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*.

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With 35 Figures in the Text.

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

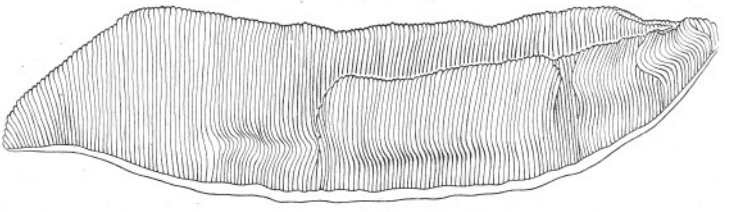


Fig. 1.—Sketch of the right inner gill of an uninfected* *Mytilus edulis* from Trelissick Reach, Fal River, showing a large fold—composed of three folds in series—on the ascending lamella. From preserved material. ×3.

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

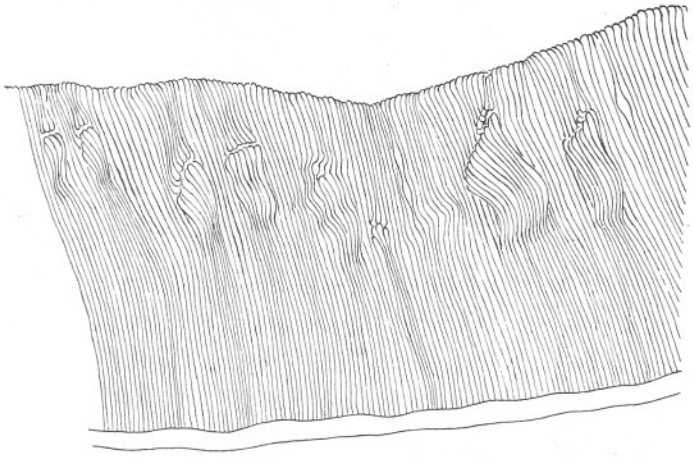


FIG. 2.—Sketch of part of a gill of an uninfected Mytilus from Trelissick Reach, Fal River, showing a series of small folds or pockets on the ascending lamella. From preserved material. ×4.

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

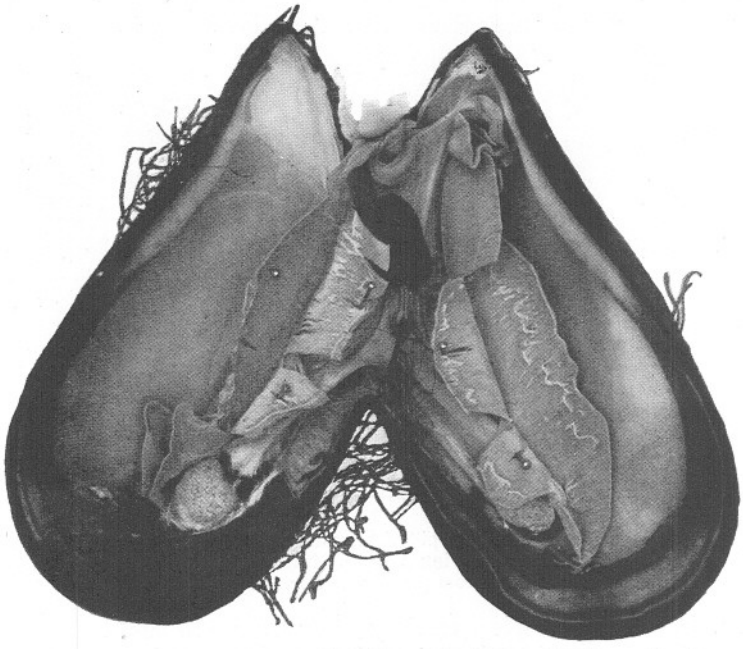


Fig. 3.—Photograph of a mussel (10·0 cm. long) from Padstow, showing numerous secondary food grooves on the descending lamellæ of the gills. In some places the free edge of the two right gills is permanently folded over. From preserved material.

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

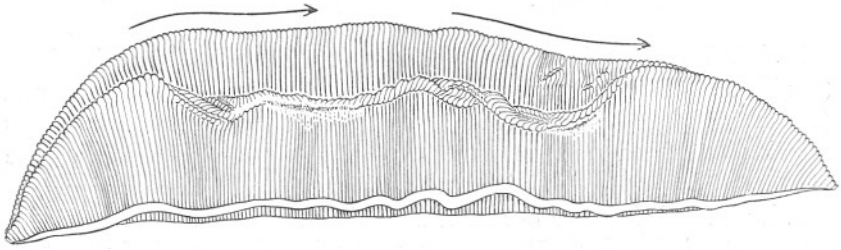


FIG. 4.—View of gills of the right side of a Padstow mussel, which harboured a large ♀ *Pinnotheres pisum*. The inner gill is short for most of its length, the free edge is in part folded over ; in one place a food groove is wanting and considerable fusion of the filaments has occurred, while elsewhere 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

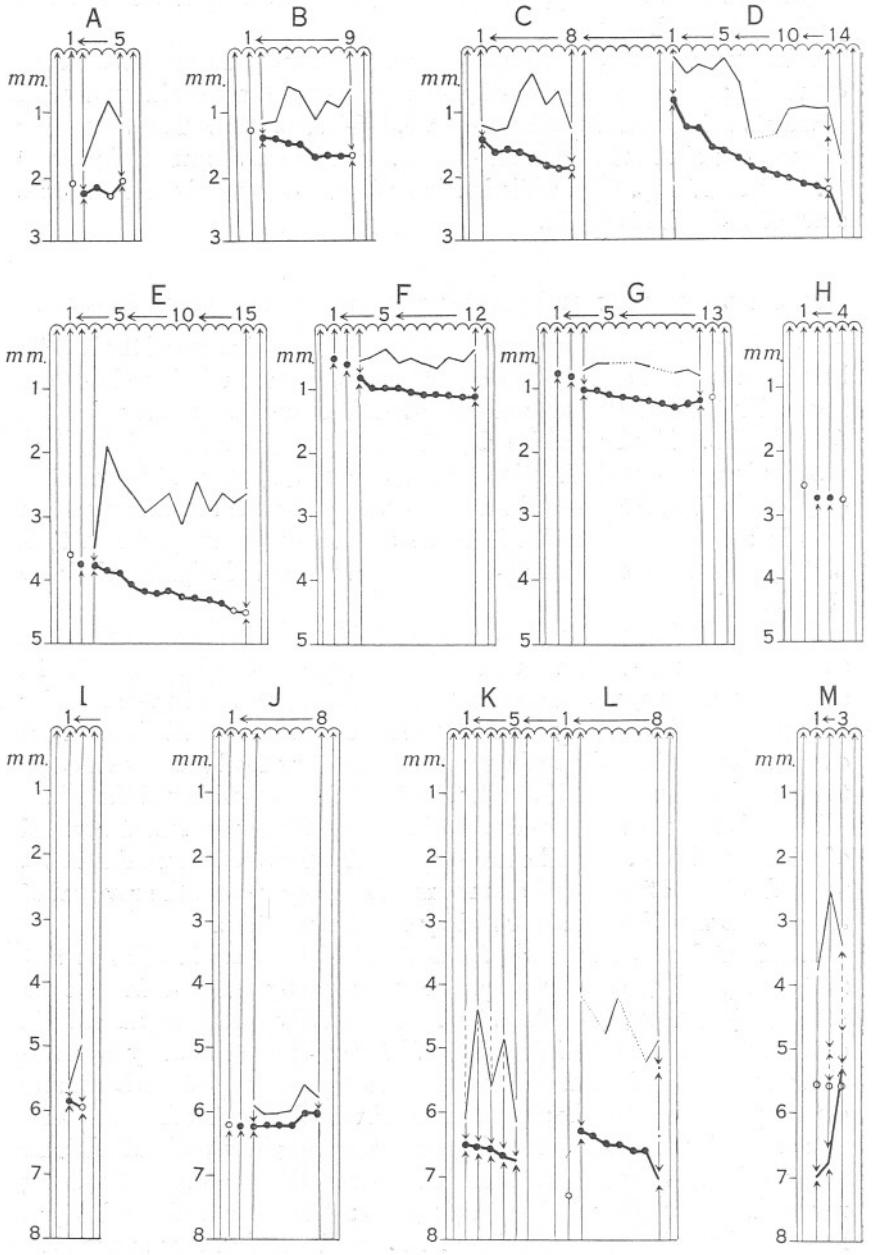


FIG. 6 (description opposite).

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, G „ L3, H „ L3 } of different specimens of Mytilus.

F „ L3, 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

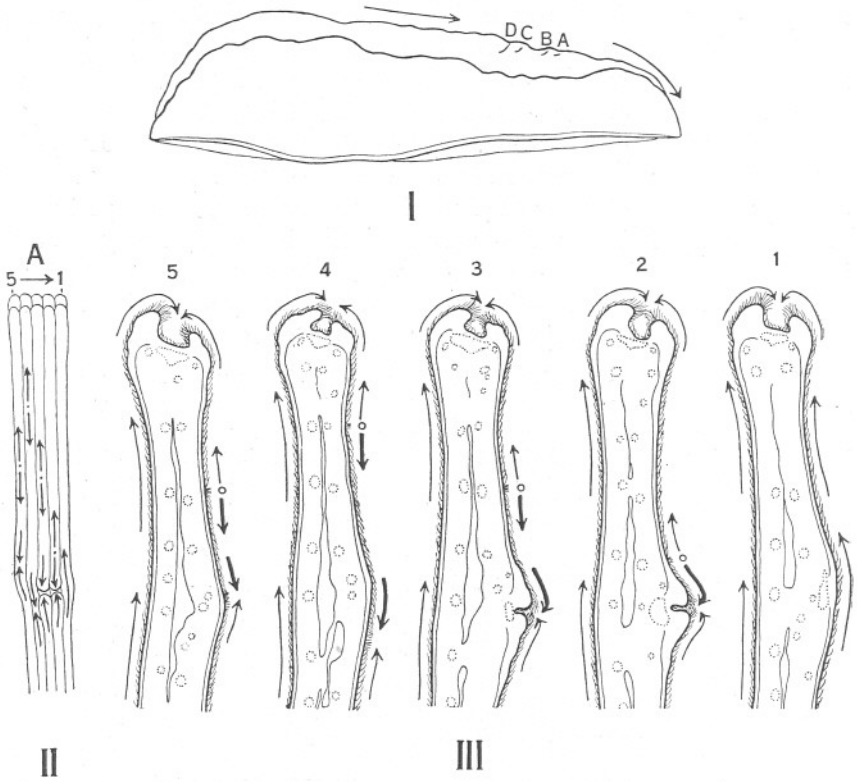


Fig. 7.—I. Sketch of gills of the right side of an infected Mytilus to show the position of the secondary food grooves A–D. The arrows indicate the direction of the current in the main food groves. From life, natural size.

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

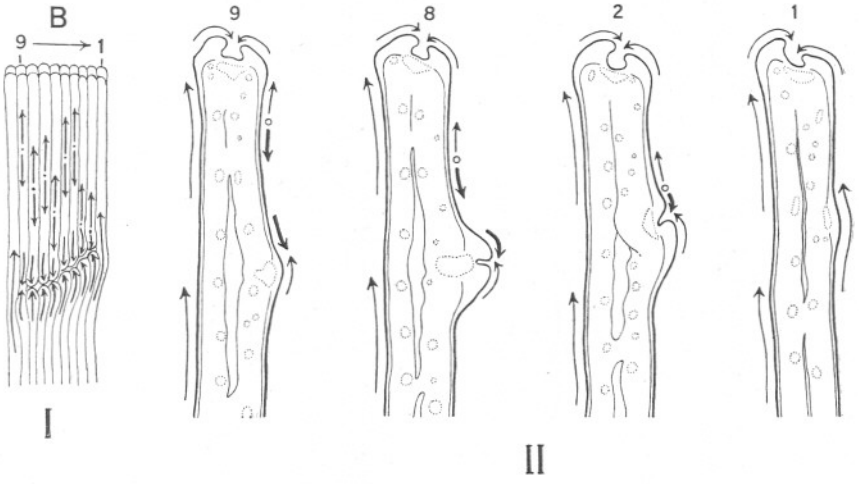


FIG. 8.—I. Surface view of filaments composing the secondary groove B (see Fig. 7, I).
II. Lateral views of representative living filaments. I–II × 18¼.

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

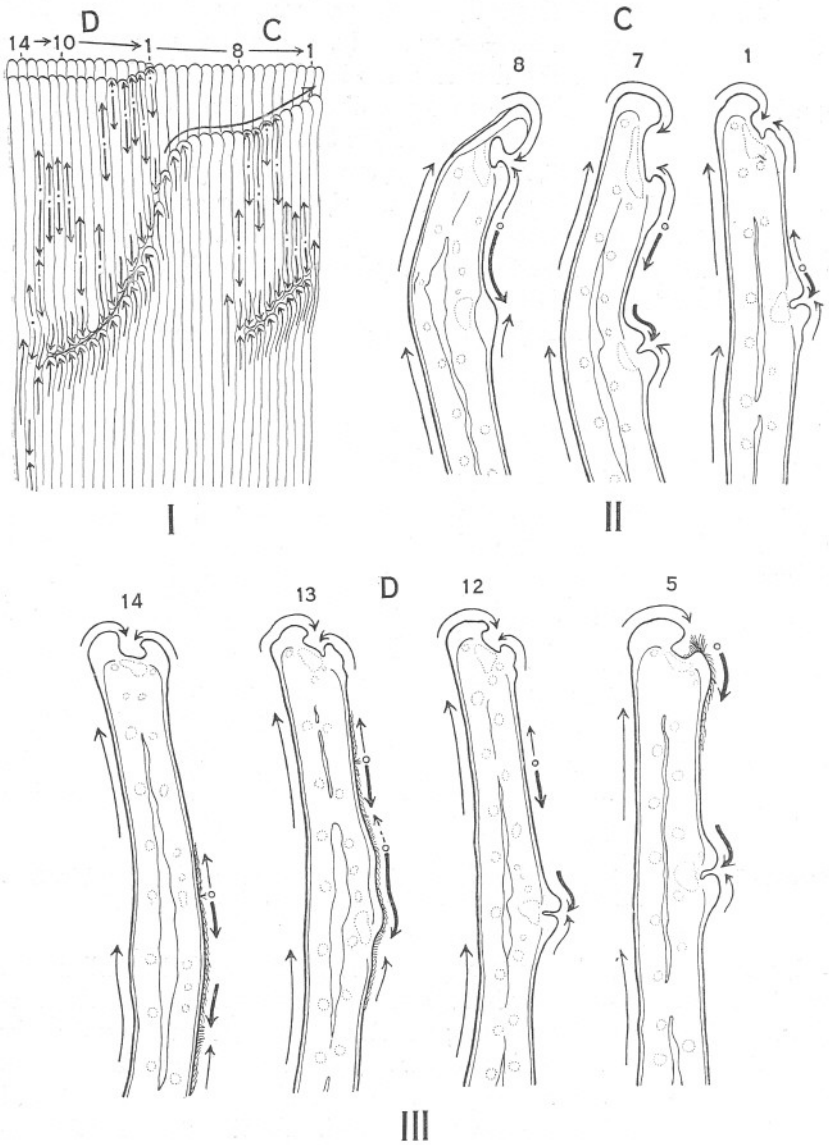


FIG. 9.—Secondary grooves C and D of the gill sketched in Fig. 7, I × 18½.

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

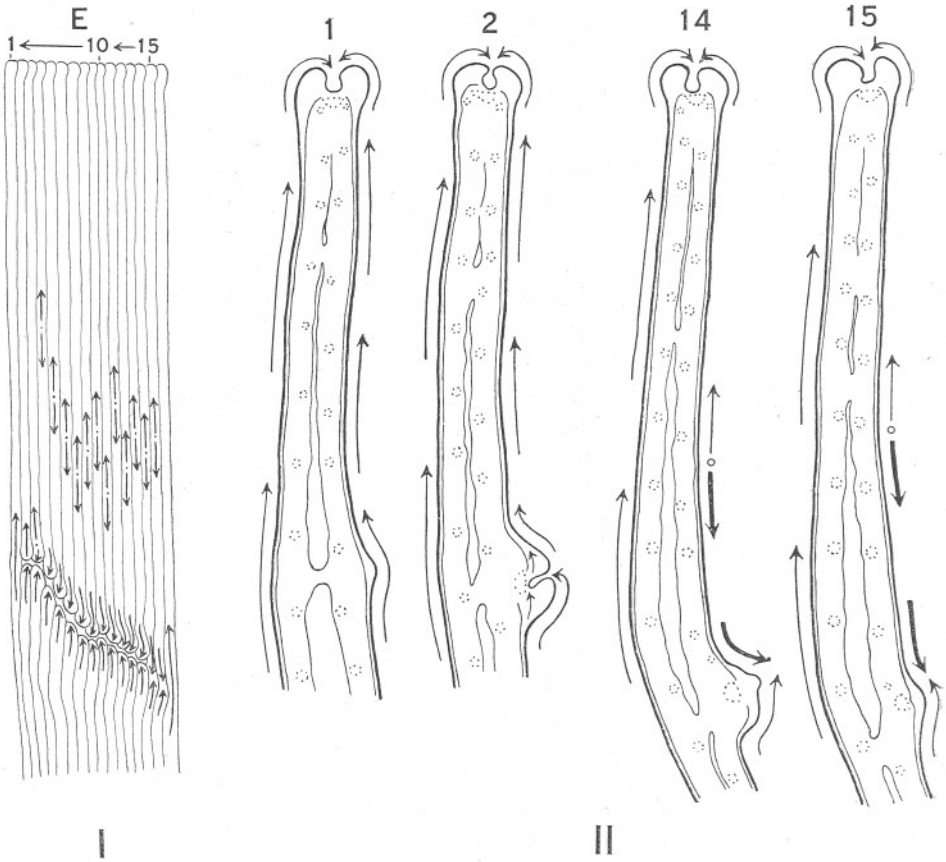


FIG. 10.—I. Surface view of filaments composing a secondary groove (E) on the descending lamella, left outer gill of an infected Mytilus.
II. Lateral views of certain of the living filaments.
I–II × ca. 18¼.

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

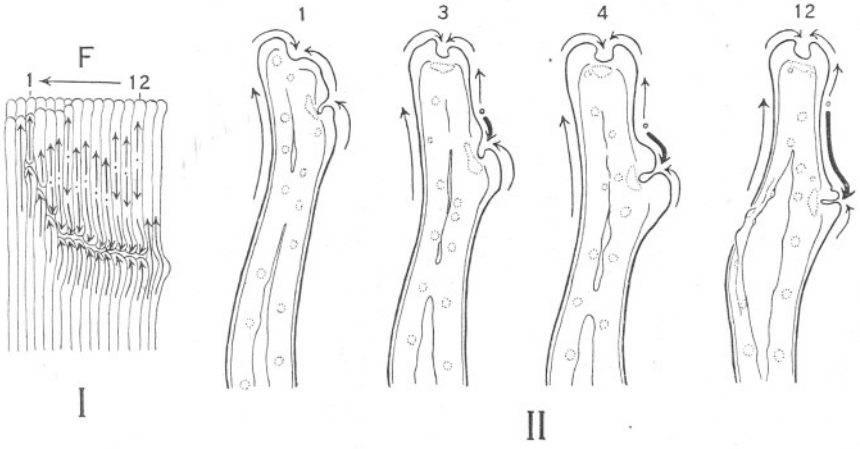


FIG. 11.—I. Surface view of filaments composing a secondary groove (F) on the descending lamella, left outer gill of an infected Mytilus.
II. Lateral views of representative living filaments.
I–II × 18¼.

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

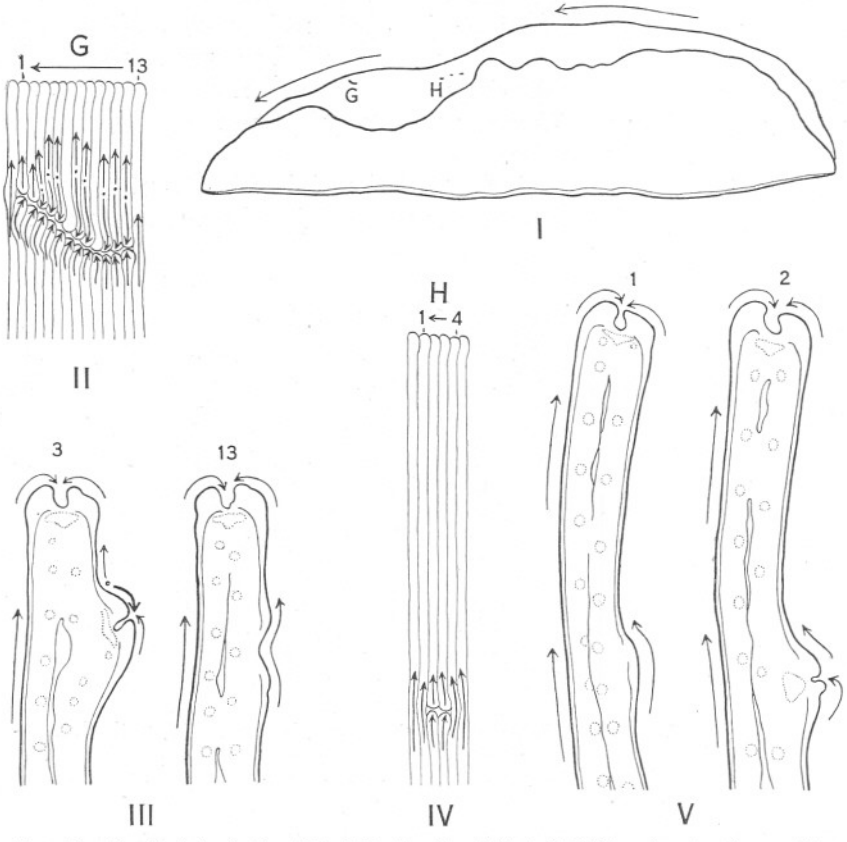


FIG. 12.—I. Sketch of gills of the left side of an infected Mytilus, showing the position of secondary grooves (those investigated are lettered) on the descending lamella of the outer gill where it was exposed owing to the shortness of the inner gill. From life.

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

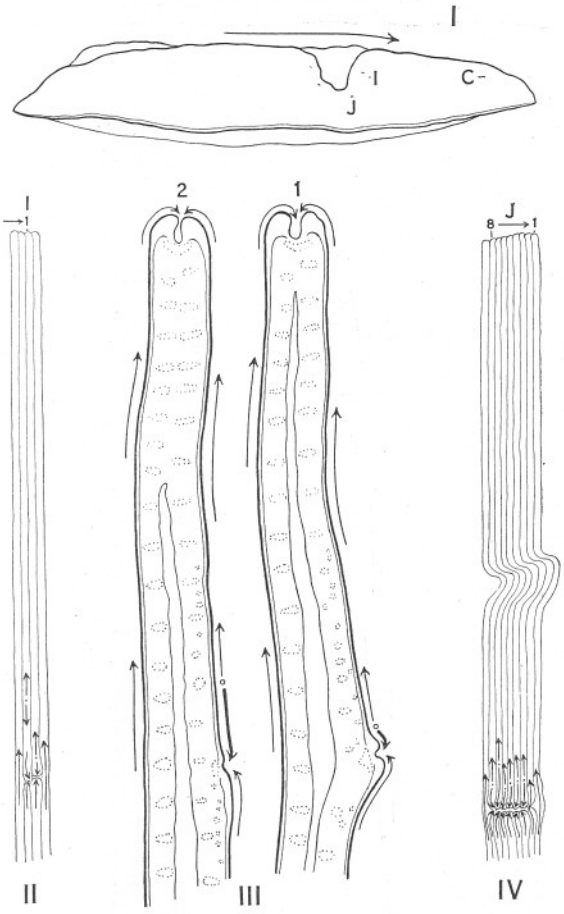


FIG. 13.—I. Sketch of gills of the right side of a specimen of *Modiolus modiolus*, which harboured a large female Pinnotheres, showing shortness of the inner gill in a small V-shaped area and several secondary grooves : those investigated are lettered ; I and J are on the ascending lamella of the inner gill, and C indicates the position of a secondary groove on the ascending lamella of the outer gill. Drawn from life. $\times \frac{2}{3}$

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 $\times$ 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*

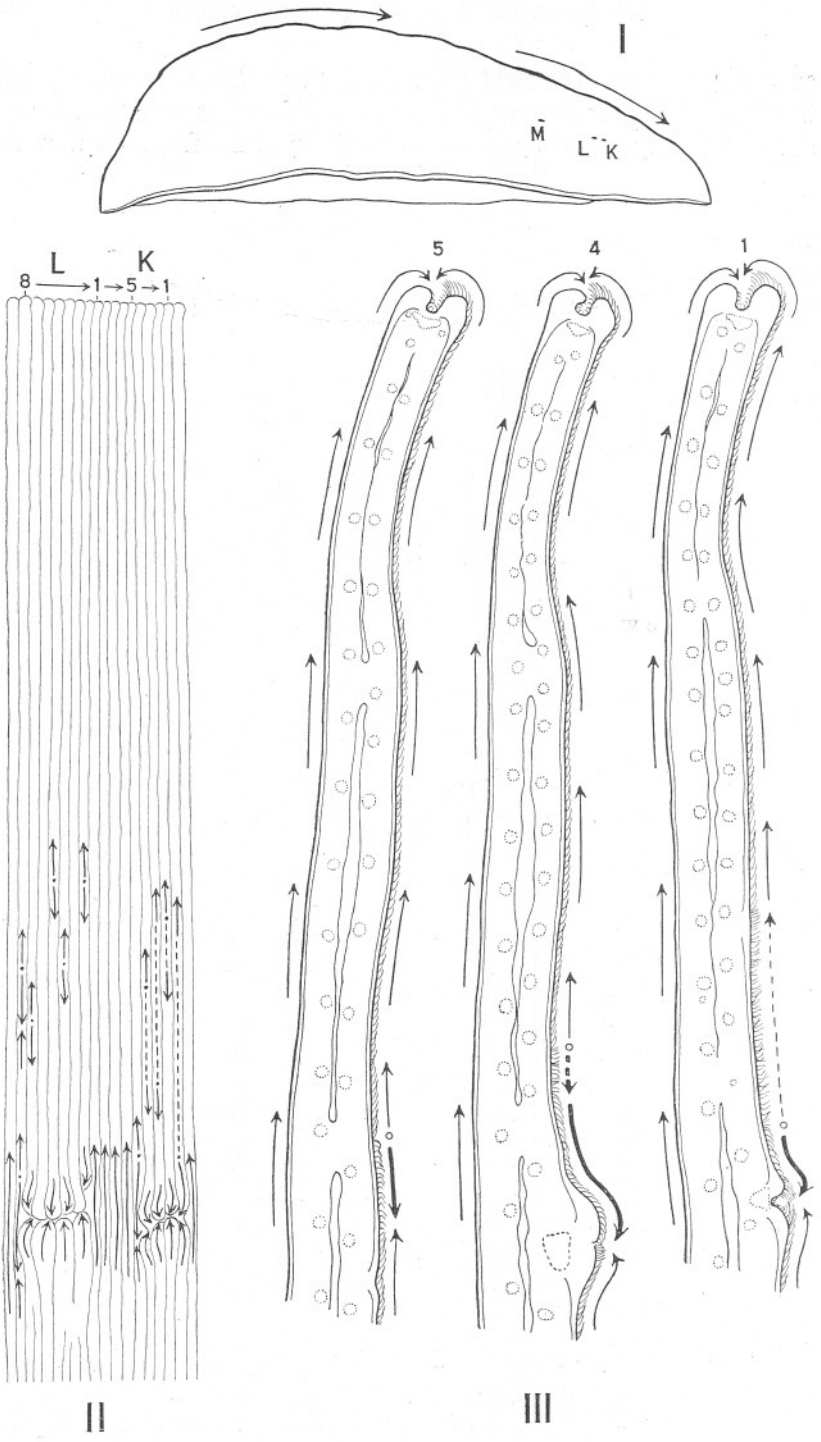


FIG. 14 (description opposite).

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 × 18¼.

* 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.

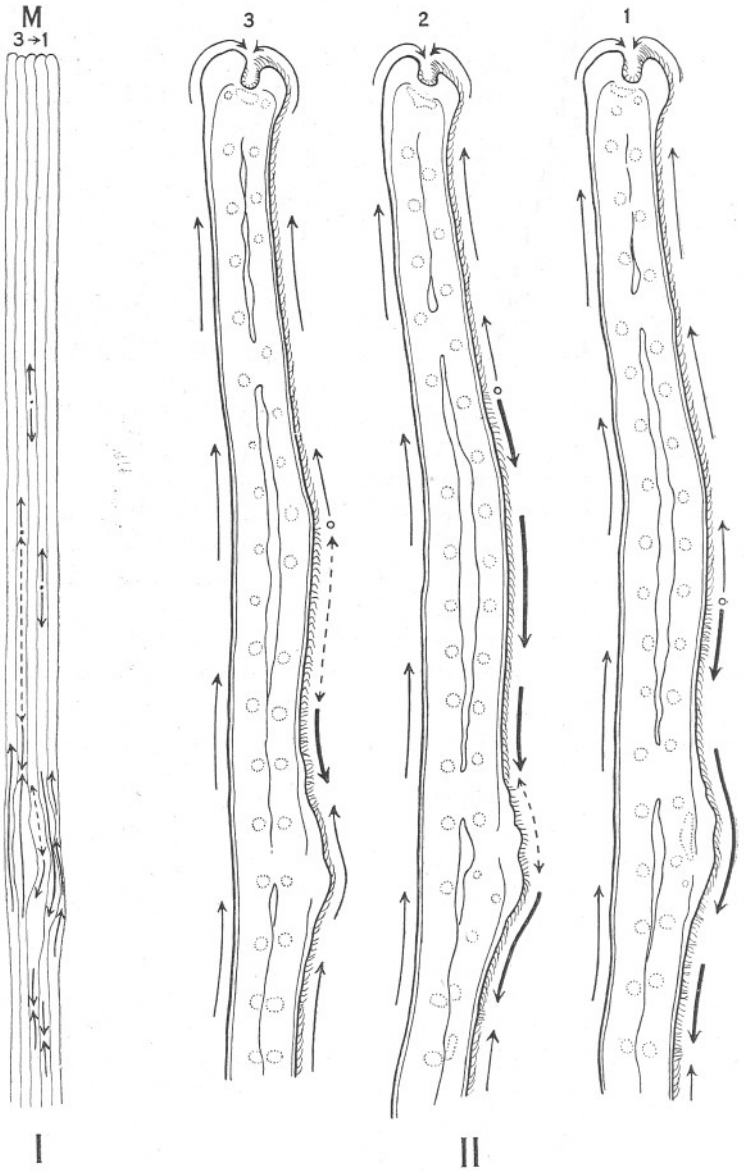


FIG. 15.—I. Surface view of filaments composing the region of enlarged filaments M (see Fig. 14 I). The double-headed arrows indicate stretches over which the current caused by the frontal cilia passed at different times in opposite directions.
II. Lateral views of three living filaments of this region.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

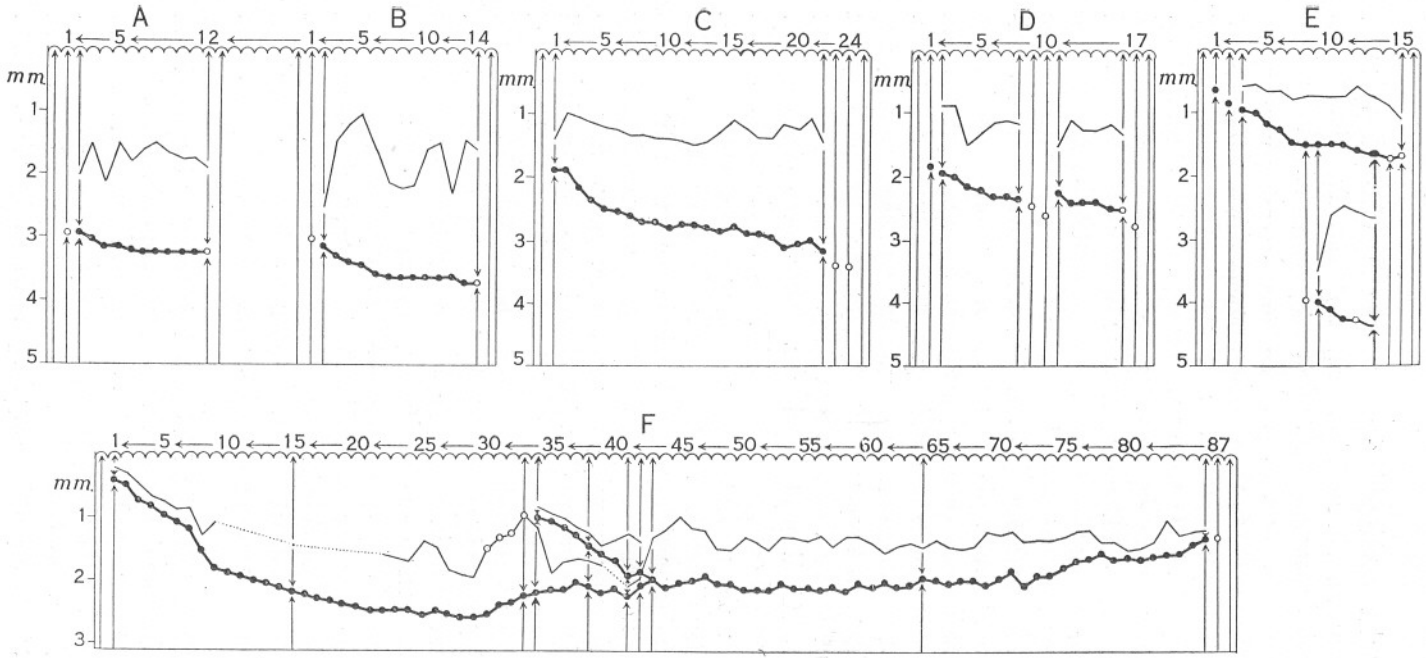


FIG. 16.—Graphs showing the relation of the distance of a secondary groove—raised on a slight projection above the surface of the lamella—from the main food groove, and the points of reversal of the frontal cilia on filaments composing the secondary groove. The direction of beat of the frontal cilia 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

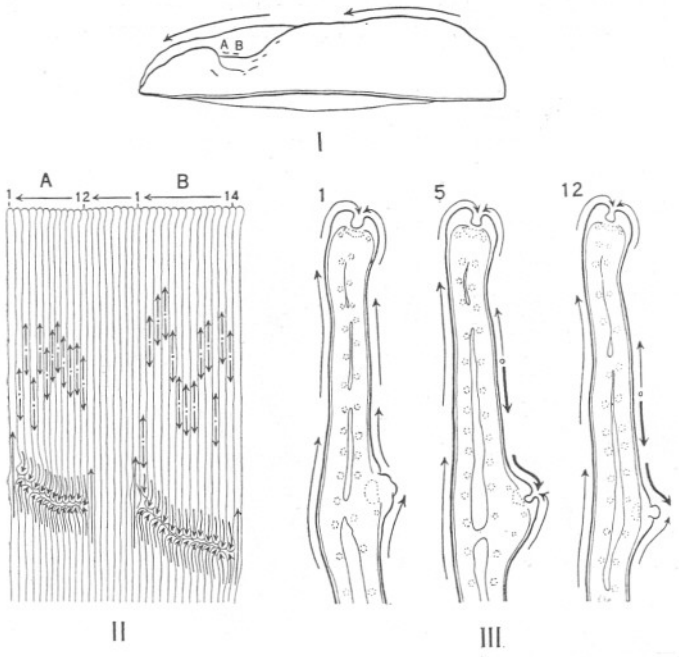


FIG. 17.—I. Sketch of gills of the left side of an infected Mytilus, showing shortness of the inner gill and several secondary food grooves. The two investigated, A and B, are on the descending lamella of the outer gill where it is exposed owing to the shortness of the inner gill. From life, $\times \frac{2}{3}$.
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

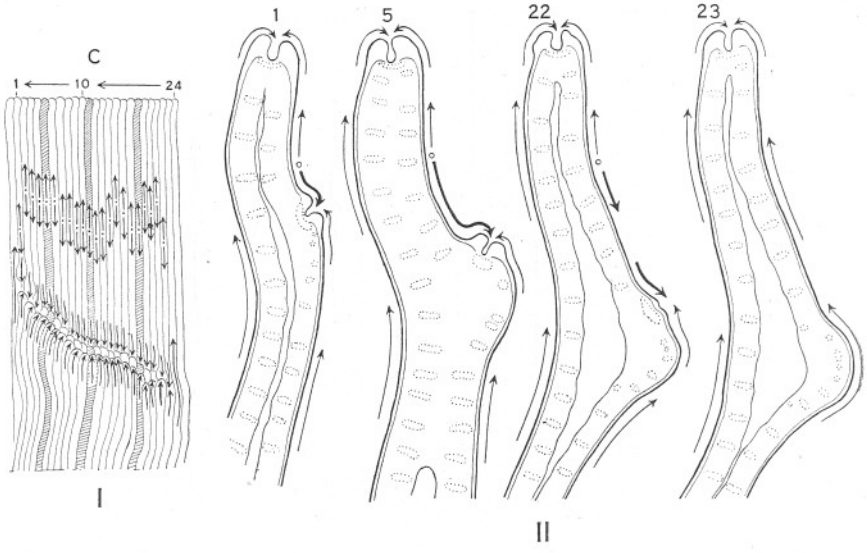


Fig. 18.—*Modiolus modiolus*.

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

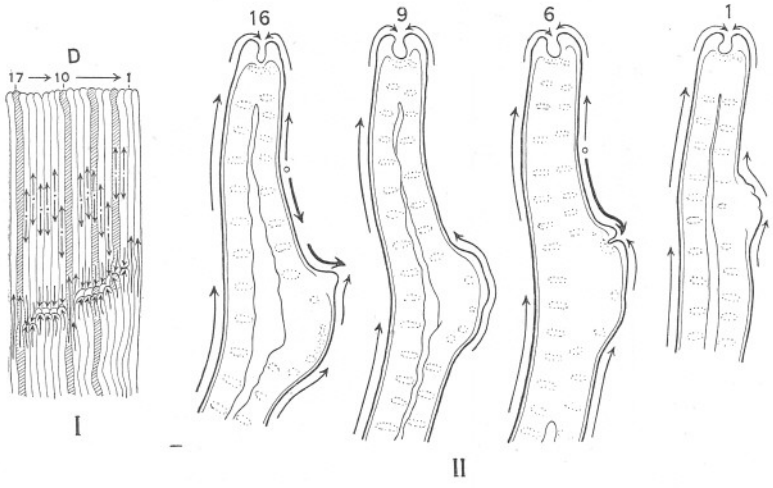


FIG. 19.—*Modiolus modiolus.*

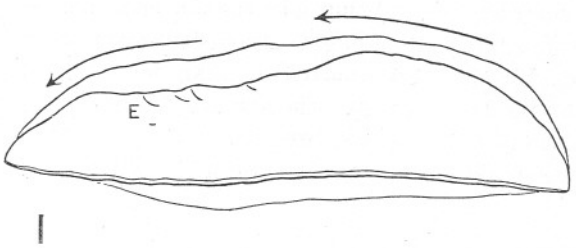
I. Surface view of filaments composing secondary groove D. This was on the ascending lamella of the outer left gill in a similar position to that of secondary groove C on the right gill (see Fig. 13 I, p. 937). The septate filaments are indicated by shading.

II. Lateral views of representative living filaments.

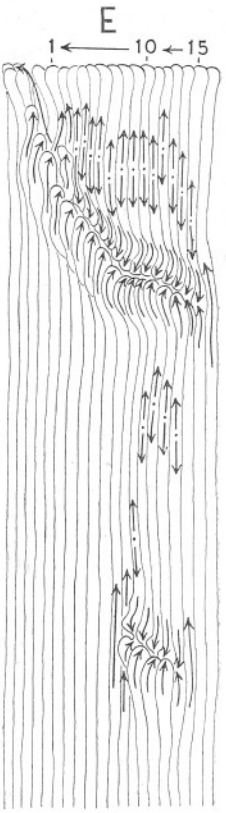
I–II × ca. 12.

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. 18¼.

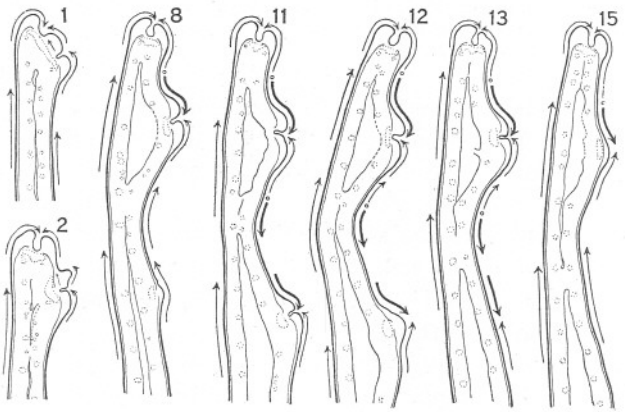


FIG. 21.—Lateral views of certain of the living filaments from the secondary grooves E (see Fig. 20). × ca. 9.

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

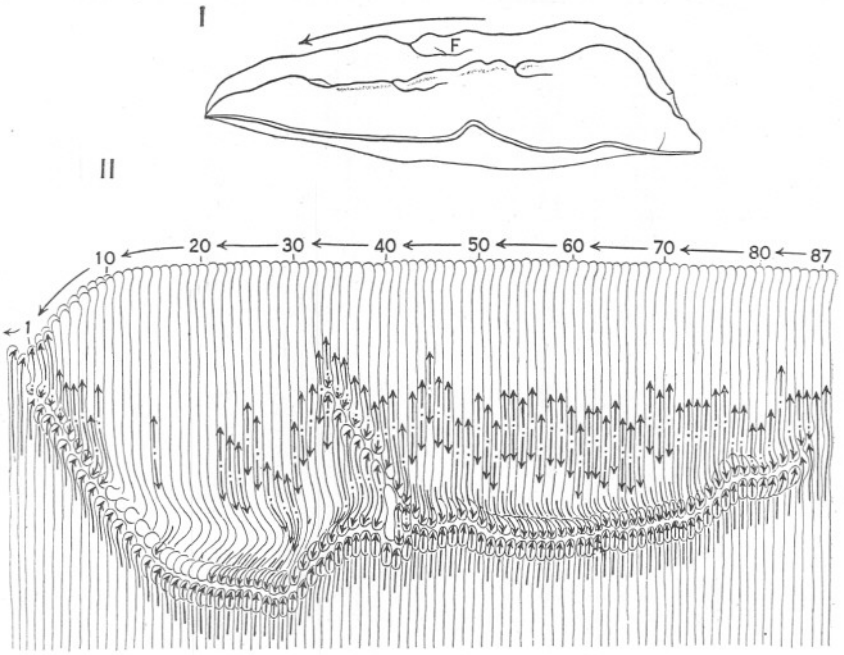


FIG. 22.—I. Sketch of left gills of an infected Mytilus, showing secondary grooves; that marked F was investigated. The stippling indicates abnormally heavy pigmentation. From life, natural size.

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. 18¼.

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

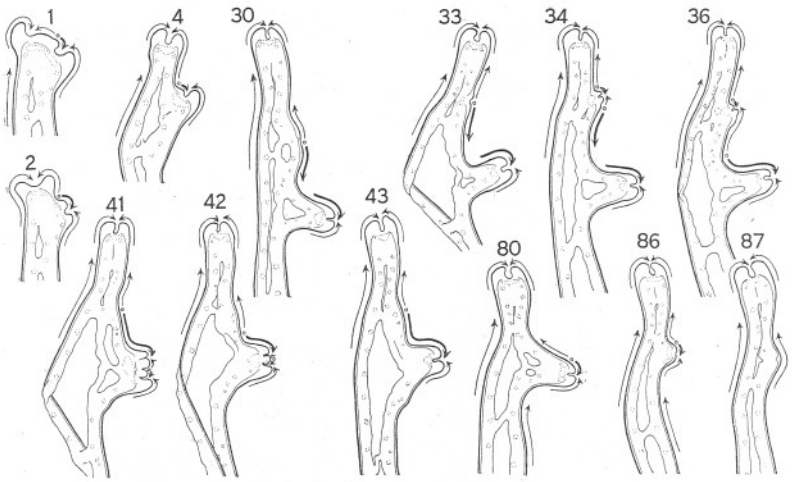


FIG. 23.—Lateral views of representative living filaments of secondary groove F (see Fig. 22). There was a tendency for the non-groove-bearing filament to be longer than that bearing the secondary groove, which made the spreading of the filaments on the slide for examination difficult. × ca. 9.

descending filaments) 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

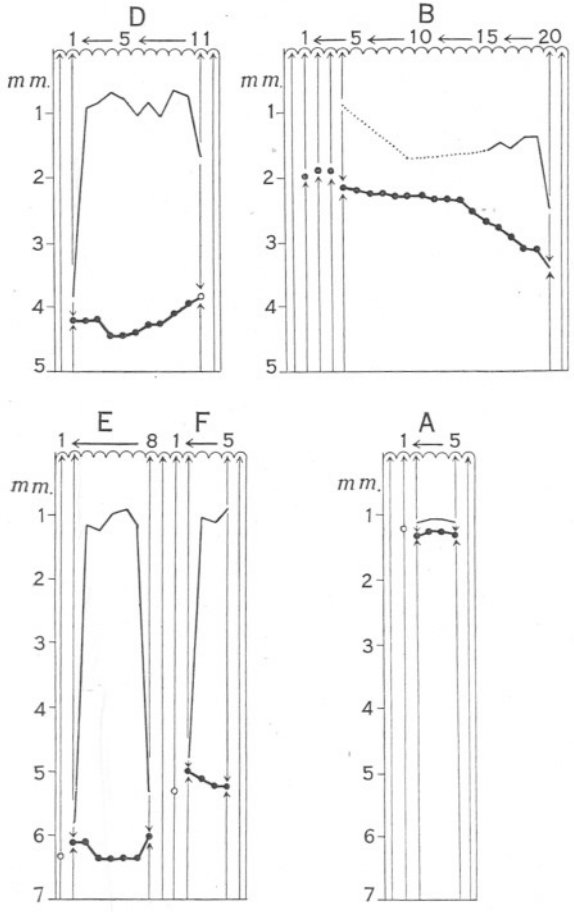


FIG. 24.—Graphs showing the relation of the distance of a secondary groove—on the edge of a secondary fold—from the main food groove on the gill of *Mytilus edulis*, and the points of reversal of the frontal cilia on filaments composing the secondary groove. The direction of beat of the frontal cilia 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

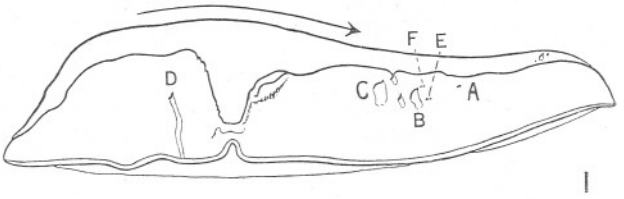
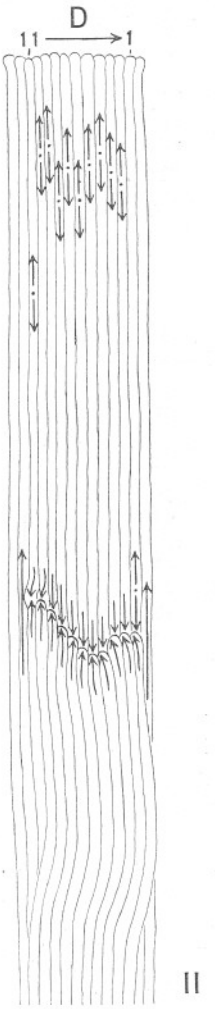


FIG. 25.



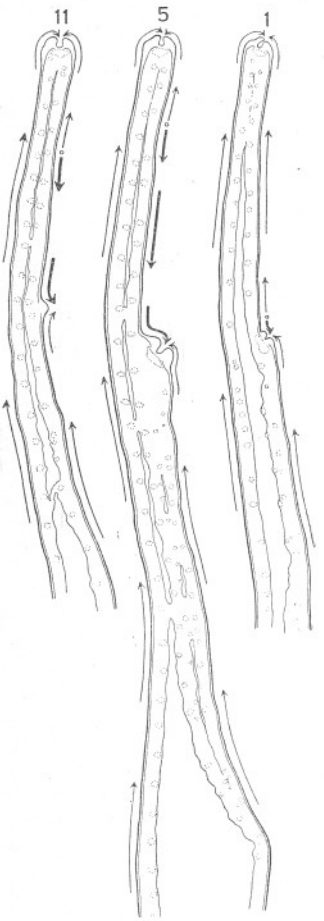


FIG. 25.—I. Sketch of gill of right side from an infected Mytilus, showing shortness of the inner gill and several secondary grooves and folds. Those investigated are lettered; E and F indicates the position of two secondary grooves on the descending lamella of the outer gill. The stippling indicates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

II. Surface view of filaments composing secondary groove D. ×18¼.

FIG. 26.—Lateral views of representative living filaments of secondary groove D (see Fig. 25). × 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

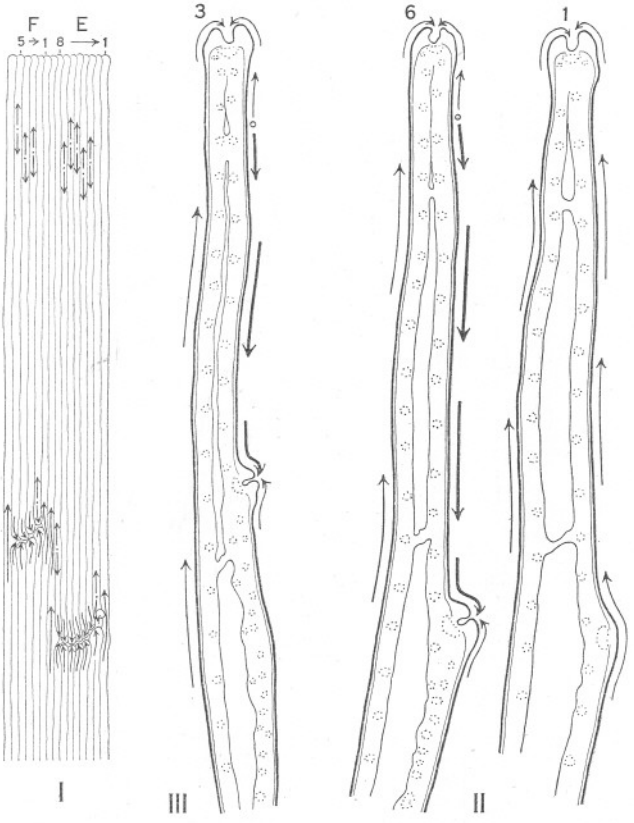


FIG. 27.—I. Surface view of filaments composing secondary grooves E and F (see Fig. 25 I, p. 950).
II. Lateral views of two living filaments from secondary groove E.
III. Lateral view of living filament from secondary groove F.
I–III× ca. 12.

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).

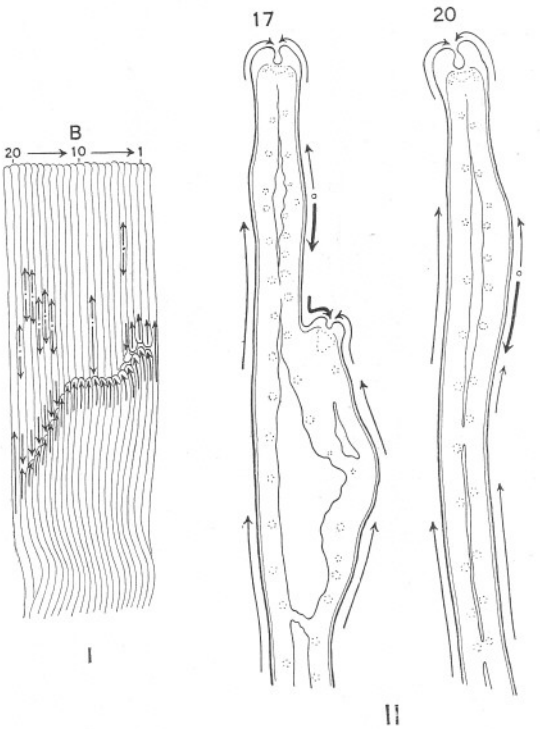


FIG. 28.—I. Surface view of filaments composing secondary groove B (see Fig. 25 I, p. 950).
Owing to the fusion of certain of the filaments the point of reversal of beat of the frontal cilia was not determined for filaments 5–8 and 10–14.
II. Lateral views of two living filaments from secondary groove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

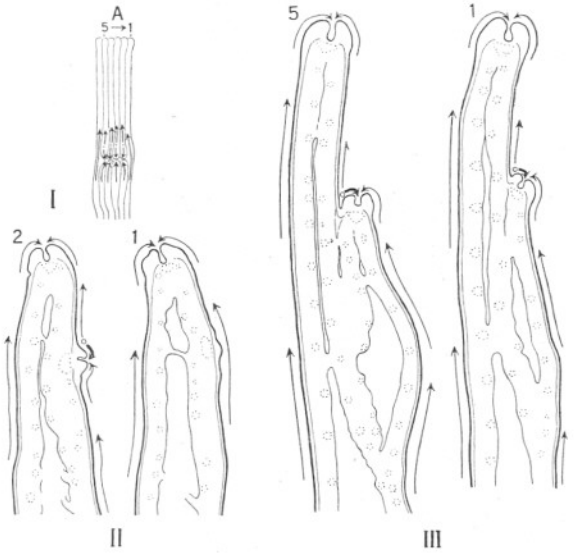


FIG. 29.—I. Surface view of filaments composing secondary groove A (see Fig. 25 I, p. 950).
II. Lateral views of two living filaments of secondary groove A.
III. Lateral views of two living filaments of secondary groove C (see Fig. 25 I).
I–III × ca. 12.

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,

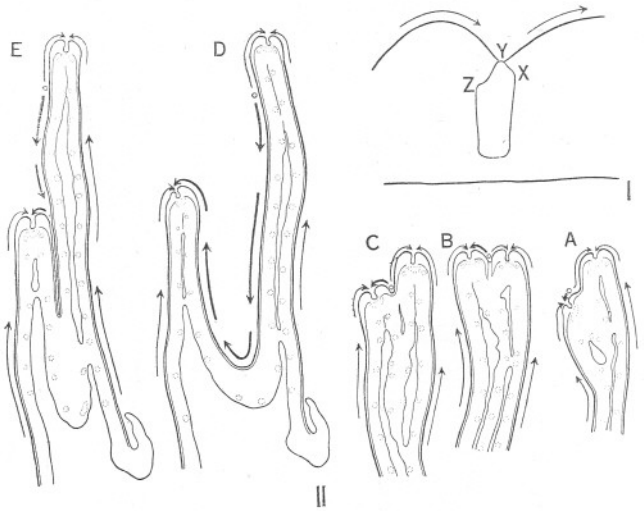


FIG. 30.—I. Rough sketch of a secondary fold or pocket on the descending lamella of the right outer gill of a Mytilus, near the posterior adductor muscle.
II. Lateral views of living filaments from the fold. Filament A was from position X, filament B from about the position Y, and filaments C, D, and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

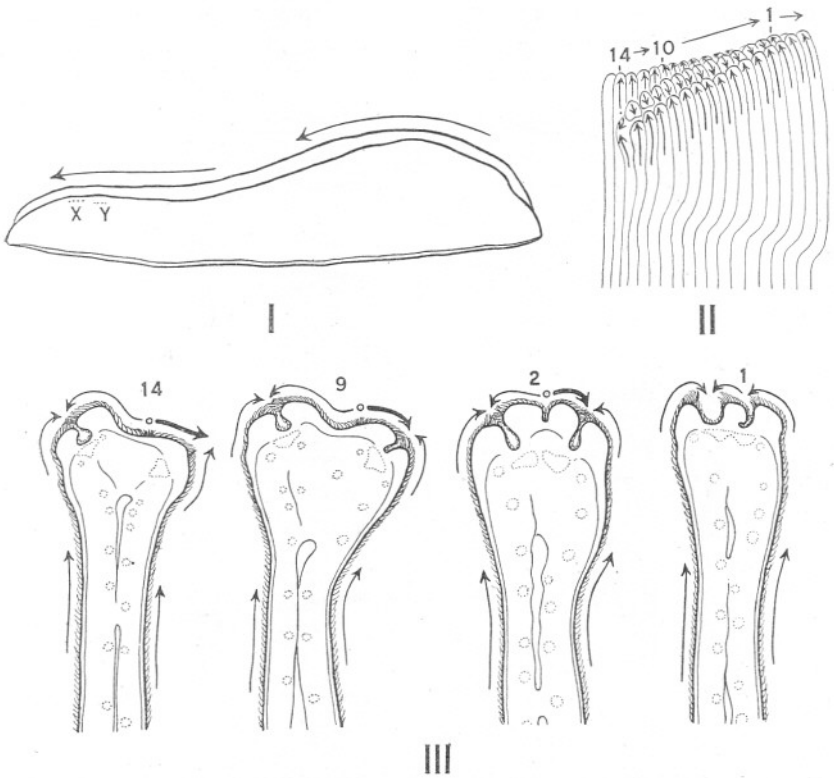


Fig. 31.—I. Sketch of left gills of a specimen of Mytilus: X indicates the position of a secondary groove on the descending lamella of the inner gill, and Y the position of one on the descending lamella of the outer gill. (Secondary groove Y was not investigated.) Drawn from life, natural size.

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

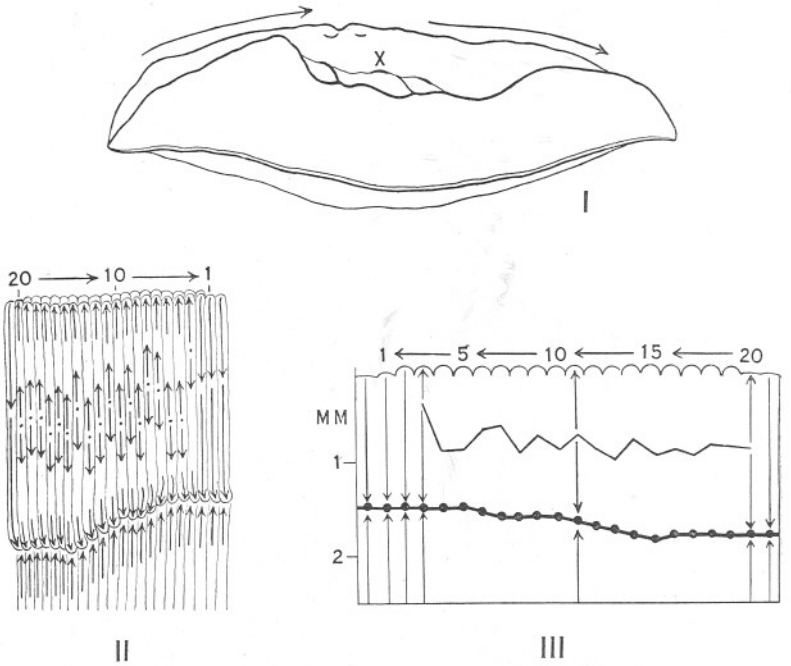


Fig. 32.—I. Sketch of gills of right side of an infected Mytilus, showing shortness of the inner gill and folding over of the free edge with, in certain places, the formation of secondary grooves at what is now the free edge of the gill. The part marked X was investigated. Two secondary grooves are present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

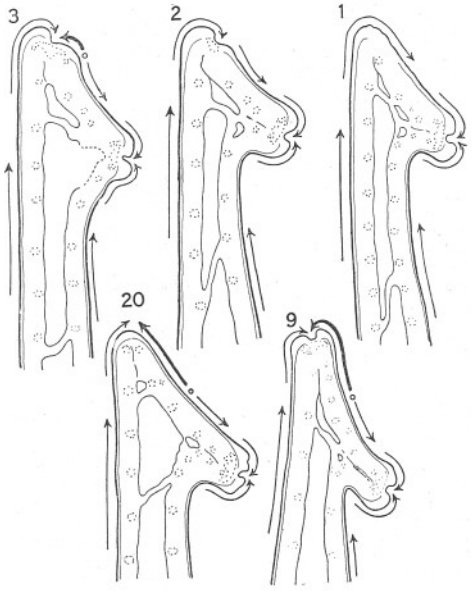


FIG. 33.—Lateral views of representative living filaments from secondary groove X (see Fig. 32). × ca. 12.

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

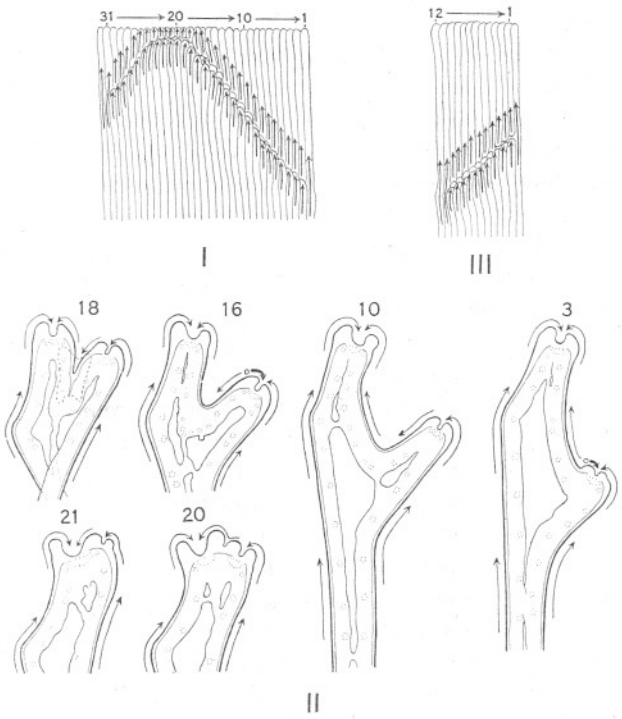


FIG. 35.—I. Surface view of filaments (Mytilus gill) composing a secondary groove which joined the main groove and then diverged. Little or no change of current occurred on the filaments.

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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