.c.*) and vestiges of ciliary interfilamentar junctions (*i.c.*). *ch.*, chitin; *f.c.*, frontal cilia; *h.m.*, horizontal muscle-fibres; *l.c.*, lateral cilia; *p.ch.*, pale-staining chitin. Bouin-Duboscq's fixative; iron haematoxylin and acid fuchsin. ×ca. 262.

Fig. 3.—Transverse section of junction between dorsal edges of ascending lamellae of two inner demibranchs. A, Placuna placenta (?). The union is mostly organic but with a short ciliary junction ventrally. B, Isognomon alata. The junction is mostly ciliary but with a short organic union ventrally. *c.j.*, ciliary junction; *ch.s.*, chitinous supporting structure; *i.c.*, interlocking cilia; *l.m.*, longitudinal muscle; *n.*, nerve; *t.m.*, transverse muscle-fibres. Alcohol fixation; iron haematoxylin and acid fuchsin. ×ca. 56.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Printed in Great Britain by John Johnson at the OXFORD UNIVERSITY PRESS