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THE BEHAVIOR OF PLANKTOTROPHIC ECHINODERM LARVAE: MECHANISMS, REGULATION, AND RATES OF SUSPENSION FEEDING

by

RICHARD RAY STRATHMANN

A dissertation submitted in partial fulfillment
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

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Approved by Alan J. Kohn

Department Zoology

Date February 16, 1970

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Date: January 13, 1970

We have carefully read the dissertation entitled Behavior of Planktotrophic Echinoderm Larvae; Mechanisms, Rates and Regulation of Suspension Feeding. submitted by Mr. Richard Ray Strathmann in partial fulfillment of the requirements of the degree of Doctor of Philosophy and recommend its acceptance. In support of this recommendation we present the following joint statement of evaluation to be filed with the dissertation.

The planktonic larval stages of bottom-dwelling marine invertebrates are very small, delicate and fragile organisms drifting for weeks or months in the sea before settling to metamorphose and assume a benthic mode of life and a more robust body form.

Such larvae, whose ability to swim or maintain position usually depends solely on cilia, survive the planktonic period only if they avoid the hazards of predation, collision with large objects, the bottom, and the surface, and unfavorable water masses. While some larvae are provided with sufficient nutrient stores for maintenance through this stage, the echinoderm larvae studied by Mr. Strathmann are not; they must feed in addition to meeting the challenges of their environment listed above. Mr. Strathmann's dissertation is a highly original, pioneering effort to understand the strategies and tactics such larvae employ in meeting the problems posed by their environment. Mr. Strathmann learned that the environment often imposes conflicting demands on larval structure and behavior. The most clear-cut case is swimming versus feeding, the necessity for locomotion and avoidance behavior by moving against the water, activity which opposes the simultaneous requirement of bringing food particles toward the body and into the mouth. Another is the necessity of moving particles suitable as food to the mouth versus rejection of unsuitable particles.

Mr. Strathmann has combined a comparative approach employing detailed observations of structure and function of locomotor and feeding mechanisms in larvae of four classes of echinoderms with experiments designed to provide stronger inferences and test hypotheses generated by the observations. He has demonstrated fundamental similarities in functional morphology despite the strikingly different appearance of the larvae of different classes; the differences he has elucidated also help to explain alternative solutions to similar problems in the different classes.

DISSERTATION READING COMMITTEE: Alan J. Kohn
Eugene N. Kozloff
Robert L. Fernald

This dissertation contains the first demonstration that (1) retention of particles by pre- and post-oral transverse bands appears to be necessary for active feeding and that the peripheral cilia of the band can and probably must retain particles; (2) the rate of which the larva clears a volume of water of food particles is proportional to the length of the ciliated band, regardless of the form of the larva; (3) several different mechanisms exist for the rejection of unsuitable particles, and some of these may be used in combination; (4) the larvae are able to distinguish and treat separately edible and inedible particles in the gut, and this sorting is not based on size alone; (5) larvae can reject particles without stopping swimming or expending extra energy; and (6) the size of food particles capable of being eaten is much larger than had previously been estimated and approximates the diameter of the esophagus.

Mr. Strathmann has made two independent estimates of the clearance rate or amount of water processed, direct and based on the morphological and functional properties of the ciliated regions, and both are in close agreement. He has critically evaluated the hypotheses purporting to account for the concentration of food particles in the buccal cavity and has provided strong evidence that models based on centrifugal force and inpingement separation should be rejected. A more satisfactory model, only incompletely formulated in the dissertation, involves only activity of the ciliated bands, mucus production in the circumoral field, and cilia of the circumoral field if they are present.

In presenting this thesis in partial fulfillment of the requirements for an advanced degree at the University of Washington I agree that the Library shall make it freely available for inspection. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by my major professor, or, in his absence, by the Director of Libraries. It is understood that any copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Signature Richard R. Strathman

Date Feb. 11, 1970

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ACKNOWLEDGMENTS

I would like to thank Drs. R. L. Fernald, A. J. Kohn, and E. Kozloff for advice on many aspects of this work. Drs. R. Guillard and J. Lewin generously provided algal cultures. I am grateful to Drs. K. Banse, R. Cloney, A. R. Fontaine, D. Hoffman, J. Prothero, E. Richey, A. W. Whiteley and other investigators at the Friday Harbor Laboratories and University of Washington for suggestions and assistance.

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INTRODUCTION

Feeding, pelagic larvae have been described in four classes of the phylum Echinodermata. These larvae bear no resemblance to the adults and represent a type of organization as unique as if they belonged to a separate phylum. Each class has a characteristic larva: the auricularia in holothuroids, the bipinnaria in asteroids, the ophiopluteus in ophiuroids, and the echinopluteus in echinoids. The similarities between these larvae suggest that the four classes are derived from a form with a planktotrophic larva.

Non-feeding pelagic larvae of the same classes have greatly reduced larval structures, yet manage all the other activities of the planktotrophic forms from which they are presumably derived. Therefore the organization of the planktotrophic larvae has been determined primarily by the requirements of feeding.

The larvae feed on suspended particles--phytoplankton or detritus. Their manner of feeding is of interest in regard to both the evolution and ecology of echinoderms and the biology and strategy of suspension feeding. The descriptions of larval feeding of Gemmill (1914, 1916), Runnstrom (1918), and Tattersall & Sheppard (1934) indicate a considerable degree of complexity in feeding but admit to few generalizations. Because these authors studied different types of larvae, it is hard to compare their results.

I have undertaken a more comparative study in an attempt to answer the following questions. How do the planktotrophic echinoderm larvae remove particles from suspension? Are different structures involved in swimming and feeding, or do single structures function in both? Does the pluteus type of larva feed much differently from the auricularia or bipinnaria? What is the rate at which they process water, in volume per unit time? Are these rates comparable to those of other small suspension feeders? Do they reduce this clearance rate in response to high concentrations of particles or other factors? How do they reject particles? Do the mechanisms of rejection differ in each class? Does rejection interfere with swimming? More generally, have these larvae, although they are but a transient stage in development, evolved the feeding capacity and complexities of behavior typical of adult suspension feeders?

A discussion of these matters leads to more speculative questions concerning the evolution of clearance rates and ways in which each type of larva may be suited to the type of metamorphosis and development of juveniles of its class.

METHODS

Most of the larvae used in this study were reared from eggs, although larvae were obtained from the plankton for comparison. Most of the adult animals (Table I) were collected near San Juan Island, Washington, USA, but *Brisaster latifrons* was obtained from Puget Sound near Seattle, *Strongylocentrotus purpuratus* and *Allocentrotus fragilis* from the Straits of Juan de Fuca, and *Patiria miniata* from the west coast of Vancouver Island.

The species reared in culture are listed in Table I and will be referred to by generic name where this is unambiguous. *Patiria* was reared to brachiolaria stage, and only the early bipinnaria of *Evasterias* was used. The rest were reared at least once through metamorphosis. *Parastichopus* is the only holothuroid in this region known to have an auricularia and I could find no other species of auricularia in the plankton. *Ophiopholis* was the only ophiuroid which spawned in the laboratory, but ophioplutei of other species were abundant in the plankton and were studied for comparison, although I do not know the names of the species to which they belong.

Fertilizable eggs of echinoids and asteroids were obtained by the methods of Harvey (1956), Chaet (1966), and Kanatani *et al*. (1969) with the exception of *Brisaster*, which spawned without treatment, and *Luidia*, from which eggs were obtained by dissection and fertilized before germinal vesicle breakdown. Eggs of *Parastichopus* were obtained by the method of Strathmann & Sato (1969). *Ophiopholis* were induced to spawn by removing them from sea water, leaving them at room temperature for about an hour, and then placing them in individual bowls of sea water at temperatures of 8 to 14°C. Active sperm could be obtained from all species by dissection and suspension in sea water.

Larvae were reared in 3-litre jars with slow, constant motorized stirring with paddles. The jars were cooled by the sea water system. The sea water temperature at Friday Harbor varies between about 7 to 13°C during the year and the temperature of the laboratory sea water system varies between about 5 and 15°C. The salinity at Friday Harbor is about 28 to 30 o/oo. *S. purpuratus* could only be reared through metamorphosis when the salinity was raised 2 or 3 o/oo with NaCl. *Allocentrotus* was also reared in water of increased salinity.

The asteroid larvae proved particularly sensitive to crowding and were thinned to about 100 per litre by the later stages. Other larvae could be raised at higher densities. Water was changed several times in the first month by thinning the cultures. Later-stage larvae did not require water changes more often than once every two months.

Algae were added to the cultures about once every five days. A mixture of *Phaeodactylum tricornutum* Bohlin, *Dunaliella tertiolecta* Butcher, and *Isochrysis galbana* Parke was sufficient for rearing larvae, although the open jars often became inoculated with other algae from the sea water system. Other algal species were occasionally used as food but were primarily used in observations of feeding. All the algae were cultured in Provasoli's (1968) ES enriched sea water medium. *Phaeodactylum tricornutum*, *Cyclotella nana* Hustedt, *Thalassiosira fluviatilis* Hustedt, *Isochrysis galbana*, *Cricosphaera carterae* (Braarud and Fagerland) Braarud, and *Amphidinium carteri* Hulburt were obtained from Dr. Robert

Guillard. *Dunaliella tertiolecta* was obtained from Dr. Joyce Lewin. *Ditylum brightwellii* (T. West) Grunow ex Van Heurck was isolated from the plankton at Friday Harbor.

Protargol silver-impregnation (Galigher & Kozloff, 1964) was used to examine the distribution of cilia in whole mounts. For study of the distribution of cilia and secretory cells in sections, larvae were fixed in glutaraldehyde and then osmium or with osmium and s-collidine and embedded in Epon epoxy resin (Luft, 1961). Sections were stained with methylene blue and azure II (Richardson, *et al.*, 1960).

Currents and particle movements were observed with the larvae held in desired orientations with a suction pipet of polyethylene or glass. Suction was regulated with a three way stopcock. A solution of blue food coloring in sea water, a suspension of algae or carmine particles, or a mixture of food coloring and particles was introduced near the larva with another micropipet and the paths of water and algae observed under a dissecting microscope at 50 or 100x.

Quantitative observations were made on larvae freely swimming in a glass chamber, which was cooled by sea water flowing through a surrounding jacket.

Clearance rates were determined by two methods. In method 1, I counted the number of algal cells entering the mouth of a larva during periods of one to three minutes. *Amphidinium* was used in these determinations because it was large enough to be seen under the stereomicroscope and yet remained rather evenly suspended in still water for the brief periods required. Cells entering the mouth could be counted most accurately at a concentration of 5000/ml. In some of the asteroid larvae, cells entering the mouth from only one side were counted and the results doubled to obtain the feeding rate. An advantage of method 1 was that the behavior of the larvae could be observed. Larvae usually fed at high rates for at least the first ten minutes in the bowl.

In method 2, I placed larvae in gently rocked flasks with a 50 ml suspension of algae for periods of 5.5 to 13 minutes depending on the feeding rate. The number of cells taken into the gut were then counted. These cells were recognized because the larvae were previously starved or had been feeding on a different algal species. This method was adequate for comparisons but poor for absolute rates because the larvae were initially disturbed by transfer to the flask and frequently ejected algae from the buccal cavity and esophagus when placed on the slide for counting.

Clearance rates were calculated assuming an even distribution of algae. However, the algae in suspension were more likely randomly distributed or clumped. Also, in both methods the periods of feeding were short. Therefore the maximum clearance rates calculated for individual larvae may be too high. For these reasons the mean values were used as a minimum estimate of the actual maximum clearance.

Luidia, *Ophiopholis*, and *S. droebachiensis* fed at high rates more consistently after being starved overnight. *Parastichopus* and *Pisaster* fed at greatly decreased rates after a period in filtered sea water and fed at higher rates when taken directly from the culture jars. The reduced feeding rate of Parastichopus was apparently not a result of starvation or lack of stirring, because one hour in filtered sea water was sufficient to reduce feeding significantly and lack of stirring of larvae in the culture water was not (tested by two sample rank test at 95%). Since I wished to estimate the maximum clearance rate, I treated each species according to its behavior.

Decrease in the number of cells in suspension was not used to measure clearance rate because algal cells frequently pass through the gut with no apparent change. The feces of the larvae do not remain compact, so that the defecated algae may be returned to suspension. The calculated feeding rate would be too low, particularly at higher concentrations of algae.

Horizontal swimming rates were measured with drawing tube and stop watch. Current velocities were measured by analysis of movies, but these larvae were confined on slides, so the estimates of velocities are only approximate.

RESULTS

External Ciliation

All the planktotrophic echinoderm larvae have a conspicuous ciliated band (Figs. 16 to 38). The area between this band and the mouth is the circumoral field. The area outside this band is the aboral field. The portions of the ciliated band anterior and posterior to the mouth are referred to as the pre- and postoral transverse bands. The mouth lies in a depression between these sections of the ciliated band called the transverse groove. There is a less conspicuous band of cilia, the adoral band, around the rim of the mouth. The upper part of the adoral band runs close to the preoral transverse band (Figs. 1, 2). The inflated buccal cavity narrows to an esophagus, which is separated from the stomach by a sphincter.

Holothuroidea. In the auricularia of the holothuroids (Figs. 16 to 20, 39, 40), the ciliated band is continuous though varying in width. The ciliated band extends in loops or processes similar to the more pronounced arms of the other types of larvae (Figs. 16, 17). In Parastichopus the aboral and circumoral fields and the buccal cavity are unciliated. No cilia were revealed in silver-impregnated whole mounts or by examination of living larvae with phase contrast or Nomarski interference optics. Some other species of auricularia are reported to have a few cilia on the circumoral field. On the circumoral field of giant auricularia larvae, Garstang (1939a) found a narrow band of cilia, which followed the ridge between the pre- and postoral transverse bands at each end of the transverse groove. He mentioned that this corresponds with the position of the "larval nervous system" described by Mortensen (1920) and others. The thin bands of cilia corresponding to the "larval nervous system" will be termed paroral bands in this study. The adoral band of Parastichopus encircles the mouth and is continuous with a wider band of cilia around the top of the esophagus (Figs. 19, 40). The upper adoral band is not as close to the preoral transverse band as in other types of larvae observed here.

Asteroidea. The bipinnaria of asteroids (Figs. 21 to 28) looks rather like an auricularia except that the ciliated band is divided into two loops. However, in the bipinnaria the circumoral and aboral fields and the buccal cavity are ciliated. Cilia of the circumoral field are not more than about 10μ apart. Luidia, Patiria, Pisaster, and Pycnopodia all have this distribution of cilia and Gemmill (1914, 1916) observed it in Asterias rubens and Porania pulvillus. Garstang (1939b) supposed Gemmill to be in error in describing cilia on the circumoral field because Field (1892) had found none there. A ciliated circumoral field probably occurs in every bipinnaria and Field was probably in error.

Gemmill (1914, 1916) noted that in Asterias and Porania the lower part of the adoral band is divided into a labial loop on the lower rim of the mouth and esophageal strips extending down the ventral side of the esophagus. All the asteroid larvae of this study have this pattern of ciliation. The line of demarcation between the adoral band and other areas is not always clear because the buccal cavity and esophagus are also well ciliated.

In Pisaster and Pycnopodia the arms become circular in cross section and heavily ciliated, with the ciliated band on the arms indistinct (Figs. 3, 26, 27). In Luidia and Patiria the arms are flattened or even grooved on the circumoral field side and the band remains distinct (Figs. 24, 25). Most asteroids have a brachiolaria larva later in development (Figs. 26, 27, 28). In addition to the other larval arms there are brachiolar arms and an adhesive disk, which are used for attachment during metamorphosis. Luidia does not develop into a brachiolaria but becomes a large larva with well developed median dorsal and median ventral processes in addition to the other arms (Figs. 24, 25). Thus Luidia has by far the longest ciliated band and most extensive circumoral field of any of the larvae examined in this study.

Ophiuroidea. The ophiuroids have a pluteus (Figs. 29, 30, 31) with arms supported by skeletal rods. In ophioplutei the ciliated band is continuous. The ophioplutei first develop four arms, the anterolateral and posterolateral pairs. The postoral and posterodorsal pairs are soon added and all the arms lengthen considerably during development. The posterolateral arms are usually somewhat broader than the others. Only two arms, the anterolateral pair, are associated with the oral hood. The paroral band of cilia consists of a single line of cilia bordering the suboral pocket and connecting the ends of the pre- and postoral transverse bands on each side. Other than these, there are very few cilia on the circumoral field in Ophiopholis or in the ophioplutei which I collected from the plankton. The aboral field is also very sparsely ciliated except near the posterior end of the larva. However, the buccal cavity and esophagus are well ciliated. A narrow gap develops in the midline of the lower adoral band of cilia.

Echinoidea. The echinoids also have a pluteus (Figs. 32 to 38) with the arms supported by skeletal rods. The echinoplutei first develop the anterolateral and postoral arms (Figs. 32, 33, 34). Then the posterodorsal arms and finally the preoral arms are added (Figs. 35, 36, 37, 38). In the eight-armed echinopluteus, four arms are associated with the oral hood. Spatangoid larvae have a posterior process, and some spatangoid echinoplutei have additional pairs of arms.

In the echinoplutei of Brisaster, Dendraster, and the strongylocentrotids observed in this study, the portions of the ciliated band descending from the anterolateral arms became looped ventrally towards the ends of the preoral transverse band (Fig. 4). This occurs as the preoral arms develop and the oral hood expands over the transverse groove. In Brisaster this part of the ciliated band remains continuous with the rest. In the strongylocentrotids the upper portion of the loop becomes faint, but traces of it can be seen. In Dendraster the upper portion disappears and the remainder appears to originate near the preoral transverse hand in the eight- armed echinopluteus (Fig. 36). It also lies next to the paroral band for part of its length. The development of the oral hood is thus more complex than in the ophioplutei.

In the strongylocentrotids and some other families, sections of the ciliated band between the arms become separated from the rest of the band and form epaulettes (Figs. 4, 38) specialized for locomotion. The posterior pair eventually join forming a complete ring. The anterior pairs join ventrally and dorsally. In Brisaster and Dendraster the band extends between the arms as lobes (Fig. 36) but these remain continuous with the rest of the band except in Dendraster larvae at a very late stage. In these the anterior and ventral pairs join in much the same manner as anterior and ventral epaulettes.

The cilia of the circumoral field are more apparent in the strongylocentrotids, which have broad arms, than in Dendraster, which is smaller and has thin arms. Runnstrom (1918) described the circumoral field of Parechinus microtuberculatus, P. miliaris, and Paracentrotus lividus as being ciliated. The aboral field is most heavily ciliated at the posterior end. The posterior process of Brisaster is quite heavily ciliated.

There are paroral bands on the rim of the suboral pocket (Mortensen, 1920). In the earlier stages they appear to extend from the postoral transverse band to the ends of the preoral transverse band, but in later stages they are rather indistinct, with only a slightly greater density of cilia than the rest of the circumoral field. The buccal cavity and esophagus are ciliated. The lower adoral band continues down the ventral esophagus as esophageal strips (see also Runnstrom, 1918), but these are not clearly demarcated from the other cilia of the upper esophagus.

Number, length, and motion of cilia. Remiers (1912; cited by Hyman, 1955) found only one cilium per cell in sections through the ciliated band of the auricularia of Synapta digitata. I found no more than one cilium per cell in sections across or along the bands of larvae of Parastichopus, Luidia, Patiria, Pisaster, Ophiopholis, Dendraster, and S. droebachiensis. An approximately tangential section along the postoral transverse band of

Luidia demonstrates one cilium per cell clearly (Fig. 6). In sections, living larvae, and silver-impregnated wholemounts, I could not find more than one cilium per cell on the circumoral and aboral fields and in the buccal cavity (Fig. 5). The greater density of cilia near the band is due to the greater number of cells and not an increase in the number of cilia per cell.

The species examined here vary considerably in the number of cilia per unit length of the ciliated band. If these species are representative of the four types of larvae, there are consistent differences between classes. The number of cilia in a strip one cell in width at right angles to the band is a measure of band width. In asteroid larvae of later stages (Luidia, Patiria, Pisaster), there are 10 or more cilia across the band, and the band width is fairly constant. In the advanced auricularia of Parastichopus there are about 3 to 7 cilia across the band, and the width of the band varies. On the arms of echinoplutei or ophioplutei, there are 3 to 5, usually 4, cilia across the ciliated band, but the band widens in some other places.

The external cilia are about 25 to 30 μ long in Parastichopus, Luidia, Patiria, Pisaster, Ophiopholis, Dendraster, and most parts of S. droebachiansis. The cilia of the epaulettes of the strongylocentrotids are about 35 μ long.

The metachronal waves of the epaulettes of the strongylocentrotids and lobes of Dendraster move toward the midline. Knight-Jones (1954) first noted this unusual combination of laeoplectic and dexioplectic waves in the epaulettes of echinoplutei, and suggested that it might be a means of suppressing rotation, which might otherwise interfere with feeding. Metachronal waves were not clearly observed in the ciliated bands, but the rather regular intervals between straight extended cilia along the band (Fig. 7) suggests a diaplectic metachronal beat.

The apparent motion of cilia of the epaulettes can be slowed stroboscopically or in movies at 16 frames per second. The hook-shaped recovery stroke is reversed when the current direction past the epaulette is reversed (Figs. 8, 9). The effective stroke appears to be straight.

The form of beat of other cilia is more difficult to observe directly. The direction of beat was therefore inferred from movement of particles and water.

Distribution of Secretory Cells

Tattersall & Sheppard (1934) found secretory cells near the ciliated band of Luidia larvae and suggested that they might secrete mucus aiding in the capture of particles. I looked for cells which might be specialized for mucus secretion and found that the distribution of cells which could conceivably serve this function was different in each class. Although not all of these cells are necessarily involved in mucus secretion, they will be tentatively regarded as mucus-secreting cells here.

Conspicuous secretory cells were visible near the ciliated band of all asteroid larvae observed in this study but they were much more numerous on the aboral side of the ciliated band. Secretory cells were also scattered on the aboral field, particularly on the posterior end of later stage larvae, but not on the circumoral field or in the buccal cavity. Thus their distribution does not suggest a role in the feeding mechanism.

A greater variety of secretory cells could be seen in sections. In asteroid larvae (*Luidia*, *Patiria*, *Pisaster*) the secretory cells near the ciliated band and some of those on the aboral field are not stained with methylene blue and azure II (Figs. 6, 10). Other larger secretory cells on the posterior end (Fig. 11), the brachiolar arms, and the adhesive disk (Fig. 12) probably account for the stickiness of these regions. The larvae could be towed backward with a glass rod attached to strands of mucus on the posterior end.

In *Parastichopus* numerous unstained secretory cells occurred on both sides of the ciliated band. In *Ophiopholis*, *Dendraster*, and *S. droebachiensis* very few secretory cells were found. One of these rare secretory cells appears in the anterolateral arm of *Ophiopholis* in Fig. 1. In *S. droebachiensis* another type of cell of secretory aspect was located at the arm tips. No specialized secretory cells were found near the adoral band or in the buccal cavity in any of the larvae.

Other epidermal cells might secrete mucus necessary for feeding. In sections of *S. droebachiensis* there was a slight metachromatic shift to purple and small reddish granules in the cells of the buccal cavity and esophagus.

Either the specialized secretory cells near the band are involved in functions other than mucus secretion related to feeding, or there are considerable differences in the role of mucus in the feeding of these species. One interpretation is that the plutei require less, or more localized, mucus secretion than the other types, and that the auricularia, with its unciliated circumoral field, needs more mucus secretion on the inner side of the ciliated band than the bipinnaria. However, I did not see any differences in feeding which could be related to the differing distributions of these secretory cells, and it is quite possible that the small secretory cells near the ciliated band (Fig. 10) are not secreting mucus at all but serve some other function.

Feeding Mechanism

Aspects common to all four classes. The ciliated band produces a current away from the circumoral field and at right angles to the band (Fig. 13: A, B), drawing water in towards the circumoral field from the anterior end or sides (Figs. 13, 15: C). The ciliated band is arranged in each type of larva so that in most parts of the band the cilia create a current with posterior or transverse components. In very few parts of the band is there an anterior component to the current. Thus the cilia of this band both draw a current across the circumoral field and propel the larva through the water (see discussions of each larval type below).

When the larvae are not feeding, particles pass over the band with the water (Fig. 15: path x-z). When the larvae are feeding, water is still passed over the band, but particles approaching the inner side of the ciliated band are retained on the circumoral field (Fig. 13: a and Fig. 15: x-y).

I could not see any difference in the beat of cilia in feeding or non-feeding larvae but there must be some difference in ciliary beat or mucus secretion at the ciliated band.

Particles are transported toward the mouth in several ways. In some larvae cilia on the circumoral field aid in transporting particles to the mouth. In larvae in which cilia are sparse or absent on the circumoral field, particles are transported toward the mouth along the band (Fig. 13: a) or in water currents. Particles in the anterior part of the circumoral field are carried toward the mouth in the general posteriorly directed current (Fig. 13: h). Another current toward the mouth is created by the pre- and postoral transverse bands, which produce an outward current between them (Figs. 13, 14: B) which draws water and particles into the transverse groove from the nearer portions of the lateral circumoral field (Fig. 13: D, d). Particles therefore enter the mouth from the side (Fig. 13: h, d) or enter the transverse groove from the side and the mouth from below (Fig. 13: i, Fig. 14: e).

Particles are carried into the mouth past the upper or lateral adoral band (Fig. 13: d, h) and are either carried directly down the esophagus (Fig. 14: g) or rotated in the buccal cavity (Fig. 14: f). Particles are retained by the adoral band and preoral transverse band while water is passed out over the transverse ciliated bands (Fig. 14).

Although particles accumulate in the buccal cavity and esophagus, it is unlikely that the interior of the buccal cavity is a major site of separation of particles and water, as suggested by Tattersall & Sheppard (1934).

When feeding actively on high concentrations of algae, the larvae can pack the esophagus and part of the buccal cavity above the level of the lower adoral band. Therefore an outward current at this location is probably not present during feeding. The lower adoral band probably beats into the mouth just as the upper adoral band does. I could not relate the differences in configuration of the lower adoral band in each class to any difference in function. During feeding there is an anteriorly directed current passing in front of the mouth towards the preoral transverse and upper adoral bands (Fig. 14: E). Water leaving through the mouth would rejoin this feeding current.

Observations with mixtures of particles and colored water support the interpretation that particles are removed from suspension on the outer surface and that concentration in the buccal cavity plays a small role. When a suspension of particles in colored water is introduced near parts of the circumoral field far from the transverse groove, the colored water is removed while particles are still moving across the circumoral field towards the mouth.

When colored water is introduced at the lateral circumoral field near the transverse groove, some water is drawn into the transverse groove and rapidly passed over the pre- and postoral transverse bands. Sometimes a little also enters the buccal cavity. The color remains visible in the buccal cavity for more than five seconds. Therefore, there cannot be a very rapid exchange of water here. Colored water did not enter the esophagus in discernible quantities.

Particles are carried into the esophagus down the lateral or dorsal walls of the buccal cavity by the adoral band alone or with the help of cilia lining the buccal cavity when these are present. The many cilia lining the upper esophagus transport particles into the posterior esophagus where they accumulate until moved into the stomach by a wave of contraction of circular muscles beginning at the top of the esophagus. The cardiac sphincter opens and the mass of particles is pushed into the stomach.

It is difficult to determine the role of mucus in feeding. The particles usually move quite rapidly near the ciliated band and circumoral field, as much as 0.5 mm/sec at 13°C. Particles approaching the circumoral field move somewhat faster, from 0.5 to 0.9 mm/sec in the bipinnaria of Pisaster and 0.5 to 1.4 mm/sec in the eight-armed echinopluteus of S. droebachiensis.[1]

In larvae with cilia on the circumoral field particles could be held loosely while transported by cilia, but in larvae without cilia in this region mucus would only impede transport in currents toward the mouth. Mucus secreted near the ciliated band might help retain particles during feeding. There is some indication that the particles in the upper buccal cavity are held in a loose mass by mucoid material. The particles are definitely stuck together in the lower esophagus.

There was no indication that any of the larvae feed with different mechanisms on different types of particles, nor was there any indication of qualitative sorting of particles during feeding. I was unable to confirm the observations of Runnstrom (1918) that cilia were individually stimulated by the presence of algal cells but not by carmine. This would provide a mechanism for sorting particles as they are transported towards the mouth.

Auricularia. The ciliated band on the loops and processes is arranged so that it creates a posteriorly directed current which propels the larva through the water. The extensions of the circumoral field on these processes are exposed to the posteriorly directed currents (Fig. 20). However, the band along the posterior extensions of the circumoral field also creates transversely directed currents, possibly also with an anterior component (Figs. 17, 18: I). Apparently these currents are necessary for the transport of particles anteriorly to the transverse grooves though direct contact with cilia may also aid in this movement of particles.

Because there are no cilia on the circumoral field, particles are often in contact with the ciliated band for considerable distances as they move jerkily along the band toward the mouth (Figs. 16, 17, 18, 20: j, k). On the anterior extensions of the circumoral field, some particles move down the center of the lateral groove (Figs. 16, 20: h) or make fewer contacts with the band (Figs. 16, 20: 1) as they are swept along in the posteriorly directed current. Particles at the extreme posterior end of the circumoral field are transported along the ciliated band dorsally or ventrally (Figs. 16, 17, 18: j) before they are caught by the cilia or currents which move them anteriorly (Figs. 16, 18: i).

The current of water produced by the pre- and postoral transverse bands (Fig. 16, 18: D, d) draws particles into the transverse groove. There is an anteriorly directed current up towards the mouth in the transverse groove; this current carries particles toward the preoral transverse and upper adoral bands (Fig. 19: E).

Since the upper buccal cavity lacks cilia, particles usually travel from buccal cavity to esophagus along the lateral wall of the buccal cavity just above the adoral band (Fig. 19: g).

Bipinnaria. Gemmill (1914) describes the ciliated band of the binpinnaria as beating "everywhere backwards". Garstang (1939b) thought it more likely that the cilia beat at right angles to the band. Actually, as in the auricularia, the band is arranged in loops and processes so that the cilia beat both away from the circumoral field and posteriorly (Figs. 21, 22, 23: A). The cilia of the circumoral field aid in transporting particles to the mouth. Gemmill (1914, 1916) found that these cilia beat towards the mouth and are more active during feeding. Particles make fewer contacts with the ciliated band than in the auricularia, but when they do contact the inner side of the ciliated band they are retained (Figs. 22, 23: m). Particles entering the transverse groove from the posterior extensions of the circumoral field usually enter the well developed suboral pocket before they are carried anteriorly into the mouth (Figs. 21, 22: i, e). Particles sometimes circulate in the buccal cavity for more than 20 minutes while they are bound into a more compact mass, but individual particles can also be carried directly down into the esophagus. This may result from the varying activity of cilia lining the buccal cavity. Particles are carried into the esophagus either along the inner side of the adoral band or down the dorsal wall of the buccal cavity.

In later stages of development loops in the ciliated band become extended out on arms. In larvae of *Luidia foliolata* the ciliated band on the arms continues to create a posteriorly directed water current away from the circumoral field (Figs. 24, 25: A). Particles contacting the inner side of the band or the extensions of the circumoral field on the arms are carried toward the mouth (Figs. 24, 25: n). This conforms to Tattersall & Sheppard's (1934) observations on the function of the arms in *Luidia ciliaris* and *L. sarsi.* These two species differ from *L. foliolata* in that they swim by muscular action whereas *L. foliolata* swims by ciliary action alone.

In larvae of *Pisaster* and *Pycnopodia* the cilia on the arms are more evenly distributed and create a strong current toward the arm tip, and this current carries both particles and water away from the larvae (Figs. 26, 27, 28: P, p). The arms serve mainly for locomotion and are usually directed somewhat posteriorly, particularly the three posterior pairs. This confirms Gemmill's (1914) observations (questioned by Garstang, 1939b) on the function of the arms in *Asterias rubens*. In these species the arms' only contribution to feeding is that water sent out along the arms is replaced by a slower, broader current elsewhere.

Ophiopluteus. The ophioplutei, when feeding in still water, swim with the arms directed upward. The ciliated band on and between the arms produces currents outwards and downwards (Figs. 29, 30: A). This draws water down from above. Some water also moves in from the side between the postoral and posterodorsal arms and above the posterolateral arms. When the larvae swim up against the surface film or coverglass, water cannot move down from directly above, and the horizontal components of the incoming and outgoing currents become greatly exaggerated (Fig. 31: O).

Particles are retained on the inner side of the ciliated band and can be carried along the ciliated band for considerable distances. Thus particles are carried towards the mouth along the extensions of the circumoral field on the arms, even the very long posterolateral arms (Figs. 29, 30, 31: q) although the circumoral field is very sparsely ciliated. The combination of the direction of the currents down past the larva and the angle of the arms might account for some of the movement along the band towards the mouth, but the cilia of the band probably transport particles along the band as well as retain them.

Thus both the water currents between the arms and direct contact with the ciliated band on the arms transport particles toward the transverse groove. Particle movement in this region is rapid and I could not assess the relative importance or interaction of these two means of transport.

Particles travel into the transverse groove past the paroral bands. The cilia of the paroral bands (Fig. 30, 31: r) may help move particles into the current crossing the suboral pocket towards the adoral and preoral transverse bands (Fig. 30: E). Particles seldom reach the bottom of the deep suboral pocket, which is almost unciliated. Particle transport in this region is therefore different from that in the bipinnaria.

Cilia lining the buccal cavity help transport particles down into the esophagus.

Echinopluteus. The echinoplutei, when feeding in still water, swim with the arms directed upward. The ciliated band on and between the arms produces currents outwards and downwards (Figs. 32 to 37: A). This draws water down from above the larva, and to a lesser extent, in from the sides. As in the ophiopluteus, the horizontal components of the currents are exaggerated when the larvae swim up against the surface (see also the figures of Runnstrom, 1918). I saw little change in the horizontal component of currents during feeding. In the four-armed echinopluteus, water moves in through the gap between the postoral arm and oral hood (Fig. 34: O). In the eight-armed echinopluteus there is a similar pattern with water moving in between the postoral and posterodorsal arms on the side and out past the postoral transverse band, the postoral and posterodorsal arms, and the oral hood.

Particles are carried along the inner side of the ciliated band, even on the thinner arms (Figs. 33 to 38: q). Thus, as in ophioplutei, particles are moved towards the transverse groove by both currents and contact with the ciliated band. However, the echinoplutei studied here have a more densely ciliated circumoral field and more extensive and complex oral hood.

The cilia of the circumoral field appear to transport particles toward the mouth (Figs. 35, 36, 38: s). In the strongylocentrotids the arms are broad and the circumoral field extends farther posteriorly between the postoral and posterodorsal arms (Figs. 4, 38). The circumoral field is therefore relatively and absolutely more extensive than in the smaller

Dendraster and the circumoral field cilia play a relatively greater role in transporting particles to the mouth. However, it is difficult to distinguish the effects of currents and cilia in moving particles across the circumoral field.

The expansion of the oral hood in the echinopluteus makes it a more important food collecting area than in the ophiopluteus. I could not determine the functioning of the ventral loop of the band descending from the anterolateral arm (Figs. 4, 36). In the four-armed larvae this portion of the ciliated band creates a current away from the circumoral field (Fig. 33). In the eight-armed larvae of *Dendraster* particles appear to move across this band toward the mouth (Fig. 36: t) though it is difficult to see whether these particles may not be farther from the oral hood and beyond the reach of the cilia. If the cilia of this portion of the band beat toward the mouth, then the direction of effective stroke has changed during formation of the loop. Other particles moved through the gap between this band and the preoral transverse band (Fig. 36: u). This gap is narrower in *Dendraster* than in the other echinoplutei studied here. Since particles sometimes appear to be passing over the ventral loop and sometimes not, this portion of the band, in *Dendraster*, may serve to regulate feeding.

In *Brisaster* and *Dendraster* the ciliated band near the arms becomes extended, forming lobes. When these are developing, particles contacting the inner side of the band are retained and carried toward the mouth (Fig. 36: s). At later stages the lobes extend farther from the arms and transverse groove and particles seldom contact the band on the lobes. Particles contacting the anterior side of an epaulette are not retained (Fig. 38: X, x).

As might be expected, the posterior process of Brisaster does not serve in feeding but has a strong posteriorly directed current.

Particles travel into the transverse groove past the paroral bands (Figs. 34, 35, 36: r). As in the ophiopluteus, the cilia of the paroral bands may help move particles into the currents crossing the suboral pocket toward the adoral and preoral transverse bands (Figs. 32 to 36: E).

Particles which have entered the mouth are usually carried down the esophagus quite rapidly. Cilia of the buccal cavity and esophagus help carry particles down to the bottom of the esophagus. Runnstrom (1918) observed that cilia of the buccal cavity were stimulated to beat toward the esophagus by the proximity of algal cells but not by carmine. I was unable to find any local response of these cilia, but the effect, if it exists, would be difficult to observe.

Rejection Mechanisms

Aspects common to all four classes. Rejection is stimulated by high concentrations of particles or particles unsuitable as food, such as carmine or diatoms too large to be ingested. The rejection mechanisms and rejection behavior of planktotrophic echinoderm larvae are quite varied, but a few activities are common to all four classes.

The larvae can stop or reduce feeding by passing particles over the ciliated band with the water (Fig. 15: path x- z). Few particles enter the mouth when the ciliated band is not retaining particles, even when the cilia of the adoral band are beating into the mouth. Retention of particles by the pre- and postoral transverse bands appears to be necessary for active feeding.

The larvae can reject particles from the buccal cavity or upper esophagus past any part of the adoral band by ciliary reversal. This was noted by MacBride (1914), Gemmill (1914, 1916), and Runnstrom (1918). Particles are then carried out past the pre- and postoral transverse bands, which continue to beat outwards but do not retain particles (Fig. 39: a, b, c). I could not determine whether cilia of all parts of the adoral band and upper esophagus reversed or altered beat together. Gemmill (1914, 1916) found that in Asterias and Porania the cilia of the ventral esophagus stopped beating while the cilia of the labial loop beat outwards. In some larvae (Luidia, Patiria, S. droebachiensis) cilia of the ventral esophagus reverse beat for ejection particles. In the other species reversal of cilia below the lower adoral band was not seen, but may occur. Tattersall & Sheppard (1934) appear to have interpreted rejection currents past the lower adoral band as part of the feeding currents.

Particles which have been carried into the esophagus can be ejected by a contraction of esophageal muscles (as in Fig. 39: 2). Contraction of the circular esophageal muscles begins at the posterior end and continues for varying distances towards the anterior end (Fig. 39: 1). During such a contraction the cardiac sphincter remains closed and the mass of particles is forced into the buccal cavity or out of the mouth. Occasionally the mass of particles reenters the esophagus when the esophagus expands again. Reversal or stopping of the adoral band and other cilia of the buccal cavity is necessary for complete removal and usually accompanies this type of esophageal contraction.

These three types of rejection behavior are often accompanied by other activities peculiar to each class. Larvae of all four classes can cease feeding or reject particles while continuing forward swimming and can reject particles even after they have reached the bottom of the esophagus.

Ciliary reversal and muscular contractions are reversibly blocked by a mixture of equal parts of sea water and isotonic $MgCl_2$ (*Parastichopus*, *Pisaster*, *Ophiopholis*, *S. droebachiensis*). The beating of cilia of the ciliated band and adoral band continues and the larvae swim until they lodge against some object or surface. The beating of the epaulettes is reversibly stopped by $MgCl_2$, which suggests that ciliary beat of the epaulettes may require nervous stimulation. Curiously, $MgCl_2$ also stops feeding, and the algae pass over the ciliated band as in rejection. Apparently the autonomous activity of the ciliated and adoral bands alone is not sufficient for feeding.

Auricularia. I observed five types of successful rejection or avoidance in the auricularia of *Parastichopus*. (1) They stop feeding while swimming forward. They eject particles from the buccal cavity by (2) ciliary activity alone or (3) by cilia and muscles acting together. (4) They eject particles from the esophagus by muscles and cilia acting together. (5) They disengage themselves from a mass of particles or other object by reversing the beat of cilia of the ciliated band and backing up.

The muscular activity aiding rejection from the buccal cavity is a contraction of muscle strands on the dorsal wall of the buccal cavity (Fig. 39, m) which forces water out of the mouth. Contraction of these muscles does not eject particles if the contraction is not accompanied by a change in ciliary beat. These muscles, along with the esophageal muscles, also contract when the larva moves particles into the stomach.

The larvae usually back up when they are electrically shocked, encounter a high concentration of particles, or bump into something, though these circumstances do not always stimulate reversal and reversal can occur at other times. During reversal, particles travel inward over the ciliated band and all portions of the band appear to have reversed beat. The pre- and postoral transverse bands carry particles into the transverse groove (Fig. 40: j). These particles are often carried into the buccal cavity and down into the esophagus (Fig. 40: k), which indicates that the adoral band does not always reverse beat along with the ciliated band. At other times the particles carried in past the preoral transverse band enter the reversed circulation in the transverse groove (Fig. 40: l) and are not carried into the esophagus, which indicates that cilia of the adoral band can reverse beat at the same time as the ciliated band.

Bipinnaria. The cilia of the ciliated band and circumoral field apparently can change beat independently in rejection. When the ciliated band stops retaining particles, particles sometimes still move toward the mouth over the circumoral field, which suggests that the cilia of the circumoral field are still transporting particles toward the mouth. In other instances the ciliated band does not retain particles and there is little transport of particles toward the mouth, which suggests that the cilia of the circumoral field have also changed beat or ceased beating. Gemmill (1914, 1916) noted that a decrease in the activity of the cilia of the circumoral field accompanied a decrease in feeding.

Ejection of particles from the buccal cavity occurs very rapidly. Presumably the cilia of the adoral band and buccal cavity reverse beat only for a very short period. Ejection from the buccal cavity is sometimes accompanied by contraction of muscles which lie against the dorsal body wall. Such a contraction, with the attendant opening of the oral region (Figs. 41, 42), is necessary for the ejection of larger particles or masses of particles past the transverse bands since at most stages of development these bands are close together. Gemmill (1914, 1916) also noted the role of dorsal flexion in rejection.

When particles are ejected from the esophagus by muscular contractions, they may be rotated in the upper buccal cavity for some time before they are ejected from the buccal cavity. Close coordination between contraction of esophageal muscles and reversal of the adoral band is not required in the asteroid larvae as in other forms. Inactivity of cilia of the buccal cavity may be sufficient to prevent particles from reentering the esophagus.

I have often seen bipinnaria and brachiolaria larvae of Patiria and Pisaster bring the pre- and postoral transverse bands into an overlapping position. This must interfere with feeding and may alter swimming direction, but I could not determine its function.

The cilia of the ciliated band never reverse beat. Instead of backing, the bipinnaria turn in a back loop by contracting the dorsal muscles (Figs. 41, 42). This contraction can occur without reversal of the adoral band or loss of particles from the buccal cavity.

The later stage larvae of Pisaster and Pycnopodia can stop or back up by pointing the arms anteriorly and pointing the median dorsal process ventrally (see also Gemmill, 1914). This results in a strong anteriorly directed current (Fig. 43: P). The arms and median dorsal process usually all contract together, although they can also contract individually. The contraction of the arms can also be accompanied by dorsal flexion. Muscle strands issue from the arms and extend considerable distances under the body wall, occasionally crossing or connecting with strands from other arms. When an arm is raised in response to being touched, the other arms most likely to respond are one or more of those on the same side of the larva.

The advanced larvae of Luidia seldom move their arms although they are capable of moving arms singly or together. They can also bring the anterior median processes together, perhaps to alter direction or speed of swimming or decrease feeding.

Ophiopluteus. The ophiopluteus of Ophiopholis can continue to swim with the arms upward while particles are passed over the ciliated band, but frequently this type of rejection is accompanied by a change in swimming pattern. The larva moves horizontally, tilting in the direction of movement or with one of the posterolateral arms leading and the arms upright. My impression is that these different types of swimming are controlled by the larva, rather than arising from proximity to the surface film or slight currents in the bowl, but I do not know what changes in ciliary beat might be responsible for such motions.

I could not ascertain the role of the paroral band cilia in rejection. The other cilia of the circumoral field are too sparse to have much effect on feeding.

Ejection of particles from the buccal cavity is aided by contraction of a pair of dilator muscles which raise the preoral transverse band and widen the mouth (Figs. 44, 45). These muscles usually contract together but can contract singly. In Ophiopholis and most of the ophioplutei that I found in the plankton, there is only one muscle cell on each side. In one species from the plankton, some individuals had two muscle cells on each side and some only one. These muscles insert on the body wall near the preoral transverse band and originate on the body wall in the anterolateral arm.

Muscle strands lying against the dorsal wall of the buccal cavity can contract independently of the esophageal muscles to aid ejection from the buccal cavity (as in Parastichopus, Fig. 39, m).

Ejection of particles from the buccal cavity is often aided by reversal of the ciliary beat of most of the ciliated band. The current past the preoral transverse band is not reversed and thus aids in ejecting particles.

Thus there are three mechanisms aiding the cilia of the adoral band and buccal cavity in ejecting particles from the buccal cavity. These three can operate singly or together, or ejection can be accomplished by reversal of the cilia of the adoral band and buccal cavity alone.

These mechanisms also aid in the ejection of particles from the esophagus.

Reversal of ciliary beat along most of the ciliated band also results in backing, and can occur without ejection of particles from the buccal cavity, indicating that cilia of the ciliated band can reverse beat without a comparable reversal of ciliary beat at the adoral band.

Echinopluteus. When the ciliated band is not retaining particles there is sometimes also a change in swimming pattern. The larva travels horizontally in the direction it is leaning. Runnstrom (1918) has described a variety of types of horizontal movement and asymmetrical patterns of water currents across the circumoral field. Some of these are probably under the control of the larva, though some patterns might be due to slight changes in orientation of the larva relative to the surface film.

Runnstrom (1918) found that the cilia of the circumoral field aided rejection of particles. This is quite likely, though I was unable to confirm it.

In four-armed larvae, a pair of posterior dilator muscles (Runnstrom, 1918; Arrau, 1958)(Figs. 46, 47) are present, which insert on the upper ventral esophagus and originate near the junction of the anterolateral and ventral transverse rods. These muscles widen the mouth at the lower edge (Fig. 48). In six- and eight-armed larvae anterior dilator muscles also become active. The several muscle cells on each side insert on the body wall near the preoral transverse band and originate on the body wall of the anterolateral arm. The lengthening preoral rod grows to the inside of these muscle strands (Figs. 46, 47). The anterior dilator muscles raise the preoral transverse band, widening the mouth (Fig. 48) and draw the preoral arms back towards the anterolateral arms, reducing the overhang of the oralhood (Fig. 4). Anterior and posterior dilator muscles are present in all the species studied. Other muscle strands alongside the mouth and esophagus serve to dilate the mouth or oppose the anterior and posterior dilator muscles, but there is less regularity in their location (see also Runnstrom, 1918). These connect to esophagus and body wall, or sometimes to skeletal rods. These muscle strands act in various combinations to aid ejection of particles from the buccal cavity or esophagus.

Muscle strands on the dorsal wall of the buccal cavity can contract independently to aid ejection from the buccal cavity.

Ejection of particles from the buccal cavity is frequently accompanied by reversal of the beat of cilia of the ciliated band. Ejection was possible during forward swimming but was much more rapid during backing. The cilia of the preoral transverse band do not reverse beat with the rest of the ciliated band and so aid ejection of particles.

These three mechanisms of ejecting particles can occur separately or together, as in ophioplutei.

Reversal of ciliary beat along the ciliated band results in backing. Particles sometimes entered the mouth during such a reversal, which suggests that the adoral band can continue forward beat when the ciliated band is reversed. Runnstrom (1918) observed a larva in which cilia of the ciliated band beat forward on one side and reversed on the other. I saw a similar instance, but the larva was confined under a coverglass and the reaction may not be a normal one.

The epaulettes of the strongylocentrotids often stop beating while cilia of the ciliated band continue forward beat. The cilia of the epaulettes either stop or reverse when the beat along the ciliated band is reversed. Usually all the epaulettes changed beat together.

Difference between the rejection mechanisms. The principal difference between the ophiopluteus and the echinopluteus (if the species here are representative) is the absence of posterior dilator muscles and the earlier development of the anterior dilator muscles in the ophiopluteus. Both ophioplutei and echinoplutei frequently utilize reversal of beat along most of the ciliated band as an aid to rejection from the buccal cavity, and the action of cilia of the preoral transverse band is not reversed. I could not determine the role, if any, of the paroral bands in rejection.

The auricularia lacks oral dilator muscles, the cilia of the preoral transverse band reverse along with the rest of the ciliated band, and reversal of the ciliated transverse band does not appear to aid ejection of particles from the buccal cavity. The asteroid larvae use dorsal flexion for turning and rejection and cilia of the ciliated band do not reverse beat at all. Since asteroid larvae are similar to the auricularia in form, the differences in turning and rejection are rather surprising.

There are major differences among the four types of larvae in the muscular mechanisms aiding the action of the reversed beat of cilia of the adoral band or buccal cavity. The presence or absence of cilia on the circumoral field or in the buccal cavity apparently makes little difference in rejection mechanisms since these tend to reinforce the action of the ciliated band or adoral band in rejection.

Gut Function

Anatomy of gut and passage of food. Gemmill (1914) and Runnstrom (1918) describe the gut and the passage of food in *Asterias rubens* larvae and echinoplutei. The gut of echinoderm larvae consists of three sections: esophagus, stomach, and intestine. There are three sphincters: a cardiac sphincter between esophagus and stomach, a pyloric sphincter between stomach and intestine, and an anal sphincter (at cs, ps, as in Fig. 14).

When the larvae ingest particles, the circular muscles surrounding the esophagus contract in a wave beginning at the anterior end, the cardiac sphincter opens, and the accumulated mass of particles is pushed into the stomach. In the stomach the mass is broken up and circulated by cilia. Particles accumulated in the posterior portion of the stomach are carried into the intestine whenever the pyloric sphincter opens. Particles are carried to the end of the intestine by cilia. When the anus opens the mass is defecated. In asteroid larvae the cilia of the intestine are largely responsible for expelling feces and the intestine does not greatly expand or contract when filling or emptying. In the auricularia of *Parastichopus*, the ophiopluteus of Ophiopholis, and in echinoplutei, contraction of the intestine accompanies defecation.

Microvilli are abundant in both the intestine and stomach and are particularly conspicuous in Ophiopholis (Fig. 1, m)

Sorting of particles in the gut. Runnstrom (1918) suspected that sorting of particles might occur in the stomach near the pyloric sphincter, but he could not demonstrate it. In this study algae (Cricosphaera of 10 to 12.5 μ diameter or Phaeodactylum about 2.5 μ wide by 30 μ long) and other particles (carmine or calcium carbonate about 5 to 15 μ wide) were fed to the larvae in a mixed suspension. Individuals which had eaten roughly equal quantities of both were placed in filtered sea water for observation. Carmine and calcium carbonate crystals were frequently passed from stomach to intestine and defecated while the algal cells remained in the stomach. Larvae of Parastichopus, Pisaster, Ophiopholis and S. droebachiensis separated calcium carbonate from Cricosphaera. Luidia and Dendraster separated carmine from Cricosphaera. Pycnopodia, Ophiopholis, and S. droebachiensis separated carmine from Phaeodactylum. Thus sorting in the gut occurs in larvae of all four classes with at least some combinations of materials.

In some cases the clumps of particles which passed to the intestine were smaller than the individual Crisosphaera remaining in the stomach. Sorting is therefore not based on size alone.

The separation of the two kinds of particles often began before they had reached the lower part of the stomach. Calcium carbonate or carmine would clump before reaching the posterior end of the stomach and remained there until the pyloric sphincter opened. The algae were less clumped and circulated about in the upper stomach for a longer time.

Some individuals exhibited incomplete or no separation but in no case were algae eliminated first and other particles retained. In larvae which had ingested many particles, separation was less complete and some of the algal cells were rapidly eliminated along with other particles.

Rate of passage of particles through the gut. When larvae ingest algae at high rates, the algal cells pass through the gut more rapidly. The most rapid passage of particles from esophagus, at the time of contraction, through the anus was 6 minutes (observed in an auricularia of Parastichopus). However, the times for passage through the gut usually exceeded 15 minutes even at high ingestion rates in larvae of all four classes. Passage through the gut commonly took more than 30 minutes at lower ingestion rates.

The time for passage from the mouth through the anus could be regulated by the frequency at which sphincters open or the length of time particles are circulated in the stomach by cilia. However, Runnstrom (1918) observed no relation between the frequency of contraction of the esophagus or sphincters and the quantity of food in the gut. My observations indicate that if there is an increase in frequency it is not great. The esophagus or intestine can be packed with cells and the sphincters still not open for a considerable time. The rate of passage through the gut must be regulated primarily by the rate at which particles pass out of the circulation in the upper stomach and accumulate in the lower stomach near the pyloric sphincter (Fig. 14: t).

Quantity of particles passed through the gut. The number of particles passing through the gut is regulated by other mechanisms. It usually is regulated by rejection mechanisms at high algal concentrations. In some cases, however, it seemed to be limited by the frequency of contraction of the esophagus, which was filled to overflowing.

Contractions of the esophagus can be inexplicably irregular. Incomplete contractions and contractions which eject material from the mouth also complicate analysis of any periodicity. Two *S. droebachiensis* larvae, observed in filtered sea water at about 13°C, exhibited successive intervals of 13.0, 2.5, and 0.5 minutes and 2.5, 0.8, and 5.1 minutes, although they were ingesting few, if any, particles. Runnstrom (1918) obtained similar results.

Appearance of algal cells passed through the gut. The appearance of algal cells passed through the gut is not a very reliable indicator of their value as food or the degree of assimilation but because no other information is available for echinoderm larvae, the condition of algal cells in the gut is of some interest. Several species of algae passed through the gut with no change apparent at 400x magnification other than a loss of motility in the flagellates. *Cricosphaera*, a coccolithophorid, and *Amphidinium*, a dinoflagellate, passed through the stomachs of *Patiria*, *Pisaster*, *Ophiopholis*, *Dendraster*, and *S. droebachiensis* without changing shape or color. *Ditylum* frustules came apart and chloroplasts of *Thalassiosira* changed color and form soon after they entered the stomachs of *Ophiopholis* and *S. droebachiensis*, so diatoms are probably easily digested. *Dunaliella* rapidly disintegrated in the stomachs of *Parastichopus*, *Patiria*, *Pisaster*, *Ophiopholis*, *Dendraster*, and *S. droebachiensis* when larvae began feeding on it. In larvae which had ingested large quantities of *Dunaliella* for several hours, cells still in one piece, and in some cases with no apparent change, were passed to the intestine. *Isochrysis*, unlike *Dunaliella*, did not break up rapidly on entering the stomachs of larvae which had begun feeding on it, but its small size prevented clear observation of its condition through the gut wall.

Largest Particles Eaten

Thorson (1946) estimated the maximum diameter of particles eaten by many larvae as about half the diameter of the esophagus, since larger particles would stop free movements of the cilia carrying the particles through the esophagus. He accordingly estimated the maximum size of food for echinoderm larvae to be 40 to 50 μ in diameter, because Mortensen's figures indicated that the esophagus is 80 to 100 μ in diameter. The larvae observed in this study had esophagus diameters as small as 50 μ in the early stages, but more advanced stages were used to estimate the maximum size of food ingested.

Sephadex spheres (Pharmacia), a highly polymerized polysaccharide, are readily ingested by the larvae and are available in a range of sizes.

Larvae were offered spheres of varying diameters and the largest ones in the stomachs were measured. The maxima observed here are somewhat greater than Thorson's estimate.

The auricularia of *Parastichopus* with esophagus width of 70 μ ate spheres up to 70 μ in diameter; the *Pisaster* brachiolaria with an esophagus width of 100 μ ate spheres up to 85 μ; eight-armed *Ophiopholis* plutei with esophagus of 85 μ ate spheres up to 65 μ; eight-armed *S. droebachiensis* plutei with esophagus of 100 μ ate sphers up to 75 μ. The esophagus was measured at the narrowest point, at the top. The largest particles could have been moved into the esophagus with the incoming flow of water following a contraction, rather than by cilia.

When larvae were offered phytoplankton from net tows, eight-armed *S. droebachiensis* plutei ate armored dinoflagellates with dimensions up to 90 μ x 60 μ x 40 μ and other larvae ate somewhat smaller dinoflagellates, but only the shortest chains of *Skeletonema costatum* or *Thalassiosira* spp. were found in the stomachs, although chain forming diatoms were quite abundant.

The larvae were fed cultured *Ditylum* ranging up to a little over 200 μ long (including the spike) and about 15 to 30 μ in diameter. The maximum lengths of frustules found in the stomach are as follows:

auricularia of *Parastichopus*, 160 μ

advanced bipinnaria of *Luidia*, brachiolaria of *Pisaster*, 210 μ

early stage bipinnaria of *Evasterias*, 150 μ

eight-armed pluteus of *Ophiopholis*, 150 μ eight-armed pluteus of Dendraster, 100 µ

four- and eight-armed plutei of S. droebachiensis, 150 µ

The mean length of Ditylum eaten by Parastichopus, Ophiopholis, and Dendraster was less than the mean length in the suspension, but Ditylum eaten by the brachiolaria of Pisaster were about the same mean length. There was less tendency for the Ditylum to jam in the oral region of the large Luidia and Pisaster than in the other larvae tested. Ditylum which were too long to be ingested were ejected from the buccal cavity.

Thus these, and probably most, echinoderm larvae cannot eat chains or rods longer than 100 to 200 µ or discs or spheres more than 65 to 85 µ in diameter. When the larvae feed on particles of the maximum size, they probably feed at a lower rate (see below: Amphidimium-Ditylum comparisons).

Feeding Rates

Maximum clearance rates. Clearance rate is the volume of water cleared of particles per unit time and ingestion rate is the number or quantity of particles ingested per unit time. In method 1 clearance rate is calculated from the rate at which algal cells (Amphidinium) are carried into the mouth when the larva is feeding in a suspension of known concentration. In method 2 clearance rate is calculated from the number of cells in the gut after the larva has been placed in a suspension for a short time. Rates determined by method 2 are usually lower and more variable than those by method 1 but method 2 can be used with more algal species and is useful for comparisons.

Estimates of the maximum clearance rates at 9.5 to 15°C are listed in Table II. Most rates were determined by method 1 with larvae previously left overnight in filtered sea water (A) or taken directly from culture jars (B). Also included are high rates measured by method 2 in a suspension of 1000 Cricosphaera per ml with larvae previously left overnight in filtered sea water (C) or in a suspension of 1000 Dunaliella per ml (D). Rates for each species are listed by advancing stage. Distance to oral hood (o.h.) or posterolateral arm tip (p.l.) is measured from the posterior end. Asteroid larvae are measured from the posterior end in the midline to the tip of the median process.

Only in Ophiopholis were the highest rates from method 2 considerably above those obtained in method 1. This may have resulted from the less accurate timing in method 2. On the other hand Cricosphaera, used in method 2, was cleared more rapidly than Amphidinium by all the larvae tested (Table IV). The larvae may clear some particles at twice the rates determined by method 1 with Amphidinium.

With the exception of Luidia, suspensions of Amphidinium are cleared by advanced larvae at rates of between 2 and 4 µl/min or about 3 to 6 ml/day. As one would expect, the earlier stages and smaller larvae have lower clearance rates. In the larva of Pisaster, the length of the ciliated band does not increase in proportion to the size of the larva because of the development of arms for swimming and attachment. This may partly account for the failure to find an increased clearance rate in the later and longer brachiolaria stage. In Fig. 49 clearance rates determined by method 1 are plotted against approximate length of the ciliated band, as estimated from drawings or photographs. Differences between larval types, differences correlated with the presence or absence of cilia on the circumoral field, and differences related to the number of cilia across the band could not be detected, though estimates of both clearance rates and band length may be biased. All the species cleared at least 0.3 to 0.6 µl per mm of ciliated band.

Reduction in clearance rates. Echinoderm larvae, just as other suspension feeders, reduce their clearance rate when exposed to higher concentrations of algae. In Table III clearance rates of larvae from filtered sea water (*Luidia*, *Ophiopholis*, *S. droebachiensis*) or culture jars (*Parastichopus*) are compared with clearance rates of larvae from the same conditions but subsequently placed in high concentrations of *Amphidinium* for about an hour. In the second set of observations on *Ophiopholis* the larvae were simply left in the suspension of 5000 *Amphidinium* per ml for about 10 to 20 minutes, and the initial feeding rate compared to the later feeding rate. Clearance rates were measured by method 1 at 9.5 to 13.5°C with eight to eleven observations for each treatment. In each case there was a significant reduction in clearance rate following exposure to high concentrations of *Amphidinium*. (Significance was tested by a two sample rank test at 95%).

All observations were made while the larvae were swimming forward, although backing, stopping, or contraction of dorsal muscles was more frequent after exposure to high concentrations of algae. Cells entering the mouth were counted as eaten even if rejected later, so that the decrease in feeding recorded here was entirely due to rejection at the ciliated band or circumoral field. Thus the echinoderm larvae can reduce clearance rate without an extra expenditure of energy or stopping swimming.

Change in clearance with concentration of particles. The effect of concentration of particles on clearance rate (Fig. 50) was determined by leaving groups of larvae overnight in three or four different concentrations of *Dunaliella* and then transferring the larvae to suspensions of *Cricosphaera* for determination of rate of feeding by method 2. The larvae were transferred to a concentration of *Cricosphaera* equal to that of the concentration of *Dunaliella* in which they had spent the night. *Dunaliella* was selected because a gentle rocking motion was sufficient to keep it suspended evenly overnight and because it gave little obstruction to counts of *Cricosphaera* in the gut. *Cricosphaera* is eaten readily and is easily counted in the gut. Since the larvae feed on both species in the same way and the interval in *Cricosphaera* was short, the feeding rates on a given concentration of *Cricosphaera* should be a simple index of the effect of the preceding exposure to the same concentration of *Dunaliella*.

The ingestion rate reaches a maximum at closer to 5000/ml for *Parastichopus* and *S. droebachiensis* and closer to 1500/ml for *Ophiopholis*. The clearance rate declined above about 1000/ml. Ingestion and clearance rates vary with concentration in much the same manner as in other suspension feeders (Conover, 1968).

The maximum ingestion rates observed in this experiment were 25 cells/min in Parastichopus, 14 cells/min in Ophiopholis, and 15 cells/min in S. droebachiensis. These maximum rates do not represent a mechanical limitation on the rate at which algae can enter the mouth or the number of cells which can be packed into the esophagus between contractions. Considerably higher rates of ingestion were observed in each type of larva while estimating clearance rates by method 1 without any such limitation being approached. Ingestion rates are controlled by the larvae, and they do not continue to pack the esophagus or gut with algae over long periods of time.

Comparison of clearance rates with different algae. The echinoderm larvae exhibit a single feeding behavior for all kinds of algae tested and apparently do not select one species and reject another during active feeding. Therefore, when a larva is feeding on a mixture of two species of algae, the relative rates at which they are eaten indicates the relative efficiency with which they can be removed from suspension.

In Table IV clearance rates on Amphidinium are compared with rates on other algal species. Clearance rates were measured by method 2 at 10 to 12.5°C at concentrations of 1000 cells per ml for each species. Six to nineteen observations were made on each species. When two species were offered separately (S), the significance of differences between rates was tested by a two sample rank test at 95%. When offered in mixture (M), by a paired difference t-test at 95%. In most cases only the number of cells in the stomach and intestine were counted.

More Cricosphaera than Amphidinium were eaten by all echinoderm larvae tested, whether fed separately or together. The algae are of similar size, though Cricosphaera is somewhat larger and non-motile. However, neither of these differences appears to be important in determining the difference in feeding rate because the larger and non-motile Thalassiosira (single cell form) was not eaten at a significantly higher rate than Amphidinium by either Ophiopholis or S. droebachiensis although it was eaten at a higher rate by Pisaster. The small Cyclotella was not eaten at consistently higher or lower rates by the larvae tested. The clearance rates determined with Amphidinium (by method 1) are probably representative of clearance rates on many algal species, but the results with Cricosphaera indicate that the larvae can clear suspensions of some kinds of particles at twice the rates indicated in Table II and Fig. 49.

Interference with feeding by larger algae. If the feeding rate is lower on an algal species in a mixture than on the species separately, then it is probably being rejected along with the less desirable or edible species in the mixture. Ditylum is a centric diatom which approaches the maximum length some of the echinoderm larvae can ingest, although the larger asteroid larvae eat it readily (see Largest Particles Eaten). In order to determine whether Ditylum is cleared at lower rates of feeding on Amphidinium, I compared clearance rates of larvae feeding on a mixture of the two species with clearance rates of larvae feeding on each species separately

(Table V). Clearance rates were measured by method 2 at 12°C at concentrations of 1000 cells per ml for each species. Only the number of cells in the stomach and intestine were counted. Significance of the differences between rates was tested by a two-sample rank test at the 95% level. Significance of differences between rates on mixed Amphidinium and Ditylum was also tested by a paired difference t-test at 95% (indicated in Table V in parentheses). The means are for eight to seventeen observations. Since the larvae fed for only short periods, lowered feeding rates are due to rejection, not satiation.

In Ophiopholis and S. droebachiensis the presence of Ditylum reduced the rate of feeding on Amphidinium, but the presence of Amphidinium did not change the clearance of Ditylum significantly. S. droebachiensis ate more Amphidinium than Ditylum both separately (rank test) and in mixture (paired difference test) despite the reduction in feeding in the presence of Ditylum. Ophiopholis ate significantly more Amphidinium than Ditylum when fed separately and significantly more Ditylum when fed in mixture. Presumably Ditylum is cleared more efficiently but ejected from the buccal cavity, or alternatively, Amphidinium may be more easily ejected from the buccal cavity and therefore more Ditylum was eventually swallowed. The reversal in "preference" when fed singly or together is curious but easily explained.

Pisaster ate both species at the same rate when they were fed separately but ate more Ditylum when fed in a mixture. The rate of feeding on Amphidinium was unaffected by the presence of Ditylum but the rate of feeding on *Ditylum* was increased in the presence of *Amphidinium*. *Pisaster* apparently clears *Ditylum* more effectively but is stimulated to feed more by *Amphidinium*. This stimulation of feeding by Amphidinium was quite unexpected.

The degree to which *Ditylum* interferes with feeding accords with the observations on the maximum length of particle these larvae can ingest. The concentrations of *Ditylum* were unnaturally high, but the results suggest that when chain-forming or rod-shaped diatoms are abundant, some echinoderm larvae may suffer reduced feeding rates because of the frequent rejections from the buccal cavity. However, longer chains often go past the larvae without entering the mouth; so the range of lengths inhibiting feeding may be quite limited.

DISCUSSION

Feeding of echinoderm larvae. The action of the ciliated band is the most important aspect of the feeding mechanism and is the same in the four classes with planktotrophic larvae. However, the mechanism by which the ciliated band passes water while retaining and transporting particles is unclear. The changes in mucus secretion or ciliary beat occurring when the band switches from retention to passing of particles are also unknown.

It is difficult to assess the relevance to feeding of those differences in configuration and current pattern which set the auricularian and bipinnarian type of larva apart from the pluteus type. If the volume cleared per unit length of band in plutei is really comparable to that in the auricularia and bipinnaria (as indicated in Fig. 49), then the plutei may produce feeding and swimming currents more efficiently. The plutei have a smaller circumoral field and body size relative to band length and, judging from the larvae studied here, the ciliated bands on the arms of the ophiopluteus and echinopluteus have fewer cells and cilia per unit length of band than in the auricularia and bipinnaria larvae. However, again judging from the species studied here, the bipinnaria can ingest larger particles than the pluteus and may obtain more food from the same volume of water cleared.

The cilia on the circumoral field aid in capture and transport of particles; however, the ophiopluteus and auricularia, with few and no cilia on the circumoral field, feed at rates comparable to the echinopluteus and bipinnaria, which have abundant cilia on the circumoral field. Larvae lacking these cilia may expend less energy but may forego other advantages.

The ciliated circumoral field in the asteroids and echinoids seems to have freed the ciliated band for locomotory specializations such as the epaulettes of some echinoplutei and the current-directing arms of Asterias, Pisaster, and Pycnopodia.

The feeding rate increases as the larvae develop. The adult rudiment does not increase much in size until the larval feeding structures are fully developed and feeding rates have probably reached a maximum. Energy first goes into developing feeding structures capable of a high clearance rate, then into development of the adult rudiment.

Jørgensen (1966) mentions that the maximum capacity for processing water depends to a considerable degree on the size and structure of the feeding organs and must be more or less genetically fixed, though "it is not known to what extent ontogenetic adaptation to the food concentration in the surrounding water is possible in the various suspension feeders." In this connection it is interesting that starved echinoplutei have shorter arms, and presumably both a lower feeding rate and lower respiratory rate. If the distal part of an arm contributes less to feeding, then respiration might be decreased more than feeding, and this could be the best response to low concentrations of food.

Comparison of expected and measured clearance rates. Clearance rates measured in the laboratory can fall considerably below the maximum rates of which an animal is capable. The rates here agree well with the rates predicted from swimming speeds or current velocities and the area swept clear, estimated from size of larvae and current pattern or from length of cilia and ciliated band.

The horizontal swimming rates are about 0.3 to 0.5 mm/sec. Velocities of particles moving posteriorly toward the transverse groove were 0.5 to 1.4 mm/sec in eight-armed S. droebachiensis (see Feeding mechanisms). The fully developed larvae of most species studied here probably sweep an area of about 0.1 mm^2 or more, judging from the size of the larvae and pattern of incoming currents. With swimming speeds of 0.5 mm/sec, this gives a clearance rate of 3 µl/min. With current velocities of 1.4 mm/sec, this gives a clearance rate of 8.4 µl/min. These estimates are in good agreement with clearance rates calculated from ingestion rates. Fully developed larvae may sweep a larger area.

In Parastichopus larvae all particles eaten appear to be retained by the band. At least 0.5 µl/min are cleared per mm of ciliated band, and the cilia of the band are about 0.025 mm long. Therefore, the velocity of the current past the band must be at least 0.33 mm/sec. This is somewhat below the current rates measured from movies or the rates one might expect judging from the swimming rates. A more fanciful means of evaluating this clearance rate is to consider the rate of ciliary beat which might be needed to maintain this current. If the cilia moved all the water in a 90° arc each beat, they would need to beat at a rate of 17 per second, which is well within the range of frequencies found for cilia of a number of other organisms (Sleigh, 1962).

The rates measured by method 1 are only a little below the maxima deduced from larval size, swimming rate, or feeding mechanism. Since

Cricosphaera was eaten at about twice the rate of *Amphidinium*, the larvae may process twice the volume of water indicated by method 1, and clear some particles at this rate.

Interpretations of feeding by other authors. The results of this study are largely in agreement with those of previous authors when two sources of confusion are taken into account. Gemmill (1914, 1916), Runnstrom (1918), and Tattersall & Sheppard (1934) all studied a single type of larva. Gemmill and Runnstrom probably overlooked the role of the ciliated band in retaining particles because they studied larvae with abundant cilia on the circumoral field. Tattersall & Sheppard studied the unusual larvae of *Luidia sarsi* and *L. ciliaris*, which swim by muscular action and therefore did not consider the importance of the band in passing water. The simpler auricularia and ophiopluteus proved to be the most instructive types for me.

The second source of confusion is the difficulty of distinguishing whether a larva is feeding or rejecting. The larvae are most easily observed when confined on a slide in a dense suspension of algae, and under these conditions they are likely to pass particles over the band. Tattersall & Sheppard's suggested mechanism (see below) for concentration of particles in the buccal cavity is probably based on an erroneous interpretation of the current system. The outward current past the lower adoral band may have been observed during ejection of particles from the buccal cavity or esophagus.

Otherwise, the observations of these authors are largely in agreement with the observations I have made. The only major point of difference which I have been unable to resolve is Runnstrom's observation of the stimulation of individual cilia by the presence of algal cells, which would provide a mechanism for the sorting of particles on the circumoral field. I could demonstrate sorting in the stomach, but not on the outer surface.

Mechanisms of concentrating particles by density. Tattersall & Sheppard (1934) have suggested that particles might be concentrated by centrifugal action. This method of concentration was suggested for the buccal cavity but might also be applied to the curving particle paths over the circumoral field. Assuming a circular path (Fig. 51), the force accelerating the particle out of orbit (toward the surface of the larva) is

$$F_1 = \frac{V(\Delta\rho)v_1^2}{r}$$

where V is the volume of the particle, $\Delta\rho$ is the difference in density between particle and water, v_1 is the velocity of the water current and r is the radius of the arc. The particle will move out of orbit with velocity approaching terminal velocity (v_2) because it is retarded by the drag force,

$$F_2 = 3\pi\eta D v_2$$

where η is the viscosity of the water (1.3×10^{-2} g/cm sec) and D is the diameter of the particle. At equilibrium $F_1 = F_2$, and the particle moves a distance relative to the water of $d = v_2 t$, where t is the time the particle circulates. This time will be $2n\pi r/v_1$ where n is the number of completed circuits. Then

$$d = \frac{2n\,V\,(\Delta\rho)\,v_1}{3\eta D}$$

For echinoderm larvae the current velocity is unlikely to be more than 0.2 cm/sec (currents in the buccal cavity are even slower than above the outer surface) and particle diameters are on the order of 10^{-3} cm. The $\Delta\rho$ of algal cells and sea water is no more than 0.2 g/cm^3 (Eppley et al., 1967). Therefore the distance the particle moves towards the larva is not more than 10^{-6} cm or 10^{-2} μ per circuit. Thus a centrifugal model cannot account for the concentration of algal cells by echinoderm larvae.

Bullivant (1968b) has suggested another concentration mechanism based on density differences. He has indicated that lophophorates may be impingement feeders with a mechanism of concentrating particles analagous to certain industrial particle separators. The current paths over the circumoral field of echinoderm larvae invite comparison with current paths figured by Bullivant (1968b) for a bryozoan. Garstang (1962) puts this well in 'Echinoderm Larvae':

> Their feeding streams converge upon the circumoral floor
> and altogether constitute a bilobed lophophore.

Zenz & Othmer (1960), in their discussion of impingement separators, derive an expression for the stopping distance of a particle, which is a measure of the tendency for its momentum to carry it across flow lines. This distance is

$$L = \frac{v_1 \rho D^2}{18\eta}$$

In the echinoderm larvae v_i, the initial velocity of the particle, would be about 0.2 cm/sec or less and ρ the density of algal cells, no more than 1.2 g/cm^3. The stopping distance is then only about 10^{-6} cm or 10^{-2} μ. This is the distance it will travel before it "has lost sufficient momentum to be completely under the influence of the fluid motion" (Zenz & Othmer, 1960). Therefore echinoderm larvae cannot concentrate particles to a significant degree by impingement feeding.

There are also mechanisms of concentrating particles which do not depend on density differences (electric field, velocity gradients) but which still would act at a distance from the animal. These mechanisms do not appear to be applicable to echinoderm larvae.

The interpretation of the feeding mechanism which I have presented in this study is adequate to account for the concentration of particles and the observed feeding rates. The ciliated band produces a feeding current. Particles are removed from suspension by contact with cilia and probably mucus at the ciliated band and circumoral field. Particles are retained at the inner side of the ciliated band or by cilia of the circumoral field and transported toward the mouth by water currents, by cilia of the circumoral field, and probably by cilia of the ciliated band.

Comparison with tornaria larvae of hemichordates. The echinoderm larvae resemble the tornaria larva of hemichordates, and the similarity has prompted phylogenetic speculation. The feeding mechanisms are surprisingly different. Garstang (1939b) described the feeding of tornaria and pointed out the great difference between tornaria and echinoderm larvae in the structure and probable function of the oral region. Judging from Garstang's description, the ciliated band of the tornaria functions differently also. In the tornaria, particles become lodged on the equivalent of the aboral field and are carried over the band into the grooves of the circumoral field. The direction of beat of the ciliated band is opposite to that in echinoderms, and during feeding particles pass over it instead of being retained by it. In echinoderm larvae, particles contacting the aboral field are not carried toward the mouth.

Larval nervous system. The complexity of the rejection behavior of the echinoderm larvae suggests that a larval nervous system may be present. Each type of larva can coordinate contraction of muscles and ciliary reversals in several combinations to eject particles from the buccal cavity or esophagus. A number of suspected nervous structures have been described: MacBride's (1914) apical complex in the echinopluteus; Mortensen's (1920) nerves in the auricularia, ophiopluteus, and echinopluteus; Gemmill's (1914, 1916) and Tattersall & Sheppard's (1934) subepidermal network in asteroid larvae. These structures have not yet been demonstrated to be nervous. Mackie et al. (1969) suggested non-nervous conduction as an additional possibility.

Mackie et al. (1969) recorded potentials not exceeding 20 μV with a frequency of about 3/sec which always accompanied reversal of the ciliated band in S. droebachiensis. Very short periods of reversal were accompanied by a single potential. Removal of most of the oral hood, and presumably the apical complex, did not stop reversal, but muscular activities and ciliary reversal were blocked by $MgCl_2$. Feeding is also stopped by $MgCl_2$.

Comparisons with clearance rates of other animals. The clearance rates measured here for echinoderm larvae are somewhat lower than the maximum rates which have been measured for small marine copepods and a bryozoan, which are of similar size (Table VI). The ranges in the table indicate differences between authors or variations related to different types of particles or different temperatures. Since echinoderm larvae appear to clear a suspension of Cricosphaera twice as fast as a suspension of Amphidinium, the upper estimate given in Table VI is twice the mean rate with Amphidinium.

Whiteley & Baltzer (1958) measured a respiratory rate of 0.32×10^{-3} μl O_2/hr for Paracentrotus lividus (four-armed pluteus at 18°C). The clearance rate of this larva, estimated from a band length of about 1 mm, is probably greater than 0.25 μl/min. This four-armed echinopluteus may therefore clear as much as 47 litres per ml O_2 consumed. This may be an overestimate, but the ratio of volume cleared per ml O_2 consumed may exceed the 10 to 20 litres per ml O_2 found for ascidians, bivalves, cladocerans, and sponges (Jørgensen, 1966), and the clearance rates determined here appear adequate to meet the food requirements of the echinoderm larvae.

Changes in feeding rate with concentration. The ingestion rate and clearance rate follow the same pattern in the echinoderm larvae as in other suspension feeders, although in some suspension feeders the ingestion rate does not decline so precipitously at high concentrations (Conover, 1968).

Reeve (1963) suggested a connection between maximum ingestion rate and maximum growth rate and reasoned that (1) the more food digested per unit time the faster the growth rate, but (2) as food passes through the gut faster there is less thorough digestion; so the animal has apparently stabilized its maximum ingestion capacity at the point where further increase in food no longer results in faster growth. Maximum ingestion rates are thus intimately related to the capacity of the gut.

The maximum sustained ingestion rates of echinoderm larvae are not the maximum rates of which they are capable. The larvae feed at much higher rates when first introduced to a high concentration of algae. High ingestion rates are accompanied by more rapid passage of food through the gut and a decrease in the sorting of particles in the stomach.

Evolution of clearance rates. It seems reasonable that the evolution of maximum clearance rates should have some relation to the concentration of food in the water, but the relationship between clearance rate and concentration of food, in an evolutionary sense, is not very clear. An animal must compromise between the requirements of feeding and those of swimming, escape from predators, and other activities. If this were the only limitation, then at lower concentrations of food, animals might be expected to increase the feeding structures at the expense of some other anatomical advantages in order to maintain a high ingestion rate.

On the other hand, clearance rate could be optimized in terms of energy expended in feeding, and this could have an opposite effect. Though the relationships between energy expended and clearance rate could take a variety of forms, depending on the way which a given type of animal undertook to evolve a higher clearance rate, it is probable that more energy would be expended per volume cleared as clearance rate increased. This type of optimization is diagrammed in Fig. 52. In this case an animal should decrease its clearance rate at lower concentrations.

One type of limitation on clearance rate could be imposed by drag forces, but the simplest and most obvious model based on this assumption has some peculiar and unrealistic consequences (though, admittedly, some of the other assumptions of this model are rather peculiar also). At low Reynolds numbers the rate at which energy is expended in moving an object through the water is proportional to the square of the velocity. An animal which creates its own feeding current must do work to overcome drag. If clearance rate is altered by changing the velocity of the currents, and if the clearance rate is proportional to the velocity of the current, then the rate at which energy is expended in feeding is proportional to the square of the clearance rate. If assimilation efficiency is constant, then the rate at which energy is gained is proportional to the clearance rate at a given concentration of food. The net energy gain to be optimized is then

$$E_{net} = qC - kC^2$$

where q is the concentration of assimilable food and C is the clearance rate. The quadratic equation can be solved for the maximum net energy gain and optimum clearance rate;

$$E_{net} = \frac{q^2}{4k} , \qquad C_{opt} = \frac{q}{2k}$$

The optimum clearance rate is directly proportional to the concentration of food unless the animal can alter the constant k at the expense of some other advantage. However, this also implies that at the optimum clearance rate the energy expended in feeding would be more than half of the total energy expenditure of the animal. This is unlikely (Zeuthen, 1946). Apparently drag forces do not play such a direct, obvious, and dominant role in the evolution of clearance rates.

Why does each class have its characteristic type of larva? The embryologists who first described the development of echinoderms were concerned with evidence for phylogenetic relationships and the nature of ancestral types (MacBride, 1914). The type of development was considered to be a very conservative trait. More recently, studies of adult morphology and the fossil record indicate that many similarities in the development of echinoderms of different classes are the result of convergent evolution (Fell and Pawson, 1966). The asteroids and ophiuroids have most recently diverged from a common ancestor, and the similarity of larvae of echinoids and ophiuroids does not indicate a close relationship between these classes. The selective pressures which might be responsible for these adaptive modifications have not been studied.

The situation is complicated by the strikingly different patterns of rearrangement of parts at metamorphosis. In ophiuroids and holothuroids the hydrocoel wraps around the larval esophagus and the adult mouth develops at the site of the larval mouth. In asteroids and echinoids the adult mouth develops at a new site on the lower left side of the larva. This aspect of the transformation from bilateral to pentaradial symmetry is therefore not correlated with either larval type or the supposed phylogenetic relationships.

The following speculations are an attempt to relate some of the differences in development to settling behavior and the feeding behavior of early juveniles. At present little is known about these stages but further observations could provide a partial test of these ideas.

The echinoderms with planktotrophic larvae may, in each class, have evolved a manner of metamorphosis combining maximum preparation for a benthic existence with the ability to feed during the search for a suitable attachment site. The formation of the adult mouth from the larval mouth before settling in ophiuroids and holothuroids may be related to the ability of these animals to feed on suspended material after metamorphosis and before settling. This depends on the mouth reopening before settling. Echinoids and asteroids, which may not be able to feed on suspended material after metamorphosis, use larval feeding structures up to the time of settling, and the adult mouth is then formed at a new site. The asteroids, which generally have the most restricted feeding habits, also undergo the least change in larval structures prior to settling.

In echinoplutei which are ready to metamorphose the postoral and posterodorsal arms tend to be partially resorbed or moved out of position due to the development of adult structures. The expanded oral hood, with two pairs of arms, may contribute to more efficient feeding while the larva waits for a suitable attachment site. The ophiopluteus does not need an expanded oral hood because it has metamorphosed before attachment, and is no longer using larval feeding structures.

The pluteus type of organization may provide a capacity for carrying a heavier adult rudiment. Locomotory specializations such as epaulettes and lobes are quite pronounced in many echinoplutei. In the ophioplutei the posterolateral arms serve this function in some species. They support the young adult until it attaches and are then cast off. In some ophiuroids, unfortunately for this hypothesis, all the arms are resorbed at metamorphosis and young adults can be found in the plankton.

The auricularia form may be best for holothuroids because there is not a bulky adult rudiment to be carried around and an elongated larva may be most readily converted into an elongated adult. However, the larva does shrink considerably at metamorphosis and the mouth must migrate from the midpoint of the larva to the anterior end of the adult, so there is still considerable need for rearrangement.

It seems to me that asteroids should have a larva similar to an echinopluteus. The plutei may feed more efficiently (see above) and there would be no need to resorb such an enormous larval body at metamorphosis. One explanation for the absence of an asteropluteus may lie in the feeding habits of the juveniles. Most asteroids are largely carnivorous. The newly metamorphosed asteroids are commonly only half a millimeter across, have only two pairs of tube feet per arm, and may have considerable difficulty finding an adequate supply of sufficiently small prey. The relatively large larval body, which is resorbed at metamorphosis, may constitute an energy reserve for the newly metamorphosed juvenile during the interval before its first meal. This is the least convincing of all these explanations. If small juvenile size is a problem, why should an asteroid not develop a larva capable of bearing a larger juvenile? Luidia sarsi and L. ciliaris have developed a muscular swimming mechanism which can, and does, carry large juvenils. Luidia sarsi sometimes casts off the larval body at metamorphosis instead of resorbing it (Tattersall & Sheppard, 1934).

In asteroid larvae the dorsal muscle strands which function in rejection and turning are also involved in settling behavior. Muscles first functioning in settling may have later come to replace reversal of beat of the ciliated band.

In the absence of a fossil record for echinoderm larvae, the evolution of these forms is a matter for after the fact speculations. Further studies may show how differences in larval feeding, swimming, and patterns of metamorphosis might be related to settling behavior and the feeding behavior of postmetamorphosis juveniles in each class.

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FOOTNOTES

[1] These current velocities, determined from movies, are what one might expect from the swimming rates. The horizontal swimming rates of *Parastichopus*, *Luidia*, *Pisaster*, *Ophiopholis*, *Dendraster*, *S. droebachiensis*, and *S. purpuratus* were all about 0.3 to 0.5 mm/sec or less at about 10 to 15°C. Some advanced echinoplutei with epaulettes or lobes specialized for locomotion could swim somewhat faster. Otherwise I could find no large difference between stages.

TABLE I

Species cultured

CLASS	ORDER	SPECIES
HOLOTHUROIDEA auricularia	Aspidochirotida	Parastichopus californicus (Stimpson)
ASTEROIDEA bipinnaria	Phanerozonida	Luidia foliolata Grube
	Spinulosida	Patiria miniata (Brandt)
	Forcipulatida	Evasterias troscheli (Stimpson) Pisaster ochraceus (Brandt) Pycnopodia helianthoides (Brandt)
OPHIUROIDEA ophiopluteus	Ophiurida	Ophiopholis aculeata (Linnaeus)
ECHINOIDEA echinopluteus	Echinoida	Allocentrotus fragilis (Jackson) Strongylocentrotus droebachiensis (O.F. Müller) S. franciscanus (A. Agassiz) S. pallidus (G. O. Sars) S. purpuratus (Stimpson)
	Clypeasteroida	Dendraster excentricus (Eschscholtz)
	Spatangoida	Brisaster latifrons (A. Agassiz)

TABLE II

Estimates of maximum clearance rates

Larva	Clearance Rate (µl/min)			Prior
	Mean	(range)	No. Obs.	Treatment
Parastichopus, auricularia				
0.7 to 0.8 mm	0.7	(0.4, 1.0)	6	B
0.7 to 0.9 mm	1.9	(0.4, 3.2)	15	B
0.85 to 1.1 mm	2.2	(1.4, 3.1	11	B
0.85 to 1.1 mm	1.8	(0.7, 3.0)	10	B
0.9 to 1.1 mm	2.8	(1.2, 4.3)	17	B
about 1 mm	3.5	(1.7, 5.6)	13	D
Luidia, bipinnaria				
0.75 to 0.9 mm	2.4	(0.9, 4.1)	15	B
1.6 to 1.8 mm, arms forming	2.4	(0.9, 6.6)	11	B
1.6 to 1.8 mm, arms forming	3.7	(1.5, 6.7)	8	A
2.5 to 3.0 mm. full size	7.1	(4.2, 11.7)	11	A
2.2 to 3.3 mm, full size	8.8	(6.0, 11.8)	10	A
Evasterias troscheli				
0.8 mm bipinnaria	1.5	(0.6, 2.4)	17	A
Pisaster, bipinnaria, brachiolaria				
0.9 to 1.0 mm	3.4	(2.9, 3.7)	10	B
1.5 mm	4.2	(2.9, 6.3)	5	B
1.85 to 2.2 mm, brachiolaria	3.4	(0.9, 4.6)	10	B
Ophiopholis, ophiopluteus				
4-arms, 0.3 mm o.h., 0.4 to 0.5 mm p.l.	1.1	(0.5, 1.4)	8	B
8-arms, 0.35 to 0.45 mm o.h., > 1 mm p.l.	1.8	(0.7, 3.4)	11	A
" 0.4 to 0.5 mm o.h. "	1.8	(1.0, 3.2)	16	A
" " "	2.0	(1.0, 4.4)	12	A
" " "	3.0	(1.9, 4.0)	9	A
" " "	7.0	(4.5, 9.7)	11	D
" " "	4.3	(0.7, 9.4)	13	C
Dendraster, echinopluteus				
4-arms, 0.3 mm o.h.	0.5	(0.2, 1.0)	10	B
8-arms, 0.4 mm o.h.	2.2	(1.9, 2.5)	5	B
8-arms, 0.4 mm o.h.	2.3	(2.1, 2.5)	2	A
S. droebachiensis, echinopluteus				
4-arms, 0.35 to 0.4 mm o.h.	1.5	(0.7, 2.6)	10	A
6-arms, 0.4 to 0.5 mm o.h.	2.1	(1.1, 2.9)	10	A
6- to 8-arms (pr.o. arms forming)	2.7	(1.8, 4.4)	5	A
8-arms, epaulettes forming	4.0	(1.6, 6.8)	12	B
8-arms, epaulettes, 0.5 to 0.6 mm o.h.	2.2	(1.3, 3.4)	15	A
8-arms, podia moving in amniotic cavity	3.5	(1.8, 4.4)	8	A

TABLE III

Reduction in clearance rates following exposure to high concentrations of the alga *Amphidinium*. Controls listed first for each comparison.

Larva	Clearance Rates (µl/min)	
	mean	range
Parastichopus		
advanced auricularia	2.2	1.4, 3.1
	0.6	0, 1.8
Luidia		
advanced bipinnaria	8.8	6.0, 11.8
	0.8	0, 1.5
Ophiopholis		
advanced ophiopluteus	1.8	0.3, 3.4
	0.9	0.2, 1.9
	3.0	1.9, 4.0
	0.4	0, 1.0
S. droebachiensis		
4-armed echinopluteus	1.5	0.7, 2.6
	0.6	0.1, 1.2
6-armed echinopluteus	2.1	1.1, 2.9
	0.4	0, 1.1
8-armed echinopluteus	3.5	1.8, 4.4
	0.4	0, 1.1

TABLE IV

Clearance rates on *Amphidinium* compared with rates on other algal species. Amp - *Amphidinium,* Cri - *Cricosphaera,* Cyc - *Cyclotella,* Tha - *Thalassiosira.*

Larva	Algae		Mean Clearance Rate (µl/min)	Significance
Parastichopus	Amp	(M)	0.3	+
auricularia, 0.8-0.9 mm	Cri		0.7	
Parastichopus	Amp	(M)	0.8	+
advanced auricularia	Cri		1.6	
Luidia	Amp	(M)	2.1	+
advanced bipinnaria	Cri		4.0	
Pisaster	Amp	(M)	0.9	+
bipinnaria, arms forming	Cri		2.2	
Ophiopholis	Amp	(M)	0.9	+
8-arm ophiopluteus	Cri		1.9	
Dendraster	Amp	(M)	0.5	+
8-arm echinopluteus	Cri		0.8	
S. droebachiensis	Amp	(M)	1.6	+
6-arm echinopluteus	Cri		2.3	
Parastichopus	Amp	(S)	1.2	+
advanced auricularia	Cri		2.3	
Pisaster	Amp	(S)	0.8	+
bipinnaria, brachiolaria	Cri		2.8	
Ophiopholis	Amp	(S)	1.1	+
8-arm ophiopluteus	Cri		4.0	
S. droebachiensis	Amp	(S)	2.0	+
6-arm, 8-arm echinopluteus	Cri		3.3	
Pisaster	Amp	(S)	0.8	+
bipinnaria, brachiolaria	Tha		2.2	
Ophiopholis	Amp	(S)	1.1	-
8-arm ophiopluteus	Tha		1.9	
S. droebachiensis	Amp	(S)	2.0	-
6-arm, 8-arm echinopluteus	Tha		2.6	
Parastichopus	Amp	(M)	1.4	-
advanced auricularia	Cyc		1.2	
Pisaster	Amp	(M)	1.0	-
bipinnaria, arms forming	Cyc		1.0	
Ophiopholis	Amp	(M)	4.4	+
8-arm ophiopluteus	Cyc		5.3	
S. droebachiensis	Amp	(M)	2.5	+
6-arm echinopluteus	Cyc		1.6	

TABLE V

Comparison of clearance rates on *Amphidinium* and *Ditylum* offered separately (S) or in mixture (M).

Larva	Clearance Rates (µl/min)		Comparisons	
	Algae	Mean	Algae	Significance
Ophiopholis	Amp (S)	2.9	Amp (S), Amp (M)	+
8-arm ophiopluteus	Amp (M)	0.5	Dit (S), Dit (M)	-
full size	Dit (S)	1.0	Amp (S), Dit (S)	+
	Dit (M)	1.3	Amp (M), Dit (M)	+ (+]
S. droebachiensis	Amp (S)	2.0	Amp (S), Amp (M)	+
8-arm achinopluteus	Amp (M)	1.1	Dit (S), Dit (M)	-
full size	Dit (S)	0.6	Amp (S), Dit (S)	+
	Dit (M)	0.8	Amp (M), Dit (M)	- (+)
Pisaster	Amp (S)	0.7	Amp (S), Amp (M)	-
bipinnaria	Amp (M)	0.7	Dit (S), Dit (M)	+
about 1.4 mm long	Dit (S)	0.6	Amp (S), Dit (S)	-
arms forming	Dit (M)	2.0	Amp (M), Dit (M)	+ (+)

TABLE VI

Clearance rates of several small marine suspension feeders

Animal	Maximum clearance ml/day	length mm	Reference
bivalve veligers			
Mytilus edulis	0.4 to 0.8	0.25	Bayne, 1965
Ostrea edulis	0.4 to 0.6	0.25	Walne, 1956
			Jørgensen, 1943
bryozoan			
Zoobotryon verticillatum	9 to 25	< 1	Bullivant, 1968a
small marine copepods		≤ 1, cephalothorax	
Acartia tonsa	10 to 25		Conover, 1956
Centropages hamatus	15		Marshall & Orr, 1962
Temora longicornis	27		Berner, 1962
"	150		Cushing, 1958
Echinoderm larvae (fully developed)			
Luidia foliolata	12 to 25	2 to 3	
others	4 to 8	≤ 1	
"	6 to 12	≤ 1	

FIGURE 1. Sagittal section to one side of the midline of the ophiopluteus of Ophiopholis aculeata. The body wall of the circumoral and aboral fields and buccal cavity consists of a single layer of cells about 1 to 3 μ thick. The cells of the ciliated band are columnar. Dark spots in the band are nuclei.

FIGURE 2. Sagittal section of the oral region of the bipinnaria of Patiria miniata to one side of the midline.

FIGURE 3. Section across an arm and the ciliated band of the brachiolaria of Pisaster ochraceus. The ciliated band on the arm is less distinct.

ad b- - adoral band, bc- - buccal cavity, cil b- - ciliated band, cf- - circumoral field, es l- - esophageal loop, m- - microvilli of intestine, ptb- - postoral transverse band, prtb- - preoral transverse band, s- - secretory cell in anterolateral arm, sp- - suboral pocket

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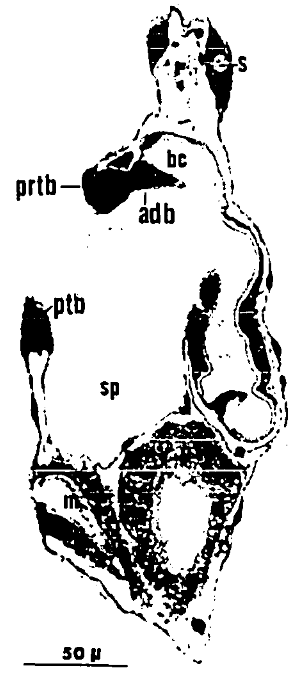
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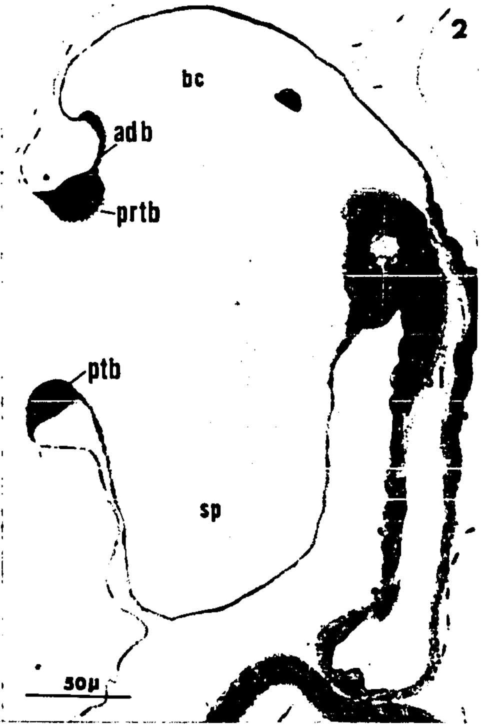
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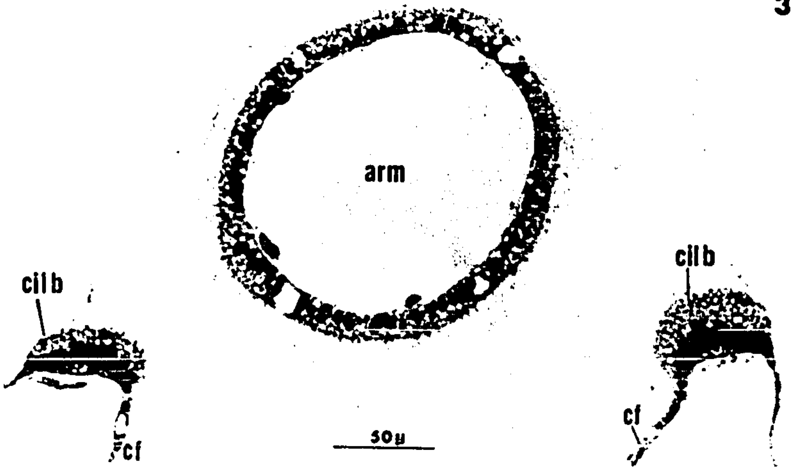
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FIGURE 4. Lateral view of the eight-armed echinopluteus of *Strongylocentrotus franciscanus*. Arrow indicates motion of preoral arm when anterior dilator contacts.

FIGURE 5. Protargol-impregnated whole mount of the circumoral field of the postoral arm of the echinopluteus of *Strongylocentrotus droebachiensis*, demonstrating one cilium per cell. There is one cilium and basal body within each cell boundary.

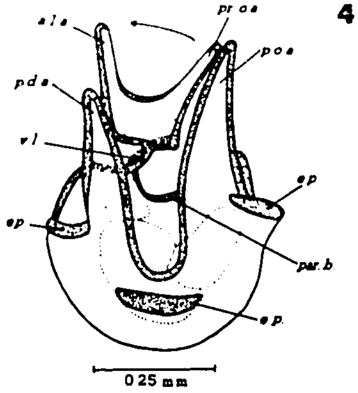
FIGURE 6. Section tangential to the postoral transverse band of *Luidia foliolata*. The distal part of each cell includes the base of only one cilium. The density of cilia (middle) appears slightly greater than the density of nuclei (left) because the cells of the band are packed together with the nuclei two layers deep. Secretory cells are visible on the outer edge of the band (far right).

FIGURE 7. Ciliated band on the postoral arm of *Strongylocentrotus droebachiensis*. Beating cilia photographed with phase contrast and electronic flash (photo by Ann James Frazier).

FIGURE 8. Beating cilia of the posterior epaulette of *S. droebachiensis*. Forward beat with hook-shaped recovery stroke.

FIGURE 9. Beating cilia of the posterior epaulette of *S. droebachiensis*. Reversed beat with hook-shaped recovery stroke.

a. l. a. - - anterolateral arm, ep. - - epaulette, par. b. - - paroral band, p. d. a. - - posterodorsal arm, p. o. a. - - postoral arm, pr. o. a. - - preoral arm, v. l. - - ventral loop of ciliated band on side of oral hood.



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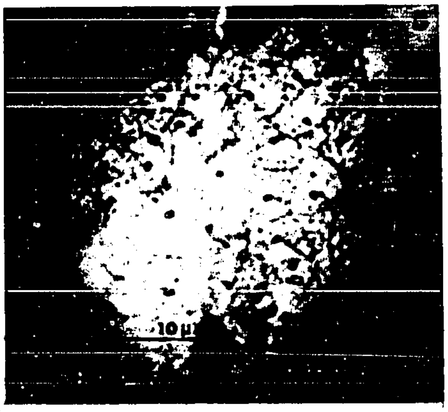

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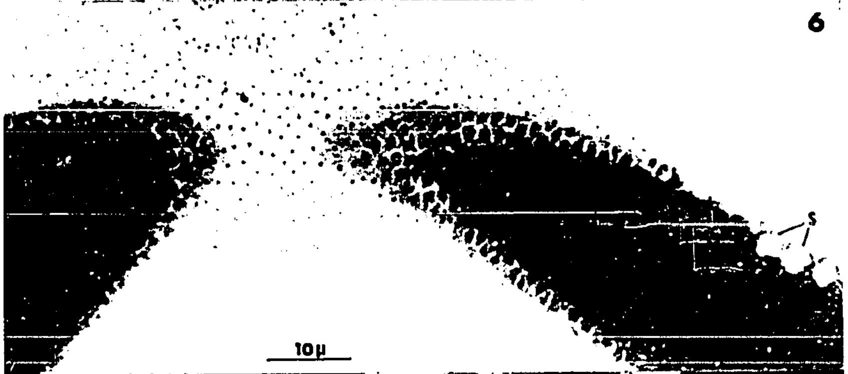


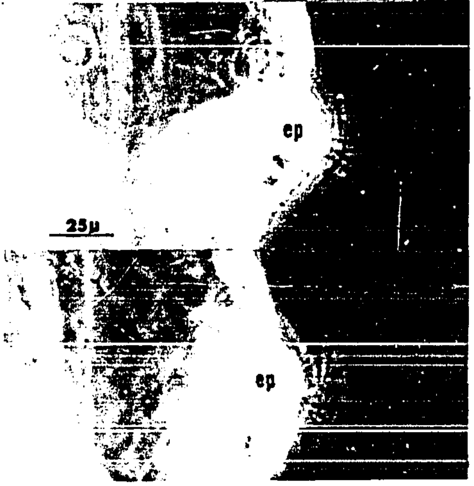
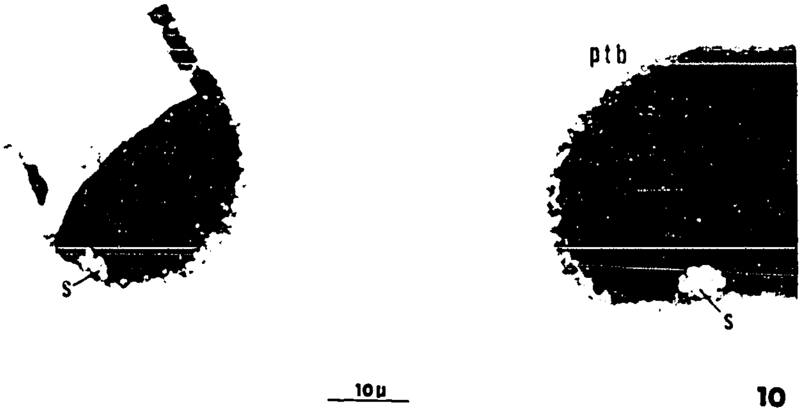


FIGURE 10. Secretory cells along the outer edge of the ciliated band of the bipinnaria of *Luidia foliolata*. Section tangential to postoral transverse portion of the ciliated band and across dorsal portion of the ciliated band.

FIGURE 11. Secretory cells at the posterior end of the brachiolaria of *Pisaster ochraceus*. The smaller type of secretory cell of Fig. 10 is also present here.

FIGURE 12. Secretory cells of the adhesive disk of the brachiolaria of *Pisaster ochraceus*. Each cell appears to extend the entire thickness of the disk. The outer surface of the disk is at the upper edge of the figure.

ptb- - postoral transverse band, s- - small secretory cell,
S- - large secretory cell.



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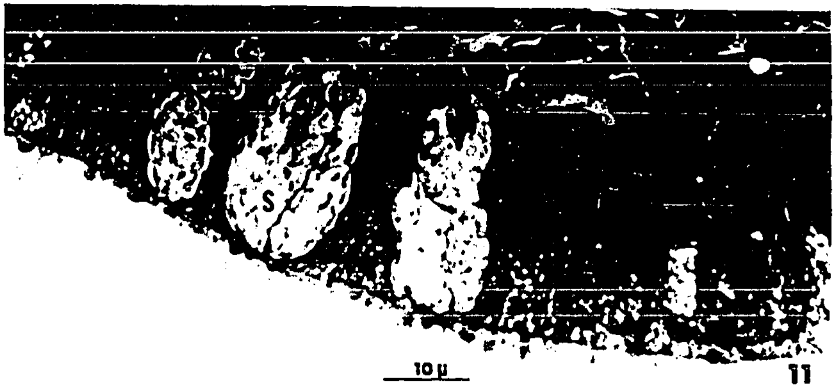

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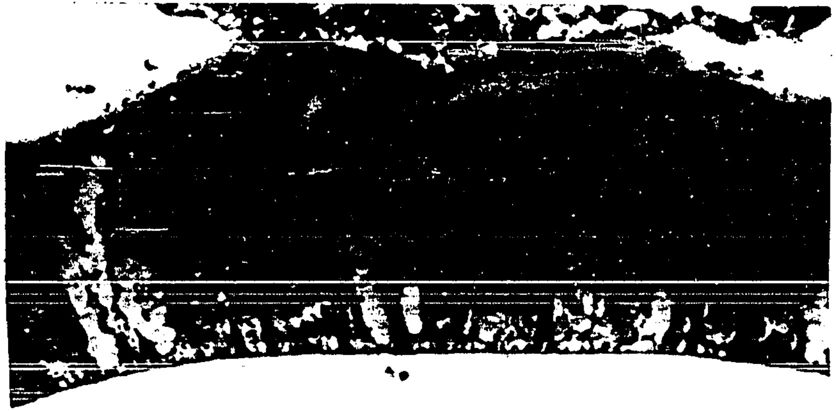

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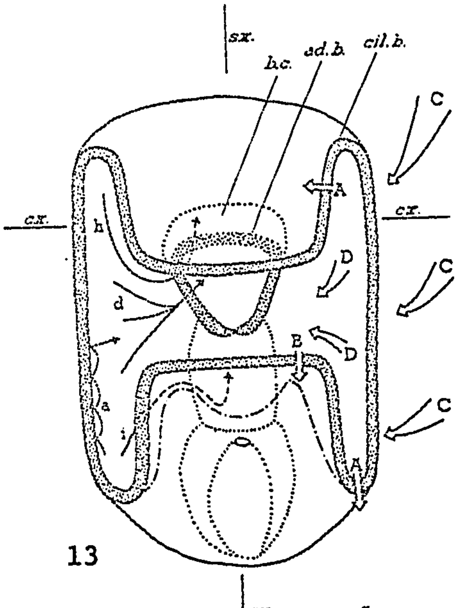
FIGURES 13, 14, 15. Generalized diagrams illustrating the common aspects of the feeding mechanisms of the four types of echinoderm larvae. Figure 13 is a ventral view. Figure 14 is a sagittal section in the plane marked sx in Figure 13. Figure 15 is a cross section at the level of the upper buccal cavity (marked cx in Figure 13).

Open arrows marked by capital letters are water currents. Arrows with single line marked by small letters are particle paths. Particle paths behind structures are marked by a dashed line. The gut and portions of the adoral band behind other structures are marked by a dotted line. The depth of the groove of the circumoral field and suboral pocket is indicated by a dot-dash line where they are behind other structures.

ad.b. - - adoral band, a.s. - - anal sphincter, b.c. - - buccal cavity, c.s. - - cardiac sphincter, cil.b. - - ciliated band, es. - - esophagus, int. - - intestine, l.ad.b. - - lower adoral band, l.st. - - lower stomach, p.s. - - pyloric sphincter, p.t.b. - - postoral transverse band, pr.t.b. - - preoral transverse band, s.o.p. - suboral pocket, u.ad.b. - - upper adoral band, u.st. - - upper stomach.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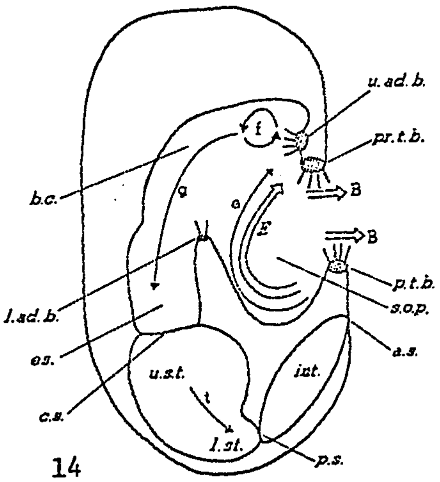
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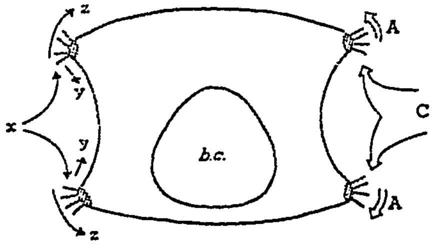
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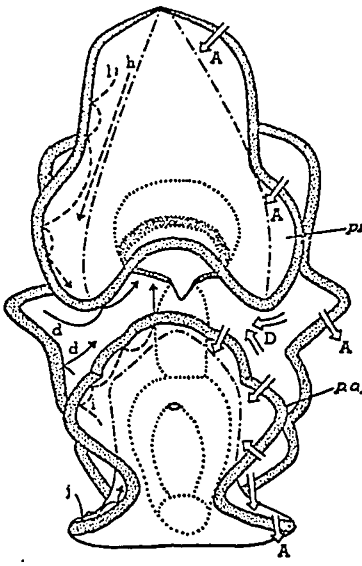
FIGURES 16, 17, 18, 19, 20. Diagrams of feeding of the auricularia of Parastichopus californicus. Figures 16, 17, 18 and 20 are ventral, dorsal, lateral, and anterior views respectively. Figure 19 is a sagittal section in the plane marked sx in Figure 17, showing currents in the oral region with portions of the bands and circumoral field out of the plane of section also indicated (dotted line).

FIGURES 21, 22, 23. Ventral, lateral, and anterior views illustrating feeding of a bipinnaria, based on Patiria miniata but similar to earlier stages of all asteroid species studied here.

Open arrows marked by capital letters are water currents. Arrows with single line marked by small letters are particle paths. Particle paths behind structures are marked by a dashed line. The gut and portions of the adoral band behind other structures are marked by a dotted line. The depth of the groove of the circumoral field is indicated by a dot-dash line where it is behind other structures.

a.d.p. - - anterodorsal process, b.c. - - buccal cavity, es. - - esophagus, m.d.p. - - mid-dorsal process, p.d.p. - - posterodorsal process, p.l.p. - - posterolateral process, p.o.p. - - postoral process, pr.o.p. - - preoral process, p.t.b. - - postoral transverse band, pr.t.b. - - preoral transverse band, s.o.p. - - suboral pocket



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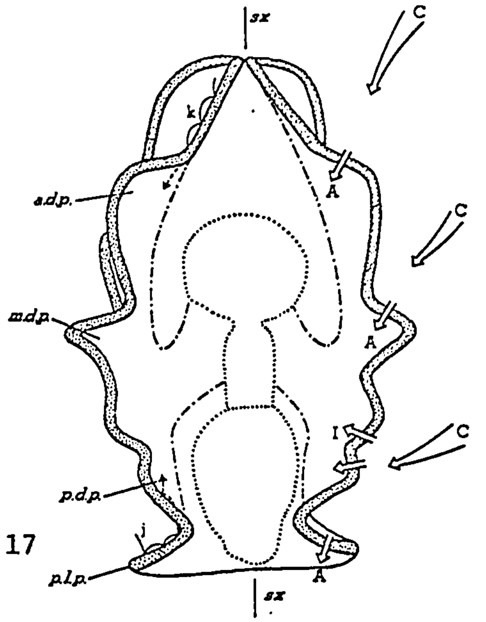

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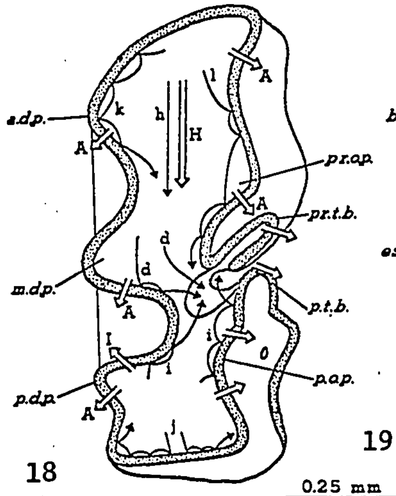

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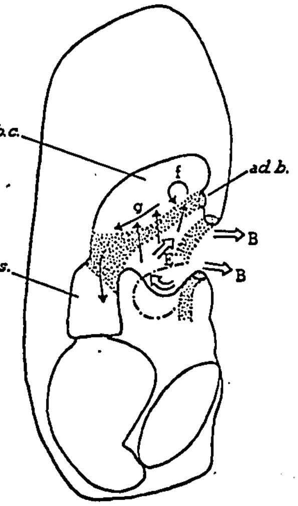
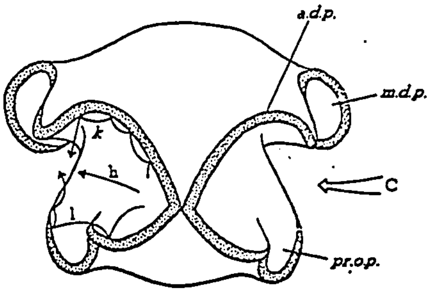
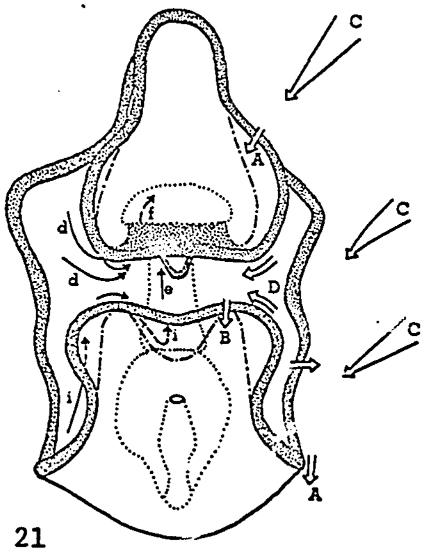


19

0.25 mm

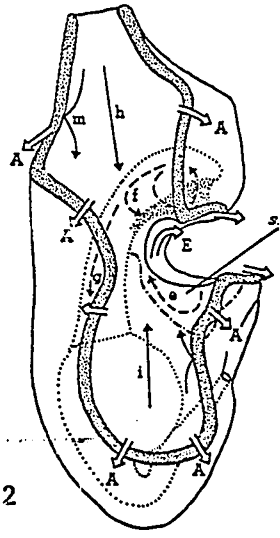


20

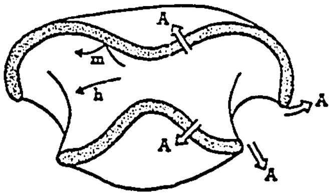


21

0.25 mm



22



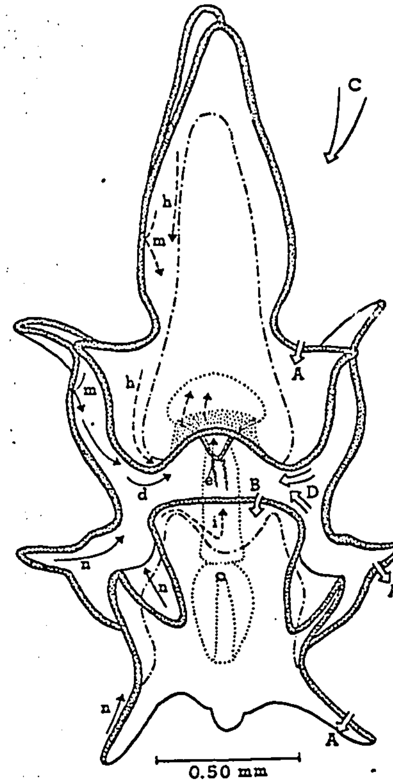
23

FIGURES 24, 25. Ventral and lateral views of the bipinnaria of *Luidia foliolata* illustrating feeding.

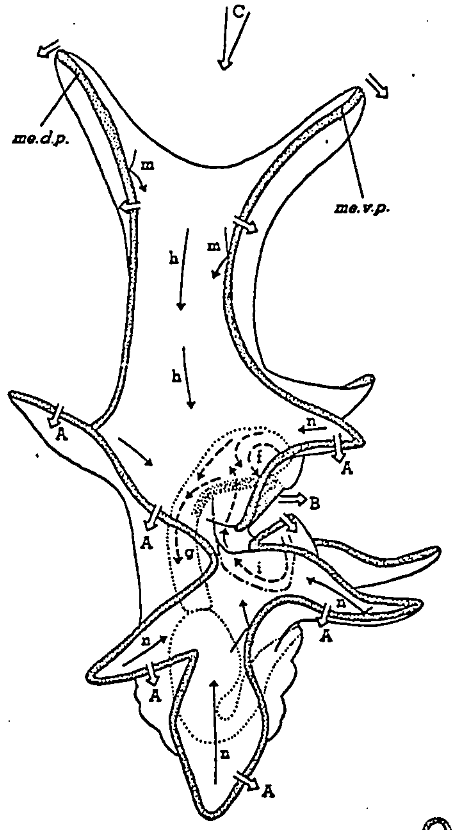
FIGURES 26, 27, 28. Ventral, lateral, and anterior views of the brachiolaria of *Pisaster ochraceus*, illustrating feeding.

Open arrows marked by capital letters are water currents. Arrows with single line marked by small letters are particle paths. Particle paths behind structures are marked by a dashed line. The gut and portions of the adoral band behind other structures are marked by a dotted line. The depth of the groove of the circumoral field and suboral pocket is indicated by a dot-dash line where they are behind other structures.

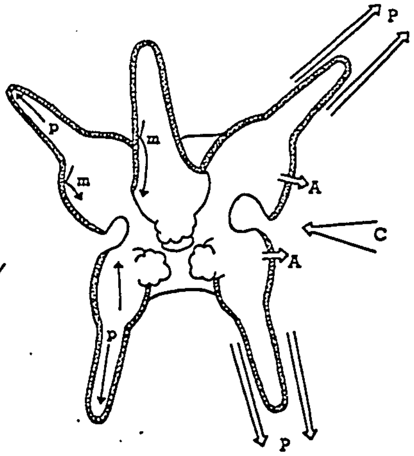
a. d. a. - - anterodorsal arm, *adh.* - - adhesive disk, *br.* - - brachiolar arm, *me. d. a.* - - median dorsal arm, *me. d. p.* - - median dorsal process, *me. v. p.* - - median ventral process, *p. d. a.* - - posterodorsal arm, *p. l. a.* - - posterolateral arm, *p. o. a.* - - postoral arm, *pr. o. a.* - - preoral arm


C
C
C
h
m
h
m
A
B
D
d
e
i
n
n
n
A
A
0.50 mm

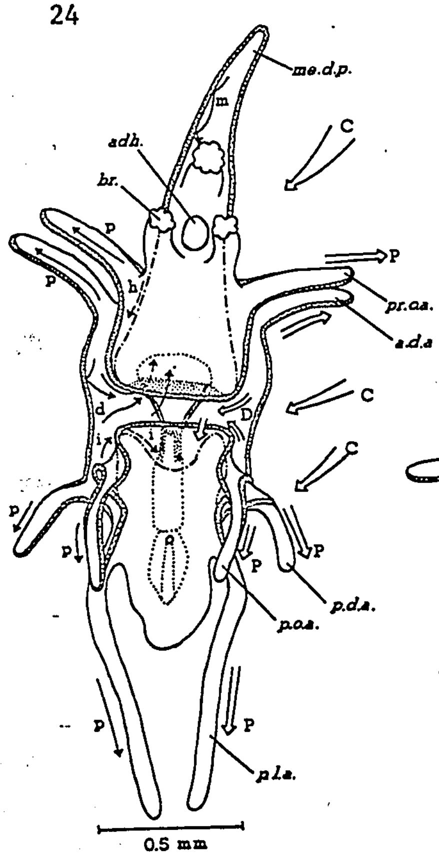
24


C
me.d.p.
me.v.p.
m
m
h
h
n
f
A
B
A
A
g
i
n
n
n
A
A
n
A

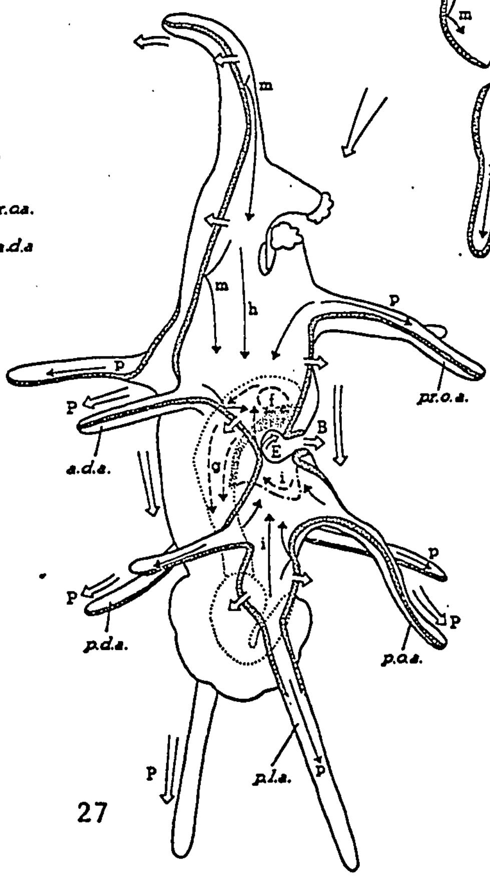
25


P
P
p
m
m
A
C
A
p
P

28


me.d.p.
m
C
adh.
br.
p
p
h
P
pr.o.a.
a.d.a
C
d
D
C
i
i
p
p
P
P
p.d.a.
p.o.a.
p
P
p.l.a.
0.5 mm

26

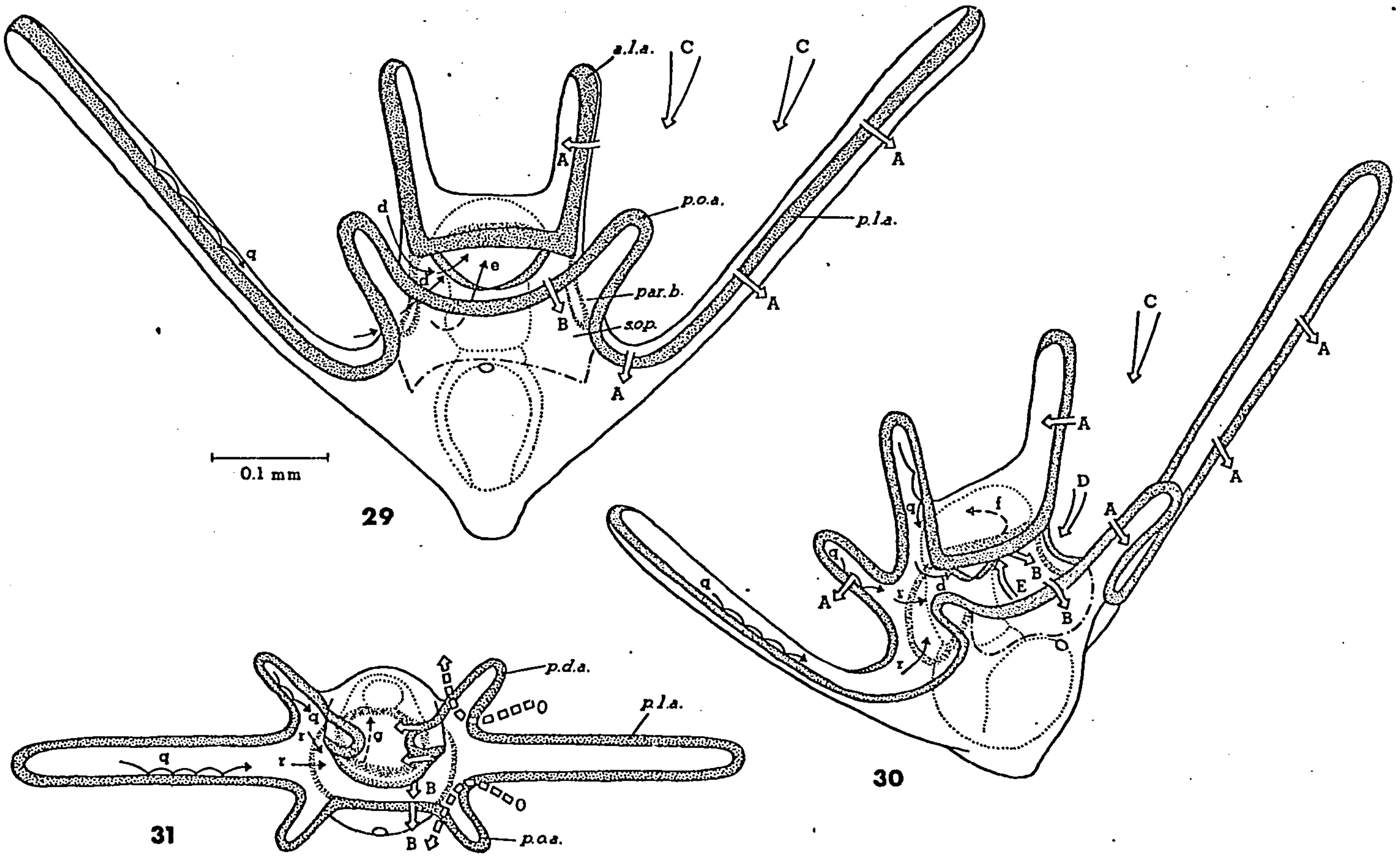

m
m
h
p
p
pr.o.a.
P
f
B
a.d.a.
E
g
i
i
p
P
P
p.d.a.
p.o.a.
P
p.l.a.
P

27

FIGURES 29, 30, 31. Ventral, ventro-lateral, and anterior views of the ophiopluteus of Ophiopholis aculeata, with eight arms but not fully developed, illustrating feeding.

The open, dashed arrow marked 0 is the exaggerated horizontal current path when the larva has swum up against the surface or a coverglass. Open arrows marked by capital letters are water currents. Arrows with single line marked by small letters are particle paths. Particle paths behind structures are marked by a dashed line. The gut and portions of the adoral band behind other structures are marked by a dotted line. The depth of the suboral pocket is indicated by a dot-dash line where it is behind other structures.

a. l. a. - - anterolateral arm, par. b. - - paroral band, p. d. a. - - posterodorsal arm, p. l. a. - - posterolateral arm, p. o. a. - - postoral arm, s. o. p. - - suboral pocket


a.l.a.
C
C
A
A
p.o.a.
p.l.a.
d
q
d
e
par.b.
B
sop.
A
A
0.1 mm
C
A
A
A
D
A
f
q
d
A
r
d
B
E
B
r
q
p.d.a.
p.l.a.
q
g
r
r
B
B
p.a.a.

29

30

31

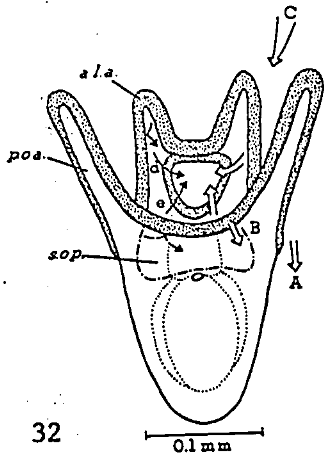
FIGURES 32, 33, 34. Ventral, anterolateral, and anterior views illustrating feeding of the four-armed echinopluteus of Dendraster excentricus.

FIGURES 35, 36, 37. Ventral, anterolateral, and anterior views illustrating feeding of the eight-armed echinopluteus of Dendraster excentricus.

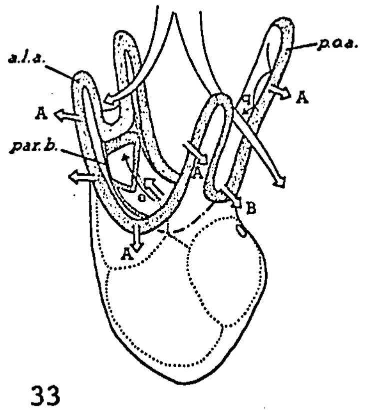
FIGURE 38. Ventral view illustrating aspects of particle and water movement near an eight-armed echinopluteus, based on Strongylocentrotus purpuratus but similar to the other strongylocentrotids.

The open dashed arrow marked 0 is the exaggerated horizontal current path when the larva has swum up against the surface or a coverglass. Open arrows marked by capital letters are water curreents. Arrows with single line marked by small letters are particle paths. Particle paths behind structures are marked by a dashed line. The gut and portions of the adoral band behind other structures are marked by a dotted line. The depth of the groove of the circumoral field and sub-oral pocket is indicated by a dot-dashed line when they are behind other structures.

a.l.a. - - anterolateral arm, ep. - - epaulette, par.b. - - paroral band, p.d.a. - - posterodorsal arm, p.o.a. - - postoral arm, pr.o.a. - - preoral arm, s.o.p. - - suboral pocket



32



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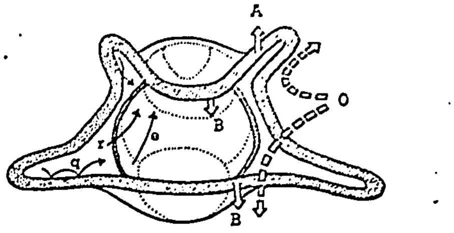

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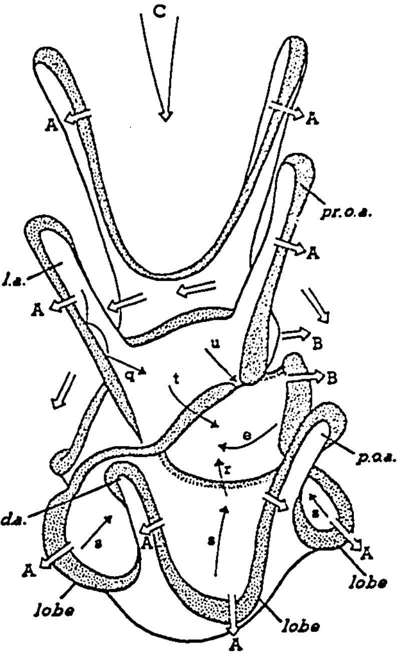
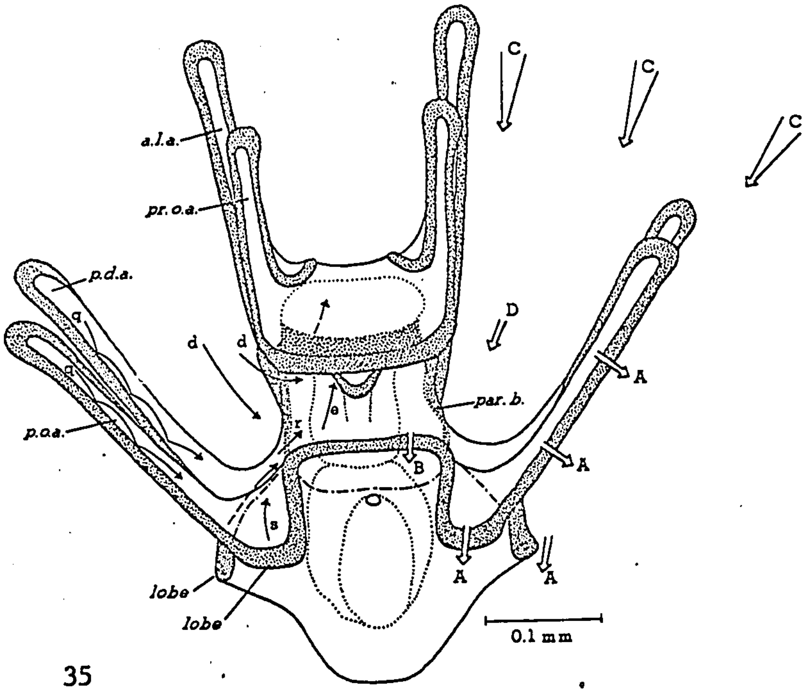


36



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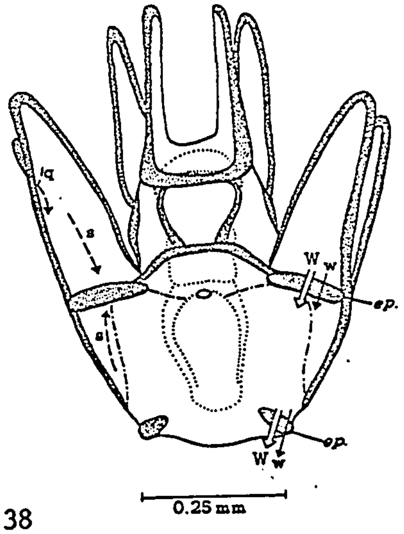

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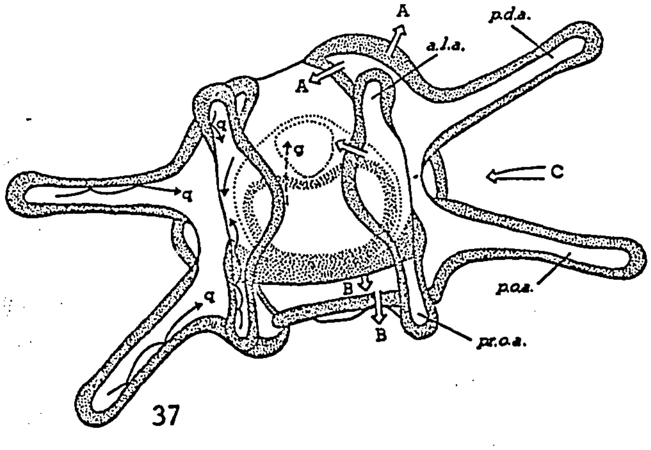


37

FIGURE 39. Rejection from the buccal cavity and esophagus of the auricularia of *Parastichopus californicus*, lateral view. (For relation to the whole larva see Figures 18, 19.) Only a few of the muscle strands are indicated. Larvae of the other classes exhibit similar types of rejection.

FIGURE 40. Particle movement in the oral region of the auricularia of *Parastichopus californicus* during reversal of ciliary beat along the ciliated band.

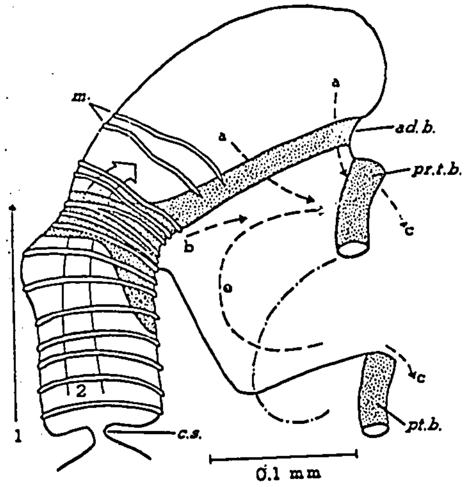
FIGURES 41, 42. Dorsal flexion of the earlier stage bipinnaria of *Patiria miniata* and the advanced bipinnaria of *Luidia foliolata*. The oral region is opened aiding rejection, and the changed orientation of the ciliated band results in turning. Compare with Figures 22 and 25.

FIGURE 43. Movement of the larval arms of the brachiolaria of *Pisaster ochraceus* to an anteriorly directed position for stopping and backing. Compare with Figure 26.

FIGURE 44. Position of the anterior dilator muscles of the ophiopluteus of *Ophiopholis aculeata* when relaxed.

FIGURE 45. Effect of contraction of the anterior dilator muscles of an ophiopluteus.

ad.b. - - adoral band, *a.di.* - - anterior dilator muscle, *a.l.a.* - - anterolateral arm, *c.s.* - - cardiac sphincter, *m.* - - muscles, *pr.t.b.* - - preoral transverse band, *p.t.b.* - - postoral transverse band



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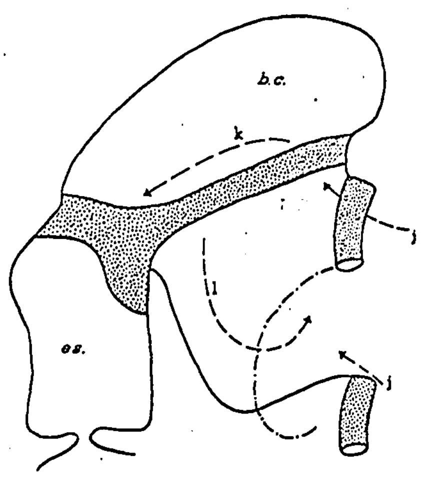
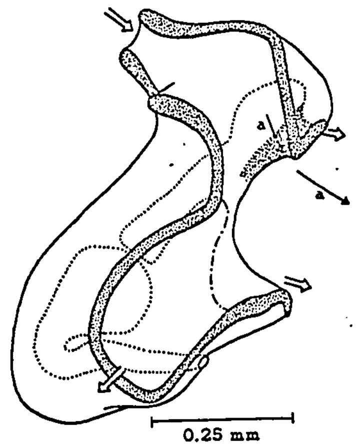


40



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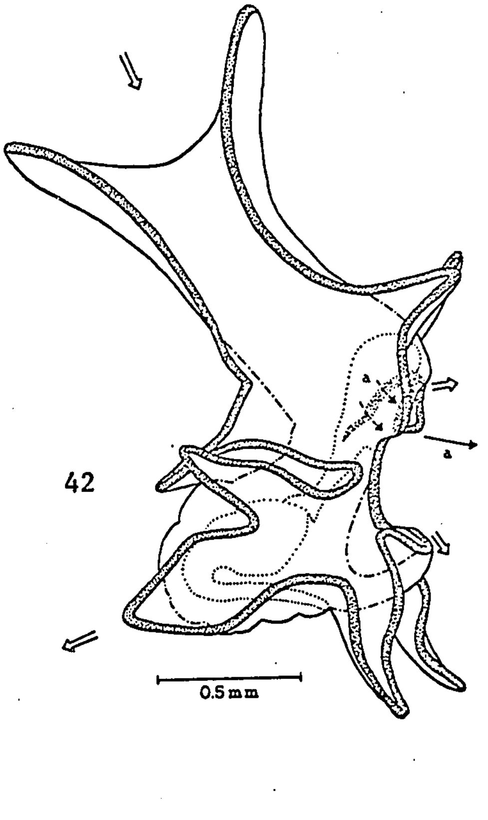

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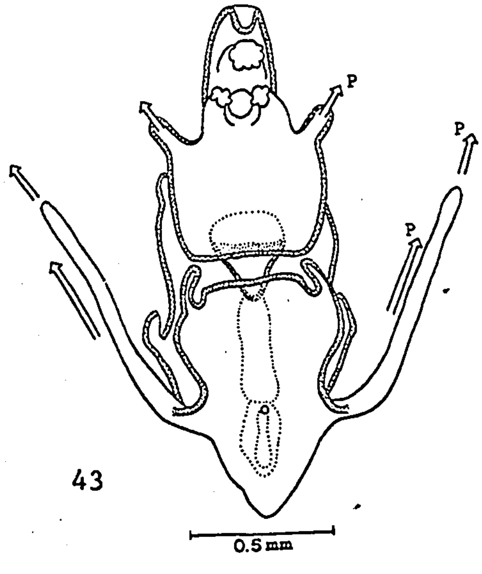
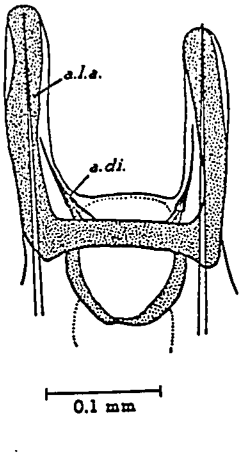


43



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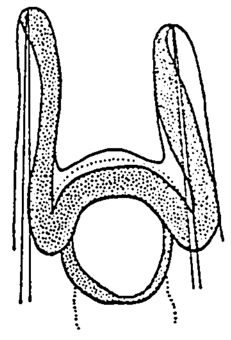
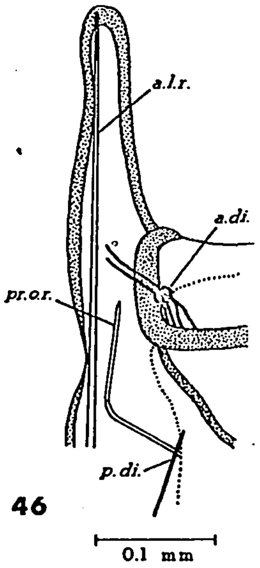


45

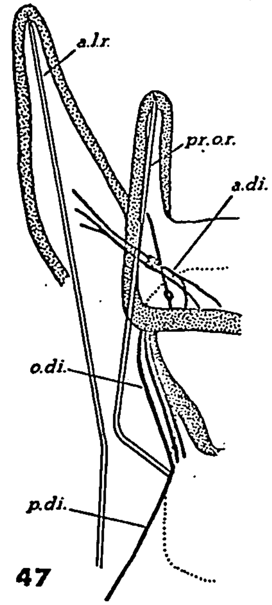
FIGURES 46, 47. Dilator muscles of six- and eight-armed echinoplutei of Strongylocentrotus droebachiensis.

FIGURE 48. Effect of simultaneous contraction of posterior and anterior dilator muscles in late six-armed stage echinopluteus of Allocentrotus fragilis, mouth viewed from dorsal side.

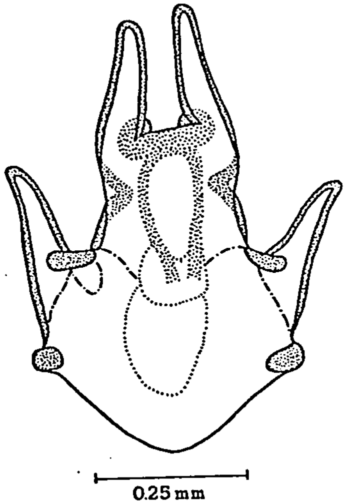
a. di. - - anterior dilator, a. l. r. - - anterolateral rod, o. di. - - muscles possibly opposing dilator muscles, p. di. - - posterior dilator, pr. o. r. - - preoral rod



46



47



48

FIGURE 49. Relation between clearance rates (measured with Amphidinium) and length of the ciliated band in larvae of four classes at several stages of development. Traces of the band on the arms of Pisaster larvae were not included in the measurement.

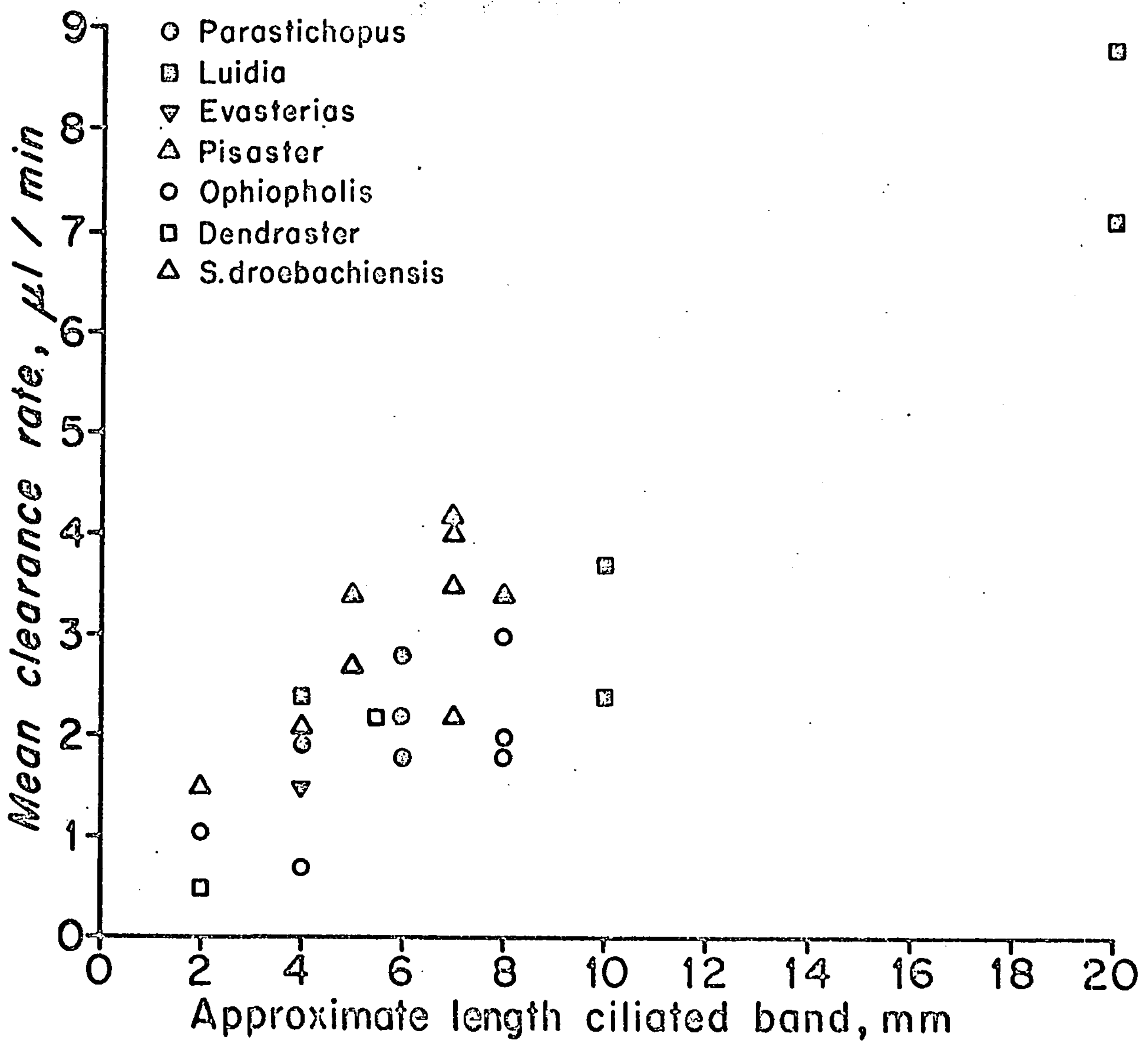

Parastichopus
Luidia
Evasterias
Pisaster
Ophiopholis
Dendraster
S. droebachiensis
Mean clearance rate, μl / min
0
1
2
3
4
5
6
7
8
9
0
2
4
6
8
10
12
14
16
18
20
Approximate length ciliated band, mm

FIGURE 50. Relation between clearance and ingestion rates and the concentration of algae. Eleven to nineteen observations at each concentration for each species.

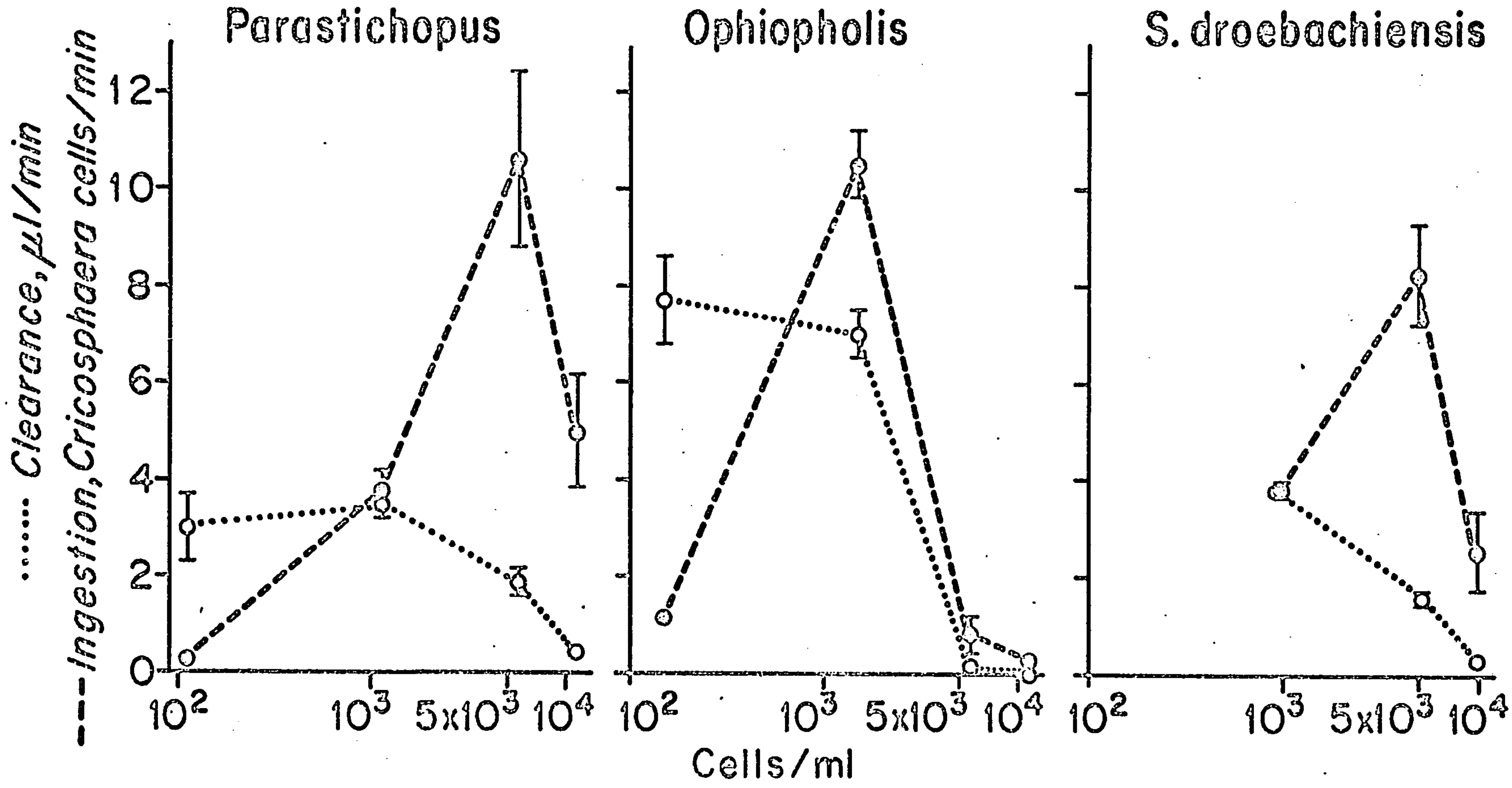
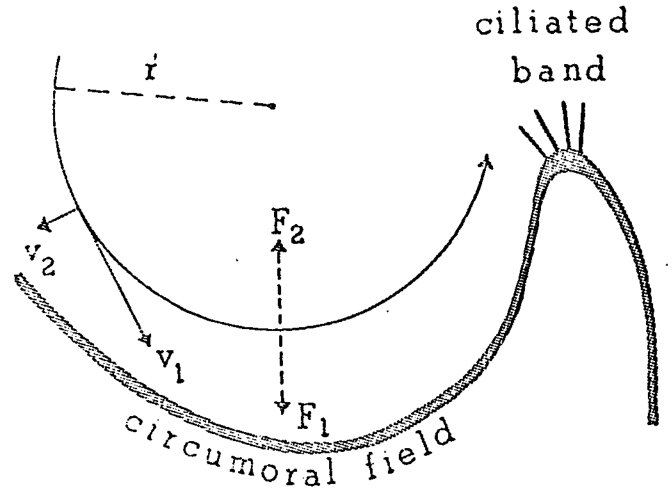
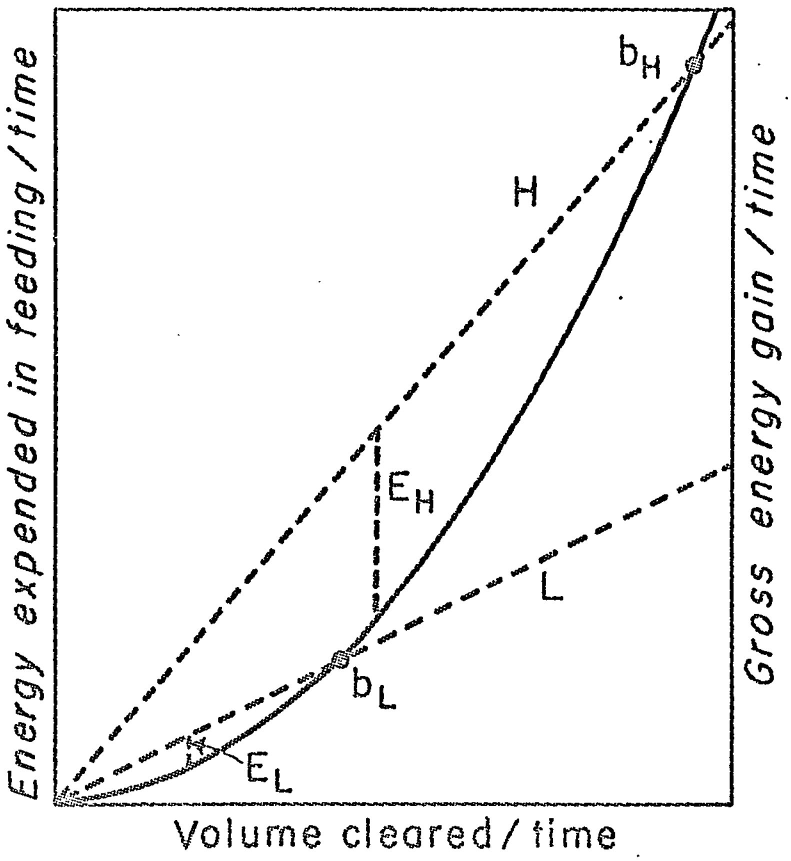

Parastichopus
Ophiopholis
S. droebachiensis
...... Clearance, μl/min
--- Ingestion, Cricosphaera cells/min
0
2
4
6
8
10
12
10²
10³
5x10³
10⁴
Cells/ml

FIGURE 51. Centrifugal model for concentration of particles.

FIGURE 52. Optimization of clearance rates when energy expended in feeding is assumed proportional to the square of the clearance rate and assimilation efficiency is constant. Solid line is energy expended in feeding. Dashed lines, L and H, are energy gained at low and high concentrations of food. The intersections, b_L and b_H are break even points at low and high concentrations. C_L and C_H are the optimum clearance rates at low and high concentrations. The vertical dashed lines, E_L and E_H are the maximum net rate of energy gain at the optimal clearance rates at low and high concentrations.


ciliated
band
r
F_2
F_1
v_2
v_1
circumoral field

51


b_H
H
E_H
L
b_L
E_L
Energy expended in feeding / time
Gross energy gain / time
Volume cleared / time

52