

Description of Two New, Mycophagous Soil Ciliates (Ciliophora, Colpodea): *Fungiphrya strobli* n. g., n. sp. and *Grossglockneria ovata* n. sp.

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ABSTRACT. The morphology and infraciliature of two new, mycophagous soil ciliates are described. Specimens were isolated from dried, rewetted soil samples with the non-flooded Petri dish method and investigated in vivo and with various silver impregnation techniques. *Fungiphrya strobli* n. g., n. sp. was discovered in the mud of rock-pools on the summit of Table Mountain, Republic of South Africa. It is a holotrichously ciliated, about 50 × 40 µm-sized grossglockneriid with the oral apparatus on the right side of the cell. The adoral ciliature, minute in all other members of the group, is well developed and has a mean of eight kineties forming a conspicuous left, oral polykinetid, highly reminiscent of that found in small species of the genus *Colpoda*. The ejected extrusomes have a unique, inflated distal end. *Grossglockneria ovata* n. sp. was discovered in leaf litter from the Lackawanna State Forest in Pennsylvania, USA. It differs from the other members of the genus by the ovate shape, smooth cortex, and the sparse, irregularly-shaped mucocysts. Taxonomic characters and ranking of grossglockneriids are discussed. Because of the complex, unique feeding tube associated with a unique feeding strategy, mycophagy, it is argued that grossglockneriid ciliates should be classified in a separate order, in spite of their close genetic relatedness to members of the order Colpodea.

Supplementary key words. Infraciliature, Pennsylvania, Republic of South Africa, Table Mountain, taxonomic ranking, USA.

GROSSGLOCKNERIIDS are a particular group of soil ciliates with a minute ($\leq 4 \mu\text{m}$) feeding tube in the centre of the small, flat oral field. The tube is used to perforate the cell wall of yeasts, fungal hyphae, and spores to take up their contents. No other food can be ingested because the paroral and adoral ciliature are weakly developed and the minute, highly specialized feeding tube is the sole feeding organelle [6]. Although globally distributed and present in almost every soil sample, grossglockneriids were only discovered in 1980 [3]. Very likely, they were misidentified or not identified at all previously. Foissner [3, 6] recognized the close relationship between the strictly mycophagous grossglockneriids and the classical, bacterivorous and predaceous colpodeids, such as *Colpoda* and *Bresslaia*, and thus assigned them to this group. Recently, this has been confirmed by SSrRNA sequence data [12].

The grossglockneriids are a small group of six, described species distributed over four genera. In the present paper, two new, very distinct species are described, substantiating my earlier claim [9] that most soil ciliates are still undiscovered.

MATERIALS AND METHODS

Fungiphrya strobli n. g., n. sp. was discovered in the mud/soil mixture of some flat, granitic, dry rock-pools on the flat summit (about 1,000 m above sea-level) of Table Mountain (Republic of South Africa, surroundings of Cape Town, lat 33°53'S, long 18°25'E). The pools were about midway between the Upper Cableway Station and MacLears Beacon. The dark grey mud/soil mixture had a pH 5.4 (in water), was slightly saline (some salt crystals formed when a drop of the soil solution was evaporated on a slide), and contained a typical terrestrial ciliate community composed of about 43 species, of which several were new. The sample was collected on 19. 2. 1995 and investigated on 26. 9. 1995.

Grossglockneria ovata n. sp. was discovered in a leaf litter sample from the Lackawanna State Forest (USA, Pennsylvania, Lackawanna County, intersection of Pittston Road and Sassafras Hill Road, lat 41°N, long 76°W). The sample consisted mainly of leaf litter (Maple, Oak, Sassafras, Mountain Laurel), with some soil interspersed, and had a pH 5.0 (in water). It was collected by Joe Slusark on 28. 12. 1994 and investigated on 21. 12. 1995 in the Salzburg laboratory.

Samples were air-dried for ~ 4 wk in the Salzburg laboratory and then sealed in plastic bags. For the investigation, ciliates were reactivated from the resting cysts using the non-flooded

Petri dish method [5]. Briefly, this simple method involves placing 10–50 g terrestrial material in a Petri dish (10–15 cm in diameter) and saturating, but not flooding, it with distilled water. Such cultures were analysed for ciliates by inspecting about 2 ml of the run-off on d 2, 7, 14, and 28.

Cells were studied in vivo using a high-power, oil immersion objective and differential interference contrast optics. The infraciliature was revealed by the silver impregnation techniques described in [4]. Counts and measurements on prepared specimens were performed at a magnification of 1,000×. In vivo measurements were conducted at a magnification of 100–1,000×. Although these provide only rough estimates, it is worth giving such data as specimens may change in preparations. Illustrations of live specimens were based on free-hand sketches and micrographs, while those of impregnated cells were made with a camera lucida. Terminology is according to [6].

RESULTS

Fungiphrya n. gen.

Diagnosis. Completely ciliated Grossglockneriidae with oral apparatus on right side of cell. Adoral ciliature well developed, consisting of more than 5 kineties forming a conspicuous left oral polykinetid. Ejected extrusomes with inflated anterior end.

Type species. *Fungiphrya strobli* n. sp.

Etymology. Composite of the Latin noun *Fungus* (fungus) and the Greek noun *Ophrya* (eyebrow = cilium), meaning "a ciliate associated with fungi". Feminine gender.

Fungiphrya strobli n. sp.

(Table 1, Fig. 1–32)

Diagnosis. Size in vivo about 50 × 40 µm. Broadly ellipsoidal; anterior left end bluntly pointed, left body margin flat, right distinctly convex. Two kinds of extrusomes: large extrusomes very numerous and 5 × 1 µm in size, form conspicuous fringe, sperm-shaped when extruded; small extrusomes granular, around base of somatic dikinetids. On average, 12 ciliary rows and 8 kineties in left oral polykinetid.

Type location. Mud/soil mixture from dry rock-pools on summit of Table Mountain, surroundings of Cape Town, Republic of South Africa (about lat 33°53'S, long 18°25'E).

Type material. Two holotype slides (one Chatton-Lwoff silver nitrate-impregnated, the other protargol-impregnated) and one paratype slide (protargol-impregnated) have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria, Accession Numbers: 1998/47–49. The slides contain several

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Table 1. Morphometric data from *Fungiphrya strobli* (upper line) and *Grossglockneria ovata* (lower line).

Character ^a	Method ^b	\bar{x}	M	SD	CV	Min	Max	n
Body, length	CL	45.0	45	4.1	9.2	39	56	18
	CL	38.9	38	3.5	8.9	33	49	21
Body, width	CL	34.5	33	3.2	9.2	30	40	18
	CL	25.2	25	2.2	8.8	20	30	21
Anterior end to paroral, distance	CL	4.7	5	0.8	16.4	4	6	18
	CL	2.7	3	0.5	18.0	2	4	21
Anterior end to end of paroral, distance	CL	11.7	11	1.5	12.8	10	16	18
	CL	7.5	7	0.8	10.1	6	9	21
Anterior end to macronucleus, distance	P	25.4	25	4.6	18.1	17	32	18
	P	17.7	19	5.9	33.1	8	25	15
Macronucleus, length	P	10.3	10	0.9	8.8	9	12	18
	P	7.3	7	0.8	11.5	6	9	15
Macronucleus, width	P	9.9	10	0.8	7.7	9	11	18
	P	7.0	7	0.7	9.6	6	9	15
Left oral polykinetid, length	CL	7.2	7	0.9	13.1	5	9	18
	CL	<4 μm						
Kineties in left polykinetid, number	CL, SC	7.9	8	1.2	15.0	6	11	18
	CL	3.0	3	0.0	0.0	3	3	16
Somatic kineties, number	CL	12.0	12	0.0	0.0	12	12	18
	CL	10.0	10	0.0	0.0	10	10	21
Kinetics in 2nd kinety right of paroral, number	CL	24.4	25	3.4	14.1	19	32	18
	CL	15.7	16	1.6	10.4	13	21	21

^a Data based on prepared and mounted specimens cultivated with the non-flooded Petri dish method. Measurements in μm . CV—coefficient of variation in %, M—median, Max—maximum, Min—minimum, n—number of individuals investigated, SD—standard deviation, \bar{x} —arithmetic mean.

^b CL—silver nitrate according to Chatton-Lwoff, as described in [4], P—protargol impregnation (protocol A in [4]), SC—silver carbonate impregnation, as described in [4].

specimens with relevant cells marked by a black ink circle on the cover glass.

Dedication. I dedicate this new species to Mag. Eric Strobl, a native South African, who for many years has helped to improve the English in my manuscripts.

Description. Size in vivo 45–60 \times 35–45 μm , usually about 50 \times 40 μm , as calculated from measurements of live specimens and values shown in Table 1, assuming a shrinkage of 5–10% due to the preparation procedures; colourless and non-contractile. Shape in vivo fairly constant and very characteristic (Fig. 1, 6, 9, 11): anterior left end bluntly pointed and slightly projecting, right margin (dorsal side) distinctly convex, left (ventral) flat, posterior end broadly rounded, laterally flattened up to 2:1; poorly preserved in preparations where most specimens are ovate (Fig. 2, 10, 28, 32). Macronucleus subequatorial, in vivo about 12 μm across with reticulate nucleolus. Compact, conspicuous micronucleus 5 \times 2.5 μm (in vivo) in size (Fig. 1, 19, 21) in indentation of macronucleus. Contractile vacuole in posterior end, with single excretory pore in centre of posterior pole (Fig. 1, 28). Cortex flexible, distinctly furrowed by ciliary rows and bright due to attached blister-like extrusomes (Fig. 1). Two kinds of extrusomes. Large extrusomes, very numerous and closely spaced, in vivo about 5 \times 1 μm , hyaline, form conspicuously bright fringe in live cells (Fig. 1, 5, 13, 14) and small circles (if attached) or granules (if released) in the silverlines (Fig. 10, 28, 30, 31), impregnate with protargol (Fig. 4, 32), are released when cells are pressed or methyl green-pyronin is added. They become sperm-shaped, up to 15 μm long filaments with a 2–3 μm wide, inflated anterior end, which is very hyaline and thus easily overlooked (Fig. 7, 8, 15–18). Small extrusomes recognized only in protargol preparations, about 0.5 μm across, found only around ciliary bases (Fig. 4, 32). Cytoplasm usually packed with globular to irregular, bright, compact food inclusions (contents of fungal hyphae) 1–10 μm across, making cells almost black at

low ($\leq 100\times$) magnification (Fig. 1, 21). Glides quickly on slides and swims by rotation about main body axis.

Somatic cilia in vivo about 8 μm long and paired throughout, arranged in 12 strongly spiralling rows, half of which curve around right side of oral apparatus to form a distinct suture with postoral kineties in left anterior region (Fig. 1, 2, 10, 19, 20, 24, 27, 29); no elongated caudal cilia. LKM-fibres (overlapping transverse microtubule ribbons) conspicuous after protargol impregnation (Fig. 4, 32). Silverline system colpodid [6], that is, with distinct lines extending between kineties, usually contains many granules (attached extrusomes) and circles (just released extrusomes; Fig. 10, 28, 30, 31).

Oral area distinctly subapical and semicircular, comparatively large and slightly concave. Feeding tube about 4 \times 3 μm extends at right angles from body surface (Fig. 1, 11, 12, 24). Its base surrounded by a ring of minute granules recognizable only in protargol preparations (Fig. 2), and, on right half, by hair-shaped structures extending to paroral membrane (Fig. 3, 26). Adoral kineties of varying length. Those at ends of ribbon usually shortened, bear about 5 μm long cilia, obliquely arranged and comparatively widely spaced, form conspicuous, obliquely extending polykinetid (ribbon) posterior to and left of feeding tube (Fig. 1–3, 10, 22–27, 29). Paroral membrane semicircular, composed of about 25–30 narrowly spaced kinetids, which bear about 5 μm long cilia (Fig. 1–3, 11, 12, 22–25). These kinetids appear paired after silver carbonate (Fig. 3, 22–25) and silver nitrate (Fig. 10, 27, 29) impregnation and, at least in anterior region, also in vivo. However, only a single row of granules is recognizable in protargol preparations (Fig. 2), indicating that the inner granule row is composed of parasomal sacs [1].

Occurrence and ecology. *Fungiphrya strobli* n.g., n. sp. was observed to feed on fungal hyphae and was associated with 43 other, mainly terricolous ciliate species, of which four were undescribed. Among about 1,000 soil samples from all the main

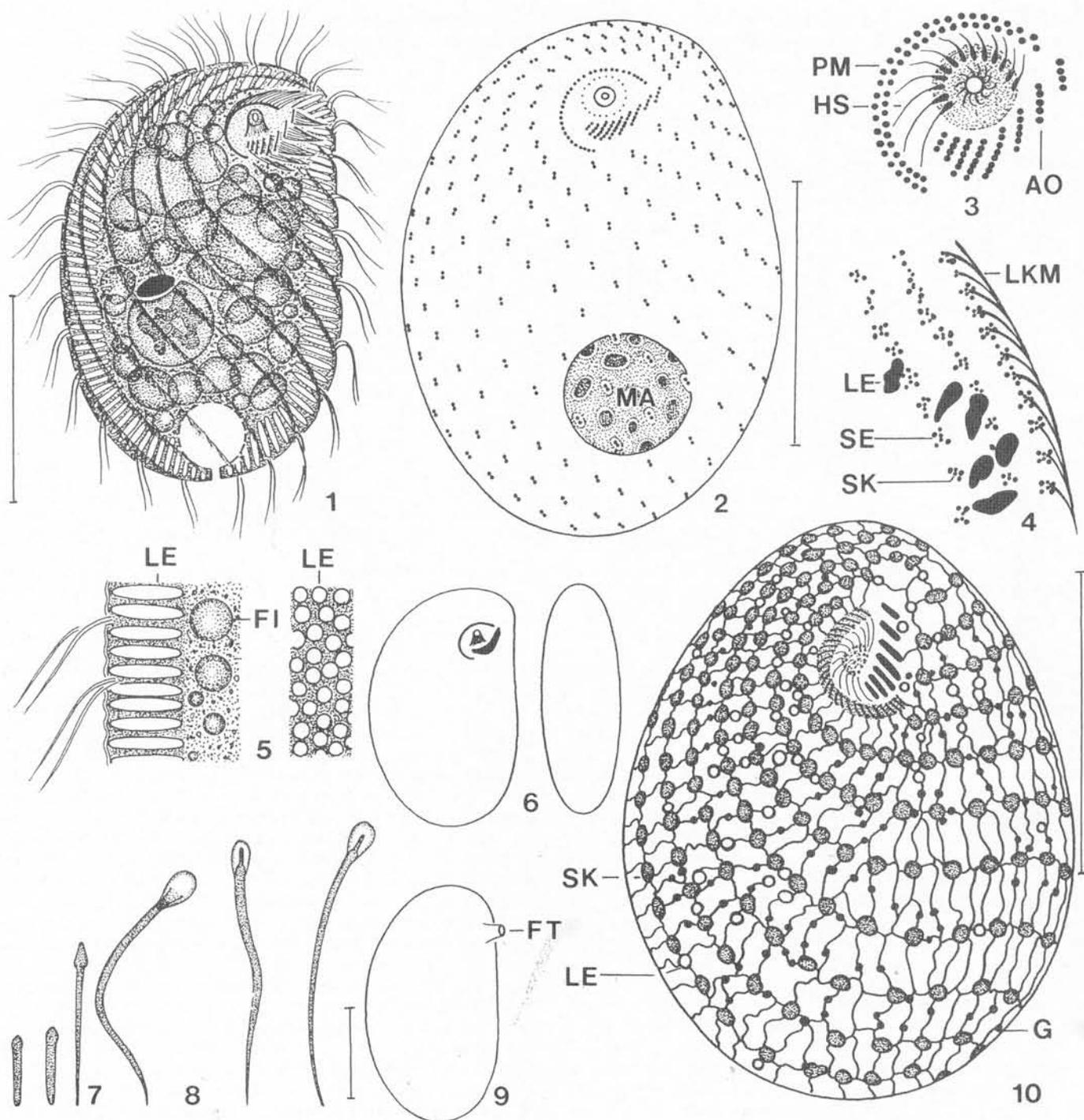


Fig. 1–10. *Fungiphrya strobli* n. sp. from life (1, 5, 6, 9), after methyl green-pyronin staining (7, 8), protargol impregnation (2, 4), silver carbonate impregnation (3), and Chatton-Lwoff silver nitrate impregnation (10). 1. Right lateral view of a representative specimen packed with food inclusions (contents of fungal hyphae) and large, ellipsoidal extrusomes forming conspicuous, bright fringe. 2. Infraciliature of right side. 3. Oral apparatus (composite from several specimens). Note that the paroral membrane (PM) consists of a double row of granules after silver carbonate impregnation, while only a single row is recognizable after protargol impregnation (Fig. 2). Hair-shaped structures (HS) extend from the base of the feeding tube to the paroral membrane. 4. Surface view of left lateral cortex, showing that *F. strobli* has two kinds of extrusomes. 5. Optical section and surface view of cortex. The extrusomes form a conspicuous fringe and give the cortex a reticulate appearance in surface view (cf. Fig. 11, 12). 6, 9. Right lateral, dorsal, and dorsolateral view of same specimen to show body flattening and feeding tube. 7, 8. Exploding and extruded extrusomes, which are up to 15 μm long (drawn to scale). 10. Infraciliature and silverline system of ventral side. AO, adoral organelles (left oral polykinetid); FI, food inclusion; FT, feeding tube; G, granule remaining after extrusion of an extrusome; HS, hair-shaped structures; LE, large extrusomes; LKM, LKM-fibre formed by transverse microtubule ribbons; MA, macronucleus; PM, paroral membrane; SE, small extrusomes; SK, somatic kineties, respectively, somatic dikinetids. Bars 5 μm (Fig. 7, 8) and 25 μm (Fig. 1, 2, 10).

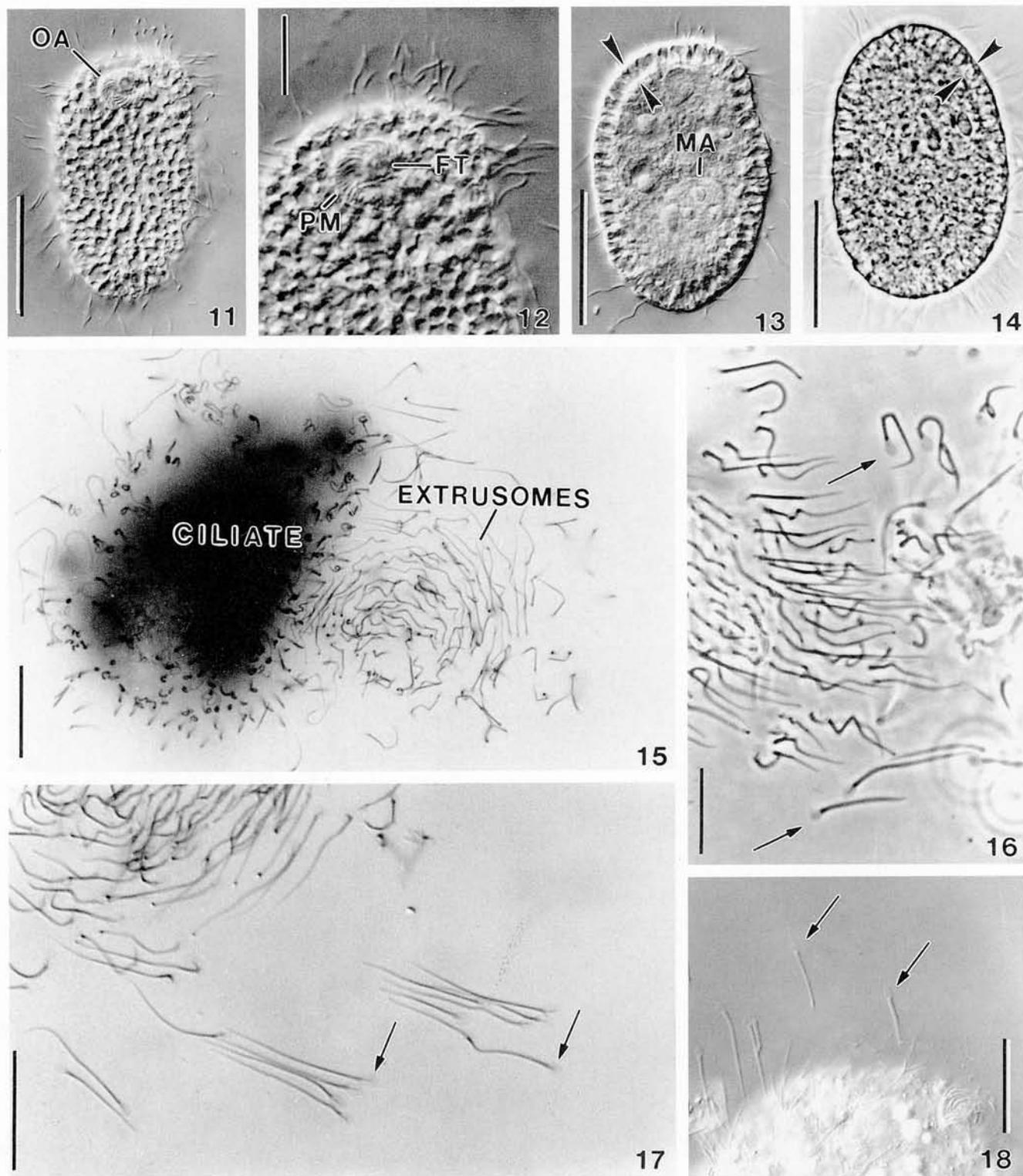


Fig. 11–18. *Fungiphrya strobli* n. sp., general morphology and extrusomes from life (11, 12, 18), after mercuric chloride fixation (13, 14), and methyl green-pyronin staining (15–17). 11, 12. Representative specimen showing oral apparatus and cortex, which is conspicuously vesicular due to many large extrusomes (cp. following figures). 13, 14. Optical sections (interference contrast, bright field) showing the conspicuous fringe (marked by arrowheads) formed by the large, blister-like, tightly spaced extrusomes. 15. *Fungiphrya strobli* has many extrusomes, which are released and elongate to 15 μm -long-rods, when methyl green-pyronin is added. 16, 17. Released, methyl green-pyronin stained extrusomes in phase contrast and interference contrast. The extrusomes have a sperm-like shape, the “sperm-head” (arrows) is very hyaline and thus difficult to recognize. 18. Released extrusomes in vivo, interference contrast. Arrows mark inflated distal end. FT, feeding tube; MA, macronucleus; OA, oral apparatus; PM, paroral membrane. Bars 10 μm (Fig. 12, 16–18) and 20 μm (Fig. 11, 13–15).

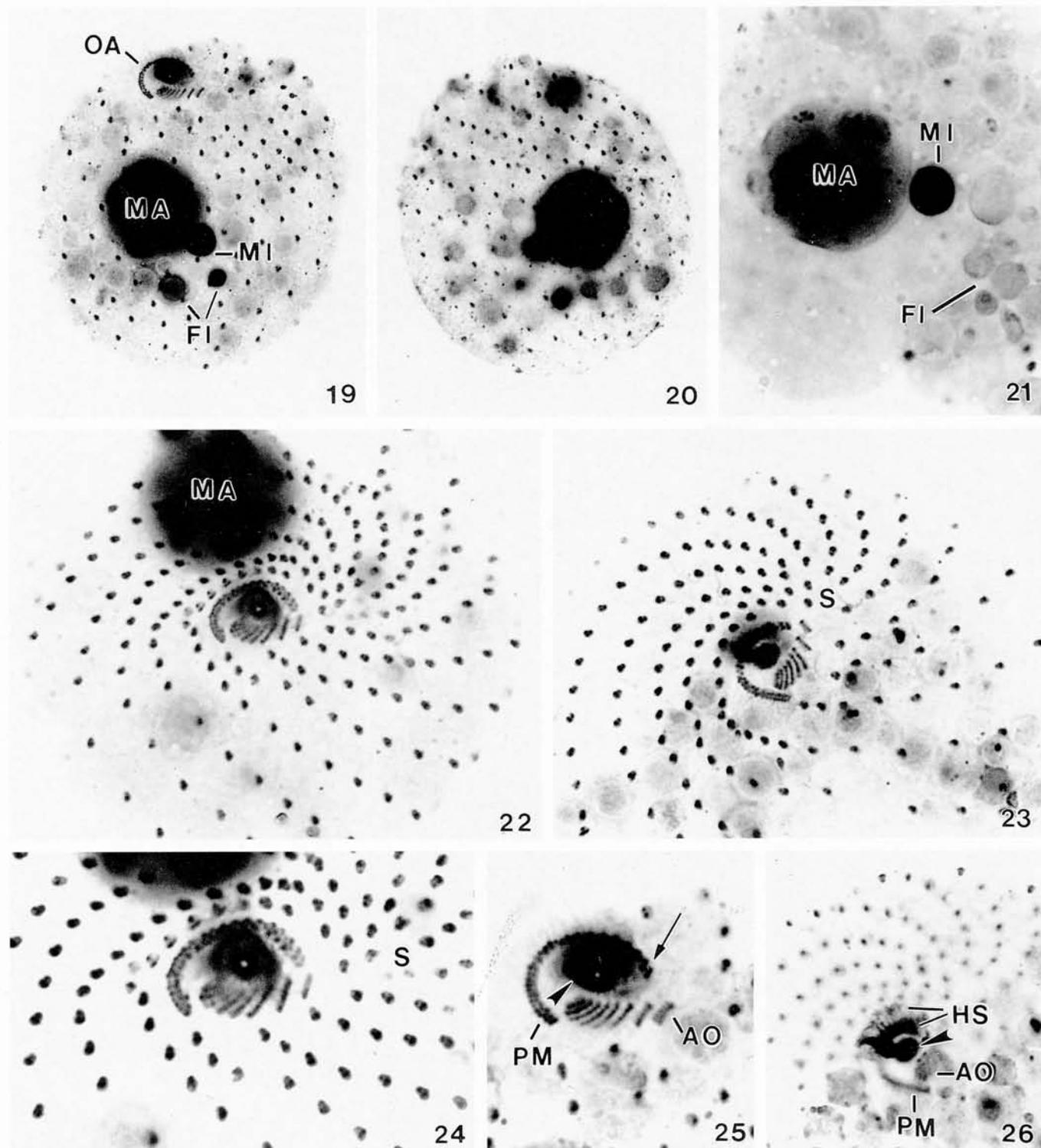


Fig. 19–26. *Fungiphrya strobli* n. sp., somatic and oral infraciliature (ciliary pattern) after silver carbonate impregnation. Figures purposely without scale bars since the applied staining technique causes unavoidable distortions of the cells, making measurements meaningless. 19, 20. Total ventral and dorsal view of same specimen. Note strongly spiralling ciliary rows. 21. Nuclear apparatus. 22–26. Anterior polar views showing oral structures and 12 strongly spiralling somatic ciliary rows, which commence in the surroundings of the oral apparatus. The paroral membrane is composed of granule pairs, clearly recognizable in Fig. 25 (arrow). Figures 23 and 26 show the same specimen at different focal plane. Arrowheads mark feeding tube, the centre of which has a minute opening. AO, adoral organ (left oral polykinetid); FI, food inclusions; HS, hair-shaped structures; MA, macronucleus; MI, micronucleus; OA, oral apparatus; PM, paroral membrane; S, preoral suture.

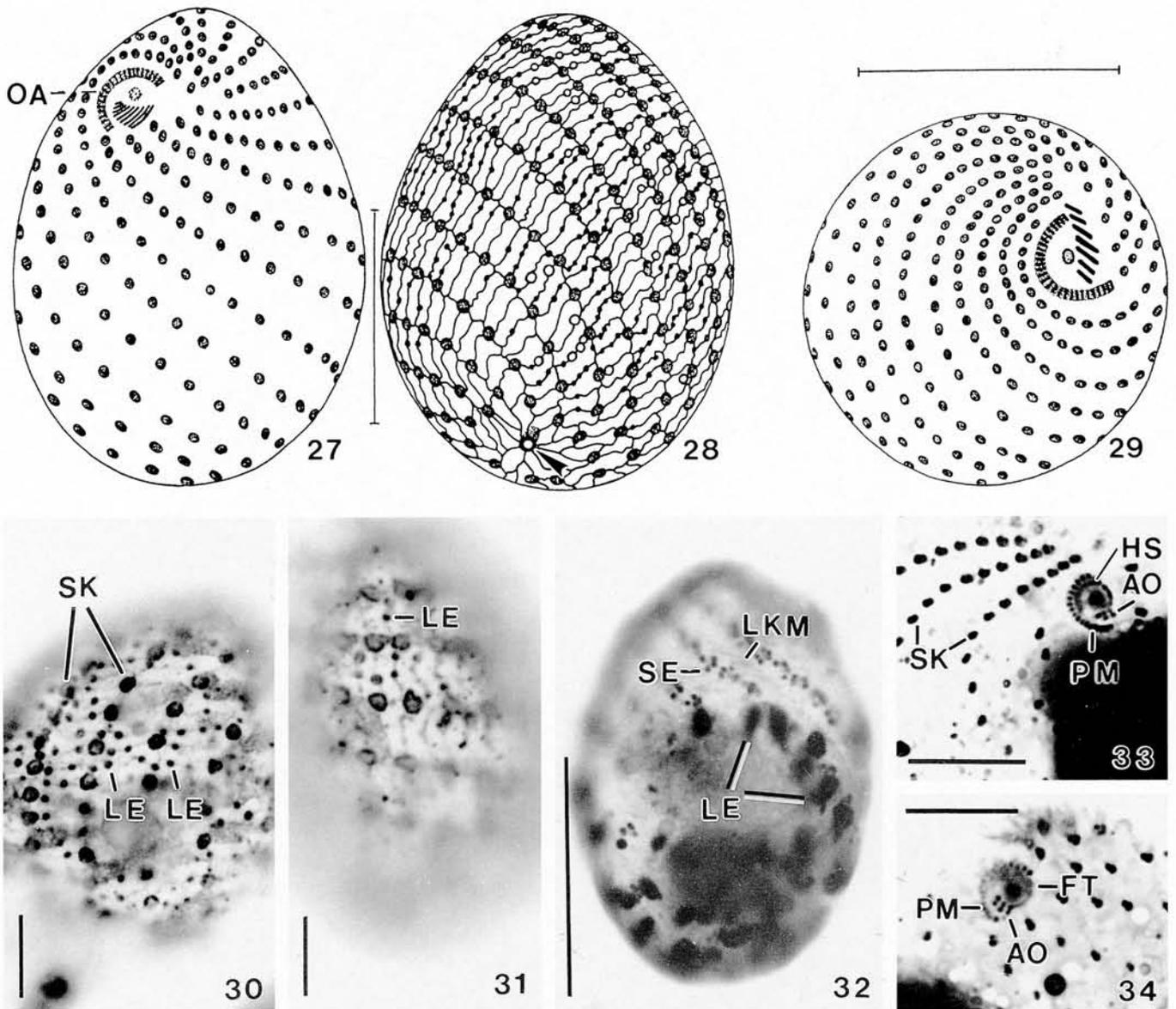


Fig. 27–34. Somatic and oral infraciliature and silverline system of *Fungiphrya strobli* n. sp. (27–32) and *Grossglockneria acuta* (33, 34) after Chatton-Lwoff silver nitrate impregnation (27–31), protargol impregnation (32), and silver carbonate impregnation (33, 34). 27, 28. Ventral and dorsal view of same specimen to show general organization. Arrowhead marks excretory pore of contractile vacuole in centre of posterior pole. 29. Anterior polar view showing strongly spiralling ciliary rows. 30, 31. Silverline system of right and left side. A small granule remains at each site where an extrusome was ejected due to the preparation procedures. 32. Left lateral view showing two kinds of extrusomes after protargol impregnation. 33, 34. The oral apparatus of *G. acuta* is very similar to that of *F. strobli*, but the adoral organelle consists of only three kineties. AO, adoral organelles (left oral polykinetid); FT, feeding tube; HS, hair-shaped structures; LE, large extrusomes; LKM, LKM-fibre formed by overlapping transverse microtubule ribbons; OA, oral apparatus; PM, paroral membrane; SE, small extrusomes; SK, somatic kineties (ciliary rows). Bars 25 μ m (Fig. 27–29, 32) and 10 μ m (Fig. 30, 31, 33, 34).

biogeographical regions, including circa 100 samples from Africa (Kenya, Namibia, Republic of South Africa), *F. strobli* was found only on the Table Mountain [10]. This area is known to be inhabited by a great number of endemic plants and animals [2]. Accordingly, there is some probability that *F. strobli* is endemic to the region or the Gondwanaland. At least, I am convinced that I could not have overlooked *F. strobli* in any of the other samples because of its characteristic shape. However, endemism is difficult to prove in single-celled organisms because they are minute, heavily underinvestigated, and each sam-

ple, especially from soil, represents an almost unique habitat due to the small size of the organisms.

Grossglockneria ovata n. sp.

(Table 1, Fig. 35–47)

Diagnosis. Size in vivo about $40 \times 27 \mu$ m; distinctly ovate. Cortex smooth and with sparse, irregularly-shaped mucocysts around ciliary bases. 10 somatic and 3 adoral kineties.

Type location. Leaf litter from Lackawanna State Forest (in-

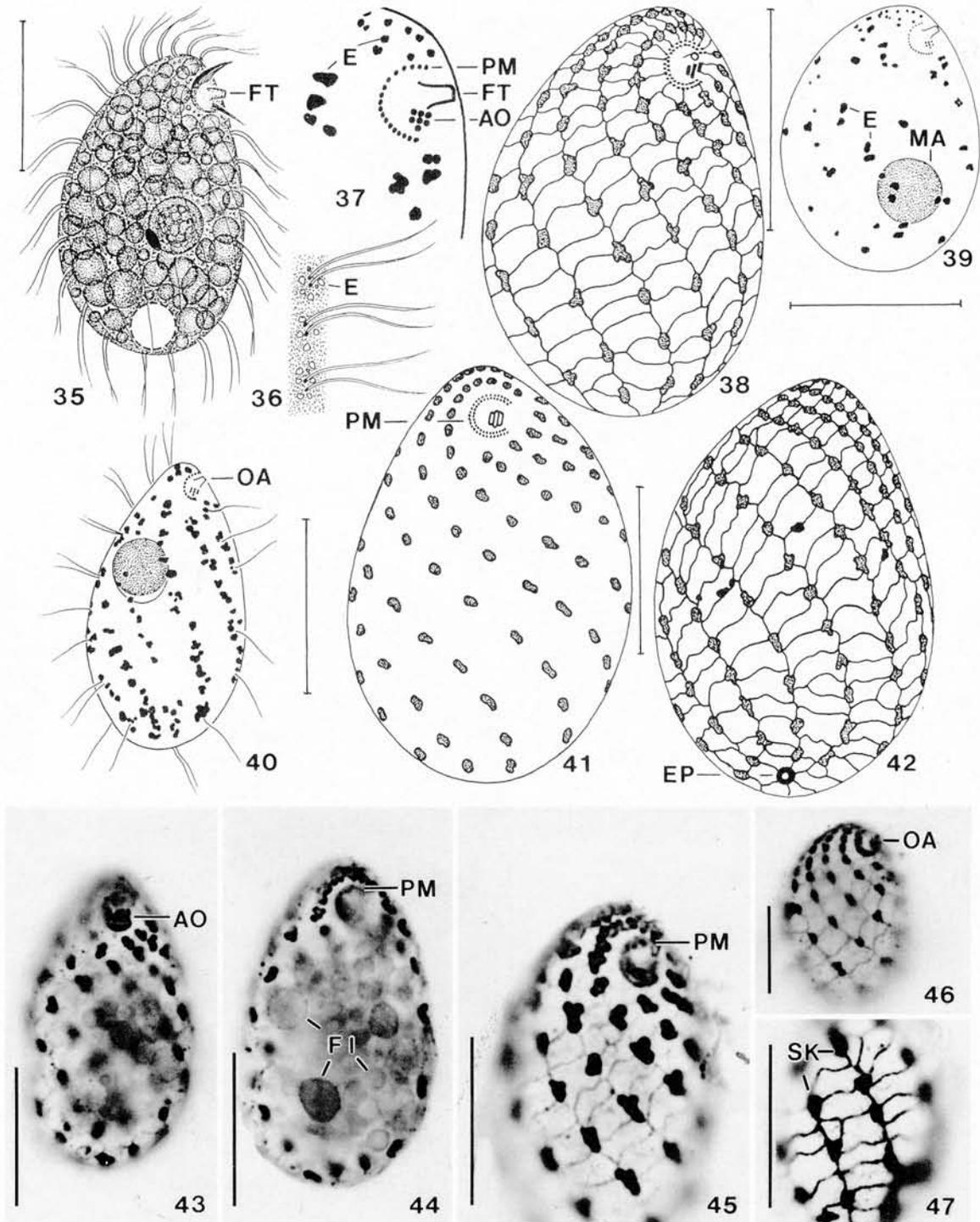


Fig. 35-47. *Grossglockneria ovata* n. sp. from life (35, 36) and after protargol (37, 39, 40) and Chatton-Lwoff silver nitrate (38, 41-47) impregnation. 35. Right lateral view of a representative, ovate specimen packed with globular and irregular food inclusions. 36. Surface view of cortex showing pale, inconspicuous extrusomes (mucocysts) around bases of cilia (cf. Fig. 39, 40). 37. Detail from Fig. 39 showing the oral apparatus. 38. Infraciliature and silverline system of right side of a representative specimen. 39, 40. Shape, mucocyst pattern, and oral apparatus of the broadest, respectively, most slender specimens found. 41, 42. Infraciliature and silverline system of ventral and dorsal side. 43, 44. Ventral views of same specimen focused to body surface and body centre to show the strongly spiralling ciliary rows and the globular food inclusions. 45, 47. Infraciliature and silverline system of right and left side. Note the irregular shape of the ciliary bases, possibly caused by impregnated parasomal sacs and/or mucocysts. The silverline system has a typical colpodid pattern. 46. Infraciliature and silverline system of right side of a broadly ellipsoidal specimen. AO, adoral organelles (kineties); E, extrusomes, very likely mucocysts; EP, excretory pore of contractile vacuole; FI, food inclusions; FT, feeding tube; MA, macronucleus; OA, oral apparatus; PM, paroral membrane; SK, somatic kineties (ciliary rows). Bars = 20 μ m.

tersection of Pittston Road and Sassafras Hill Road), north of Scranton, Pennsylvania, USA (about lat 41°N, long 76°W).

Type material. Two holotype slides (one Chatton-Lwoff silver nitrate-impregnated, the other protargol-impregnated) and two paratype slides (one Chatton-Lwoff silver nitrate-impregnated, the other protargol-impregnated) have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria, Accession Numbers: 1998/50–53. The slides contain several specimens, with relevant cells marked by a black ink circle on the cover glass.

Etymology. “*ovata*” (Latin) because of its distinct egg shape.

Description. Size in vivo 35–50 × 20–35 µm, usually about 40 × 27 µm, as calculated from some measurements of live specimens and values shown in Table 1, assuming a shrinkage of about 5% due to the preparation procedures; non-contractile and unflattened. Shape very constant and highly characteristic, that is, distinctly ovate with dorsal side slightly more convex than ventral (Fig. 35, 38, 41, 43); rarely broadly ellipsoidal (Fig. 39, 46) or slenderly ovate (Fig. 40). Macronucleus in middle third of body, globular to slightly ellipsoidal, with reticulate nucleolus in central area. Micronucleus attached to macronucleus, lenticular, about 3.5 × 2 µm in vivo (Fig. 35, 39, 40). Contractile vacuole in rear end, with single excretory pore in centre of posterior pole (Fig. 35, 42). Cortex inconspicuous, flexible, not, or indistinctly furrowed by ciliary rows and thus smooth. Extrusomes (very likely mucocysts) mainly around bases of cilia, sparse and flaky, 0.5–1.5 µm across, very inconspicuous in vivo (Fig. 36) but impregnated darkly with protargol (Fig. 39, 40) and lilac after application of methyl green-pyronin. Cytoplasm invariably packed with globular to irregular, bright, compact food inclusions (contents of fungal hyphae), 1–10 µm (usually 3–6 µm) across, making cells almost black at low magnification (≤ 100×); between food inclusions numerous minute (≤ 1 µm) crystals sparkling under interference contrast illumination. Movement inconspicuous, glides quickly on slides, interrupted by short periods of rotation; but does not jump like *Pseudoplatyophrya saltans*.

Somatic cilia in vivo about 10 µm long, usually paired, arranged in 10 strongly spiralling kineties, of which about 5 curve around right side of oral apparatus to form indistinct preoral suture with postoral kineties at left side of oral apparatus; no elongated caudal cilia. Dikinetic bases large and irregularly shaped after silver nitrate impregnation, possibly due to parasomal sacs and/or mucocysts (Fig. 38, 41–47). Silverline system colpoid [6], that is, with distinct lines extending between kineties (Fig. 38, 42, 45–47).

Oral area subapical and circular, minute, slightly concave. Feeding tube about 3 × 2 µm in vivo. Three adoral kineties composed of 2, 3, 2 basal bodies with about 5-µm-long cilia forming a rather distinct bundle (Fig. 35, 37, 38, 41, 45). Paroral membrane semicircular, composed of about 23 narrowly-spaced basal bodies with 5-µm-long cilia forming rather conspicuous membrane in vivo (Fig. 35, 37, 39, 44, 45); invariably composed of two rows of granules in silver nitrate prepared specimens, very likely due to parasomal sacs at left side of kinetids [1].

Occurrence and ecology. *Grossglockneria ovata* as yet, was found only at the type location where it appeared 2 d after rewetting the sample. It was associated with three other grossglockneriids, namely, *Pseudoplatyophrya nana*, *P. saltans*, and *Nivaliella plana*, which were readily distinguishable from *G. ovata* by their smaller size; no specimens resembling *G. acuta* or *G. hyalina* were observed; I observed a few specimens attached to fungal hyphae by the feeding tube.

The whole run-off from the sample was collected on day two

for preparations and fresh water was added. After 4 d (6 d after rewetting) the grossglockneriids mentioned above had disappeared and large numbers of *G. acuta* appeared (Fig. 33, 34), which grew for about 1 wk.

DISCUSSION

See [6, 8] for authorship and detailed description of all taxa mentioned.

***Fungiphrya strobli*.** *Fungiphrya strobli* is a well-defined genus and species, differing from other grossglockneriids by having the oral apparatus on the right side and a conspicuous left oral polykinetid (Fig. 1, 11, 19, 24). The oral apparatus of all other grossglockneriids (*Grossglockneria*, *Pseudoplatyophrya*, *Nivaliella*, and *Mykophagophrys*) is at the left anterior margin and the left oral polykinetid is minute, consisting of only three (rarely four) small kineties (Fig. 33, 34). Furthermore, *Fungiphrya* has unique extrusomes, assuming a peculiar, sperm-like shape when released (Fig. 16, 17). All other grossglockneriids have globular extrusomes, except for *Mykophagophrys* [8], whose extrusomes are similar to that of *Fungiphrya* except that they have a cone-shaped distal end, that is, lack the apical blister found in *F. strobli*. *Mykophagophrys terricola* is considerably smaller than *F. strobli* (30 × 20 µm vs. 50 × 40 µm, respectively) and has two very short kineties right of the paroral and a distinct caudal cilium. Thus, *F. strobli* is easily distinguished from *M. terricola* and all other grossglockneriids.

At first glance, the oral apparatus of *F. strobli* looks rather different from that of other grossglockneriids, especially because of the comparatively large, left oral polykinetid and the hair-shaped structures at the base of the feeding tube (Fig. 2, 3, 22–26). However, a reinvestigation of *Grossglockneria acuta* (Fig. 33, 34) showed hair-shaped structures too, which are more difficult to recognize than in *F. strobli* because the whole oral apparatus is smaller. Likewise, the ring of minute granules at the base of the feeding tube is present in *G. acuta* (Fig. 33). Possibly, the hair-shaped structures are identical with the microtubular lamellae composing the feeding tube of grossglockneriids [1].

In an elegant study, Wright & Lynn [14] calculated the maximum ages of major ciliate lineages using a small subunit rRNA molecular clock. They found that the grossglockneriid *Pseudoplatyophrya* evolved about 280 million years ago, while *Colpoda*, the sister group of the grossglockneriids [12], is only about 180 million years old. This is supported by fossil records from amber [Schönborn, W., Dörfelt, H., Foissner, W., Krienitz, L. & Schäfer, U., manuscript in preparation] and the present data. *Fungiphrya strobli* has a mixture of grossglockneriid and colpoid features because it has, like typical colpoids, a conspicuous left oral polykinetid.

***Grossglockneria ovata*.** Two other *Grossglockneria* species are known: *G. acuta* and *G. hyalina*, whose somatic and oral infraciliature are very similar to that of *G. ovata*. Thus, species distinction depends on other characters, such as body shape and the number and distinctiveness of the extrusomes. Admittedly, these features are not very conspicuous but, nevertheless, serve to separate live specimens unequivocally. *Grossglockneria acuta* is easily distinguished from *G. ovata* by its more slender shape, especially the tapered anterior portion, the usually distinctly furrowed (by the ciliary rows) surface, and the mucocysts, which form conspicuous stripes. *Grossglockneria hyalina* differs from *G. ovata* by the distinctly furrowed cortex and the obovate, fusiform or roughly triangular shape, which is distinctly different from the highly characteristic ovate shape of *G. ovata*.

In vivo and at low magnification (≤ 100×), *G. ovata* is easily confused with *Mykophagophrys terricola*, which has a similar

shape and is also often darkened by food inclusions. However, *M. terricola* is smaller (25–35 × 12–20 μm) than *G. ovata* (35–50 × 20–35 μm) and has a conspicuous, bright fringe due to many narrowly spaced, ellipsoidal extrusomes, which become nail-shaped when extruded [8]. Furthermore, the infraciliature is different. *Pseudoplatyophrya saltans* has the same body shape as *G. ovata* but is distinctly smaller (14–20 × 10–15 μm vs. 35–50 × 20–35 μm, respectively) and has a highly characteristic, jumping movement; in silver slides, it can be distinguished from *G. ovata* by its different infraciliature.

Taxonomic ranking of grossglockneriids. Foissner [3, 6, 7] assigned ordinal rank to the grossglockneriids because of their unique and complex feeding tube, which is used to penetrate the cell walls of fungal hyphae and conidia and take up their contents. The general organization [6] and somatic ultrastructure [1] are very similar to those found in members of the order Colpodida. Recent data [12] on the SSrRNA gene sequences of *Pseudoplatyophrya* (a typical grossglockneriid) and *Bresslaia* (a typical colpodid) have confirmed the sister group relationship proposed by Foissner as early as 1980 [3]. However, the sequence data also show that the molecular distance between two other colpodid sister taxa, the bryometopids and bursariomorphids, is considerably larger than that between *Bresslaia* and *Pseudoplatyophrya*. Thus, Lynn & Small [11, and pers. commun.] classified the grossglockneriids only as a family of the Colpodida.

I agree with Mayr [13] and others that taxa ranking should be practical and reflect the significance of traits. The grossglockneriids, whose complex feeding tube probably did not evolve by a single, simple evolutionary process and which is associated with a dramatic change in the ecology and physiology of the organisms, entered a new adaptive zone and have diversified as eight distinct species (very likely, some more have not yet been discovered) with a variety of specializations. Thus, separation at ordinal level seems appropriate, so much the more as the whole colpodids have class rank [11].

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