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THE METHOD OF FEEDING OF TUNICATES

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Introduction

This, the second of a series of papers (MacGinitie, 1939) on the feeding mechanisms of marine invertebrates, deals with the method of feeding in three tunicates, namely, *Ciona intestinalis* (Linn.), *Ascidia californica* Ritter and Forsyth, and *Diplosoma pizoni* Ritter and Forsyth. The first two are simple ascidians and the latter is a colonial form. Since both simple and colonial forms have been investigated, I feel that it is fairly safe to state that the method described below is typical of all ascidians.

Young specimens of *Ciona intestinalis* and of *Ascidia californica,* especially those which have been reared in the laboratory, are quite transparent, and the observations here recorded were made upon animals which were in no way disturbed while they were carrying on their natural feeding activities. The same can be said of *Diplosoma pizoni,* as the matrix of the colony is perfectly clear and transparent. All observations were made upon undisturbed individuals of the colony.

Mechanism for Feeding

The structures which are strictly connected with the feeding activities of tunicates are the endostyle with its mucous glands, the peripharyngeal grooves, the dorsal groove, the stigmata, the esophagus, and the cilia lining all grooves, bars and the inner edges of the stigmata. The pharynx or branchial basket has been too well described in textbooks of zoology to make it necessary to redescribe it here. A current of water is maintained through the branchial cavity almost continually, whether the animal is feeding or not. The only time that the current is stopped is when the animals are left exposed by the tide or when they have been disturbed by some outside stimulus, and at such times the oral aperture and atriopore are usually closed.

The cilia lining the stigmata and the branchial basket may be divided into two groups, each group having a particular function. Those lining the stigmata have the function of maintaining the current of water, while those on the inner surface of the branchial bars and in the endo-

style, the peripharyngeal grooves and dorsal groove have the function of moving mucus.

Food and the Method of Feeding

The endostyle is richly supplied with mucous glands, and when a tunicate starts to feed it begins to secrete mucus throughout the length of the endostyle. This mucus is moved by the cilia of the branchial bars around the branchial basket in two sheets, one on either side. When the edges of the mucous sheets arrive at the dorsal groove, they are taken up by it and formed into a thread, and this string is passed posteriorly along the dorsal groove to the esophagus. The function of the peripharyngeal grooves is to hold and move the oral ends of the two mucous sheets.

The water entering the branchial basket through the oral funnel passes into the atrial cavity through the stigmata in all directions with the exception of the region of the endostyle and dorsal groove, and when the animal is feeding such water must also pass through the sheet of mucus which covers the interior of the basket. This mucus intercepts and entangles all solid material entering with the water, and such material comprises the food of tunicates. On rocky shores it consists almost entirely of plankton, often greatly enriched by algal spores from seaweeds. Within the estuaries it consists largely of material in suspension, mainly stirred-up detritus from the shores and bottom. During the summer season in Southern California this detritus in suspension is usually enriched by one or more species of dinoflagellates.

While a tunicate is feeding mucus is constantly being secreted, and the mucous sheets covering the inner walls of the branchial basket move continuously from the endostyle toward the dorsal groove. Hence, while the tunicate is feeding, the food-laden thread of mucus enters the esophagus in an unbroken string. As it enters the stomach this mucous string is folded back and forth and remains intact for some time. It is only that portion near the pyloric valve that coalesces and becomes semi-liquid as it passes into the intestine.

Although the cilia of the stigmata and branchial basket beat almost continuously, the mucous sheets are formed discontinuously. Upon the least disturbance the animals will cut off the secretion at the endostyle, and the remnants of the mucous sheets will continue to pass around to the dorsal side until the ends reach the dorsal groove. From then on until the animal begins to feed again the branchial basket is practically free of mucus. When a tunicate is not feeding, small particles may be seen to pass readily through the stigmata into the atrium and out with the atrial current.

If material which is foreign to the usual run of food material is introduced into the current of water entering the oral funnel, feeding will cease at once, and the undesirable material will be quickly forced from the branchial basket by a quick contraction of the body wall. The current will be renewed immediately, and, if no further undesirable material is taken in, feeding will soon be resumed. If the stimulus from the introduced material is rather strong the animal will cease feeding and will forcibly eject what water is in the branchial basket and atrium, and will remain closed for a considerable length of time, depending upon the strength of the stimulus.

In tunicates there is a ring of tentacles which interlace across the oral funnel which prevents the entrance of large particles. Such large particles as do find their way into the branchial basket are not incorporated in the mucus, but are in some way dropped from it into the branchial basket, and at intervals are forcibly ejected from the oral funnel by a sudden contraction of the body wall of the tunicate.

It is characteristic of animals which use mucus to entrap their food that they are able to drop from such mucus at least a portion of the undesirable material which is entrapped. Just how this is accomplished is not at present clear. It may be that the cilia which move the mucus can, by pressing outward through the mucus cause such particles to drop out. Many animals have specialized regions where the cilia perform this function. In the tunicates it is the cilia bordering the dorsal groove, in the pelecypods (future paper) it is the cilia of the lower edge of the gills and those of the labial palps, and in the echiuroid *Urechis* it is the outer cilia bordering the proboscis. In such regions the cilia are usually considerably larger than elsewhere.

When large particles strike the tentacles of the oral funnel they are usually blown away by a quick contraction of the mantle wall with little cessation of the feeding current. As most single tunicates hang vertically with the osteum downward one ejection movement serves to remove the large object. But, because of the separate action of individuals of a colony, a particle upon the surface of a colonial form which is fairly level may be bounced over the surface for some time before it is carried away by currents or is rolled over the edge. Since there is a constant current out of the atriopore (which in colonial forms may be common to several individuals), no particles find their way into the atrium and no tentacles are necessary, for if the current is stopped the atriopore closes.

As has been stated above, the cilia beat almost continually, and normally when the tunicate is not feeding most of the solid particles pass through the stigmata and out the atriopore. However, even when the

branchial basket is not lined with the mucous sheets, some of the solid particles may find lodgment upon the ciliary tracts lining the branchial basket (particularly those of the endostyle, peripharyngeal grooves and dorsal groove), and will follow more or less the definite tracts. This is especially true of specimens that are handled or cut open, since they may secrete mucus along these grooves, whereas normally they would not do so. The mucus which carries such particles as are transported along these ciliary tracts may enter the esophagus or may be dropped into the branchial basket and be ejected through the oral funnel. The more or less abnormal performance just described has led to the erroneous ideas found in textbooks about the feeding of tunicates.

Ciliary Action

The ciliary action of *Ascidia californica* was studied in detail. The oral aperture, the atriopore, the cilia of the basket, and the cilia of the stigmata may all function independently of each other or they may all function together. The cilia of the stigmata may be stopped without stopping those of the basket. When the cilia of the stigmata cease vibrating they lie down against the edges of the openings, leaving the stigmata wide open. However, when the animal is contracted the edges of the stigmata are approximated and the openings closed. At such times, of course, the cilia are still and lie flat against the sides of the openings.

After the cilia have been stopped they resume their beating by starting to vibrate in a small circle at the center of the stigmatal opening, and this ring spreads towards either end of the opening until all are again beating. The beating cilia surrounding a stigmata remind one of an elongated wheel organ of a rotifer or a veliger larva. In the ascidian investigated the apparent movement was in an anti-clockwise direction as viewed from the outside.

There is no doubt that the cilia of the branchial bars, ridges and grooves actually hold and move mucus. The cilia seem partially to enter the sheet of mucus and force it forward. During part of the beat the cilia are more or less hooked into the mucus and this serves to hold it so that the cilia following are able to penetrate and in turn do their share of pushing and holding. This action of the cilia is further evidenced by the fact that the mucous sheet which is present on the inside of the basket when the animal is feeding has in it waves which correspond to the wave motion of the cilia. These waves in the mucus appear when water heavily laden with food is introduced into the oral funnel. As the food material collects in the mucous sheet it sometimes

appears in streaks which are more accentuated as the mucus nears the dorsal groove.

Summary

1. The feeding method of *Ciona intestinalis* and *Ascidia californica* (simple ascidians), and of *Diplosoma pizoni* (a colonial form) was investigated.

2. Tunicates feed by straining the solid material from a current of water as it passes through a thin film of mucus lining the branchial basket.

3. The mucus is constantly secreted at the endostyle and is continually moved to the dorsal groove in two sheets which line the interior of the basket. The dorsal groove forms the edges of the food-laden sheets into a thread which is passed posteriorly to the esophagus and enters it in an unbroken string. The peripharyngeal grooves serve to hold the anterior ends of the mucous sheets and move them around to the dorsal groove.

4. When a tunicate is not feeding, the inside of the branchial basket is not lined with mucus, and the solid materials pass out with the atrial current.

5. Some sorting is carried out by the cilia of the dorsal ridges. The cilia which line the openings of the stigmata, and whose vibration creates the current of water passing through the basket, may be stopped without stopping the cilia lining the basket or without closure of the oral aperture and atriopore.

6. After the cilia lining the stigmata have been stopped they commence to beat in what appears to be a ring at the center of the opening. The cilia of one side of a stigmata are in perfect synchronism with those of the opposite side of the opening, and, by the continual inclusion of other cilia, all finally vibrate and resemble somewhat an elongated wheel organ of a rotifer.

LITERATURE CITED

MacGinitie, G. E., 1939. The method of feeding of Chaetopterus. *Biol. Bull.*, **77**: 115.