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THE CYTOPYGE OF CILIATA

I. ITS FUNCTION, REGENERATION AND MORPHOGENESIS IN URONEMA PARDUCZI

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Abstract

The cytopyge of *Uronema parduczi* has been investigated. The changes in the silver-line system have been discussed with special thoroughness. Our present knowledge of the cytopyge of Ciliata is reviewed. (1) The cytopyge serves for excreting undigestible solid metabolic products. The excreted faecal ball, consisting of a granular mucous ground substance, is approximately spherical and often contains relatively large inclusions. (2) The cytopyge is located in the direction meridian, its aperture being preformed. It is active relatively rarely. The excretion process lasts several seconds and leads to an increased lability in the silver-line system. At the same time, the occlusion membrane and the silver line of the cytopyge and parts of the direction meridian are destroyed. (3) Excretion is followed by regeneration. First of all the argyrophil substance accumulates in the vicinity of the cytopyge. The destroyed parts of the direction meridian and the cytopyge silver line are reorganized in this substance. (4) After repeated functionings, the cytopyge silver line develops a high degree of branching, a phenomenon which may serve as an indicator of age, or of erosion, and disappears during the reorganization of the silver-line system. The daughter cytopyge silver line originates from a branch of the silver lines of the buccal cavity. (5) An active co-operation of the silver-line system in the regeneration, reorganization and morphogenesis of the cytopyge has been demonstrated.

Introduction

The cytopyge, also called cell bottom anus or cytoproct, is an organelle characteristic of many Ciliata. As generally accepted [6, 11, 12, 13, 22, 23, 25, 46] it serves for excreting undigestible solid metabolic products.

Mainly due to methodical difficulties, cytopyge is one of the least examined organelles of Ciliata. Hence, its mechanism of function is not quite understood. The first detailed reports in this field were published by DOFLEIN [11], KAHL [25], KLEIN [30], GELEI [20] and PÁRDUCZ [40]. More recently, the cytopyge in different Ciliata has been subjected to thorough light- and electronmicroscopic studies [12, 13, 23, 24, 46], which have resulted in the discovery of numerous morphological peculiarities and in clarifying the basic cytopyge mechanism in *Paramecium caudatum* [13]. However, the electronmicroscopic knowledge in this field is still incomplete and partially contradictory [13, 46].

Since the cytopyge always opens and is localized at the same site, its

opening must pre-exist even in those Ciliata in which it cannot be detected by light microscopy after a complete regeneration.

Several authors have reported on the cytopyge of the family *Uronematidae* without going in detail [9, 10, 16, 40, 48].

The object of the present study has been to investigate the cytopyge of *Uronema parduczi* and several other Ciliata. Besides, special attention is paid to the dynamic actions of the silver-line system.

Considering that no comprehensive review on the cytopyge of Ciliata has been published, we have made an attempt to review the available literature.

Material and method

In general, *Uronema parduczi* [16] served as test material. For comparison, the following Ciliata species were studied: *Uronema marinum*, *Colpidium kleini*, *C. colpoda*, *C. campylum*, *Tetrahymena pyriformis*, *Cyclidium glaucoma*, *Colpoda steini*, *Euplotes* sp., *Prorodon teres*, *Spirostomum ambiguum*, *Stentor polymorphus*, *Thuricola folliculata* and other *Vorticellidae*.

Most of these species were isolated from infusions and cultured on hay or lettuce extract. Some others (e.g. *Thuricola folliculata*) had to be examined immediately after having been caught, for we failed to culture them.

Besides various cytological staining methods, none of which except GELEI's [18] osmium—toluidine blue method have resulted in clear pictures, mostly silver methods both "dry" [15, 19, 32] and "wet" [4, 19] were applied. All the silver methods led to approximately the same results. The silver preparations shown in the figures in this paper were prepared by the technique evolved by us [15].

Especially great attention was paid for years on *in vivo* observations. In spite of this, defaecation could rarely be observed. We often failed to induce defaecation by mild pressure. Even the stimulating effect of slow dehydration or overnutrition was weak. Defaecation almost regularly occurred soon after excystation (e.g. *Prorodon*).

Results

The function of cytopyge

Defaecation ensues in all the species under study very quickly, within 2—60 seconds. First of all, a small bulge appears at the corresponding site of the pellicle; subsequently, the faecal ball may penetrate the pellicle, abruptly or gliding. The pellicle in numerous Ciliata (e.g. *Uronema*) does not recede before the egestion of faecal ball. Instead, it is destroyed at the specific site. The faecal ball under excretion is more or less spherical, sometimes tapering posteriorly [30] and it is often (e.g. *Prorodon*) surrounded by a case.

Silver preparations show few animals the cytopyge of which is just functioning at the moment of excretion. On the other hand, specimens with cytopyges in various phases of regeneration occurred more frequently. In silver preparation, the late function phase cannot be distinguished clearly from the early regeneration phase. In many small Ciliata (e.g. *Uronema*), the function leads to an increased lability of the silver-line system.

In *U. parduczi*, the cytopyge lies in the direction meridian (Richtungsmeridian) (Fig. 1, CYP, RM), appearing in the impregnated animal as a more or less ramified, highly argyrophil line (Figs 8—15). The direction meridian continues both posteriorly and anteriorly (Fig. 1, RM).

Fig. 4 shows a cytopyge in function or in a rather early phase of regeneration. A large round hole about 6 μm in diameter is clearly seen in the pellicle,

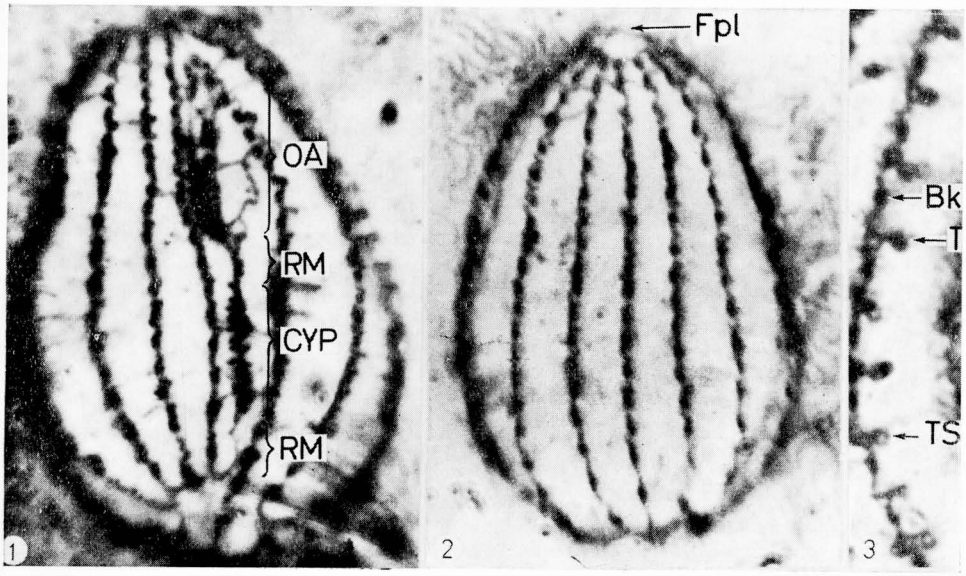


Fig. 1. Uronema parduczi, ventral view. OA = typical tetrahymenid oral apparatus, RM = direction meridian, CYP = cytopyge. Approx. ×1 800
Fig. 2. Uronema parduczi, dorsal view. Fpl = frontal plate having no cilia. Approx. ×1 800
Fig. 3. Uronema parduczi, high-power magnification of the ciliary meridian with trichocysts (T), trychocyst excretion holes (TS) and basal bodies (Bk). Approx. ×3 200

below the oral apparatus. The silver line of the cytopyge ran there and the bordering parts of the direction meridian have already been destroyed for comparison (see Figs 1, 10 and 18). At the edge of the open cytopyge, a highly argyrophil substance has already appeared.

The regeneration of cytopyge

Regeneration as controlled under the light microscope proceeds in all species under study in principally the same manner. Immediately after the discharge of the egestion vacuole, a new pellicle appears at the site of discharge, whereafter the site of discharge becomes invisible again. Nevertheless, according to the silver preparations the whole regeneration process must last at least 10—30 minutes. Otherwise, so many animals (approx. 4 percent) should not show cytopyge in regeneration.

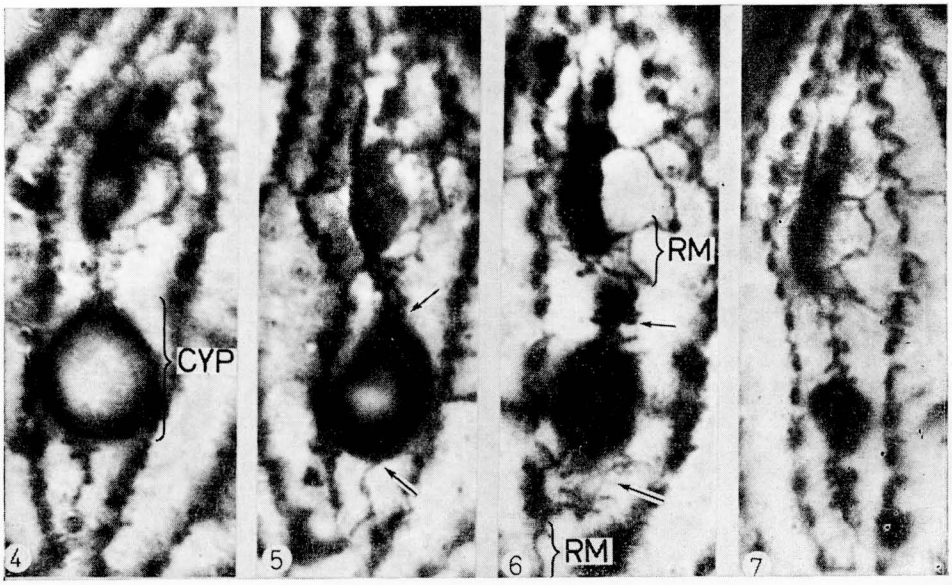


Fig. 4. Uronema parduczi, the function of the cytopyge. Note the wide opening of the cytopyge. Approx. × 2 200

Figs 5—9. Uronema parduczi, five successive phases of the cytopyge regeneration. Note the early increase and the subsequent decrease in the amount of the argyrophil substance. The new cytopyge silver line and the newly-formed parts of the direction meridian are formed in the argyrophil substance. Approx. × 2 200

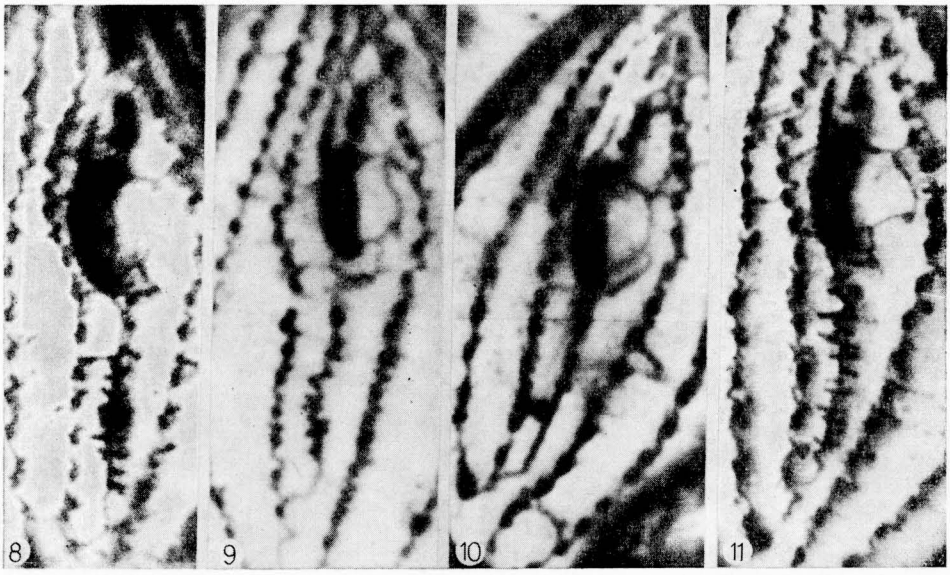
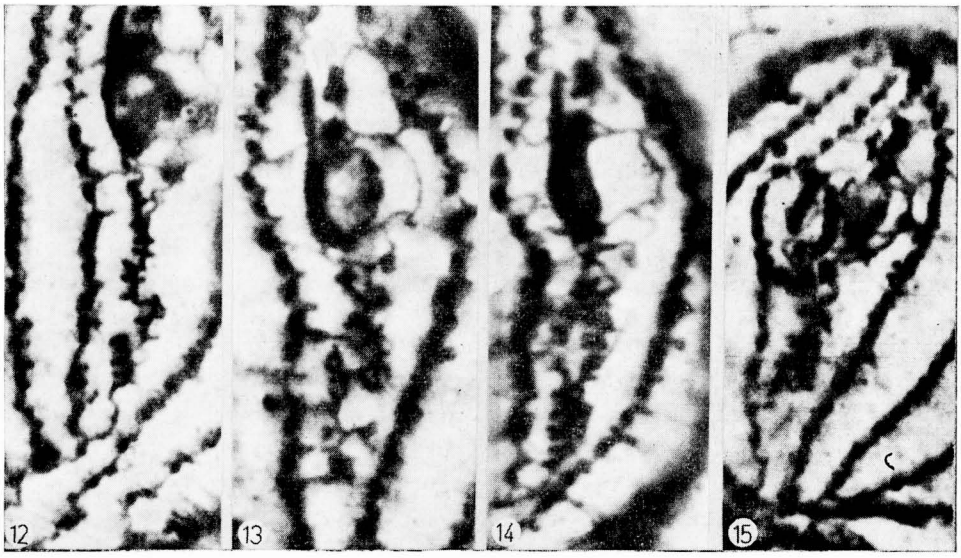


Fig. 10. Uronema parduczi, straight, unbranched cytopyge silver line of a very young specimen whose cytopyge, supposedly, has not yet been active. Approx. × 2 000



Figs 11—14. Uronema parduczi, examples for the advancing cleavage and branching of the cytopyge silver line after repeated functionings of the organelle. Approx. ×2 200
Fig. 15. Uronema parduczi, start of cytopyge re-organization during morphogenesis. A narrow-meshed silver-line system is formed in the cytopyge area. Approx. ×1 700

In *U. parduczi* the following parts of the organism are destroyed or impaired by the functioning of the cytopyge and should be regenerated subsequently: (1) the corresponding piece of the pellicle, viz. the occlusion of the cytopyge, (2) the cytopyge silver line, (3) parts of the direction meridian.

Figs 5—9 show the successive stages of regeneration. The extraordinarily intensive accumulation of the argyrophil substance indicates that this substance plays an important role in the regeneration process. Starting from the cytopyge opening (Figs 4 and 5) it covers, at last, the whole "wound surface" (Figs 5 and 6). The persisting part of the direction meridian is in close connection with this argyrophil mass (Fig. 5, arrows). In Fig. 6, a slight decrease in size of the cytopyge opening and a further accumulation of the argyrophil substance are to be seen. Consequently, the direction meridian gains more room and its regeneration becomes more or less complete. Parts of the cytopyge silver line have also been regenerated (Fig. 6, arrows). Fig. 7 shows an advanced stage of regeneration. The opening of the cytopyge is already rather small and the argyrophil substance, though reduced in mass, is still of high concentration. The cytopyge silver line has mostly regenerated and the direction meridian is already complete. In the further course of regeneration, the cytopyge opening steadily decreases in size and the argyrophil substance decreases in mass (Fig. 8) until the latter disappears (Fig. 9): the cytopyge has regenerated. As the regeneration attains an advanced stage, the lability of the silver-line

system decreases and becomes more and more normal [comp. 32] (Figs 4—9, compare with increased lability, p. 162).

Since, after each function, the cytopyge silver line becomes more argyrophil than the direction meridian (presumably, silver is deposited in a newly-formed fissure), both can be separated from each other without any difficulty.

Changes in the cytopyge during the life cycle

Morphogenesis of the cytopyge

Although little is known of the morphogenesis of the cytopyge, there is no doubt that the peculiarities of its morphogenesis are very variable.

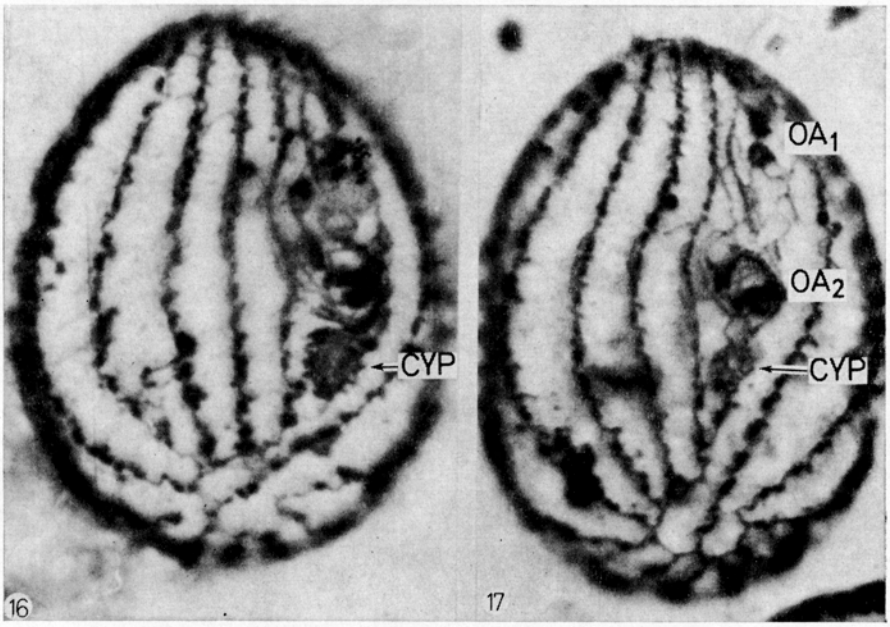
According to KLEIN [29], the new excretion vacuole in *Euplotes moebiusi* is in close relation to the caudal cirrus-forming fields. EBERHARDT [12] demonstrated in *Spirostomum* and *Blepharisma* the existence of a special gradient which, localized in the field of the cytopyge, presumably creates the posterior end. The cytopyge comes about in these Ciliata as an autonomous organelle in a certain anlage field and is already capable of functioning long before the end of the division. KACZANOWSKA and KOWALSKA [24] described in *Chilodonella cucullulus* a *de novo* formation and a continuous growth of the cytopyge during morphogenesis. They conclude that the actual position of the cytopyge is epigenetically determined.

In *U. parduczi*, like in many other Ciliata possessing a direction meridian, the cytopyge of the anterior division animal ("daughter animal") has no direct connection with that of the posterior division animal ("mother animal"). Apparently, indirect connections exist only through the silver-line system. It is not clear how the morphogenesis proceeds. It has only been demonstrated that the cytopyge, or the cytopyge silver line, which is reorganized during morphogenesis (see p. 167), derives from an originally poorly determined branch of the silver line of the buccal cavity. Fig. 18, showing a late stage of division, is especially instructive: both the cytopyge silver line and the direction meridian are constructed of several silver lines each of which arise in the buccal cavity (Fig. 18, arrow). Immediately before the separation of mother and daughter animals, the individual silver lines come into still nearer contact to each other and, at last, they appear as a single silver line (Fig. 10).

Re-organization of the cytopyge

Based on alterations in the argyrophil structures during morphogenesis, KLEIN [29] and KACZANOWSKA and KOWALSKA [24] described a re-organization of the cytopyge in *Euplotes* and *Chilodonella*, respectively.

In *U. parduczi*, too, the re-organization of the cytopyge ensues during morphogenesis. In numerous other Ciliata (e.g., *Colpidium*) on the other hand,



Figs 16—17. Uronema parduczi, the peak of cytopyge re-organization, which is in general closed already before furrowing. Note the newly-formed narrow-meshed lattice. Approx. ×1 900

no re-organization of the cytopyge could be demonstrated. Fig. 15 shows a very early stage of division. The re-organization of the oral apparatus has just started; the cytopyge silver line appears to be more or less unchanged; only some lattice-like formations, presumably the earliest signs of re-organization, appear in the immediate neighbourhood of the cytopyge. In a subsequent stage of morphogenesis (Fig. 16, arrow), the re-organization is clearly recognizable. Over the cytopyge, there is a narrow-meshed silver-line system, the edges of which are especially well visible. In a still later stage of division, when two oral apparatuses (OA_1 and OA_2 in Fig. 17) are already visible, the narrow-meshed lattice is especially pronounced. This is the top of re-organization. As the segmentation starts, the lattice formation begins regressing and is replaced by a single unbranched silver line (Fig. 18, see below).

Changes of the cytopyge silver line in the interphase individual

EBERHARDT [12] was the first to estimate the post-division age of *Spirostomum* and *Blepharisma* specimens on the basis of the position of the cytopyge.

The more or less abundant branching of the cytopyge silver line in *U. parduczi* represents an analogous phenomenon. As mentioned above, the cyto-

pyge is fully re-organized during morphogenesis and, at last, a straight unbranched silver line is formed (Figs 10 and 18). Obviously, the first branchings appear after division, more strictly, after the first function of the organelle.

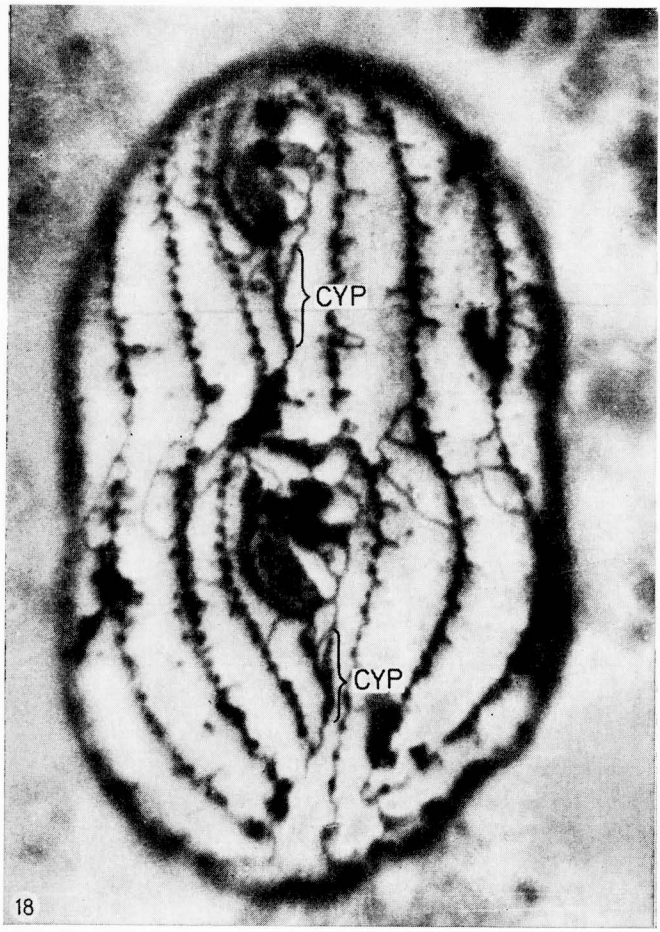


Fig. 18. Uronema parduczi, end of cytopyge re-organization. The animal is already furrowed. Note the cytopyge silver line and the direction meridian, both being formed from silver lines having originated from the buccal cavity. Approx. ×3 500

Since old cultures in which division activity is very weak are the richest in branches, it is clear that the more branchings are present the more times the cytopyge has functioned (Figs 11—14). An exhaustion phenomenon may also appear: branching may reach a level at which, more or less separated, two cytopyge silver lines exist (Fig. 14).

Shape, size and position of the cytopyge in different Ciliata

The cytopyge has often been described as a fissure-like formation in the pellicle [e.g. 6, 7, 24, 48]. It is not very variable in shape if there are special formations, such as cirri and silver lines in its surroundings (compare with [25)]. It has been found ranging from 5 μm *(Cyclidium)* to 50 μm *(Neobursaridium)* [39] in length. KAHL [25], who published an extraordinary large size for the cytopyge of the family *Sciadostomidae* and for that of the genus *Placus*, stated that it was as long as a half of the body and that it was visible in the living organism. Recent investigations on *Placus luciae* have not confirmed these data [17]. As to the location and existence of the anus contradictory data have been published (compare with [17, 25, 41].)

The anus is often near the terminal end of Ciliata. This is especially valid for *Holotrichida*. In *Peritrichida* and many (e.g., *Thuricola*), but not all, *Heterotrichida* (e.g., *Blepharisma*), the cytopyge is to be found in the vestibulum. The cilia of the adoral membranelles and/or those of the vestibulum take over the function of whirling faecalia from the immediate vicinity of the infusor [25]. The same has well been demonstrated in *Thuricola folliculata*.

The cytopyge has reached its highest differentiation in the order *Entodiniomorphida*. Here, several authors distinguish a rectal part from the real anal opening [33, 49]. In the rectum of *Ophryoscolecida*, a complex fibrillar network of unknown function has been demonstrated [49].

The occurrence of cytopyge in different Ciliata

Not all Ciliata possess a defaecation apparatus corresponding to cytopyge. It has clearly been demonstrated for the following taxons: *Gymnostomatida* [11], *Rhabdophorina* [25], *Cyrtophorina* [24], *Trichostomatida* [45], *Hymenostomatida* [6, 30], *Tetrahymenina* [6], *Peniculina* [31, 50], *Pleuronematina* [32], *Peritrichida* [22, 25], *Sessilina* [22], *Mobilina* [22], *Heterotrichida* [39], *Tintinnida* [21], *Entodiniomorphida* [33, 49], *Hypotrichida* [32]. In spite of thorough studies, cytopyge could not yet been demonstrated for the orders *Suctorida*, *Apostomatida*, *Astomatida*, *Thigmotrichida*, *Oligotrichida* and *Odontostomatida*, and the suborders *Arhynchodina*, *Rhynchodina* and *Licnophorina* [2, 3, 5, 14, 26, 27, 28, 35, 36, 43, 44]. Further studies should decide whether it is really absent.

This, surely incomplete, list shows a rather great variability in the occurrence of cytopyge, which is, however, independent of the degree of organization accepted within the system of these Ciliata. The cytopyge is absent, first of all, in parasitic and ectocommensal Ciliata.

Discussion

Function of the cytopyge

Recently, ESTÈVE [13] has revealed the basic features of the cytopyge mechanism of *Paramecium caudatum* by electronmicroscopic studies. Accordingly, the egestion vacuole is advanced to the cytopyge by long tubular fibrils extending deep into the animal. At last, it is pushed out due to a sphincter-muscle-like contraction of these fibrils which run conically over the opening of the cytopyge.

The simple elementary membrane closing the cytopyge, which was first described by SCHNEIDER [46], is fully destroyed. Based on electronmicroscopical observations JURAND [23] has concluded that in the moment of defaecation the cytopyge opens widely and so the egestion vacuole will be discharged. This view, though agrees with the light-microscopic observations of numerous authors [11, 25, 30, 34], has been refuted by SCHNEIDER [46] on the basis of WICHTERMAN's finding. The latter author described the excrement of the *Paramecium* as a flow of fine particles instead of being a spherical mass. However, since WICHTERMAN [50] did not describe the methods he used, the validity of his experience is doubtful.

ESTÈVE's "sphincter-muscle" theory is consistent with light-microscopical experiences. In fact, contraction-like movements of the neighbouring cytoplasm have often been observed ("deutlich wahrnehmbares Pressen") as characterized by DOFLEIN [11]. In this way, it can be understood that the pellicle, i.e., the membrane closing the cytopyge is torn and destroyed (e.g., in *Uronema* and *Colpidium*). This view is supported by JURAND's [23] observation that, together with the contents of the cytopyge, parts of the cytoplasm are pushed out.

According to the investigations carried out so far, the faecal ball leaves the cytopyge as a relatively large (e.g., in *Nassula ornata* 20×12 μm in size, [34]) spherical or ellipsoid mass. The fact that the faecal vacuoles are often larger than the nutrient vacuoles suggests that several egestion vacuoles may form a common faecal ball. This phenomenon already attracted KAHL's [25] attention. RUDZINSKA [45] demonstrated the same by electron microscopy in *Colpoda*.

The role of the silver-line system in the regeneration of the cytopyge

In *U. parduczi* and many other Ciliata [30], argyrophil substance accumulates at the edge of the open cytopyge early in the regeneration process, then it intensely increases in amount and after or still during the regeneration, disappears. For this reason, an essential function is attributed to this substance in the regeneration of the cytopyge. There is no doubt that the destroyed

parts of the direction meridian as well as the new cytopyge silver line originate from the argyrophil substance of the regenerating cytopyge (Figs 4—9). It is, however, unclear how this process develops in detail and how the function of the argyrophil substance in the regeneration process is realized. Similarly, it is difficult to tell how far the relation between the silver-line system and the regeneration process extends. Nevertheless, the described processes unequivocally indicate a tendency of the silver-line system to actively co-operate in the basic functions of the cell and to restitute itself by an autoplasmatic formation after a partial destruction [32].

The problem of excretion by Ciliata without cytopyge

It has been shown that many Ciliata possess no defaecation mechanism comparable to the cytopyge-mechanism. These are to some extent comparable to cells of many metazoa which are not supplied with a defaecation mechanism [47]. The accumulation of undigested, undischargeable metabolic products is considered as a cause of ageing of both meta- [47] and protozoa [44].

The interesting investigations of RUDZINSKA [44] on *Tokophyra infusionum* have shown that in this Suctoria, having no cytopyge, resting bodies accumulate with advancing age. The resting bodies presumably consist of undigestible food. Pigment-like metabolic products, never occurring in Ciliata with cytopyge, (e.g., *Colpoda* [45]), were especially pronounced. Various other "pigments" (see the summary in ANDERSON [1]) found in protozoa might also be interpreted as undigestible metabolic products.

Recent investigations on *Ancistrocoma pelseneri* [27], another Ciliata having no cytopyge, suggest that undigestible solid (!) food may be excreted by the contractile vacuoles. In this context, these Ciliata (e.g., *Euplotes*, [29] *Spirostomum* [12], *Blepharisma* [12]) are of special interest which possess only one temporary opening for the cytopyge and the contractile vacuole. In these cases the discharge of fluid and solid metabolic products occur in the same organelle. It seems therefore reasonable to suppose that contractile vacuole and cytopyge are phylogenetically related organelles, and this view is supported by electronmicroscopic findings [13]. In this way also the excretion by Ciliata having no cytopyge might be understood. Supposedly, they excrete a large part of their undigestible metabolic products in a more or less liquefied state by the contractile vacuole. The substances having not been liquefied or discharged will accumulate as resting bodies.

The nature of the excreted material

Little is known of the composition of the faeces of Ciliata. The present investigations have shown that its composition depends on the species and on the nutrition. In *Colpidium*, *Tetrahymena*, *Glaucoma* and *Uronema*, the

approximately spherical faecal balls are light gray in colour and granular in structure. Sporadically, also larger forms and intensively refractile grains occur inside faecal balls. In the faeces of *Spirostomum* small, highly refractile grains were found which resembled the body pigment of the animal (compare with p. 171). Besides, round, yellowish inclusions of variable size were often noted. *Stentor* and *Thuricola* excrete very little corpuscular excrement. In the granular basic substance more or less large undefined particles occur.

Electronmicroscopic investigations allow us to obtain some information on the composition of the excrement during discharge. Unequivocally, filamentous and granular structures, sometimes bacterial membranes were found inside egestion vacuoles [13, 23, 45, 46]. According to RUDZINSKA [45] even living undigested bacteria seem to be excreted. We have found no chemical analysis of the excrement in literature.

Systematic value of the cytopyge

According to the investigations carried out so far, the taxonomical value of the cytopyge is very little. KAHL [25] has found some relationship between the location of the cytopyge and the organization level of a ciliate, stating that "bei primitiveren Formen meistens dem Hinterende (terminal), bei höheren Formen meist dem Hinterende (Vorderende?!) genähert ist, sonst aber sehr verschieden liegt". GELEI [see 42] and, recently, RAABE [42] are of similar opinion. According to these authors, due to the sessile habit and axial symmetry of *Peritrichida*, their cytopyge has been shifted superiorly. The infundibulum functions in this case as a "cloaca oralis". WICHTERMAN [50] could demonstrate little differences in the cytopyges of various *Paramecium* species, and these differences were of little diagnostical value. Finally, NANNEY [38] found a relationship between the location of the cytopyge and various "corticotypes" of *Tetrahymena pyriformis*. Accordingly, the location of the cytopyge is determined by the corticotype of the animal. In *Uronema*, the cytopyge silver line shows a variability which may be introduced in the diagnostics of several species [16].

The present work also points to the poor taxonomic value of the cytopyge. In spite of this, its location, shape and size should not be neglected when a new taxon is described.

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