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Taxonomic characterization of *Epicarchesium granulatum* (Kellicott, 1887) Jankowski, 1985 and *Pseudovorticella elongata* (Fromentel, 1876) nov. comb., two peritrichs (Protozoa, Ciliophora) from activated sludge

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Summary

Epicarchesium granulatum (Kellicott, 1887) Jankowski, 1985, type and sole species of the genus, and *Pseudovorticella elongata* (Fromentel, 1876) nov. comb. (basionym: *Vorticella elongata* Fromentel, 1876) were rediscovered in activated sludge. Their morphology and infraciliature is redescribed using live observation and silver impregnation. The genus *Epicarchesium*, poorly defined previously, is confirmed. It has a tuberculate pellicle and, as supposed by Jankowski, a reticulate silverline system. *Epicarchesium granulatum* has a J-shaped macronucleus, two contractile vacuoles at the ventral wall of the vestibulum, and an average of 57 silverline mesh rows between the anterior end and the aboral ciliary wreath and 31 between the ciliary wreath and the stalk (scopula). The myoneme system shows an unusual specialization, viz. a basket of fine strands extending from mid-body to scopula. *Pseudovorticella elongata* has a J-shaped macronucleus, a single contractile vacuole at the ventral wall of the vestibulum, and an average of 58 silverline mesh rows between the anterior end and the aboral ciliary wreath and 15 between the ciliary wreath and the scopula. Live specimens show a high shape variability under certain conditions and are easily confused with some common *Vorticella* species because the pellicular tubercles are inconspicuous. Taxonomic and ecologic literature of both species is reviewed.

Key words: Activated sludge; Ciliate taxonomy; Peritrichida; *Epicarchesium granulatum*; *Pseudovorticella elongata* nov. comb.

Introduction

Peritrich ciliates are a dominant and diverse group within the activated sludge fauna. They play an essential role in flocculating suspended bacteria thereby improving effluent quality [7, 8]. Thus, they are frequently used as indicators of sludge and effluent quality [4, 6, 13, 33]. For this, however, a correct species identification is often useful.

Unfortunately, species identification in peritrich ciliates is still extremely difficult, not only because of many incomplete original descriptions but also because descriptions and redescriptions by modern authors are frequently of poor quality, too. In fact, descriptions are often performed as they were 60 years ago, and the suggestions by Foissner and Schiffmann [15] to improve peritrich taxonomy by extensive photographic documentation of live specimens and by investigating the silverline system have been almost completely ignored. New genera and species are still established solely on live observations and more or less insufficient, ancient descriptions [22, 23, 32, 46]. *Epicarchesium*, redescribed in this paper, is a typical example. It was established by Jankowski [23] on Kellicott's [26] *Carchesium granulatum*, assuming that the pellicular tubercles mentioned by Kellicott are indicative of a reticulate silverline system.

In our opinion, the description of a new or insufficiently known ciliate should be performed in such a way that not only taxonomists can cope with the identification but also ecologists, who usually are not trained in applying the rather complicated and capricious silver methods. Thus, it is the duty of the specialists to provide ecologists with reliable characters recognizable in live specimens, a task unfortunately increasingly neglected by taxonomists who frequently describe species from silver slides only. As concerns peritrichs, whose generic and species characters are often rather inconspicuous, an ample illustration is indispensable for achieving the goal mentioned above. This has already been emphasized by Foissner and Schiffmann [16], and the experience collected since that time fully supports their demand. Otherwise, taxonomy of peritrichs will remain in the poor state it is and eventually end in irrationality.

Material and Methods

Epicarchesium granulatum and *Pseudovorticella elongata* were found on 15. 11. 1990 and 08. 06. 1995 in plant B of a two stage activated sludge plant at Siggerwiesen, Salzburg, Austria. A second population of *Epicarchesium granulatum*, not studied in detail, occurred on 28. 11. 1994 in an underloaded sludge plant at Asten, Linz, Austria.

Cells were studied in vivo using a high-power oil immersion objective and differential interference contrast. The infraciliature and other cytological details were revealed with protargol, the silverline system was impregnated with the "dry" silver nitrate method. *Epicarchesium granulatum* was also impregnated with silver carbonate. See Foissner [12] for detailed descriptions of all methods mentioned.

Counts and measurements on silvered specimens were performed at a magnification of ×1,000. In vivo measurements were conducted at a magnification of ×250–1,000. Although these provide only rough estimates, it is convenient to give such data as specimens shrink in preparations and contract during fixation. Standard deviation and coefficient of variation were calculated according to statistics textbooks. Drawings of live specimens were based on free-hand sketches and micrographs, those of impregnated cells were made with a camera lucida. Terminology is according to Corliss [3] and Warren [44].

Results

Genus *Epicarchesium* Jankowski, 1985 [23]

Improved diagnosis: Colonial Vorticellidae with interrupted stalk myoneme, tuberculate pellicle and reticulate silverline system.

Type species (original designation): *Carchesium granulatum* Kellicott, 1887 [26].

Redescription of *Epicarchesium granulatum* (Kellicott, 1887) Jankowski, 1985 (Figs. 1–46; Tables 1, 2)

Improved diagnosis: Size in vivo 90 × 40 µm on average, slenderly campanulate. Macronucleus usually J-shaped in main body axis. Two contractile vacuoles at ventral wall of vestibulum. Colonies irregularly dichotomous with 2–16 ($\bar{x}$ = 5) zooids. On average 57 silverline mesh rows between anterior end and aboral ciliary wreath and 31 between aboral ciliary wreath and scopula.

Neotype material: Two slides each with protargol (Foissner and Wilbert techniques) and silver nitrate (Klein-Foissner technique) impregnated cells have been deposited in the collection of microscope slides of the Oberösterreichische Landesmuseum in Linz (LI), Austria.

Redescription (Figs. 1–46; Table 1): Zooids colourless, in vivo 65–105 × 30–60 µm, cylindroid to slenderly campanulate, occasionally slightly clavate (Figs. 3, 22, 23, 25), length up to 3 times width, common ratio 2:1 (Table 1); sometimes more or less distinctly bent over to produce subterminal notch (Fig. 3). Contracted specimens globular to broadly fusiform (Fig. 13). Macronucleus invariably (n > 30) in longitudinal axis of cell, usually J-shaped but occasionally C- or 3-shaped, both ends additionally sometimes slightly curved, long horizontal upper portion at level of peristomial collar, middle portion extends along ventral side (Figs. 3, 9–12, 24, 32). Micronucleus ellipsoidal, in 3 out of 8 specimens near anterior end of macronucleus, in others near posterior end (Figs. 36, 39). Two contractile vacuoles invariably at ventral wall of vestibulum, one underneath vestibular opening, the other above mid-body near cytostome (Figs. 3, 26), about 5 µm across, pulsate alternately or simultaneously; both vacuoles unite to canal-like structure or form single vacuole above mid-body in dying or slightly squashed specimens; thus, observation without cover glass at magnifications of ≥ ×250 is indispensable. Cytopyge at dorsal wall of vestibulum closely underneath peristomial collar (Fig. 3). Cytoplasm granular, contains few to many 5–14 µm sized food vacuoles filled with bacteria. Mitochondria immediately underneath cortex between myoneme strands (Fig. 38). Frequently parasitized by suctorians of genus *Endosphaera*.

Pellicular tubercles rather inconspicuous, 0.7–1.5 µm across, at first glance appearing as narrow transverse striae well recognizable with interference contrast (Figs. 3, 4, 24, 30, 31), some containing an argyrophilic substance, invisible in live specimens, revealed in silver carbonate and protargol impregnated cells as few to many distinct granules (Figs. 35, 42). Furthermore, 1–4 µm sized cortical blisters occur forming irregular transverse rows; number and distinctness of these blisters vary highly within and between populations, sometimes even lacking or very abundant giving cells coarse, granular appearance easily recognized at low magnification (Figs. 1, 3, 4, 24, 29–31); distort when slightly pressed, apparently releasing some contents, becoming more hyaline; impregnate with neither protargol nor silver nitrate.

Silverline system like in peritrichs of the *Pseudovorticella* type, i.e. composed of square to slightly hexagonal meshes, arranged like pellicular tubercles, more irregular on peristomial collar; frequently transverse-elongate, especially underneath aboral ciliary wreath where distances between mesh rows slightly decrease, possibly due to increased contraction during preparation (Figs. 19, 20, 43–45). Silverlines associated with

Table 1. Morphometric characteristics from *Epicarchesium granulatum* and *Pseudovorticella elongata.*

Character [1])	Method[2])	Species[3])	$\bar{x}$	M	SD	$SD_{\bar{x}}$	CV	Min	Max	n
Body, length	L	Eg	85.8	90.0	12.3	2.5	14.3	65.0	105.0	25
	L	Pe	74.6	76.0	13.9	5.3	18.6	48.0	92.0	7
Body, length	P	Eg	56.2	56.0	5.6	1.0	10.0	44.0	70.0	30
	P	Pe	49.6	50.0	7.3	1.3	14.6	37.0	65.0	30
Body, width	L	Eg	40.9	40.0	8.7	1.7	21.3	30.0	60.0	25
	L	Pe	41.1	44.0	4.5	1.7	10.8	32.0	44.0	7
Body, width	P	Eg	41.1	39.5	4.3	0.8	10.5	37.0	54.0	30
	P	Pe	41.5	40.5	5.1	0.9	12.2	30.0	55.0	30
Peristomial collar, width	L	Eg	38.5	37.0	7.2	1.4	18.8	30.0	55.0	25
Peristomial collar, width	P	Eg	21.0	20.5	3.1	0.6	14.7	16.0	29.0	30
Zooids in a colony, number	L	Eg	5.0	4.0	4.1	0.6	75.5	2.0	16.0	53
Main stalk, width	L	Eg	6.4	6.2	0.7	0.1	10.5	5.0	8.0	22
Lateral stalk, length	L	Eg	61.3	60.0	35.6	7.1	58.0	10.0	145.0	25
Lateral stalk, width	L	Eg	6.6	6.2	1.0	0.2	15.6	5.0	9.0	25
Silverline mesh rows from anterior	N	Eg	57.0	57.5	2.1	0.4	3.7	53.0	61.0	30
end to aboral ciliary wreath, number	N	Pe	58.0	58.0	3.8	0.6	6.6	51.0	66.0	43
Silverline mesh rows from aboral	N	Eg	31.0	30.0	2.0	0.4	6.4	27.0	34.0	30
ciliary wreath to scopula, number	N	Pe	15.0	15.0	2.2	0.3	14.6	10.0	20.0	43
Distance between silverline	N	Eg	1.2	1.2	0.1	0.02	8.6	0.9	1.4	30
mesh rows in mid-body	N	Pe	1.0	1.0	0.2	0.03	18.8	0.7	1.6	43
Macronucleus, length	P	Eg	39.2	39.0	5.5	1.0	13.9	31.0	52.0	30
	P	Pe	37.7	37.0	5.9	1.1	15.5	28.0	51.0	30
Macronucleus, diameter in	P	Eg	8.5	8.8	1.0	0.2	12.2	6.0	10.0	30
mid-ventral portion	P	Pe	6.3	6.0	0.9	0.2	14.8	5.0	9.0	30
Micronucleus, length	P	Eg	4.4	5.0	1.0	0.3	22.8	3.0	6.0	10
	P	Pe	4.5	4.0	0.2	0.2	18.0	3.5	6.0	20
Micronucleus, width	P	Eg	2.9	3.0	0.3	0.1	11.8	2.5	3.5	10
	P	Pe	2.9	3.0	0.4	0.09	13.1	2.5	3.7	20

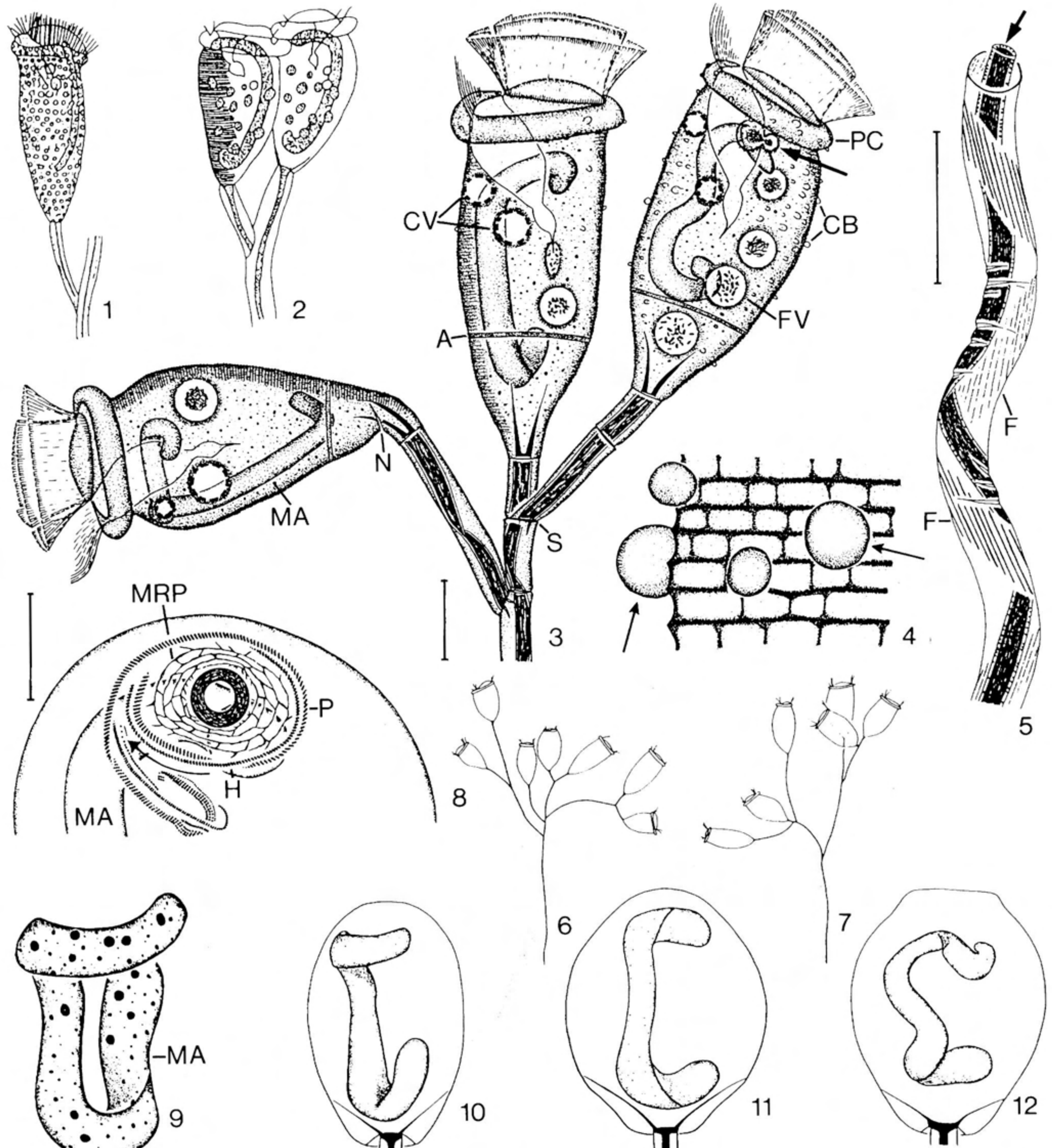
[1]) Measurements in µm. CV = coefficient of variation in %, M = median, Max = maximum, Min = minimum, n = number of specimens investigated, SD = standard deviation, $SD_{\bar{x}}$ = standard deviation of arithmetic mean, $\bar{x}$ = arithmetic mean.
[2]) L = from life, N = dry silver nitrate impregnation, P = protargol impregnation.
[3]) Eg = *Epicarchesium granulatum*, Pe = *Pseudovorticella elongata*.

few to many granules, 0.5–1.3 µm across, possibly pellicular pores; some meshes filled with argyrophilic substance.

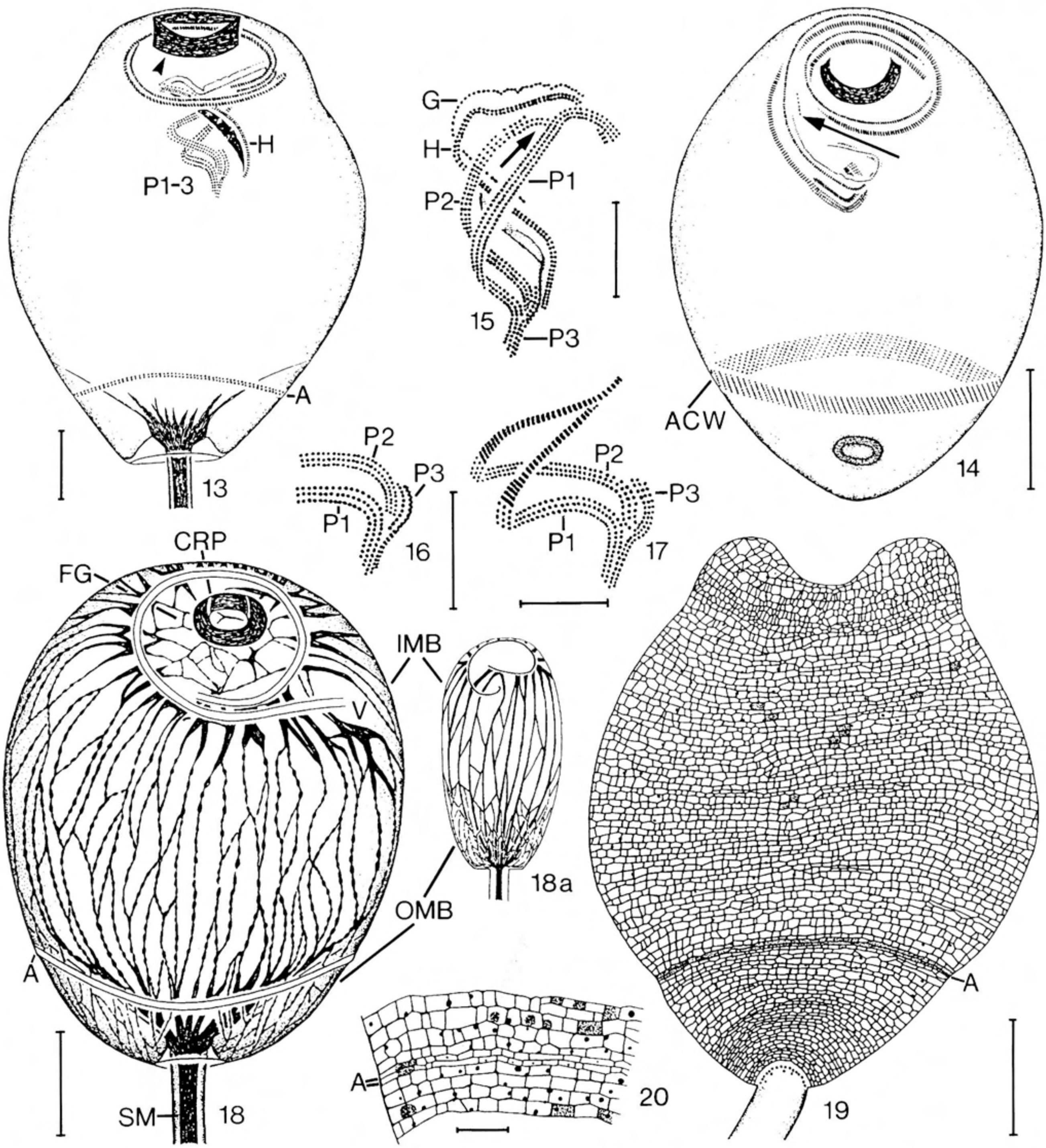
Myoneme system similar to that of *Vorticella* spp. (cp. [11]) and consisting of (i) a conspicuous, compact strand in peristomial collar followed by 3–5 thin, closely spaced, more or less distinctly anastomosing rings (Figs. 8, 37); (ii) a fibrous reticulum in peristomial disk (Fig. 18); and (iii) an "inner basket" consisting of many conspicuous, granular myonemes, more or less distinctly linked to each other by fine strands, originating from stalk myoneme and extending to adoral ciliary spiral (Figs. 18, 37); a special "outer basket" formed by tiny myonemes separates subequatorially from the main strands and extends to the scopula closely underneath the cortex (Fig. 18a).

Anlage of aboral ciliary wreath composed of closely spaced, oblique dikinetids in protargol impregnated cells (Fig. 13); more complicated after silver nitrate impregnation, i.e. consisting of 2–3 closely spaced mesh rows sometimes studded with minute granules (Figs. 19, 20, 45). Swarmers, still attached to colony, studied in detail only in protargol slides, ellipsoidal to slightly ovoid, infraciliature as in sessile specimens, except for seemingly enlarged adoral spiral describing 1.3 turns (about 500°) at peristomial disk before plunging down into vestibulum, and anlage of aboral ciliary wreath, which develops to oblique kineties each consisting of about 8 basal bodies bearing long cilia (Figs. 14, 23).

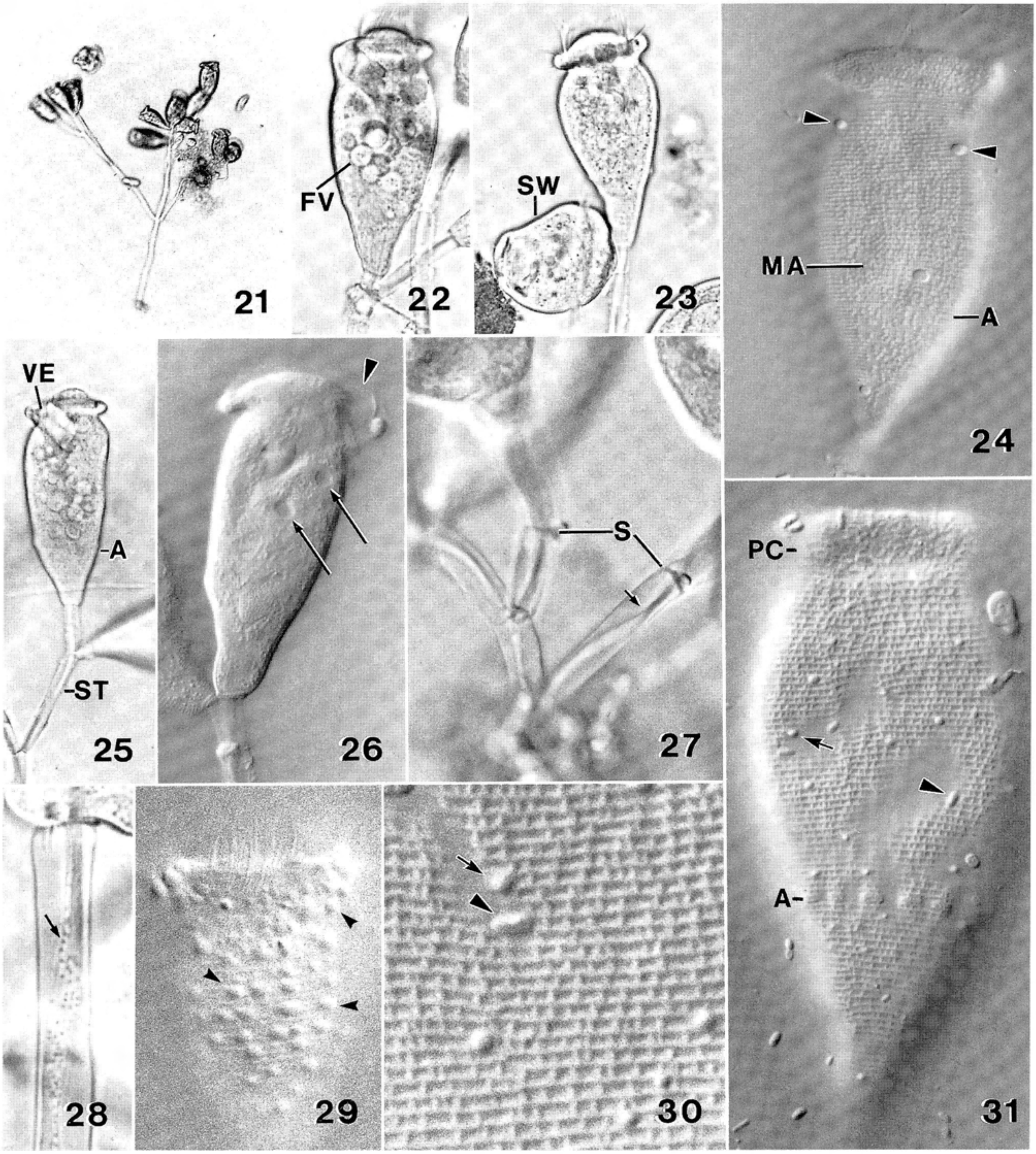
Oral apparatus of usual structure. Peristomial collar about 6 µm thick, about of same width as broadest body portion. Peristomial disk moderately elevated and convex, but not umbilicate, in feeding specimens. Vestibulum (infundibulum) of usual size, obliquely extending to cell centre. Oral infraciliature very much like in other vorticellids, thus the detailed illustrations



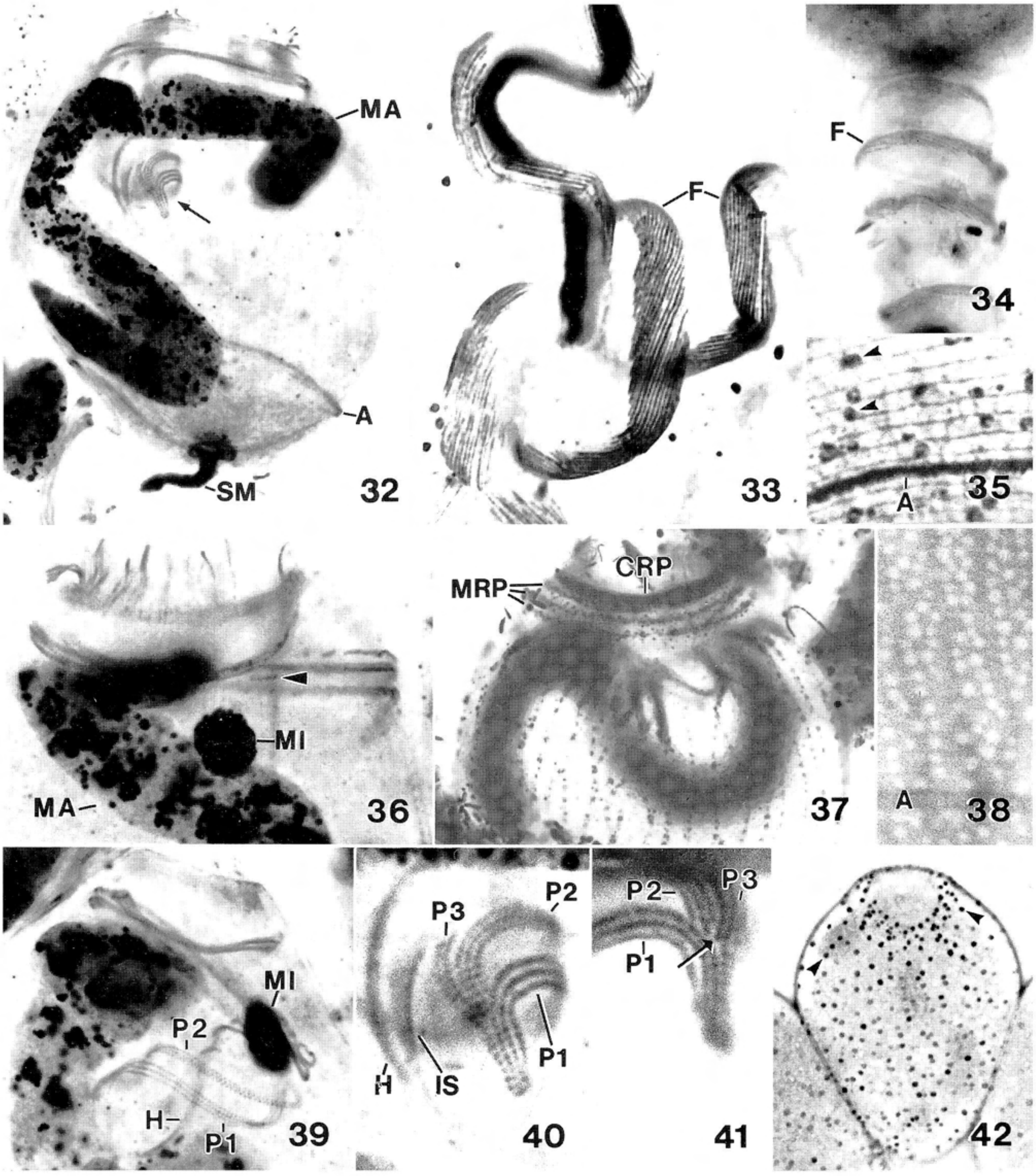
Figs. 1–12. *Epicarchesium granulatum*, morphology and synonymy from life (Figs. 1–7) and after protargol impregnation (Figs. 8–12). **1.** *Carchesium granulatum* from Kellicott [26], length 100 µm. **2.** *Carchesium* cf. *aselli* from Stamm [37], length 64–90 µm. **3.** Colony with typical zooids. Arrow marks cytopyge. **4.** Tuberculate pellicle. Arrows mark cortical blisters. **5.** Fine structure of stalk. The stalk sheath contains fibres (F) extending a quarter to a third of a coil, covering about one third of its circumference. Arrow marks flattened stalk myoneme. **6, 7.** Variability of branching pattern. **8.** Oblique frontal view of oral infraciliature and myoneme rings in peristomial collar. Arrow marks epistomial membrane. **9–12.** Variability of macronuclear shape, length of nucleus 31–52 µm. Bars = 20 µm. A = anlage of aboral ciliary wreath, CB = cortical blisters, CV = contractile vacuoles, F = fibres in stalk sheath, FV = food vacuole, H = haplokinety (undulating membrane), MA = macronucleus, MRP = myoneme rings in peristomial collar, N = subterminal notch, P = polykinety (adoral zone of membranelles), PC = peristomial collar, S = stalk septa.



Figs. 13–20. *Epicarchesium granulatum*, infraciliature and silverline system after protargol (Figs. 13–18) and dry silver nitrate (Figs. 19, 20) impregnation. **13.** Ventral total view. Arrowhead marks compact myoneme ring in peristomial collar. **14.** Lateral total view of swarmer with epistomial membrane (arrow) and fully developed aboral ciliary wreath. **15–17.** Oral infraciliature. Arrow denotes site where peniculus 2 branches off from peniculus 1. **18, 18a.** Myoneme system. The longitudinal nodular myonemes form an "inner myoneme basket" (IMB) and a special "outer myoneme basket" (OMB) commencing subequatorially and extending to the stalk. **19, 20.** Silverline system. In adults, the anlage of the aboral ciliary wreath is composed of 2–3 closely spaced mesh rows (cp. Figs. 43, 45). Bars = 10 µm (Figs. 13–16, 18, 19) and 5 µm (Figs. 17, 20). A = anlage of aboral ciliary wreath, ACW = fully developed aboral ciliary wreath, CRP = compact myoneme ring in peristomial collar, FG = fibrous myoneme reticulum in peristomial disk, G = germinal kinety, H = haplokinety, IMB = inner myoneme basket, OMB = outer myoneme basket, P 1–3 = peniculi (adoral membranelles) of adoral polykinety, SM = stalk myoneme, V = vestibular entrance.



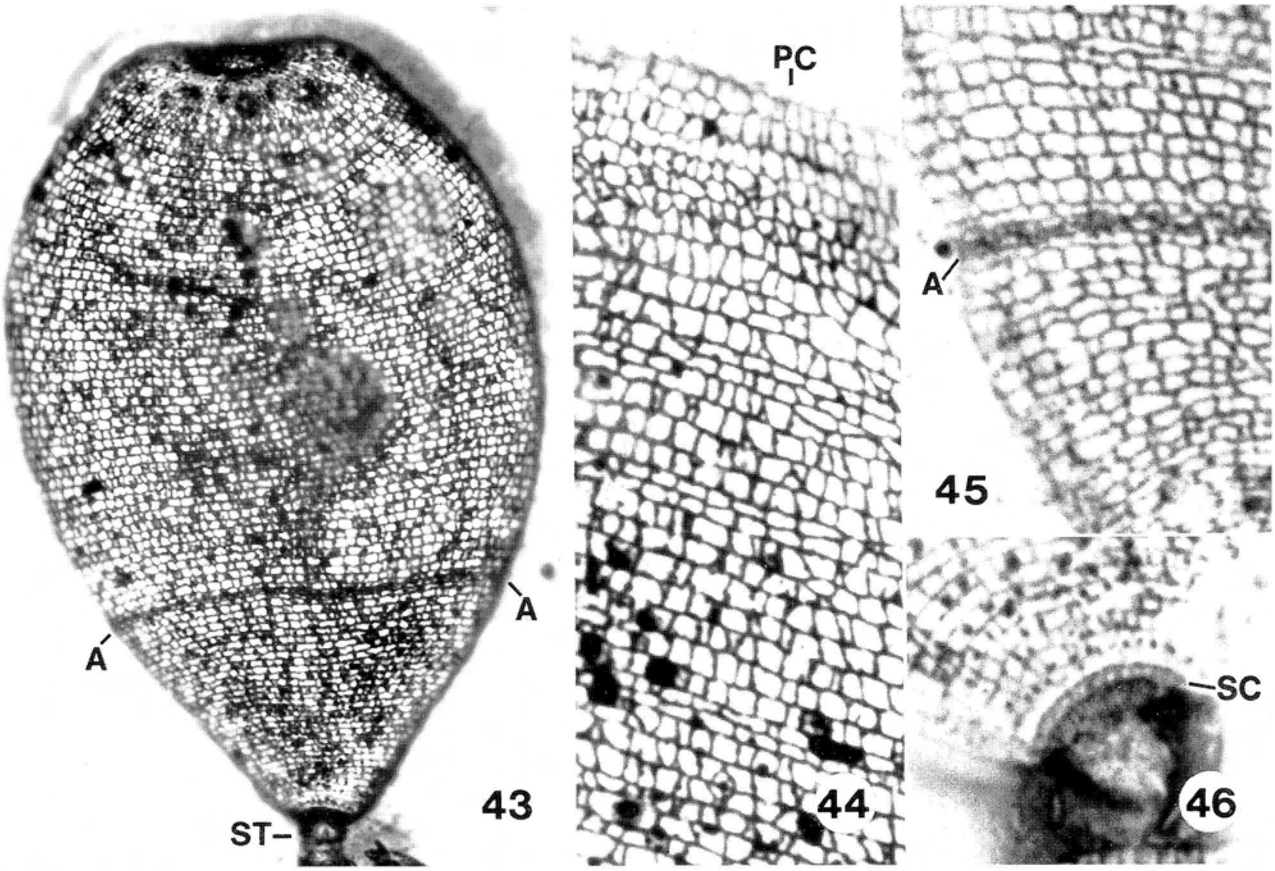
Figs. 21–31. *Epicarchesium granulatum* from life. **21.** Typical colony. **22, 23, 25.** Variability of zooid shape. **24.** The tuberculate pellicle appears transversely striated at low magnification. Arrowheads denote large pellicular blisters (cp. Fig. 29). **26.** *Epicarchesium granulatum* has two contractile vacuoles at the ventral vestibular wall (arrows). Arrowhead marks vestibular entrance. **27.** Stalk and branching nodes with septa. Arrow marks distinctly flattened stalk myoneme. **28.** The myoneme sheath is studded with tiny granules (arrow). **29.** Cortical blisters (arrowheads) in a specimen from the Asten population (photograph kindly supplied by R. Oberschmidleitner). **30, 31.** Total view (Fig. 31) and detail (Fig. 30) of tuberculate pellicle. Arrows mark large cortical blisters, easily confused with the more rod-shaped bacteria (arrowheads). A = anlage of aboral ciliary wreath, FV = food vacuole, MA = macronucleus, PC = peristomial collar, S = septa, ST = stalk, SW = swarmer, VE = vestibular entrance.



Figs. 32–42. *Epicarchesium granulatum*, infraciliature after silver carbonate (Figs. 32–37, 39, 40, 42) and protargol (Figs. 38, 41) impregnation. **32.** Lateral total view. Arrow marks proximal portion of adoral ciliary spiral shown at higher magnification in Fig. 40. **33, 34.** The stalk sheath contains closely spaced, short fibres lying outside in the coiled stalk (Fig. 34). **35.** Rarely, a cortical lattice, very similar to the silverline system, weakly impregnates with silver carbonate. Arrowheads mark argyrophilic substance in pellicular tubercles. **36.** Nuclear apparatus and distal portion of oral infraciliature. Arrowhead marks epistomial membrane. **37.** Myoneme system in anterior body half. **38.** The mitochondria, which are immediately underneath the cortex between the myoneme strands, appear as whitish dots. **39–41.** Oral infraciliature. The inner kinety of peniculus 3 is posteriorly shortened by about half of length (arrow). **42.** Many pellicular tubercles contain argyrophilic granules (arrowheads). A = anlage of aboral ciliary wreath, CRP = compact myoneme ring in peristomial collar, F = fibres in stalk sheath, H = haplokinety, IS = faintly impregnated structure, MA = macronucleus, MI = micronucleus, MRP = tiny myoneme rings in peristomial collar, P 1–3 = oral peniculi, SM = stalk myoneme.

(Figs. 8, 13, 15–17, 32, 36, 39–41) and some remarks on relevant details should suffice to orientate the reader. Adoral spiral conspicuously short, i.e. haplokinety (paroral ciliature) and polykinety (adoral ciliature) describe only 1.1 turns (about 400°) at peristomial disk before plunging down into vestibulum and accomplishing a further turn. Haplokinety accompanied by faintly impregnated structure, commences 3–5 (n = 5) basal bodies behind polykinety (Fig. 8). Peniculus (adoral membranelle) 1 twisted once, composed of 3 kineties (ciliary rows) terminating at different levels with longest (inner) kinety next to peniculus 3 and shortest kinety opposite; rarely, inner kinety appears shortened because covered by peniculus 3. Peniculus 2 also twisted once, terminates distinctly above and between peniculi 1 and 3, kinety neighbouring peniculus 1 usually shortened posteriorly by 1–2 basal bodies (in 2 out of 8 specimens unshortened), anteriorly by 3–7 (n = 8) basal bodies. Peniculus 3 also composed of 3 kineties, 6.3–8.5 µm ($\bar{x}$ = 7.4 µm; n = 13) long, proximally usually slightly projecting above peniculus 1 (85% of specimens), its inner kinety, next to peniculus 2, posteriorly shortened by about half of length and thus terminating at same level as peniculus 2; outer kinety anteriorly (85% of specimens) and posteriorly shortened by about 1 basal body each. Epistomial membrane composed of 5–6 basal bodies impregnating more intensively in swarmers than in sessile specimens, possibly because not ciliated in the latter; located near distal end of adoral ciliary spiral, i.e. at vestibular entrance, possibly linked to a somatic myoneme terminating very close to epistomial kinety (Figs. 8, 36).

Colonies with 1–16 zooids, up to 400 µm high, irregularly dichotomous, causing zooids to be at different levels (Figs. 3, 6, 7, 21). Main stalk attached to sludge flocks, 5–8 µm ($\bar{x}$ = 6.4 µm) across, equidistant, i.e. does



Figs. 43–46. *Epicarchesium granulatum*, silverline system after dry silver nitrate impregnation. **43.** Total view. **44, 45.** Silverline system in anterior and subterminal body portion at higher magnification. **46.** Scopula region. A = anlage of aboral ciliary wreath, PC = peristomial collar, SC = scopula, ST = stalk.

not narrow distally, thickness increased to about 10 µm at ramification sites and septa found in branching nodes and along main stalk at irregular intervals; lateral branches 10–145 µm (n = 25) long (Table 1). Main stalk and lateral branches contract helicoidally both simultaneously and separately; stalk myonemes distinctly flattened, longer axis 3–4.5 µm ($\bar{x}$ = 3.5 µm; n = 20) wide, regularly twisted and studded with pale, inconspicuous granules about 0.5 µm across attached to myoneme sheath (Figs. 5, 27, 28). Main stalk myoneme extends to distal end of stalk; lateral myonemes end at septa of branching nodes with inconspicuous fibres penetrating main stalk but not contacting its myoneme (Figs. 3, 27). Stalk sheath occasionally covered by rod-shaped bacteria, distinctly wrinkled when contracted; about one third of its circumference, on outer side of coiled stalk, contains closely spaced, obliquely arranged short fibres each extending a quarter to a third of a coil; fibres recognizable with interference contrast, deeply impregnated by silver carbonate, faintly by protargol and silver nitrate (Figs. 5, 33, 34). Scopula margin formed by double row of more or less tightly spaced argyrophilic granules (Fig. 46).

Occurrence and ecology: *Epicarchesium granulatum* was found in an activated sludge plant at Siggerwiesen (Salzburg) and in an underloaded plant at Asten near Linz. Specimens placed in petri-dishes survived only when aerated. However, *E. granulatum* very likely occurs in various freshwater biotopes having no particular substrate preference because Kellicott [26] found his specimens in the Niagara river and the Seajaquada creek (USA) attached to plants and *Cambarus* (now *Orconectes* [42]), a large crustacean. Apparently, *E. granulatum* is not a common species because we did not find definite records in the literature since the original description. However, several records of *Carchesium* spp. [21, 31, 43] from activated sludge and land-filtered sewage effluent might belong to this species (see Discussion). See ecology section of *P. elongata* for species associated with *E. granulatum*.

Pseudovorticella elongata (Fromentel, 1876) nov. comb. (Figs. 47–93; Tables 1, 2)

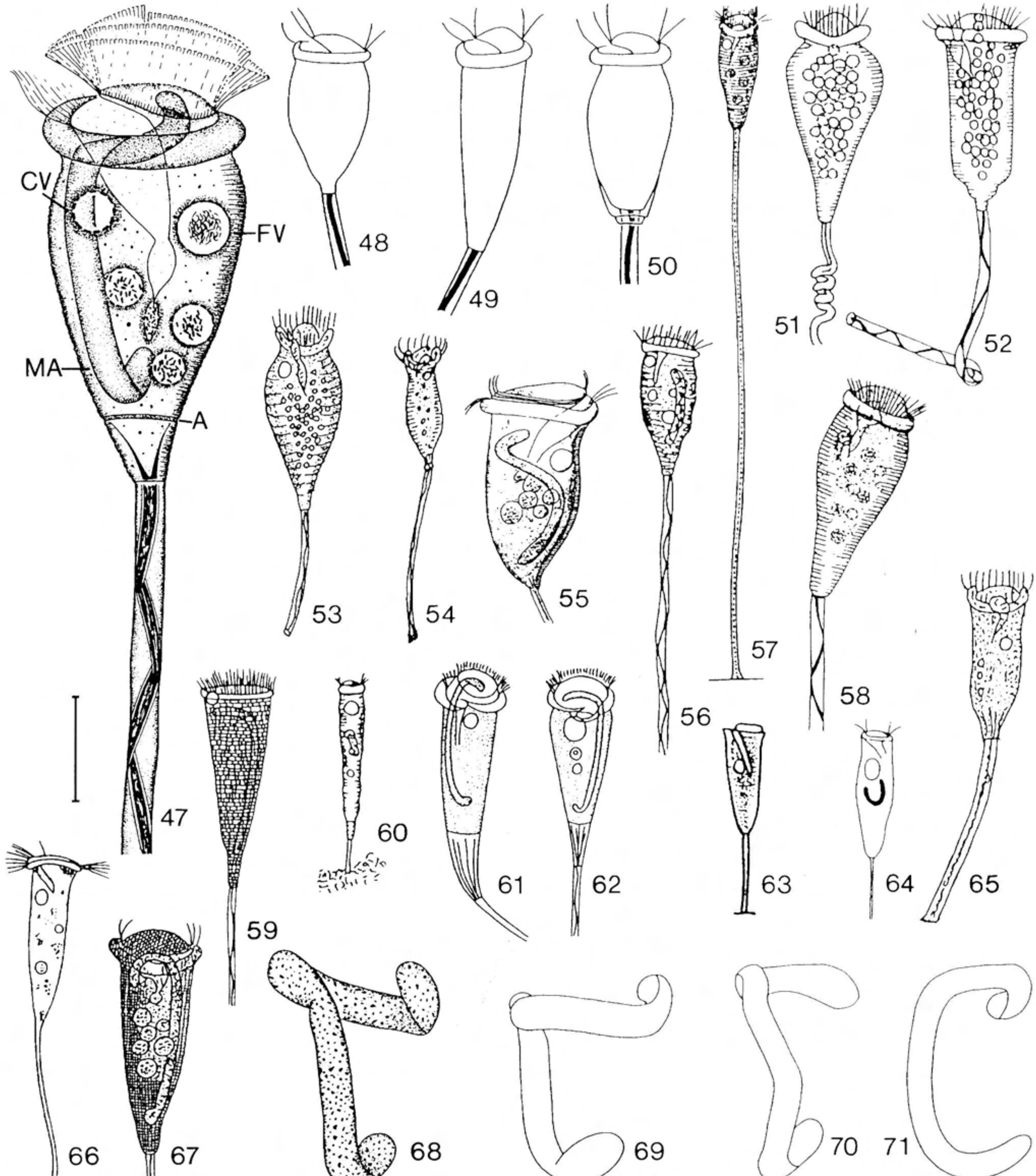
Improved diagnosis: In vivo 75 × 40 µm on average, slenderly campanulate; distressed specimens conspicuously cylindroid or conical, length up to three times width. Macronucleus J-shaped in main body axis. One contractile vacuole at ventral wall of vestibulum. On average 58 silverline mesh rows between anterior end and aboral ciliary wreath and 15 between ciliary wreath and scopula.

Neotype material: Two slides each with protargol (Foissner and Wilbert techniques) and silver nitrate (Klein-Foissner technique) impregnated cells have been deposited in the collection of microscope slides of the Oberösterreichische Landesmuseum in Linz (LI), Austria.

Redescription: Size in vivo 50–100 × 30–45 µm (Table 1). Slenderly campanulate to slightly clavate or barrel shaped, i.e. very much like *V. convallaria, V. infusionum* and *V. microstoma* (Figs. 47, 48, 50, 80–82). Shape distinctly and quickly changed in distressed specimens, for instance under very slight cover glass pressure, becoming cylindroid or conical, length up to three times width (Figs. 49, 83–86); such specimens even increase in length up to about 100 µm (up to 130 µm, if synonymy [1] is taken into account) and are easily mistaken for another species. Contracted cells obovoid with stalk slightly invaginated, in protargol preparations more distinctly globular. Stalk slightly shorter to up to twice as long as body, 5–7 µm across, attached to sludge flocks, contracts helicoidally but rarely; closely spaced argyrophilic granules at scopula margin (Fig. 78). Stalk myoneme without distinct granules, extends regularly twisting to distal end (Fig. 87). Macronucleus invariably (n > 30) in longitudinal axis of cell, usually J-shaped, occasionally C-shaped, both ends additionally often slightly curved, long anterior portion traverses peristomial disk, middle portion extends along ventral side; in protargol preparations often containing innumerable minute granules (nucleoli?), rarely, larger irregular (chromatin?) patches as in other peritrichs (Figs. 68–71, 74). Micronucleus ellipsoid, near anterior end of macronucleus, in 2 out of 11 specimens between transverse portions of macronucleus (Fig. 74). Contractile vacuole at ventral wall of vestibulum rather close to peristomial collar (Figs. 47, 81, 86).

Cortex distinctly transversely striated (Figs. 47, 88) and slightly roughened by minute tubercles 1–2 µm across (Fig. 89); tubercles recognizable only with interference contrast, many contain some substance, invisible in live specimens, giving protargol impregnated cells a blackish, spotted cortex (Figs. 72, 74). Silverline system as in congeners, but meshes more minute than in comparably sized species due to extraordinarily high total number of mesh rows (Table 2); meshes square to slightly hexagonal, some filled with an argyrophilic substance, arranged in same pattern as pellicular tubercles, rather irregular and slightly enlarged on peristomial collar in fully contracted cells, transverse-elongate and more narrowly spaced underneath aboral ciliary wreath, possibly due to increased contraction during preparation (Figs. 77, 90–92). Silverlines associated with few to many granules, possibly pellicular pores.

Myoneme system very similar to that known from peritrichs of the *Vorticella convallaria* type [11], i.e. consisting of a compact ring in peristomial collar, a fibrous reticulum in peristomial disk, and many longi-



Figs. 47–71. *Pseudovorticella elongata*, morphology and synonymy from life (Figs. 47–67) and after protargol impregnation (Figs. 68–71). **47.** Typical specimen. **48–50.** Shape variability; distressed specimens become conical. Stalk slightly invaginated in Fig. 50. **51–57.** *Vorticella elongata* Fromentel, 1876; Figs. 51, 52 from Fromentel [17], length about 60 µm; Fig. 53 from Dumas [9], length not given; Fig. 54 from Dumas [10], length given, however with uncertain units; Fig. 55 from Smith [35], length 95 µm; Fig. 56 from Biernacka [2], length 85 µm; Fig. 57 from Kent [27], length 85–102 µm. **58.** *Vorticella multangula* from Fromentel [17], length about 75 µm. **59–62.** *Vorticella conica* Stokes, 1887; Fig. 59 from Stokes [41], length 93–112 µm; Fig. 60 from Biernacka [2], length 105 µm; Figs. 61, 62 from Banina [1], length 90–130 µm. **63, 64.** *Vorticella subcylindrica* Ghosh, 1922;

Table 2. Comparison of silverline mesh row numbers in *Pseudovorticella elongata*, several congeners, and *Epicarchesium granulatum*. From Foissner and Brozek [14], supplemented.

Species	Number						
	Specimens investigated	Contractile vacuoles	Mesh rows from anterior end to aboral ciliary wreath		Mesh rows from aboral ciliary wreath to scopula		Mesh rows
			Extremes	Mean	Extremes	Mean	Ratio
Pseudovorticella elongata	43	1	51–66	58	10–20	15	0.26
P. chlamydophora	6	1	17–20	18	14–17	16	0.89
P. monilata	56	2	15–23	19	9–18	14	0.74
P. mutans	3	1	24–28	26	16–19	17	0.65
P. fasciculata	60	1	28–32	30	15–21	18	0.60
P. difficilis	20	1	25–31	28	14–18	16	0.57
P. pseudocampanula	5	1	28–33	30	16–18	17	0.57
P. quadrata	10	1	28–33	31	16–21	17	0.55
P. sauwaldensis	20	1	18–21	19	8–12	10	0.53
P. sphagni	22	2	25–30	27	8–10	9	0.33
Epicarchesium granulatum	30	2	53–61	57	27–34	31	0.54

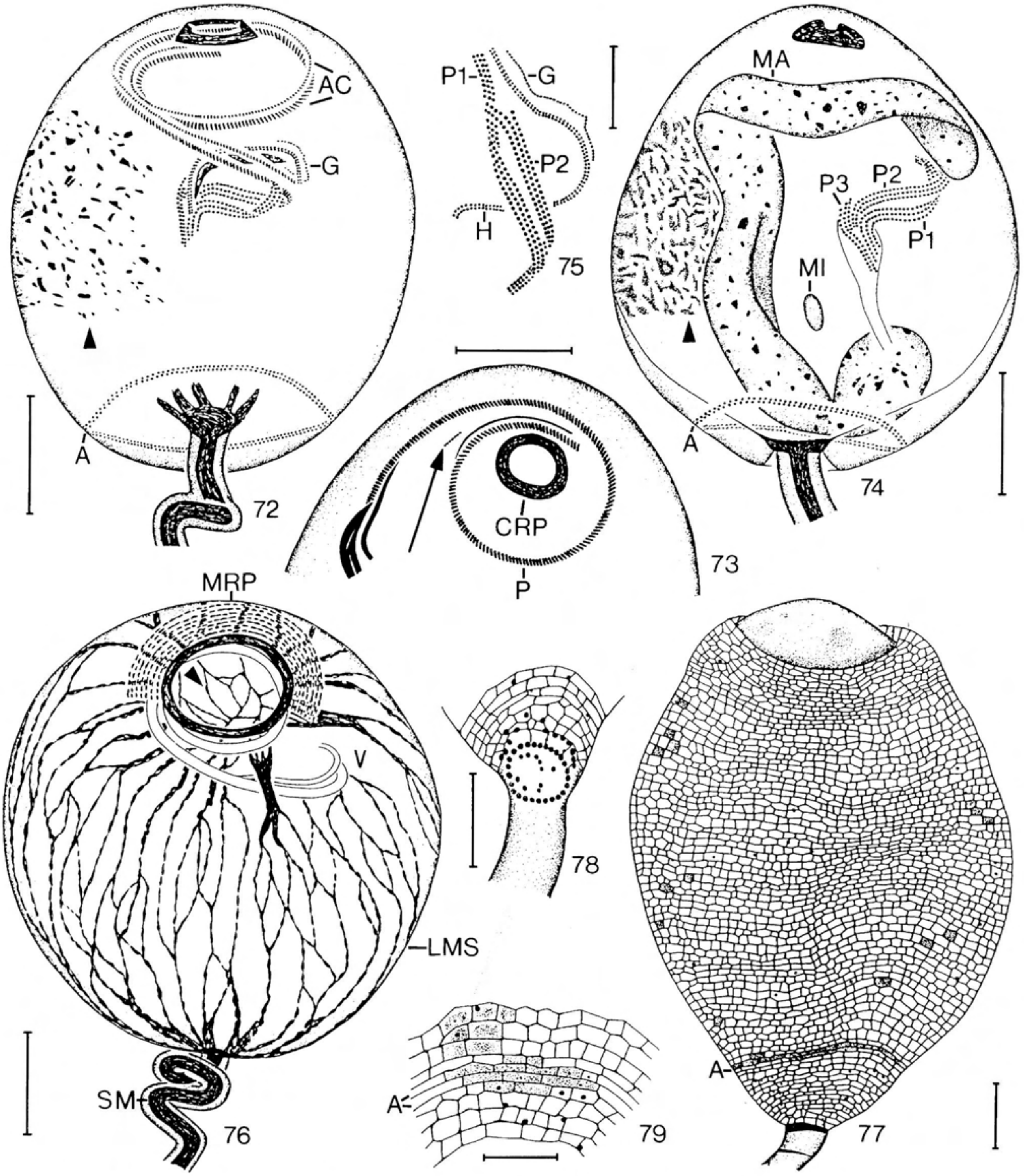
tudinal, more or less distinctly anastomosing strands originating from stalk myoneme and extending anteriorly to become anchored at adoral ciliary spiral (Fig. 76).

Anlage of aboral ciliary wreath composed of closely spaced, oblique dikinetids in protargol slides (Figs. 72, 74); after silver nitrate impregnation consisting of 2 closely spaced mesh rows framed by slightly narrowed somatic ones, whole complex thus composed of 4 more or less closely spaced silverline mesh rows (Figs. 79, 91).

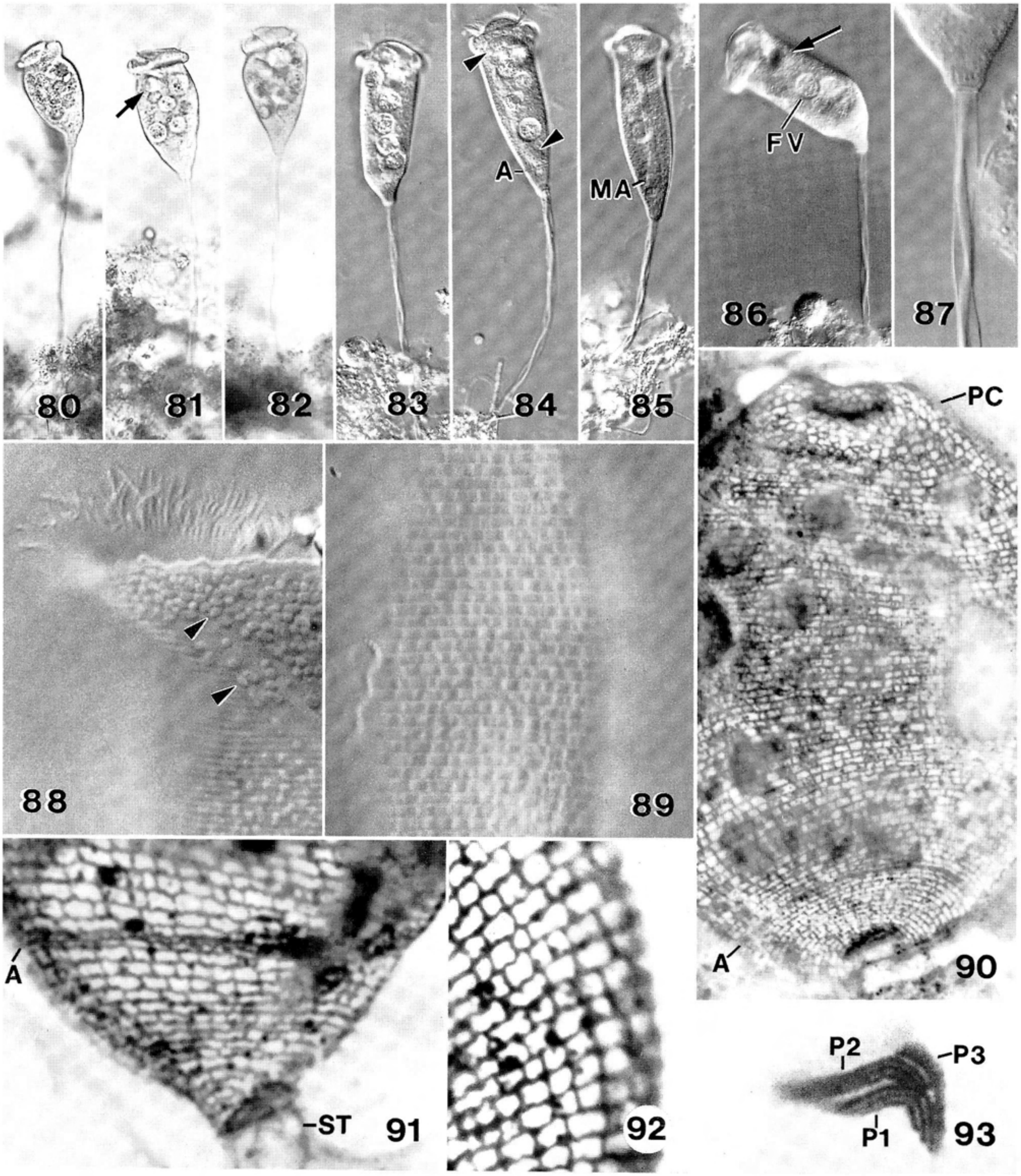
Oral apparatus of usual structure, peristomial collar about 6 µm thick, not projecting above body, except in stressed specimens. Peristomial disk usually convex, rarely flat; not umbilicate. Vestibulum (infundibulum) obliquely extending to body centre. Oral infraciliature quite similar to other members of genus (Figs. 72–75, 93). Haplokinety (paroral ciliature) and polykinety (adoral ciliature) describe 1.3 turns (about 500°) at peristomial disk before plunging down into vestibulum accomplishing a further turn. Haplokinety accompanied by faintly impregnated structure, commences, like in *E. granulatum*, a few basal bodies behind polykinety (Figs. 72, 73). Peniculi (adoral membranelles) composed of 3 kineties each, their proximal ends form arrow-like figure because peniculus 2 is slightly shortened and interposed between peniculi 1 and 3. Peniculus 1 twisted twice, its kineties terminate obliquely, i.e. at different levels, with (inner) longest kinety next to peniculus 3 and shortest kinety opposite. Peniculus 2 twisted once, terminates distinctly above peniculi 1 and 3, its inner kinety invariably slightly shortened proximally, its outer kinety shortened distally by about 4–5 basal bodies each. Peniculus 3, 6.3–8.0 µm ($\bar{x}$ = 7.1 µm; n = 12) long, proximally invariably slightly projecting above peniculus 1, its inner kinety, next to peniculus 2, proximally shortened by about half of length and thus terminating at same level as peniculus 2; outer kinety shortened anteriorly and posteriorly by about one basal body each. Epistomial membrane difficult to recognize, consists of 5–7 basal bodies very likely not ciliated in sessile specimens, located near vestibular entrance, i.e. about 90° distant from distal end of adoral ciliary spiral (Fig. 73).

Occurrence and ecology: *Pseudovorticella elongata* was found in activated sludge together with various other ciliates, e. g. *Epicarchesium granulatum* (described above), *Epistylis entzii*, *Carchesium polypinum*, *Vorticella convallaria*, *Trochilia minuta*, *Thigmogaster oppositevacuolatus* and *Acineria uncinata*. Taking into

◄
Fig. 63 from Ghosh [18], length 150 µm; Fig. 64 from Naidu [28], length 60 µm. **65.** *Vorticella subcylindrica* from Dumas [10], length given, however with uncertain units. **66, 67.** *Vorticella plicata* Gourret and Roeser, 1886; Fig. 66 from Gourret and Roeser [19], length not given; Fig. 67 from Stiller [38], length 85 µm. **68–71.** Variability of macronuclear shape, length of nucleus 28–51 µm. Bar = 20 µm. A = anlage of aboral ciliary wreath, CV = contractile vacuole, FV = food vacuole, MA = macronucleus.



Figs. 72–79. *Pseudovorticella elongata*, infraciliature and silverline system after protargol (Figs. 72–76) and dry silver nitrate impregnation (Figs. 77–79). **72–74.** Ventral, frontal and lateral view of infraciliature. Arrow marks epistomial membrane. Arrowheads denote argyrophilic substance in pellicular tubercles. **75.** Vestibular portion of adoral ciliary spiral. **76.** Myoneme system. Arrowhead marks fibrous reticulum in peristomial disk. **77.** Silverline system. **78, 79.** Scopula and anlage of aboral ciliary wreath, composed of two narrowly spaced silverline mesh rows (cp. Fig. 91). Bars = 10 µm (Figs. 72–74, 76, 77) and 5 µm (Figs. 75, 78, 79). A = anlage of aboral ciliary wreath, AC = adoral ciliary spiral, CRP = compact myoneme ring in peristomial collar, G = germinal kinety, H = haplokinety (undulating membrane), LMS = longitudinal myoneme strands, MA = macronucleus, MI = micronucleus, MRP = myoneme rings in peristomial collar, P 1–3 = peniculi of polykinety (adoral zone of membranelles), SM = stalk myoneme, V = vestibular entrance.



Figs. 80–93. *Pseudovorticella elongata* from life (Figs. 80–89) and after dry silver nitrate (Figs. 90–92) and protargol (Fig. 93) impregnation. **80–86.** Shape variability, without cover glass (Figs. 80–82) and under cover glass (Figs. 83–86). Arrows mark contractile vacuole. Arrowheads denote ends of macronucleus. **87.** Stalk. **88.** The pellicle appears transversely striated at low magnification. Arrowheads mark mitochondria. **89.** The reticulate pellicular structure is recognizable only at high magnification (oil immersion ×100). **90.** Total view of silverline system. **91.** Silverline system in posterior body portion. **92.** Silverline system at high magnification. **93.** Proximal end of adoral ciliary spiral showing the three peniculi. A = anlage of aboral ciliary wreath, FV = food vacuole, MA = macronucleus, PC = peristomial collar, P 1–3 = oral peniculi, ST = stalk.

account the synonymy (see Discussion), *P. elongata* is very likely a rather common species, but possibly frequently misidentified as *Vorticella* spp.; it has even been recorded several times from activated sludge [1, 2, 5, 6]. Others found it in various freshwater biotopes attached to submerged plants [25], algae [10, 27] and a crustacean [41]; Fromentel [17] did not mention the biotope. Sládeček et al. [34] classified *P. elongata* as sharp indicator (indicative weight, G = 5 in a five-point rating scale) for beta-mesosaprobity (saprobic index of species, S = 2.0), i.e. of slight water pollution. However, the records from activated sludge indicate that *P. elongata* has a broader range of occurrence. We suggest to distribute the saprobic valencies, rated by a 10-point scale [34], as follows: β-mesosaprobity, $\beta = 6$; α-mesosaprobity, $\alpha = 4$; indicative weight thus, G = 3; saprobic index of species, S = 2.4.

Discussion

Identification and comparison of *Epicarchesium granulatum* with related genera and species

Jankowski [23] established the genus *Epicarchesium* solely on the brief description of *Carchesium granulatum* by Kellicott [26], assuming that the tuberculate pellicle is indicative of a reticulate silverline system. Our study confirms Jankowski's speculation, and thus we recognize *Epicarchesium* as a distinct genus (Figs. 19, 30, 31, 43–45). *Epicarchesium*, as yet monotypic, is easily confused with *Carchesium* and *Pseudocarchesium*, the tuberculate pellicle and reticulate silverline system being the sole distinguishing characters; these are, however, not easily recognized in live specimens, although the tuberculate cortex is conspicuous under interference contrast at high magnification (Figs. 30, 31). Furthermore, *Pseudocarchesium* contracts in zigzag and thus belongs to the zoothamniids [36].

Our population of *E. granulatum* matched the original description almost perfectly, differing solely in a minor detail, viz. the stalk septa, which were obviously lacking in Kellicott's [26] colonies. Kellicott [26] even mentioned the pellicular tubercles and that the two contractile vacuoles are difficult to recognize. However, Kellicott possibly did not see the inconspicuous pellicular tubercles but the curious and more prominent pellicular blisters described above (Figs. 1, 3, 4, 24, 29–31).

Apparently, *Epicarchesium granulatum* has never been found since the original description. However, *Carchesium* spp. were frequently reported in the sewage treatment literature [21, 31, 43], and *Carchesium* cf. *aselli* Engelmann, found by Stamm [37] in a Swiss wastewater treatment plant (Fig. 2), was very likely *E. granulatum* because most characters mentioned match Kellicott's and our observations. Stamm [37] observed stalk septa as we did.

Epicarchesium granulatum in vivo bears a strong resemblance to several *Carchesium* species because the pellicular tubercles are inconspicuous and clearly recognizable only at high magnification (Figs. 30, 31). *Carchesium gracilis* [29] and *C. batorligetiense* [39, 40] are very similar to *E. granulatum* in size, shape and macronucleus, but have only a single contractile vacuole. *Carchesium dipneumon* (Penard, 1922) Schödel, 1987 [32], an epizoite of *Gammarus* has, like *E. granulatum*, two contractile vacuoles at the ventral wall of the vestibulum. Unfortunately, this species has not yet been silver-stained and thus its generic classification remains doubtful. The same applies to *C. pectinatum* (Zacharias), a euplanktonic species, which has a distinctly tuberculate pellicle and thus might belong to *Epicarchesium*.

Solitary specimens of *E. granulatum* can be easily confused with *Pseudovorticella* spp. However, no *Pseudovorticella* is known to have such a high total number of silverline mesh rows as *E. granulatum* (Table 2).

Taxonomy and identification of *Pseudovorticella elongata*

Foissner and Schiffmann [15] split *Vorticella* into two genera, *Vorticella* and *Pseudovorticella*, depending on the somatic silverline pattern. This decision was readily accepted and extended to other groups of peritrichs [22, 23, 46]. *Vorticella elongata* has a helicoidally contracting stalk and a reticulate silverline system (Figs. 77, 90–92) and thus undoubtedly matches the diagnosis of *Pseudovorticella*. It is readily distinguished from other *Pseudovorticella* species by its high number (51–66; $\bar{x} = 58$; Table 2) of silverline mesh rows between the anterior end and the aboral ciliary wreath. However, in vivo it is easily confused with *P. micata* (marine), *P. mollis* (< 50 µm long), *P. mutans* (inseparable with conventional characters) and *P. sauwaldensis* (< 50 µm long), which have a similar shape, size, nucleus and contractile vacuole (see [45] for authorships and dates of species). Thus, the number of silverline mesh rows, which can be estimated also in live specimens using interference contrast (Fig. 89), is indispensable for a correct identification. In vivo, *Pseudovorticella elongata* is also easily confused with *Vorticella convallaria*-type species because the pellicular tubercles are inconspicuous (Figs. 88, 89). However, the overall appearance of *P. elongata* is slightly different from *V. convallaria* and related forms. In fact, it came to our attention because it looked like a transition form of *V. convallaria* and *V. in-*

fusionum, i.e. was a little bit smaller and less campanulate than *V. convallaria* usually is, but a little bit larger and more campanulate than the common forms of *V. infusionum* and *V. microstoma* (Figs. 47, 48, 50, 80–82).

Species identification in peritrich ciliates is difficult because the group is highly split and most original descriptions and redescriptions are of poor quality. Furthermore, some of the characters commonly used, for instance, stalk length and body shape, are rather variable [29]. *Pseudovorticella elongata* is particularly complicated because it has an extreme shape variability, not recognized by previous authors, and, as mentioned above, bears a strong resemblance to some common *Vorticella* species (Figs. 47–50, 80–86). In fact, several authors possibly described or identified the shape extremes as different species. In evaluating the synonymy, the reticulate pellicular structure of *P. elongata* should not be used as key character because the tubercles are inconspicuous and thus easily overlooked. However, some of the more experienced and careful observers noticed them [10, 38, 41]; others mentioned at least a distinct pellicular striation [2, 9, 10, 17, 27, 35].

Noland and Finley [30] synonymized two species, viz. *V. multangula* Fromentel, 1876 (often misdated with 1874; e. g. [30, 44]) and *V. conica* Stokes, 1887, with *V. elongata*, while Kahl [24] recognized all as distinct species. The last reviser [44] followed Noland and Finley [30] and added two further synonyms, viz. *V. subcylindrica* Ghosh, 1922 and *V. plicata* Gourret and Roeser, 1886. None of the revisers mentioned substantiated the synonymy suggested. Thus, we shall discuss this matter in some detail.

Vorticella multangula Fromentel, 1876 [17] was distinguished from other species of the genus by its strongly spiralized stalk myoneme, an inappropriate character because it is common to the whole genus, as already noted by Kent [27]. However, Fromentel's *V. elongata* (Figs. 51, 52) and *V. multangula* (Fig. 58) reflect the shape variability we observed very well (Figs. 47–50, 80–86). Whether the *V. elongata* populations described by several authors [2, 9, 10, 27, 35] actually belong to this species is difficult to ascertain because data and figures (Figs. 53–57) are too incomplete. However, Biernacka [2] figured as *V. conica* and *V. elongata* two forms highly resembling those we observed (Figs. 56, 60). Furthermore, Biernacka [2] found these species, as we did, in activated sludge.

The second synonym, *Vorticella conica* Stokes, 1887 [41], has rarely been reported, notably, however, from activated sludge plants in Russia [1] and Poland [2]. The figures (Figs. 59–62) and descriptions by these authors and especially by Stokes [41] perfectly matched our distressed specimens (Figs. 49, 83–86). Stokes even noticed the tuberculate pellicle, the weak contractility, the short stalk and the posterior annuli in contracted cells. However, neither Stokes [41], who found only 6–8 specimens attached to a single *Cyclops*, nor Banina [1] and Biernacka [2] recognized the unhampered shape of *P. elongata*, very likely because it distorts, as described above, quickly under the cover glass and normal specimens are easily mistaken for another species (see Biernacka's [2] *V. elongata*, Fig. 56).

The third synonym of *P. elongata*, *Vorticella plicata* Gourret and Roeser, 1886 [19], is a marine, rather incompletely described species whose shape matched that of our distressed specimens (Fig. 66). Stiller [38] redescribed *V. plicata* from a highly saline sulphur spring in Croatia and mentioned that it has a tuberculate pellicle (Fig. 67). Thus, *V. plicata* might indeed be a junior synonym of *P. elongata*. However, more detailed studies on marine peritrichs are needed.

Vorticella subcylindrica Ghosh, 1922 [18], another possible synonym of *P. elongata*, has been described very superficially (Fig. 63). However, if the length (150 μm) given by Ghosh [18] is correct, then it can hardly be identical with *P. elongata*. Naidu [28], who briefly redescribed *V. subcylindrica* from a single specimen, mentioned a length of only 60 μm and a horseshoe-shaped macronucleus (Fig. 64). *Vorticella subcylindrica* Dumas, 1930 [10], a junior primary homonym of *V. subcylindrica* Ghosh, 1922, also matched our specimens of *P. elongata*, especially because Dumas [10] mentioned that it has a tuberculate pellicle and is similar to *P. elongata* found by him at the same site (Figs. 54, 65). Thus, we suggest synonymy and do not replace the homonymy (article 60 b of the ICZN [20]).

Very likely, *P. elongata* has additional synonyms which, however, can be discovered only by very detailed revisions of the genera *Vorticella* and *Pseudovorticella*.

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