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

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With 27 Figures in the Text.

CONTENTS.

INTRODUCTION.

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

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

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

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

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

DESCRIPTION OF STRUCTURAL ABNORMALITIES OF THE GILLS.

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

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

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

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

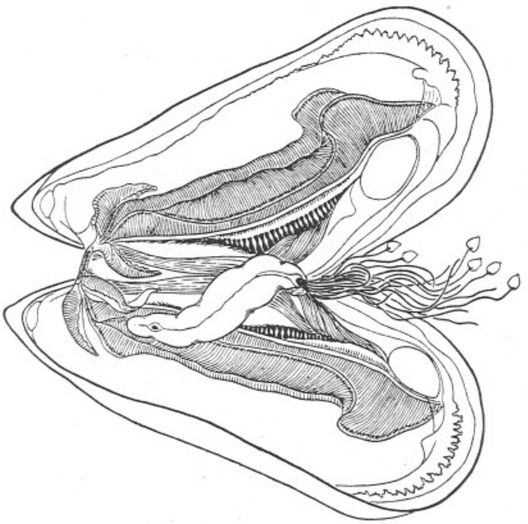

FIG. 1.—Sketch from life of a mussel from the Fal Estuary, October 28th, 1927, showing folding over of the four gills. The folded portion of the left inner gill alone was entirely fused; that of the other three gills could be raised almost to the bend. Natural size.

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

The appearance in surface view of a small part of a gill in which the fold had become completely fused, is shown in some detail in Figure 2 (p. 492). The main food groove now runs across the surface of the lamella (at G), and just dorsal to it there is a narrow zone in which fusion of the filaments side by side, and considerable irregular proliferation of the frontal surfaces of the filaments has occurred. Fusion of the filaments has also taken place along a narrow region ventral to the food groove, as well as near the bend of the fold, at what is now the free edge of the gill. The occurrence of fusion of the filaments laterally, added to the fact that the folding is

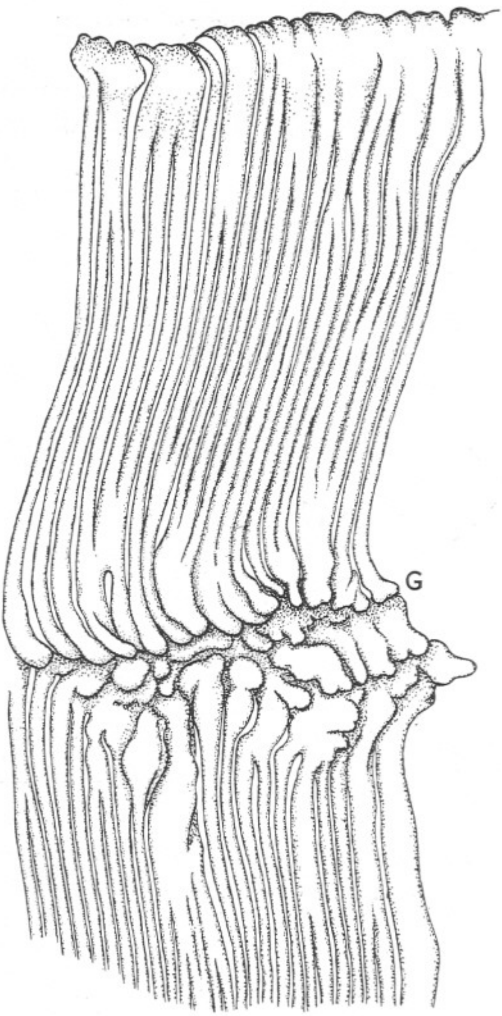

Fig. 2.—Surface view of a small area of a gill of which the folded portion had entirely fused, the main ventral food groove (G) now running across the surface of the lamella. The fusion of the gill filaments side by side is shown, and the irregular growth of the frontal epithelium in a narrow region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

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

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

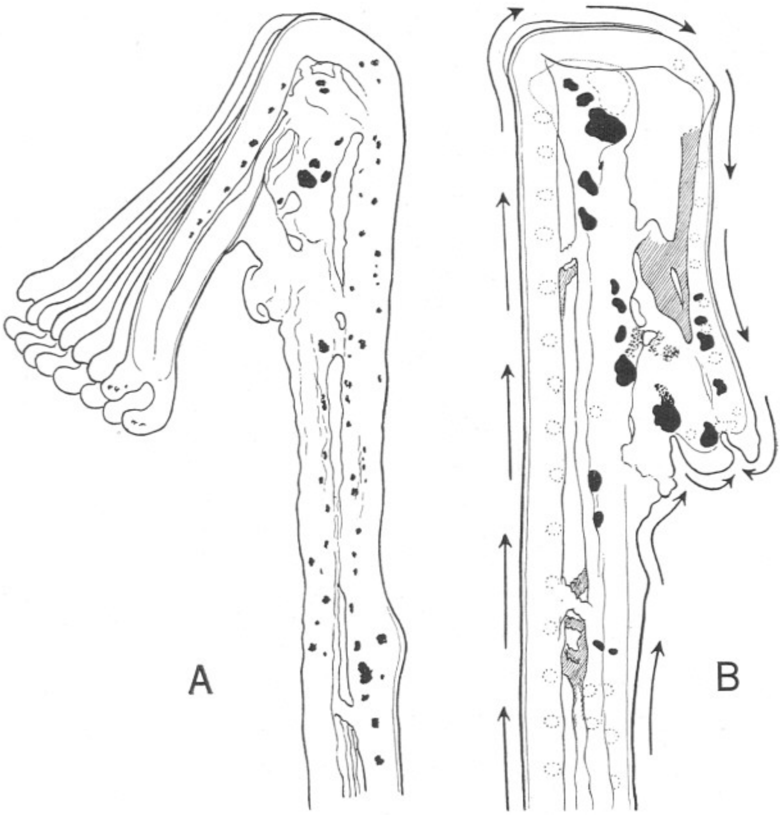

Fig. 3.

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

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

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

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

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

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

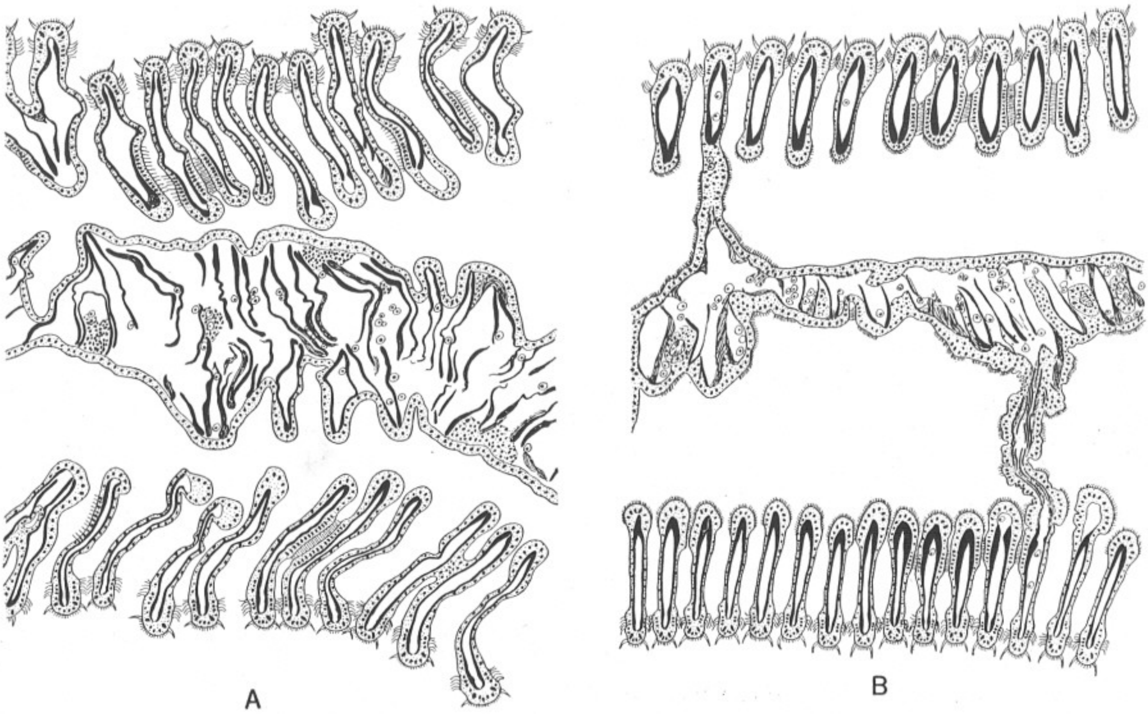

Fig. 4.

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

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

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

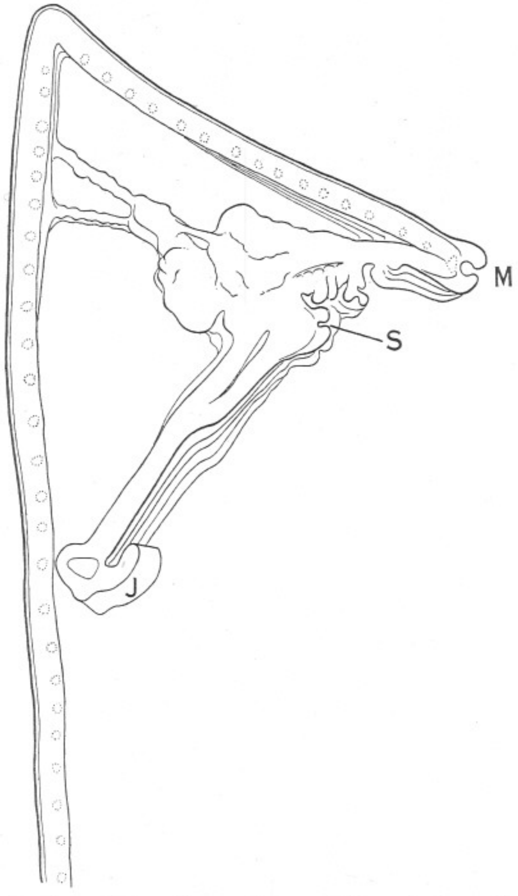

FIG. 5.—Lateral view of a small group of filaments from the gill of a mussel from East Bank, Fal Estuary, November 23, 1927, which showed an apparent fold in surface view. M, main ventral food groove; S, secondary food groove; J, junction area of interlocking cilia on outer surface of dorsal food groove. From preserved material. × ca. $12\frac{1}{6}$.

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

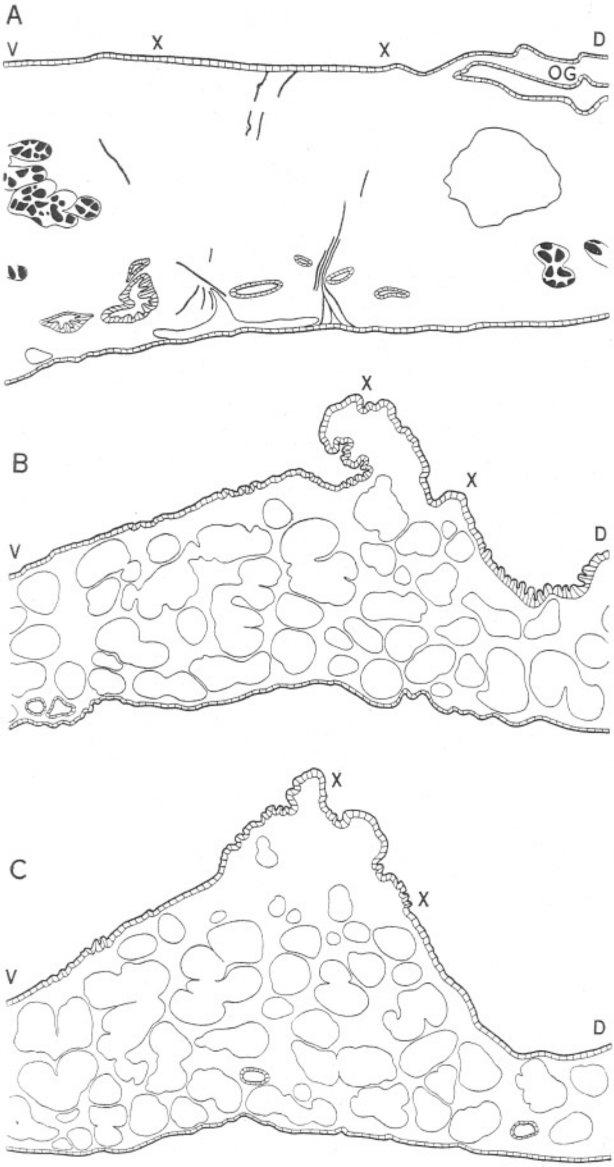

FIG. 6.

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

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

D and V, Dorsal and Ventral.

A–C. × ca. 27½.

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

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

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

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

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

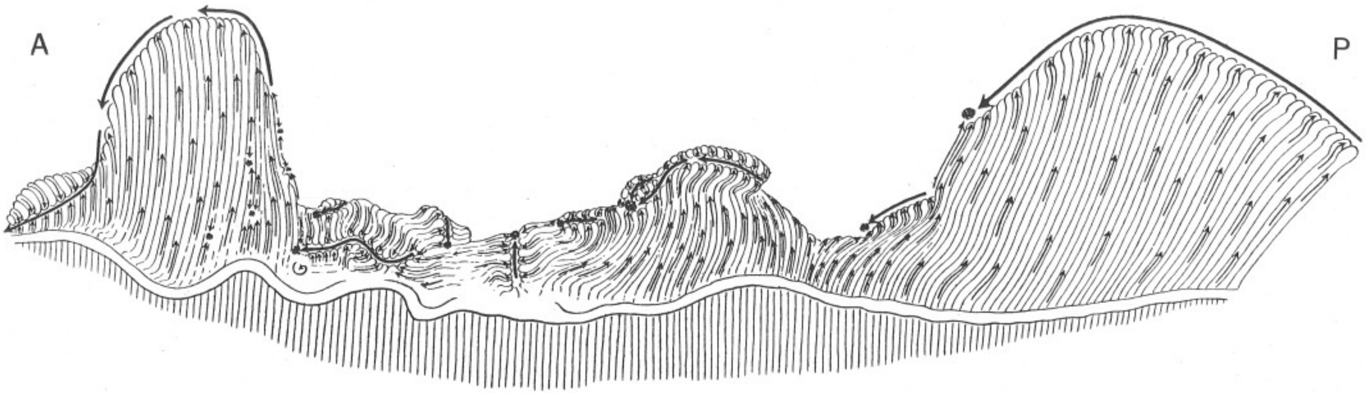

FIG. 7.—Sketch of living gill from a mussel from North Bank, Fal Estuary, 1930, showing disorganisation of food currents by what is, presumably, irregular folding of the gill with fusion. All four gills of this mussel were in a similar state. The direction of the currents along food grooves is indicated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

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

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

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

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

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

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

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

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

† The interpolation is mine.

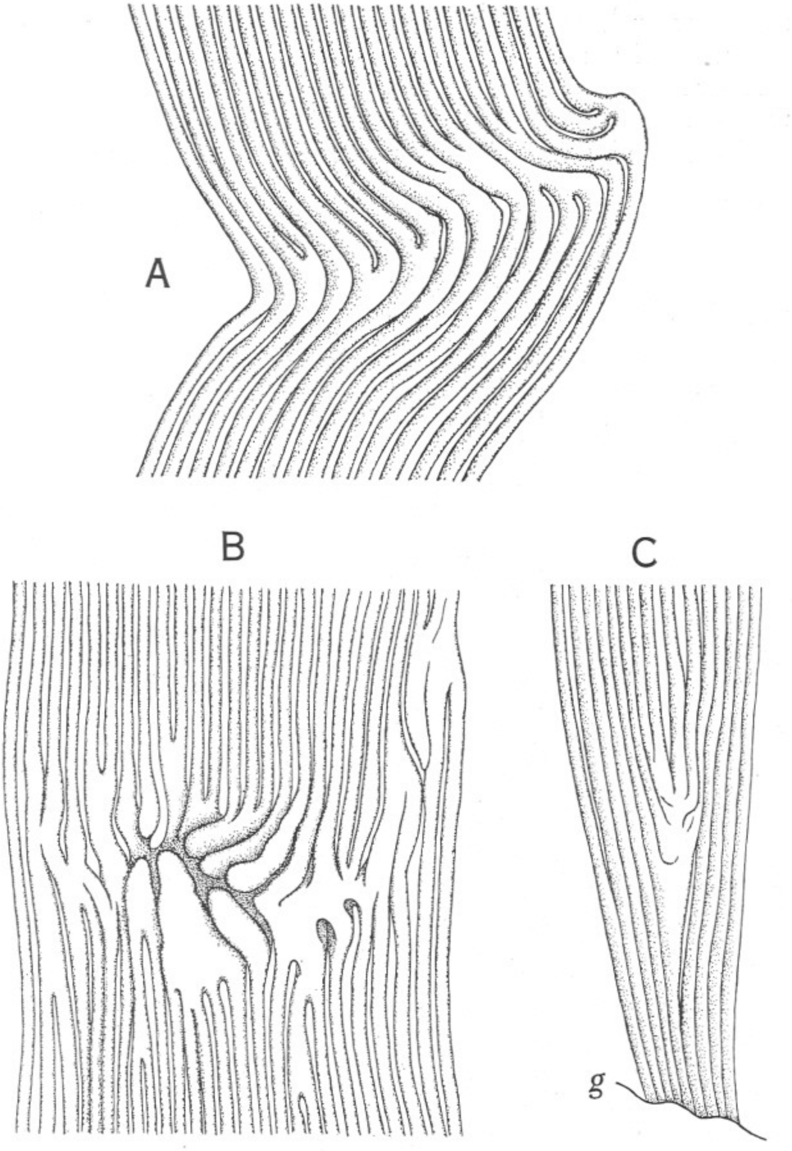

FIG. 8.—Sketches showing fusion of gill filaments on the gills of a mussel from Trelissick Reach, Fal River, November 1, 1927. From preserved material. × ca. 41½.

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

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

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

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

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

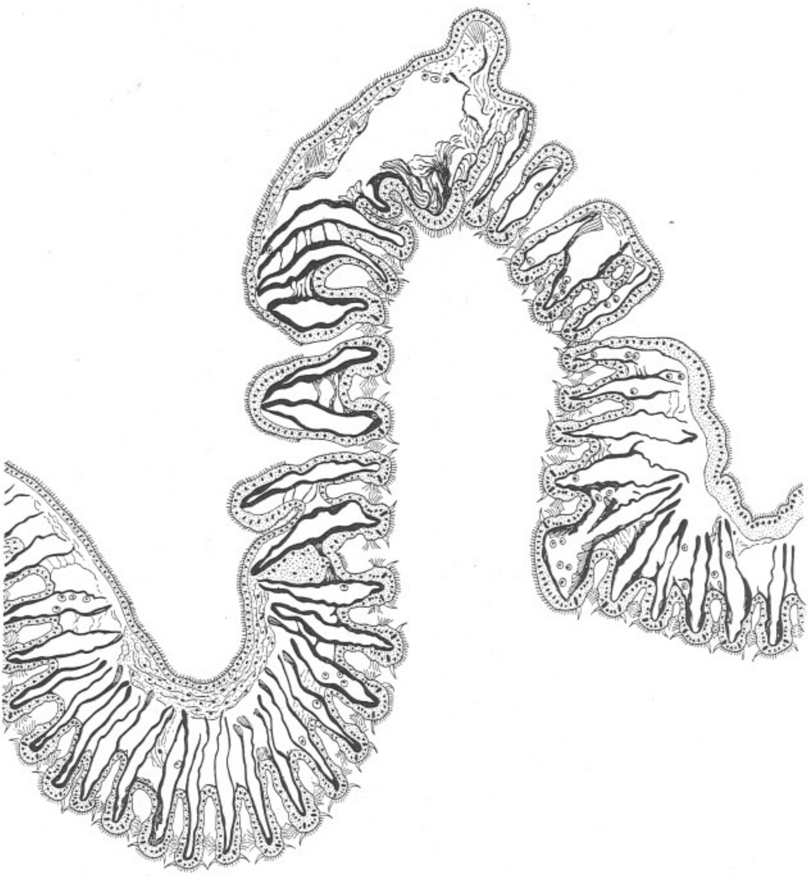

FIG. 9.—Transverse section through dorso-ventral folds in an ascending lamella, near the dorsal food groove, of a mussel from North Bank, Fal Estuary, 1930. The distribution of the cilia and nuclei is represented diagrammatically. The extensive area of ciliation on the abfrontal surface of the lamella, is, however, noteworthy. Bouin's fixative; Mann's methyl-blue-eosin. × ca. 93⅓.

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

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

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

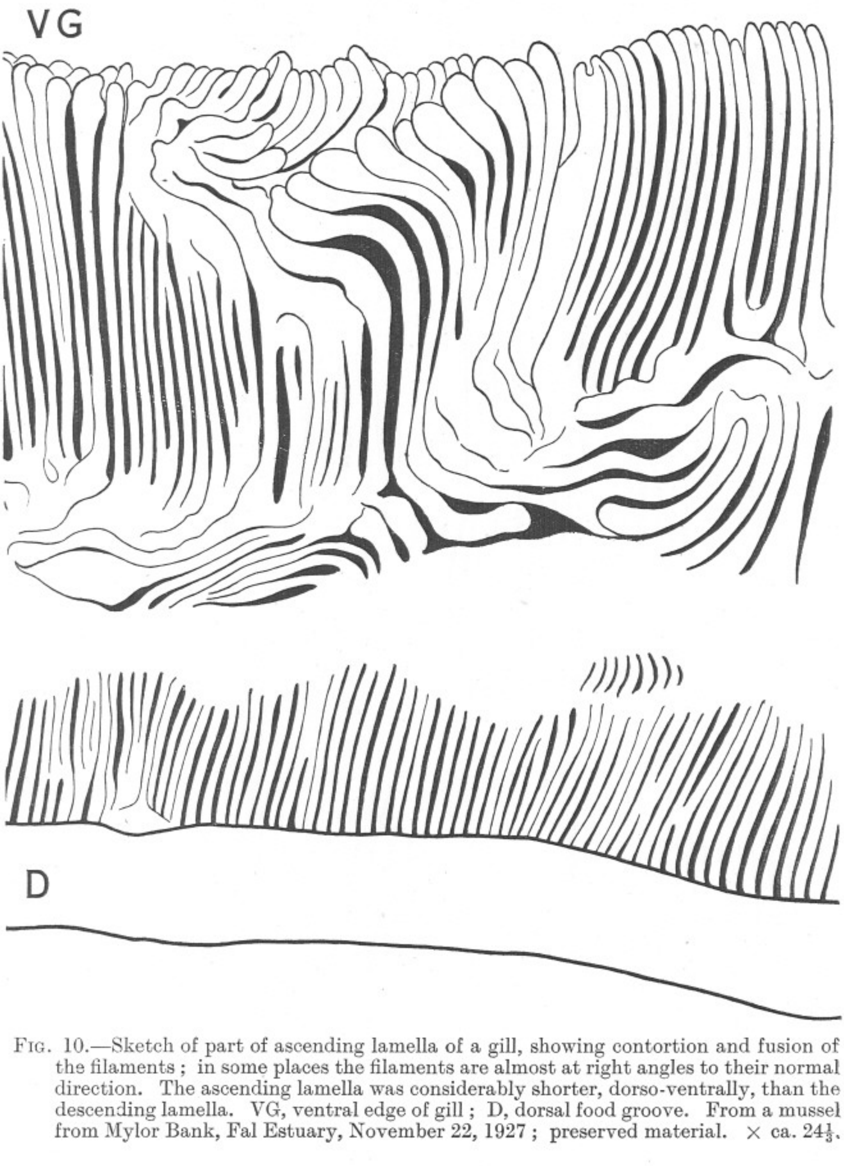

Fig. 10.—Sketch of part of ascending lamella of a gill, showing contortion and fusion of the filaments; in some places the filaments are almost at right angles to their normal direction. The ascending lamella was considerably shorter, dorso-ventrally, than the descending lamella. VG, ventral edge of gill; D, dorsal food groove. From a mussel from Mylor Bank, Fal Estuary, November 22, 1927; preserved material. × ca. $24\frac{1}{3}$.

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

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

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

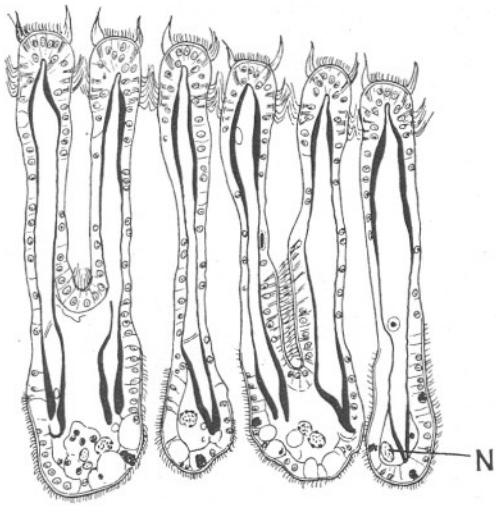

FIG. 12.—Transverse section, single gill lamella, showing fusion of the interlamellar (abfrontal) ends of filaments. N, ? nerve. Bouin's fixative; Mann's methyl-blue-eosin. × 210.

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

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

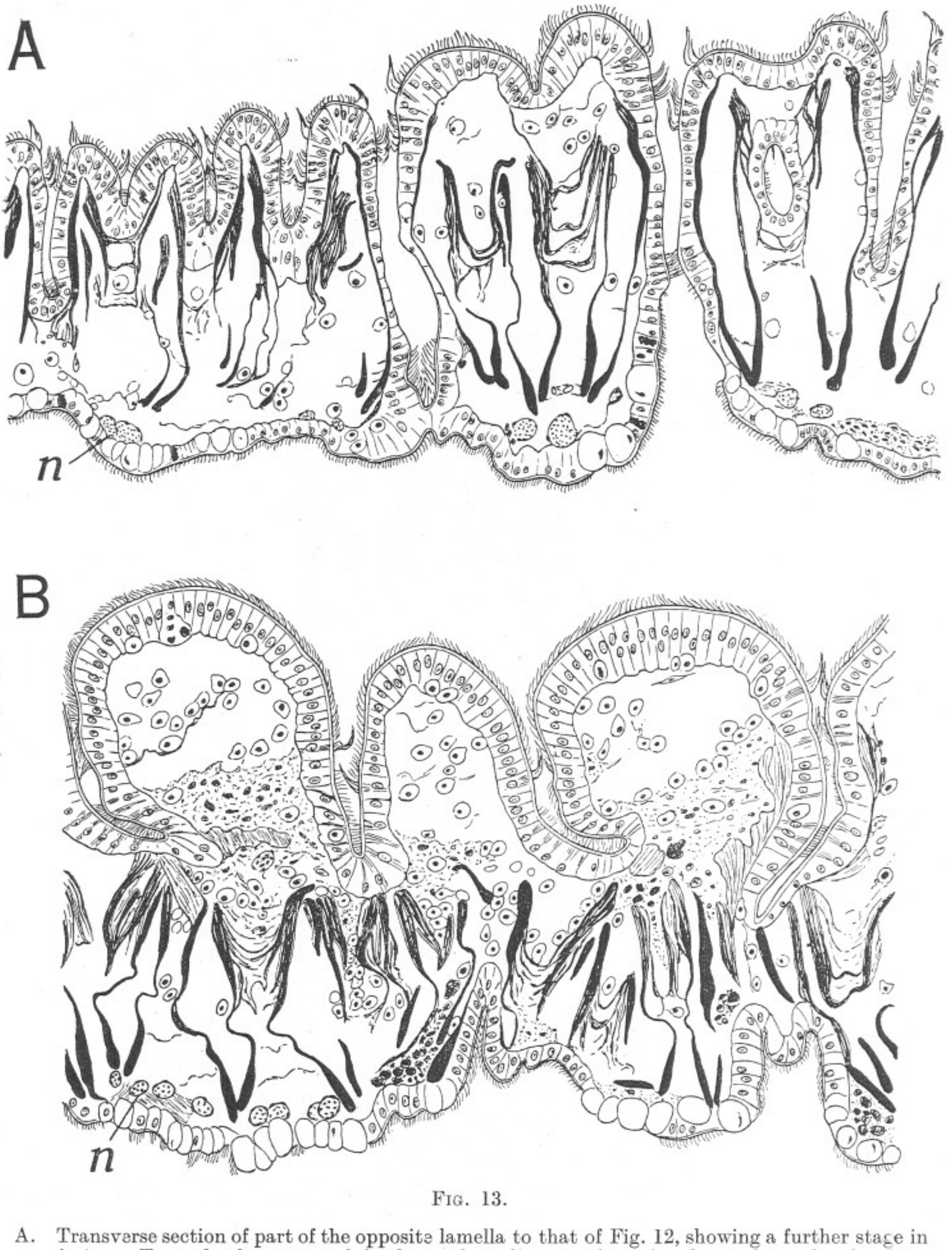

FIG. 13.

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

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

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

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

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

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

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

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

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

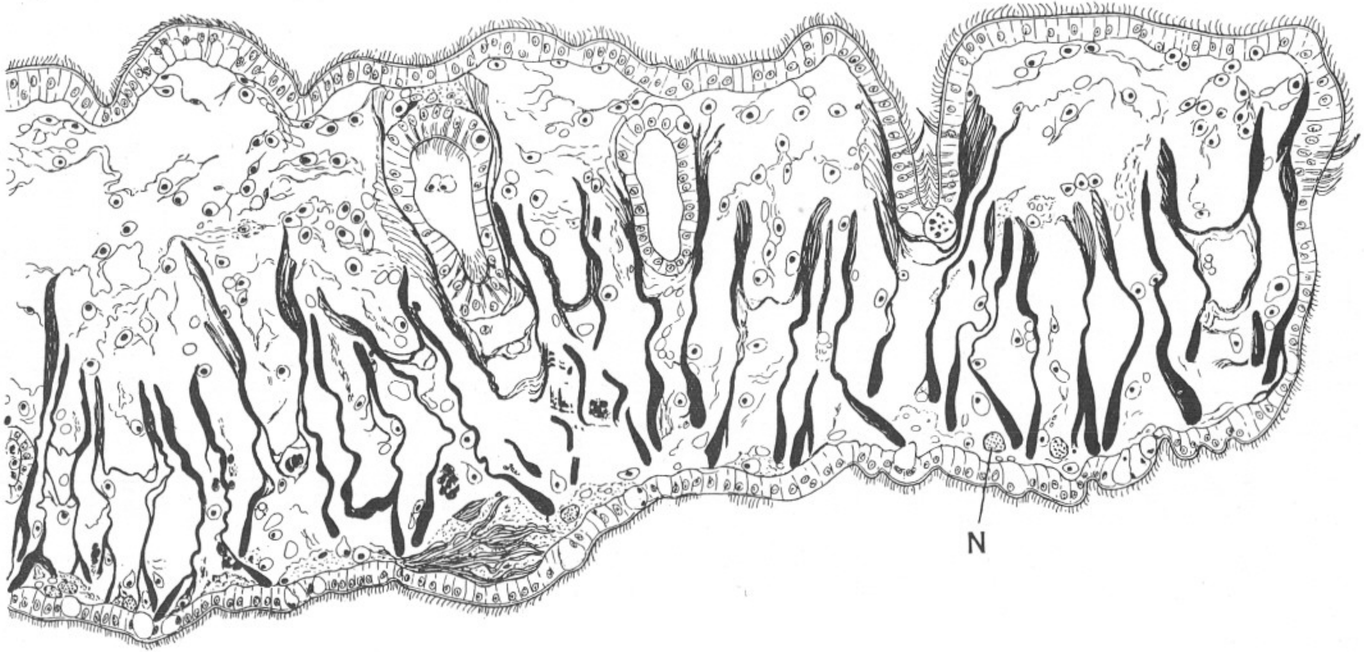

FIG. 14.—Transverse section, ascending lamella, showing extensive fusion of the filaments (17 filaments in the part sketched). This is from the lamella, part of which is shown in surface view in Fig. 11. The frontal surface is approximately flat except for a deep furrow towards the right side of the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

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

(*c*) Enlargement of the Gill Filaments.

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

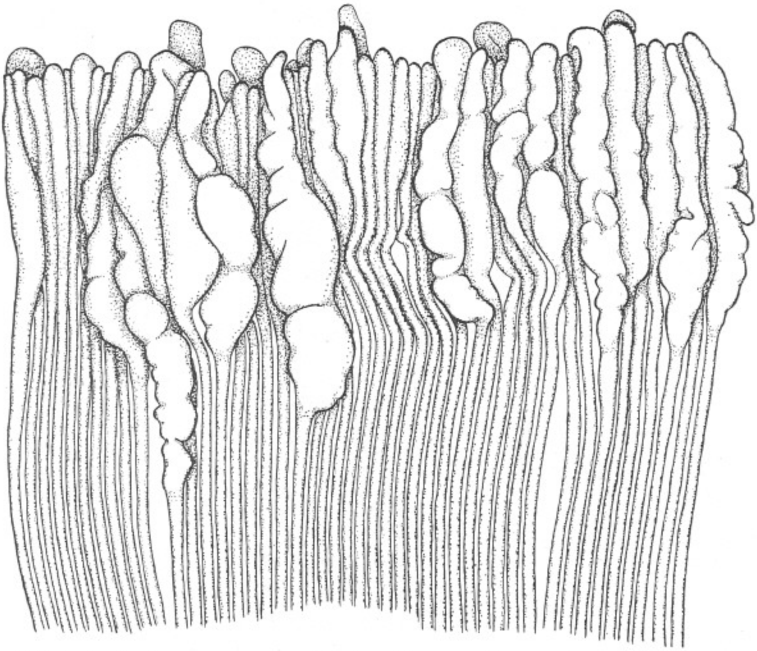

Fig. 15.—Surface view of a small region of an ascending lamella to show enlargement of the filaments in a zone 2·0 to 3·0 mm. wide at the ventral edge of the gill. The main food groove has an irregular appearance owing to the extension ventrally of some of the filaments. From a mussel from Teignmouth,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

(August 21st, 1928) which showed enlargement of the filaments, generally in small groups, in a zone about 2·0 to 3·0 mm. wide along both sides (descending and ascending lamellæ) of the free ventral edges of all four gills. The enlarged filaments had an irregularly swollen appearance, being pitted in some places with small pockets, and tended to overlie laterally the normal filaments, where these occurred (Fig. 15). While the width across the frontal surface of a normal filament is about 0·05 mm., in an enlarged filament it may reach 0·3 mm. or more. Fusion of filaments laterally, however, was of somewhat rare occurrence and where it had taken place was restricted to the fusion of the abfrontal ends of the filaments. A single filament in side view is shown in Figure 16, A (p. 510). Out-growth of the lobes of the ventral food grooves had occurred giving an irregular appearance to the ventral edges of the gills (Fig. 15), which appeared otherwise to be straight and uninjured.

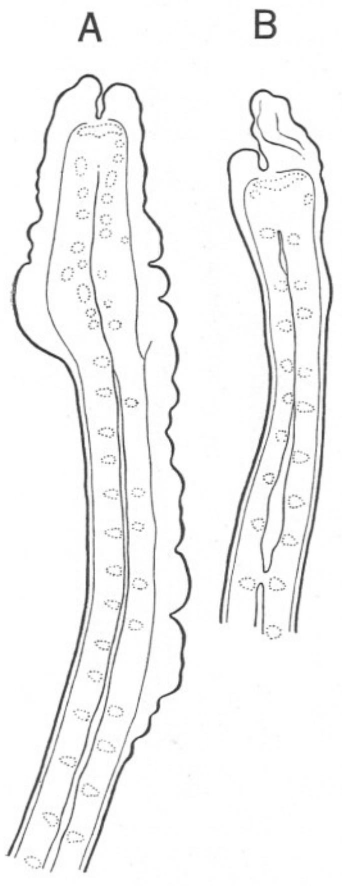

FIG. 16.—Lateral views of two filaments which have suffered enlargement of the frontal surface. B, shows extension of one side of the main ventral food groove. The fine inner line indicates the position of the lateral cilia. From preserved material. × ca. 18¼.

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

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

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

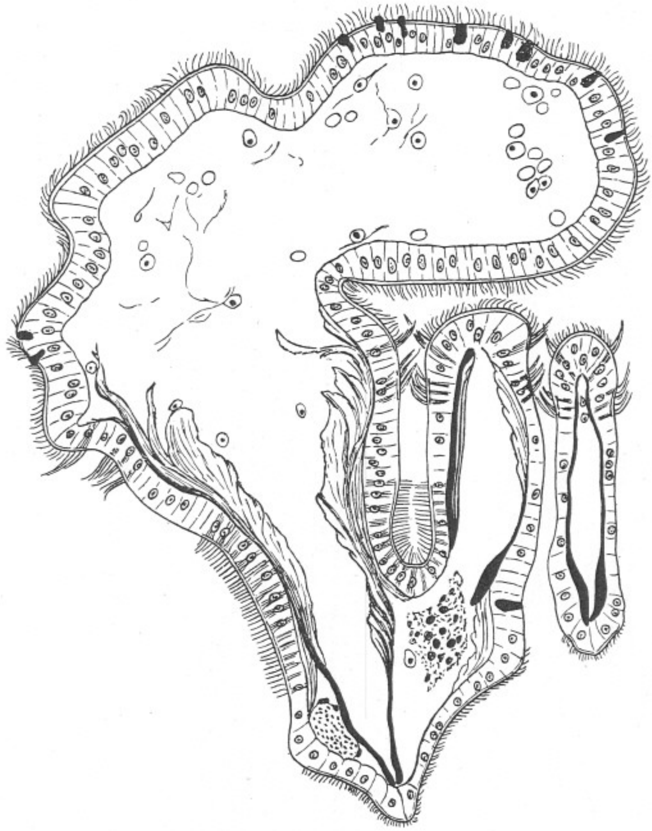

FIG. 17.—Transverse section of filaments from the gill of a mussel from Teignmouth (the same individual from which Fig. 15 was taken), showing one much enlarged filament. As shown by the position of the lateral and latero-frontal cilia, the increased size is largely, or almost entirely, due to the great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

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

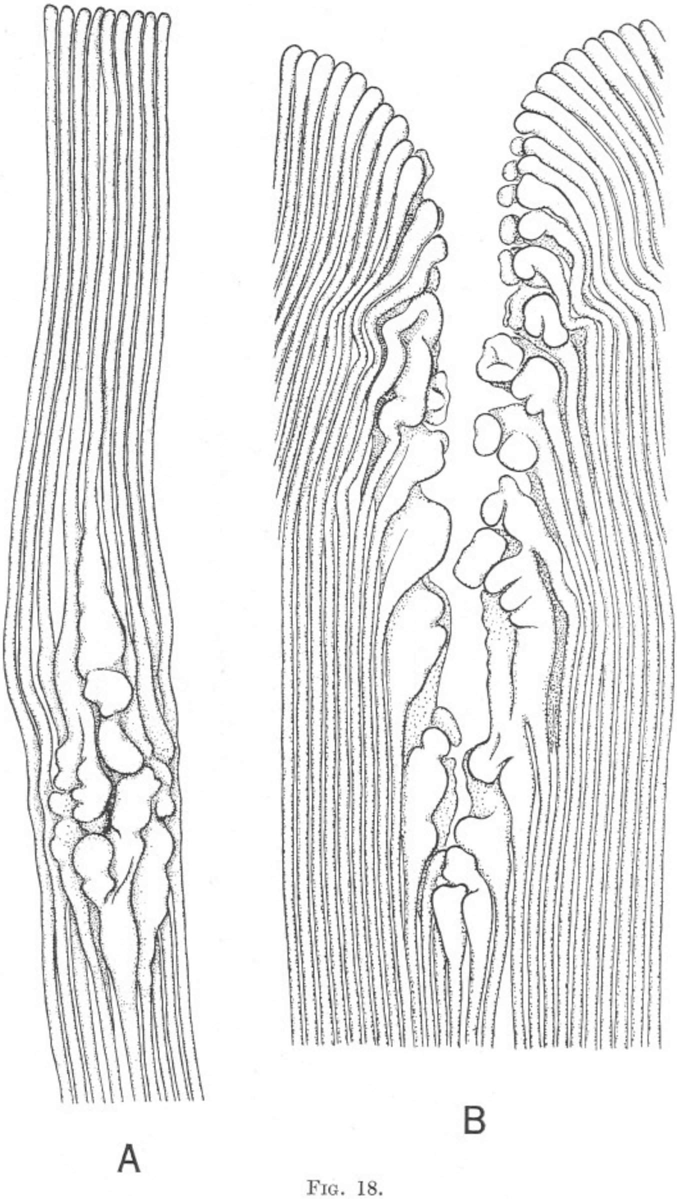

FIG. 18.

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

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

A–B. From preserved material. × ca. $24\frac{1}{3}$.

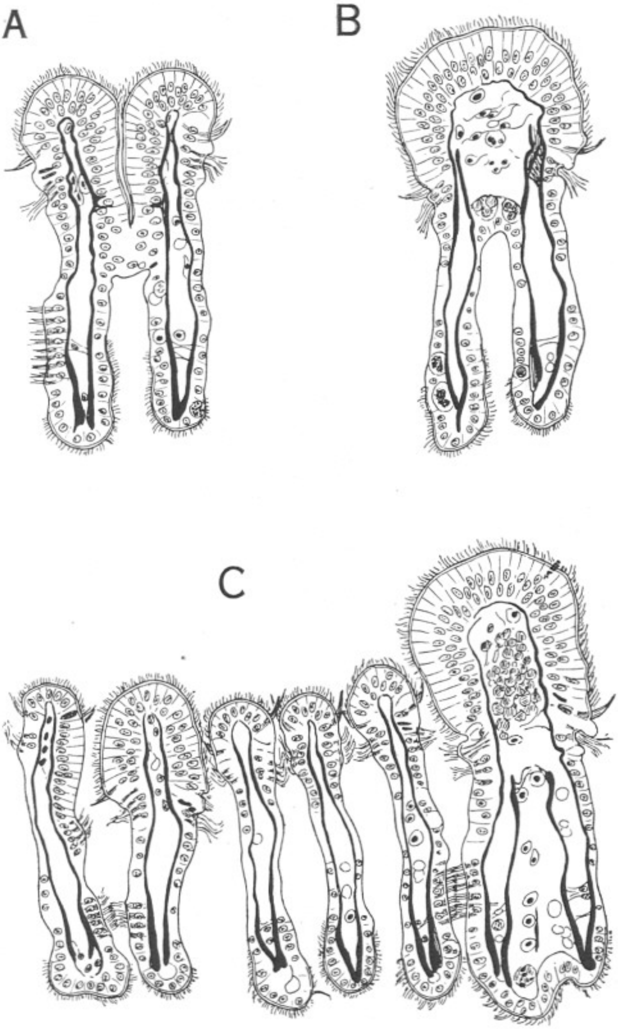

Fig. 19.—Transverse sections (from the same series as that of Fig. 20) showing filaments with abnormally deep cells towards the frontal face; one filament shows deep cells on one side only. To the right of C two fused filaments show a similar condition of the cells. A and B are sections of these same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

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

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

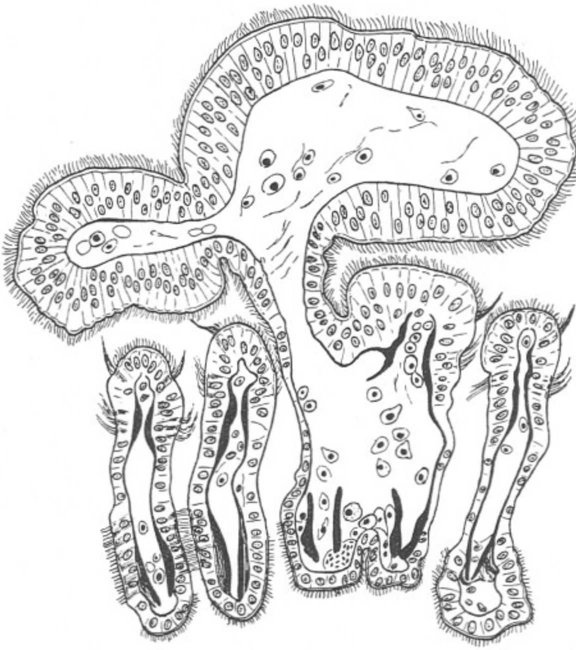

FIG. 20.—Transverse section of five filaments from the gill of a mussel from North Bank, Fal Estuary, 1930, showing a filament with greatly increased frontal surface and great depth of cells, fused with a filament on the right in which the frontal cells are also of great depth. There is no increase in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

ventral ends of occasional filaments increased the irregular appearance. The scattered groups of swollen filaments were mostly found near the ventral margins of the gills, but rarely the swelling was continued to almost half the width of the gill; the swellings had a much pitted appearance. Some of the lamellæ, however, also showed many of the filaments slightly widened, but otherwise normal. In transverse sections of such filaments it was seen that the widening was due to the unusually great depth of the cells towards the frontal part of the filament (Fig. 19, p. 513) (cf. the condition of the frontal epithelium near the ventral food grove of normal filaments). Filaments were observed with the cells of one side of normal depth, while those of the opposite side were much deeper. Figure 19, A, B and C (right-hand part of section), which are sections through the same two filaments at different levels, show three stages in the gradual fusion of two filaments with enlarged frontal cells. Transverse sections of much enlarged gill filaments showed in this case, as in those from Teignmouth, that it was mostly proliferation of the frontal cells that had produced the swelling (Fig. 20, p. 514): these cells were of abnormal depth, in some instances almost as deep again as those of the enlarged filaments of the Teignmouth mussels of August 21st, 1928 (cf. Figs. 17 and 20). There was no increased production of chitin, as in the Teignmouth example sectioned.

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

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

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

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

A Mytilus from Teignmouth (July 10th, 1928) showed a curious condition of the gills of the right side. Anteriorly, for about 7·0 mm., the two gills appeared to be fused side by side, and, since the outer one was somewhat shorter than the inner, the two ventral food grooves were at different levels; immediately behind for about 7·0 mm. the two gills were fairly distinct: throughout this anterior region the gill filaments showed much crumpling. The gills then appeared to have fused again, so that in the middle region for about 18·0 mm. there was one "gill" only, but here it appeared to be formed of two lamellæ only —they could be clearly separated to within 3 mm. of the ventral edge, where they were connected by interlamellar junctions—and as both were provided with a dorsal food groove, they were presumably ascending lamellæ; the gill was entirely free from the body. At this part the gill was about 7 mm. deep. While the gill filaments of the outer lamella appeared from surface view to be normal, those of the inner lamella were in places bent somewhat out of the true dorso-ventral direction (i.e. crumpled), with some slight fusion side by side. For the remaining posterior 20·0 mm. the gills were normal and about 11·0 mm. deep. The shell had suffered no injury, and the inner surface of the valve was perfectly smooth.

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

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

GENERAL CONDITION OF MYTILUS FROM THE VARIOUS LOCALITIES INVESTIGATED.

Fal Estuary.*

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

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

TABLE I.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

* Identified by Mr. D. P. Wilson.

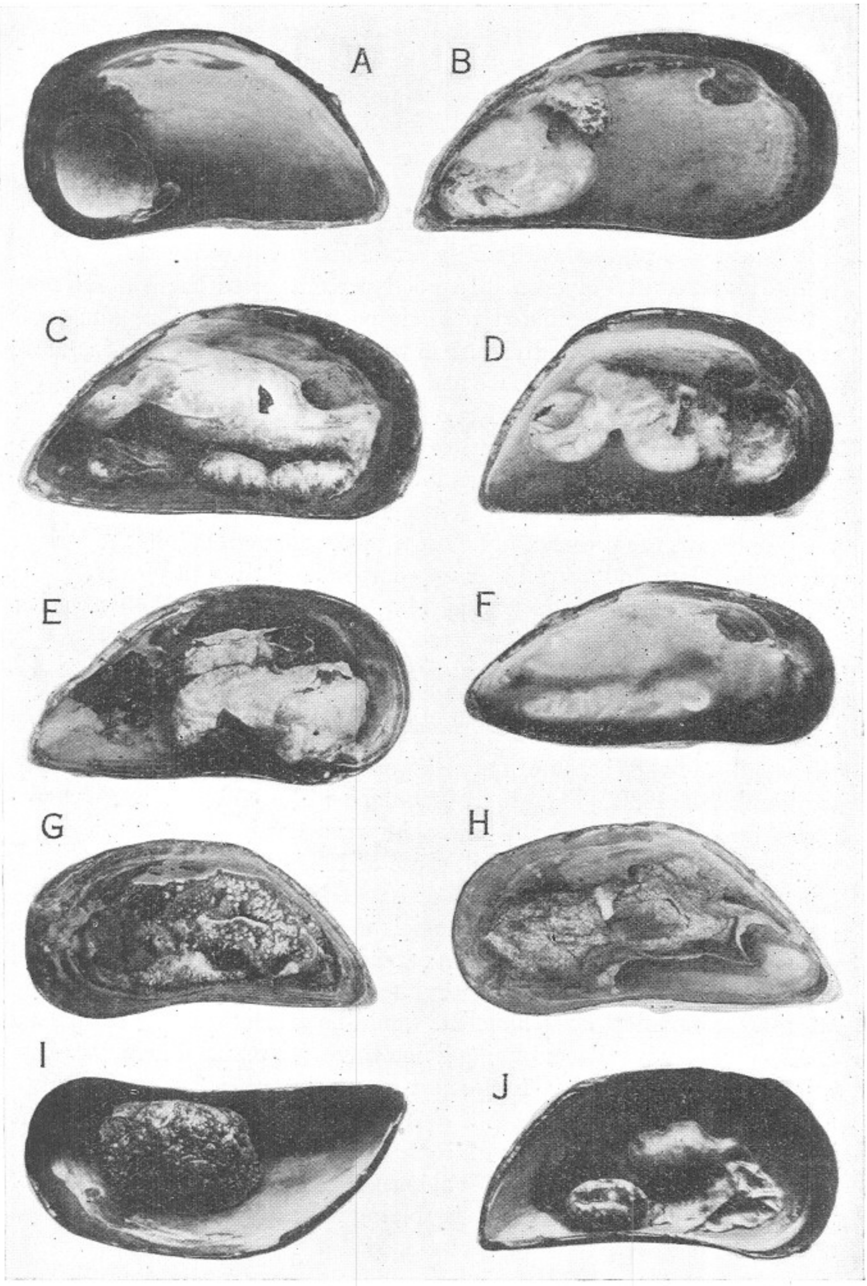

FIG. 21.

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

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

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

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

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

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

Estuaries of the Hamoaze, near Weir Point.

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

Estuary of the Yealm.

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

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

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

Estuary of the Teign.

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

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

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

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

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

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

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

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

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

* The Trematode is being investigated at Leeds University.

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

The Promenade Pier, Plymouth.

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

DISCUSSION.

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

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

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

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

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

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

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

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

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

The most comprehensive account of the physiology of the mussel is to be found in the section on " The Physiology of the Mussel with special reference to purification " in Dodgson's " Report on Mussel Purification " (**12**). He observed the conditions under which mussels will function normally, and one is impressed with their hardiness and tolerance to widely differing conditions. Their behaviour with regard to much silt in the water (**12**, p. 175), strength of tidal currents (p. 191), variations in temperature (pp. 194, 198), and in salinity (pp. 208, 209), and lack of oxygen (p. 221) is dealt with in his work. The fact that mussels may exist for as long as 40 days under anærobic conditions, whilst ciliary action may persist for at least 25 days (**12**, p. 221), is especially interesting in view of conditions—such as temporary silting up of mud on the beds, sudden decrease in salinity, etc.—which might exist on the beds causing mussels to remain closed for long periods, with a possible adverse effect on the gills. According to Gray (**21**, p. 79), however, in closed mussels (removed from sea-water) ciliary movement would most probably be inhibited in two or three hours, owing to the concentration of CO_2 in the shell water, and thus the oxygen requirements of the animal would be reduced.

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

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

The factor or factors acting on the Fal Estuary mussels have apparently resulted in some cases in a tendency for the gill to collapse, the middle region—the part least supported—folding over longitudinally. Once folding had occurred, fusion of the folded over portion with the surface of the lamella beneath it would appear almost inevitably to follow. In other instances crumpling or puckering had arisen, most probably resulting in the crowding together of the filaments in certain areas, which, when it became marked, would cause fusion of the filaments. It is curious that in gills which showed numerous areas of fusion it was frequently only one lamella of a gill which was affected, and that most usually the ascending lamella.

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

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

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

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

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

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

Drew's (**14**) suggestion, that the intrafilamentar septum (in Pecten) is a brace to keep the filaments from swelling laterally owing to pressure of the blood, and in this way becoming circular and obstructing the flow of water between the filaments (see **10**, p. 44), is especially interesting in view of the swelling of the filaments of this gill. It may be noted that difference of opinion exists as to the nature of the intrafilamentar septum ; various authors, including Ridewood (**43**, pp. 166, 168), holding it to be composed of chitin, while Kellog (**26**, p. 421) believes it to be endothelium (in *Pecten irradians*). Dakin (**10**, p. 43) found in *P. maximus* that it appeared to stain quite differently from the chitinous skeleton, appearing almost as if it were cellular, while nuclei, which were not adhering blood corpuscles, were seen in it. Setna (**45**, p. 376) states that in Pecten (three species), material fixed in Bouin and stained with Dobell's

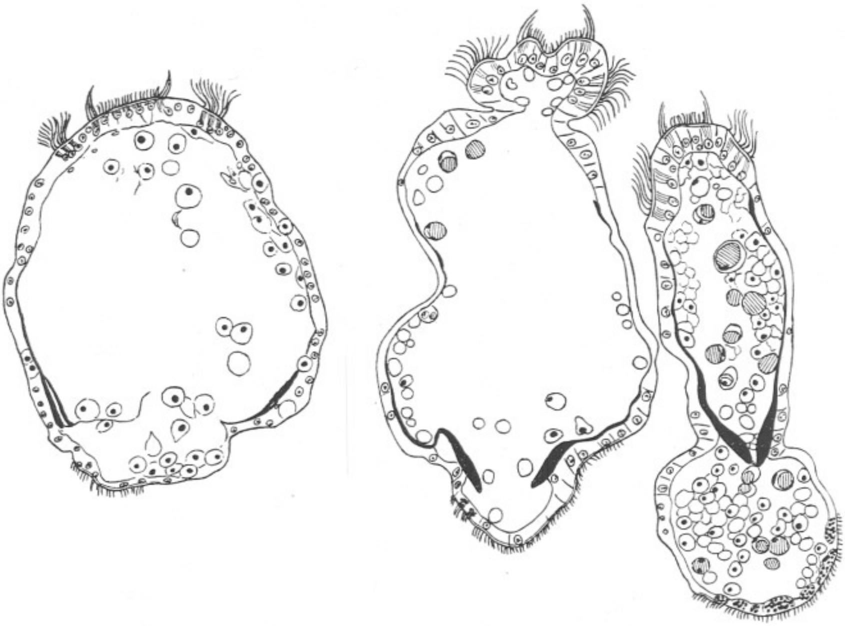

FIG. 22.—Transverse section of filaments from gill which showed increase in size of some of the filaments, after the gill had been cut from the mussel and left three days in a finger bowl of sea-water. The slight development of the chitinous supports and the numerous phagocytes in the filament on the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

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

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

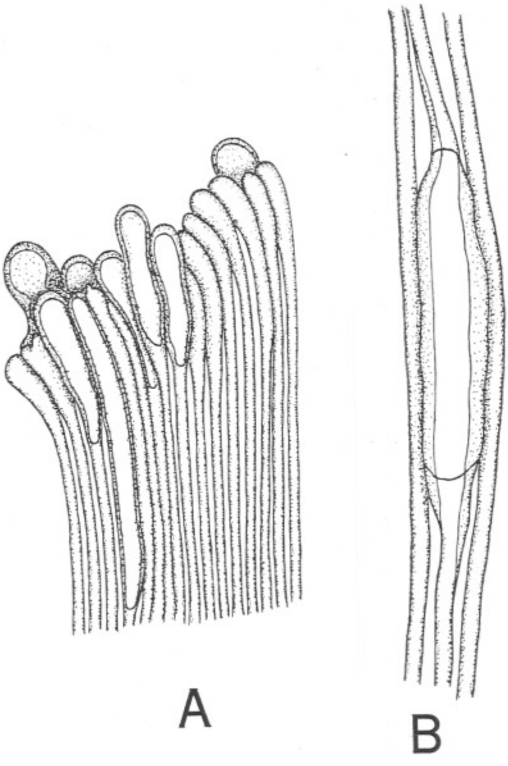

FIG. 23.—Sketches of living gill with sporocysts of a Trematode within the gill filaments. The main ventral food groove in A has an irregular appearance, due to the active sporocysts attempting to push forward. From both A and B it may be seen that the gill filaments recover their normal size after the passing of the Trematode. A, ca. $24\frac{1}{3}$; B, ca. $76\frac{1}{3}$.

through the mussel by way of the blood vessels ; in some instances they are seen crowded in the pallial vessels, causing them to assume a deep orange colour against the creamy white of the mantle ; the colour of the sporocysts varies, however, from cream to orange in different mussels. In badly infested mussels, the plicate canals (*organes godronnés*) of Sabatier, **44**) are packed with them, as are the mantle and parts of the visceral mass. The dorsal food grooves on the ascending lamellæ are occasionally crowded with the active sporocysts and cercariæ of this Trematode, but on few occasions have they been seen actually within the gill filaments, though they have at times been noticed pushing their way along the interfilamentar spaces, in which case they may have actually burst through the gill epithelium, or may possibly have been individuals liberated in opening the mussel. When inside the filaments the active sporocysts would seem to tend to work their way towards the ventral free edge of the gill, where they cause extension of the lobes of the main food groove, giving the ventral edge of the gill an irregular appearance (Fig. 23, A, p. 529); and towards the dorsal food groove on the ascending

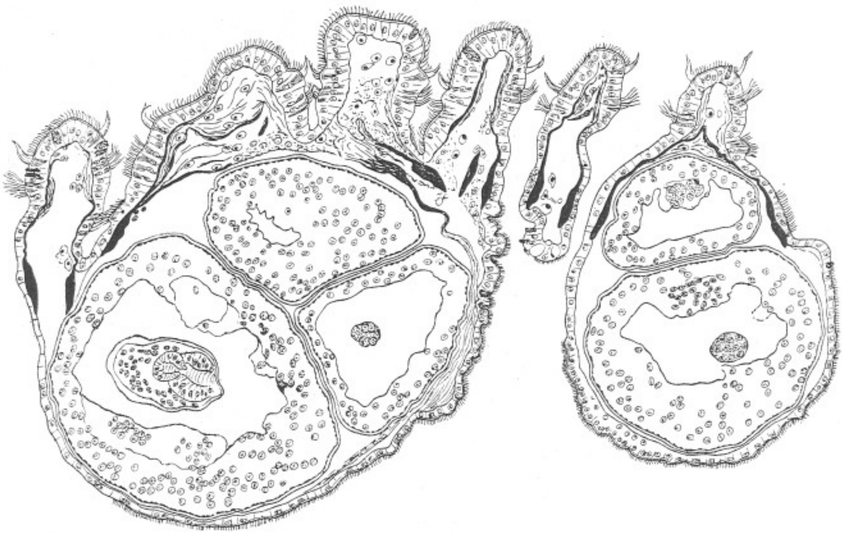

FIG. 24.—Transverse section of part of single lamella of a gill, near the dorsal food groove, showing great enlargement of the interlamellar (abfrontal) ends of the gill filaments owing to the presence of the sporocysts of a Trematode. In the filament on the right, two sporocysts are present side by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

lamella. The parasites can be seen to cause such great distension of the filaments that it is surprising they do not burst through the epithelium; it is manifest that the filaments are highly elastic as these resume the normal size after the passage of the parasite. The presence of the sporocysts gives to the filaments containing them an appearance somewhat similar to that described previously (p. 509, and Fig. 15); but the swelling is smooth and also the lines of latero-frontal cilia can be seen running across the swelling (Fig. 23, B), showing that the frontal epithelium experiences no more stretching—possibly less—than the rest of the epithelium. The extreme enlargement of the filaments is strikingly shown in transverse sections, such as Figure 24, where there are two sporocysts side by side in the same filament. The enlargement of the area of ciliated abfrontal epithelium may be noted. This section also shows that fusion of the filaments may presumably be caused where swollen filaments are forced against each other. One would imagine that fusion from this cause is only likely to occur in areas where the active sporocysts tend to congregate for some time, e.g. near the ventral and dorsal edges of the gills. As mussels infected with the Trematode came from Padstow, where exceedingly little abnormality of the gills occurred among the mussels—apart from those infected with either Pinnotheres or the Trematode—the fusion in this case may be fairly safely attributed to the presence of the Trematode. Figure 25 shows

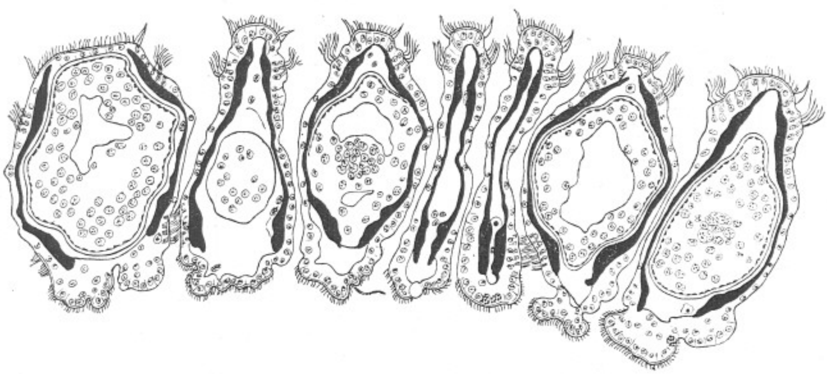

FIG. 25.—Transverse section of part of a single lamella of a gill, to show the crowding of filaments caused by the presence of sporocysts of a Trematode in five out of the seven gill filaments drawn. Bouin's fixative, Mann's methyl-blue-eosin. × ca. 171.

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

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

SUMMARY.

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

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

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

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

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

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

(*c*) Enlargement of the gill filaments.

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

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

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

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

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

METHOD OF DIVISION OF THE MANTLE CAVITY IN NORMAL INDIVIDUALS.

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

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

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

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

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

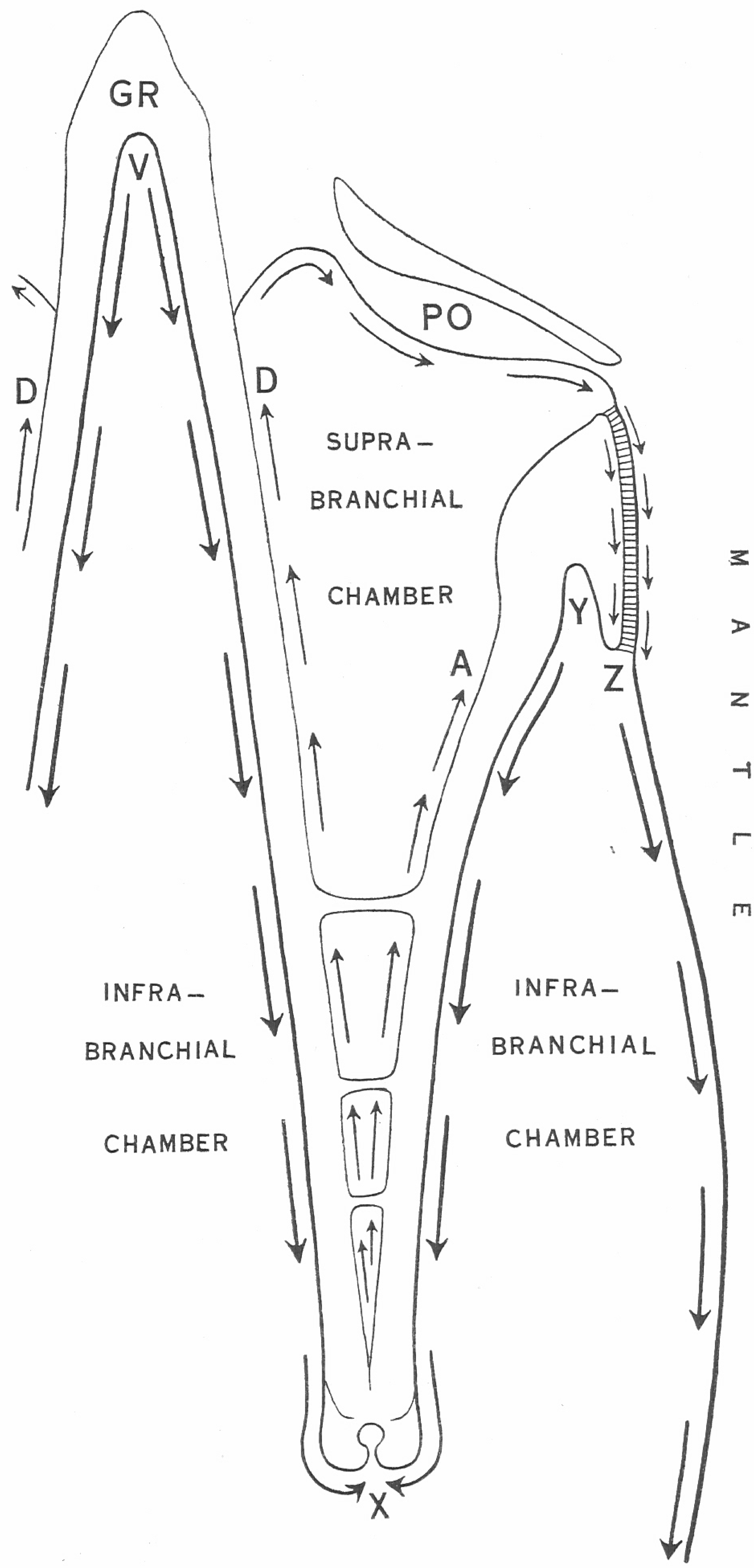
GR
V
D
D
PO
SUPRA–
BRANCHIAL
CHAMBER
A
Y
Z
MANTLE
INFRA–
BRANCHIAL
CHAMBER
INFRA–
BRANCHIAL
CHAMBER
X

FIG. 26.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

When the gill is interlocked with the mantle, the anteriorly directed current on the mantle forms, with that along the dorsal groove of the gill (Fig. 26, Z and Y), a single anteriorly directed current. In this condition the current is more clearly defined, and there seems to be less tendency for particles to be drawn from the dorsal groove on to the frontal faces of the filaments, probably because the groove may be more widely open when gill edge and mantle are interlocked. The animal is able to alter the form of the food groove considerably, and in specimens of Modiolus killed without narcotising, the outer wall of the groove may be reflected, so that the groove is non-existent ; while in Mytilus there is much contraction.

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

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

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

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

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

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

In Pecten the temporary nature of the division of the mantle cavity has been observed by Orton (**33**, p. 461), who says "the upturned edges of the outer gill filaments touch the mantle during feeding, and in this way form at this point a temporary food groove." It may be noted that preparatory to the clapping of the valves the free posterior ends of the gills swing forward by contraction of the ctenidial muscles (see also **45**) and any connection between the gills and the mantle is broken.

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

The plicate canals are found on the roof of the supra-branchial chamber, the width of each division of the chamber being roughly the length of these organs. The external surfaces of the canals are highly ciliated, rapid currents passing over them, in the main, in a dorso-ventral direction (see Fig. 26). These canals, to which Sabatier gave the name of *organes godronnés* (**44**, p. 56), have a respiratory function.

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

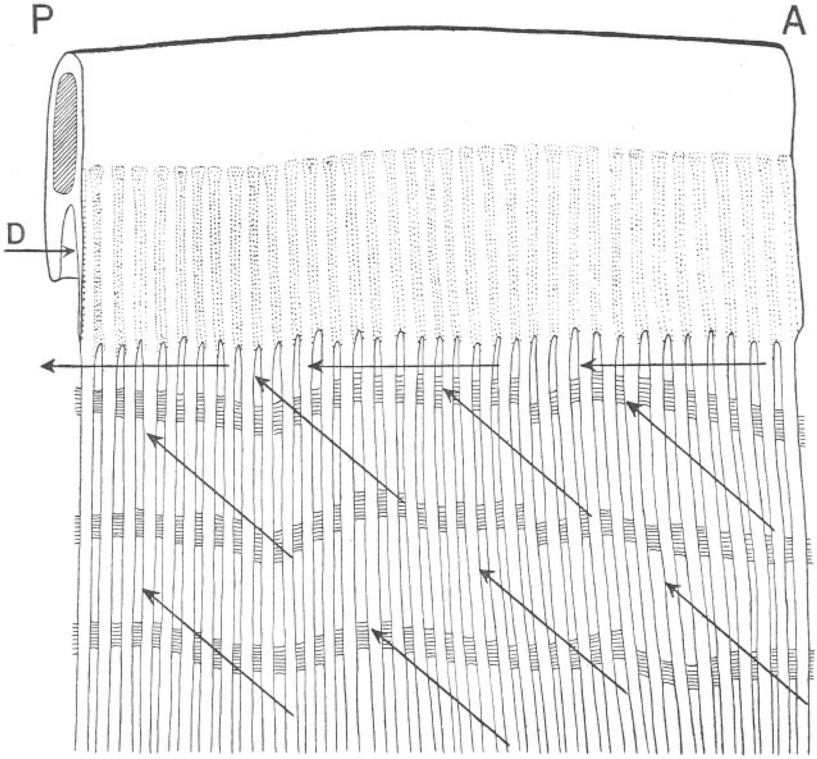

FIG. 27.—Mytilus. View of the abfrontal surface of an ascending lamella in the region of the dorsal food groove, to show the ciliary currents.

A and P. Anterior and posterior.

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

which is anterior-ventral to posterior-dorsal (Fig. 27). Across the dorsal ends of the gill filaments—in the region where they become fused together—of both descending and ascending lamellæ, the cilia maintain a posteriorly directed current (Figs. 26, D and A; 27). In most of the individuals which were examined the epithelium covering the fused ends of the filaments was either feebly ciliated, or destitute of cilia with the exception of scattered very large cilia (see p. 537), and there was only occasional slight movement dorsalwards of particles jerked forward by the latter: in such individuals the posterior ciliary current across the base of the filaments was very clear. Very rarely individuals were seen in which the abfrontal cilia were continued on to the epithelium covering the fused ends of the filaments; there was in consequence a ciliary current across this surface, in a postero-dorsal direction, and the purely posteriorly directed ciliary current was not then as clear.

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

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

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