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Morphogenesis and Ultrastructure of the Soil Ciliate *Engelmanniella mobilis* (Ciliophora, Hypotrichida)

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SUMMARY

The morphogenetic pattern, freeze-fracture, transmission, and scanning electron-microscopy of interphasic cells were used to elucidate the enigmatic systematic position of *Engelmanniella mobilis*. Frontal, buccal, parabuccal, and marginal cirri are distinguishable during cortical development; transverse, frontoterminal (migratory), and caudal cirri are absent. Ontogenetic peculiarities include the conservation of parental and grandparental marginal cirri and the apokinetal origin of a dorsal kinety in the opisthe. Thus, interphasic cells of *E. mobilis* possess three generations of cirri. The pellicle is multilamellated. Prominent, undischargeable subpellicular granules consisting of a homogeneous osmiophilic mass develop from bundles of long fibers. Rhomboid crystal-like structures projecting from the lithosomes and regularly patterned mitoribosomes are additional remarkable ultrastructural characteristics. The somatic and frontal cirri comprise 2–10 kinetosomes. Very likely, all cirri are composed of closely adjacent "dikinetids" because their kinetosomes form pairs each possessing a transverse and a postciliary microtubular ribbon. The fourth row of kinetosomes of the adoral membranelles shows the usual transverse microtubular ribbons, while one or two transverse microtubules are closely adjacent to the third and the second row of its basal bodies. Our data suggest that *Engelmanniella* has descended from a kahliellid lineage. However, its placement in a well-founded (!) stichotrichid family is impossible at present.

Introduction

Engelmanniella mobilis (Engelmann, 1862) Foissner, 1982 is the type species of a genus assigned to the Oxytrichidae, Cladotrichidae, and Kahliellidae [13, 20, 37, 42]. The taxonomic assignments above were based entirely on the uniform cirral pattern observed in non-dividing cells.

Although 102 genera have been included in the recently proposed classification of the order Hypotrichida [42], only single species belonging to 21 genera have been investigated at electron-microscopical level [2, 5, 6, 14, 19, 23–25, 27–29, 39, 46–48, 50 and references therein]. Certainly, this is too few to understand the phylogenetic value of ultrastructural features. Morphogenetic data of hypotrichs are more abundant, but still too inconsistent to allow a definite conclusion about their systematic value at familial and genus level [21]. Their significance is even ambiguous at subordinal level as evident from the recent revisions of Small and Lynn [37] and Tuffrau [42], who still use symplesiomorphies to characterize the subordinal taxa. Thus, it was only a slight surprise to us that we were unable to give our peculiar genus a definite home at the end of the investigation.

Material and Methods

Engelmanniella mobilis was collected from the top soil (0–10 cm) of a forest *(Asperulo-Fagetum)* near Baumgarten (Lower Austria). The methods of cultivation and protargol silver staining are described in Foissner [20]. Protargol and a modified Feulgen

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stain [31] were used to study the nuclear cycle. Furthermore, a silver carbonate method was employed to examine the fibrillar associates of the ciliature [3]. For transmission electron-microscopy, cells were fixed according to Franke et al. [22]. They were dehydrated in a graded ethanol series, transferred through propylene oxide into Epon 812, and flat-embedded in aluminium weighing pans. Individual specimens were cut from the flat molds with a heated scalpel and cemented at the desired orientation onto the face of epoxy blocks. 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 an AEI Corinth 500 or a Philips EM 300 electron microscope. For scanning electron-microscopy, starved (1 day) cells were fixed with Párducz's solution [34]. Further processing corresponded to standard procedures [e.g., 25]. The freeze-fracture technique followed Bardele [6]. The terms right and left are employed from the organism's "point of view" that is with the observer inside the cell; to facilitate the comparison of light- and electronmicroscopic observations, all Figs. are orientated as seen from outside the cell.

The cells of a Japanese population from a rice field near Kumamoto were exposed to alcian blue, methyl green-pyronin, cold and hot (50 °C) acetone, sudan black, and sudan red III to study the nature of the subpellicular granules [1, 36]. Specimens of the *Tetrahymena pyriformis* complex served as control organism. Ultrathin sections were used for acid hydrolysis to reveal the RNA nature of the polysome-like granules in the mitochondria [1].

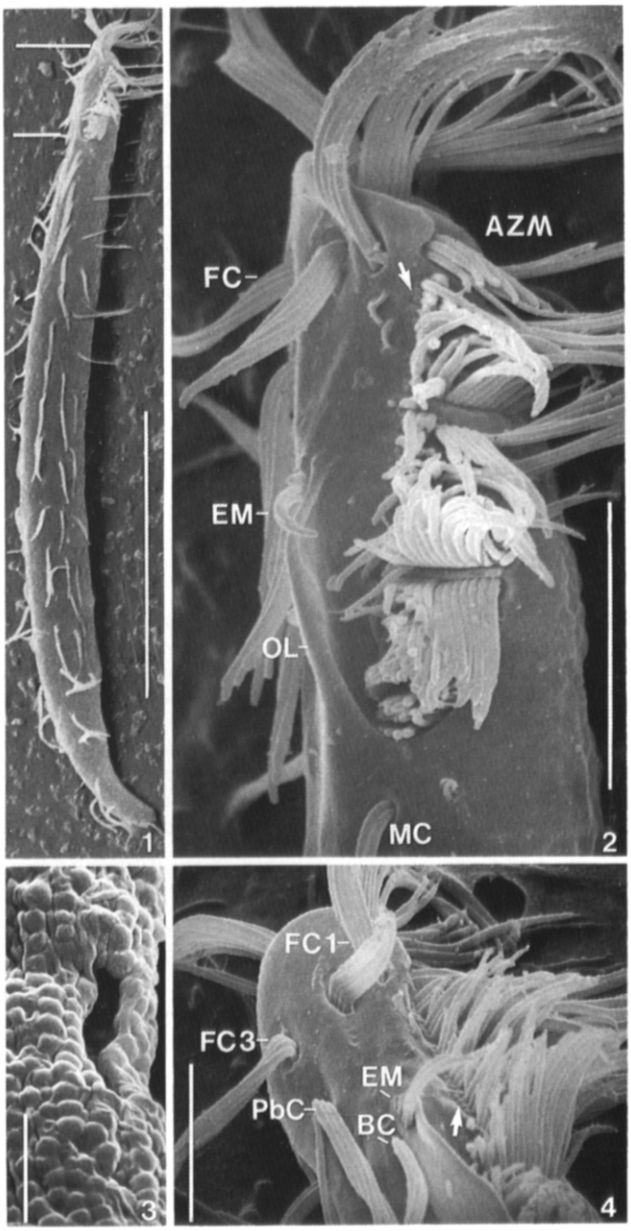
Results

This study concentrates on the morphogenesis and the ultrastructure of the infraciliary elements. Some details of other cytoplasmic structures, e.g. the subpellicular granules, are given as preliminary results. For comparison, the infraciliature of interphasic specimens of *Engelmanniella mobilis* is shown in Figs. 1, 2, 4, 5.

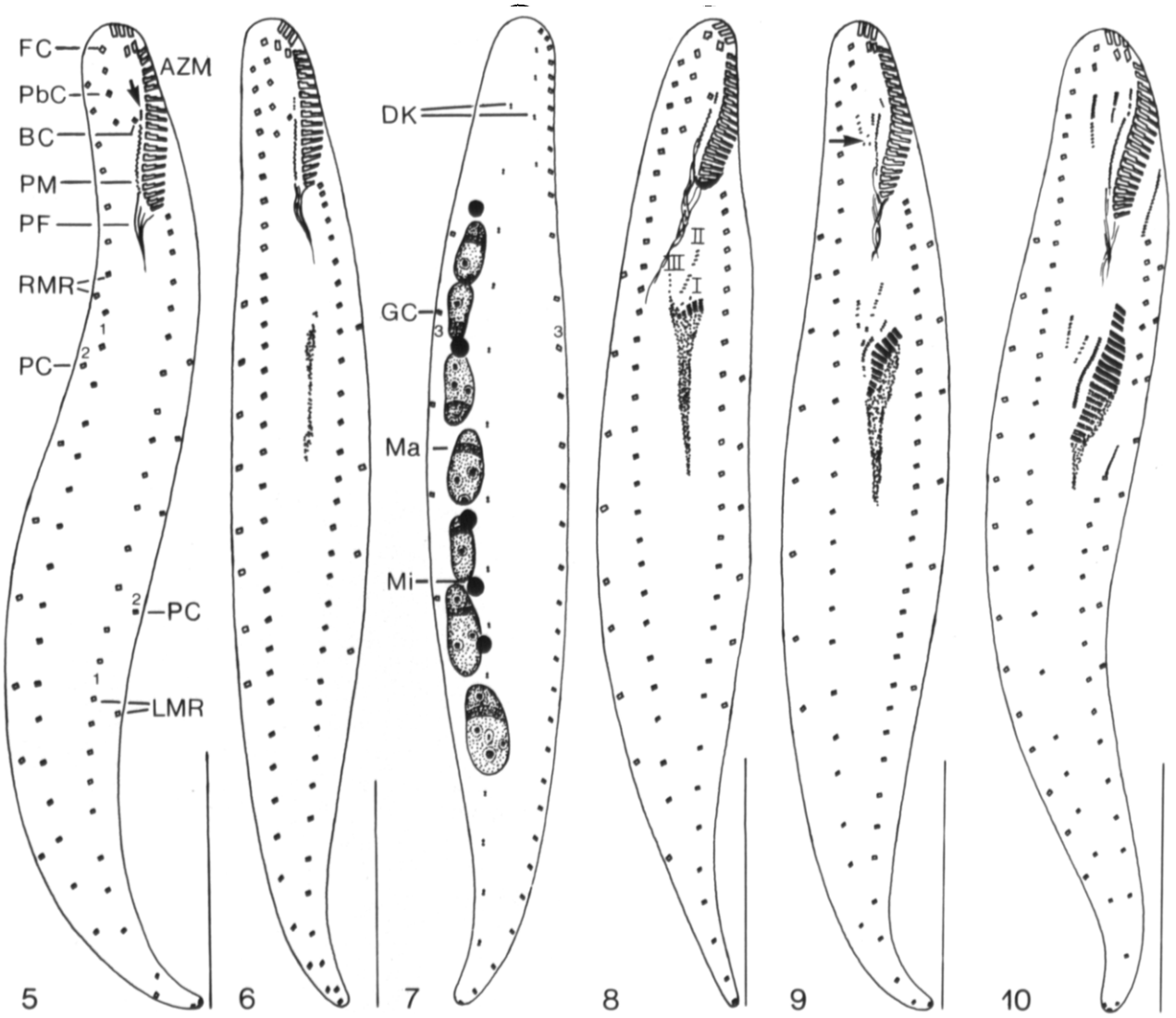
Foissner [20] used a rather general terminology to describe the infraciliature of *E. mobilis*, because he was unable to distinguish the different kinds of cirri. The morphogenetic investigation permits a precise nomination of the cortical elements. The "first cirral row to the right of the mediam" [20] is composed of the third frontal cirrus and several parabuccal cirri which are characterized by their origin in the frontal anlage III and their position on the frontal area beside the buccal cirrus. This distinction allows the separation from frontal cirri arising in the anlagen IV, V and so on in other hypotrichs. The "cirral rows" [20] develop by self-replication (within row proliferation) in the anterior and the middle region of the cell; thus, they correspond to marginal rows which belong to the somatic ciliature [7, 46].

Morphogenesis of cell division

Stomatogenesis. The oral primordium originates apokinetally close to the center of the ventral surface. It comprises a small, lengthened field of newly formed kinetosomes (Fig. 6). Soon, from its broadened anterior part, three adoral membranelles differentiate (Fig. 8),



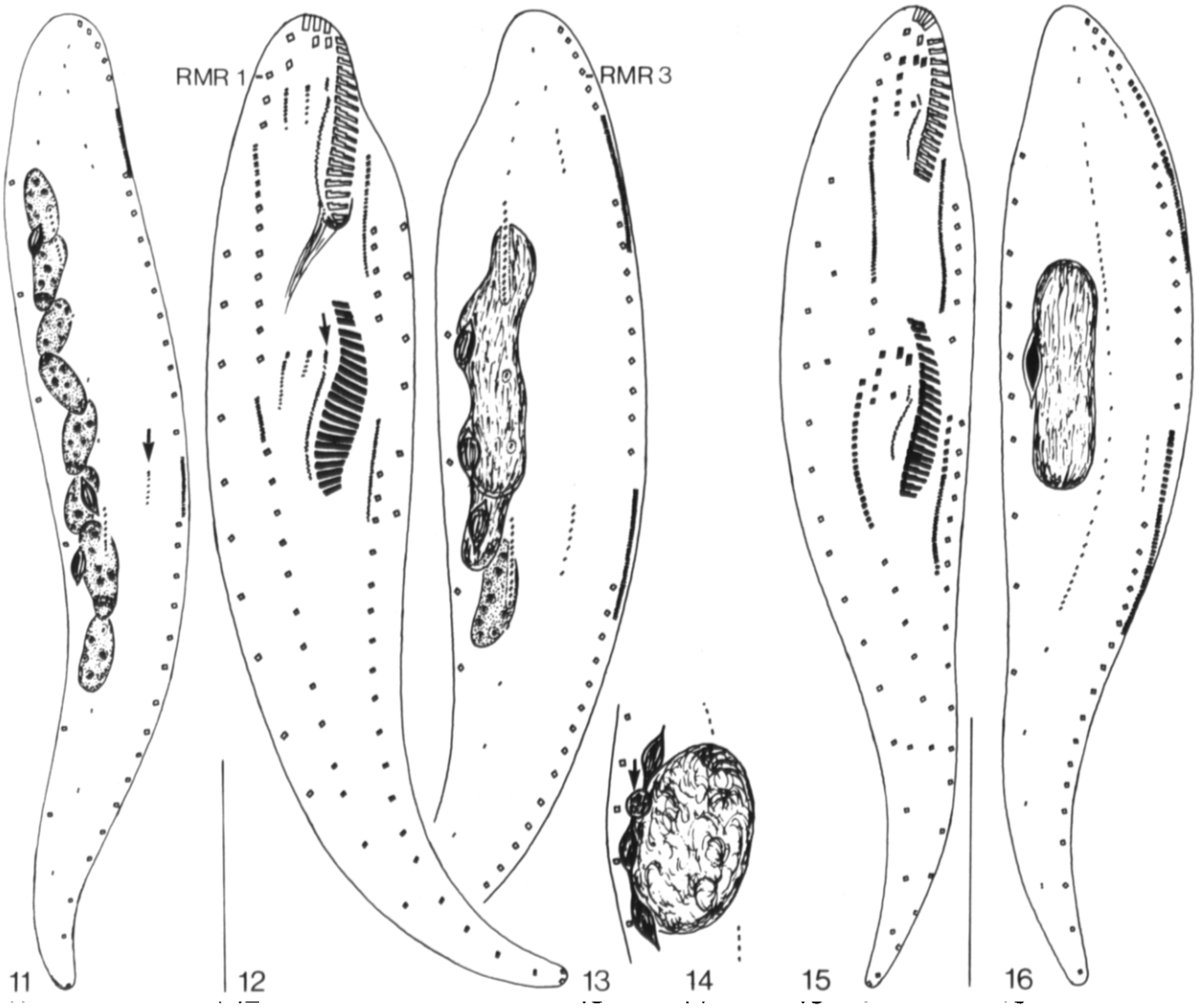
Figs. 1–4. Scanning electron micrographs of *Engelmanniella mobilis*. – Fig. 1. General organization. The lines denote the very small oral area. Bar = 70 µm. – Fig. 2. Detail of the oral area. The frontal cirri (FC), the endoral membrane (EM), and a marginal cirrus (MC) of the 1st left row are visible. Note the ciliary stubs (arrow, comp. Fig. 4) of the rightmost basal bodies of the adoral membranelles (AZM). The short cilia of the paroral membrane are invisible because they lie in the fold of the oral lip (OL). Bar = 10 µm. – Fig. 3. Pore of the contractile vacuole. The subpellicular granules appear as hemispherical elevations in this slightly shrunken cell. Bar = 5 µm. – Fig. 4. View of the oral area illustrating the short endoral membrane (EM) neighbouring the buccal cirrus (BC) which comprises four cilia. The 1st (FC 1) and the 2nd frontal cirrus consist of eight cilia, while the 3rd one (FC 3) and the 1st parabuccal cirrus (PbC) comprise six cilia. Bar = 5 µm.



Figs. 5–10. Interphasic morphology (Fig. 5) and early morphogenetic stages (Figs. 6–10) from protargol impregnated specimens of *Engelmanniella mobilis*. – Fig. 5. Ventral view of a non-dividing cell. Note the endoral membrane (arrow) in front of the paroral membrane (PM). AZM = adoral zone of membranelles, FC = frontal cirri, LMR = left marginal rows, PbC = parabuccal cirri, PC = parental cirri, PF = pharyngeal fibers, RMR = right marginal rows, 1–3 = marginal rows (comp. Fig. 7). – Figs. 6, 7. The longitudinal oral primordium develops de novo. The 3rd right marginal row and the 3rd left one which consists of grandparental cirri (GC) are situated on the dorsal side. Each macronuclear segment (Ma) shows one replication band. DK = dorsal kineties, Mi = micronucleus. – Fig. 8. In the opisthe, the anlagen (I–III) separate from the oral anarchic field. – Fig. 9. In the proter, the anlagen II and III arise from a dispersion of the buccal cirrus and the posteriormost parabuccal cirri. Probably some kinetosomes originate de novo (arrow). – Fig. 10. The parental endoral membrane evolves the primordium of the 1st frontal cirrus. Streaks appear in the 1st left marginal row. Bars = 30 μm.

which can be easily recognized as the detached frontal adoral membranelles of the interphasic cell (Figs. 2, 5, 46, 48). A group of basal bodies segregates from the oral primordium forming the anlagen of the undulating membranes and of two frontal cirral streaks in the opisthe (Figs. 8, 9).

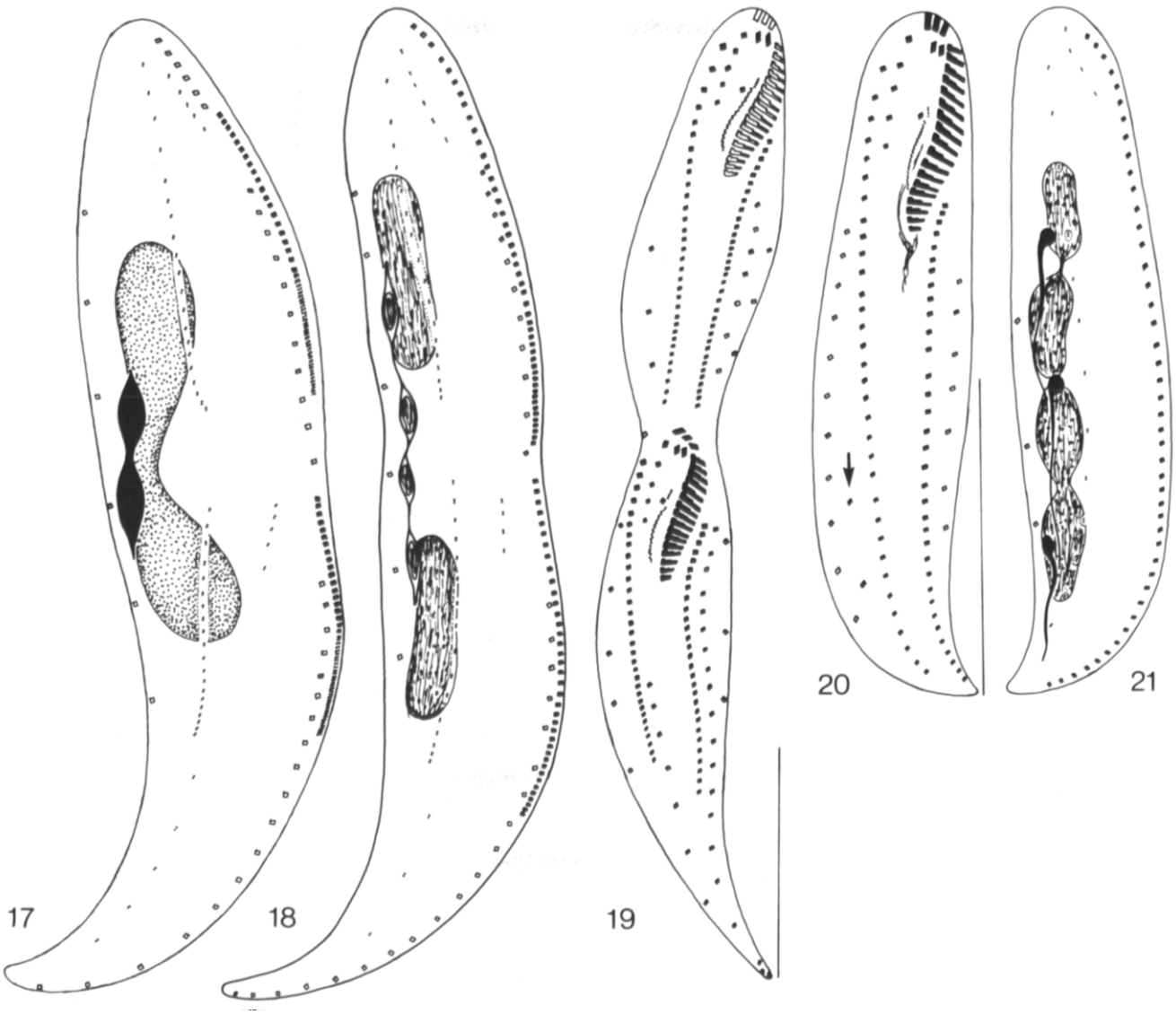
In the proter, the primordium of the first frontal cirrus develops from the endoral membrane (Fig. 10). The parental paroral membrane is slightly disordered in later divisional stages (Fig. 12) indicating that it is also reorganized, at least in part; however, details are too small in this species to stress a firm conclusion. Remarkable is the displacement of the extraordinarily short endoral membrane in front of the paroral one (Figs. 15, 19, 20). At first, we had the impression that it arises by a terminal segmentation; however, careful examination of a lot of divisional stages convinced us that the new endoral membrane originates in the usual way, that is by an anterior longitudinal splitting of the paroral membrane [e.g., 9, 10]. The parental adoral zone of membranelles is maintained throughout the division. The pharyngeal fibers, however, are invisible in later morphogenetic stages



Figs. 11–16. Middle morphogenetic stages of *Engelmanniella mobilis* (protargol impregnation). – Fig. 11. Note the apokinetal origin (arrow) of the very short dorsal kinety in the opisthe. – Figs. 12, 13. Formation of primordia in the 1st (RMR 1) and the 3rd (RMR 3) right marginal row and in the 1st left row. The 3rd left (grandparental) marginal row remains unchanged. In the opisthe, the 1st frontal cirrus (arrow) originates from the primordium of the undulating membranes. The macronuclear segments fuse and the micronuclei became prophasic. – Fig. 14. The macronuclear mass condenses; some micronuclei do not divide (arrow). – Figs. 15, 16. Differentiation of cirri proceeds in the 1st right and the 1st left marginal row, but no changes occur in the 2nd right and the 2nd left one (rows consisting of parental cirri). Bars = 30 μm.

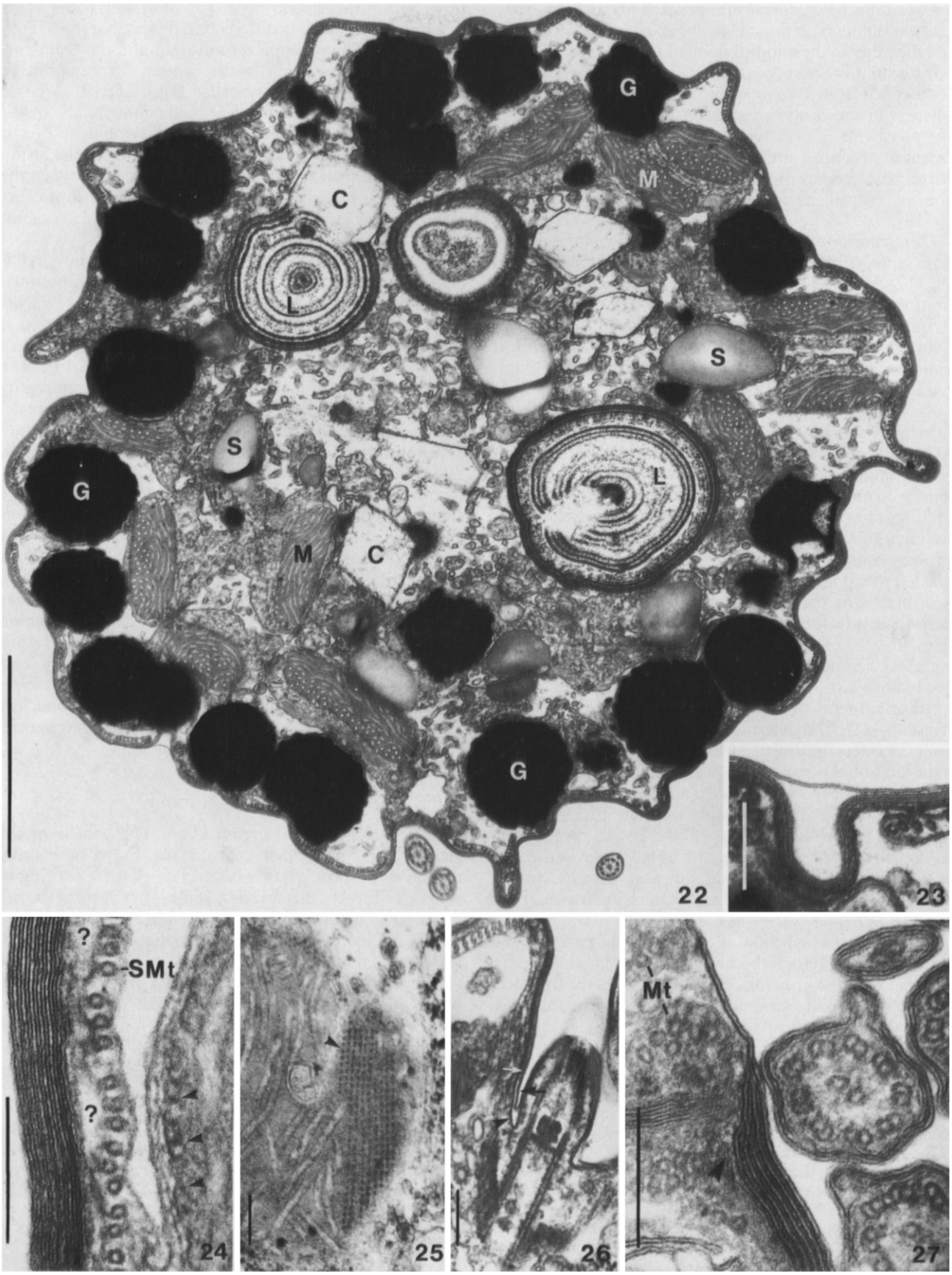
(Figs. 15, 19). Thus, they may be reorganized as proposed for other hypotrichs [e.g., 7, 9, 21].

Development of cirral primordia. Three frontal anlagen (including the primordium of the undulating membranes) arise in each filial product. Each develops in a different manner: in the opisthe all of them separate from the oral anarchic field, while in the proter the anlagen originate by a dispersion of parental structures (Figs. 8–10) including the endoral membrane, the buccal cirrus, and two to four of the posteriormost parabuccal cirri. In some specimens, basal bodies have been observed posterior to these cirri (a less distinct stage is shown in Fig. 9). They may have originated de novo because the parental buccal and parabuccal cirri were sometimes still intact. Further primordia develop within the first left and right marginal row and the rightmost (third) marginal row which is situated on the dorsal side (Figs. 10–12). Parental cirri in the anterior part and in the middle of the cell participate in the formation of these anlagen according to the development of typical marginal rows. It is remarkable that the proliferation starts latest in the first right row (comp. Figs. 10–13). No anlagen are generated within the second right and the two leftmost marginal rows (Figs. 10–13, 15–18).



Figs. 17–21. Late morphogenetic stages of *Engelmanniella mobilis* (protargol impregnation). – Figs. 17, 18. Division of the nuclear apparatus and formation of the division furrow. Several micronuclei are covered with a single envelope. – Fig. 19. The elongation of the daughter cells and the resorption of some parental and grandparental cirri cause enlarged distances among the conserved cirri. – Figs. 20, 21. Ventral and dorsal view of the proter after division. Two grandparental cirri of the old 2nd right marginal row are still present (arrow). The micronuclei are still in telophase as indicated by the thin projecting filaments. Bars = 30 μm.

Figs. 22–27. Transmission electron micrographs of *Engelmanniella mobilis*. – Fig. 22. Cross section in the middle region of the cell. ▶ Prominent subpellicular granules (G), crystal-like structures (C) projecting from the lithosomes (L), mitochondria (M), and starch grains (S) are visible. Bar = 3 μm. – Fig. 23. Transverse section of a structure probably corresponding to the pellicular invaginations shown in Figs. 28, 29. Bar = 200 nm. – Figs. 24, 25. Multilamellate pellicle accompanied by the alveoli (?) and a single layer of subpellicular microtubules (SMt). Regularly patterned mitoribosomes (arrowheads) are visible on the inner side of the mitochondrial membrane. Bars = 200 nm. – Fig. 26. In the vicinity of cirri, an external perilemma (large arrow) and the cell membrane (arrowhead) are recognizable. Additional membranes (small arrow) are disposed between these structures. Bar = 200 nm. – Fig. 27. The cytopharyngeal area is partly covered by a single unit membrane and is enforced by membrane layers and microtubules (Mt). The individual members of a membrane stack may extend into the cytoplasm (arrowhead). Several membranes cover the cilia. Bar = 200 nm.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Development of dorsal primordia. Two anlagen originate within the right dorsal kinety, one in the anterior part and the other in the middle region of the cell (Fig. 11). The extraordinarily short (on the average four pairs of basal bodies) left row develops apokinetally in the opisthe, whereas in the proter the primordium proliferates from one or two pairs of parental basal bodies (Figs. 11, 13). Parental structures are resorbed after the new pairs of dorsal basal bodies move to their final positions. Formation of caudal cirri has never been observed (Figs. 16–18).

Differentiation of cirri. The first frontal cirrus develops from the primordium of the undulating membranes (Fig. 12). The second frontal cirrus and the buccal cirrus are formed in the anlage II (Figs. 12, 15, 19, 20). Frequently 2–4 supernumerary cirri arise in this primordium which are resorbed later. From anlage III the third frontal cirrus and 3–5 parabuccal cirri differentiate (Figs. 12, 15, 19, 20).

As mentioned above, some marginal rows do not participate in the formation of primordia; moreover 30%–80% of their cirri are *not* resorbed in later morphogenetic stages. Therefore, different generations of cirri are conserved on the lateral areas of the filial products. To the left three cirral generations can be distinguished: the newly built marginal cirri constitute the first left row; the second left row consists of parental cirri remaining from the old first left row (Figs. 15, 19, 20); whereas the old second row is displaced to the left, thus representing grandparental cirri which now form the third left row in the filial products (Figs. 16–18, 21). On the right border two generations of marginal cirri persist: the first and the third row consist of newly built cirri, whereas the second right row is constituted of parental cirri formerly comprising the third row (Figs. 15–21). The determination of the different generations considers the directed increase of the primordia to the right side of the parental marginal rows (Figs. 12, 15). Consequently new marginal cirri are generated to the right of the old ones. (The seemingly opposite process in the rightmost row shown in Figs. 13 and 16–18 results from an optical artefact; the correct focus level proves the new primordia next to the dorsal kineties, but due to the restricted space the parental row has to be drawn at the "wrong" side).

The transverse splitting of the remaining parental and grandparental marginal rows on two daughter cells, together with the growing cell cortex, causes the distances among the somatic cirri in the two leftmost (conserved) rows and in the second right (parental) row to be wider than those in the newly differentiated marginal rows (Figs. 19–21, 29). The parental second right and the grandparental third left somatic row, the frontal cirri, and one or two parabuccal cirri are resorbed (Figs. 15, 19).

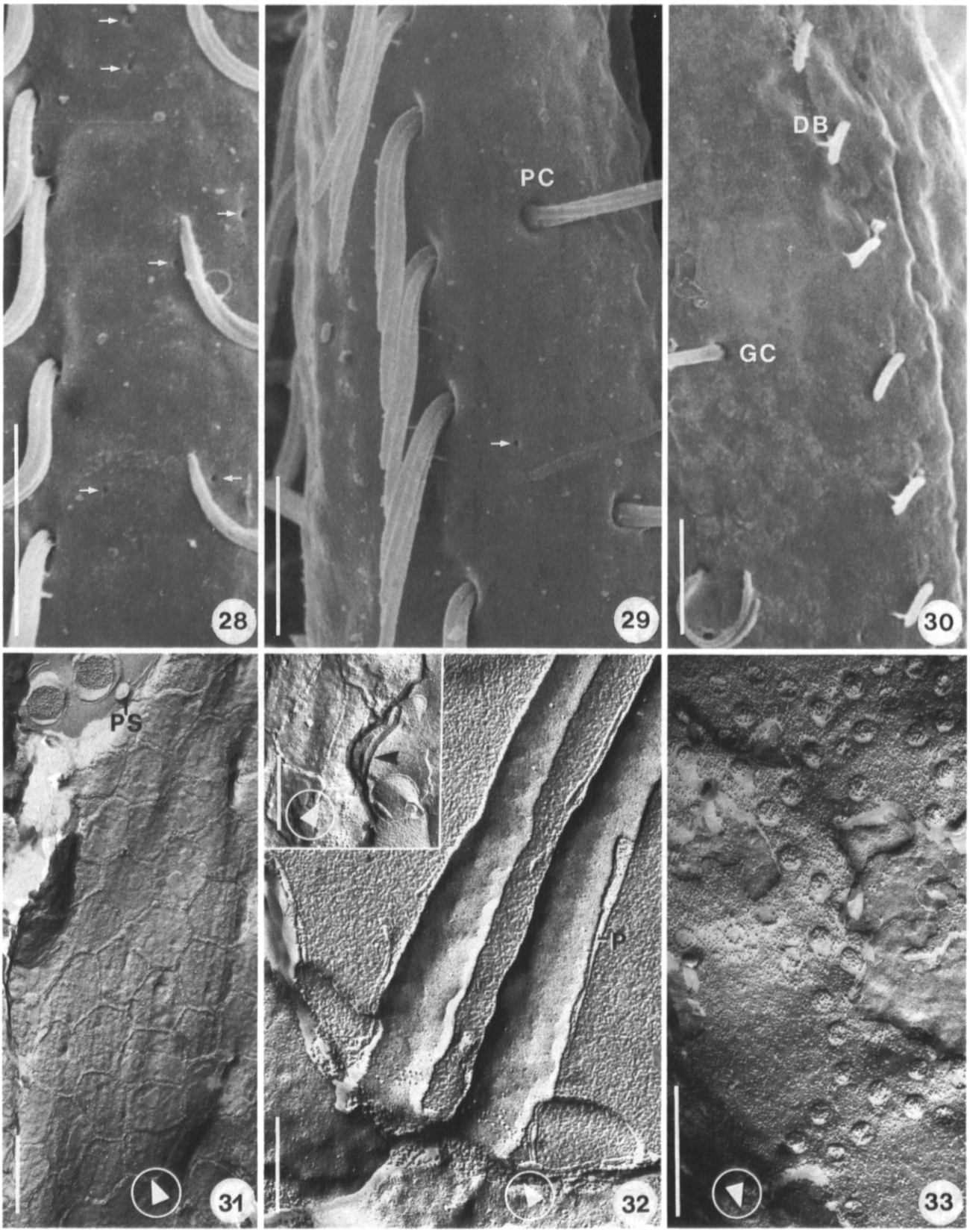
Nuclear cycle. The nuclear behaviour tends to be remarkably independent from the development of the cortical pattern: in about half of the specimens, the fusion of the macronuclear segments is completed just when the frontal primordia arise; in the other half, this fusion occurs when the new cirri are differentiated (Figs. 15, 16) or even during their final displacement.

As usual the macronuclear segments often show replication bands (Figs. 7, 11) before any cortical divisional processes can be detected. After their passage, the segments fuse to an irregularly shaped aggregation showing a fibrous content (Fig. 13). Further condensation results in an elliptical mass with whirling fibers (Fig. 14). The original number of macronuclear segments is restored by subsequent divisions (Figs. 16–18, 21). Some micronuclei became prophasic, start to stretch and the chromosomes appear arranged along the future spindle (Figs. 11, 13, 14). Other micronuclei obviously do not divide (Fig. 14), because we frequently (14%, n = 29) found only a single spindle-like micronucleus or two yet connected micronuclei (Figs. 16, 17), although the interphasic cells have at least two micronuclei. The non-dividing micronuclei are invisible in late morphogenetic phases (Figs. 16–18, 21). However, among 68 corresponding stages micronuclear ghosts could not be detected. A further uncommon attribute of this strain is a "chain" of three or four micronuclei covered by a single envelope (Fig. 18). This situation occurred in 7% of 55 cells investigated. Nevertheless, in later morphogenetic stages the micronuclear division seems to be quite normal in showing micronuclei in the telophase (Fig. 21).

Electron-microscopical observations

Pellicle and internal organization. The pellicle of the ventral and the dorsal cell surface shows a varying thickness: in most parts it is multilamellate consisting of 3–6 three-layered membranes, while other parts of the cell are covered by up to 17 of such membranes (Figs. 22–24, 26, 27, 32, inset). Somatic and oral cilia show at least two, sometimes three membranes (Figs. 26, 27, 32). In the vicinity of the cirri, the pellicle consists of two membranes which might be identified as an external "perilemma" and

Figs. 28–33. Scanning electron (Figs. 28–30) and freeze-fracture micrographs (Figs. 31–33) of *Engelmanniella mobilis.* – Figs. 28, 29. Note the irregularly distributed pellicular invaginations (arrows). The cirri of the 1st left marginal row are closer situated than those of the 2nd left row consisting of parental cirri (PC). Bars = 5 μm. – Fig. 30. The grandparental cirri (GC) of the 3rd left marginal row comprise two cilia, while the dorsal bristle complexes (DB) have a single ciliary stub. Bar = 5 μm. – Fig. 31. P-face of the alveolar layer and face-on view of a kinetosomal territory showing two broken cilia and a parasomal sac (PS). Bar = 2 μm. – Fig. 32. The E-face of the ciliary membrane shows the usual double-stranded ciliary necklace and unpatterned particles; parts of the perilemma (P) are visible too. The inset at the upper left illustrates the P-face of some membranes (arrowhead) of the multilamellate pellicle and a few alveoli. Bars = 2 μm. – Fig. 33. Roughly hexagonally arranged pore complexes in the E-face of the nuclear envelope. Bar = 2 μm. The encircled arrowheads in Figs. 31–33 give the direction of shadowing. ▶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the cell membrane (Fig. 26). Figure 26 illustrates that further layers are interposed between these membranes; thus, the additional layers probably represent stacks of perilemma. Single unit membranes occur most frequently in the cytopharyngeal area (Fig. 27). In such sections, however, it is difficult to decide if this structure corresponds to the perilemma or the cell membrane (Fig. 27). The individual members of the membrane stacks can be confluent or extend into the cytoplasm leaving one-layered membranes (Fig. 27). Alveoli are indistinct in ultrathin sections, but clearly revealed by freeze-fracturing; many randomly distributed intramembranous particles can be observed (Fig. 31). The same is true for the membrane stacks of the perilemma (Fig. 32, inset). We could not find out the definite location of the alveoli. Probably, they are situated between the cell membrane and the subpellicular microtubular layer (Fig. 24).

Below the somatic pellicle, there is a single layer of longitudinal subpellicular microtubules enclosed by the inner alveolar (?) membrane and a cytoplasmic membrane (Figs. 22–24). An epiplasm could not be identified.

Several randomly distributed pellicular invaginations measuring about 100 nm in diameter were observed (Figs. 28, 29). A single ultrathin section showed a structure which might correspond to such an invagination (Fig. 23). We can not exclude the possibility that these structures are artefacts because pellicular invaginations have never been observed in other hypotrichs.

A great number of starch grains and lithosomes typically accompanied by projecting rhomboidal crystal-like structures occur in the artificially (?) vacuolated cytoplasm (Fig. 22). Frequently the mitochondria show polysome-like granules (mitoribosomes) lined up in regular rows on their inner membrane (Figs. 24, 25); this has also been observed in *Pseudourostyla* spp. [38]. Their RNA nature was verified by the hydrochloric acid hydrolysis. The macronuclear segments contain relatively large, irregularly formed chromatin. The freeze-fracture technique reveals roughly hexagonal arranged pore complexes of usual structure [24, 45] in the macronuclear envelope (Fig. 33). Two ultrathin sections of the replication band obtained from different specimens show a conventional forward and rear zone [14, 33]. The micronuclei were not observed.

A characteristic feature of *E. mobilis* are rows of spherical subpellicular granules, 0.5–1 μm in diameter, which have been described light-microscopically [20]. The granules cause a distinctly wrinkled surface in suboptimally critical-point dried cells (Fig. 3). These organelles are very likely not extrusive during the interphase because (1) no empty granules were found electron-microscopically (Figs. 3, 22); (2) no anchoring rosettes [26] could be observed in freeze-fracture replicas; (3) they do not stain with alcian blue; (4) heat, methyl green-pyronin, acetone, and various other reagents cause no extrusion. Each granulum is covered with a membrane (Fig. 39), which has many disordered intramembranous particles. The granules are colourless to slightly yellow in the light microscope, but very dark stained by the electron-microscopical procedures (Figs. 22, 39) and by silver carbonate (Figs. 46, 47). Their strong osmiophily, their slightly Feulgen positive reaction, and their lamellar structure during development suggest that they contain complex lipids [1, 16, 36]. However, they are insoluble in ethanol (during dehydration) and cold as well as hot acetone which is a reaction indicative of phosphatides [36]. Sudan III and sudan black did not clearly stain these granules.

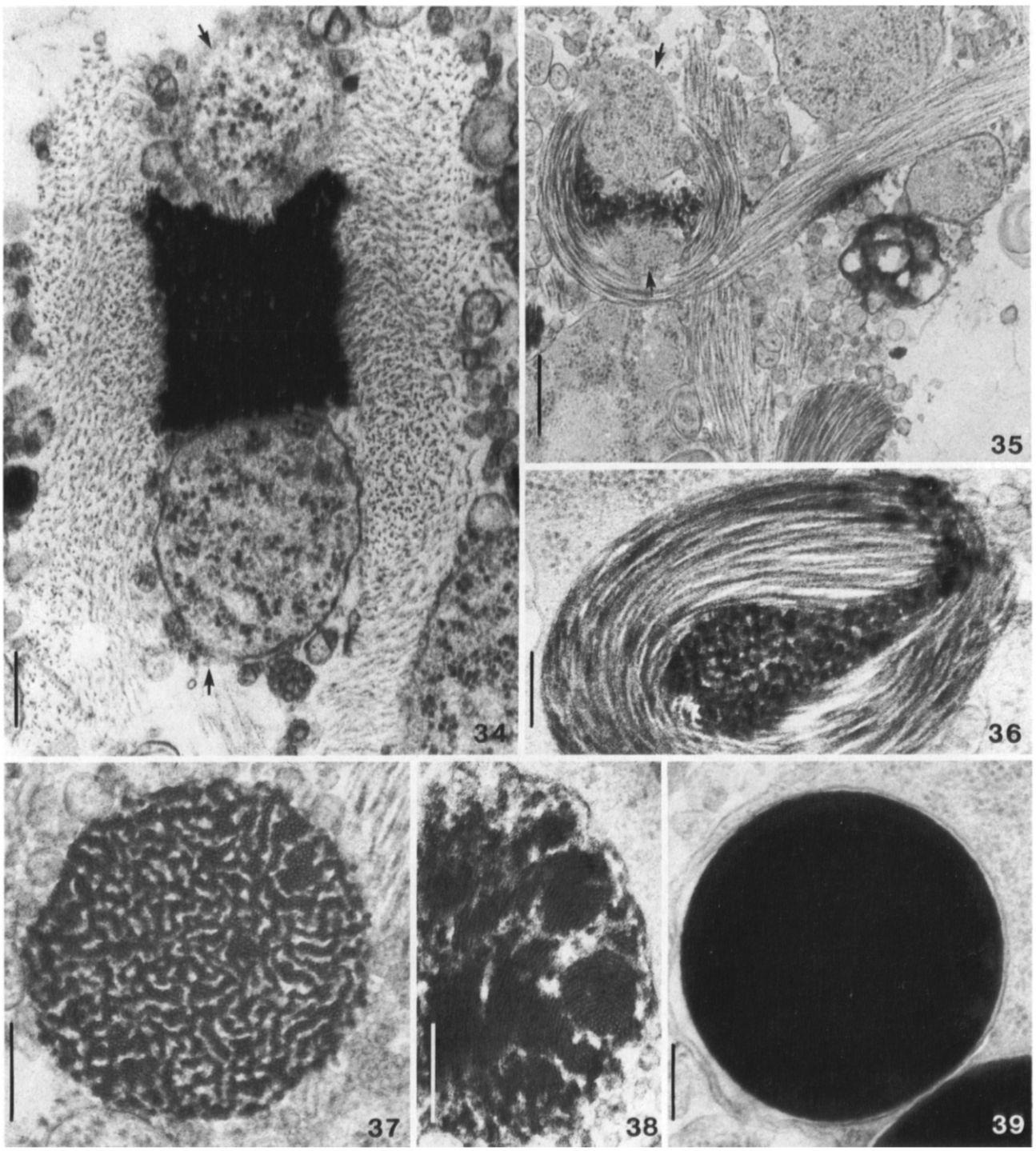
In the non-dividing cells prepared for electron microscopy, we frequently observed structures very probably representing different developmental stages of these granules. Straight bundles of fibers roll up and form a dark stained mass which is often associated with segregated cytoplasmic (?) material (Figs. 34, 35). The dark central part enlarges (Figs. 34–37). At first sight it looks like a micronucleus, but in fortunate sections the fibers comprising this mass are still visible. With increasing condensation, they appear tubule-like (Figs. 36–38); however, this could result from a decoration of the fibers with osmiophilic material. In the fully developed granules usually no substructure is recognizable (Figs. 22, 39). Sometimes a spongious central part is visible.

The subpellicular granules are absent from the pellicle and the cytoplasm of encysted cells suggesting that they contribute to the formation of the cyst wall. A detailed study is in progress.

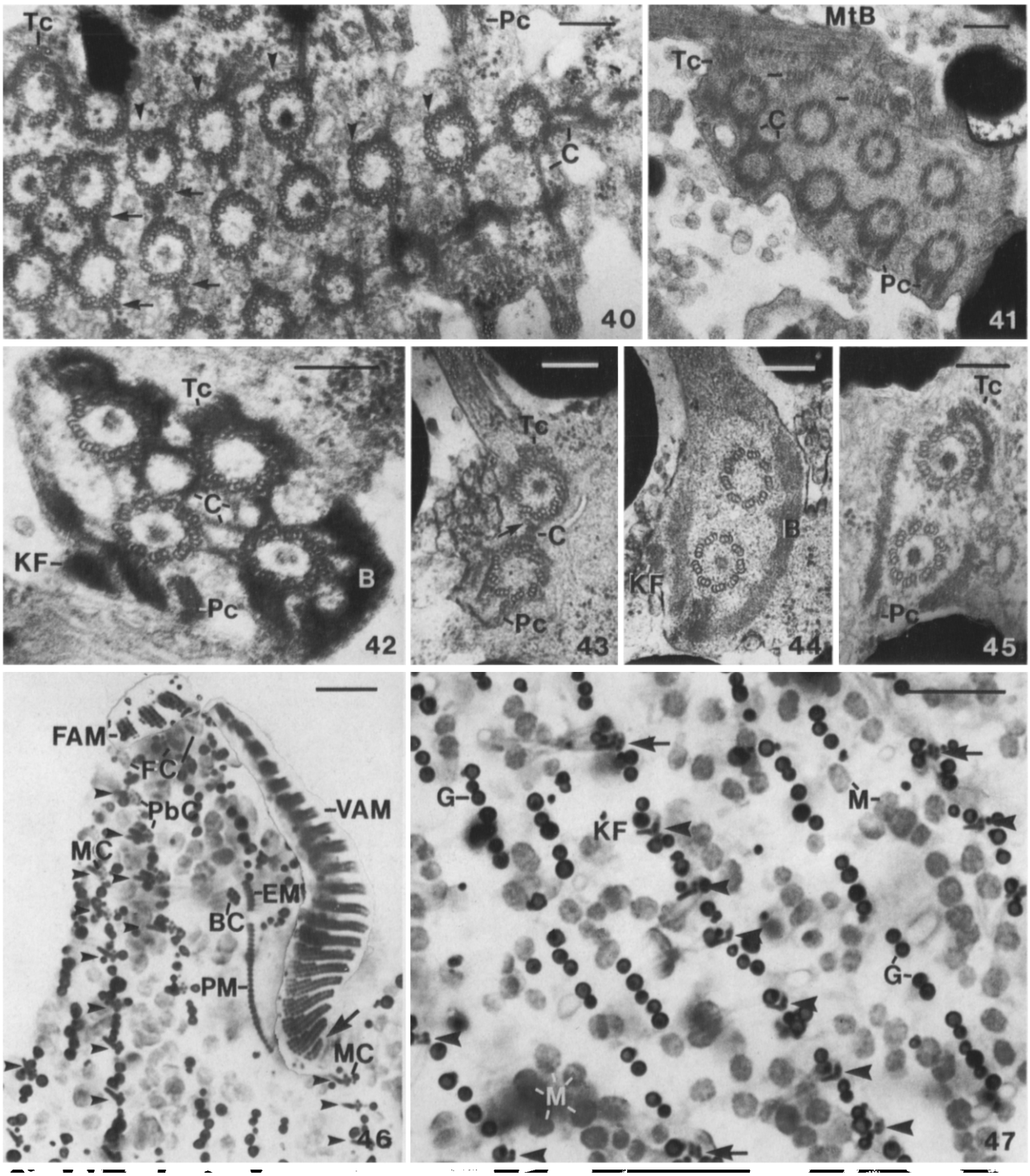
Somatic and oral ciliature. The first and second frontal cirrus comprise 8–10 kinetosomes, whereas the third one has only six basal bodies; the buccal and the first parabuccal cirrus consist of 4–6 kinetosomes (Figs. 2, 4, 41, 46), the other parabuccal cirri regularly have four basal bodies. The marginal cirri of the youngest generation generally comprise four basal bodies in the anterior two thirds (Figs. 2, 28, 29, 42) and two kinetosomes in the posterior third of the cell (Fig. 47). In contrast, those of the parental and grandparental ones nearly regularly consist of only two basal bodies (Figs. 29, 30, 43, 44). The exact pattern is shown in the schematic Fig. 48 and has been proved to be rather constant.

All cirri are ciliated (Figs. 1, 2, 4, 28–30) and show the same basic organization as other hypotrichs (Figs. 41–44) [14, 19, 23–24, 27, 32; and references within those works]. Nonetheless, their structure is strongly reminiscent of dikinetids, because all basal bodies form "pairs" each showing a transverse and a postciliary microtubular ribbon. Thus, the cirri of *E. mobilis* consist of groups of "paired" kinetosomes and simple dikinetids surrounded by a typical cirral basket (Figs. 41–44, 49). Silver carbonate impregnation shows very clearly the absence of the kinetodesmal fibers in the three frontal cirri and the buccal cirrus (Figs. 46, 48). The cilia show a double-stranded ciliary necklace and a medium number of unpatterned particles (Fig. 32); this has also been observed in *Urostyla* sp. [5].

The dorsal bristle complex of *Engelmanniella mobilis* is almost identical to that of e.g. *Kahliella, Paraurostyla, Laurentiella,* and *Oxytricha* [19, 25, 29, 39]. Macrotubules were not observed [19, 29, 39]. The dorsal bristle complex can be distinguished from the "paired kinetosomes" of the cirri by the following characteristics: (1) only the anterior basal body of a dorsal pair is ciliated (Fig.



Figs. 34–39. Possible genesis of the subpellicular granules in *Engelmanniella mobilis*. – Figs. 34, 35. Cross and longitudinal section of the fibers which seemingly roll up and probably compose the dark stained mass. Segregated cytoplasmic material (arrows) is associated with the fibrillar bundles. Bars = 200 nm and 500 nm, respectively. – Figs. 36–38. The tubular appearance of the condensating organelle possibly results from a decoration of the fibers with osmiophilic material. Bars = 200 nm. – Fig. 39. The fully developed granules are covered with a membrane and show no substructure (comp. Fig. 22). Bar = 200 nm.



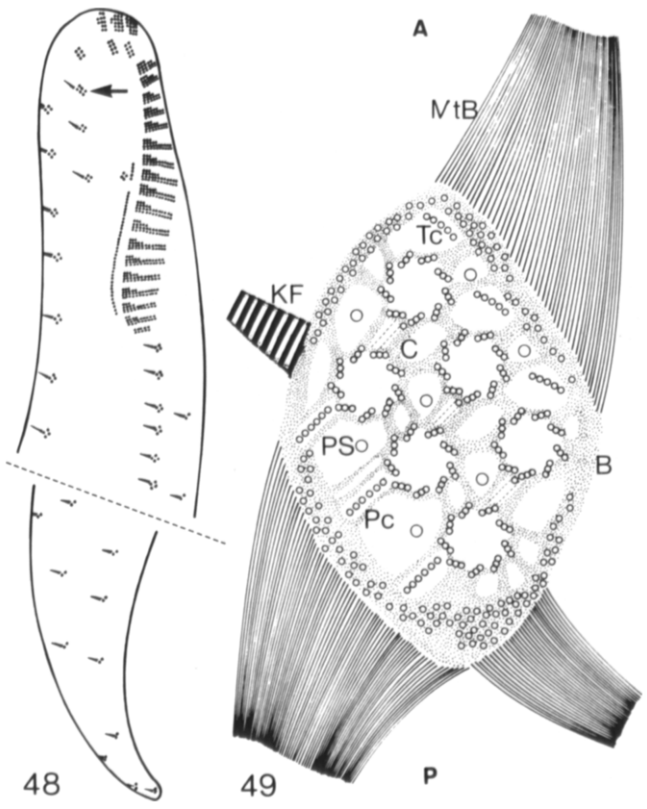
Figs. 40–47. Oral and somatic ciliature of *Engelmanniella mobilis*. Transmission electron micrographs (Figs. 40–45; Bars = 200 nm) and silver carbonate impregnation (Figs. 46, 47; Bars = 5 µm). – Fig. 40. Kinetosomes of the 4th row of the adoral membranelles bear transverse microtubular ribbons, while two microtubules (arrowheads) are associated with the 3rd and 2nd row of basal bodies. Single proximal and double distal electron-dense connections are visible. The posteriormost kinetosomes show postciliary microtubular ribbons and the internal ones have a single postciliary microtubulus (arrows). – Fig. 41. Grazing section of the 1st frontal cirrus. Each "pair" of basal bodies shows a transverse (lines) and a postciliary microtubular ribbon. – Figs. 42–44. Marginal cirri consisting of one or two "dikinetids" show the same microtubular and microfibrillar associates. Distally the kinetosomes are interlinked and connected with the cirral basket by electron-dense material (Fig. 42). Proximally a single interkinetosomal link is present; the arrow in Fig. 43 denotes a single postciliary microtubulus emerging from the anterior kinetosome. – Fig. 45. Asymmetrically arranged electron-dense material of a dorsal bristle complex (comp. the cirral basket in Fig. 44). B = fibrillar basket, C = electron-dense connections, KF = kinetodesmal fiber, MtB = microtubular bundle, Pc = postciliary microtubules, Tc = transverse microtubules. – Fig. 46. The rightmost frontal adoral membranelle (FAM) consists of three rows of kinetosomes; next to the cytopharynx there is a single one comprising only two rows (arrow), while the other ventral adoral membranelles (VAM) and two FAM have four rows of basal bodies (comp. Fig. 48). Kinetodesmal fibers (arrowheads) are associated to the marginal (MC) and parabuccal cirri (PbC); they are absent in the frontal cirri (FC) and the buccal cirrus (BC). – Fig. 47. The marginal cirri comprise four basal bodies (arrows) in the anterior region, while they consist of two kinetosomes (arrowheads) in the posterior 3rd of the cell (comp. Figs. 46, 48). Note the rows of the argyrophilic subpellicular granules (G) and numerous mitochondria (M; comp. Fig. 46). EM = endoral membrane, PM = paroral membrane.

30); (2) possession of only a proximal interkinetosomal connective; (3) the electron dense material surrounding the pair is asymmetrically arranged (comp. Figs. 44, 45); (4) the microtubules originating from this material are relatively few in number and short (Fig. 45); (5) the absence of the kinetodesmal fiber (proved by silver carbonate impregnation [3]).

The two left frontal adoral membranelles consist of four rows of basal bodies, whereas the rightmost membranelle is composed of only three rows (Figs. 46, 48); probably only two of them are ciliated. The ventral adoral membranelles consist of four rows of basal bodies, with exception of the adoral membranelle next to the cytopharynx which comprises only two rows (Figs. 46, 48). In addition to the usual microtubular and microfibrillar associates [e.g., 4, 19, 24, 28, 39], we observed one or two transverse microtubules closely adjacent to the basal bodies of the second and third row (Fig. 40). The scanning electron-microscope shows some evidence that the rightmost kinetosomes of the adoral membranelles have only ciliary stubs (Figs. 2, 4).

The paroral membrane is invisible in scanning electron-micrographs (Fig. 2). Light- and transmission electron-microscopical observations indicate that it is covered with the oral lip. The oral lip is an u-shaped structure with its open part directed to the center of the cell. A few sections of two cells indicate that the paroral membrane consists of a single row of closely arranged cilia. However, the occurrence of a second unciliated row of kinetosomes can not be ruled out since in silver carbonate preparations the basal bodies appear sometimes zigzag-like arranged. Light-microscopical observations show small (about 3–4 μm) immobile structures projecting from the kinetosomes of the paroral membrane. We were unable to decide whether these are short cilia or nematodesma.

The endoral membrane consists of 3–7 cilia (6–7 μm long; Figs. 2, 4); a single section indicates that its kinetosomes may bear only postciliary microtubules.



Figs. 48, 49. Diagrams of the infraciliature of *Engelmanniella mobilis*. The number of basal bodies comprising the oral and somatic ciliature (comp. Fig. 5 for terminology) is rather constant. The arrow in Fig. 48 denotes the 1st parabuccal cirrus, the microtubular and microfibrillar associates of which are shown in Fig. 49. Note the "paired" condition of the cirral basal bodies (comp. Fig. 41). The broken lines indicate the single proximal interkinetosomal link. A = anterior, B = basket, C = electron-dense connections, KF = kinetodesmal fiber, MtB = microtubular bundle, P = posterior, Pc = postciliary microtubules, PS = parasomal sacs, Tc = transverse microtubules.

Discussion

Morphogenetic comparison

The most remarkable ontogenetic feature of *Engelmanniella mobilis* is the transfer of three marginal cirral generations to the post-dividers. A conservation of parental marginal cirri has also been described in *Kahliella acrobates* and *Parakahliella macrostoma* [7, 17, 40]. We suppose from published figures that some marginal cirri persist in *Kahliella simplex* [8] and *Cladotricha koltzowii* [11], too. In the meantime, the morphogenesis of *Kahliella franzi* and *Parakahliella haideri* has been studied [9, 10]. These species seem to reorganize all cirri, although some of the cirral fragments of *P. haideri* strongly resemble conserved cirri. *Kahliella franzi* is perhaps not congeneric. *Cladotricha koltzowii* and *Engelmanniella mobilis* share the small number of frontal streaks and the apokinetal stomatogenesis [11]. The origin of a variable number of marginal rows (perhaps by conservation of parental cirri) and the genesis of the dorsal ciliature in *Cladotricha* spp. are unknown. *Cladotricha variabilis* in Borror and Evans [11] is in our opinion not congeneric. We agree with Berger et al. [7] that the persistance of old cirri in the post-dividers is an apomorphic character (and probably "primitive" because it is absent in the so-called advanced hypotrichs, e.g. in *Oxytricha*), since it is a rare feature; the occurrence of grandparental structures in *Engelmanniella mobilis* is even unique among ciliates, as far as we know the literature. The conservation of parental cirral structures in both, *E. mobilis* and some species of the kahliellids sensu lato *(Kahliella, Parakahliella, Cladotricha)* implies some sort of relationship between these taxa.

Supernumerary (parental?) marginal rows have also been observed in *Gastrostyla steinii* [23, 44], *Paraurostyla weissei* [30], and *Holosticha multistilata* [12]. However, these cases are extraordinary phenomena in clones or mutants. Here, these supernumerary marginal rows may arise by segmentation and overlapping of the newly

developing marginal rows like in the albino mutant of *Pseudokeronopsis rubra* [49] or by a de novo (?) formation of additional marginal primordia [44]. Clearly, all these processes are different from those in *Engelmanniella mobilis,* where the conservation of parental and grandparental cirral rows is a genus specific character.

In *Engelmanniella mobilis,* the left of the two dorsal kineties originates de novo in the opisthe. This mode of dorsal development is unknown in other hypotrichs. In general, shortened dorsal kineties are supposed to evolve from the right marginal primordium [7, 9, 10, 17, 21, 25, 29, 46]. This is obviously not the case in *E. mobilis,* because the anlagen are situated far away from each other (Figs. 11, 13). The apokinetal origin of a dorsal kinety in *E. mobilis* indicates that the ancestor has generated its long dorsal kineties by self-replication, as it is still the case, for instance, in *Kahliella acrobates* [17]. Then the left row became shortened and the corresponding kinety in the opisthe has to originate de novo. Consequently, the developmental pattern manifested in *Engelmanniella mobilis* is supposed to be a strong apomorphic character.

Calkins [13] has studied the nuclear cycle in an American variety of *E. mobilis.* He noticed that, despite the variable number of 2–6 micronuclei in interphasic cells, they are generally reduced to two during division. Contrary to our observations, he never found a "single micronucleus stage". For this reason and the fact that he detected faintly staining ghosts, Calkins [13] suggested their resorption and rejected the possibility of a micronuclear fusion. Indeed, degeneration of some micronuclei during morphogenetic processes has been observed occasionally in several species [e.g. 43], whereas a fusion of micronuclei only occurs during conjugation. Thus, we conclude that *E. mobilis* shows a relatively high tendency to resorb some of the micronuclei. Its 3–4 micronuclei covered with a single envelope could be explained by the observation that the daughter nuclei form a new envelope inside the old one [35, 43]. In *E. mobilis,* the micronuclei apparently divide more than once to produce the usual number of 2–4 and fail to separate for a while.

Ultrastructural comparison

A somewhat enigmatic finding is the multilamellate pellicle of *E. mobilis.* Considering the difficulties with fixation in hypotrichs, we can not completely rule out that this is an artefact; however, its very regular appearance in ultrathin sections and freeze-fracture replicas argues against this possibility. Numerous of our sections suggest that the innermost layer corresponds to the normal cell membrane, whereas the additional layers are stacks of perilemma (Fig. 26). The perilemma is a characteristic feature of tintinnids and several hypotrichs of different families [comp. 6]; however, numerous layers of it are mainly found in the cytopharynx [6], but occasionally also in the somatic region, e.g. in *Epiclintes felis* [15]. Bardele [6] speculates that the perilemma in hypotrichs is a temporary structure which is quite often renewed. In contrast, we could not find a cell (in the several specimens sectioned) only covered by a single membrane. Therefore, we rather assume that the multilamellate pellicle is a characteristic feature of *Engelmanniella mobilis.* Its origin and function remains unclear.

The present study provides a previously unknown organization of the cirri because all basal bodies form "pairs" each possessing a transverse and a postciliary ribbon. Thus, a cirrus of *E. mobilis* may be considered as group of 2–5 "dikinetids"; furthermore, single kinetosomal pairs occur in the conserved marginal rows and regularly in the cirri of the posterior third of the cell. The same paired condition of the basal bodies is evident, although unmentioned, in the spirofilid *Parastrongylidium martini* [19], while all other electron-microscopically known hypotrichs add kinetosomes to the original pairs [2, 14, 19, 23, 24, 27, 32, 39, 46–48, 50]. The cirral organization found in interphasic cells of *Engelmanniella* and *Parastrongylidium* strikingly resembles the cirral primordium of *Paraurostyla* [27], with exception of the fibrillar basket. Therefore, the "second round of proliferation", which causes a lateral expansion of a streak and consequently an enlargement of cirri in most hypotrichs [24, 27, 32], is obviously absent in *Engelmanniella* and *Parastrongylidium.* This conclusion is sustained by the light-microscopical observations of the morphogenesis. The number of kinetosomal pairs in the streaks is in accordance with that composing the cirri (Fig. 12).

The detailed investigation of the seemingly undifferentiated cortical pattern of *Engelmanniella mobilis* revealed a considerable degree of cirral differentiation, particularly the absence of the kinetodesmal fiber in the frontal cirri and the buccal cirrus, whereas two of them are reported in *Kahliella* [19] and even six in *Histriculus* [32]. Since the various kinds of cirri are difficult to distinguish in ultrathin sections, for instance the anterior and posterior frontal (parabuccal) cirri, a precise comparison is impossible at present. Interestingly the frontal cirri, especially the first and second one, of *Engelmanniella mobilis* are "enlarged" to a similar extent as those of the so-called advanced hypotrichs; for example, in *Gastrostyla* the number of basal bodies is three times higher in frontal than in marginal cirri [23], while in *Engelmanniella* this ratio is 2 : 1 to 5 : 1.

The adoral membranelles of *Engelmanniella mobilis* possess one or two transverse microtubules closely adjacent to the third and the second row of basal bodies. They occur in addition (!) to the usual transverse microtubular ribbons (comprising 4–7 microtubules) of the fourth kinetosomal row. *Kahliella acrobates* and *Gastrostyla steinii* (members of different suborders) have only single transverse microtubules emerging from the kinetosomes of 1–3 rows of the adoral membranelles [19, 23]. The transverse microtubular ribbons associated with the second and the third row of adoral kinetosomes disappear during morphogenesis in *Paraurostyla* [28] and are absent in the interphasic cells of, for instance, *Histriculus, Parastrongylidium,* and *Oxytricha* [14, 19, 24]. This suggests that *Engelmanniella mobilis* may have retained an ancestral state.

Shortened cilia in the fourth row of the frontal adoral membranelles have been described in *Paraurostyla* [4]. In *Engelmanniella mobilis,* perhaps even the third row of the frontal adoral membranelles and the rightmost kinetosomes of the ventral ones bear only ciliary stubs. Shortened cilia might have been widely overlooked in hypotrichs.

A paroral membrane consisting of a single row of basal bodies has been described in various stichotrichid hypotrichs [2, 19]. However, like in *Engelmanniella,* none of these claims have been proved by serial sections.

The prominent undischargeable subpellicular granules and the rhomboidal crystal-like structures projecting from the lithosomes of *E. mobilis* are hardly comparable with the data available in the literature. These characters obviously need further detailed investigations, particularly cytochemical ones, which are beyond the scope of this paper.

Conclusions

Engelmanniella mobilis shares the undifferentiated interphasic cortical pattern with taxa of the suborder Stichotrichina [comp. 11, 17, 18, 37, 40–42]. Symplesiomorphies with urostylids and oxytrichids are the probably homologous frontal anlagen I–III, the self-replication of most parts of the somatic ciliature, and the basic organization of the microtubular and microfibrillar associates of the oral and somatic ciliature. The absence of frontoterminal (migratory), midventral, transverse, and caudal cirri, the lack of a second round of proliferation during the development of cirri, and the ability to conserve parts of the infraciliature suggest that *E. mobilis* is a rather primitive stichotrichid which has descended from a *Kahliella*-like ancestor. There is, however, at present no possibility to exclude that these characteristics (as well as the shortened dorsal kinety that requires de novo development in the opisthe) may be secondary reductions that are correlated with life in the interstices of soil particles.

Nevertheless, the "usual" cirri (including a second round of proliferation; see above) present in *K. acrobates* [19], strongly argues against a confamilial position of *Engelmanniella* and *Kahliella,* as proposed by Tuffrau [42]. Likewise, we reject its inclusion into the Cladotrichidae [37] since the type-genus and consequently the family are still insufficiently diagnosed. At present, *Cladotricha, Engelmanniella, Uroleptoides, Perisincirra,* and *Lamtostyla* constitute this family, although their frontal ciliature, which is used to define the family [37], is dissimilar even in the non-dividing cells. We dislike to add a further unsubstantiated familial diagnosis, but argue for detailed studies to improve the genus characteristics. An emended diagnosis of *Engelmanniella* will be given in a separate paper including the cyst morphology and a morphometric comparison of several geographically distant populations (in prep.).

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Key words: Engelmanniella mobilis – Ciliophora, Hypotrichida – Morphogenesis – Ultrastructure – Systematics

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