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Ultrastructure of the Mycophagous Ciliate *Grossglockneria acuta* (Ciliophora, Colpodea) and Phylogenetic Affinities of Colpodid Ciliates

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SUMMARY

Ultrastructural features of *Grossglockneria acuta* Foissner, 1980 are very similar to those known in the confamilial species, *Pseudoplatyophrya nana*. The somatic infraciliature corresponds to the typical colpodid dikinetid pattern. The peculiar oral apparatus is described in detail. The feeding tube contains about 17 concentric cytostomial microtubular lamellae and postciliary microtubules. The lamellae are interconnected by dense plaques and their innermost microtubules anchor in dense material at the distal end of the tube. The postciliary ribbons of the paroral kinetosomes extend subpellicularly into the proximal region of the tube. It is supposed that supernumerary postciliary microtubules are proliferated and assemble to the cytostomial microtubular lamellae during stomatogenesis. Few transverse microtubules are associated to some adoral and presumably all paroral kinetosomes; they do not extend into the tube. Most basal bodies of the single adoral organelle lack kinetosomal derivates. The Grossglocknerida and Colpodida are suggested to be sister groups because they undergo a telokinetal stomatogenesis in reproductive cysts. The colpodid kinetid is characterized by a compound microtubular structure of posterior transverse ribbons to the left of the kinety. Several hypotheses as to the origin of the typical colpodid kinetid pattern, especially the posteriorly extending transverse microtubules, are discussed. Available evidence suggests haptorid or nassulid ancestors of the colpodids. Some data indicate a paraphyletic composition of the class.

Introduction

The order Grossglocknerida represents a very homogeneous group of mycophagous ciliates restricted to terrestrial habitats. It is characterized by an outstanding synapomorphy, the feeding tube, which is used to perforate fungal hyphae and spores and to engulf their content [46, 47]. At present, the order consists of a single family, the Grossglockneridae, including 3 genera, *Grossglockneria*, *Pseudoplatyophrya* and *Nivaliella* [11]. Morphogenetic and ultrastructural data on *Pseudoplatyophrya nana* convincingly showed that the Grossglocknerida are colpodid ciliates with affinities to the Cyrtolophosidida (oral apparatus) and the Colpodida (telokinetal stomatogenesis within reproductive cysts) [12, 51]. The fine structure of the peculiar feeding tube is not yet fully known. Here, we present a three-dimensional reconstruction from serial sections.

Colpodid ciliates have been related to karyorelictids, heterotrichs, haptorids, hypostomes, hymenostomes and oligohymenophorans mainly due to their diverse oral structures [5–8, 13, 23, 25, 41, 43, 53]. All these different types, however, show a uniform somatic ultrastructure, i.e. posterior transverse ribbons which extend posteriorly to

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form a compound microtubular structure on the left of the kinety, the LKm fibre [22, 40, 41, 53]. This characteristic pattern could not be related to other kinetid patterns. Thus, the ancestors of the colpodid ciliates are still enigmatic [18, 41]. New data, which has since accumulated, demands a re-evaluation of this question.

Material and Methods

Grossglockneria acuta was collected from the litter (0–3 cm) of a spruce forest near Aigen (Böhmerwald, Upper Austria; 48° 42'N, 14°E). The culture method as described by Petz et al. [46] was applied.

Cells were fixed in 2.5 % glutaraldehyde both with and without postfixation in 2 % osmium tetroxide in 0.05 M Na-cacodylate buffer (pH 7). They were dehydrated in a graded ethanol series and either embedded in Spurr or Lowicryl K4M or transferred through propylene oxide into Epon 812 or Araldite. Ultrathin sections were cut with a diamond knife mounted on a Reichert ultracut. Double stained sections (aqueous uranyl acetate and lead citrate) were examined and photographed on a Philips EM 300 or a Zeiss EM 109 electron microscope.

The triplets of the kinetosomes are numbered according to Puytorac [48]. The terms right and left are employed from the organism's "point of view", that is with the observer inside the cell. All figures are orientated as seen from outside the cell in the light microscope to facilitate the comparison of light and electron microscopic observations.

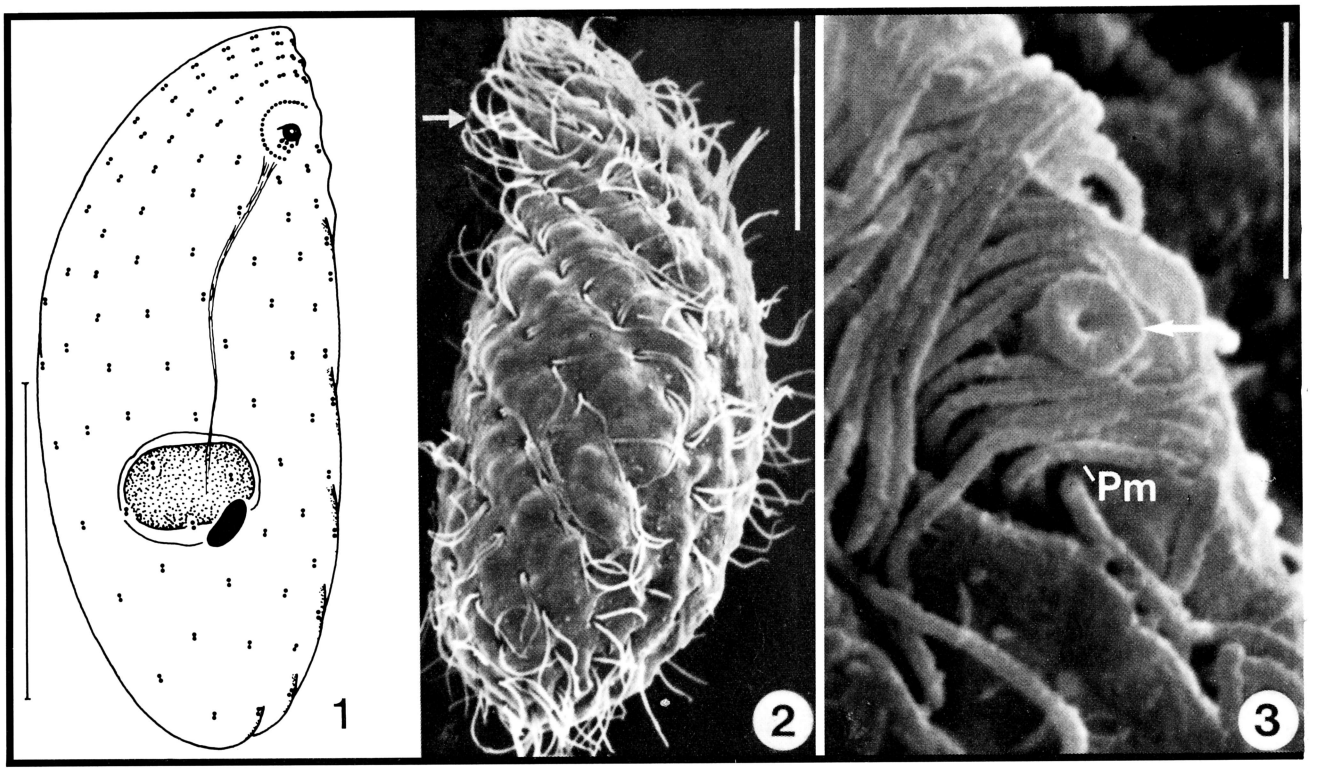
Results

Detailed light microscopic and morphometric descriptions of *Grossglockneria acuta* have already been published earlier [11, 13, 46]. The general organization is thus referred to in only few figures (Figs. 1–3).

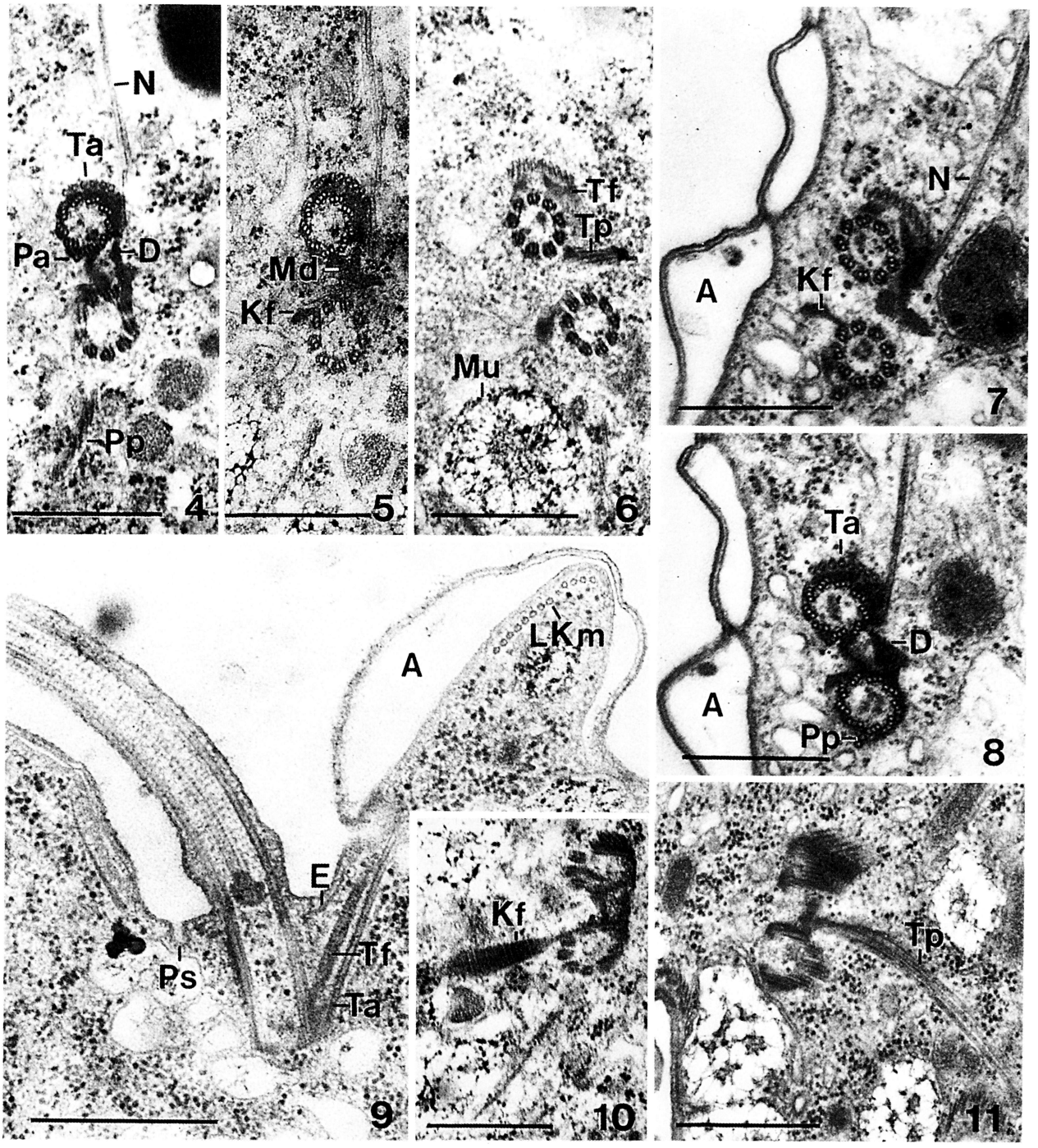
Somatic Cortex

A typical cell membrane covers the usually large pellicular alveoli which are at least partially underlaid by rough endoplasmic reticulum (Fig. 23). The epiplasm is very thin and thus sometimes almost not recognizable (Figs. 7–9).

The somatic kineties are separated by rather distinct interkinetal crests and composed of paired, ciliated basal bodies, which are orientated slightly oblique (10–20°) to the longitudinal kinety axis (Fig. 2). Cohering cilia, mentioned by Foissner [11] in some populations, could not be found. The basal bodies are about 450 × 200 nm (n = 4) in size and unremarkable in structure (Fig. 9). Their proximal ends are surrounded by dense material, where the anterior transverse ribbon, postciliary ribbons, the kinetodesmal fibre, the nematodesmal microtubules and the interkinetosomal linkages are anchored (Figs. 4–10). The posterior transverse ribbon originates more distally from the median desmose (Figs. 4, 11).



Figs. 1–3. *Grossglockneria acuta*, general organization. – Fig. 1. Infraciliature, ventro-lateral view after protargol impregnation (from Foissner [13]). Bar = 15 μm. – Figs. 2, 3. Scanning electron micrographs of left side and face view of the oral area (from Petz et al. [47]). Note the short cilia of the paroral membrane (Pm); arrows mark the feeding tube. Bars = 10 μm and 2 μm, respectively.



Figs. 4–11. *Grossglockneria acuta*, transmission electron micrographs of the somatic cortex. – Figs. 4–6. Transverse serial sections of a dikinetid showing the kinetodesmal fibre (Kf), postciliary and transverse ribbons of the anterior (Pa, Ta) and posterior (Pp, Tp) kinetosomes, nematodesmal microtubules (N), 2 proximal desmoses (D) and the median desmose (Md) as well as a mucocyst (Mu). Bars = 500 nm. – Figs. 7, 8. Transverse sections of another dikinetid distally and proximally. Note the posterior thickening of the left desmose and the conspicuous aveoli (A). Bars = 500 nm. – Fig. 9. Longitudinal section of the anterior kinetosome of a dikinetid showing the LKm fibre, the dense transverse fibre (Tf; cp. Fig. 6), a parasomal sac (Ps) and the very thin epiplasm (E). Bar = 500 nm. – Figs. 10, 11. Oblique sections showing the fan-shaped kinetodesmal fibre (Kf) to the right and the posteriorly directed transverse microtubules (Tp) to the left of the dikinetid. Bars = 500 nm.

The basic pattern of the microtubular associates has been investigated in detail, whereas their length has not been determined precisely. The anterior basal body of a dikinetid has a transverse ribbon, few postciliary and nematodesmal microtubules (Figs. 4–9). 6–12 (n = 12) transverse microtubules are situated near triplets 3–5 (Figs. 4–8); the marginal microtubules are connected to the prominent transverse fibre by fine filaments (Fig. 6). They extend to the anterior-left and pass between the epiplasm and the posterior transverse ribbons of the neighbouring anterior dikinetids. 1 to 2 (n = 8) postciliary microtubules extend upward into the crest, where they curve to the posterior-right. 1–3 nematodesmal microtubules occur, at least in the anterior region of the cell. They originate beside triplets 2, 3 and extend anteriorly, slightly oblique to the longitudinal kinety axis and parallel to the dikinetid axis (Figs. 4, 5, 7, 8).

The posterior basal body of a dikinetid has a transverse and a postciliary ribbon and a kinetodesmal fibre (Figs. 4–8, 10, 11). 5–7 (n = 9) transverse microtubules are situated near triplets 3–5. They are usually sectioned very obliquely indicating a relatively flat course to the posterior-left (Fig. 11), where 2 or 3 transverse ribbons of a kinety lie side by side, sometimes also overlapping, thus corresponding to the colpodid LKm fibre (Fig. 9). Since the postciliary ribbons also extend into the interkinetal crest, they usually cannot be exactly distinguished from the LKm fibre (Fig. 26). 2–7 (n = 8) divergent postciliary microtubules course posteriorly to the right (Fig. 4). The kinetodesmal fibre at triplets 5, 6 is directed laterally and upward into the crest; it is short and fan-shaped as described for *Colpoda maupasi* [34] (Fig. 10).

Desmose 1 extends between triplet 9 of the anterior kinetosome and triplets 5, 6 of the posterior. Desmose 2 joins triplet 2 of the anterior basal body and triplets 3, 4 of the posterior; its posterior part is usually thickened (Figs. 4, 8). Serial sections show that more distally, a median desmose joins triplet 9 of the anterior kinetosome and the desmose 2 (Fig. 5).

Parasomal sacs are situated anterior (and possibly posterior) to the kinetodesmal fibre, posterior to the posterior transverse microtubules and to the left of the anterior transverse microtubules (Figs. 9, 26).

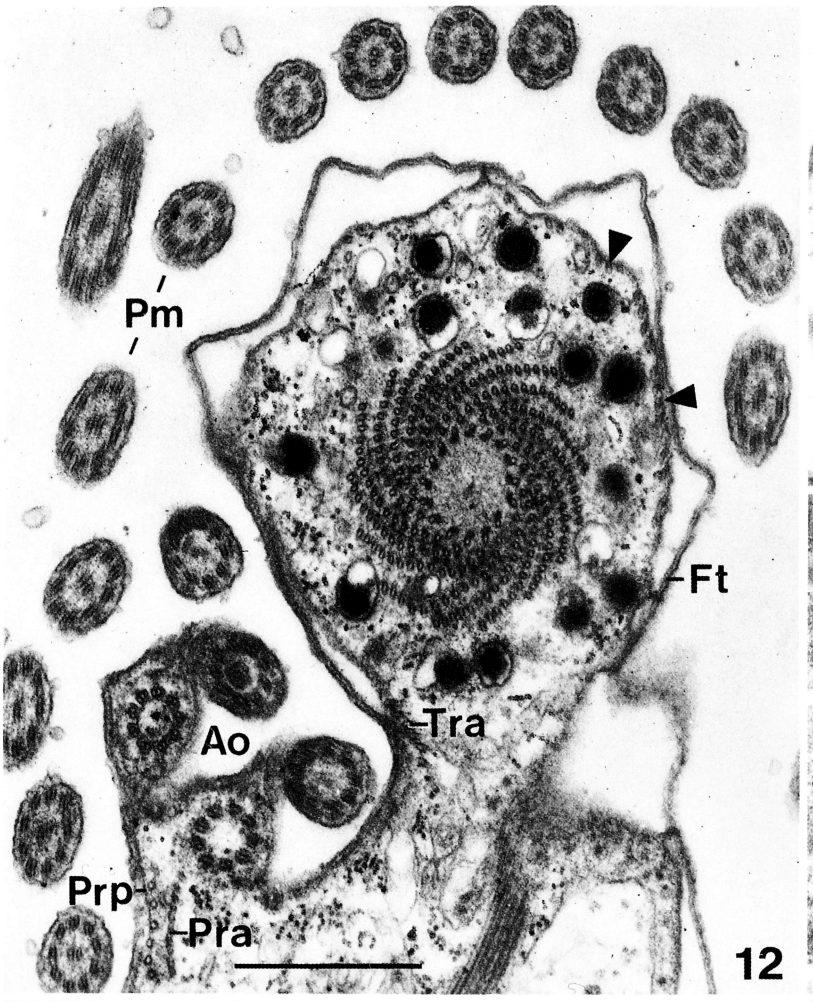
Oral Apparatus

The oral apparatus consists of the feeding tube, the paroral membrane and a very small, presumably functionless adoral organelle (Figs. 12, 24, 25). The oral cilia, measuring about 2 μm in prepared specimens, are very short compared to the somatic cilia (Fig. 3).

The feeding tube is a truncated cone, about 1.5 μm in height and 1.5 μm across the base; distally it tapers slightly and terminates in a more or less distinct bulge (Fig. 14). In the centre of the distal part of the tube is a small funnel, the so-called endocytotic duct [47], which is about 400 nm in height and 100 nm in diameter (Figs. 13, 14). The cytoplasm surrounding the central microtubular core contains numerous osmiophilic granules, 50 nm in diameter (Figs. 12, 14, 17), whereas proximally, at the base of the tube, many elongated phagoplasmic vesicles occur in feeding cells (Fig. 15). The feeding tube is supported by 15–19 (n = 4) concentric microtubular lamellae and the postciliary ribbons of the paroral membrane (Figs. 12–15, 17, 18). The lamellae overlap clockwise when viewed from outside the cell. Adjacent lamellae are joined by dense plaques, which are especially distinct in the distal third of the tube, i. e. along the endocytotic duct (Fig. 13). Each lamella consists of a single-layered ribbon of 14–18 (n = 25 from 3 individuals investigated) microtubules; their number varies within a single specimen. Its innermost microtubules, which are distinguished from the rest by a dense ridge, form a cylinder delimiting the cytopharyngeal area (Fig. 12). The ridges extend from the base of the feeding tube to the proximal end of the endocytotic duct. About 5 of the internal (more central) microtubules are distally anchored in dense material in the distal bulge of the feeding tube (Fig. 14). The remaining peripheral microtubules of each lamella terminate close below the bulge. Several microtubules of some lamellae on the right side elongate into long pharyngeal fibres. The probable arrangement of the different components of this peculiar feeding apparatus is shown in Fig. 24, a three-dimensional reconstruction based on transverse and longitudinal serial sections.

The paroral membrane surrounds the right half of the feeding tube semicircularly as a single row of about 17 ciliated kinetosomes, which are proximally anchored in a plate of dense material (Figs. 12, 17). Nematodesmata originate from this dense plate and course beneath the kinety (Fig. 17). Each basal body has 2 microtubular systems: approximately 5 microtubules face the feeding tube (Figs. 12, 17–21), while a small group of 2 or 3 microtubules is situated on the opposite side of a paroral kinetid (Fig. 19). The first system is interpreted as postciliary ribbon because of its convergent arrangement (Fig. 12;

Figs. 12–16. *Grossglockneria acuta*, transmission electron micrographs of the oral apparatus and mucocysts. – Fig. 12. Overall view of the oral structures which consist of the paroral membrane (Pm), the adoral organelle (Ao) and the feeding tube (Ft). Note the transverse (Tra) and postciliary (Pra) microtubules of the adoral kinetosomes and the postciliary microtubules (Prp) of the paroral kinetosomes which extend to the feeding tube where they form a layer of subpellicular microtubules (arrowheads). The feeding tube shows dense globules and concentric microtubular lamellae, each innermost microtubule having a dense ridge. Bar = 500 nm. – Fig. 13. Transverse section of the distal part of the feeding tube. The large alveoli (A), the endocytotic duct and the dense plaques (P) each connecting two adjacent microtubular lamellae (L) are recognizable. Bar = 500 nm. – Fig. 14. Longitudinal section of the feeding tube showing the endocytotic duct (arrow) and the dense bulge (B) where the microtubular lamellae (L) anchor distally (arrowhead). Bar = 1 μm. – Fig. 15. Transverse section through the proximal region of the oral apparatus of a feeding cell. Note the postciliary microtubules (Prp) extending from the paroral kinetosomes and the elongated phagoplasmic vesicles (Pv). Bar = 500 nm. – Fig. 16. Mucocysts (Mu) surrounding a somatic dikinetid. Mitochondria (M) have tubular cristae. Bar = 500 nm. ▶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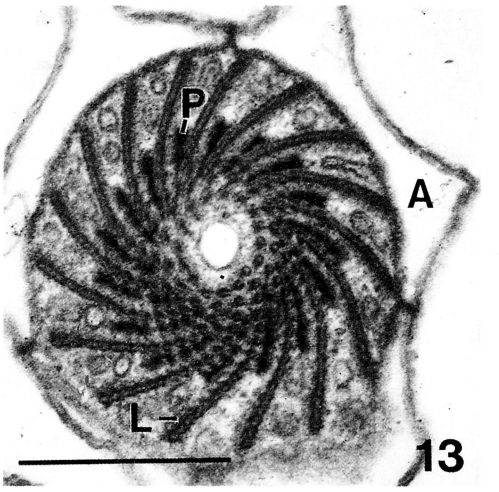
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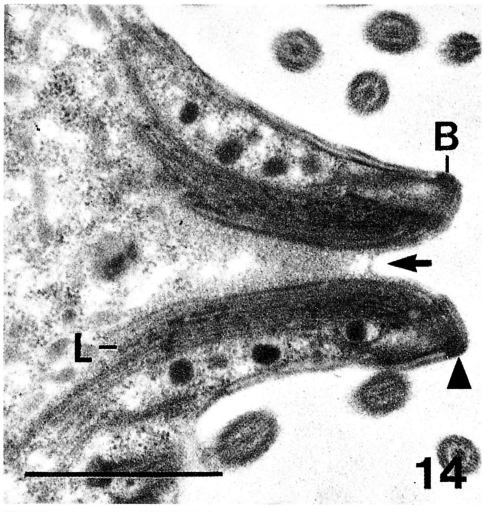
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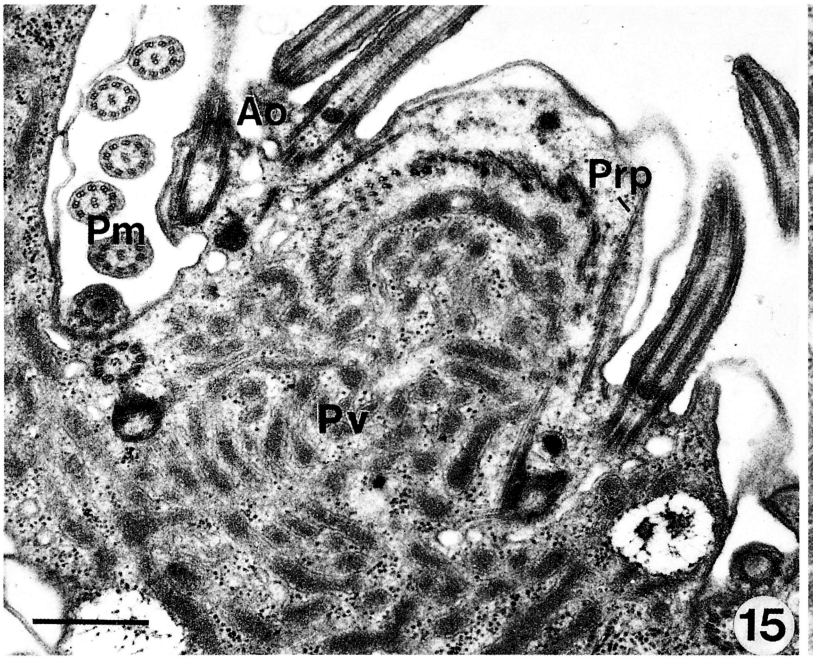
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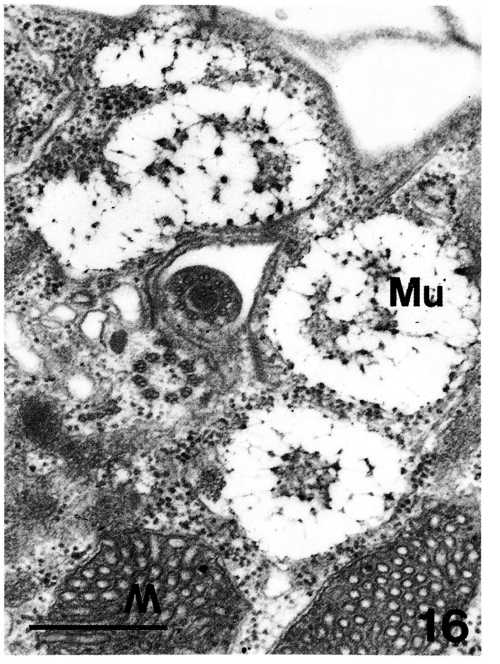
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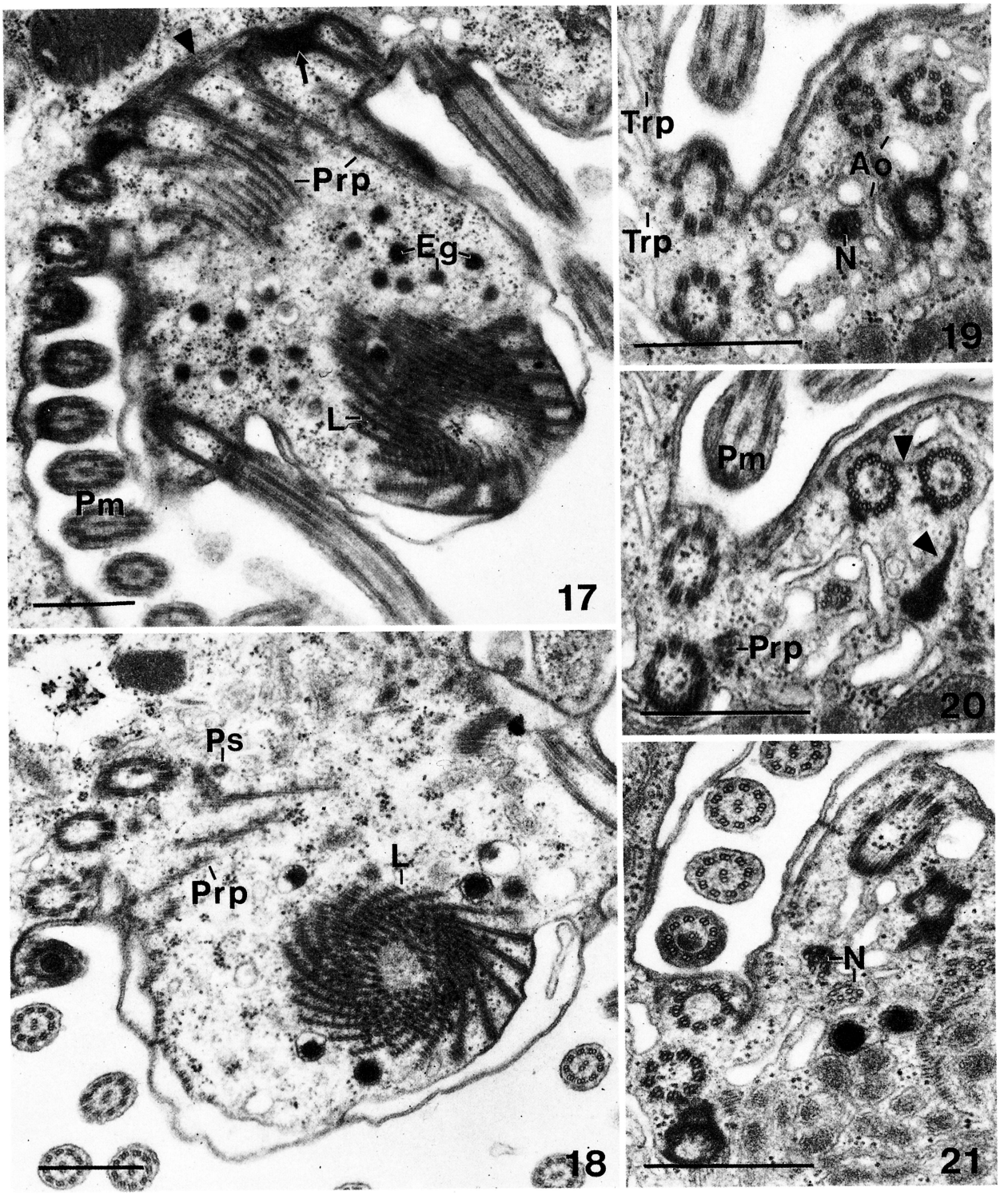


Figs. 17–21. *Grossglockneria acuta*, transmission electron micrographs of the oral structures. – Figs. 17, 18. Oblique sections showing the subpellicularly extending postciliary microtubules (Prp) of the paroral membrane (Pm), which is anchored in dense material (arrow) and underlaid by nematodesmal microtubules (arrowhead). Note the dense globules (Eg), the microtubular lamellae (L) of the feeding tube and a parasomal sac (Ps). Bars = 500 nm. – Figs. 19–21. Transverse sections of the adoral organelle (Ao) and the paroral membrane (Pm). Two transverse microtubules (Trp) each are associated with a paroral kinetosome. Nematodesmata (N) and interkinetosomal linkages (arrowheads) are weakly developed. Bars = 500 nm.

for definition see [40]) and its position perpendicular to the longitudinal axis of the paroral membrane (Figs. 17, 18), which is obtained by an oral dikinetid rotation of 90 degrees to the right [cf. 10, 29, 42]. The second system is interpreted as transverse ribbon due to its position which corresponds to that of the posterior transverse microtubules in the somatic dikinetid (Figs. 25, 26), i. e. the anterior basal body of the paroral dikinetid is resorbed during stomatogenesis resulting in a single-rowed paroral membrane as proposed by Puytorac et al. [51] in *Pseudoplatyophrya nana*. Verification of these assumptions, however, would require stomatogenetic analyses using transmission electron microscopy. The postciliary ribbons extend subpellicularly into the distal region of the feeding tube (Figs. 12, 15, 17, 18) where they terminate close below the bulge. The transverse ribbons reach only a short distance into the cytoplasmic ridge opposite the feeding tube. Kinetodesmal fibres are absent. One parasomal sac is situated anteriorly and posteriorly to each basal body (Fig. 18).

The adoral organelle is very small and was only infrequently sectioned. Light microscopic results indicate that the number of kinetosomes comprising the organelle may vary from 5–6. We observed 5 ciliated kinetosomes and 1 unciliated basal body, some of these are connected by inconspicuous desmoses (Figs. 12, 20). The left basal body of the posteriormost pair bears about 5 transverse microtubules, the right has approximately 9 divergent postciliary microtubules (Figs. 12). These microtubular ribbons are apparently absent from the second and third pair (Figs. 19, 20). Nematodesmata originate at the proximal ends of the first and the second pair of basal bodies, probably contributing to the long pharyngeal fibres (Figs. 19–21).

The arrangement of the microtubular associates of the oral kinetosomes is shown in a schematic drawing (Fig. 25).

Internal Organization

At light microscopic level the mucocyst-like extrusomes are globular, about 1 µm in diameter. They are located mainly along the somatic kineties and impregnate heavily with protargol [11]. Ultrastructurally a crystalline content was never seen, but merely a fluffy core composed of 1–3 dense aggregates and a loose, lattice-like periphery (Figs. 6, 16). Extruded granules and developmental stages have not been observed. A similar fine structure of the mucocysts has been found in many other colpodids, e. g., *Bryometopus, Bryophrya, Cyrtolophosis* [7, 23, 55]. Whether this rather unusual appearance (as compared with typical mucocysts) is caused by poor fixation or represents a special type of extrusomes needs to be clarified by further investigation.

The cytoplasm is rich in rough endoplasmic reticulum and reserve granules (Figs. 22, 23). Mitochondria have tubular cristae (Figs. 16, 22). Contractile vacuole and excretory pore seem to be of usual structure [e. g., 14, 33], but were not studied in detail.

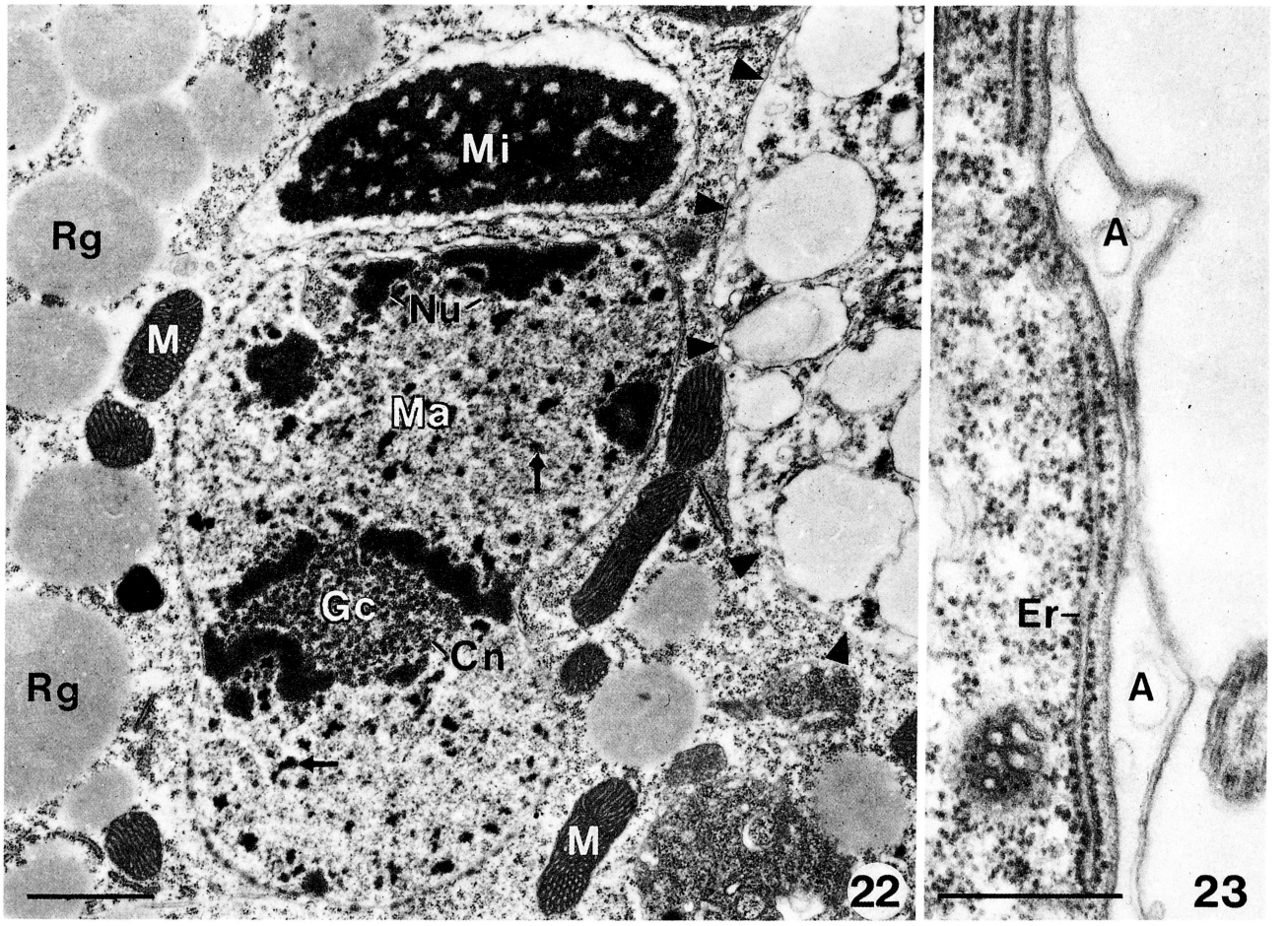
The nuclear apparatus of *G. acuta* is quite similar to that of *Colpoda steinii*, e. g. in having a fairly conspicuous central composite nucleolus [33, 52]; additional peripheral nucleoli may appear (Fig. 22). The micronucleus is ellipsoid and situated in an unfixed position close to the macronucleus. It is of the chromosomal type [52] and covered by its own membrane (Fig. 22).

Discussion

Intrafamilial Variation of Ultrastructure

The cortical and internal organization of *Grossglockneria acuta* is almost identical to that described for *Pseudoplatyophrya nana* [51]. The alveolar layer is less conspicuous in *P. nana* and its feeding tube is composed of only 8–10 microtubular lamellae. Obviously, these differences, as in *Colpoda* spp. [36, 37], are related to its small size. Such differences are, however, not found in the number of microtubules associated with the somatic basal bodies. The anchorage and linkages of the lamellae at the distal end of the feeding tube have not been described in *P. nana*; however, some micrographs of Puytorac et al. [51] indicate their presence in this species too. The few oral transverse microtubules and the nematodesmata beneath the paroral membrane are perhaps absent in *P. nana*. It is, however, very difficult to get appropriate sections of the extremely small oral apparatus of grossglocknerid ciliates. These microtubules might thus have also been overlooked in *P. nana*.

The microtubular core of the feeding tube of *P. nana* is formed by "postciliary *and* other microtubules" originating from the paroral membrane and extending directly to the distal end of the tube [51]. However, the figures in Puytorac et al. [51] are not conclusive in this respect; e. g., the structures designated as "microtubules (N)" may in fact, due to their orientation, represent paroral postciliary microtubules (Fig. 18 in [51]) or pharyngeal fibres originating from the adoral kinetosomes and the cytostomial lamellae (Figs. 13–15, 21 in [51]). Furthermore, their figures show subpellicular microtubules lining the feeding tube as in *G. acuta*; they were, however, not interpreted by Puytorac et al. [51]. In our opinion, the situation for both species is as follows: The cytostomial microtubular lamellae are anchored in the distal bulge and reach into the cytoplasm. The postciliary ribbons of the paroral kinetosomes extend subpellicularly into the distal part of the feeding tube and terminate below the bulge (cp. Figs. 13, 17–21 in [51] and Figs. 15, 17, 18, 24 in our paper). We assume, however, that the microtubular lamellae arise from the paroral postciliary ribbons during stomatogenesis, since the number of lamellae corresponds roughly to that of the paroral basal bodies. The number of microtubules per lamellae is, however, about three times larger than that of a paroral postciliary ribbon; we assume thus that supernumerary postciliary microtubules are proliferated during stomatogenesis. These microtubules presumably detach once morphogenesis is completed, as described also for several cyrtophorid ciliates [10, 27, 29]. Verification would of course require stomatogenetic analyses using transmission electron microscopy; a difficult undertaking



Figs. 22, 23. *Grossglockneria acuta*, transmission electron micrographs of the nuclear apparatus and the pellicle. – Fig. 22. The macronucleus (Ma) contains small chromatin bodies (arrows), peripheral nucleoli (Nu) and a large composite nucleolus (Cn) comprising a weakly stained granular (Gc) and a heavily stained (fibrous?) component. The chromatin of the micronucleus (Mi) has a lattice-like appearance. A large food vacuole (bordered by arrowheads), several reserve granules (Rg) and mitochondria (M) surround the nuclear apparatus. Bar = 1 μm. – Fig. 23. The pellicular alveoli (A) are at least partially underlaid by a large cisterna of rough endoplasmic reticulum (Er). Bar = 500 nm.

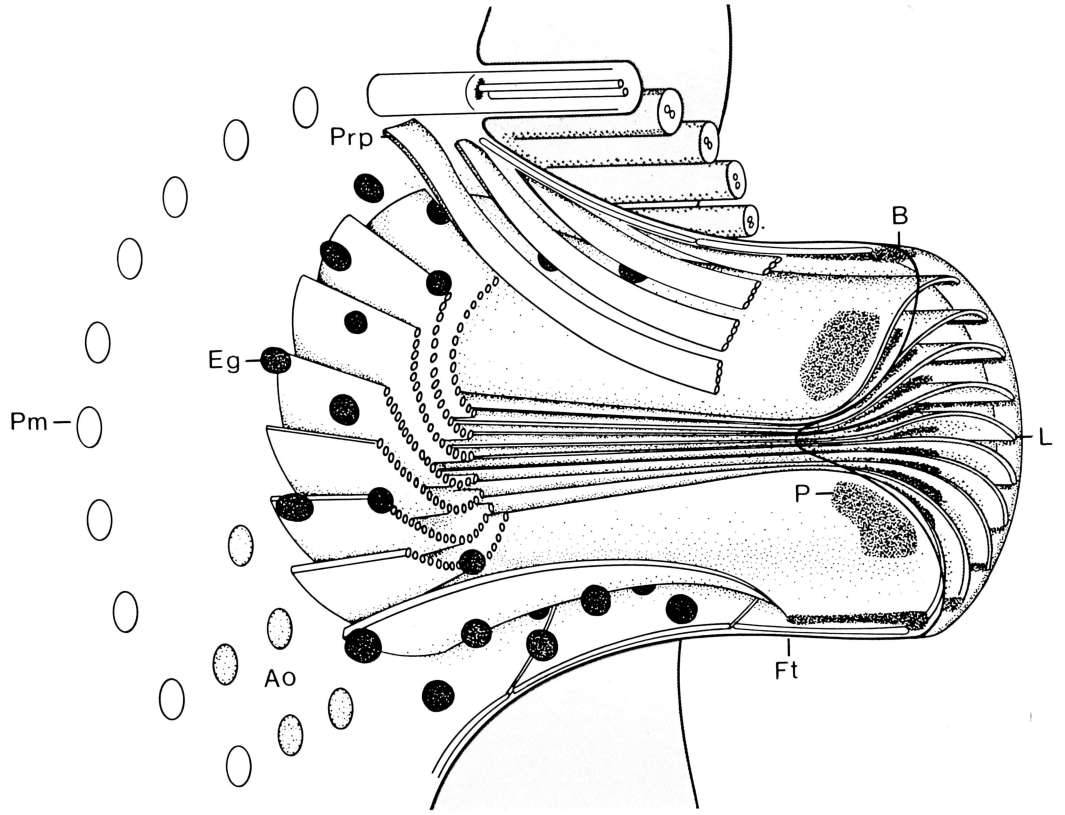
due to the small size of the oral structures and the division of grossglocknerids in reproductive cysts, where the appropriate orientations are only to be found at random.

The exact course of the microtubular ribbons in the feeding tube is not easy to analyze. We thus cannot entirely rule out the possibility that the postciliary ribbons of the paroral membrane extend subpellicularly along the feeding tube, bending sharply at the distal end, where further microtubules are added to each ribbon. These could then plunge into the centre of the tube to form the cytostomial microtubular lamellae. This alternative hypothesis is in our opinion, however, rather unlikely since one must assume that the paroral postciliary ribbons, which originate from the *semicircular* paroral membrane, are assembled to the *circular* core shown by the microtubular lamellae.

In conclusion, the ultrastructure of grossglocknerid taxa seems quite homogeneous. All apomorphies (feeding tube, single rowed paroral membrane, single adoral organelle) are confined to the oral apparatus, whereas the somatic ultrastructure is very similar to small-sized species of the genus *Colpoda*, e.g. less pronounced LKm fibre [34].

Phylogenetic Relationships of the Grossglocknerida within the Colpodea

Puytorac et al. [51] stated affinities between *Pseudoplatyophrya nana* and *Cyrtolophosis* regarding the ordered arrangement of the right oral structures. However, colpodids s. str. have recently been discovered, the right oral ciliary field of which also consists of an ordered row of dikinetids, namely *Avestina, Ilsiella* and *Kuehneltiella* [1, 15, 17]. Morphogenetic evidence suggests, however, that ordered right ciliary fields could evolve by convergence. The grossglocknerids have, like the colpodids s. str., a typical telokinetal stomatogenesis, i. e. new basal bodies



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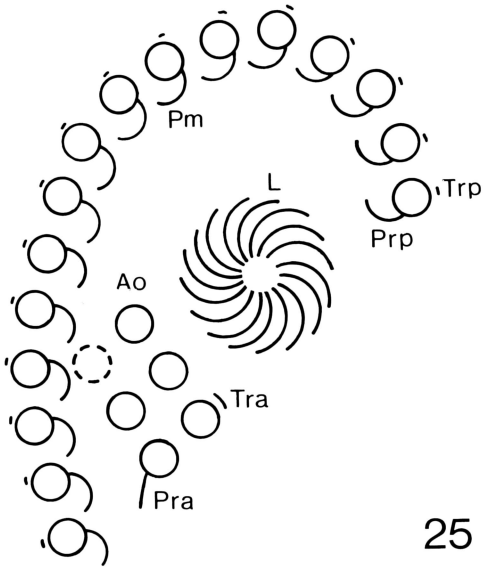

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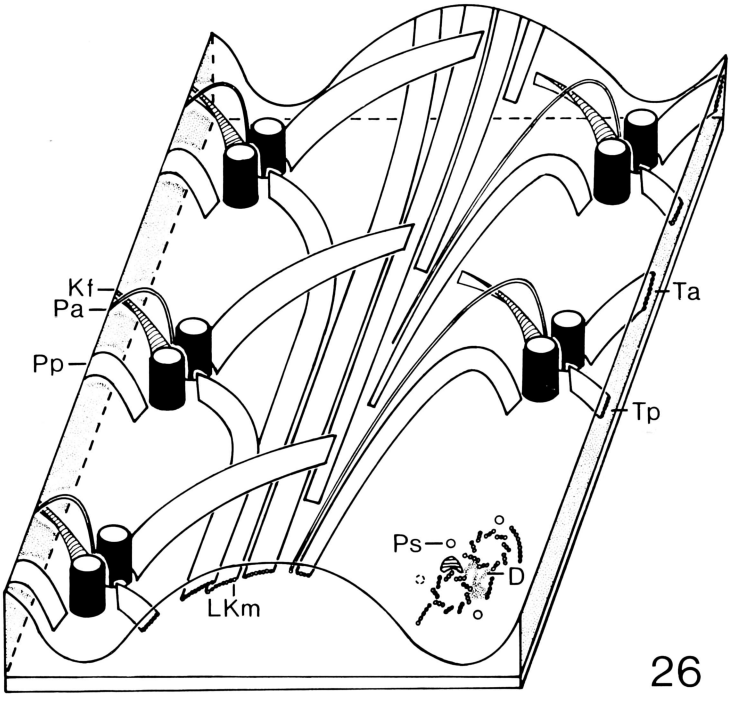

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are added only at the ends of the somatic kineties [12, 19, 26, 44]. The cyrtolophosidids have some sort of parakinetal stomatogenesis where the primordia develop within the parental ciliary rows and proliferate basal bodies laterally too [4, 8, 25, 49]. Thus, in grossglocknerids the single rowed (secondarily reduced [12]) right oral structure, which originates from a single stomatogenetic kinety, may be considered as an "oligomerized" colpodid polykinety rather than a cyrtolophosidid paroral membrane. Similarly the grossglocknerid "adoral organelle" corresponds to a colpodid polykinetid rather than to a cyrtolophosidid "pavé" because the left oral structures of the Grossglocknerida and Colpodida assemble to a composite organelle (polykinety), while they arrange in groups (adoral organelles, pavés) in the Cyrtolophosidida [4, 8, 12, 19, 25, 26, 44, 49].

Concerning the oral ultrastructure, grossglocknerids resemble some cyrtolophosidid families, such as the Platyophryidae and Woodruffiidae. In both orders microtubular lamellae occur which circularly line the cytostomial area and are not connected to oral kinetosomes [8, 43, 49]; presumably these lamellae are postciliary microtubules which have detached from the oral basal bodies. Oral transverse microtubules have never been observed in the Cyrtolophosidida, whereas they are associated to the paroral and some adoral kinetosomes of *Grossglockneria acuta* and possibly colpodids s. str. In *Colpoda magna* (formerly *Tillina* [cp. 18]) Lynn [36], for instance, observed 2 or 3 short microtubules associated to kinetosomes near the peripheral somatic edge of an oral polykinetid. He interpreted them as nematodesmata, although they are arranged like transverse ribbons (Fig. 24 in [36]). Remarkably, in these colpodids s. str. the transverse microtubules do not extend to the cytopharynx as indicated in the colpodids s. l., *Bursaria* and *Bryometopus* (Fig. 20 in [45]; Fig. 23 in [55]).

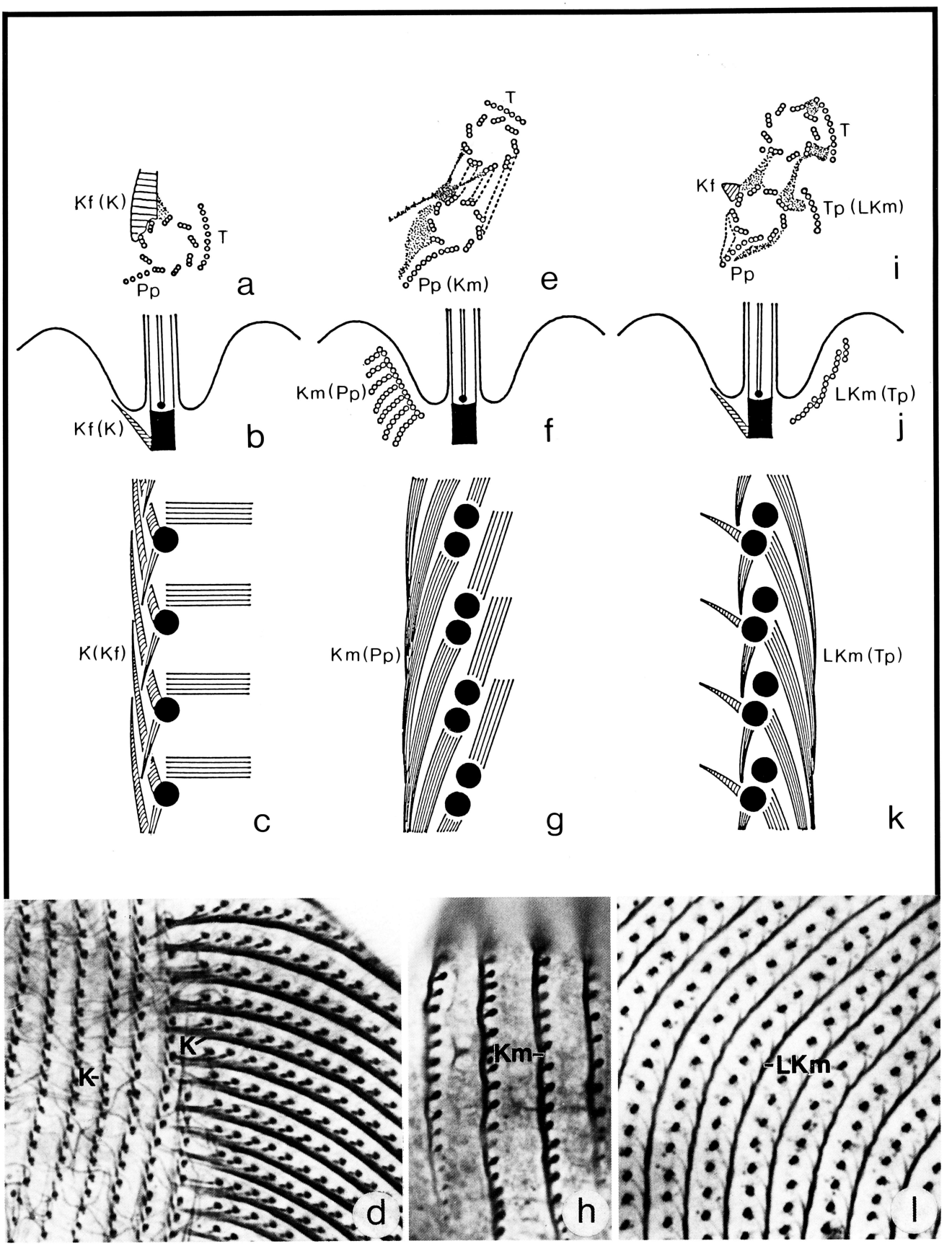
The comparison of the oral structures and the morphogenesis suggests that the Grossglocknerida are more closely related to the Colpodida than to the Cyrtolophosidida. The silverline system furthermore becomes very tightly and irregularly meshed during morphogenesis in *Pseudoplatyophrya nana* and *Colpoda* spp., whereas it assumes a widely and more regularly meshed (platyophryid) pattern in *Cyrtolophosis* [12, 13]. The Grossglocknerida and Colpodida are moreover related in terms of their nuclear structure: both have a separated macronucleus and micronucleus [12, 33–36], whereas the micronucleus is included in the perinuclear space of the macronucleus in the Cyrtolophosidida [5, 7, 8, 13, 43]. All these data confirm the close affinity between the Grossglocknerida and Colpodida proposed by Foissner [12, 13]. A sister group relationship is very probable and justified by the apomorphy – telokinetal stomatogenesis in reproductive cysts.

Phylogenetic Affinities of Colpodid Ciliates

The class Colpodea is characterized by the LKm fibre of the somatic kinetids [13, 53]. The evolution of this special pattern is still enigmatic [41]. Recently published data, however, enables a new approach to this problem. Before discussing this complicated matter, we provide a somewhat elaborated preface, because inexperienced workers always have great difficulties to orientate within the ciliate cortex and to understand the conclusions drawn by specialists. Surprisingly, simple schematic drawings of the basic types of cortical fibrillar systems *and* their light microscopic equivalents are still lacking. We therefore prepared a comparative illustration showing the most common somatic fibrillar patterns (Fig. 27).

Somatic kinetids of ciliates are characterized by a classic set of fibrillar associates consisting of a kinetodesmal fibre, postciliary and transverse microtubules [40]. Three basic patterns can be distinguished according to the predominating component (Fig. 27): overlapping kinetodesmal fibres (kinetodesma) occur in apostomes, hymenostomes, scuticociliates, peritrichs and certain astomes; overlapping postciliary ribbons (postciliodesma or right Km fibres) are to be found in karyorelictids, heterotrichs, haptorids and some cyrtophorids; overlapping posterior transverse ribbons (LKm or left Km fibres) characterize the colpodids [22, 40, 41]. In general, kinetids may be anchored to the right of a kinety (kinetodesma, postciliodesma) or to the left (LKm fibres); its main fibrillar associates can be directed anteriorly (kinetodesma) or posteriorly (postciliodesma, LKm fibres). Kinetodesma and postciliodesma

◀ Figs. 24, 25. *Grossglockneria acuta*, schematic drawings of the oral apparatus. – Fig. 24. Three-dimensional reconstruction based on serial sections. The concentric microtubular lamellae (L) of the feeding tube (Ft) overlap clockwise, are joined by dense plaques (P) and surrounded by dense globules (Eg). The paroral membrane (Pm) semicircularly borders the right side of the feeding tube. The postciliary microtubules (Prp) of the paroral kinetosomes extend subpellicularly into the tube and terminate beneath the bulge (B). The kinetosomes of the adoral organelle (Ao) are dotted. – Fig. 25. Microtubular associates of the oral structures. – Fig. 26. Three-dimensional reconstruction of the microtubular associates of the colpodid somatic cortex. The dikinetid pattern in the lower right corner corresponds to that of *Grossglockneria acuta*. The most characteristic feature of the colpodid cortex is the LKm fibre which is formed by overlapping transverse microtubules (see text for detailed explanation). Ao = adoral organelle, B = bulge, D = desmose, Eg = dense globule, Ft = feeding tube, Kf = kinetodesmal fibre, L = microtubular lamella, LKm = LKm fibre, P = dense plaque, Pa = postciliary microtubules of anterior somatic kinetosome, Pm = paroral membrane, Pp = postciliary microtubules of posterior somatic kinetosome, Pra = postciliary microtubules of adoral kinetosome, Prp = postciliary microtubules of paroral kinetosome, Ps = parasomal sac, Ta = transverse microtubules of anterior somatic kinetosome, Tp = transverse microtubules of posterior somatic kinetosome, Tra = transverse microtubules of adoral kinetosome, Trp = transverse microtubules of paroral kinetosome.


Kf (K)
T
Pp
a
T
Pp (Km)
e
T
Kf
Tp (LKm)
Pp
i
Kf (K)
b
Km (Pp)
f
LKm (Tp)
j
K (Kf)
c
Km (Pp)
g
LKm (Tp)
k
K
K
d
Km
h
LKm
l

are scattered in very different ciliate groups, whereas the LKm fibres are obviously confined to the colpodids and are thus characterized in detail.

Our three-dimensional reconstruction of the colpodid kinetid pattern is a synopsis of data available in the literature and of observations on *Grossglockneria acuta* (Fig. 26); thus, it does not correspond to a particular species. Such a reconstruction seems necessary because in the two others available the postciliary and transverse microtubules are confused [20, 21]. Unfortunately, data concerning the length of the postciliary and anterior transverse ribbons are sparse and our reconstruction can therefore only provide a schematic idea of them. The LKm fibres are composed of transverse microtubular ribbons associated with the posterior kinetosomes of the dikinetids [e. g., 22, 39]. These ribbons extend posteriorly to the left of the kinety and align and/or overlap with other ribbons from more anterior dikinetids (Fig. 26). The number of microtubules associated with the colpodid dikinetid varies in detail as does the size of the LKm fibre, i. e. it is inconspicuous in *Colpoda steinii*, but very prominent in *Woodruffia* [33, 49] and *Bresslaua* [38]. This is very probably a size-related (allometric) phenomenon [37].

In search of possible colpodid ancestors, we focused on groups having kinetid patterns which could most simply explain the origin of the LKm fibre. We have thus excluded ciliate groups showing a distinct "right compound structure", comprising either kinetodesmal fibres or postciliary ribbons, from the following considerations, since it is unlikely that they are more closely related to the colpodids. Likewise, we do not suppose that the posterior transverse ribbon is a new acquisition of colpodids. Such a "de novo" origin is implied in the proposal by Lynn [33, 40] who considers the dikinetid pattern to be ancestral. Although this possibility cannot be ruled out, we assume the monokinetid to be ancestral due to its morphogenetic potency to give rise to all the complex patterns observed in the somatic and oral cortex of ciliates [10, 27, 31]. The following discussion will lead to the hypothesis that colpodids are related to haptorid and nassulid ciliates:

1. Phylogenetic relationships of colpodids and haptorids have already been proposed with respect to the somatic dikinetid pattern of colpodids and the haptorid dorsal brush dikinetids [13, 31]. A gymnostome ancestor of colpodids was also proposed by Gerassimova [20], based, however, on the misinterpretation of colpodids as having postciliodesma. The anterior and posterior transverse ribbon of the colpodid dikinetid is in fact reminiscent of the transverse microtubular system of the haptorid monokinetid (named T1 and T2, respectively) since in both groups the ribbons have a different origin (proximally or more distally of the kinetosome) and direction (anteriorly or laterally and even slightly posteriorly) [e. g., 3, 14, 16, 31, 40, 54]. One can indeed imagine that the colpodid pattern evolved from 2 haptorid monokinetids, which did not separate during morphogenesis and where the anterior basal body preserved the T1 ribbon and lost the T2, while the posterior retained the T2 and lost the T1 (Fig. 28a). Consequently, the anterior transverse ribbon of the colpodids would be homologous to the first transverse system (T1) of haptorids, while the colpodid posterior ribbon would be homologous to the second, laterally directed haptorid transverse system [T2]. This hypothesis of a different origin of the 2 transverse ribbons is however weakened by the following observations: (i) The anterior basal body of the brush dikinetids usually lacks all fibrillar associates and the T2 ribbon is, in all known cases, absent from the posterior kinetosome [3, 14, 16, 31, 54]; (ii) The postciliary system dominating the haptorid cortex has to be reduced dramatically to obtain a colpodid pattern [54]; (iii) The postciliary ribbons are convergent in somatic and oral kinetids of haptorids and phyllopharyngids, while those of nassulids, colpodids and all other ciliate groups differentiated into divergent (somatic) and divergent and/or convergent (oral) postciliary ribbons [40].

A further, perhaps more simple explanation of the origin of a colpodid dikinetid can be constructed from recent results on nassulids and *Coleps* [9, 28] supposing that the anterior transverse ribbon and the LKm fibre evolved from the same microtubular ribbon (Fig. 28b). The nassulids and *Coleps* have a weakly developed fibrillar system, but show transverse microtubles extending slightly to the posterior-left, resembling the transverse ribbon of the posterior kinetosome of the colpodid dikinetid. Although the infraciliature of these taxa largely consists of monokinetids, there are few somatic dikinetids at the anterior end of all (*Coleps*) or some (nassulids) kineties. In *Furgasonia blochmanni* these dikinetids are equipped with a double set of fibrillar systems [9]. This corresponds to the proposal that the dikinetid pattern evolved from 2 monokinetids, which do not separate during morphogenesis, each with a complete set of microtubular associates [cp. 9, 10, 27, 31]. Interestingly, the monokinetid of *Nassula citrea* has a desmose-like fibrillar structure which is strongly reminiscent of the desmose of its dikinetid [9]. Furthermore, the left desmose of colpodids resembles the single interkinetosomal linkage of several nassulids [9], because it connects the same triplets and shows a posterior-left thicken-

◀ Fig. 27. Basic types of the cortical fibrillar systems of ciliates at electron and light microscopic level. Each type is shown in transverse (a, e, i) and longitudinal (b, f, j) section, in face view (c, g, k) and in silver-impregnated specimens (d, h, l). All figures are orientated as seen from outside the cell in the light microscope. The line diagrams are schematic figures and do not refer to a particular species. The kinetodesma type (K; a–d) is characterized by overlapping kinetodesmal fibres (Kf) extending anteriorly to the right of a kinety, e. g. in the peniculine *Paramecium caudatum* (d). The right Km or postciliodesma type (Km; e–h) is characterized by overlapping postciliary microtubules of the posterior kinetosomes (Pp) extending posteriorly to the right of a kinety, e. g. in the heterotrich *Blepharisma japonicum* (h). The left Km type (LKm; i–l) is characterized by overlapping transverse microtubules of the posterior kinetosomes (Tp) extending posteriorly to the left of a kinety, e. g. in the colpodid *Bresslauides terricola* (l). T = transverse microtubules.

ing anchoring the transverse ribbon. Although both transverse ribbons of the Colpodea are classified as tangentially oriented to the kinetosomal diameter, their different course may indicate that the posterior transverse ribbon was originally radial, as in nassulids and *Coleps* [9, 28]. The few transverse microtubules associated with the anterior dikinetid basal body of *Furgasonia blochmanni* may even represent a transition between a radial and transverse oriented ribbon. Short postciliary ribbons and inconspicuous kinetodesmal fibres are further characters shared by colpodids and nassulids. However, there are no indications that they are real sister groups, but some further plesiomorphies may possibly be found in future.

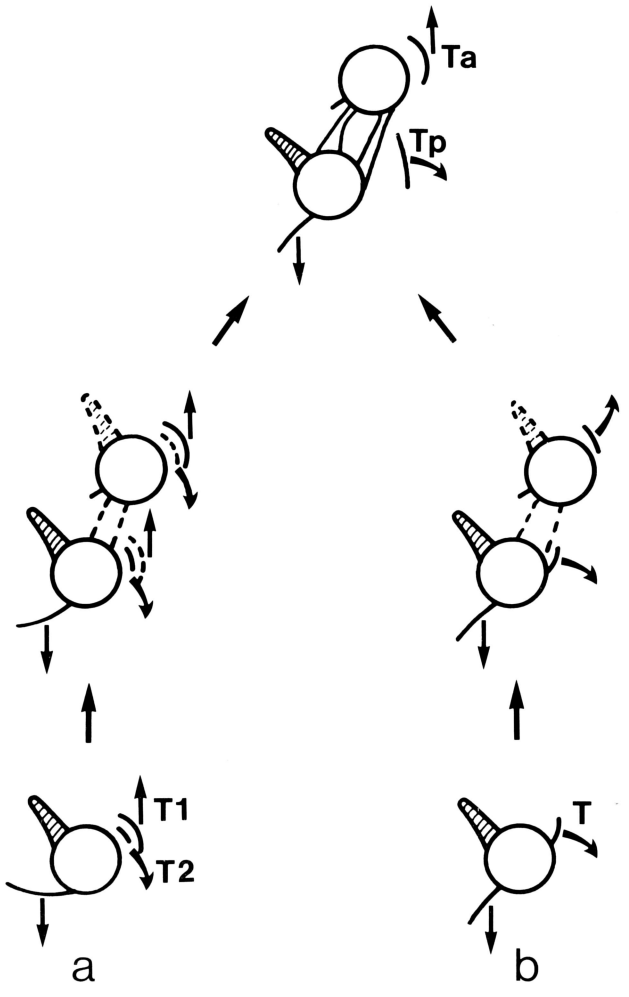


Fig. 28. Evolution of the colpodid LKm fibre. Smaller arrows indicate direction of microtubular ribbons; broken lines mark structures in resorption (kinetodesmal fibre, T1, T2) or formation (desmoses). Both hypotheses are based on the assumption that the dikinetid evolved from two monokinetids which did not separate during morphogenesis. The first hypothesis (a) assumes that the transverse microtubular system derived from two different transverse microtubular ribbons, the haptorid T1 and T2, where the anterior kinetosome of the colpodid dikinetid preserved the anteriorly directed T1, while the posterior kinetosome retained the laterally directed T2. The second hypothesis (b) assumes that the anterior and posterior transverse microtubular ribbons of colpodids derived from the same original structure, i. e. the nassulid radial transverse microtubules (T) which are slightly directed posteriorly. In the anterior kinetosome of the dikinetid the transverse microtubules were transformed to a transversely arranged and anteriorly directed ribbon (Ta), while they obtained a distinct posterior direction in the posterior kinetosome (Tp).

One of the reviewers commented that it is more parsimonous to argue an heterotrich ancestor with dikinetids (e. g., *Condylostoma, Climacostomum, Protocruzia*) which polymerized and extended the transverse system of its posterior kinetosome posteriorly. We accept this suggestion as third hypothesis concerning the origin of the colpodid kinetid pattern. Heterotrichs, however, have a right Km fibre (Fig. 27e–g) and a rather advanced type of stomatogenesis (see below), therefore we consider this hypothesis as rather unlikely. Lynn & Small [41] also emphasized the lack of homology in the somatic dikinetids of the Postciliodesmatophora and the Colpodea.

2. Although colpodids s. str. and grossglocknerids divide exclusively in reproductive cysts, their stomatogenesis is telokinetal as in haptorids and certain cyrtophorids, e. g. *Chilodonella* [12, 19, 26, 27, 29, 44]. Compared to the haptorids, their stomatogenesis appears advanced, since a reduced number of somatic kineties generates the oral structures. The colpodids s. l., e. g., *Bryometopus, Bursaria* and *Cyrtolophosis*, divide mostly in free-swimming condition and show some sort of parakinetal stomatogenesis, resembling those of heterotrichs [4, 42, 45, 55]. The heterotrich oral structures, however, originate from an anarchic field, which is absent in colpodids. If the anarchic field is considered as a new acquisition, the colpodids could have given rise to the heterotrich ciliates. In this context it is worth noting that *Bryometopus* and *Bursaria* have long been considered heterotrich ciliates due to their oral structures [13, 21, 45, 50, 55]. "Evolved" bucco- or apokinetal types of stomatogenesis, which are common in nassulid ciliates, do not occur in colpodids with the very doubtful exception of *Woodruffia metabolica* [10, 18, 49]. Concerning ontogenesis, colpodids are thus widely separated from nassulids, but fairly closely related to haptorids.

3. The widely, regularly meshed (platyophryid) type of silverline system occurring in several cyrtolophosidid families is similar to that extending between the haptorid dorsal brush kineties, while the tight, irregularly meshed (kreyellid) type resembles that of nassulid ciliates. Foissner [13] has postulated that the Colpodea presumably evolved from haptorid ancestors by a spiral expansion of the haptorid brush pattern to the entire cell surface. However, the same can be hypothesized for nassulids, namely an increase of the dikinetids which were originally restricted to the anterior end of some somatic kinetids.

4. The oral apparatus of the colpodid genera *Bryometopus* and *Bursaria* has rhabdos-type structural elements, i. e. the transverse ribbons extend to the right vestibular wall [45, 55]. Remarkably, as in *Grossglockneria* and *Colpoda magna*, few, presumably functionless oral transverse microtubules have also been found in the nassulid *Furgasonia blochmanni* and some heterotrichs [10, 36, 42]. The

oral structures of all Colpodea (including *Bryometopus* and *Bursaria* [45, 55]), however, principally correspond to the cyrtos-type because postciliary microtubules are the main component. The postciliary ribbons lining the vestibular wall are associated to the oral kinetosomes in colpodids s. str., while additional microtubular lamellae (cp. above) occur in grossglocknerids and some cyrtolophosidids as in the Cyrtophorida and Nassulida [10, 27, 29]. These orders are further distinguished by the origin of the external cyrtos (basket) components: in Cyrtophorida the outer ring of nematodesmata originates from the somatic subkinetal microtubules, while the nematodesmal lamellae of Nassulida derive from paroral and adoral nematodesmata [10, 27]. The latter presumably also occurs in the Platyophryidae and Woodruffidae [8, 43, 49]. The feeding tube of Grossglockneridae resembles the tentacles of the Suctorida [e. g., 24] and the sucking tube of the Rhynchodida [e. g., 32], which belong to the cyrtophorid Phyllopharyngea [41]. Recently, a similar feeding apparatus was found in a flagellate [30]. Since the stomatogenetic modes and several other aspects of these groups are quite different, it may be argued that the so-called cyrtos-type of oral apparatus has several independent origins. To sum up, the colpodid oral structures show rhabdos- and cyrtos-type elements. The relationships to the rhabdophorid (haptorid) oral apparatus are weak; within the cyrtos-type they are more closely related to the Nassulida than to the Cyrtophorida.

In conclusion, phylogenetic relationships of colpodids remain rather enigmatic. Nassulid ancestors are indicated mainly by some details of the somatic and oral ultrastructure and are not excluded by the silverline pattern. Haptorid ancestors are reflected mainly by ontogenetic data and some details of the somatic and oral ultrastructure as well as the silverline pattern. Evidently the available data indicate a similar probability of haptorid and nassulid ancestors of the colpodids. As mentioned above, the posteriorly directed LKm fibre is the sole character uniting the class Colpodea and thus may be considered as an apomorphy [22]. At the present state of knowledge, however, we cannot rule out the possibility that the LKm fibre originated convergently. In addition, the very diverse oral structures and the different types of stomatogenesis and silverline patterns indicate a paraphyletic assemblage of the class. Several obervations could be more readily explained by this assumption, e. g. the different ciliary plaques in colpodids s. str. and cyrtolophosidids [2] and the occurrence of conjugation in *Bursaria* which is not reliably documented in other colpodids [18].

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