The Ciliary Feeding Mechanism of the Entoproct Polyzoa, and a comparison with that of the Ectoproct Polyzoa.

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With 12 Text-figures.

CONTENTS.

Introduction ................................................. 393
The Structure of the Lophophore and of the Tentacles in the Entoprocta .......................... 394
The Ciliary Feeding Mechanism of the Entoprocta .............. 401
The Behaviour of the Lateral Cilia on the Tentacles of Loxosoma crassicauda ............... 406
A Résumé of Borg's Work on the Ciliary Feeding Mechanism of the Ectoprocta, with a Note on Flustrella hispida ....................... 411
The Method of Rejection of Unwanted Particles in Flustrella hispida ............................. 415
Discussion .................................................. 419
Summary ..................................................... 422
Literature ................................................... 422

Introduction.

The ciliary feeding mechanism of the Entoproct Polyzoa does not seem to have been worked out in any detail, as has that of the Ectoproct Polyzoa (4, 5, 18), although certain references to it occur in the literature of the group (27, 9). The following account of the ciliary feeding mechanism of the Entoprocta is based chiefly on an investigation of Loxosoma, though Pedicellina was also observed. L. crassicauda was chosen for the greater part of the work on account of the large size of its lophophore; the method of feeding of the other species of Loxosoma found at Plymouth, namely, L. singulare, L. claviforme, L. phaseolosomatum, and L. obesum (3), is, however, identical.
THE STRUCTURE OF THE LOPHOPHORE AND OF THE TENTACLES IN THE ENTOPROCTA.

In Pedicellina, as is well known, the plane of the lophophore is at right angles to the main axis of the stalk and calyx; in Loxosoma the lophophore is set obliquely. In at least some species of Loxosoma, however, the dorsal half of the lophophore is generally bent backwards during feeding, and the lophophore is then practically at right angles to the calyx (Text-fig. 1) (see also Assheton on L. saltans 2, p. 125, and Pl. 6, fig. 10). The numbers of tentacles springing from the lophophore varies in the different species of Loxosoma, and is generally somewhat variable within the species. The smallest number known to be present is eight, as in L. nitschei (25), L. obesum (3), &c., and the largest number twenty-nine in L. davenporti (19). In Pedicellina cernua the number is fourteen to twenty-four. In Loxosoma and Pedicellina new tentacles arise on either side of the median plane in the mid-distal (dorsal) region of the lophophore.

A narrow platform, or diaphragm, is present at the base of the tentacles; ventrally it is continuous with the large bilobed epistome; dorsally it is interrupted in the middle line where the new tentacles originate (see Text-fig. 5, p. 402). On the diaphragm is a ciliated tract, the vestibular groove, leading to the mouth. The ventral lip is considerably smaller than the epistome, and appears as a ciliated lobe between the bases of the two most ventral tentacles (Text-fig. 5, p. 402).

Normally in Loxosoma and Pedicellina the tentacles are extended, but when the animals are disturbed, or many distasteful particles are present in the water, the tentacles are bent inwards and folded away within the vestibule, while a delicate fold of skin, the velum or tentacular membrane, growing from the edge of the calyx at the bases of the tentacles, is drawn over the retracted tentacles by the contraction of a sphincter muscle present in its circular margin. The opening into the vestibule is thus reduced to a very small orifice. The appearance of L. crassicauda with tentacles withdrawn and lophophore closed is sketched in Text-fig. 2. The sphincter
L. crassicauda. Sketch of a living, unnarcoitized animal to show the backward bending of the lophophore during feeding, the direction of the water currents set up by the lateral cilia of the tentacles, and of the rejection current (R.C.) caused by the epistomial cilia. ×70.

is not as strongly developed in this species as in some, for instance, L. singularare, and in consequence the opening left into the vestibule is fairly large. Even in individuals killed
unnarcotized, the sphincter contracts little more than is shown in Text-fig. 2. In *L. crassicauda* the two most ventral tentacles—those on either side of the mouth—fold outside and across the adjacent tentacles.

The tentacles of *Loxosoma* and *Pedicellina* are supplied with nerves; one nerve enters each tentacle and gives off branches to the sense-cells (Harmer 13, pp. 271, 273). In *L. crassicauda* the nerves are visible in the living animal. Muscle-fibres also enter the tentacles, and to these are due the movement of the tentacles during feeding. Independent bending movements of a tentacle—sideways, and inwards and outwards—are observable. To the contraction of these longitudinal muscles, together with the sphincter in the velum, is due the
folding away of the tentacles into the vestibular cavity, when the animal is disturbed. In *Loxosoma* and *Pedicellina* there appear to be two longitudinal muscles in each tentacle; these run close to the lateral ciliated cells. The fibres are not easily identified in transverse sections.

The tentacles of *Loxosoma* are roughly triangular in cross-section, with the base of the triangle facing the lophophoral space (Text-fig. 6, p. 403). In *L. obesum* the triangle is almost equal-sided (Text-fig. 3, b), in *L. crassicauda* elongated (Text-fig. 3, a), and in this latter species, especially the two long sides of the triangle, are somewhat concave. This concavity is not due entirely to shrinkage of the tentacles on fixation, for it is seen in the living animal. The tentacles of *Pedicellina cernua* tend to be roughly rectangular in cross-section (Text-fig. 3, d), except near the tips, where they are triangular.

The epithelium of the tentacles consists of three kinds of cells: (1) ciliated cells; (2) non-ciliated cells; and (3) a few scattered sense-cells, bearing one or more stiff tactile hairs, which occur among the unciliated cells. The non-ciliated epithelium is found on the outer and lateral surfaces of the tentacles; there appears to be no regular arrangement of the cells: the nuclei are roundish. The cells on the inner or ciliated surface are in three tracts; a frontal (middle) and two lateral. The appearance in surface view of the ciliated cells of the tentacles of *L. crassicauda* is shown in Text-fig. 4. The frontal cells forming the middle tract are in three rows, and there is no interlocking of the cells. The middle row is slightly depressed to form a very shallow groove (see Text-fig. 3). The cells are rectangular in surface view, the two outer rows being especially elongated. The nuclei are long and narrow, and generally placed horizontally, but they may be twisted. The nuclei of the frontal cells, especially of those towards the bases of the tentacles, are frequently irregular in shape, as are also those of the cells forming the vestibular groove at the base of the tentacles. The frontal cells bear short cilia, those on the two outer rows being somewhat longer than those on the middle row (Text-fig. 4).
TEXT-FIG. 3.
Transverse sections of the tentacles of *Loxosoma* and *Pedicellina*. A. *L. crassicauda*. B, C. *L. obesum*. C, section towards the base of a tentacle. D. *Pedicellina cernua*. B.G., basal granules; C.R., ciliary rootlets; F.C., frontal cilia; GR., granules in lateral ciliated cells; L.C., lateral cilia; M., ? muscle-fibres; M.C., large cells in tentacle of *Pedicellina*. A and C, fixed in strong Flemming's fluid without acetic acid; B, Bouin's fixative; D, corrosive sublimate: all stained in Heidenhain's iron haematoxylin and acid fuchsir. × ca. 1200.
The cells of the lateral series are almost cubical, and have large oval nuclei (Text-fig. 4). They each bear a single row of long cilia. On fixation each cilium separates into its constituent fibres, and therefore in sections has the appearance of a tuft of fine cilia (Text-fig. 3).

Assheton (2, p. 136) described the cells of the ciliated surface of the tentacles of _L. saltans_ as being in three rows, as did Kowalewsky (15, p. 3) in _L. neapolitanum_; Nickerson
(19, p. 354) found no definite arrangement in L. davenporti. Kowalewsky says that the middle row is depressed to form a groove, but that the two lateral rows alone bear cilia; the latter statement is most probably incorrect, for while transverse sections of the tentacles of L. crassicauda and L. obesus show them to be very slightly grooved, the middle tract of cells also is ciliated. In figures of transverse sections of the tentacles of L. saltans (2, Pl. 7, fig. 18) and L. davenporti (19, Pl. xxxii, figs. 9 and 10) cilia uniform in length are shown over the whole of the inner surface, and it may be noted that a similar uniformity in the length of the cilia is shown by Cori (9, Text-fig. 5, p. 9) on the tentacles of Pedicellina cernua. An examination of living specimens of the species of Loxosoma found at Plymouth, and also of Pedicellina cernua, showed that while all the rows of cells on the inner face of the tentacles bear cilia, those of the middle rows are much shorter and finer than those on the two outer rows. An examination of the living tentacle is desirable, as sections do not always show clearly the difference in length of the frontal and lateral cilia. The cilia on the two outer rows of cells are very long, being about 35μ to 45μ long in L. crassicauda, and lash inwards (from the abfrontal to the frontal surface) across the length of the tentacles, except at the tip—occupied by a single cell—where they beat along the length. The short frontal cilia beat along the length of the tentacles and towards the base.

In the living L. crassicauda the lateral cilia are seen to be in groups of about twelve to fifteen to a cell, separated by slight intervals corresponding to the cell-walls: the number of cilia may be counted in a cell which has worked out of the epithelium. The metachronal rhythm of these cilia is characteristic, but difficult to describe: viewed from the frontal or abfrontal surface the appearance is of a double row of dots—one of which is very close to the bases of the cilia and is not always visible when the tentacles are viewed from some positions—while, at more or less regular intervals, cilia are extended. The effect of the rows of dots is no doubt due to the bending of the cilia during the stroke. All the cilia arising from a single cell do not beat in the same phase: if, however, the animal has been long
narcotized, and the rate of beat is much reduced, there is a tendency for them to beat more or less in the same phase.

The Ciliary Feeding Mechanism of the Entoprocta.

An undisturbed Loxosoma in the act of collecting food particles has the tentacles well expanded. The degree of expansion of the tentacular crown, however, varies; under natural conditions the tentacles form a shallow funnel (Text-fig. 1), but when under the influence of a narcotic, e.g. stovaine, they may bend outwards so that an almost flat plate is produced, and in extreme instances, the tips of the tentacles may even bend downwards. Text-fig. 5, which is a sketch of a narcotized animal, shows the tentacular crown rather more widely open than it would be under normal conditions. In Pedicellina the tentacles generally seem to be curved slightly towards the lophophoral space, though when the animals are narcotized the tentacular crown may become as widely expanded as that of Loxosoma under similar conditions. While feeding, the calyx, with the lophophore, is turned in different directions. In Loxosoma (L. crassicauda), as previously mentioned, the dorsal half of the lophophore is generally bent backwards, so that it is almost at right angles to the calyx. During expulsion of faeces the backward bending movement of the lophophore is marked.

Water is drawn into the tentacular funnel by the action of the long lateral cilia on the tentacles. The action of these is so energetic that it may be seen to shake the tentacles. The current enters between the outstretched tentacles (see Text-fig. 6), and sets away in front of the animal (see Text-fig. 1, p. 395). When the tentacles are fully expanded the current is therefore roughly from the direction of the attached end of the animal towards the free end: this causes the free-swimming bud to move with the lophophore hindmost. Particles carried in suspension in the water passing between the tentacles are thrown by the lateral cilia on to their inner, or frontal, surface, and passed by the short frontal cilia towards the base, and into the ciliated, vestibular groove, which leads to the mouth (Text-fig. 5). The grooved tract is interrupted in the median dorsal line of the
Sketch of the tentacular crown of *L. crassicauda* showing the ciliary currents, and the direction of beat of the lateral cilia of the tentacles. Only the cilia (*C.*) arising from the edge of the diaphragm are shown. *D.*, diaphragm carrying ciliated vestibular groove; *EP.*, epistome; *M.D.*, mid-distal (dorsal) region of lophophore; *OE.*, oesophagus; *R.*, rectum; *R.C.*, rejection current set up by the cilia on the epistome; *S.M.*, sphincter muscle in the velum; *V.L.*, ventral lip of mouth. The tiny arrows show the direction of beat of the lateral cilia of the tentacles. × 140.

Lophophore, and particles travelling down the tentacles on either side of this point pass in opposite directions towards the mouth. The path followed by particles from the tentacles slopes in the direction of the mouth in passing into the vestibular
groove, except in the case of those from the tentacles on either side of the mouth, which follow a path sloping slightly away from it, and join the collected stream from the tentacles of its side, at the right and left corners of the mouth respectively (Text-fig. 5). During feeding, muscular movements of the

epistome, mouth region—including that part of the lophophore carrying the two most ventral tentacles—and oesophagus occur.

While feeding with expanded tentacular crown the animal may partly close it with a sudden clutching motion (the movement of the lateral cilia ceasing), and as rapidly extend the tentacles again (the ciliary beat recommencing): or one
tentacle may be flicked inwards, without the others being affected; this appears to occur when a particle—perhaps usually a free-swimming ciliate—strikes the outer surface of a tentacle, where the tactile hairs are found; even the presence of large particles on the inner surface does not appear to call forth this response. Occasionally a single tentacle is bent slowly inwards into the vestibule, and may remain in this position for some minutes, and then be slowly straightened.

*L. crassicauda* may occasionally add to its diet organisms too large and active to be captured in the usual manner. Small, actively swimming ciliates, which are too powerful swimmers to be carried by the water current of the *Loxosoma*, at times blunder within the circket of tentacles and penetrate into the vestibule. The *Loxosoma* immediately and rapidly approximates the tentacles, bunching them tightly together, and reducing the circumference of the lophophore. The ciliate is thus trapped within the vestibule, and it either accidentally, or helped by the activity of the cilia of the vestibular groove, reaches the mouth and is swallowed. Not till then does the *Loxosoma* expand its tentacles. One individual was observed to capture six ciliates, at intervals, in this manner, and others were seen behaving in a similar way, with two or three already in the stomach.

Particles may be accepted as food or rejected from one cause or another. When unwanted, unpleasant, or too numerous food particles are carried in the food current the animal may reject them in one of several ways, its behaviour seeming to be rather capricious. In extreme instances it rejects them in a most definite manner, by closing the lophophore and contracting violently. On other occasions the mouth may be closed, but more generally the particles are allowed to enter and are then rejected. In the latter case the upper part of the oesophagus is constricted by circular muscle-fibres (see Text-fig. 2, *OE.M.*), and particles entering the right and left corners of the mouth are carried out again in two converging streams on to the oral surface of the epistome, from which they pass off between the two lobes in a median stream (see Text-fig. 5) to join the main water current setting away in front of the animal. The rejection
current (Text-figs. 1 and 5, B.C.) set up by the cilia on the epistome is easily distinguished in animals in which the lateral cilia of the tentacles are more or less motionless, and therefore the main water current almost in abeyance.

If the water were made thick with much powdered carmine or strings of large diatoms, the lophophore was observed, on occasions, to bring about rejection by partly closing—to about the position shown in 3, Text-fig. 1, b—with most of the long lateral cilia of adjacent tentacles motionless, with their tips interlaced; thus while the main water current was very greatly reduced, the interlaced cilia would act as a filter. The frontal cilia and those of the vestibular groove, continued to beat, and particles already within the lophophoral space were being drawn on to the inner faces of the tentacles, thence into the vestibular groove, and so on to the epistome, continuously.

*L. crassicauda* was found to feed freely on *Nitzschia closterium* var. *minutissima*.¹ When, however, too great a quantity of the culture was added, the animals very soon, perhaps in a minute or two, had swallowed sufficient. They then, though continuing to hold the tentacles expanded, much reduced the supply of diatoms by keeping the lateral, water-current producing, cilia practically motionless wrapped across the inner surfaces of the tentacles. Those towards the bases of the tentacles were generally active, but those on the distal halves were either all motionless, or only an odd group of cilia here and there showed activity. The activity of the lateral cilia was fitful, numerous intermissions occurring, the tentacular crown being suddenly half closed and then slowly opened, these movements coinciding respectively with the stopping and the recommencement of the beat. Occasionally a single tentacle might be curved slowly inwards and downwards to the vestibule. During this time such diatoms as reached and entered the mouth were carried out and expelled from off the epistome. The behaviour described above has also been observed to occur for no apparent reason, in sea-water almost free of organisms, but there is a possibility that it might be due to the methods of observation.

¹ Dr. E. J. Allen, F.R.S., very kindly supplied the culture of diatoms.
A few *L. crassicauda*, with the stomach full, occasionally reacted to the presence of numerous diatoms (*Nitzschia*) in the water in a different way: the tips of the tentacles were approximated, the tentacles being bunched together, and the circumference of the lophophore reduced. They might remain like this for several minutes, then slowly expand the tentacles.

At other times when *L. crassicauda* was observed in water with numerous diatoms, after obtaining sufficient food, they kept the tentacles well expanded, with the lateral cilia especially active, and relied on the rejection current from the epistome to carry off the unwanted diatoms, in the manner previously described (see p. 404).

**The Behaviour of the Lateral Cilia on the Tentacles of Loxosoma crassicauda.**—While the frontal cilia of the tentacles, and those clothing the vestibular groove at the bases of the tentacles, beat continuously, the lateral cilia of the tentacles of a healthy *Loxosoma* frequently cease beating, and would appear to be under the nervous control of the animal. Intermission of the ciliary beat of the main water-current producing cilia also occurs in the Ectoproct Polyzoa, both in the fresh-water (see Nitsche on *Alcyonella fungosa* 21, p. 27) and in the marine forms (see Borg 5, p. 248), and in *Phoronis* (11, p. 163). *Phoronis hippocrepia* at Plymouth, though left undisturbed in their stone during observation, held the lateral cilia more or less motionless, and several attempts made to observe the animals feeding were unsuccessful.

A healthy *Loxosoma* while feeding frequently clutches all the tentacles inwards, while all the lateral cilia suddenly and simultaneously become motionless, held wrapped across the inner surface of the tentacles in the position of the end of the effective stroke. Such behaviour may occur in response to no perceptible stimulation, or may occur when large particles strike the tentacles, or when the tube of the microscope is gently tapped. If the tube is tapped sharply the animal retracts the tentacles entirely, closing the lophophore. After successive gentle tappings the animal becomes less sensitive, and sharper ones are needed to call forth the reaction.
If the stimulation has been slight the tentacles almost immediately begin to straighten out, and the cilia to start beating. The ciliary beat may begin while the tentacles are still curved, or not until they are practically fully extended.

The recommencement of the beat after a period of quiescence is not simultaneous on all the tentacles, or even on the same tentacle. A wave of activity passing over the cilia may begin at the base of the tentacle and travel rapidly towards the tip; this is perhaps the most usual behaviour. The two sides of a tentacle, however, appear to be independent, for the movement may not begin at the same moment, or travel at the same rate, on both sides. The recommencement of the beat does not invariably take the form of a wave of activity passing from the base to the tip of the tentacle. A slight variation is that the cilia on the first two or three cells of one side at the base may be late in starting. At other times the cilia on two or three cells at the tip may start beating first, followed by those on the basal part of the tentacle, but there is irregularity in the sequence in which the cilia on the different cells become active. During a series of gentle stimulations the cilia of a certain cell of a tentacle of one individual were consistently slow to begin beating after an intermission, and might be several seconds behind those on adjacent cells. It would seem that the cilia arising from a single cell generally become active more or less simultaneously, but it has been observed that the start of beat of the separate cilia may be independent; this is especially seen when the cilia of a cell lag considerably behind those on other cells in becoming active.

As previously mentioned, under certain conditions—for instance when numerous Nitzschia are present in the water and the animal has taken sufficient food—L. crassicauda reduces the water current by holding many of the cilia motionless. A certain number of cilia, however, are active, chiefly those on the basal halves of the tentacles springing from the ventral half of the lophophore. Such groups of cilia as are beating appear to be beating metachronically. The cilia on the distal halves of some of these tentacles may remain motionless, wrapped across the inner surface, during successive periods of
activity and quiescence of the cilia on the basal halves: they may remain motionless for as long as ten minutes, though this is probably unusual.

Although sudden inward bending movements, of all the tentacles together, appear to be invariably accompanied by the stoppage of the beat of the lateral cilia, slow bending movements of a single tentacle, even if the end enters the vestibule, are not so accompanied. The sudden flicking inwards of a single tentacle is unaccompanied by the stoppage of beat of the cilia on the others, or, I believe, on that concerned, though it is difficult to be certain of the latter, as, during the movement, the tentacle passes rapidly out of focus.

In *Loxosoma* the stoppage of beat of all the lateral cilia on all the tentacles is simultaneous, while the start of the beat of the group of cilia arising from a single cell, and perhaps even of separate cilia, is independent. Carter (7, p. 11) has found that in the nudibranch veliger the stoppage of beat of the velar cilia is simultaneous, but that the start of the beat of the separate cilia is independent, and he says, 'this difference between the behaviour at the beginning and end of the intermission suggests that the recommencement of the beat is due rather to the passing away of the impulse which caused the intermission than to a new impulse'. Whether this would be sufficient to explain the behaviour of the lateral cilia of *Loxosoma*, where a number of the lateral cilia on a tentacle may remain motionless for some minutes, while the remainder on the same tentacle experience successive periods of activity and quiescence, is perhaps doubtful.

In *Loxosoma* the long cilia on the single cell at the extreme tip of each tentacle, and which beat along its length, are frequently seen motionless, bent slightly in towards the inner surface; in side view they then have the appearance of a single very stout cilium. These cilia appear often to lag some time behind the others in becoming active after an intermission.

When the tentacles are withdrawn into the vestibule and the lophophore is closed (see Text-fig. 2, p. 396), the lateral cilia beat, but rather irregularly owing to the restricted space; intermissions occur, and during these the two rows of cilia are
seen wrapped across the inner surfaces of the tentacles, the tips of those of opposite side interlacing.

Under the influence of stovaine, the cilia beat without intermission, but there is a tendency, if the narcotic be used over a period of half an hour or more, for the ciliated cells to break away. Generally those towards the tips of the tentacles are shed first. Even under normal conditions there appears to be some tendency for the lateral ciliated cells gradually to work out of the epithelium, individuals being observed with cells in the process of being shed. Their place is possibly taken by new cells, and in this way worn-out ciliated epithelium renewed. It might be noted that Carter (7, p. 11) describes the breaking free of the cells bearing the velar cilia in unhealthy nudibranch veligers. Cilia on the isolated lateral cells of Loxosoma may continue to beat actively for a short time.

With ether, also, intermissions cease, but it seems that they reappear after a time. Contraction of the muscles, including those of the tentacles and lophophore were observed, both during the time intermissions were inhibited, and when they had returned. This drug, however, was only used two or three times and its action not fully studied. The animals during observation were placed in a solid watch-glass, covered with a sheet of glass, so as to prevent evaporation of the ether.

The occasional intermission of the lateral cilia in healthy individuals, together with the ceaseless beating when under the influence of a narcotic, is suggestive of the behaviour of the velar cilia of the nudibranch veliger under similar conditions (7), and it would appear not improbable that they are similarly under the nervous control of the animal. That the tentacles of Loxosoma are supplied with nerves has been demonstrated by Harmer in L. crassa cauda (13): the nerves, however, were traced to the sense-cells present on the unciliated surface of the tentacles.

In Loxosoma, inhibitory control occurs of cilia concerned with feeding; so far as is known such control is almost restricted to locomotory cilia. According to Fedele, however, the branchial cilia of Doliolum are under the control of the animal (see Gray 12, p. 125).
A tufted fringe of cilia, 20 to 30\(\mu\) long, occurs along the free edge of the diaphragm, hanging down into the vestibule, and is continuous across the epistome, a ‘tuft’ occurring on either lobe (see Text-fig. 5, p. 402). These cilia appear to be frequently motionless, with the exception of the two groups on the lobes of the epistome; on the occasions when they have been observed lashing, they do so irregularly, a few groups (a group to a cell) beating, while the rest are motionless. They seem to be rather less inactive when the lophophore is closed. The beat is at right angles to the edge of the diaphragm, but the direction of the effective stroke was not determined. Their function remains obscure; it is possible that they may prevent particles—straying from the vestibular groove—from falling into the vestibule (particles are not seen within the vestibule of a healthy \textit{Loxosoma}); or they may effect a circulation of water among embryos in the vestibule. These cilia would appear to belong to the type which is motionless, or only feebly active, except when a stimulus is applied (see Gray 12, p. 125). The stimulus which would set these cilia moving was not determined; particles passing round the vestibular groove did not necessarily cause them to become active. In a narcotized animal, in which the lateral cilia of the tentacles are beating rapidly and without intermission, the cilia hanging from the edge of the diaphragm are motionless, with the exception of the two groups on the lobes of the epistome, which may show some movement.

There appear to be no glands in connexion with the ciliated tracts on the tentacles, or with the vestibular groove; the large gland-cells which outline the vestibule parallel with the groove in \textit{L. crassicauda} have been shown by Harmer (13) to open to the exterior.

The ciliary feeding mechanism of \textit{Pedicellina cernua} is essentially the same as that of \textit{Loxosoma}. The direction of the ciliary currents on the tentacles and along the vestibular groove are shown by Cori (9) in his Text-fig. 3, p. 6, though he does not distinguish between the two kinds of cilia on the tentacles. The cilia are differentiated into lateral cilia (see Text-fig. 3, d, p. 398) beating across the length of the tentacles, with the effective beat from the abfrontal to the frontal surface.
and the frontal cilia beating along the length, from the tip towards the base. The metachronal wave of the lateral cilia of Pedicellina is of the same type as that of the lateral cilia of Loxosoma.

A Résumé of Borg's Work on the Ciliary Feeding Mechanism of the Ectoprocta, with a Note on Flustrella hispida.

A preliminary account of the ciliary feeding mechanism of the Ectoproct Polyzoa was published by Borg in 1923 (4), and a further one in 1926 (5). From his accounts it is evident that the method of feeding in the Ectoprocta is very different from that of the Entoprocta. Borg worked on the Cyclostomata, Crisiella, Crisia, Tubulipora, Berenicea, and Lichenopora, as well as several cheilostomatous and ctenostomatous species (5, p. 246): at Plymouth the feeding of Flustrella hispida, one of the Ctenostomata, was especially noticed.

The form of the tentacles in the Ectoprocta, as in Loxosoma, is more or less triangular in cross-section (Text-fig. 7), in some forms (Crisiidae), however, with the apex of the triangle truncated (5, p. 216), but while in Loxosoma the base of the triangle faces the lophophoral space, in the Ectoprocta the apex faces the space (cf. Text-figs. 6, p. 403, and 8, b). The outer surfaces of the tentacles are unciliated, but bear a number of very long, stiff, tactile hairs. The lateral cilia (see Text-fig. 7) occur near the abfrontal (outer) face of the tentacles (at either corner of the base of the triangle in cross-section), are long, and beat from the frontal to the abfrontal surface; these are the main water-current producing cilia. From transverse sections it would seem that the lateral cilia occur in a double row on either side of the tentacles. According to Borg these cilia do not beat at right angles to the length of the tentacle, but somewhat obliquely downwards, and the tip of each cilium traces out an elliptical path. They have a marked metachronal wave, which passes up one side of a tentacle and down the other, and runs, therefore, at right angles to the direction of beat of the cilia.
Transverse sections of the tentacles of Ectoproct Polyzoa. 

A. **Lichno-pora fimbriata** (Cyclistomata). (After Borg.) × ca. 2000. 
B, C, D. **Flustrella hispida** (Ctenomastata). B, through distal region of tentacle; C, through basal region of tentacle; D, through base of a tentacle forming part of the rejection tract. × ca. 1200. 
E, F. **Electra pilosa** (Cheilostomata). E, through distal region of tentacle; F, through basal region of tentacle. × ca. 1470. 

B.G., basal granules; C.R., ciliary rootlets; F.C., frontal cilia; L.C., lateral cilia; M., homogeneous membrane; M.C., mesoderm; M.F., muscle-fibres. B-D, corrosive sublimate; E, F, Bouin’s fixative; B-F, iron haematoxylin and acid fuchsin.
The development of the cilia along the frontal face would appear to vary widely in different forms.\(^1\) They may be (a) absent, or Borg (5, p. 217) states, so feebly developed that he was unable to find them, as in most Cyclostomata; in others (b) short and thinly scattered as in the Crisiidae, and in some other forms, for instance, Berenicea patina, Diplosolen obelia, and Lichenopora fimbriata (Text-fig. 7, A) (5, p. 216); or (c) fairly numerous and long as in Flustrella hispida (Text-fig. 7, B-D) and Alcyonidium (Ctenostomata). Also in Electra pilosa, one of the Cheilostomata, the frontal cilia are fairly long, at least towards the base of the tentacles, though perhaps not very thickly set (Text-fig. 7, E and F). Marcus (see Borg, 5, p. 248) says of the frontal cilia of Farella repens that they are immovable and stiff. In the first instance (a) a frontal current along the length of the tentacle is obviously absent; in the second instance (b), Borg (5, p. 248) says he has occasionally seen a particle, which has stuck to one of these cilia, moving slowly along the frontal face towards the mouth, but that these frontal cilia play quite a subordinate part in the nutrition; in (c) Flustrella hispida, where the frontal cilia are well developed, they approach the lateral cilia in length and there seems to be little or no movement of particles over them, except perhaps towards the lower part of the tentacular funnel. Here particles may occasionally be seen travelling down them into the mouth. Towards the base of the lophophore, where the tentacles are crowded together, the frontal cilia are especially long, while the laterals appear somewhat reduced in length. The chief function of the frontal cilia—especially of those towards the bases of the tentacles—in Flustrella hispida would appear to be to help produce and direct the main water current towards the mouth.

\(^1\) It is possible that the frontal cilia are longer than they appear in transverse sections. As these cilia beat along the length of the tentacles, it is possible that in preserved material they may lie at an angle to the frontal surface, and in transverse sections would be cut across. The lateral cilia, on the other hand, beating across the length of the tentacles, would be seen at their full length in transverse sections.
In the Ectoprocta the extended tentacles form a funnel with the mouth at the base; in Flustrella hispida the shape of the lophophore is bell-like, the tips of the tentacles being bent outwards. Briefly the method of feeding as observed by Borg (5, p. 247) is as follows: a water current is produced by

Text-fig. 8.
A. Diagram showing longitudinal section through tentacular crown, mouth (M.), and pharynx (PH.), in Cyclostomata. B. Diagram showing section through tentacular crown. The arrows indicate the direction of water currents caused by movements of cilia. (After Borg.)

the lateral cilia of the tentacles, between which it passes outwards (Text-fig. 8) (that is in the opposite direction to the water current in Loxosoma) incidentally carrying with it many food particles. This results in the formation of a current directed straight down the lophophore to the mouth (Text-fig. 8, A). The muscular pharynx acts as a suction-pump which receives the food, and its effect is increased through the strong cilia of the epithelium of the pharynx, which move from above downwards. As Borg points out, the feeding mechanism cannot be regarded as very perfect, many particles escaping with the
water current passing out between the tentacles, and mostly only those in, or near, the median line of the lophophore reaching the mouth. Borg (5, p. 248) details the various means by which the animal increases the number of particles brought to the mouth, chief of which are the turning of the tentacular crown in different directions, and the alteration in the direction of the water current by the spreading and the contracting of the tentacles.

The methods resorted to by the Ectoprocta to prevent distasteful particles from reaching the mouth are, according to Borg (5, pp. 248, 249):

1. Complete or partial retraction of the tentacular crown.
2. Approximation of the tips of the tentacles, thus preventing the formation of the water current towards the mouth, while particles are whirled out between the tentacles.
3. Quick movement towards the median line of a tentacle to free itself from a useless particle, which has adhered to it.

The rejection of useless particles, which have already gained the region of the mouth, is carried out in the following different ways (see Borg, 5, pp. 249, 250):

1. The mouth remains closed, and particles are then usually carried away by the water streaming out between the bases of the tentacles.
2. 'Particles that have already been swallowed can again be ejected out of the stomodaeum, through a momentary alteration of the direction of movement of the cilia of the pharynx, and a quick opening and closing of the mouth.'
3. Ejected particles, and others too large to pass through the narrow spaces between the proximal parts of the tentacles, often collect in a little heap by the side of the mouth. When this occurs the animal first widens the tentacular crown, and then contracts it with great rapidity; in this way water at first streams in between the tentacles and then is forced out through the opening of the tentacular funnel, carrying with it the heap of particles.

The Method of Rejection of Unwanted Particles in Flustrella hispida.—The method of rejection of un-
wanted particles from the mouth region in *Flustrella hispida* is more specialized than is that of the forms described by Borg. It was noticed that in *Flustrella* if the animal does not wish to feed, particles passing into the pharynx travel out again at a certain point ventrally, and, passing between the bases of two tentacles, are carried away in the main current setting away from the animal. Closer observation showed that there is a narrow ciliated rejection tract in this region, leading from the mouth outwards between the bases of the two tentacles (Text-fig. 9). These form part of the rejection tract, the cilia for a short distance beating towards the tips. This tract is a continuation of a ventral groove in the pharynx (Text-fig. 12, p. 419) along which the cilia beat outwards towards the mouth. Looking down on an expanded lophophore, this region, with the tentacles on either side of it, can easily be distinguished (Text-fig. 9); its position can be determined in transverse sections through the base of the tentacular crown, owing to the larger size of the bases of the two tentacles forming part of the rejection tract (see Text-fig. 10). On either side of the groove is a large
CILIARY FEEDING OF ENTOPROCTA

flagellum (see Prouho, 24, p. 564), or I am inclined to think a short, almost transverse, row of stout cilia (Text-fig. 11, *FL*), which beat transversely towards the groove. Their position at the end of the beat into the groove is shown in Text-fig. 9: they do not beat continuously, but at irregular intervals.

In *Flustrella*, therefore, although the cilia clothing the
walls of the pharynx beat mainly in a downward direction, there is a groove in the mid-ventral line (Text-fig. 12) along which the cilia beat upwards, thus the passing of particles, and of water, out of the pharynx is not due to a momentary alteration of the direction of movement of the cilia of the pharynx, such as Borg (5, p. 249) found in the species he investigated. It is probable that muscular movement of the walls of the pharynx determine whether particles be brought in contact with the outgoing tract of cilia, for during feeding the walls of the pharynx are in constant movement. Particles accepted as food collect, before being swallowed, in the region where the pharynx passes

**Text-fig. 11.**

*Flustrella hispida.* Transverse section through the lophophore at the level of fusion of the tentacles. *FL.*, flagellum (or short row of stout cilia?); *H.M.*, homogeneous membrane of the tentacles; *V.G.*, ventral groove or rejection tract. Corrosive sublimate; iron haematoxylin and acid fuchsin. Somewhat diagrammatic. × 430.
CILIARY FEEDING OF ENTOPROCTA

into the unciliated oesophagus, but even from here there may be some slight loss of particles, as the ventral ciliated groove is continued for a very short distance among the unciliated epithelium of the oesophagus.

The peculiarity in the form of the buccal region in Flustrella, and an allied genus Pherusa, was noted by Prouho (24, p. 564) in 1892, and he says, "La symétrie bilatérale du lophophore est ici rendue manifeste par cette disposition particulière qui, sans doute, doit être de quelque utilité à l'animal pour le choix ou la préhension de sa nourriture."

DISCUSSION.

From what is known of the structure of the tentacles and their ciliation in the fresh-water Polyzoa, it is probable that the ciliary feeding mechanism of this group is somewhat similar to that of the marine Ectoprocta, though no doubt modified owing to the horseshoe shape of the lophophore in the majority.
of forms, and the presence of a large epistome. The lateral cilia in the Phylactolaemata have been described by Allman (1, p. 20), as beating towards the tips of the tentacle on one side and towards the base on the other, but he was apparently misled by a marked metachronal wave of the type of the lateral cilia of the marine Ectoprocta, and, as pointed out by Nitsche (21, p. 26), in reality the cilia beat across the tentacles (see also Kraepelin, in Borg 5, p. 245). It is very probable that the effective beat is from the frontal to the abfrontal face as in the marine forms. It might be noted that Gilchrist (11, footnote, p. 163) also alludes to the lateral cilia of the tentacles of Polyzoa as beating in opposite directions on each side of the tentacles.

It is of interest that a similar type of metachronal wave, that is one running at right angles to the direction of beat of the cilia, and in opposite directions on opposite sides of a tentacle, filament, or gill-bar, is found for the lateral cilia in widely different groups of animals in which these cilia beat in the same direction, namely, from the frontal to the abfrontal surface, and where their function is that of producing a water current. Groups of animals in which the lateral cilia have a rhythm of this type are: Ectoproct Polyzoa, Phoronis, Lamellibranchs, those Gastropods in which the gills are formed of distinct filaments, and the cilia are differentiated into laterals and frontals (i.e. Gastropods exclusive of Tectibranchs and Nudibranchs), Ascidians and Amphioxus.

It will be evident from the foregoing account that the method of feeding in the Entoproct and Ectoproct Polyzoa is very different; not only are the main water currents in the two groups in opposite directions (cf. Text-figs. 1, p. 395, and 8, p. 414)—illustrated by the fact that in Loxosoma a free bud, or detached small adult, swims with the calyx hindmost, while the opposite occurs in the Ectoprocta—but while ciliary currents (as distinct from water currents)1 play an important part in the method of feeding in the Entoproct,  

they may be absent, or little developed, on the tentacles of the Ectoprocta. The difference in the method of feeding is reflected in the size of the particles taken in the two groups, the Entoprocta being restricted on the whole to finer particles than are the Ectoprocta.

The method of feeding in the Entoprocta is rather similar to that of Sabella pavonina as described by Nicol (20), though on a simpler plan, and without the specialized sorting mechanism of the worm. In Sabella the beat of the long cilia which maintain the main water current is also from the abfrontal to the frontal surface of the filaments, and they have a metachronal rhythm similar to that of the lateral cilia of Loxosoma. It might be noted, however, that while in Sabella these cilia when at rest have a marked S-form, those of Loxosoma are only slightly curved inwards.

The cilia producing the main water current in Loxosoma and Pedicellina are in the same position in regard to the frontal cilia, that is adjacent to them on either side, as in Sabella pavonina and certain other Cryptocephalous Polychaetes (see Nicol 20), and incidentally as on the dorsal filaments of Brachiopods (see Orton 23, p. 293)—though in the latter group the effective beat is in the reverse direction—and have been termed by Nicol latero-frontal cilia. While these cilia are undoubtedly latero-frontal in position, this term is perhaps not altogether advisable as it has been previously applied to, and has come to denote in particular, the slow beating, straining (see Gray 12, p. 145, and Orton 22, p. 466)—and not water-current producing—cilia of the Lamellibranch Mollusca. As the long cilia on the tentacles of the Entoprocta agree in their function of producing the main water current—though the effective beat is in the opposite direction—with the lateral cilia on the tentacles of the Ectoproct Polyzoa, and incidentally with those of Phoronis, Lamellibranchs, certain Gastropods, Ascidians, and Amphioxus, they have been termed lateral cilia in this paper.

The ciliary feeding mechanism of the Ectoprocta would

1 Gray (12, p. 145) also says that ‘they appear to keep individual filaments apart, so giving freedom of action to the lateral cilia’.
appear to differ considerably from that of any group so far described in any detail, in that ciliary currents, if not absent, play a subordinate part, while the chief role is played by the water current—set up by the lateral cilia—in conjunction with a suction pump formed by the muscular pharynx.

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Summary.

An account is given of the ciliary feeding mechanism of the Entoproct Polyzoa, and of the structure of the lophophore and tentacles. The long lateral cilia cause a current of water to pass inwards between the tentacles, and throw particles on to the short frontal cilia of the inner surface, which carry them to the vestibular groove leading to the mouth.

The behaviour of the lateral cilia of the tentacles of *L. crassicauda* is described, and it is suggested that they are under the nervous control of the animal.

A résumé of Borg's work on the ciliary feeding mechanism of the *Entoprocta* is given, a note on *Flustrella hispida* being added. It is pointed out that the method of feeding in this group differs widely from that of the *Entoprocta*.

Literature.

CILIARY FEEDING OF ENTOPROCTA 423

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