

## SUSPENSION FEEDING BY MARINE INVERTEBRATE LARVAE: CLEARANCE OF PARTICLES BY CILIATED BANDS OF A ROTIFER, PLUTEUS, AND TROCHOPHORE

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The means by which cilia remove particles from suspension are of ecological interest because the clearance mechanism determines how much and what kind of food can be obtained by a suspension feeder in a given environment. Clearance is of physiological interest because cilia which must remove particles from a current of water may require greater strength or more rapid alteration of beat than cilia moving in water alone. When both these aspects are considered, the organization and evolution of the ciliary feeding systems are more readily understood. The entire process of suspension feeding consists of (1) producing a current, (2) filtering or clearing particles from it, (3) transporting the particles to the mouth, and (4) ingesting them (Werner, 1959). Since clearance is the most difficult part of the process to observe, descriptions of feeding mechanisms frequently omit clearance, and discussions of ciliary motion often exclude consideration of the extra load some cilia must bear.

Although many small suspension feeders have the simple arrangement of only one or two ciliary bands, little is known about the manner in which cilia concentrate particles from suspension. There is not the division of labor which Dral (1967) found in the mussel, *Mytilus*, which uses different sets of cilia to function in current production, filtering, and transport of particles. Nor is there the distinct mucus filter found in some other suspension feeders (Werner, 1959). Some authors have suggested mechanisms such as centrifugation (Tattersal and Sheppard, 1934), impingement (Bullivant, 1968a, b), or sedimentation (Davis, 1955), but these cannot account for the high rates at which particles are cleared (Strathmann, 1971). Other authors have felt that contact between cilia and particles is necessary for removing particles from suspension but have been unable to determine just where or how particles are moved relative to the water. Observation is difficult because (1) cilia are small and move rapidly, and (2) water currents, as distinct from the motion of particles, are difficult to observe on this scale.

In this study we used high speed cinefilms of plutei, rotifers, and a trochophore to examine two mechanisms by which particles are removed from suspension by cilia. In one type of suspension feeding a single band of cilia produces a current and retains particles on the upstream side of the band. This type of feeding is exhibited by planktotrophic echinoderm larvae (Strathmann, 1971) and at least

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some of the tornaria larvae of hemichordates. We will refer to this type as the single band system. In a second type of suspension feeding, one band of cilia produces a current and particles are collected downstream in a groove between this band and a parallel band of shorter cilia. We will refer to this second type as the opposed band system. It is exhibited by bdelloid and flosculariacean rotifers (Hatschek, 1878; Zelinka, 1886; Remane, 1929, 1932), the trochophore larvae of annelids (Hatschek, 1878; Wilson, 1932) and probably also the trochophores of echiuroids (Hatschek, 1880), the veliger larvae of bivalves and gastropod mollusks (Yonge, 1926, Werner, 1955; Thompson, 1959; Fretter, 1967), and entoproct larvae (Jägersten, 1964; Mariscal, 1965).

We shall try to give a satisfactory account of the mechanisms by which particles are cleared from a suspension in these two systems. We shall then discuss the variability of the two mechanisms and indicate how their limitations may be related to differences in the size of particles which can be eaten and differences in clearance rates (volume of water processed per unit time).

#### MATERIALS AND METHODS

In California we reared from egg and sperm the plutei of the sea urchin *Lytechinus anamesus* (Echinodermata, Echinoidea) and trochophores of the serpulid worm *Spirabranchnus spinosus* (Annelida, Polychaeta). We used methods described by Costello, Davidson, Eggers, Fox, and Henley (1957). We obtained mitraria larvae, gastropod veligers, and tornaria larvae from the plankton near Catalina Island. Bdelloid rotifers resembling *Philodina* were obtained from a hay infusion culture of *Paramecium*. In Hawaii we reared tornariae of *Ptychordera flava* (Hemichordata, Enteropneusta) from egg and sperm, and we used veligers of *Charonia tritonis* (Mollusca, Gastropoda) newly hatched from egg capsules.

Plutei, a trochophore, and rotifers were filmed on "Plus X" or "4X" film (Kodak) at 100 to 200 frames per second with a Redlake Locam camera with phase contrast or Nomarski interference microscopes (Zeiss). These cinefilms included a time marker for noting rates, all of which were measured at room temperature, about 20 to 22° C.

The plutei were pressed by the coverglass just enough to slow them and to orient them for filming. In this way we could film an optical section across the lateral portion of the ciliated band between the postoral and anterolateral arms. We were less successful in orienting and slowing trochophores without interfering with feeding; but the rotifers remained stationary, fed actively, and maintained a suitable position on microscope slides.

Filmed observations were made of a trochophore feeding on *Phaeodactylum tricornutum*, rotifers feeding on plastic spheres of 1.3 or 2.7  $\mu$  diameter (Dow Chemical Co.), and plutei feeding on either *Phaeodactylum* or *Dunaliella tertiolecta*, sometimes in combination with plastic spheres. In other feeding observations we used these algae or particles and also *Amphidinium carteri*, *Cricosphaera carterae*, and Sephedex spheres (Pharmacia).

Even with unnaturally high concentrations of particles, there are relatively few contacts per 100 feet filmed between particles and the portion of the ciliated band in focus. With still higher particle concentrations the larvae ceased clearing

particles from suspension. This limited the number of particle captures we could record on film.

In even the best filmed sequences, the movement of water could not be directly observed. This would have required a technique for introducing just upstream from the ciliated band a very small (less than  $30\ \mu$  diameter) discrete volume of water colored by soluble dye and including suspended particles. (Chinese ink and other current markers commonly used in zoological studies are suspensions of particles and not suitable for observing motion of particles relative to water in clearance). The motion of water was therefore inferred from motion of particles and cilia.

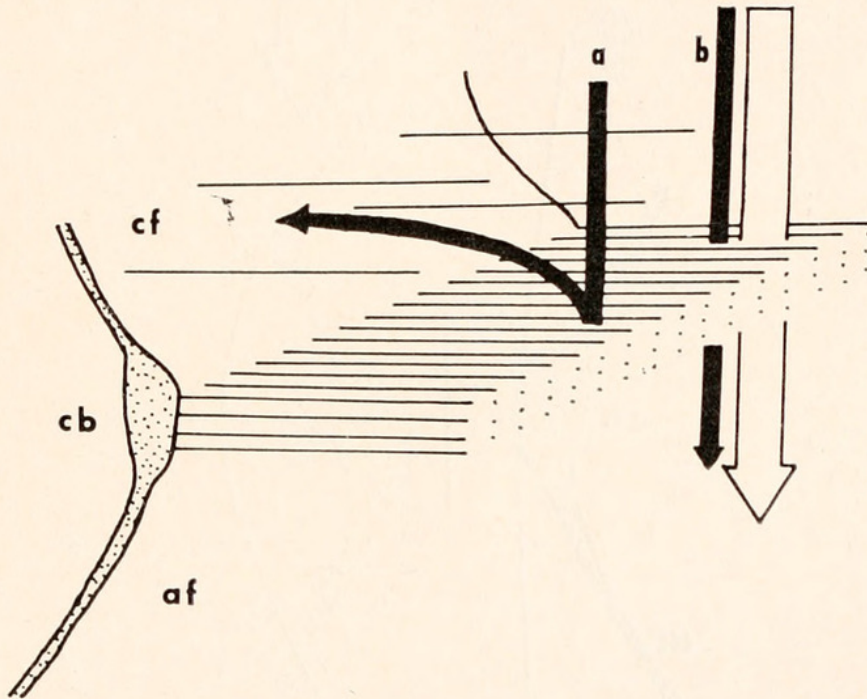


FIGURE 1. Diagram of single band of cilia with upstream collection of particles.  
For explanation of symbols and abbreviations, see text.

The close array of cilia prevented tracing of individual cilia in successive frames, but positions in a given frame and a composite picture of positions during the beat cycle could be obtained.

## RESULTS AND DISCUSSION

### *Locally induced reversal of beat in the pluteus*

The distribution of cilia in the single band system is diagrammed in Figure 1. The band of cilia produces the current (white arrow) used in feeding and locomotion. When a larva is feeding, particles are stopped at the ciliated band and passed back to the cilia of the circumoral field (Fig. 1a), which pass them on towards the mouth. Some echinoderm larvae lack cilia on the circumoral field, and particles are passed along the band of cilia in a series of jumps. When a larva is not feeding, the current is the same but particles are passed through the band of cilia with the water (Fig. 1b). In some forms the cilia of the band can also reverse the direction of the beat and the water current. During a general reversal

of beat along the band, the direction of swimming is reversed and feeding ceases or is greatly reduced. All of this can be seen without high speed cinefilms.

The high speed cinefilms of plutei indicate that a locally induced reversal of beat is the clearance mechanism operating at the band. As diagrammed in Figure 2, the cilia have a straight effective stroke and curved recovery stroke. The effective strokes of the cilia of the band sweep a little more than  $180^\circ$ . When the larva is not feeding, particles pass through the band of cilia with the water

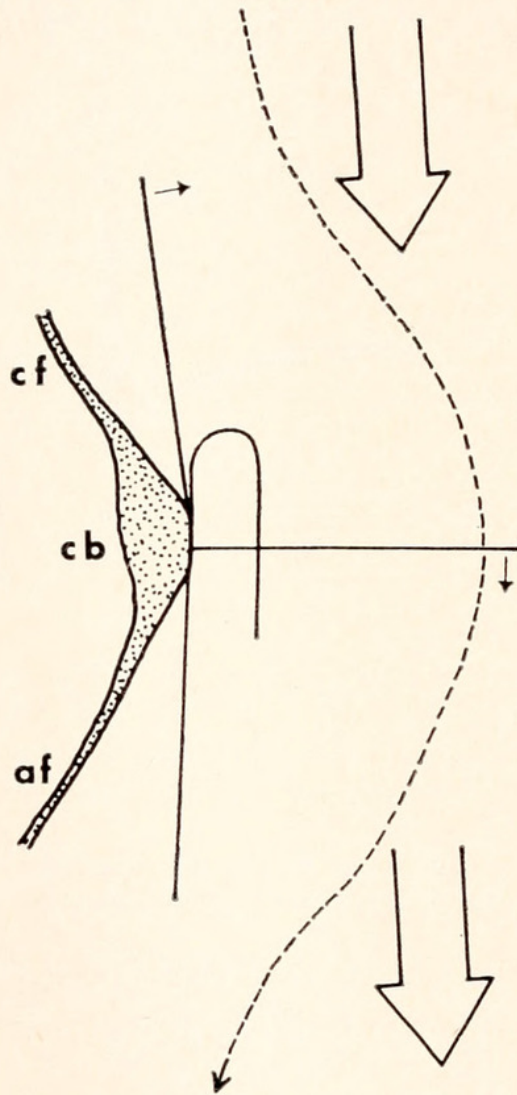


FIGURE 2. Diagram of form of beat of cilia in the pluteus and path of a particle through the band when the pluteus is not feeding. For explanation of symbols and abbreviations, see text.

(Fig. 2), and forward beating continues with no discernible change. In a feeding larva the beat is the same until a particle comes within reach of the cilia. Then an alteration of the beat of several cilia can be seen while the particle slows, changes direction, and is finally pushed back in an arc suggesting a reversed effective stroke of the cilia (Fig. 3a). In some cases the particle is only detained by the brief alteration of beat (Fig. 3b). Because a small particle can pass through the band of cilia close to the position at which a larger particle is being retained, the change of beat which retains a particle must be local.

The change in beat may be triggered by a mechanical disturbance of the cilium, and a larger particle may be a more effective trigger. Small particles (bacteria and polystyrene spheres of 1 or 2  $\mu$  diameter) pass through the band of cilia (Fig. 3c) when larger particles (*Dunaliella* or *Phaeodactylum*) are retained. When 1.3  $\mu$  polystyrene spheres and cells of *Amphidinium* were present in equal concentrations, the plutei ingested more than five times as many cells of *Amphidinium*.

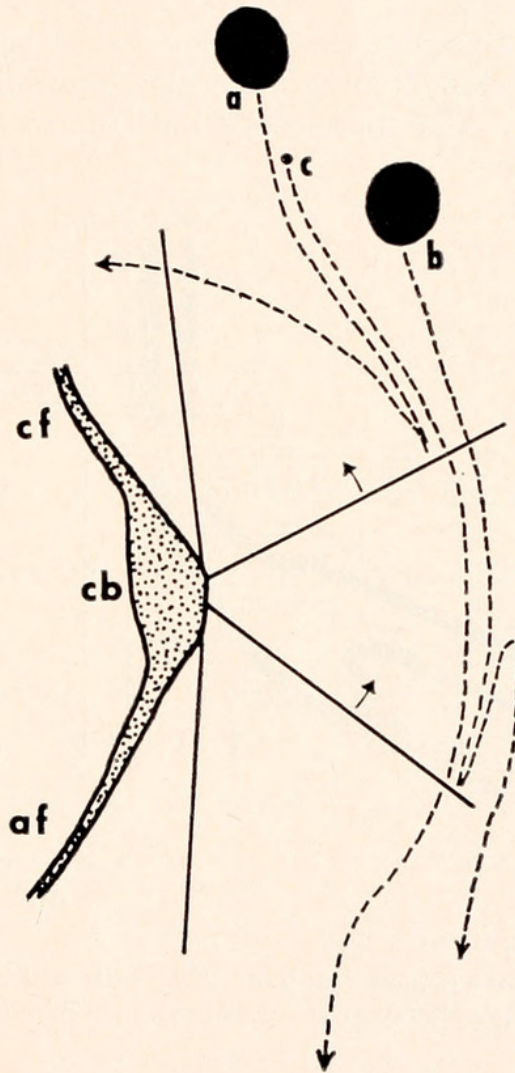


FIGURE 3. Diagram of paths of particles through the band of cilia when the pluteus is feeding. For explanation of symbols and abbreviations, see text.

The whole process of altering beat and retaining a particle occurs very rapidly. In a feeding larva particles approaching the cilia are moving about 0.07 to 0.11 cm/sec. (Some larvae which were not feeding produced a faster current across the band, but this was not a consistent difference between feeding and non-feeding larvae.) A particle's forward motion is stopped about 0.02 to 0.06 sec after it has come within reach of the cilia (estimated as 25  $\mu$  from the base of the cilia). The particles are moved back toward the circumoral field at about 0.06 to 0.10 cm/sec. Forward beat is resumed after about 0.06 to 0.14 sec.

In the sequences in which the cilia retaining a particle were clearly in focus, a reversed recovery stroke could be seen; but in these sequences no other particles

were present to indicate a forward beat elsewhere. Thus, we cannot be certain that these reversals were not general reversals coinciding with the arrival of a particle at the band. In the sequences in which alteration of beat was clearly local, the cilia pushing the particle were not as clearly in focus; and we could only deduce from the motion of the particle that the alteration of beat included a reversed effective stroke. Though an induced local reversal of the effective stroke could not be directly observed, we can find no other interpretation consistent with our observations.

That a reversal remains localized is not surprising, since there is only a single cilium per cell in echinoderm larvae. It is more difficult to account for the rapidity of the reversal. A particle carried within reach of the cilia is moving

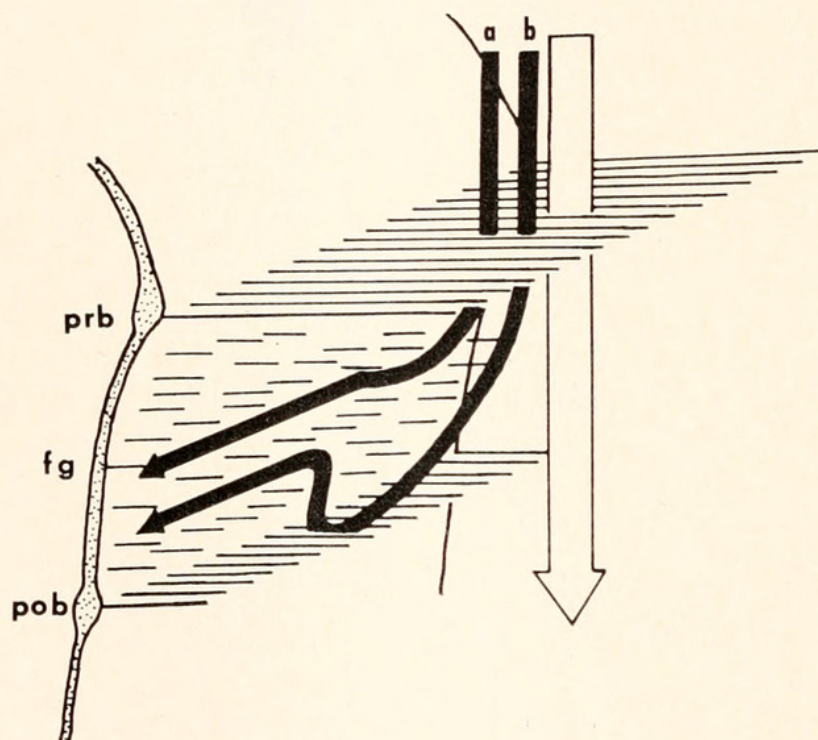


FIGURE 4. Diagram of two opposed bands of cilia with collection of particles in a food groove. For explanation of symbols and abbreviations, see text.

almost as fast as the cilia in their forward effective strokes. The cilia must be stimulated during the beginning of their forward effective stroke, and either these cilia or their neighbors must reverse beat before the forward stroke is completed. The current velocities, timing, and particle motion indicate that this very rapid reversal of beat does occur within a fraction of the time it would take to complete a forward stroke.

#### *Opposed band system of bdelloid rotifer and trochophore*

The distribution of cilia in the opposed band system is diagrammed in Figure 4. Previous investigators agree that the long cilia of the preoral band produce the major current used in feeding and locomotion, and that the short, fine cilia of the food groove convey the collected particles along the groove to the mouth, but they variously describe particles as being brought directly into the food groove by

the long cilia of the preoral band (or trochus or prototroch) (Fig. 4a) or as being first carried to the shorter cilia of the postoral band (or cingulum or metatroch) (Fig. 4b) which then convey them to the food groove. High speed cinefilms of bdelloid rotifer and trochophore and observations of rejection mechanisms of larvae indicate that both preoral and postoral bands are essential to clearance. We have concluded that the opposed beat of cilia of the preoral and postoral bands results in increased movement of the preoral cilia relative to the water in the latter half of their effective stroke and that most of the clearance of particles from water occurs at this point.

The cinefilms of bdelloid rotifers indicate that the cilia of the preoral and postoral bands beat towards each other (Fig. 5) with an approximately straight effective stroke and curved return stroke. Particles enter in the major current (Fig. 5A, upper arrow). Most of the particles within reach of the preoral cilia are swept into the food groove (Fig. 5a). A few particles observed posterior to the preoral cilia indicate a current in this region (Fig. 5A, lower arrow), but this water has been largely cleared of particles. Many of the particles swept into the food groove never come within reach of the postoral cilia (Fig. 5a). Particles just beyond the reach of the preoral cilia continue to move posteriorly (Fig. 5b). For clearance to occur, the cilia of the preoral band must push the particles relative to the water; this probably happens in the latter half of the effective stroke as the particles are carried into the food groove. Mucus could also aid in clearance; if the cilia of the preoral band were to pick up mucus as they slide past the food groove on the recovery stroke, then they might hold particles more firmly on their effective stroke. Particles in the food groove can be carried toward the base of the cilia of the preoral band by the return stroke (Fig. 5e). This action of the return stroke may help keep particles in the food groove.

Then what is the role of the postoral band of cilia? Although these cilia may help retain particles in the food groove or serve to catch particles slipping beyond the tips of the cilia of the preoral band (Fig. 5c), they also appear to play a more direct role in the clearance mechanism. In some instances particles which have slipped beyond reach of the cilia of the preoral band are also carried beyond the postoral band of cilia, only to be conveyed anteriorly into the food groove (Fig. 5d). Since many of these particles are clearly beyond reach of the cilia of the postoral band, they must be carried in currents (Fig. 5d) presumably produced by the postoral band of cilia. Since the two bands of cilia are producing currents in opposite directions, water must be pushed away from the food groove where the cilia are completing their effective stroke. This water movement would keep most particles from slipping beyond the reach of the cilia of the preoral band and would increase the movement of preoral cilia and particles relative to the water.

Observations of serpulid trochophores showed that the cilia of the two bands beat in the same manner as the cilia in the rotifers. Particles coming within reach of the cilia of the preoral band are carried into the food groove. The orientation of the filmed trochophore relative to the camera prevented detailed analysis of particle paths near the postoral band of cilia, but since the distribution and beat of the cilia and the paths of particles are very similar, it seems likely that trochophores employ the same mechanism of clearance as bdelloid rotifers.

However, in the serpulid trochophores, regulation of clearance may be different. The rotifers cleared particles continuously when the wheel organ was extended, although the collected particles were often rejected at the mouth. The trochophores

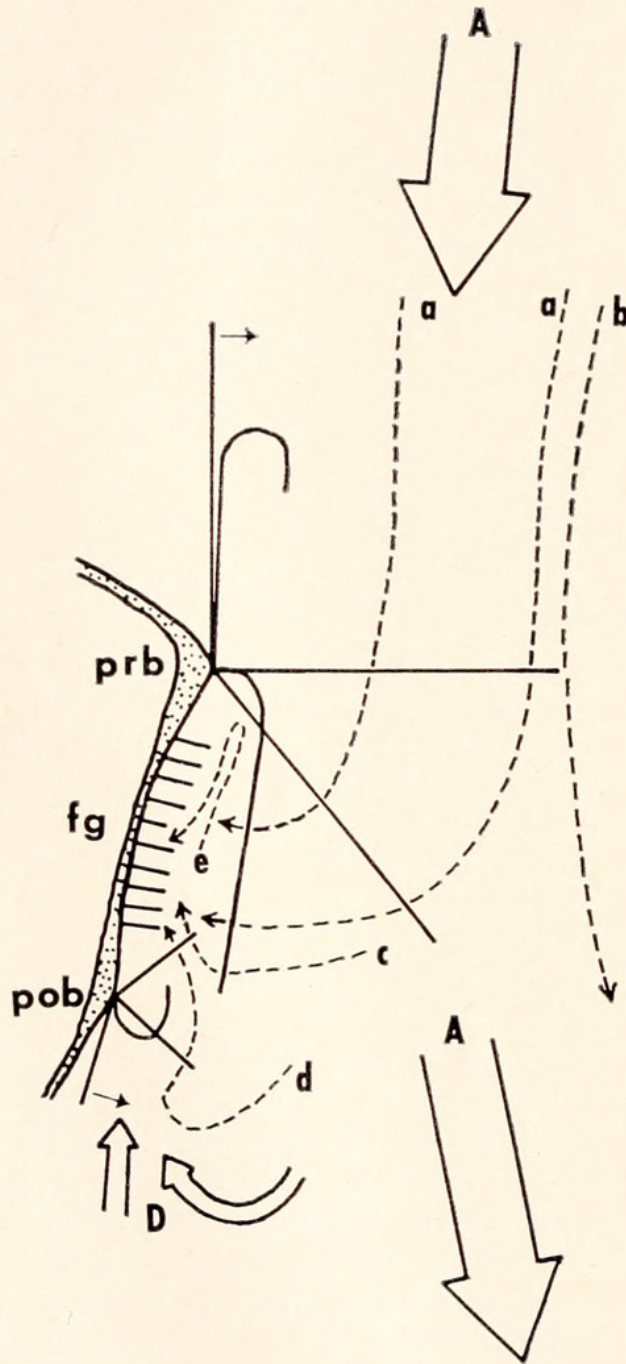


FIGURE 5. Diagram of direction of beat of cilia, currents, and particle paths in a bdelloid rotifer. Direction of ciliary beat, currents, and particle motion are similar in the trochophore. For explanation of symbols and abbreviations, see text.

could similarly reject particles at the mouth, passing them down the neurotroch; but they could also stop filtering while continuing to swim. While the preoral band of cilia and cilia of the food groove stopped beating, particles were not collected behind the preoral band of cilia but were carried posteriorly with the water. This supports our view that the function of the trochophore's postoral cilia in clearance

is the same as in the bdelloid rotifer. A mitraria larva and gastropod veligers collected from the plankton also could continue swimming without clearing particles, presumably again by stopping beat of the postoral cilia.

#### *Occurrence of the two systems*

The single band system has been found in all planktotrophic echinoderm larvae studied (Strathmann, 1971) and also occurs in the tornaria larva of hemichordates. In the tornariae which we have observed, the ciliated bands beat away from a ciliated circumoral field, and particle movement in feeding and rejection is like that in an echinopluteus or bipinnaria. These tornariae included individuals having no tentacles throughout development and early stage larvae of *Ptychodera flava*, which appeared to be developing tentacles. Garstang (1939) described a very different mode of feeding for tentaculate tornaria larvae. In Garstang's tornariae, particles first contact the aboral field and are then moved across the band onto an unciliated circumoral field. No mechanism is offered by Garstang for concentrating particles until after they have entered the mouth. It seems unlikely that the larger tentaculate stages should have such a different feeding mechanism, but further studies of tentaculate forms would be of interest.

The single band clearance mechanism, with an induced localized reversal of beat, could conceivably occur in other animals whose mechanism of clearing particles has not been satisfactorily explained. For example, the lateral and frontal cilia of some brachiopods might function much as the ciliated band and cilia of the circumoral field of the tornaria and echinoderm larvae. During feeding, the direction of ciliary beat, currents, and the movement of particles down the tentacles or filaments are quite similar (Atkins, 1956). Some brachiopods have one cilium per cell (Atkins, 1958). An induced local reversal of beat of the lateral cilia could explain how small particles are retained on the frontal surface of the filaments. But if other lophophorates were found to exhibit the single band system then we would have to alter our opinions on its limitations, for in some lophophorates there are several cilia per cell (figures in Hyman, 1959), and the lateral cilia run to somewhat greater length than the cilia of the ciliated band in tornaria and echinoderm larvae. More detailed observations of the lateral cilia of lophophorates during feeding and rejection should indicate the extent to which an induced local reversal mechanism is employed in this group. If this mechanism does occur, there should be a break in the metachronal wave when a particle is retained by the lateral cilia.

The opposed band system appears to occur in bdelloid and flosculariacean rotifers, the trochophores of echiuroids and annelids, the veligers of mollusks, and in entoproct larvae (for references see above). However, some authors have not included a postoral band of cilia when describing larvae of mollusks, annelids, or echiuroids which feed and have a well-developed preoral band. In many cases this omission is undoubtedly an oversight. The shorter cilia of the postoral band could easily be confused with the cilia of the food groove, particularly when the constituent simple cilia making up a compound cilium have separated from each other during fixation. However, Newby (1940) states that the postoral band is absent in the planktotrophic larva of *Urechis caupo*, while noting its presence in other echiuroid larvae. Either he is mistaken, or there are larvae which

superficially resemble the ones we have considered but employ a very different mode of feeding. Is it possible that a single band of cilia could concentrate suspended particles, collecting them on the downstream side? The cinefilms of the pluteus with polystyrene spheres showed that occasionally a small particle is temporarily caught downstream from a single band of cilia by being repeatedly pulled back toward the band by the return stroke. But it is difficult to imagine how such a system could achieve the clearance rates which seem to be necessary in marine larvae. If particles were to adhere with sufficient tightness to the preoral cilia, how would they be transferred to the cilia of the food groove?

The occurrence of one of these two clearance mechanisms in an animal does not mean that other clearance or feeding mechanisms are not also present. In the tornaria and bipinnaria larvae, particles can move onto the heavily ciliated circumoral field and travel along it for some distance without contacting the ciliated band. This means that the cilia or mucus on the circumoral field function to some degree in removing particles from the current produced by the ciliated band. Cilia on the circumoral field of echinoplutei may function in clearance also. Multiple feeding mechanisms may occur in trochophores. Thorson (1946) describes small trochophores with very large diatoms in their digestive tracts. These diatoms could not have been captured by the opposed band system that we have described, so another or supplementary mode of feeding must be employed by these forms. We must therefore exercise some caution in moving from a description of clearance mechanisms of ciliated bands to inferences concerning the feeding biology of the whole animal, and it will be understood that subsequent remarks apply only to clearance by the bands in the single and opposed band systems.

#### *Size of particles cleared from suspension*

The efficiency with which a particle is cleared from suspension will vary with its size, shape, and other properties, but we can see in a general way how the single and opposed band systems will differ as to the size of particles cleared. In the opposed band system the preoral and postoral bands must be close enough for the opposed action of the bands to be effective, and the size of the particles which can be collected and transported in the food groove is accordingly limited (see also Werner, 1955 and Fretter, 1967). In the single band system the circumoral field is broader, and because its curvature helps retain particles of diameter greater than the length of the cilia, the upper limit on size is less obvious. Fully developed echinoderm larvae ingest Sephadex spheres of 60 to 80  $\mu$  diameter (Strathmann, 1971) and the tornaria larvae ingest spheres over 100  $\mu$  in diameter. Garstang (1939) cites the observation of a polychaete larva passing along the circumoral field into the mouth of a tornaria.

In the opposed band system there is no obvious limit to clearance at the small end of the size range. Very small particles might not slip between cilia if held by mucus, and the bdelloid rotifer does, in fact, eat 1.3  $\mu$  diameter spheres. In the single band system in the pluteus, we did not see the 1.3  $\mu$  diameter spheres trigger a local reversal of beat and they were eaten at a lower rate than the larger cells of *Amphidinium carteri*. It seems likely that small particles cannot be cleared as efficiently by the single band system because they do not trigger a reversal of beat. Alternative possibilities are (1) that the relative inefficiency is clearing polystyrene

spheres from suspension is due to a property other than size and (2) that the plutei of *Lytechinus anamesus* cannot be taken as representative of all animals with the single band system.

#### *Components of the clearance rate*

From the description of the clearance mechanisms we can see that clearance rates might be estimated from an equation such as

$$C = l_b(1_c - 1_r)v$$

where  $l_b$  is the length of the ciliated band,  $l_c$  the length of the cilium,  $1_r$  a correction factor for the return stroke (where the cilium is not capturing particles), and  $v$  is the velocity at which the particles are carried within the capture distance,  $1_c - 1_r$ . We should therefore be able to relate clearance rate to morphological features and analyze its components; and we should also be able to calculate clearance rates using  $v$  from the cinefilms and measurements of cilia and band length.

In the bdelloid rotifer, particles passing within  $12\ \mu$  of the base of the preoral cilium were almost always conveyed into the food groove. When the cilium was about half way through the effective stroke, these particles were moving at 0.08 to 0.13 cm/sec relative to the rotifer. Particles passing closer to the tip of the cilium, 12 to  $15\ \mu$  out from the base, moved at speeds up to 0.18 cm/sec but occasionally slipped beyond the cilia and were lost. Without data on the frequency with which particles passed a given point and were captured, we must content ourselves with a rough approximation and say that for the rotifer clearance will be on the order of  $10 \times 0.1$  cm/sec or about 0.9 ml/day per mm of ciliated band.

For the pluteus we can calculate a clearance rate per unit length of band as about  $20 \times 0.1$  cm/sec or 1.7 ml/day per mm of ciliated band. Clearance rates estimated from ingestion rates for other echinoderm larvae agree with this calculated value within a factor of two. This is good agreement considering the errors which enter into both types of calculations.

Though data for  $v$  are scant and difficult to obtain, data on the length of cilia and length of band is easily acquired. We can relate variations in morphology to differences in clearance rate and see that different clearance mechanisms will evolve differently in response to the same factors.

#### *Variability in the two systems*

The animals known to have the single band system exhibit little variability. In the echinoderm larvae the cilia of the band are about  $25\ \mu$  long. The cilia are quite fine and appear to be simple rather than compound. Cilia of the band of the tornaria larvae are of similar length and appearance to those of echinoderm larvae and are probably simple cilia also. Compound cilia are present in the telotroch of tornariae, but these function in locomotion, not feeding. In all these larvae the ciliated band is long and convoluted increasing greatly during development. Within the echinoderm larvae there is some variation in band width, but clearance rate is approximately proportional to band length (Strathmann, 1971).

In the opposed band system the preoral cilia are about  $15\ \mu$  long in some bdelloid rotifers and range up to  $100\ \mu$  long in some prosobranch veligers. In some species

the band length increases greatly as the animal develops. In others, there is relatively little increase. Thus, the opposed band system exhibits much greater variation than the single band system. This greater variability in the opposed band system may be related to the presence of compound cilia in the preoral and postoral bands, whereas the single band system appears to be limited to simple cilia, though the reasons for this limitation are at present unknown.

Harris (1961) argued that single cilia all have about the same bending couple, and therefore the velocity of a cilium relative to the water can be related in an approximate manner to the length and distribution of cilia. Thus the velocity decreases with the length of the cilium and increases with the number of cilia in a compound cilium and with the number of cilia across the band. It follows that in compound cilia the velocity of beat and length of cilium can be varied somewhat independently. This must give an extra dimension in the design of a larva having compound cilia. For example, with a band of simple cilia, increasing the length of the cilia might permit clearance of larger particles from suspension but at the expense of lowering the velocity of beat and hence the clearance rate. With a band of compound cilia the number of constituent cilia could be increased as the length of a compound cilium is increased, so that larger particles could be cleared without any lowering of the clearance rate. Moreover, with compound cilia it may be possible to increase clearance rate per unit length of ciliated band by increasing both velocity of beat and length of cilium. With simple cilia a limited increase in clearance rate might be achieved by increasing the number of cilia per unit length of band, but clearance rate must be largely proportional to band length.

Variation is also found in less obvious features of the opposed band system: the number of rows of cilia in the preoral band (see Fretter, 1967 on veligers) and the relative lengths of cilia in each of these rows (see Hatschek, 1878, 1880, 1885 on trochophores). The trochophore of *Spirabranhus* has three rows of preoral cilia with the cilia of the middle row much longer than those of the other two rows. The length of the preoral cilia relative to the width of the food groove varies, as do the relative lengths of preoral and postoral cilia. In the rotifer studied here, the preoral cilia were about 12 to 16  $\mu$  long, the postoral cilia about 4 to 5  $\mu$ ; in the trochophore the longer preoral cilia were 30 to 40  $\mu$  long, the postoral cilia 13 to 17  $\mu$ ; and in the newly hatched veliger of *Charonia tritonis* preoral cilia are about 100  $\mu$ , the postoral cilia about 20  $\mu$ . The effect of these less obvious differences on the clearance mechanism and the clearance rates with variously sized and shaped particles is not known.

#### *Limitations inherent in the single band system*

The single band system appears to be limited to simple cilia and in all known cases, to one cilium per cell. Yet one might expect that compound cilia would permit a greater clearance rate per unit length of band by increased velocity of beat or increased length of cilia. Since compound cilia are present in the telotroch of the tornaria larva, their absence in the band must be related to the requirements of the clearance mechanism. Perhaps an induced local reversal of beat cannot be managed with sufficient rapidity by compound cilia. Even with simple cilia, the velocity of ciliary beat in a feeding larva may be limited by the speed with which a reversal can occur.

Given the restriction to simple cilia, two other possible limitations are the maximum bending moment or torque and the stiffness of a cilium. Our lack of knowledge of cilia and the complexity of the movement of water, particles, and cilia prevents an accurate calculation of the bending couple or stiffness exhibited by this system. In addition, the particle motion relative to the larva can be measured, but motion relative to the water is less certain and could vary between 0 and 0.2 cm/sec. Several cilia alter their beat when a particle is retained. With several cilia pushing a particle or moving a sizeable parcel of water along with it, the required bending moment or stiffness would be greatly reduced. Nevertheless, by accepting several assumptions and approximations, we can examine the nature of these limitations in terms of a simplified model.

First, what bending moment might be required for a cilium to push a particle of  $10\ \mu$  diameter back toward the circumoral field? Referring to Stoke's law, even though all the assumed conditions may not be met, we can calculate the drag force on the particle as  $F = 3\pi\eta DV$ , where  $\eta$  is the viscosity of water,  $D$  the diameter of a spherical particle, and  $v$  the velocity with which the particle is pushed relative to the water. The cinefilms show that  $v$  may be on the order of 0.1 cm/sec, which means that the drag force is therefore about  $10^{-5}$  dyne. If the particle is  $20\ \mu$  from the base of the cilium, the bending moment is about  $2 \times 10^{-8}$  dyne-cm. Yoneda (1960) found that a component cilium of the abfrontal cilium in *Mytilus* can exert a torque of  $2 \times 10^{-8}$  dyne-cm while resisting a glass needle. Brokaw (1966) calculated bending couples one order of magnitude smaller for sperm tails swimming in a viscous medium.

If the cilium were to bend too much while pushing the particle through the water, it would slip past the particle. Assuming that the cilium in the above example cannot be deflected more than  $4\ \mu$  without losing the particle, we can calculate the required stiffness as  $S = Ml^2/2d$ , where  $M$  is the bending moment,  $l$  the distance from the base of the cilium, and  $d$  the deflection at this distance. Then the stiffness is  $10^{-10}$  dyne-cm<sup>2</sup>, which is three to four orders of magnitude greater than the stiffness calculated for two kinds of cilia and a sperm flagellum (Rikmenspoel and Sleight, 1970). Either these calculations are very inaccurate, or these cilia do have a much greater stiffness, as their job might require. Since this stiffness implies that the elastic moduli of ciliary components are greater than have been found for other biologic materials (Brokaw, 1966), it seems more likely that the model is inappropriate for an exact calculation of the required bending couple or stiffness.

The three possible limitations discussed above would affect the length of the cilium or the velocity of the particle movement, and thus only the clearance rate per unit length of band. An increase in the length of the ciliated band would increase the clearance rate but at some cost to the animal. For example, if we imagine that a larva is initially to have a longer band, it must develop from a larger egg, and then fewer eggs can be produced. Other compromises could involve the requirements of swimming or escape responses, and may be too complex and varied for analysis to be profitable; but we can begin to see how the limitations of cilia ultimately restrict the evolutionary strategies of ciliary suspension feeders by limiting clearance rate per unit length of band, and as knowledge of cilia increases, so will our insight into the organization and activities of these animals.

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#### SUMMARY

1. High speed cinefilms of a serpulid trochophore, a bdelloid rotifer, and an echinopluteus show two ways cilia remove particles from suspensions.

2. In the pluteus a particle passing through the band of cilia triggers a localized change of beat which appears to be a reversal and which retains the particle on the upstream side of the band of cilia. Retention of particles by an induced local reversal of beat implies that the stimulus occurs during the forward effective stroke of a cilium and that the reversed effective stroke of this cilium or its neighbors begins before the forward stroke is completed. For this system, clearance and transport of particles, rejection of particles, and swimming can be accomplished by a single band of cilia.

3. In the bdelloid rotifer, and probably in the serpulid trochophore, the opposed action of parallel preoral and postoral bands of cilia apparently causes the longer preoral cilia to push particles relative to the water during the latter part of the effective stroke. This system has the preoral band of cilia function in clearance and swimming, the postoral band in clearance and rejection, the food groove cilia in transport of particles.

4. These two clearance mechanisms may be of wide distribution. Echinoderm larvae and the tornariae of hemichordates appear to employ the induced local reversal of beat. The trochophores of annelids and echiuroids, veligers of mollusks, entoproct larvae, and bdelloid and flosculariacean rotifers appear to employ the system with two opposed bands of cilia.

5. Clearance rates can be estimated from velocity of particle movement, length of cilia, and length of ciliated band.

6. Variations in ciliation in these two feeding systems are discussed in terms of differences in clearance rates and the size range of particles cleared from suspension.

7. Factors which may inherently limit clearance rate are also discussed.

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