

(From the Dept. of Zoology, Bristol University.)

On the Mechanism of Movement of Food Vacuoles in Peritrich Ciliates.

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With 3 figures in the text.

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Introduction.

This paper is the result of an attempt to investigate the mechanism of movement of food vacuoles inside peritrich ciliates. It was known already that in many ciliates the food vacuoles follow a more or less determined course. This movement of food vacuoles has generally been attributed to protoplasmic streaming.

According to an old theory (EHRENBERG, see PRITCHARD, 1861), now generally rejected, the course of the food vacuoles is supposed to be determined by an invisible tube or gut coiled within the organism. This theory has recently been revived by KOEHRING (1930), on the strength of observations made with the assistance of intra vitam staining with neutral red. However, the facts that food vacuoles appear to follow one another closely along a definite course, and that one vacuole in movement appears to push on those in front of it, only contribute indirect evidence as to the presence of a gut. KOEHRING has postulated a definite tube continuous from mouth to anal spot. It is interesting that in certain accounts of Peritricha there is described a narrow tube running inwards from the bottom of the pharynx. This tube was recorded and illustrated as of considerable extent in *Epistylis flavicans* by GREEFF (1870, 1871), but it is rather shorter in SCHRÖDER'S (1906 a, b, c) drawings of various other Peritricha. Both these authors represent the tube as opening at its free inner end into the general cytoplasm. The existence of such a tube has since been questioned by GREENWOOD (1894), who failed to find any trace of it in *Carchesium polypinum*. Its presence might naturally be expected to influence the movement of food vacuoles.

In this work the writer has tried to find out something of the mechanism of movement of food vacuoles from observations of their speed and course.

Material and Methods.

Peritrich ciliates were used as material. *Epistylis plicatilis* (KENT, 1880—82), *Cothurnia curvula* and *C. ingenita* (HAMBURGER und v. BUDDENBROCK, 1911), and *Carchesium* sp. (near *C. polypinum* of KENT, 1880—82), were got from slightly brackish water from the river Avon at Bristol. *Zoothamnium* sp., and *Pyxidium aselli* (PENARD, 1922) were got from a pond in the University grounds, where they infested the legs of the isopod *Asellus aquaticus*. Marine *Zoothamnium niveum* and *Cothurnia ingenita* (HAMBURGER und v. BUDDENBROCK, 1911) were received by post from Plymouth. From past experience it was known that these remain healthy if reasonable precautions are taken.

While under observation under the microscope the organisms were irrigated either with filtered pond water or with sea water, both of p_H 7.8—8.2, in the way already described (KITCHING, 1934, 1936). The temperature was not controlled, but room temperature

was between 13° and 19° C., and did not change by more than one degree during any one experiment. Measurements of the velocity of food vacuoles and of protoplasmic streaming were made by means of a stop watch graduated to $\frac{1}{5}$ second and of a micrometer eyepiece scale. Food vacuoles were timed over measured distances (of 20 μ) in various parts of their course, and the mean velocity was found for each measured distance. It is recognised that error was introduced by this procedure; but, as will be realized later, this error is of no serious account. The velocity of protoplasmic streaming was estimated by observation of granules in a similar way. Intra vitam staining was not used.

Observations.

1. The movements of food vacuoles under normal conditions.

In *Epistylis plicatilis* the food vacuoles were rather small (as compared with those of other Peritricha), and were formed very frequently — usually at intervals of a few seconds. The track of the food vacuoles (Fig. 2a) led from the bottom of the pharynx towards the base of the organism, and then curved round and ran up the other side back towards the ciliary disc. The food vacuoles appeared (under the microscope) to travel fast as they left the pharynx, but lost speed progressively. They ceased moving, relative to the protoplasm, at a position level once more with the base of the pharynx. From this point they were carried by the streaming of the protoplasm, and their course was irregular and difficult to follow. The food vacuoles were spindle-shaped when they left the pharynx, and did not round up until their movement relative to the protoplasm had ceased.

In the fresh-water *Zoothamnium* sp. the course of the food vacuoles was similar to that in *Epistylis plicatilis*, but the food vacuoles themselves were larger relative to the body size. Moreover they were found to move at a uniform speed (as nearly as could be measured) over the whole of the determined part of their course, and then to stop suddenly.

In *Cothurnia ingenita* (whether from Avon water or sea water) the determined part of the course was short and straight. Detailed measurements were not made, but it may be stated that in a typical example this part of the course was about 20 μ in length, and was covered at a more or less uniform speed of 2 μ per second.

In *Zoothamnium niveum* (marine) and *Carchesium* sp. (fresh-water) the course was essentially similar to that in *Epistylis plicatilis*, and the determined part of it was traversed at a speed greater than that of the streaming protoplasm.

2. The effects of media of increased osmotic pressure on the movement of food vacuoles.

Experiments were carried out on *Zoothamnium* sp. (fresh-water) to see whether the movement of food vacuoles over the determined part of the course was affected by the osmotic pressure of the external medium. The importance of this question will be explained in the discussion.

The time taken for food vacuoles to cover the determined part of the course was measured with a stop watch. In view of the results obtained the error in determining the moment of starting and stopping of the food vacuole is of no importance; and in any case it is not likely to have exceeded 10 per cent, as in this species stopping is sudden. As will be seen from Table 1, transference of the organism to 0.05 molar cane sugar at first made no significant difference to the velocity of the food vacuoles. Later however there was a slight decrease in the velocity, and the food vacuoles did

Table 1.

Data from two experiments on the velocity of food vacuoles over the determined part of the course in *Zoothamnium* sp. (fresh-water).

Medium	distance travelled μ	time sec.	velocity μ per sec.
Pond water	27	11	2.5
" "	"	$11\frac{4}{5}$	2.3
" "	"	$10\frac{4}{5}$	2.5
" "	"	$11\frac{1}{5}$	2.4
" "	"	$11\frac{2}{5}$	2.4
Sucrose 0.05 M.	"	$11\frac{2}{5}$	2.4
" "	"	$11\frac{3}{5}$	2.3
" "	19	$11\frac{3}{5}$	1.6
" "	16	9	1.8
" "	19	11	1.7
Pond water	20	$9\frac{2}{5}$	2.2
" "	"	$9\frac{2}{5}$	2.2
" "	"	$10\frac{1}{5}$	2.0
" "	"	$10\frac{2}{5}$	1.9
" "	"	10	2.0
Sucrose 0.05 M.	"	9	2.2
" "	"	9	2.2
" "	"	$8\frac{4}{5}$	2.3

not travel quite so far. This may probably be attributed to the obstruction caused by the accumulation of numerous food vacuoles in the cytoplasm, a phenomenon which will be discussed in a later paper. However before this obstruction became effective the food vacuoles moved at much the same velocity as when the organisms were in ordinary fresh water.

3. The effects of cyanide.

Solutions of cyanide (0.001 molar) were made up by adding potassium cyanide to pond water. The resulting solution was neutralized with hydrochloric acid to the same pH, as judged with indicators, as the untreated pond water.

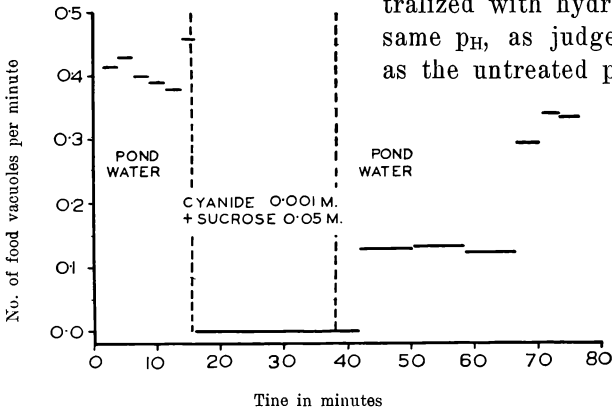


Fig. 1. Graph illustrating the effect of cyanide on the frequency of uptake of food vacuoles by *Zoothamnium* sp. (fresh-water). Frequency is measured as the no. of food vacuoles per minute, each value being calculated from the interval between two successive food vacuoles. Each such value is plotted as a line corresponding to the interval in question.

described (KITCHING, 1938). The walls of the gullet soon became pressed together by the swelling of the body, so that in any case no more food vacuoles could have been taken up. Therefore in order to eliminate the effect of swelling, various fresh-water peritrich species were examined first in filtered pond water and then in 0.001 molar cyanide and 0.05 molar sucrose made up in filtered pond water. In this latter medium there was no swelling, and yet the uptake of food vacuoles soon stopped. The organisms in most cases remained extended, with the cilia stationary. A considerable measure of recovery was achieved when the organisms were replaced in plain filtered pond water. These results are illustrated in Fig. 1 and summarised in Table 2. In a few experiments food vacuoles were

Treatment of *Zoothamnium* sp. (fresh-water) with cyanide rapidly led to a cessation of uptake of food vacuoles. The cilia and the contractile vacuole also stopped all activity, and the whole organism began to swell up in the way already descri-

Table 2.

Species used	external medium	mean interval between successive food vacuoles	standard error of mean	no. of intervals measured
Experiments on effects of cyanide				
<i>Zoothamnium</i> sp. (fresh-water)	pond water	114 sec.	7.9 sec.	5
	cyanide 0.001 M.	> 18 min.	—	—
	pond water	approx. 2—3 min., and decreasing	—	6
<i>Zoothamnium</i> sp. (fresh-water)	pond water	150 sec.	3.3 sec.	5
	cyanide 0.001 M.	> 22 min.	—	—
	+ sucrose 0.05 M.			
	pond water	approx. 3 min., and decreasing	—	6
<i>Cothurnia curvula</i> (fresh-water)	pond water	79 sec.	4.0 sec.	10
	cyanide 0.001 M.	> 26 min.	—	—
	+ sucrose 0.05 M.			
	pond water	approx. 2—3 min., and decreasing	—	5
<i>Pyxidium aselli</i>	pond water	154 sec.	3.3 sec.	8
	cyanide 0.001 M.	> 14 min.	—	—
	+ sucrose 0.05 M.			
	pond water	approx. 5 min., and decreasing	—	4
Experiments on effects of agar				
<i>Pyxidium aselli</i>	pond water	67 sec.	4.2 sec.	13
	agar $\frac{1}{16}$ — $\frac{1}{8}$ %	94 sec.	7.6 sec.	6
" "	pond water	94 sec.	7.7 sec.	9
	agar $\frac{1}{16}$ — $\frac{1}{8}$ %	108 sec.	5.7 sec.	9
" "	pond water	77 sec.	2.9 sec.	7
	agar $\frac{1}{16}$ — $\frac{1}{8}$ %	76 sec.	2.7 sec.	4
" "	pond water	80 sec.	2.4 sec.	5
	agar $\frac{1}{16}$ — $\frac{1}{8}$ %	80 sec.	1.8 sec.	8

taken up shortly after transference of the organism to cyanide, and stoppage of uptake did not take place immediately. In such cases these food vacuoles moved extremely slowly over the determined part of the course, and were more rounded in shape than normally.

4. Uptake of food vacuoles without ciliary activity.

Experiments were required to discover whether the uptake of food vacuoles was in any way dependent on the beating of the cilia of the disc or of the gullet. Accordingly *Pyxidium aselli* (fresh-water) was observed (a) in filtered pond water, and (b) in $\frac{1}{16}$ to $\frac{1}{8}$ per cent agar solution. In the agar solution the beating of the cilia either entirely stopped or was reduced to an occasional very feeble flicker; and the organisms remained expanded. The frequency of uptake of food vacuoles was unaffected. Results are summarised in Table 2.

5. Displacements of the course of food vacuoles in relation to protoplasmic streaming.

The normal direction of protoplasmic streaming in *Epistylis plicatilis* is shown diagrammatically in Fig. 2 b. Protoplasm flows down towards the base of the organism on the side of the gullet, and back towards the ciliary disc on the opposite side. Sometimes

however this general course of protoplasmic streaming is complicated by subsidiary currents. A not infrequent type is illustrated in Fig. 3 a. In this the protoplasm appeared to flow back towards the ciliary disc along a course nearer to the central axis of the organism than usual. The determined part of the course then became deflected and indented in the way shown in the diagram. Sometimes this part of the course was visible as a line within the cytoplasm; at other times it was clearly marked out by the rapid succession of food vacuoles. In each case it could be seen to be deflected by the streaming protoplasm. Sometimes it happened that a food vacuole completed the "determined" course; and then a change of protoplasmic streaming occurred so that the determined course was deflected; and as a result the next food vacuole came to rest (relative to the protoplasm) some way away from the first (Fig. 3 b). In other cases the determined part of the course became twisted in a spiral, apparently by the protoplasmic current (Fig. 3 c). It should be noted that the organisms remained still while under examination, and did not rotate or perform any other movements likely to complicate the observations.

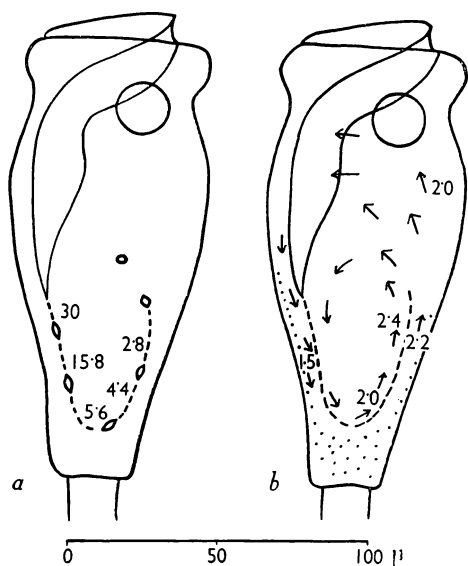


Fig. 2. The course of the food vacuoles and the streaming movements of the protoplasm in *Epistylis plicatilis*. In (a) the determined part of the course of the food vacuoles is shown as a broken line, and their velocity is given in μ per sec. In (b) the direction of the streaming of the protoplasm is indicated by arrows, and its velocity is marked in μ per sec. Dots signify stationary protoplasm.

Discussion.

The course traversed by the food vacuoles inside a peritrich ciliate consists of (a) the "determined" part, which is covered at a speed greater than that of the streaming protoplasm, and (b) the undetermined part, which is irregular and difficult to follow, and along which the food vacuoles appear to be carried in the general stream. The motive force for the first part of the course appears to be different from that for the second. It seemed possible, in view of the progressive decrease in velocity of the food vacuoles of *Epistylis plicatilis*, that a food vacuole might receive some initial "push-off" as it left the pharynx, and that it might proceed under its own momentum for the determined part of the course. However it can readily be shown that the distance travelled is many times too great in view on the minute size of the food vacuole. Thus the distance (s) travelled by a spherical body of radius a , mass m , and initial velocity v , through a medium of viscosity η , is determined by the relation: $s = \frac{mv}{6\pi a \eta}$.

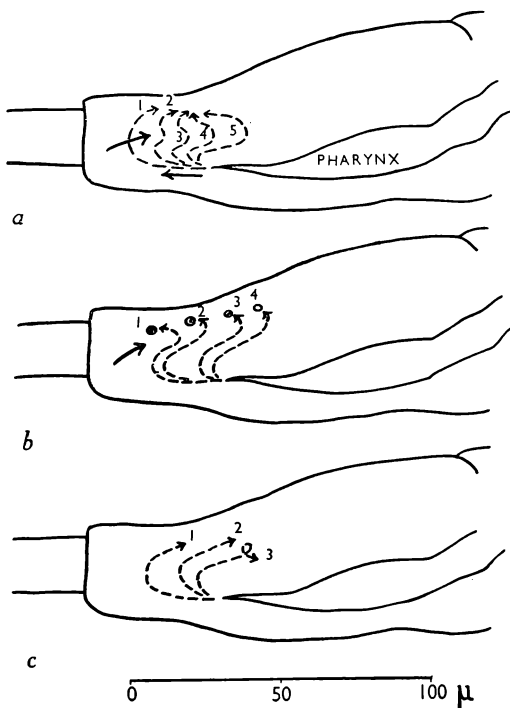


Fig. 3. Changes in the determined part of the course of food vacuoles in *Epistylis plicatilis*. The courses of successive food vacuoles are marked by broken lines and numbered to show their sequence. Heavy arrows indicate the direction of protoplasmic streaming.

For a drop of water of the dimensions of a food vacuole (radius 4μ) with an initial velocity of 50μ per second to travel a distance of 100μ (approximately the length of the "determined" part of the course), the medium would require to have a viscosity of about $10^{-6} \times$

the viscosity of water. But the viscosity of the protoplasm must be at least as great as that of water, and under such conditions the drop would in fact stop "dead", in so far as an observer could judge.

It must be concluded from what has been said above that the food vacuoles receive forwardly directed impulses en route during the determined part of their course. It might be suggested that energy is in some way derived from the considerable difference in concentration of solutes between the vacuolar contents and the cytoplasm. The vacuoles do in fact shrink from the time when they are pinched off from the pharynx. But if this explanation were correct one might have expected some immediate modification of the speed or range of food vacuoles as a result of a drastic change in the osmotic pressure of the medium; and this does not happen. For this reason the explanation under consideration seems to be an improbable one. It may therefore be suggested that kinetic energy is imparted to the food vacuoles by contractions of the protoplasm which ensheaths the determined part of the course.

Such additional evidence as could be obtained supports the view that the food vacuoles are driven by protoplasmic contraction. Their shape, which is lentoid while they are in the determined part of the course, accords with this view. The uptake of food vacuoles is stopped in the presence of cyanide, as would reasonably be expected of an active process dependent on cell respiration. Again, the uptake of food vacuoles is independent of ciliary activity. This last observation is consistent with the conclusion that the movement of food vacuoles is not the result of an initial "push-off" under the influence of pressure set up by ciliary activity, but is on the contrary due to protoplasmic contraction operating throughout the determined part of the course.

The supposed existence of a permanent tube leading inwards from the pharynx, as described by GREEFF (1871), remains problematical. The present writer was only able to receive an impression of such a tube while food vacuoles were actually passing. However the movement of food vacuoles over the determined part of their course at a speed greater than that of the protoplasmic streaming is of widespread occurrence in Peritricha. Therefore the existence is suggested, if not of a definite tube, at least of a differentiated region of protoplasm which not only guides but also propels the food vacuoles. This differentiated region is attached to the pharynx; but it is apparently free at its inner end since it can be displaced by changes in the direction of protoplasmic streaming. These dis-

placements appear to have been seen previously by GREEFF (1871), but he attributed his observations incorrectly to rotation of the whole organism. KOEHRING'S revival of the idea of a continuous gut receives no support from the observations described in this paper.

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Summary.

1. The course traversed by food vacuoles inside peritrich ciliates may be divided into a preliminary "determined" part and a subsequent "undetermined" part.

2. The determined part is covered at a speed greater than that of the protoplasmic streaming, and in it the food vacuoles follow one another strictly along the same route.

3. Over the undetermined part of the course the food vacuoles appear to be carried by the streaming of the protoplasm. This part of the course is devious, irregular, and difficult to follow.

4. In *Epistylis plicatilis* the determined part of the course is traversed with progressive deceleration. In the other species observed it is covered at an approximately uniform speed, and the food vacuoles appear to stop "dead" at the end.

5. An increase in the osmotic concentration of the external medium made little difference at first to the speed of food vacuoles in the determined part of the course.

6. The frequency of uptake of food vacuoles slowed down to zero in organisms subjected to dilute cyanide. Vacuoles taken up from media containing cyanide travelled slowly and were more nearly spherical than normal.

7. The uptake of food vacuoles proceeded normally in organisms subjected to media of sufficiently high viscosity to bring all ciliary activity to a stop.

8. The determined part of the course can be deflected by protoplasmic streaming.

9. It is concluded that food vacuoles are propelled over the determined part of the course by contractions of surrounding protoplasm.

10. No support is given to the view that a continuous gut exists in ciliates.

References.

- GREEFF, R. (1870, 1871): Untersuchungen über den Bau und die Naturgeschichte der Vorticellen. Arch. Naturgesch. **36**, 353—384; **37**, 185—221.
- GREENWOOD, M. (1894): On the constitution and mode of formation of "food vacuoles" in Infusoria, as illustrated by the history of the processes of digestion in *Carchesium polypinum*. Philos. Trans. Ser. B, **185**, 355—383.
- HAMBURGER, C. u. W. v. BUDDENBROCK (1911): Ciliata mit Ausschluß der Tintinoidea. Nordisches Plankton, Teil 13. Kiel u. Leipzig.
- KENT, W. S. (1880—82): A manual of the Infusoria. London.
- KITCHING, J. A. (1934): The physiology of contractile vacuoles. I. Osmotic relations. J. of exper. Biol. **11**, 364—381.
- (1936): The physiology of contractile vacuoles. II. The control of body volume in marine Peritricha. Ibid. **13**, 11—27.
- (1938): The physiology of contractile vacuoles. III. The water balance of fresh water Peritricha. Ibid. **15**, 143—151.
- KOEHRING, V. (1930): The neutral red reaction. J. Morph. **49**, 45—137.
- PÉNARD, E. (1922): Études sur les infusoires d'eau douce. Geneva.
- PRITCHARD, A. (1861): A history of the infusoria. London.
- SCHRÖDER, O. (1906 a): Beiträge zur Kenntnis von *Campanella umbellaria* L. sp. Arch. Protistenkunde **7**, 75—105.
- (1906 b): Beiträge zur Kenntnis von *Epistylis plicatilis* (EHRBG.). Ibid. **7**, 173—185.
- (1906 c): Beiträge zur Kenntnis von *Vorticella monilata* TATEM. Ibid. **7**, 395—410.
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