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ELECTRONMICROSCOPICAL STUDIES ON THE ARGYROPHILIC STRUCTURES OF COLPIDIUM CAMPYLUM (CILIATA, TETRAHYMENIDAE)

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Abstract

Comparative light- and electron microscopical analysis of the argyrophilic structures in wet silvered *Colpidium campylum* has led to the following results. (1) The silverline meridians order 1 and 2 are located in the epiplasm, beneath the adjacent alveolar membranes of the pellicle. They are closely connected with the basal bodies, the protrichocysts and the excretion pore. Thus, the argyrophilic substance is continuous in the cortex of *C. campylum*. (2) The basal bodies are argyrophilic mainly on their proximal thirds and are surrounded by meridians order 1 in a ring-like fashion. However, the argyrophilic substance of the meridians order 1 breaks into the basal bodies and the distal parts of the cilia and surrounds the parasomal sacs. (3) The protrichocysts, except their apices, are surrounded by silver aggregates. These are localized on the outer side of the cytoplasmic membrane limiting the protrichocysts, and this membrane is connected with the endoplasmic reticulum. The disappearance of the silver aggregates soon after the protrichocysts have been discharged suggests that the argyrophilic substance is resorbed in the cytoplasm. The electron microscopical findings enable a better understanding of the light microscopical observations concerning the location of the argyrophilic substance in both resting and functioning protrichocysts. (4) The excretion pore in its whole extension is surrounded by silver aggregates which are located tightly beneath the pellicle. (5) Attempts were made to correlate the electron microscopical findings with the light microscopical ones, and a fibrillar nature of the silverline system of tetrahymenid ciliates is suggested.

Introduction*

Recently, having demonstrated by electron microscopy the subpellicular location of the SL* system (a formation discovered by KLEIN [12, 15]) in *Colpidium colpoda*, we [6] have refuted the hypothesis proposed by PITELKA [19] and other electron microscopists [for detailed literature, see 6] for the position and structure of this system. We have mainly studied the position and structure of SL meridians order 2. The arrangement and the location of the silver deposition at the basal bodies, protrichocysts, and SL meridians order 1 require further studies.

I had performed such investigations now in *Colpidium campylum*, a species closely related to *Colpidium colpoda*. In the present work, the findings

* In this paper the following abbreviations are used: SL = silverline, AS = argyrophilic substance.

in *C. colpoda* have been reproduced in *C. campylum*, and the site of silver deposition at the protrichocysts, basal bodies, parasomal sacs, SL meridians order 1 as well as those at the excretion pore have been investigated in detail.

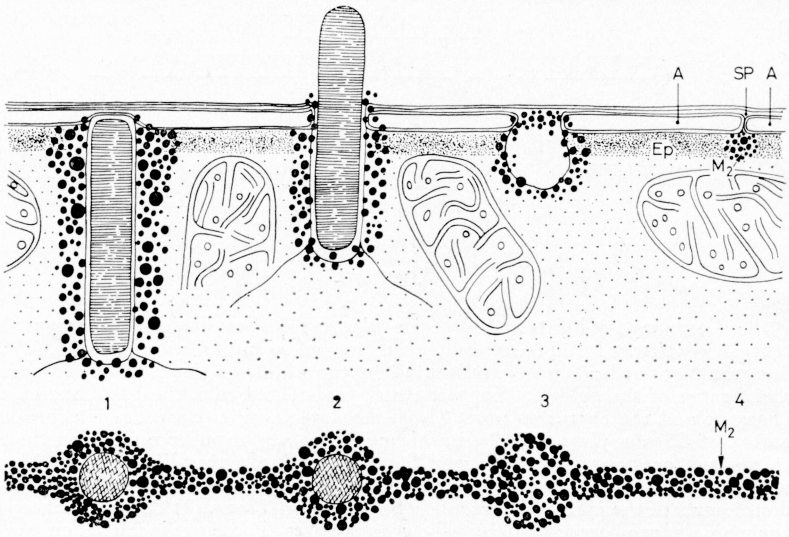


Fig. 1. The upper half is a schematic drawing of the silver deposition at resting and functioning (2—4) protrichocysts of *C. campylum* in longitudinal section. In the lower half the corresponding stages, recognizable even light microscopically, are shown in cross section. The SL meridians order 2 (M_2) are localized in the epiplasm (Ep), beneath the adjacent alveolar membranes of the pellicle (A) and enclose the protrichocysts. Further explanation in text

Material and method

Colpidium campylum, a ciliate of about 70 μm in size, very common in α-mesosaprobe and polysaprobe puddles, was cultivated in plant infusions. The species was determined according to the criteria recommended by KAHL [11], FOISSNER [5] and MAC COY [17].

For light and electron microscopy, the animals were sucked off from the surface of the infusion with a pipette, carefully centrifugated and, without any washing, poured over with the fixative.

Dry [8, 12, 15] and wet [3] silver preparations were comparatively examined under the light microscope. The procedure of wet silver impregnation was the same as described by CORLISS [3].

Preparation for electron microscopy. Fixation according to PALADE [18] at pH 7.5 for 15 min. The osmium tetroxide was washed off with the stock puffer solution, the preparation was dehydrated in an alcohol series, kept in propylene oxide for 30 min and embedded in Epon 812.

Dehydration of wet silvered specimens was interrupted at 50% alcohol concentration, then they were separated from the slide together with the gelatine layer with a razor blade. The dehydration in the alcohol series was continued subsequently (separation of completely dehydrated preparations fails!). The animals, embedded in the gelatine layer, were then placed in propylene oxide for 30 min and embedded in Epon 812.

Thin sections were made by means of a diamond knife with a Reichert OMU-2 ultramicrotome and spread on a carbon strengthened, pioloform filmed slide. Counter staining: 15 min in an alcoholic (50%) uranyl acid solution and 15 min in a lead citrate solution after REYNOLDS [20]. For electron microcopical investigations, the EM 9S of the firm Zeiss has been available for use.

Results

Light microscopical studies

The SL system in *C. campylum* as seen in dry silvered specimens (8)

Considering that numerous studies on the SL system of *Colpidium campylum* have been published [5, 10, 13, 14], we described this system very briefly, completed by several micrographs (Figs 2 –5). Based on their connec-

Fig. 2. Right lateral aspect of the SL system of *C. campylum*. The SL meridians order 2 (M_2) originate near the apical pole from the SL meridians order 1 (M_1) and return into the same below the excretion pore (Ex). Dry preparation, × 1 200

Figs 3, 4. High power magnification of the SL system of *C. campylum*. The basal bodies (Bk) located in the SL meridians order 1 appear unevenly impregnated. The appearance of the relation bodies of the protrichocysts (P) depends on the stage of function of the organelles. Wet preparation, × 3 000, × 3 200

Fig. 5. A highly argyrophilic excretion pore (arrow) connected with the adjacent SL meridians order 1 and 2. Wet preparation × 3 200

Fig. 6. A slightly oblique cross section through *C. campylum*. Note the fibril system typical of tetrahymenid ciliates (kinetodesmal fibre = kf, postciliary tubuli = pt, transverse tubuli = tt), a pellicular alveole (A), and an epiplasm (E). Method "a", × 48 000

tions with certain organelles, SL meridians order 1 (Fig. 2, M_1) and order 2 (Fig. 2, M_2) are to be distinguished. The basal bodies of the cilia (Figs 3, 4, Bk) appear located in a regularly meridional row, viz., in meridians order 1, which often show an undulant course (Fig. 4). The basal bodies appear as heavy impregnated argyrophilic granules showing no special fine structure.

The meridians order 2, which continue in the relation bodies of the protrichocysts, are located just between the rows of the basal bodies. They arise near the apex from meridians order 1 and are emptied near the antapex into the same structure (Fig. 2). Unlike meridians order 2 in *C. colpoda*, those in *C. campylum* are usually not divided into two or three SLs [comp. 5]. In the rare cases when they are, there are well defined anastomoses between the separated parts of meridians order 2. Similar anastomoses may occur between SL meridians order 1 and 2 as well (Fig. 3). The relation bodies of the protrichocysts are arranged in the SL meridians order 2 at very irregular distances (Figs 2, 3, 4). They appear as homogenous AS (Fig. 2) accumulated in an area about 1 μm in diameter. Occasionally, heavily impregnated rings about 1.5 μm in diameter have also been seen.

The excretion pore (Fig. 2 Ex, 5 arrow) is an heavily stained argyrophilic ring with a much less argyrophilic centre. The neighbouring meridian order 1, sometimes also the neighbouring meridian order 2, runs into the argyrophilic ring of the excretion pore (Fig. 5).

The SL system in *C. campylum* as seen in wet silvered specimens (3)

Like in *C. colpoda* [comp. 6], there are no principal differences in *C. campylum* between dry- and wet silvered SL systems. The latter are sometimes impregnated so finely that they are practically invisible. Similar difficulties were met in the electron microscope technique, viz., one often could not decide if an intensely impregnated specimen was present in a semi-thin section. Too finely impregnated SL systems are of limited use in the electron microscopy because in such sections the SLs are scarcely elevated over the fine nonspecific precipitates.

The impregnation mode of the basal bodies and of the relation bodies of protrichocysts provides the only differences between pictures obtained with dry and wet preparation. As shown in Figs 3 and 4, the impregnation of the basal body apparatus is quite uneven. Some appear as a heavily argyrophilic grain, others as a ring carrying one or more argyrophilic grains of variable size. I could not differentiate between basal grain and accessory grain as described by Klein [13] and Gelei et al. [10]. It is a further difficulty that protrichocysts occasionally occurring adjacent to basal bodies and are then mistaken for an accessory body. In wet silvered specimens, ring-like silver deposits are

often seen at the site of the protrichocysts (Figs 3, 4, P). This finding, very important for an understanding of the function of protrichocysts, is dicussed in detail below.

Electron microscopical studies

Examination of *C. campylum* prepared by method "a"

The fine structure of *C. campylum* has been described in some detail by PITELKA [19]. I cannot add much to his data, which have been completed more recently by very detailed observations concerning the fine structure of related ciliates [1, 4, 21]. The organization of the cortex of *C. campylum* is very similar to that described in some detail for *C. colpoda* [6].

The pellicle consists of the cell membrane, which continuously surrounds the whole cell, and the membrane bounded alveoles (Figs 1, 6, A). The silver should be deposited at the joining sites of these alveoles [19]. The fibrogranular epiplasm (Figs 6, 8, EP), about 80 nm in thickness, is located beneath the inner alveolar membrane. It becomes very thin near the basal body and then passes through this body, in which it forms the basal plate. The arrangement of the cortical fibrillar systems (Fig. 6) corresponds to the situation described by ALLEN [1] and ELLIOT et al. [4] for *Tetrahymena pyriformis*, and the same is valid for the structure of the protrichocysts (mucocysts) and the excretion pore.

Examination of *C. campylum* prepared by method "b"

Silverline meridians order 1 and 2. As shown in all the Figures presented in this paper SL meridians order 1 and 2 are located in the epiplasm, beneath the joining site of the pellicular alveoles (Fig. 9, arrows). They are about 80 nm in diameter and built up of silver aggregates of variable size. The distances between these aggregates are sufficient to separate them from one another. The size of the silver aggregates and the diameter of the SLs depend on the quality of the preparation, viz., in heavily impregnated preparations the silver aggregates are large (some 40—80 nm) and are very near to each other (Fig. 7), whereas in finely impregnated specimens they are much smaller (some 10—40 nm) and are well separated from each other (Figs 8, 9, 11). Consequently, the SLs are larger in diameter in heavily impregnated animals than in finely impregnated ones. The SLs are indistinctly limited from the cytoplasm and the epiplasm (e.g. Figs 8, 9, 10, 11). They are packed most tightly at the border between epiplasm and cytoplasm (Figs 9, 11) and decrease in both size and number towards the pellicular membranes.

The basal bodies, cilia and parasomal sacs. It has been shown without any exception that, independently of the degree of impregnation, only the proximal thirds of the basal bodies are argyrophilic (Figs 12, 13, 16, 19). Their

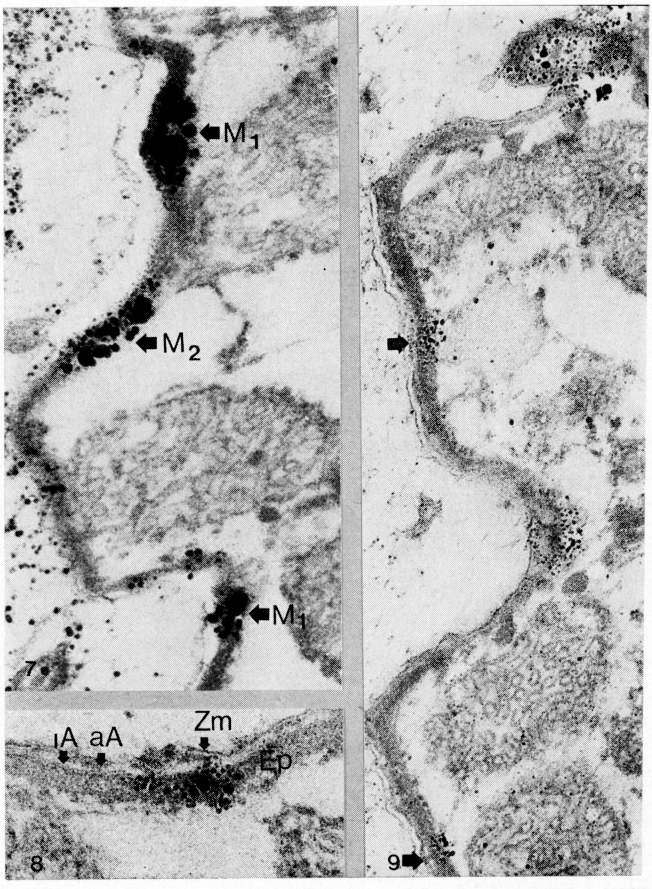


Fig. 7. A cross section showing two SL meridians order 1 (M_1) and a slightly obliquely sectioned SL meridian order 2 (M_2). SL meridians are built up of very distinctly large silver aggregates. Method "b", × 56 000

Fig. 8. High power magnification of SL meridians order 2. Silver aggregates are seen only in the epiplasm (Ep), beneath the cell membrane (Zm) and beneath the outer (aA) and inner (iA) alveolar membrane. Method "b", × 80 000

Fig. 9. A cross section showing two SL meridians order 1 with basal bodies, and two SL meridians order 2. It is clear that the latter are below the joining site of the pellicular alveoles. Method "b", × 80 000

middle and distal parts show very weak, if any, argyrophilia (Figs 12, 16). It is especially clear in cross sections (Figs 18, 20) that the majority of the silver aggregates was found around the basal bodies while much less aggregates

occurred in their centre. However, no sharp border could be demonstrated between the silver aggregates inside and those outside the basal bodies.

Beside the cilia, mainly the axonema part adjacent to the basal bodies shows argyrophilia (Figs 16, 19). Proximally to this, no specific silver deposi-

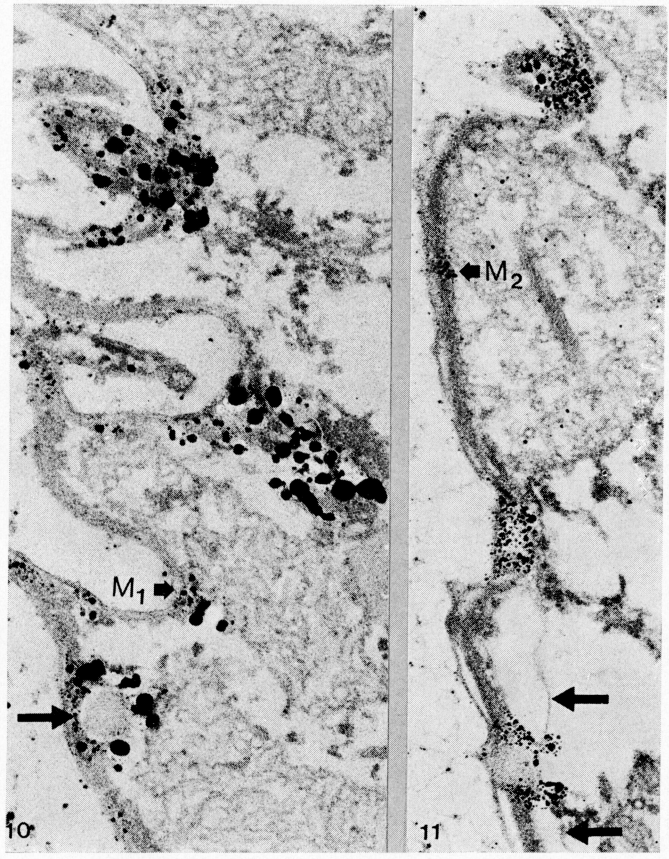


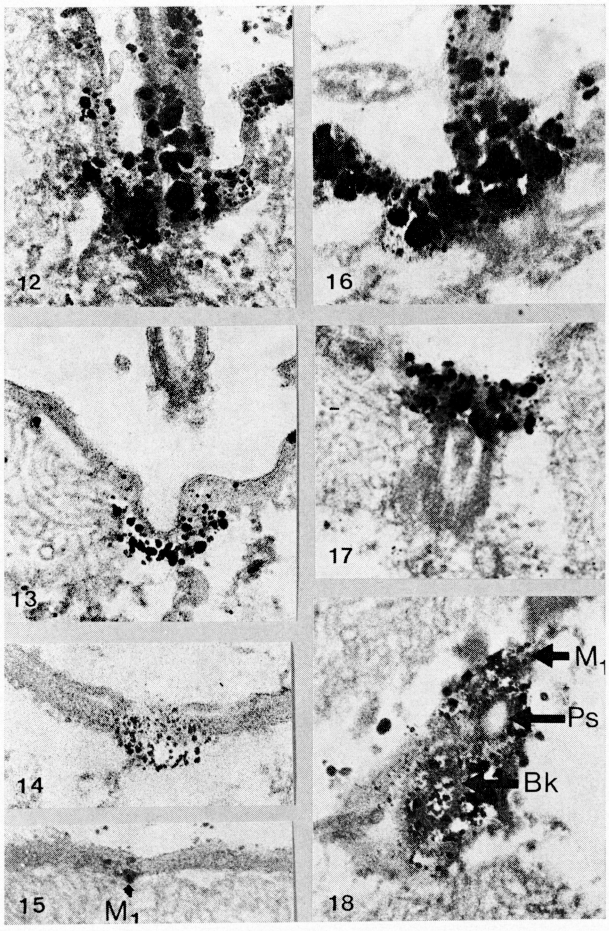
Fig. 10. An oblique section. Note the ring-like silver deposition around a protrichocyst (arrow) as well as around a basal body and a SL meridian order 1 (M_1). Method "b", × 64 000
Fig. 11. Cross section of a very finely impregnated *C. campylum* specimen. Note the SL meridian order 2 (M_2) in the epiplasm and the protrichocyst just before discharged. The membrane enclosing the protrichocyst (comp. Fig. 22) is connected with the endoplasmic reticulum (arrows). Method "b", × 56 000

tion could be demonstrated. Here, the occasionally observed aggregates were quite irregularly distributed.

The silver aggregates around the basal bodies continue without any interruption in aggregates around the parasomal sacs and build up the SL meridians order 1 (Figs 12—15, 18, 21). The parasomal sacs are surrounded

by silver aggregates in a bag-like manner (Figs 13, 18), but their central parts are free of them.

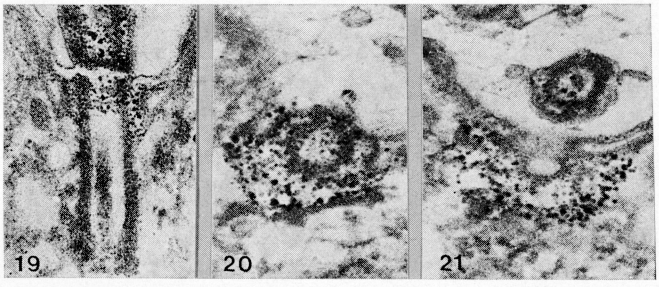
Protrichocysts. Examination of a great number of silver impregnated *C. campylum* enabled us to reconstruct, and control by light microscopy, the



Figs 12—15. This series of electron micrographs presents a good impression as regards the silver deposition at basal bodies and parasomal sacs. The silver aggregates in and around the basal bodies (Fig. 12) lead without any interruption to the parasomal sac and to the SL meridian order 1 (Fig. 15, M_1). Method "b", × 64 000, × 64 000, × 64 000, × 48 000
Figs 16, 17, 18. Irrespective of the degree of impregnation (comp. Fig. 16 with Figs 12, 19) it is clearly seen that only the proximal thirds of the basal bodies are argyrophilic. There are silver aggregates inside and around basal bodies. Method "b", × 64 000

exact location of the AS in relation to the resting and functioning protrichocysts (Fig. 1). Four phases could be distinguished, viz., (1) resting protrichocysts which are surrounded by a membrane originating in the endoplasmic

reticulum (Fig. 11, arrows); these are surrounded, in a bag-like manner, by a great number of silver aggregates (Figs 1 [1], 22). The aggregates, which continue without interruption in the SL meridians order 2 (Fig. 11), are carried tightly by the membrane surrounding the protrichocysts, but are not connected with the organelles themselves. The apex of the protrichocysts was always free of silver aggregates (Figs 22, 23). At the level of the epiplasm, however, these occur in a greater number, appearing in longitudinal sections as a wedge-like silver deposit (Fig. 22). The degree of silver accumulation as well as the size of the silver aggregates depends, just like in meridians order 1 and 2 and the basal bodies, on the preparation technique. (2) When the protrichocysts are pushed out, the pellicular membranes fuse and the organelles can leave the animal through the resulting circular gap (Fig. 1 [2]). Most of the AS remains in the animal (Fig. 23), but little amounts may be found tightly attached over the pellicle, suggesting that part of the AS is lost (Fig. 23, arrow) [compare 6]. (3) The bage-like vacuoles that contained the protrichocysts will diminish in size and soon disappear as the organelles have



Figs 19, 20, 21. Plane sections showing that silver aggregates of SL meridian order 1 (Fig. 18, M_1) continue without any interruption to the basal bodies (Fig. 18, Bk) and to the parasomal sacs (Fig. 17, 21, Ps). Method "b", × 64 000

been discharged (Figs 1 [3] 26). Meanwhile the silver aggregates are evenly distributed around the more or less spherical vacuole so that the silver aggregates appear diffusely distributed (Figs 1 [3], 25). (4) These aggregates diminish in number and eventually disappear at all as the gaps become smaller and smaller. The AS is obviously resorbed by the cytoplasm. Only SL meridian-order 2 remains visible; it runs without any interruption over the place where the organelles were released (Figs 1, 11).

The existence of four phases is consistent with the light microscopic findings (see discussion): phases 1 and 2 correspond to the ring-like silver deposit (Figs 4, P, 22—24), phase 3 correspond to the diffusely impregnated relation bodies (Figs 3, P, 25, 26) while phase 4 to meridians order 2 (Fig. 11).

The excretion pore. The light microscopical findings have been confirmed by electron microscopy also as regards the silver deposit at the excretion pore. In longitudinal sections of the excretion pores (Fig. 27) the very distinct, large silver aggregates were seen only under the pellicular membranes and under the alveolar membranes joining the pores. Although these should show light microscopically one or more uniformly impregnated grains, the silver deposit

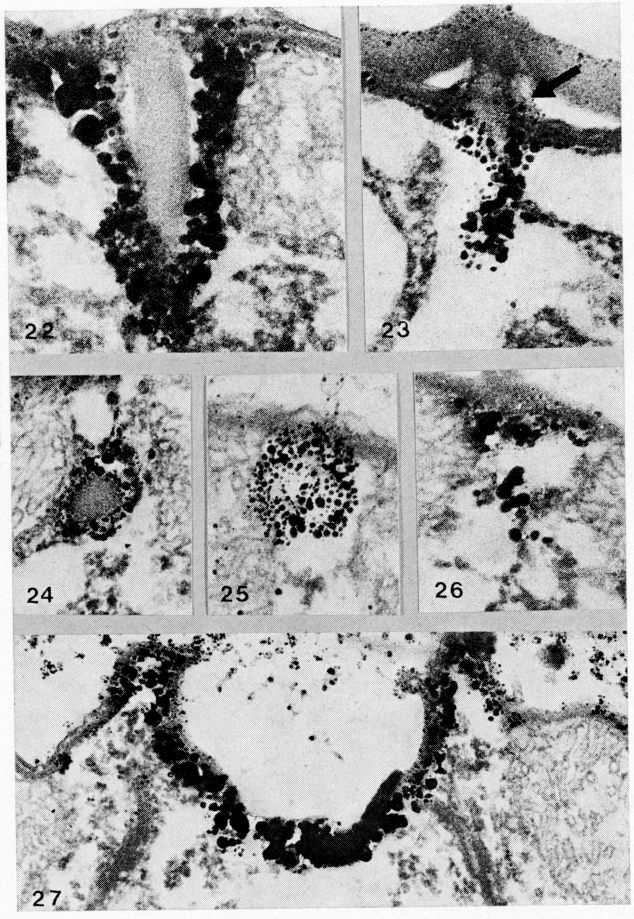


Fig. 22. Resting protrichocyst surrounded by bag-like arranged silver aggregates. These are located outside the membrane enclosing the organelle. Method "b", × 72 000
Fig. 23. When the protrichocysts are pushed out, a little AS (arrow) may escape. Method "b", × 64 000
Fig. 24. Resting protrichocyst. Cross section. Note the ring-like silver deposition. Method "b", × 64 000
Figs 25, 26. Protrichocyst "loop-holes" in plane section (Fig. 26). The silver aggregates are nearly evenly distributed on the surface of the loop-hole. Method "b", × 64 000
Fig. 27. Excretion pore, longitudinal section. Note the silver aggregates exclusively under the pellicular membranes. Method "b", × 48 000

often appears ring-like (Fig. 5). This discrepancy can easily be explained by the following considerations: (1) The ring-like formation may be an optical artefact which arises because the centres of the pores, being located considerably deeper, do not draw a sharp picture. In fact, weak argyrophilia can be seen in the centres of the pores as well if the specimens are examined correctly. (2) Furthermore, the silver-free centre may be an expression of a certain stage of function of the contractile vacuole. When the vacuole is emptied, the membranes limiting the pore are broken through [4]; consequently, the AS in the center of the pore must disappear. During the subsequent regeneration of these membranes AS must develop again beneath the membranes, making AS demonstrable by electron microscopy (Fig. 27). It is for the same reason, that homogeneously impregnated pores in variable number are seen in many light micrographs.

Discussion

SL meridians order 1 and 2

The present studies have shown that the SL meridians order 1 and 2 are located in the epiplasm of *C. campylum*. Accordingly, they can be regarded as subpellicular structures [6]. In *C. colpoda*, on the other hand, we [6] found the SL meridians order 2 in the epiplasm, whereas the meridians order 1 somewhat deeper. A revision of the *C. colpoda* preparations has recently shown that the SL meridians order 1 are located in the epiplasm too. The earlier erroneous conclusion can be explained by the fact that we did not take into consideration the silver deposit around the parasomal sacs which extends deep into the cytoplasm (comp. Figs 13, 14). Thus, we concluded that the SL meridians order 1 are located somewhat deeper, in a variable position.

The protrichocysts

KLEIN [15, 16] described the position of the AS at resting and functioning tricho- and protrichocysts as follows. (1) Tricho- and protrichocysts are connected by a relation grain, which is somewhat below the apex, with the SL system. (2) At the site where an organelle is being discharged, the SL forms a ring, i.e., a circular fibril through which the organelle leaves the animal. The relation grain, remaining on the relator, leaves the animal together with the secretion organelle. (3) The strong argyrophilia around the circular fibril is due to the activation of a finely meshed SL system at the site of discharge. (4) The gap (a "loop-hole") and the ring are closed soon after the secretion organelle has left the animal.

The present electron microscopical studies have led to a controversial interpretation of the light microscopical findings (see p. 000): (1) No relation grain as interpreted by KLEIN [15, 16] exists at the protrichocysts (Figs. 2, 23). The fact that KLEIN [16] found a relation grain in the lumen of a circular fibril might be explained as follows: as a protrichocyst has been discharged, part of the AS extends, more or less evenly, over the gap and thus a relation grain may be simulated (comp. Figs 25, 26). (2) There is no circular fibril around the protrichocysts, for the AS surrounding the protrichocysts along its full lenght leaves only its apex free (Fig. 22). KLEIN [16] himself emphasized the rarity of preparations showing such circular fibrils. This may therefore be interpreted so that resting protrichocysts around which the light microscope shows a ring-like silver deposition caused by the bag-like silver accumulation around these organelles (see Fig. 22) occur very seldom in dry prepared specimens because the protrichocysts, owing to the stimulus due to dehydration, are soon discharged and, consequently, mainly the resorption stages of "loopholes" are seen (Figs 25, 26). This interpretation is supported by the observation that such circular fibrils have been seen much more frequently in wet prepared specimens (Figs 3, 4), which had been killed by a procedure of much shorter duration. (3) The intensive argyrophilia of the "circular fibril" described by KLEIN [15, 16] arises from the bag-like AS surrounding the protrichocysts (Fig. 22). The concentration of AS here causes a light microscopically demonstrable argyrophilia, more intensive than in SL meridians order 1 and 2. (4) The AS around the protrichocysts is resorbed as the organelles have been discharged. This is supported first of all by the light microscopic findings in dry prepared specimens, viz., the majority of SL meridians order 2 show neither argyrophilic grains nor rings [13].

Based on these findings we recommend the term "relation body" (Relationskörper) instead of the terms "Zirkularfibrille" and "Relationskorn" proposed by KLEIN [16].

The basal body

The electron microscopic findings concerning the silver deposition at the basal bodies and parasomal sacs do not correlate with the light microscopic observations unequivocally. This is because the structural units are at the threshold of light microscopic visibility and thus can be misinterpreted. These difficulties point to the fact that the structure of the basal body apparatus of *C. campylum* as described by KLEIN [14] and GELEI et al. [10] is somewhat different. The circular fibrils of these authors may correspond to the silver deposits around the basal bodies (Figs 18, 20). The argyrophilic granules (basal grain and accessory grains) on and in these rings should mostly correspond

to the basal bodies with their parasomal sacs. Since these grains may occur in great number and are not always round (Figs 3, 4), we attribute some role to preparation artefacts and/or optical deformations.

Structure and function of the SL system

It was found shortly before our electron microscopical studies on *C. campylum* that, in peritrichous and hypotrichous ciliates, the silver lines are identical with certain cortical fibrils [7, 9]. The same could be not demonstrated in tetrahymenid ciliates. In conventionally prepared specimens of *C. colpoda* [compare 6] and *C. campylum* no specific material was found at the sites of silver deposits. I am nevertheless convinced that the SLs are fibrils even in tetrahymenid ciliates, though, these fibrils cannot be demonstrated with the preparation techniques used so far [compare 6]. The SL systems of ciliata show light microscopically such a very similar structure that it would be highly unlikely that they were build up of fibrils only in peritrichous and hypotrichous ciliates and not in tetrahymenid ciliates. It is however possible that the SL systems of different ciliates show some structural dissimilarities.

The present investigations emphatically suggest that the SL system is connected with several cortical structures, viz., basal bodies, protrichocysts and excretion pore. These and many other observations [see 6, 7, 9] support the view that the SL system plays part in conveying locomotoric impulses and in building up new formations [15].

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