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THE CYTOPYGE OF CILIATA

IV. AN EXPERIMENTAL STUDY OF THE INGESTION, DIGESTION AND DEFAECATION IN *OXYTRICHA FALLAX*

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Abstract

(1) The ingestion, digestion and defaecation have been investigated in *Oxytricha fallax*, in starving state and non-starving state after feeding with prey ciliates. (2) Immediately after prey ciliates have been added to starving *O. fallax*, the swimming activity of the latter substantially increased. (3) The intracellular digestion follows the pathway described for other *Ciliata*. In the course of this the size of the vacuole contents reaches extreme values four times. Changes of chemical nature rendering structures argyrophilic take already place in the ingestion vacuole: in *Paramecium caudatum* and *Uronema parduczi* these structures appear as network systems presumably corresponding to the pellicle structure. (4) The size of food vacuoles formed in *O. fallax* seems to be in correlation with the nutritional status. (5) The process of the defaecation is of the gliding type; the contents of the egestion vacuole are discharged into the outer medium, whereas the vacuole membrane presumably remains in the animal. (6) The interval ingestion—defaecation takes 30—60 min after feeding of the starving *O. fallax*. (7) The silver line system of prey ciliates responds with structural and formative changes to the changes in the chemical environment; these reactions are interpreted as signs of fibrillar nature of the silver line system. (8) The silver line system of *O. fallax* has been described for the first time; it is represented by fine network covering the whole body of this ciliate.

Introduction

Relied upon the lysosome concept of DE DUVE [6] many investigators [e.g., 6, 27, 38] consider the food or digestion vacuoles of protozoa more or less analogous to the lysosomes of metazoa. This concept is based first of all on the presence of acid phosphatase. Recently, however, UHLIG and co-workers [39] have revealed intracellular villi in the food vacuoles of *Ciliata*. Thus, the analogy has been called in question.

Owing to numerous old (reviewed by KITCHING [22]) and recent [3, 7, 8, 20, 31, 33—36, 39] publications, an abundant information is available on the chemistry and the morphology of food vacuoles and on the changes showed by the vacuoles and the ingested matter. However, little is known about many interesting questions, e.g., the interval between ingestion and defaecation in *Ciliata*. In this respect the old studies of MAST [26] and recent works published by RICKETTS [31], concerning the periodicity of the endocytosis in *Tetrahymena pyriformis*, should be mentioned. Similarly, little

is known about the reactions of the silver line systems of prey ciliates enclosed in food vacuoles of rapacious infusoria. In the corresponding experiments mainly bacteria or yeast cells were used as prey organisms. Only KLEIN [24] has dealt with prey ciliate viz., *Colpidium campylum*, enclosed in food vacuoles of *Tetrahymena patula*. The process of defaecation of *Ciliata* has also called little attention [13, 36].

The present work was undertaken to obtain further information about the above questions.

Material and method

As rapacious infusoria two strains of *O. fallax* were used. These differed from eac other only in size. Strain I, 110—150 μm in size originated from algal infusions of the territory Burgenland. Strain II 150—260 μm in size, originated from straw infusion from the north of the Danube (Gaisbach).

As prey ciliates *U. parduczi* and/or *Colpidium campylum*, both obtained from infusions in Burgenland, were used. *O. fallax* strain II was simultaneously fed with *Paramecium caudatum* and *C. campylum*. Average sizes for prey ciliates: *U. parduczi*, 31 μm; *C. campylum*, 80 μm; *P. caudatum*, 190 μm.

In the first series of experiments *O. fallax* collected fr om mould membranes of infusions, rich in bacteria, were used. The second series was perfor med several days later, when the bacterial food in the infusions had already been exhausted. In this stage the animals had very seldom food vacuoles.

1st series of experiments: non-starving *O. fallax* strain I were fed with *U. parduczi* or *C. campylum* and strain II were fed simultaneously with *C. campylum* and *P. caudatum*.

2nd series of experiments: O. fallax of strain I having starved for about 24 h were fed with either *U. parduczi* or *C. campylum*, *ad libit.*, or with a limited amount of these prey ciliates.

Prey ciliates were added to *O. fallax* on a slide and animals were killed by drying 5, 10, 15, 20, 25, 30 and 35 min thereafter. Silver impregnation was carried out in the dry preparation [9]. Living protozoa were examined by phase-contrast microscopy.

Results

Remarks concerning the applied Ciliata

O. fallax had been characterized both morphologically and physiologically [15—18, 21, 30, 32]. However, its silver line system was not described previously. This consists of fine network (Figs 1a, 12) covering the whole animal: it disappears, at least partially, during preparation. This was a great advantage in our experiments, because of this matter the change of the argyrophilic structures of the prey ciliates captured in the food vacuoles could be studied very well. Similar networks have been described in other *Ciliata* [1, 2, 4].

O. fallax can feed bacteria [15], yeast cells [18] and flagellates [17]. According to GRIMES [15] an unidentified Flagellata species must have an important role in its cultivation. A well-defined rapacious mode of life like that observed in the present experiments had not been described earlier for this species; under natural conditions it must be limited to starving animals.

The different strains of *O. fallax* are very variable in size (see above).

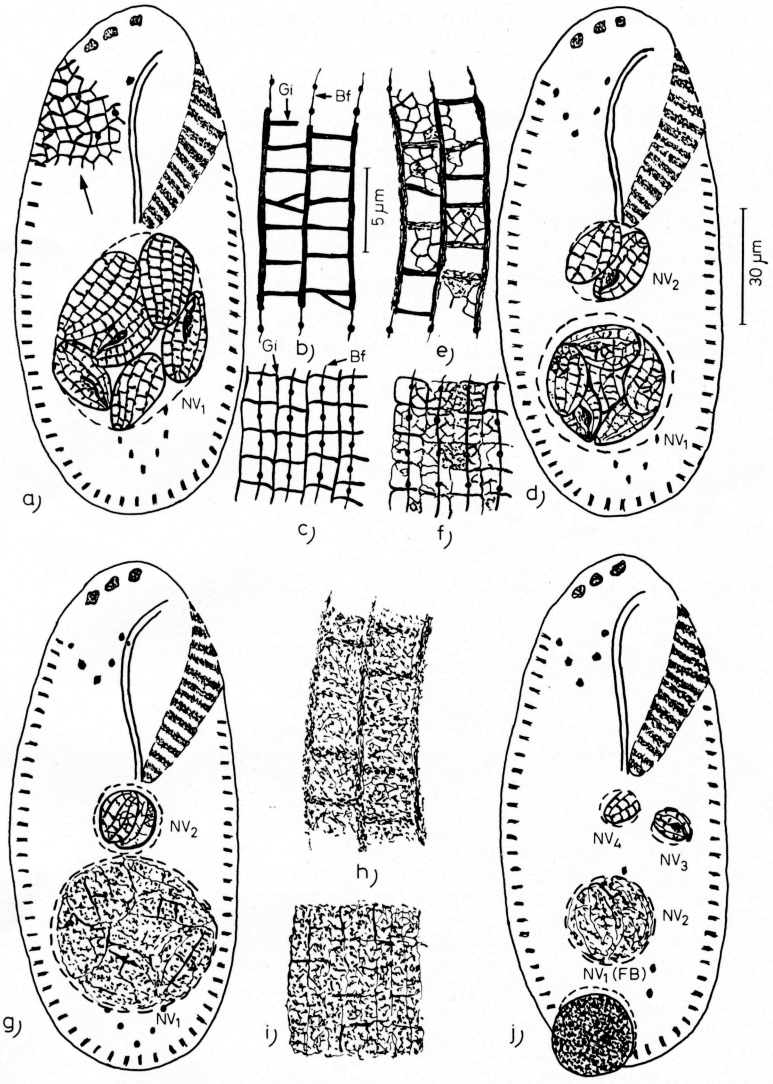


Fig. 1. Schematic illustration of cortical organization of *O. fallax* and changes in the argyrophilic structures of *U. parduczi* and *P. caudatum* during digestion in food vacuoles of starving *O. fallax*. Gi = argyrophilic network superimposing the basal fibrils (Bf) of *U. parduczi*; NV_1(FB) = first food vacuole turning into faecal ball. Arrow in a) points to a section of the silver line system of *O. fallax*. The hatched areas represent the membranes of food vacuoles

The dimensions published by GRIMES [15], KAHL [21], DINGFELDER [5] and REUTER [32] are 80 μm, 150 μm, 150—160 μm and 140—180 μm, respectively.

The normal silver line system of prey ciliates is outlined in Figs 8—11 and described in detail in our previous papers [10, 12] and in KLEIN's [23, 25] papers.

Ingestion, digestion starving and defaecation in starving O. fallax

The ingestion phase (0—5 min after feeding). Adding of prey ciliates is immediately followed by an increase in swimming activity and in the movement of the adoral membranelles of *O. fallax*. Owing to the resulting sucking effect, the prey animals stream to the mouth and are collected in the ingestion vacuole. In 3 to 5 min a very large vacuole (Fig. 2) is budding off. In the vacuole, which may contain up to 50 Uronemas (Fig. 13), 4 *Colpidia* or one *Paramecium*, the ingested animals may remain able to move for 10 min. If the three different prey ciliates are reached at the same time, *U. parduczi* is favoured. Furthermore, about 20% of *O. fallax* did not ingest ciliates even if the latter were available in excess.

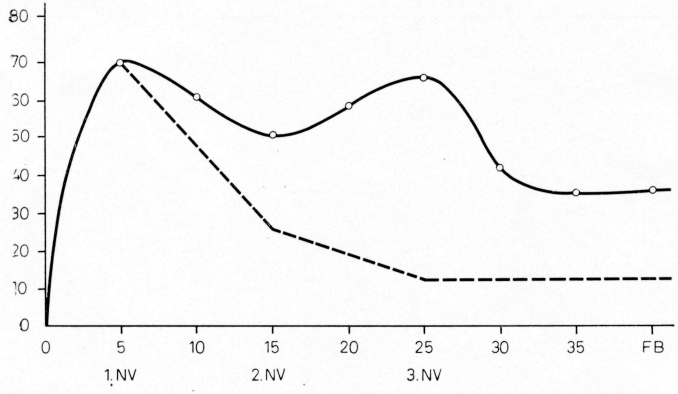


Fig. 2. Fluctuation in the size of first food vacuoles after feeding of starving *O. fallax* (solid curve). Note the four extreme values corresponding to the four steps of digestion. The sudden fall at 25 min after ingestion suggests that the absorption of food components starts at the same time. The dotted line shows a correlation between nutritional status and vacuole size. The food vacuoles developing after feeding of starving animals are extraordinarily large. Food vacuoles of the normal size begin to be formed 25 min after feeding. Absorption of food components from the first vacuole starts at the same time. Ordinate: size of food vacuoles in μm, abscissa: minutes after feeding. FB = faecal balls

Fig. 13 shows a very large ellipsoid food vacuole including more than 40 Uronemas. In the smaller vacuole in Fig. 15 only 10 are seen. The prey ciliates in these vacuoles already show remarkable changes in staining: In *U. parduczi* and *P. caudatum*, strongly argyrophilic network covering the whole animal, stain well (compare Figs 8, 9 and 11 with Figs 13—15, 21 and 22). The silver line system, on the other hand, is still unchanged both in shape and structure.

The digestion phase (5—20 min after feeding). Prey ciliates, often more or less rounded (*U. parduczi*) or apically pointed (*C. campylum*), appear as dense balls in the food vacuoles, which have become smaller (Fig. 2) and spherical (Figs 1d, 16). Some 15 min after ingestion many of the ingested animals break

up or become non-transparent and granular (Fig. 26). The silver line systems and the argyrophilic network (see above) show remarkable structural damages manifesting themselves in granular splitting (Figs 1e, f, 16, 17, 24). Silver line remnants of reticular structure are often seen (Figs 1e, f, 12, 23, 24). In *C. campylum* regression of the oral apparatus was sporadically observed (Fig. 25). Besides this first, in general very large, food vacuoles, many specimens of *O. fallax* contained another, smaller food vacuole (average diameter, 30 μm, Figs 2, 17 NV_2) adjacent to, but not fused with, the large vacuole. This is so especially in the presence of prey ciliates in excess. The digestion of these and subsequently formed vacuoles proceeds similarly to that of the first vacuole.

The resorption phase (20—30 min after feeding). As the food vacuole has reached the second maximum in size (Fig. 2) the silver line systems and the argyrophilic network of the prey ciliates are split and thus the prey ciliates become unrecognizable (Figs 1g—i, 19, 24). The rounding of the prey animals is often very pronounced, especially if only few prey animals have been enclosed in a food vacuole. If prey ciliates (*U. parduczi*) were added in excess, second and further vacuoles were often encountered; some of these contained only one or two ciliates. The food vacuoles thus formed attained the normal size, viz., 10—20 μm in diameter.

Approximately 25 min after ingestion the staining properties of the prey ciliates begin to change: the deep black staining of the silver impregnation (*acid phase*) turns into a brownish-yellow colour (*alkaline phase*).

The defaecation phase (30—40 min after feeding). By this time all argyrophilic structures of the prey ciliates have split. The first food vacuole becomes smaller in size again (Fig. 2) and the intensive argyrophilia of its contents returns, then the contents approach to the cytopyge (Fig. 1j). The discharged balls (Fig. 2) statistically agree in size with the egestion vacuoles. Most of the faecal balls were spherical or slightly elliptical in shape, pronouncedly argyrophilic in staining and relatively dense in consistence. Fig. 20 shows a faecal ball just discharged from the cytopyge.

Observations in vivo. The cytopyge base in *O. fallax* is located immediately behind the caudal cirrus, yet, not at the utmost caudal edge of the body. The defaecation was completed, in every case observed by us, between two and three sec without any phenomenon recognizable even by phase-contrast microscopy; the faecal ball glides out of the animal while the cytopyge opens widely.

Immediately after defaecation the cytopyge disappears again (Fig. 3). Figs 6 and 7 show the discharge of two egestion vacuoles placed near behind each other. The arrow in Fig. 6 points to the first egestion vacuole, whose contents had already been discharged and seem not to originate from the prey ciliates (Experiment series I). The second egestion vacuole, containing a remarkably little

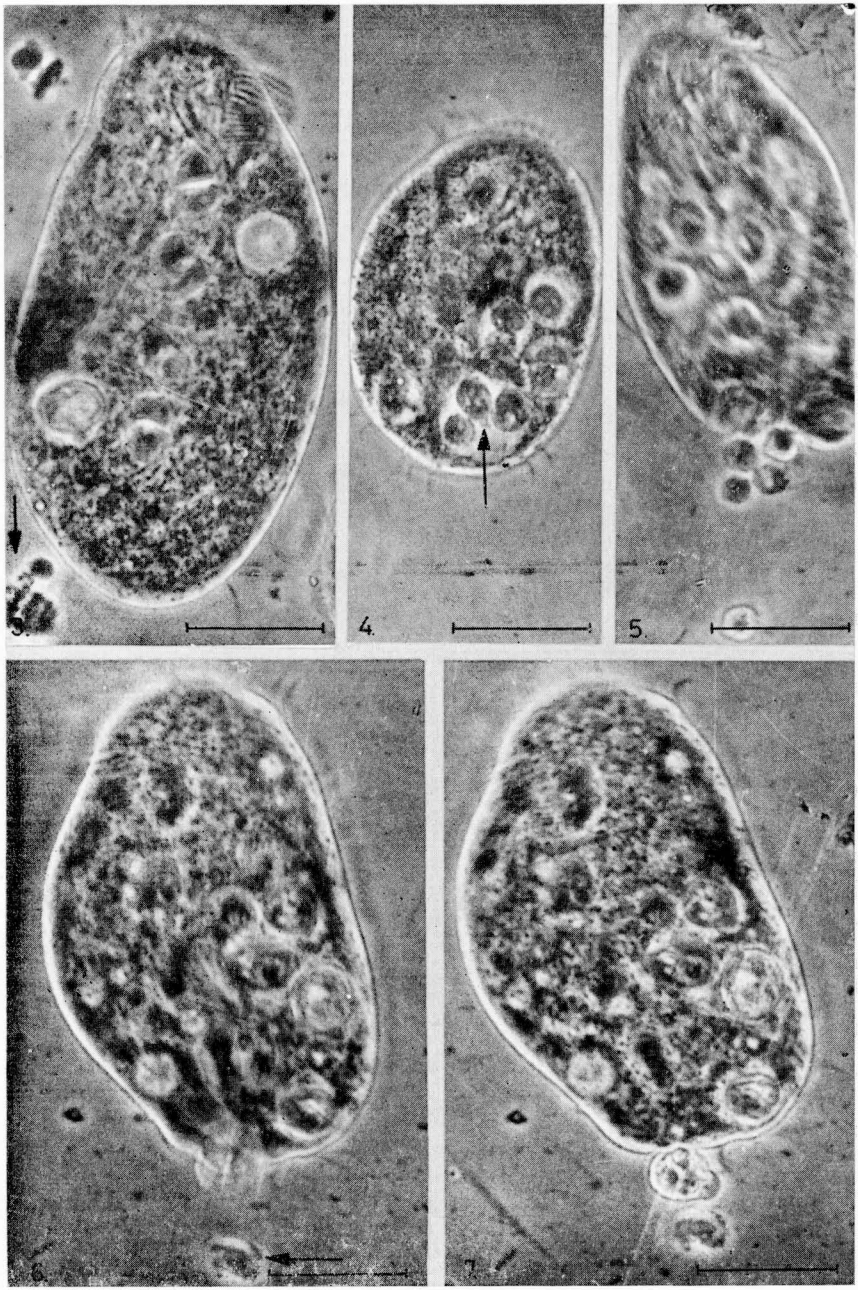
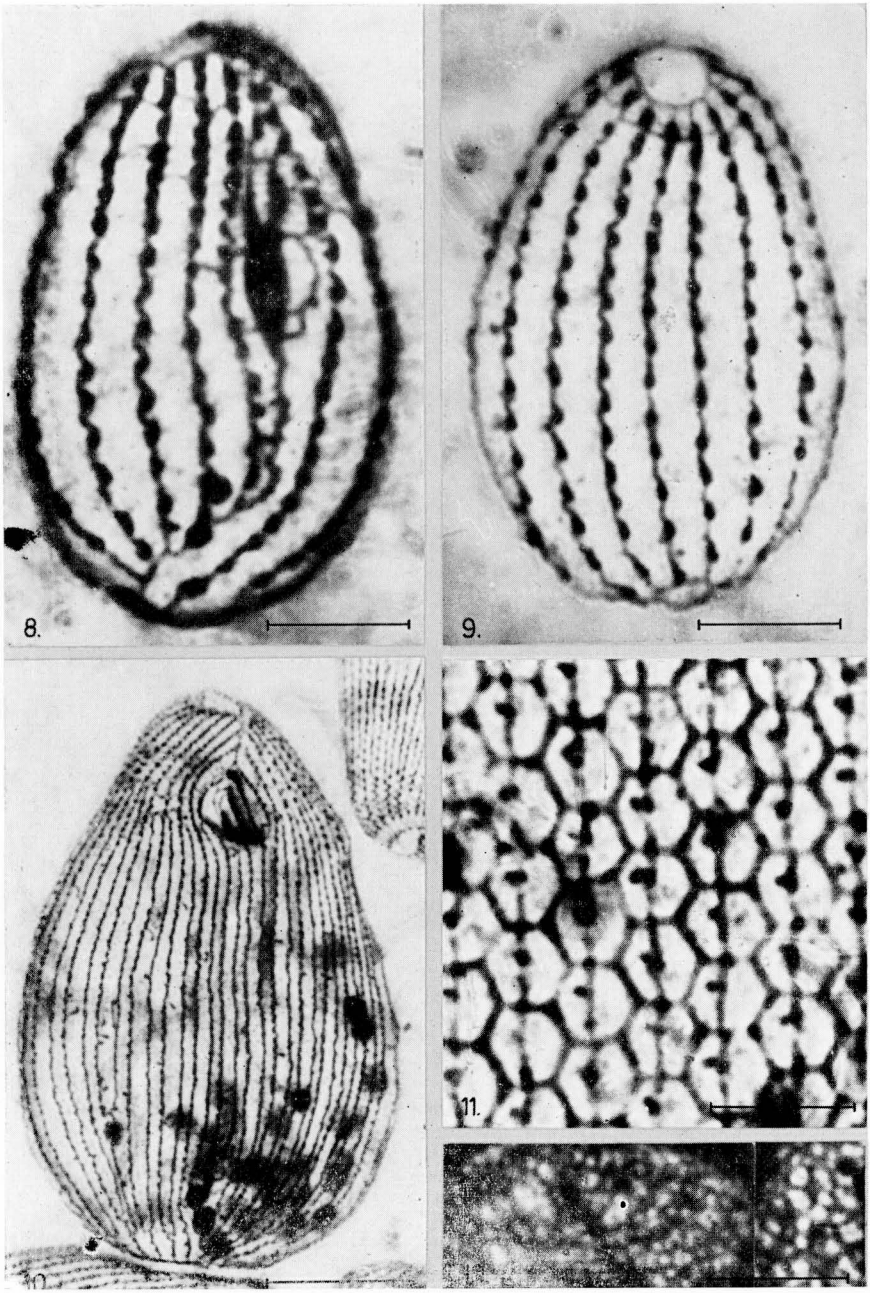


Fig. 3. O. fallax immediately after the faecal ball (arrow) has been discharged. The faecal ball is of low consistence, mainly consisting of bacterial debris. The cytopyge orifice disappears immediately after the function of the organelle. Scale=40μm

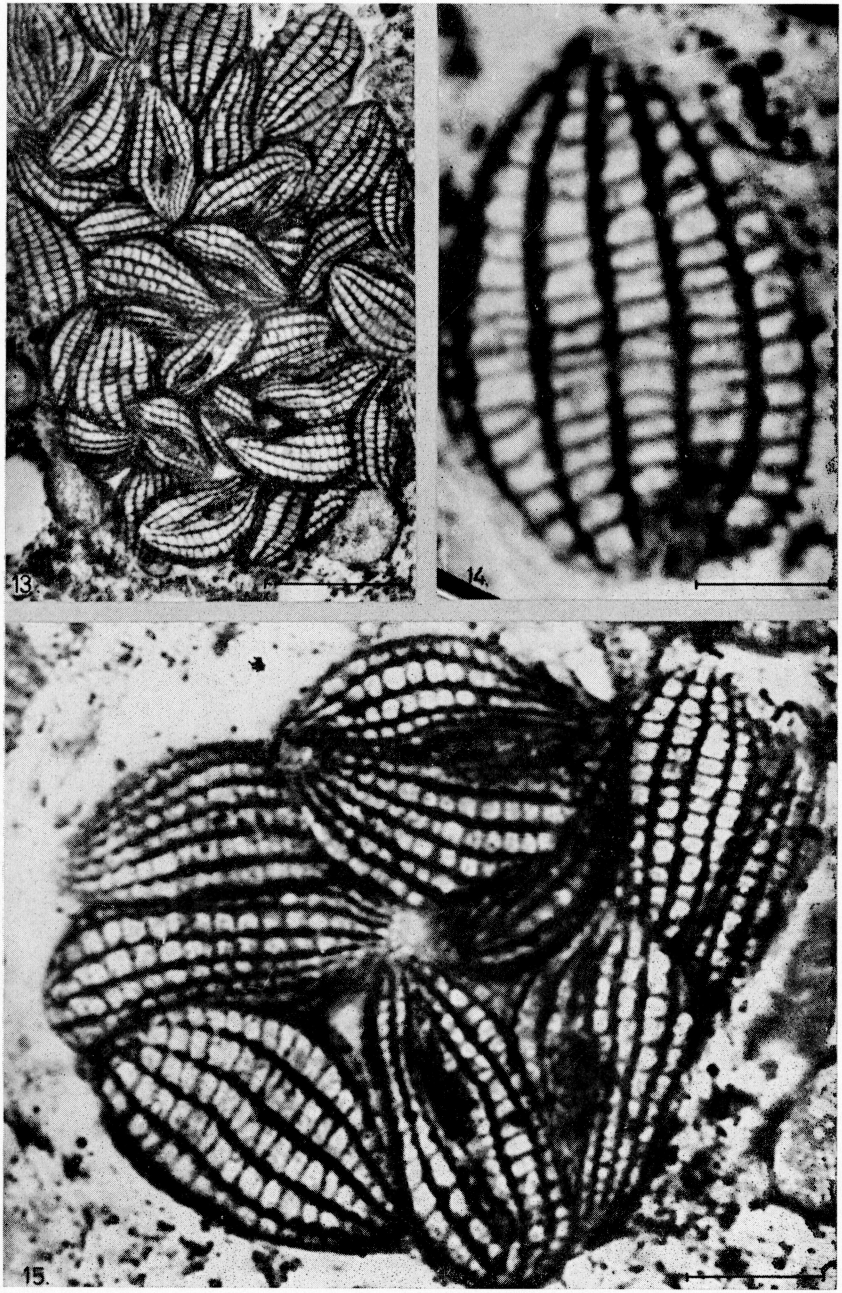
Fig. 4. O. fallax (non-starving) 25 min after having been fed with *U. parduczi*. Note the strongly digested rounded Uronemas in food vacuoles. Scale = 55 μm

Fig. 5. O. fallax in the very moment when the contents of an egestion vacuole with the undigested remnants of four *U. parduczi* is being driven out. For details see the text. Scale = 45 μm

Figs 6 and 7. Two stages in the very rapidly proceeding defaecation of the contents of egestion vacuoles in *O. fallax*. Internal 2 seconds. For details see the text. Scale = 40 μm

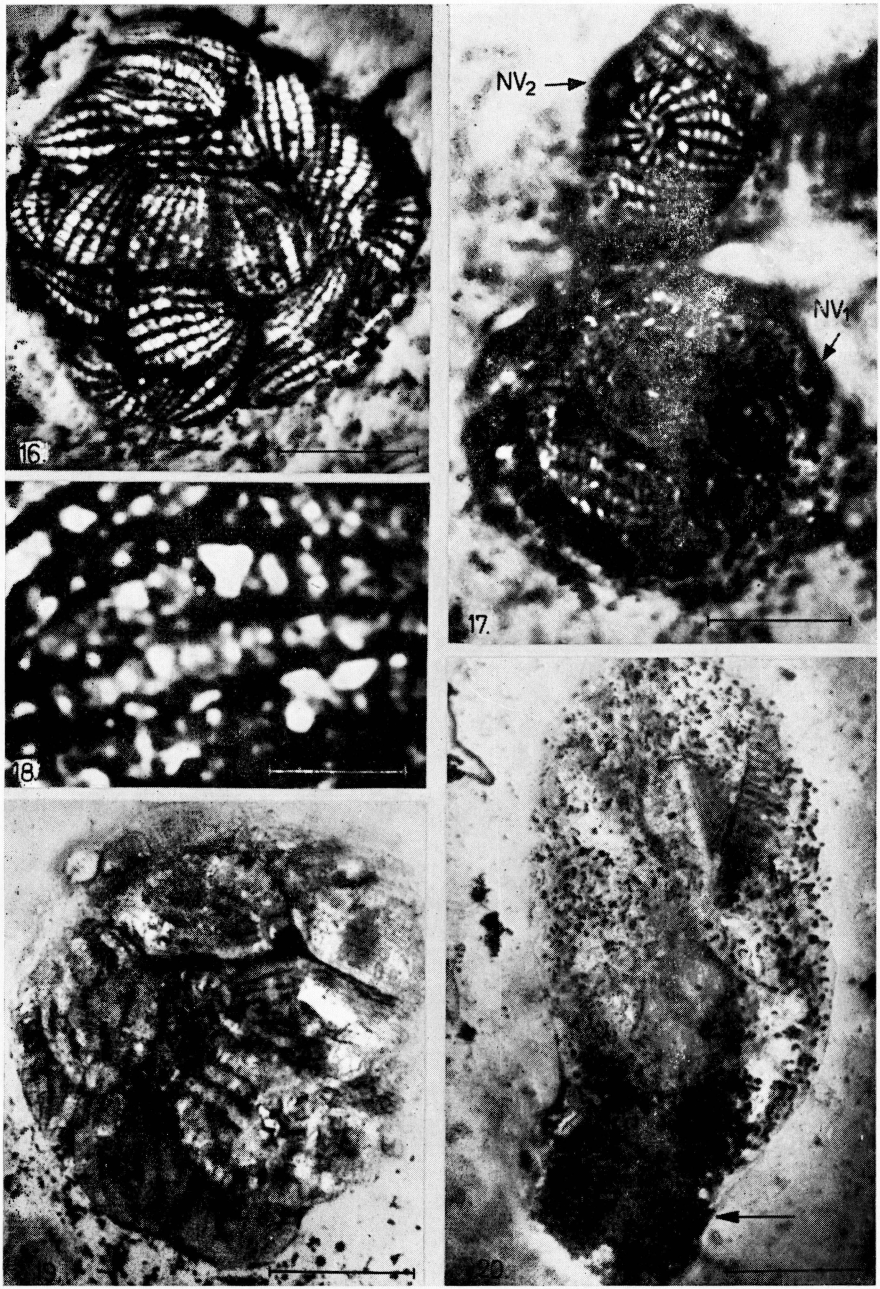


Figs 8—9. Normal silver line systems of *U. parduczi*, ventral and dorsal. Scale = 7 μm
Fig. 10. Normal silver line system of *C. campylum*, ventral. Scale = 20 μm
Fig. 11. Detail of the silver line system of the dorsal site of *P. caudatum*. The hexagonal lattice is the indirectly joining system. The vertically running silver lines represent the directly joining system. Scale = 9 μm
Fig. 12. Detail of the very fine-meshed silver line system of *O. fallax*. Scale = 20 μm

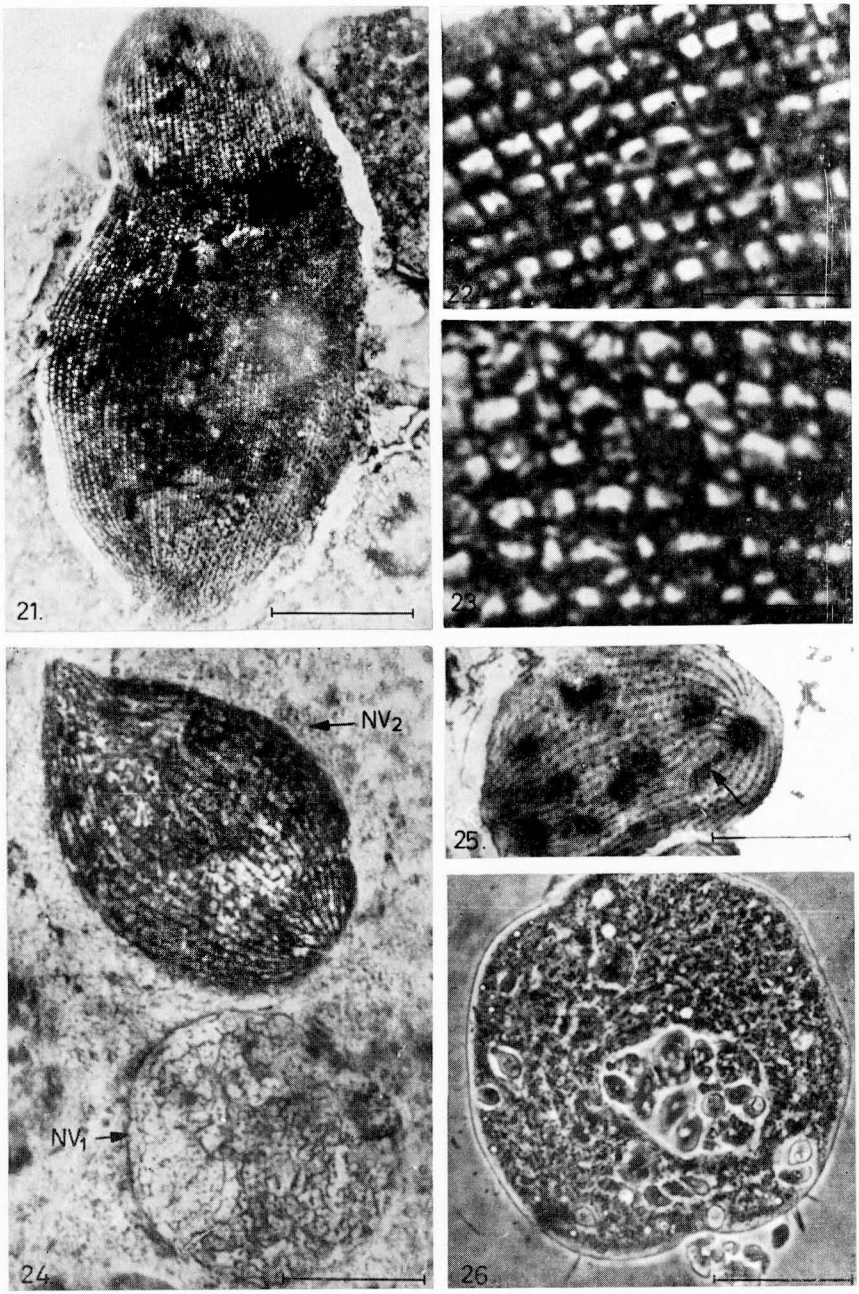


Figs 13—15. Food vacuoles in *O. fallax* 3—5 min after feeding with *U. parduczi*. For further explanation see the text. Scale = 15, 7 and 11 μm, respectively

Fig. 16. Food vacuole in *O. fallax* 10 min after feeding with *U. parduczi*. The silver lines and argyrophilic network systems of the prey ciliates are weakly damaged in structure. Scale = = 20 μm. *Fig. 17.* Food vacuoles in *O. fallax* 15 min after feeding with *U. parduczi*. The argyrophilic structures of the prey ciliates show pronounced structural and formative changes in the food vacuole ingested at first (NV_1). The second food vacuole (NV_2), having spent



only 5 min in the animal, is much smaller and the argyrophilic structures in it are practically unchanged. Scale = 20 μm. *Fig. 18.* Detail of the dorsal site of the silver line system of *U. parduczi* after 15 min staying in a food vacuole of *O. fallax*. The silver line system has turned into fine-meshed network (compare with Figs 8 and 9). Scale = 7 μm. *Fig. 19.* Food vacuole in *O. fallax* 25 min after feeding with *U. parduczi*. All argyrophilic structures are unrecognizable. Scale = 20 μm. *Fig. 20. O. fallax* 35 min after feeding with *U. parduczi*. The contents of the egestion vacuole are just being driven out. The faecal ball (arrow) shows an intensive argyrophilia, it is approximately spherical and very compact



Figs 21—22. Food vacuole in *O. fallax* 5 min after feeding with *P. caudatum*. The silver line system of the prey ciliate takes shape definitely. Note the well-staining reticular structure in Fig. 22. Scales = 45 μm and 15 μm. *Fig. 23.* Detail of the damaged silver line system (fine pale silver lines) of *P. caudatum* having stayed in a food vacuole of *O. fallax* for 15 min. Note the rounded meshes of the argyrophilic network (compare with Fig. 22). Scale = 15 μm. *Fig. 24.* Two food vacuoles of *O. fallax* having ingested one *C. campylum* each. In the first vacuole (NV_1), being 20 min old, the silver line system of the prey ciliate has split into remnants of reticular structure. In the second vacuole (NV_2), approximately 10 min old, the silver line system of the prey animal is still well-recognizable, though damaged in structure. Scale =

digested *U. parduczi*, is just being discharged (Fig. 7). If the animal is not hampered in its moving by the coverslip, an indent of the caudal body end is often observable for a short period of time (Fig. 5). If only few prey ciliates had been enclosed in the food vacuole, the digested animals, mostly rounded off and in the majority of cases reduced to half size, were still well-recognizable in the egestion vacuole (arrow in Fig. 4). These undigestable residua are then excreted, together with the fluid contents of the vacuole. The vacuole membrane, on the other hand, seemed to be retained in the animal, at least its excretion was never observed.

Ingestion, digestion and defaccation in non-starving O. fallax

In the presence of sufficient bacterial food (Serie I) only 20—30% of the *O. fallax* protozoa appeared to digest *U. parduczi* or *C. campylum*. *P. caudatum* was ingested very rarely. Large food vacuole was never formed (see p. 64); the ingested ciliate was enclosed in a small vacuole. Ingestion of more than 4—8 Uronemas or 1 or 2 *Colpidia* occurred also rarely. During digestion these food vacuoles underwent the same processes as the food vacuoles formed after feeding of starving *O. fallax*.

Discussion

Ingestion, digestion and defaecation. It may be concluded that the digestion in *O. fallax* follows the way described for other *Ciliata* [7, 8, 22, 26, 27]. The quality of the ingested food seems to exert little effect on the process of digestion. In addition to the three kinds of food vacuoles, viz., ingestion, digestion and egestion vacuoles as suggested by MÜLLER and TÖRŐ [27] a fourth term, viz., resorption vacuole as proposed by UHLIG and co-workers [39] seems to be differentiated, the more so because during the whole process of digestion the size of the vacuole contents shows, successively, four extreme values (Fig. 2).

Since recent investigations [31] have excluded the proliferation of the vacuole membrane as a limiting factor in the formation of food vacuoles, the continuous decrease in size of the food vacuole (Fig. 1) formed in the starving *O. fallax* must be in correlation with the nutritional status of the animal. This is supported by the fact that non-starving animals do not develop large vacuoles (see above). Such observations are not mentioned by RICKETTS [31], though he applied similar experimental methods.

←

= 20 μm. *Fig. 25*. Food vacuole of *O. fallax* 10 min after feeding with *C. campylum*. The oral apparatus of the prey animal has been absorbed until a membranelle remained only (arrow). Scale = 30 μm. *Fig. 26*. Starving *O. fallax* 20 min after feeding with *U. parduczi*. Note the numerous small food vacuoles besides the first large one. The animal was under intensive pressure. Scale = 45 μm

The interval between ingestion and defaecation has been given for *T. pyriformis* as 24—50 min [31]. These results are consistent with those found for *O. fallax* by us and for *P. caudatum* by MAST [26]. In *Tokophyra infusionum*, on the other hand, digestion processes can be observed even as late as 24 h after feeding [34]. However, these results are scarcely comparable with ours because *T. infusionum* has no cytopyge [13]. For amoebas fed with ciliates even intervals between 21 and 72 hrs have been published [3].

The increase in swimming activity of the starving *O. fallax* after addition of prey ciliates (see p. 64) is comparable with similar results obtained by WENZEL and BALTES [40], who fed *Spathidium stammeri* with *T. pyriformis*. These authors attribute this phenomenon to an unknown substance which, originating in the prey ciliate, exerts a chemotactic effect on *Spathidia*. This view seems to be supported by our own work, though, we did not perform special experiments. An extremely high motility of *T. pyriformis* was observed by RICKETTS [31].

Since special structures, presumably responsible for the defaecation of the contents of egestion vacuoles, have been found neither *in vivo* nor in impregnated preparations, the cytopyge mechanisms have remained unclear. It may be classified as of the "gliding" type [14]. Even HASHIMOTO [17], when describing the defaecation of different cytoplasmic inclusions (crystals, etc.) did not mention the mechanism of defaecation.

The reactions of the silver line system of prey ciliates in food vacuoles of O. fallax. In accordance with KLEIN [24] we succeeded in observing structural and formative reactions of the silver line system of prey ciliates in food vacuoles. The structural changes manifested themselves in a granular splitting of the silver line system (Figs 16, 17, 19, 24). Outgrowth of lateral silver lines from basal fibrils of *C. campylum* could not be observed by us; instead, a reticular transformation of parts of the silver line system often appeared in numerous prey ciliates shortly before the complete dissociation of the silver line system i. e., several minutes before the death of the animal (Figs 18, 23, 24). Similar network-like formations have been described in mechanically damaged *Colpidia* [11] and chemically damaged *Glaucoma* [25]. The regression of the oral apparatus observed by KLEIN [24] in every case as a phenomenon lasting for several seconds was observed by us only sporadically as a process lasting for 10—15 min.

In accordance with KLEIN [25], we interprete all these changes as a reaction to the drastically altered chemical conditions in the food vacuoles. They may be considered as a sign of the fibrillar status of the silver line system, though the electron microscope investigation carried out so far have not proved this assumption. [11,29].

The argyrophilic network system of U. parduczi and P. caudatum. The visual demonstration of the argyrophilic network system in the food va-

cuole was a surprising result of our experiments, for this system is not visible or appears in fragments outside the food vacuole [FOISSNER, unpublished]. Considering that this network system (Figs 13—17, 21, 22) was already visible before budding off of the ingestion vacuole, it must be assumed that the food vacuole has already been penetrated in this stage of development by substances rendering these structures argyrophilic. It may be excluded that the argyrophilic structure was newly formed in the vacuole for developmental structures were never seen.

The quadrangular network in *P. caudatum* reminded of the pellicle structure of this ciliate [19, 37], being obviously differen tfrom the indirectly connected hexagonal silver line system described by KLEIN [23] (compare Fig. 11). KLEIN [25] and PÁRDUCZ [28] described in *U. marinum* an indirect silver line system appearing very similar to the network in *U. parduczi* described in the present work. Nevertheless, in the light of recent research this resemblance seems to be accidental, at least as regards KLEIN's indirect system (FOISSNER, unpublished.) The argyrophilic network may be considered a pellicle structure resembling that described by PÁRDUCZ [28] in *U. marinum*.

The interpretation of the argyrophilic network system of *U. parduczi* and *P. caudatum* as a pellicle structure seems to be proved because corresponding structure could not be demonstrated in the present experiments in *C. campylum*, a ciliate having no special outer pellicle structure [29].

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