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Taxonomic Characterization of *Pseudohaplocaulus infravacuolatus* nov. spec. and *Vorticella chlorellata* STILLER 1940, Epiplanktonic Peritrichs (Ciliophora, Peritrichia) Attached to Coenobia of *Anabaena* (Cyanophyta), Including a Redescription of *V. chlorostigma* (EHRENBERG, 1831)

key words: ciliate taxonomy, infraciliature, periphyton, plankton, protozooplankton

Abstract

Pseudohaplocaulus infravacuolatus nov. spec. and *Vorticella chlorellata* STILLER, 1940, two peritrich ciliates attached to planktonic coenobia of *Anabaena* sp. (Cyanophyta), were investigated using live observation, silver impregnation, and scanning electron microscopy. *Pseudohaplocaulus infravacuolatus* differs from its nearest relative, *P. anabaenae* (STILLER, 1940), mainly by the location of the anterior contractile vacuole. *Vorticella chlorellata* has symbiotic green algae, a J-shaped macronucleus, and a single, ventral contractile vacuole. The number of silverlines is very close to that of *V. picta*, but distinctly different from that of *V. chlorostigma* (EHRENBERG, 1931), an other green *Vorticella*, red-described for the first time. *Vorticella rhabdostyloides* KELLICOTT, 1885 is recognized as a distinct species, but transferred to *Haplocaulus*: *H. rhabdostyloides* (KELLICOTT, 1885) nov. comb. Likewise, *Vorticella fasciculata* MÜLLER, 1773 is considered a distinct species and transferred to *Pseudovorticella*: *P. fasciculata* (MÜLLER, 1773) nov. comb.

1. Introduction

Epibiont associations increasingly attract general and plankton ecologists because they are an ideal experimental system for examining the structure of metapopulations (THRELKELD *et al.* 1993). Sessile peritrich ciliates associated with planktonic freshwater organisms might be an excellent model for such investigations. They colonize phytoplankters, zooplankters, and organic debris and have a high diversity.

The present paper provides a detailed taxonomic account of two epiphytoplanktonic peritrichs, one of which (*Pseudohaplocaulus infravacuolatus*) occurred in amazingly high numbers. Epiphytoplanktonic associations between peritrichs and various species of colonial cyanobacteria and/or diatoms were reported as early as 1885 by KELLICOTT and later by GAJEWSKAJA (1933), KAHL (1935), STILLER (1940) and SOMMER (1951). These authors recognized most populations as new species. More recently, DAVIS (1972, 1973), PACE and ORCUTT (1981), KERR (1983), PRATT and ROSEN (1983), and CANTER *et al.* (1990, 1992) reported on such associations, but mainly from an ecological point of view. The species concerned were usually not determined or, as we shall show, misidentified. In fact, none of the epiphytoplanktonic peritrichs has as yet been investigated with modern taxonomic methods. We were thus not too surprised in discovering a new species of *Pseudohaplocaulus* WARREN, 1988, a genus established rather recently and without sufficient evidence. As several ecologists noted (e. g. KERR 1983), associations between peritrichs and phytoplankters are very likely much more frequent than reported in the literature. Possibly, transportation, sto-

rage, and preservation of samples before observation lead to the demise of vorticellids or cause them to detach from their substrate.

The scarcity of reliable morphological studies contrasts with the detailed ecological data. CANTER *et al.* (1992), for instance, studied how many peritrichs a filament of *Anabaena* can buoy up with its gas vacuoles. Furthermore, they showed that the peritrichs, although keeping the cyanobacterial coenobia in constant motion by the action of the cilia, could not prevent colonies from sinking when the gas vacuoles were collapsed by pressure.

A detailed description of epiplanktonic and euplanktonic ciliates is not only of purely taxonomic interest. Planktonic ciliates contribute significantly to the energy flux and the clearance of the water by their filter-feeding activity in periods of peak abundances, which usually occur during bacterial and phytoplankton blooms (FENCHEL 1987, LAYBOURN-PARRY 1992, LAYBOURN-PARRY and ROGERSON 1993). Likewise, hypotheses on community structures and specificity of associations, so frequently found in the literature, are strongly dependent on a thorough taxonomy.

Our study provides also a remarkable example of the high diversity of vorticellid peritrichs, indicating that many of the synonyms suggested by NOLAND and FINLEY (1931) and WARREN (1987) could be distinct taxa. Two species, *V. chlorellata* STILLER and *V. chlorostigma* (EHRENBERG), at first glance very similar due to their symbiotic green algae and thus synonymized by WARREN (1987), are distinctly different in most other main characteristics.

2. Material and Methods

Pseudohaplocaulus infravacuolatus and *Vorticella chlorostigma* were found on 2. 11. 1991 in Lake Grabensee, Salzburg, Austria (E 13° 5' /N 48° 0'). Both were attached to planktonic colonies of *Anabaena* sp., which were collected with a plankton net. Lake Grabensee is a small (1.26 km²), shallow (max. depth 13 m), eutrophic lake described in some detail by MOOG and JAGSCH (1980). No chemical or other analyses of the water were performed when the ciliates were collected. Likewise, the number of *Anabaena* colonies and peritrichs were not counted because this was beyond the scope of the study.

Vorticella chlorostigma was collected in May 1974 in a peat-bog of the Ibmer Moor near the village of Buch (Upper Austria, E 12° /N 48°03'), where the cells formed green lawns on grass blades hanging into the water.

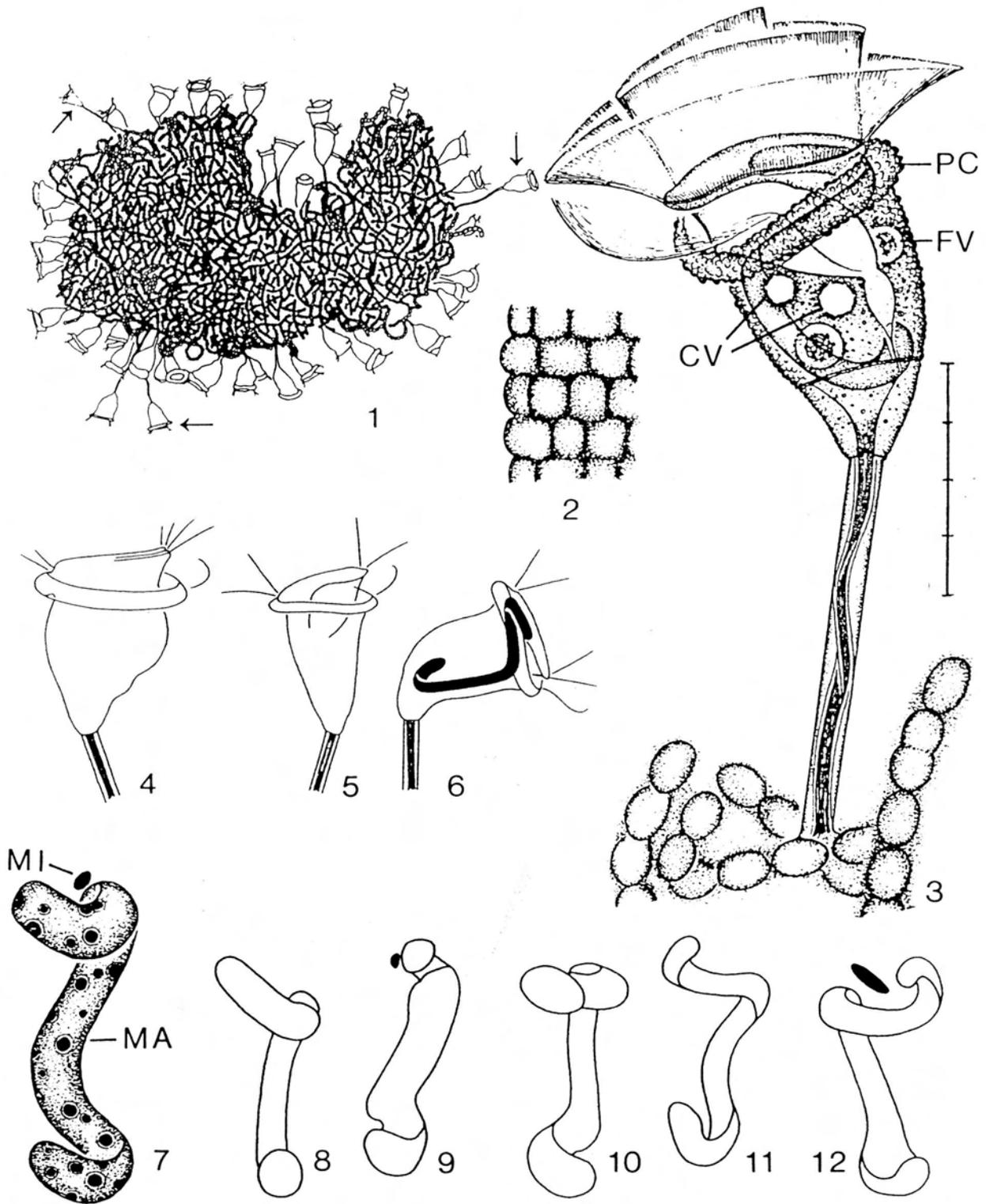
Cells were studied *in vivo* using a high-power oil immersion objective and differential interference contrast. Of course, characteristics which could change under cover-glass pressure, like cell shape and location of contractile vacuoles, were studied in uncovered, swirling specimens using magnifications between X 100 – X 400. The infraciliature (ciliary pattern) was revealed with protargol, the silverline system with the "dry" silver nitrate method. *Pseudohaplocaulus infravacuolatus*, which occurred in great numbers, was also studied with the scanning electron microscope. See FOISSNER (1991) for a detailed description of all methods mentioned.

Counts and measurements on silvered specimens were performed at a magnification of X 1,000. *In vivo* measurements were conducted at a magnification of X 250–1,000. Although these provide only rough estimates, it is convenient to give such data as specimens usually shrink in preparations and contract during fixation. Standard deviation and coefficient of variation were calculated according to statistics textbooks. Drawings of live specimens are based on free-hand sketches and micrographs, those of impregnated cells were made with a camera lucida. Terminology is according to CORLISS (1979) and WARREN (1986).

3. Description of Species and Discussion

Pseudohaplocaulus infravacuolatus nov. spec. (Figs. 1–43; Tables 1, 2)

Diagnosis: On average 60×40 µm, campanulate. Macronucleus J-shaped in main body axis. 2 contractile vacuoles at ventral wall of vestibulum. On average 24 silverlines (mesh



Figures 1-12. *Pseudohaplocaulus infravacuolatus* from life (1-6) and after protargol impregnation (7-12). - Fig. 1: Coenobium of *Anabaena* sp. heavily colonized by *P. infravacuolatus* and *Vorticella chlorellata* (arrows). - Fig. 2: Tuberculate pellicle. - Figs. 3-6: Typical specimens. - Figs. 7-12: Variability of nuclear apparatus, length 32-42 μm . CV: contractile vacuoles, FV: food vacuole, MA: macronucleus, MI: micronucleus, PC: peristomial collar. Bar division: 10 μm .

rows) between anterior end and aboral ciliary wreath and 20 silverlines between aboral ciliary wreath and scopula. Epiplanktonic.

Locus typicus: Lake Grabensee (W 13° 5'/N 48° 0'), Salzburg, Austria; attached to planktonic colonies of *Anabaena* sp.

Type specimens: Two holotypes and two syntypes of *P. infravacuolatus* as four slides of protargol- (Wilbert technique) and silver nitrate- (Klein-Foissner technique) impregnated cells, respectively, have been deposited in the collection of microscope slides of the Oberösterreichische Landesmuseum in Linz (LI), Austria.

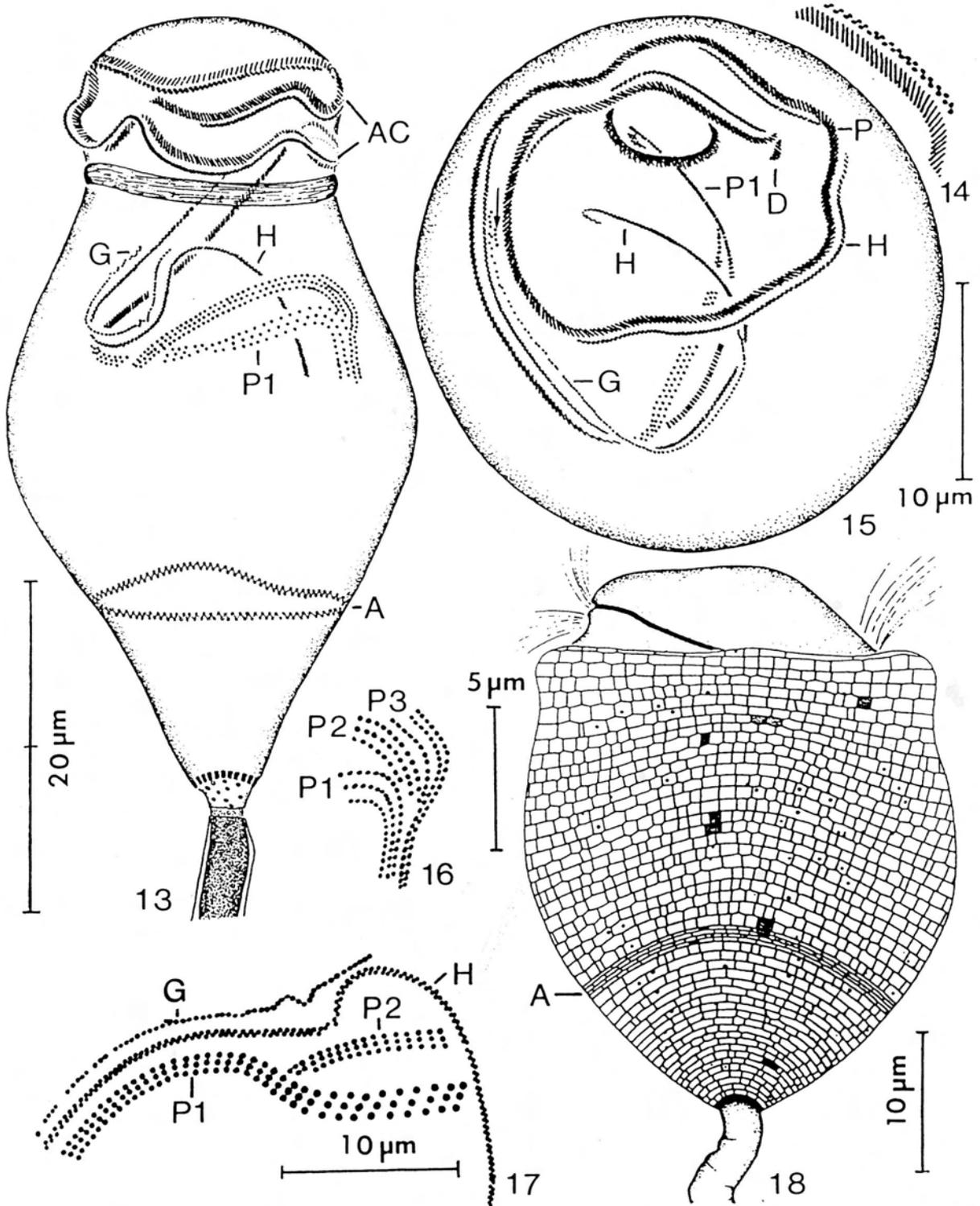
Etymology: *infra* (below) because both contractile vacuoles are below (at the ventral wall) of the vestibulum, as opposed to *P. anabaenae*, which has one of its two vacuoles above the vestibulum, i. e. at the dorsal wall.

Description: Size *in vivo* 60×40 µm on average (Table 1). Slenderly to distinctly campanulate, about half of specimens nodding, i. e. more or less obliquely attached to main stalk axis (Figs. 3–6, 25–28). Stalk usually about as long as body, rarely up to 200 µm, 4–6 µm across, directly attached to cyanobacterial filaments or, possibly, also to their slimy sheath; equidistant, i. e. does not narrow distally; without conspicuous granules; does not or indistinctly contract helicoidally but sinuously, even in cells fixed for preparations; myoneme only slightly helicoidal, sometimes with inconspicuous thickening, extends to distal end of stalk; stalk sheath distinctly wrinkled during contraction. Contracted specimens barrel-shaped or clavate; cells not as contractile as most other vorticellids and thus often remaining partially extended when fixed for preparations; myoneme system, however, very similar to that of *Vorticella* (cp. FOISSNER 1977), i. e. consisting of compact ring in peristomial collar and many thin strands extending between adoral ciliary spiral and scopula, forming rather distinct tube in posterior end continuing as stalk myoneme. Macronucleus invariably ($n > 20$) in longitudinal axis of cell, J-shaped, both ends additionally often slightly curved, long anterior portion traverses peristomial disc, middle portion extends along ventral side;

Table 1. Morphometric characteristics from *Pseudohaplocaulus infravacuolatus* (PI), *Vorticella chlorellata* (VC) and *Vorticella chlorostigma* (VH).

Character ¹	Species	\bar{x}	M	SD	SD _{\bar{x}}	CV	Min	Max	n
Body, length (<i>in vivo</i>)	PI	60.0	62.0	5.9	1.8	10.0	47	67	11
	VC	53.0	52.0	5.5	1.7	10.2	44	64	10
Body, width (<i>in vivo</i>)	PI	40.0	42.0	3.3	1.0	8.2	32	42	11
	VC	40.0	40.0	4.4	1.4	10.9	34	48	10
Silverline mesh rows or silverlines from anterior end to aboral ciliary wreath, number	PI	23.8	24.0	1.4	0.2	5.9	21	26	36
	VC	38.0	39.0	1.9	0.5	5.0	35	40	17
	VH	109.1	107.0	5.8	1.5	5.3	101	118	16
Silverline mesh rows or silverlines from aboral ciliary wreath to scopula, number	PI	19.8	20.0	1.4	0.2	7.1	16	22	39
	VC	21.4	21.0	1.7	0.5	8.2	19	24	11
	VH	50.3	50.0	3.4	0.9	6.8	41	55	14
Distance between mesh rows or silverlines in mid-body	PI	1.6	1.6	0.3	0.1	18.8	1	1.4	34
	VC	0.8	0.8	0.1	0.03	11.0	0.6	1.0	13
	VH	0.7	0.7	0.06	0.02	8.8	0.6	0.8	15
Macronucleus, diameter in mid-ventral portion	PI	5.8	6.4	1.1	0.3	19.2	4	7.2	12
	VC	4.2	4.4	0.7	0.3	17.5	3.2	4.8	5
Micronucleus, length	PI	4.8	4.8	0.8	0.4	16.7	4	5.6	5
Micronucleus, width	PI	2.7	2.4	0.4	0.2	15.3	2.4	3.2	8

¹) Data based on the investigation of silver nitrate (silverline characteristics) or protargol (nuclear characteristics) impregnated specimens. 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.



Figures 13–18. *Pseudohaplocaulus infravacuolatus* after protargol (13–17) and silver nitrate (18) impregnation. – Figs. 13–15: Lateral and frontal view of oral ciliary pattern. Distal end (D) of adoral spiral is shown at higher magnification in Fig. 14. Arrow marks epistomial membrane close to germinal kinety. – Figs. 16, 17: Mid-region and proximal end of adoral ciliary spiral. – Fig. 18: Silverline system. A: anlage of aboral ciliary wreath, AC: adoral ciliary spiral, D: distal end of adoral spiral, G: germinal kinety, H: haplokinety (undulating membrane), P: polykinety (adoral zone of membranelles) which forms three peniculi (P1–3) in the vestibulum.

rarely specimens with almost rod-shaped nucleus (Figs. 7–12). Micronucleus ellipsoid, near distal anterior end of macronucleus. Two contractile vacuoles, both invariably at ventral wall of vestibulum, one pre-equatorially slightly underneath vestibular opening, the other in body centre near cytostome (Figs. 3, 24).

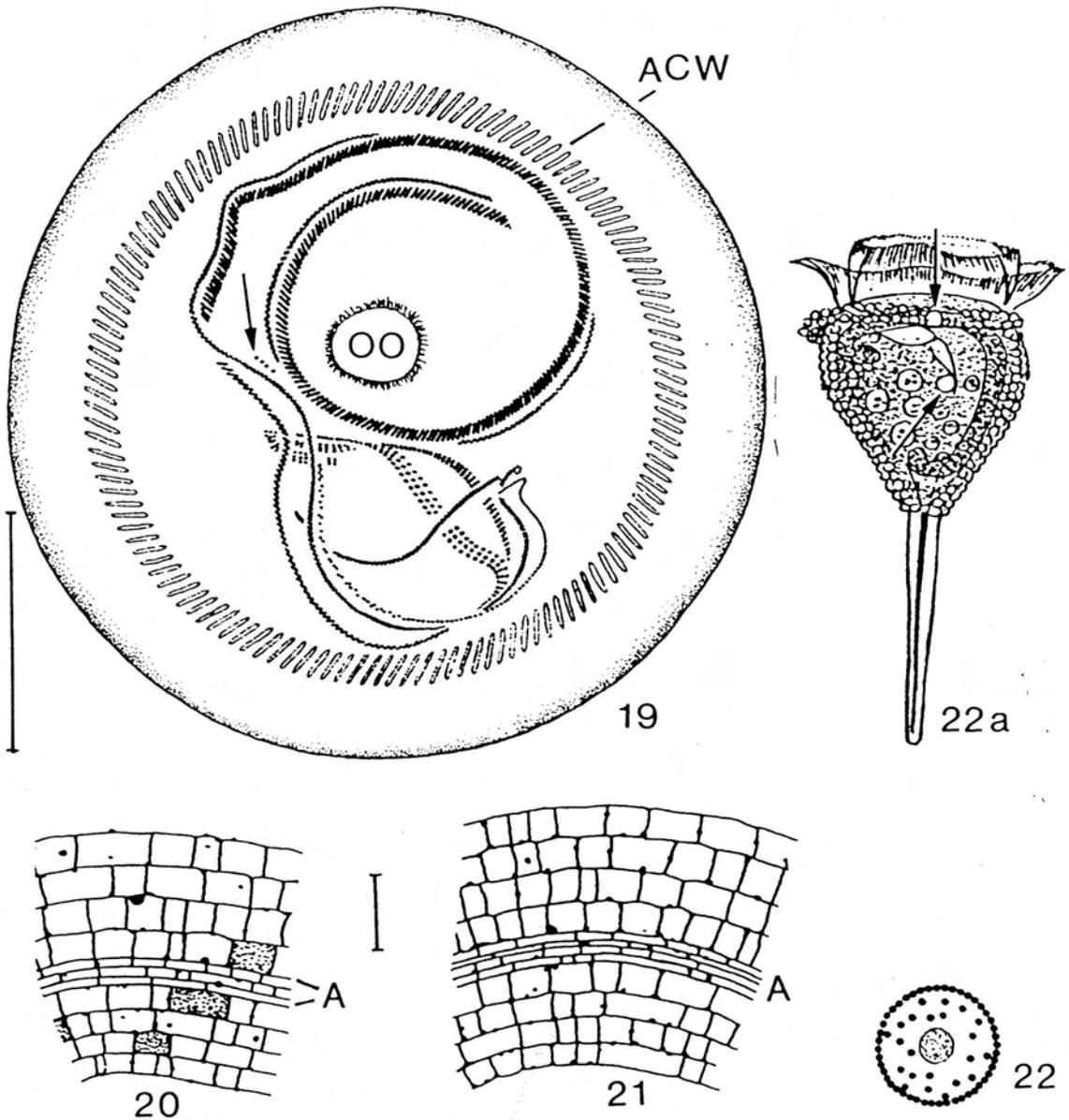
Pellicle with conspicuous tubercles, especially in anterior body half and on peristomial collar often studded with large blisters; lacking on peristomial disc; distinctiveness of tubercles varies in different specimens, but always recognizable at a magnification of $\geq X 400$, at least in anterior body half (Figs. 38, 41, 42). Tubercles usually much more irregular than underlying pellicular alveoli as evident from peeled specimens and silverline system (Figs. 36, 37, 43); contain granules and substance, both invisible in live specimens, staining with silver nitrate and protargol (Figs. 34–37). Silverline meshes square to slightly hexagonal, frequently elongate in transverse axis of cell, especially underneath aboral ciliary wreath; distance of mesh rows rather constant between anterior end of cell and aboral ciliary wreath, gradually decreasing from ciliary wreath to scopula, as also evident from almost equal number of mesh rows (Table 1, Figs. 35–37). Silverlines associated with few to many granules, possibly pellicular pores, but no pores recognizable in SEM micrographs.

Anlage of aboral ciliary wreath composed of closely spaced, oblique dikinetids in protargol slides (Fig. 13); much more complicated after silver nitrate impregnation (Figs. 20, 21, 35, 37), i. e. consisting of 2–3 very closely spaced mesh rows framed by narrow somatic ones; whole complex thus composed of 4–5 very closely spaced silverline mesh rows with tubercles recognizable also in SEM micrographs (Figs. 39, 40). Scopula margin formed by tightly spaced granules; centre faintly to heavily impregnated in swimmers (Fig. 22).

Oral apparatus conspicuous, peristomial collar slightly to distinctly projecting, of usual thickness, contains a thick myoneme distally and some thin myonemes proximally. Peristomial disc usually slightly convex, rarely flat, conspicuously protruding above peristomial collar in feeding specimens; not umbilicated. Vestibulum (infundibulum) in feeding cells almost transverse to main body axis and large as, e. g., in *Vorticella convallaria*. Oral infraciliature very much like in other vorticellids; thus the detailed illustrations (Figs. 3, 13–17, 29–32) and some remarks should suffice to orientate the reader. Cilia conspicuously long (Fig. 38), viz. about 20 μm , possibly due to the semiplanktonic mode of life, as supposed by STILLER (1940) in *P. anabaenae*. Haplokinety (undulating membrane) and polykinety (adoral ciliature) describe 1.5 turns (about 540°) at peristomial disc before plunging down into vestibulum and accomplishing a further turn. Haplokinety possibly not accompanied by impregnable structure, commences 0.8–3.2 μm (\bar{x} 2.4, n 9) behind polykinety (Fig. 14). Peniculus (adoral membranelle) 1 twisted in vestibular portion, composed of 3 kineties (ciliary rows) usually terminating at same level, rarely (inner) kinety next to peniculus 3 slightly longer. Peniculus 2 terminates distinctly above peniculus 1, its right kinety invariably slightly shortened anteriorly and posteriorly. Peniculus 3 about 5–8 μm long, posteriorly usually (80% of specimens) slightly projecting above peniculus 1, its inner kinety, next to peniculus 2, posteriorly shortened by about half of length and thus terminating at same level as peniculus 2; distance between inner and middle kinety slightly wider than between middle and outer kinety. Epistomial membrane, at least its 4–6 basal bodies, recognizable in both sessile specimens and swimmers, located at vestibular opening, i. e. far from distal end of adoral ciliary spiral (Figs. 15, 19).

Swimmers observed only in stained preparations, disc-shaped with scopula in centre of aboral pole. Infraciliature as in sessile specimens, except for aboral ciliary wreath whose anlage develop to small kineties bearing long cilia (Fig. 19).

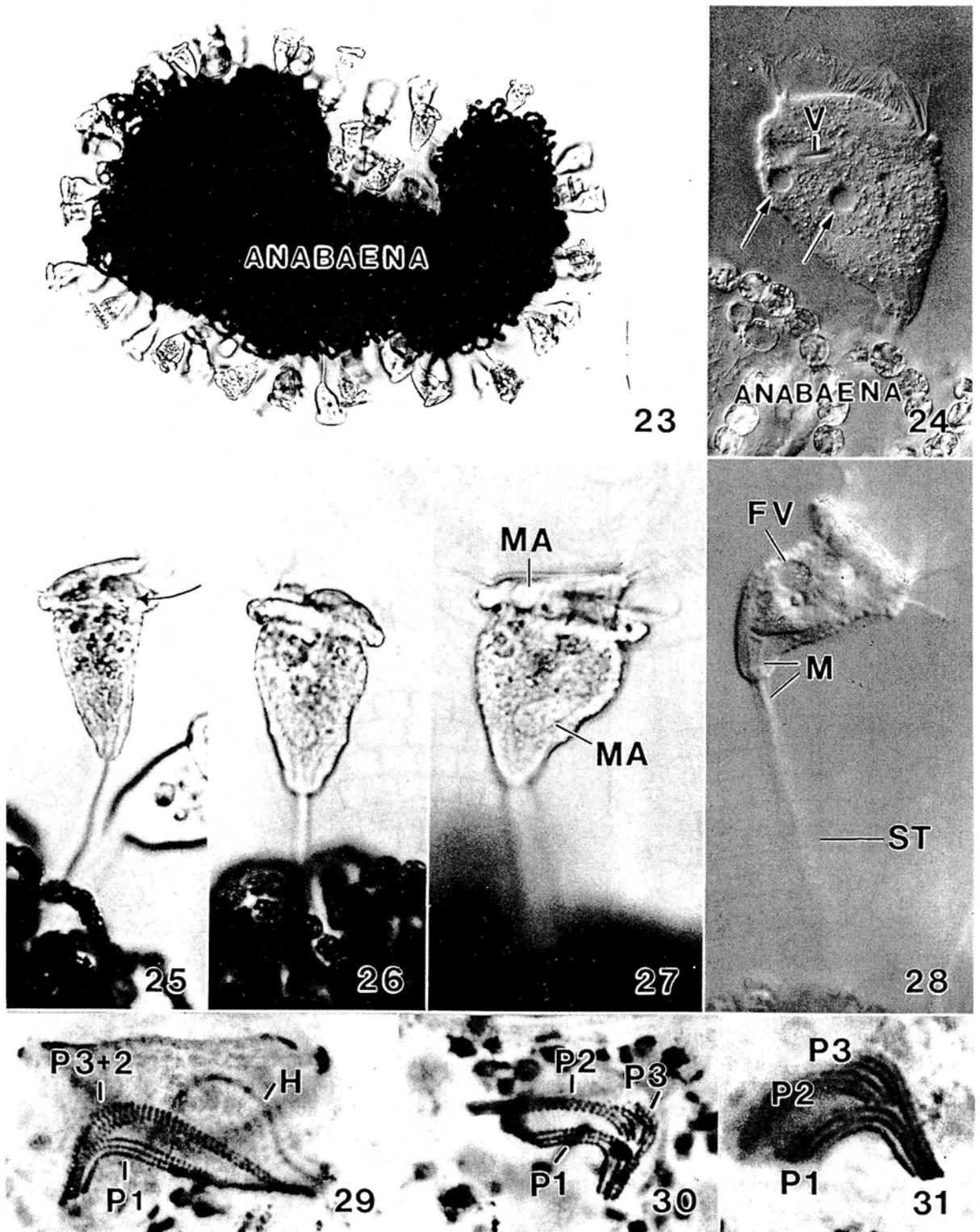
Occurrence and ecology: As yet only found at type location attached to planktonic coenobia of *Anabaena* sp., often in great numbers (Figs. 1, 23). Food vacuoles contained brownish algal remnants. See KERR (1983), PRATT and ROSEN (1983), and especially CANTER *et al.* (1992) for detailed ecological data on the same or a closely related species, *P. anabaenae* (see below).



Figures 19–22. *Pseudohaplocaulus infravacuolatus* after protargol (19, 22) and silver nitrate (20, 21) impregnation. – Fig. 19: Frontal view of swarmer with epistomial membrane (arrow) and fully developed aboral ciliary wreath (ACW). – Figs. 20, 21: In adult specimens, the anlage (A) of the aboral ciliary wreath is composed of 4–5 very narrowly spaced silverline mesh rows (cp. Fig. 35, 37, 39, 40). – Fig. 22: Scopula of specimen shown in Fig. 19. A: anlage of aboral ciliary wreath, ACW: fully developed aboral ciliary wreath, OO: contracted peristomial opening. Bars: 10 μ m (Fig. 19) and 5 μ m (Figs. 20, 21), respectively.

Fig. 22a. *Pseudohaplocaulus anabaenae* from life (from STILLER 1940). Arrows mark contractile vacuoles.

Comparison with related species: WARREN (1988) founded *Pseudohaplocaulus* with two species, namely *P. nicoleae* (PRECHT, 1935), type of the genus, and *P. anabaenae* (STILLER, 1940). *Pseudohaplocaulus nicoleae* is an epizoite of a marine polychaete, *Nicolea zostericola*, and has only a single, ventral contractile vacuole. Thus, it cannot be confused with *P. infravacuolatus*.



Figures 23–31. *Pseudohaplocaulus infravacuolatus* from life (23–28) and after protargol (29–31) impregnation. – Fig. 23: *Anabaena* coenobium heavily colonized by *P. infravacuolatus*. – Figs. 24–28: Shape variability and location of contractile vacuoles. The specimen shown in Fig. 24 has been slightly squeezed to reveal more clearly the specific location of the contractile vacuoles (arrows). Curved arrow denotes vestibular entrance. – Figs. 29–31. Oral ciliary pattern. FV: food vacuole, H: haplokinety, M: stalk myoneme, MA: macronucleus, P1–3: oral peniculi, ST: stalk, V: vestibulum.

At first glance, our species closely resembles *P. anabaenae* (STILLER, 1940) WARREN, 1988¹⁾, especially in having two contractile vacuoles and a similar size, shape, pellicular structure and habitat. However, the location of the contractile vacuoles is different: both are situated at the ventral wall of the vestibulum in *P. infravacuolatus* (Fig. 24), whereas one vacuole is located at the dorsal vestibular wall in *P. anabaenae*. This has been definitely illustrated (Fig. 22a) and described by STILLER (1940): "The animal has two contractile vacuoles; one at the dorsal pharyngeal wall at the level of the peristomial collar, the other deep in the body near the end of the pharynx". We consider this difference sufficient to separate our population from *P. anabaenae* because the number and location of the contractile vacuoles is a very constant character and is used by many authors to distinguish species in peritrich and other ciliates (FOISSNER 1975, KAHL 1935, NOLAND and FINLEY 1931). Furthermore, CANTER *et al.* (1992; Fig. 5) depict a peritrich from *Anabaena lemmermannii*, very likely a *Pseudohaplocaulus* (see below), which has the contractile vacuoles located exactly as described by STILLER (1940). In addition, CANTER's species apparently has a small vestibulum (see their Fig. 2) as mentioned by STILLER (1940) in *P. anabaenae*.

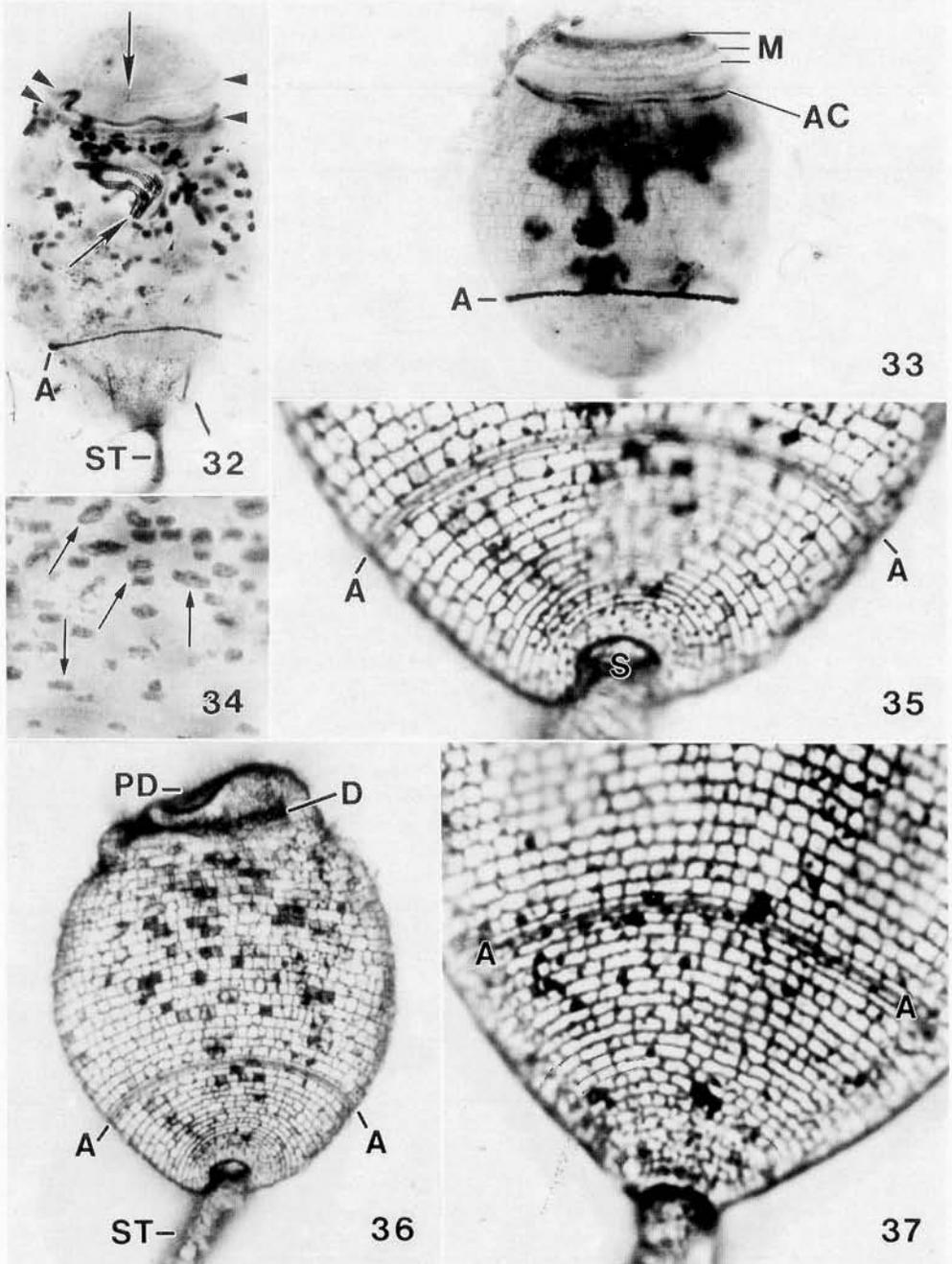
There are some other characters which differ in *P. infravacuolatus* (Fig. 3) and *P. anabaenae* (Fig. 22a), namely the size (length 47–67 vs. 40–45 μm), the vestibulum (unusually small in *P. anabaenae*), the equidistant stalk (gradually narrowed in *P. anabaenae*), and the pellicular structure (tubercles of same size and distinctiveness throughout in *P. anabaenae*). These characters are not as crucial as the contractile vacuoles but should not be neglected because STILLER's description is rather detailed and based on abundant material found in Lake Plön, Germany.

Pseudohaplocaulus infravacuolatus cannot be reliably distinguished from *Pseudovorticella chlamydophora* and *P. monilata* using the number of silverline mesh rows as diagnostic character (Table 2). Both of course differ by the stalk, which contracts helically, from *Pseudohaplocaulus*, whose stalk contracts in zigzag. *Pseudovorticella chlamydophora* differs from *P. infravacuolatus* also by its single contractile vacuole. *Pseudovorticella monilata* is very similar in all characters, even in the number and location of the contractile vacuoles. All distinguishing characters of these three species are recognizable only in live specimens. Live observation is thus essential for their correct identification.

Comparison with literature data: There are several records and micrographs in the ecological literature showing peritrichs attached to planktonic cyanobacteria. Unfortunately, the morphological data contained in these papers are too incomplete for a definite a posteriori identification. However, all very likely belong either to *P. anabaenae* (STILLER, 1940) or *P. infravacuolatus*.

KERR (1983) depicted a *Vorticella* prevailing on planktonic colonies of *Nostoc* sp. (*Anabaena* sp. according to CANTER *et al.* 1992) in Balsam Lake, USA. Its habitat, size (length about 40–50 μm according to the figures), shape, and short, weakly coiled stalk (up to length of body according to figures) suggest that it belongs to *Pseudohaplocaulus*; possibly it was *P. anabaenae* because, with some imagination, one can recognize two contractile vacuoles in the position typical for this species in Figure 4 (the upper rightmost specimen) of KERR's paper.

¹⁾ RUTTNER (1937) mentioned a *Vorticella anabaenae* already in 1937 but did never describe it, as far as we know. Thus, it is a nomen nudum and does not preoccupy STILLER's species. Interestingly, he found it on planktonic *Anabaena* in Lake Traunsee and Lake Wolfgangsee, both close to Lake Gränsee where we discovered *P. infravacuolatus*.



Figures 32–37. *Pseudohaplocaulus infravacuolatus* after protargol (32–34) and silver nitrate (35–37) impregnation. – Fig. 32: Oral and somatic infraciliature (ciliary pattern). Arrows mark distal and proximal end of adoral ciliary spiral; arrowheads denote turns of ciliary spiral. – Fig. 33: Rarely, a cortical lattice, which is very similar or even identical with the silverline system, impregnates with protargol. – Fig. 34: Many pellicular tubercles contain argyrophilic substance (arrows; see also Fig. 36). –

PRATT and ROSEN (1983) found a peritrich ciliate associated with *Anabaena flos-aquae* in Lake Douglas, USA. They identified it as *Vorticella monilata* (now *Pseudovorticella*, WARREN 1988) and provided two figures but, unfortunately, no description. *Pseudovorticella monilata* and *Pseudohaplocaulus infravacuolatus* are indeed similar in many characters (see above and Table 2) and thus PRATT and ROSEN's identification cannot be entirely refused. However, their Figure 1, which shows many contracted specimens, suggests that it was a *Pseudohaplocaulus* because the stalks are short and uncoiled, unlike in *Pseudovorticella monilata*, which usually has a long stalk distinctly coiled in contracted specimens (FOISSNER *et al.* 1992).

CANTER *et al.* (1990, 1992) provided a lot of beautiful micrographs from a peritrich attached in great numbers to planktonic colonies of *Anabaena lemmermannii* occurring in Lake Windermere, England. Like PRATT and ROSEN (1983), they identified it as *Pseudovorticella monilata*, with the help of B. J. Finlay. Again, we suggest that this was a *Pseudohaplocaulus*.

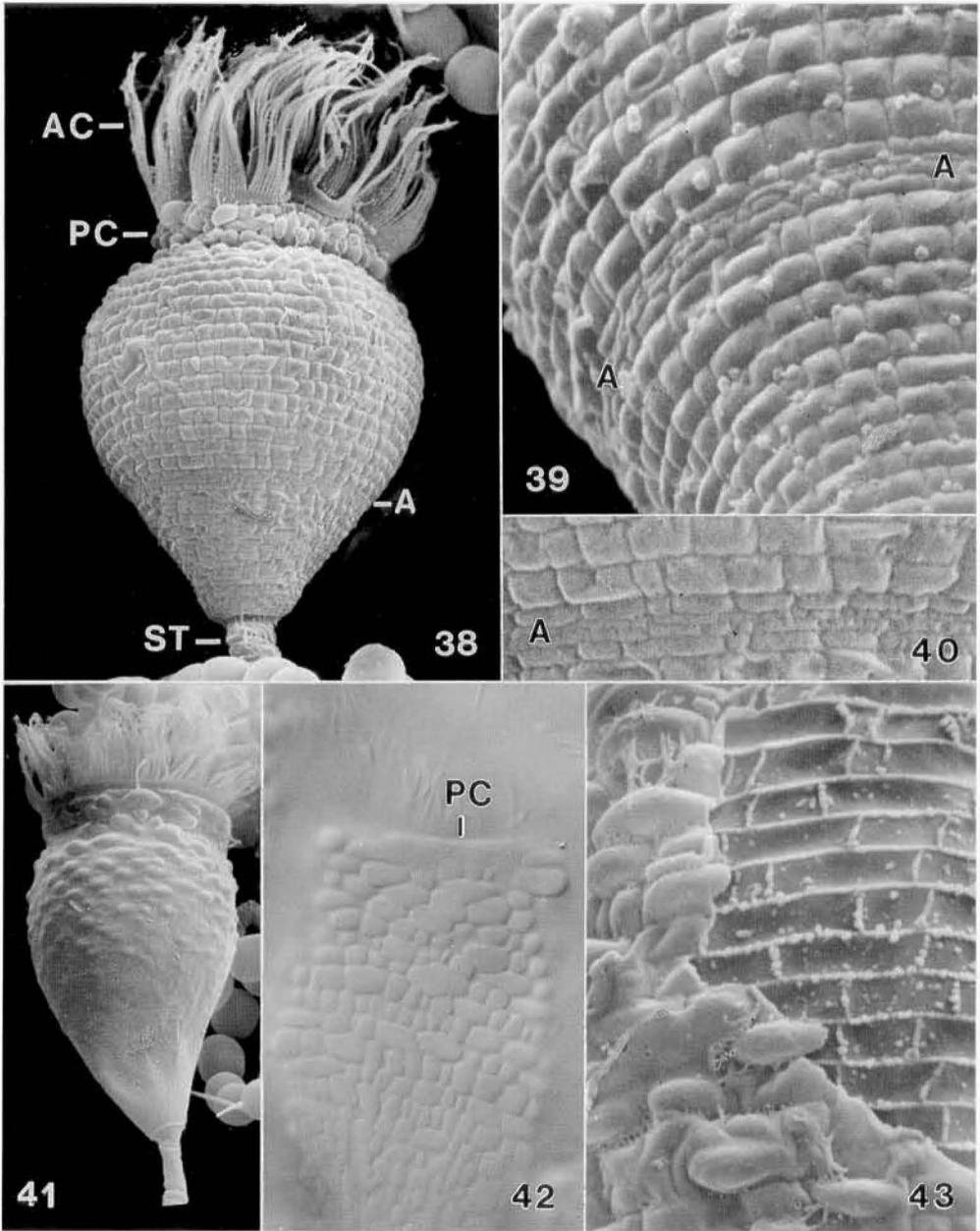
Table 2. Comparison of silverline (mesh row) numbers in *P. infravacuolatus* and several *Pseudovorticella* and *Epicarchesium* species. Data compiled from FOISSNER (1979), FOISSNER and SCHIFFMANN (1974, 1975, 1979), FOISSNER *et al.* (1992), LEITNER and FOISSNER (*Epicarchesium*, unpubl.), and SONG WEIBO and WILBERT (1989).

Species	Specimens investigated	Contractile vacuoles	Numbers				
			Silverlines from anterior end to aboral ciliary wreath		Silverlines from aboral ciliary wreath to scopula		Silverlines
			Extremes	Mean	Extremes	Mean	
<i>Pseudohaplocaulus infravacuolatus</i>	36	2	21–26	24	16–22	20	0.83
<i>Pseudovorticella chlamydophora</i>	6	1	17–20	18	14–17	16	0.94
<i>P. monilata</i>	56	2	15–23	19	9–18	14	0.74
<i>P. mutans</i>	3	1	24–28	26	16–19	17	0.65
<i>P. fasciculata</i> ¹	60	1	28–32	30	15–21	18	0.60
<i>P. difficilis</i>	20	1	25–31	28	14–18	16	0.57
<i>P. pseudocampanula</i>	5	1	28–33	30	16–18	17	0.57
<i>P. quadrata</i>	10	1	28–33	31	16–21	17	0.55
<i>P. sauwaldensis</i>	20	1	18–21	19	8–12	10	0.53
<i>P. sphagni</i>	22	2	25–30	27	8–10	9	0.33
<i>Epicarchesium granulatum</i>	30	2	53–61	57	27–34	31	0.54

¹) Formerly *P. margaritata f. chlorelligera* (see chapter 4).

(Continued Figures 32–37)

Figs. 35, 37: Silverline system in posterior body portion and details of anlage of aboral ciliary wreath (cp. Figs. 20, 21, 39, 40). – Fig. 36: Total view of silverline system showing that the number of silverlines is very similar between anterior end and aboral ciliary wreath, respectively, between aboral ciliary wreath and scopula (= stalk attachment site). A: anlage of aboral ciliary wreath, AC: adoral ciliary spiral, D: distal end of adoral ciliary spiral, M: myonemes in peristomial collar, PD: peristomial disc, S: scopula, ST: stalk.



Figures 38–43. *Pseudohaplocaulus infravacuolatus* from life (42) and in the scanning electron microscope (38–41, 43). – Figs. 38, 41, 42: Slightly contracted cells showing variability of pellicular ornamentation. – Figs. 39, 40: Posterior region showing anlage of aboral ciliary wreath. – Fig. 43: Peeled specimen showing that pellicular tubercles are more irregular than cortical pattern (cp. Figs. 36, 37, 42). A: anlage of aboral ciliary wreath, AC: adoral ciliary spiral, PC: peristomial collar, ST: stalk.

lus because of the short stalk which obviously contracted in zigzag and not spirally as in *Pseudovorticella* (see Fig. 5 in CANTER *et al.*, 1992; Fig. 10 shows a dead specimen with a helicoidally contracted stalk sheath, whereas the stalk myoneme is uncoiled indicating that this species cannot contract the stalk helicoidally). Furthermore, Figure 5 in CANTER *et al.* (1992) strongly suggests that it was *P. anabaenae* because the contractile vacuoles are exactly in the position described for this species (STILLER, 1940).

Vorticella chlorellata STILLER, 1940 (Figs. 44–53, Tables 1, 3)

Improved diagnosis: On average 55×40 µm, campanulate, green by symbiotic algae. Macronucleus J-shaped in main body axis. One contractile vacuole at ventral wall of vestibulum. On average 39 silverlines (pellicular striae) between anterior end and aboral ciliary wreath and 21 silverlines between aboral ciliary wreath and scopula. Epiplanktonic.

Neotype specimens: No type material of *V. chlorellata* has been mentioned in the literature. Thus, we have deposited two neotype slides with specimens from Salzburg, prepared as described, in the collection of microscope slides of the Oberösterreichische Landesmuseum in Linz (LI), Austria.

Redescription: Size *in vivo* 53×40 µm on average. Urceolate (Figs. 44, 50) to pyriform-campanulate (Fig. 49). Stalk up to 3 times as long as body, with inconspicuous granules, contracts distinctly helicoidally. Contracted specimens pyriform to ellipsoid; myoneme system very similar to that in other *convallaria*-type vorticellids (FOISSNER 1975), details, however, could be not recognized because it stained too faintly. Macronucleus in longitudinal axis of cell, J-shaped (n = 3); micronucleus not observed. One contractile vacuole at mid-ventral portion of vestibulum. Cells packed with symbiotic green algae and thus conspicuously green-coloured. Symbiotic algae globular, 5–6 µm across, with bowl-shaped chloroplast containing distinct pyrenoid, thus very likely belonging to genus *Chlorella*.

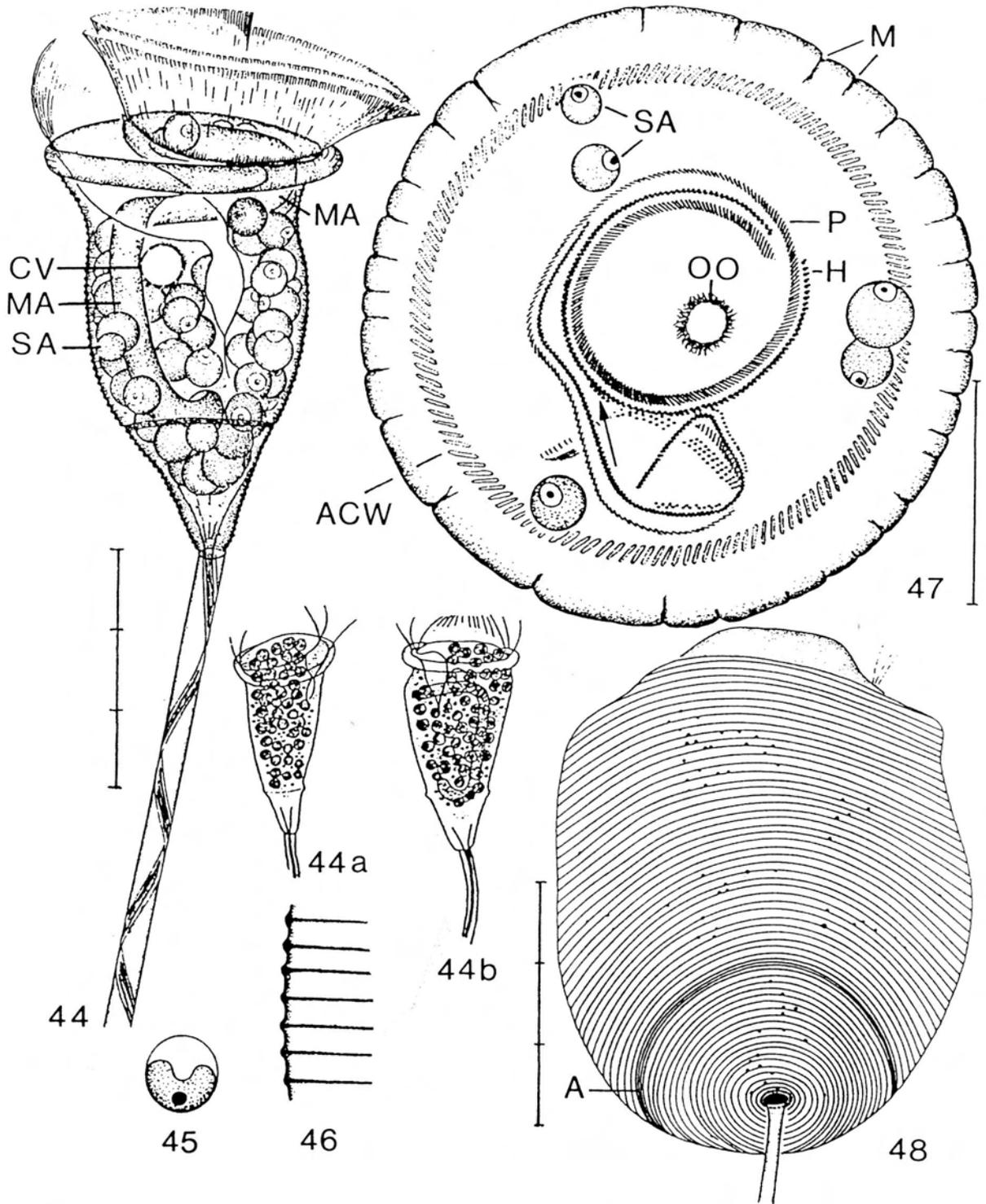
Pellicle and silverline system as in other members of genus, transverse striation distinct in living specimens (Fig. 53), pellicular pores present but not countable because preparations were too mediocre. Structure of inactive and active aboral ciliary wreath also as in other vorticellids. Scopula margin formed by rather widely spaced granules surrounding argyrophilic centre.

Oral apparatus of usual structure, peristomial collar distinctly projecting, in fully extended specimens spread brim-like (Fig. 50). Peristomial disc slightly convex. Vestibulum large,

Table 3. Comparison of silverline numbers in several common *Vorticella* species. Data, except for those of *V. chlorellata* and *V. chlorostigma*, from FOISSNER *et al.* (1992).

Sample size (n) > 30, except of *V. chlorellata* and *V. chlorostigma* (cp. Table 1).

Species	Numbers				
	Silverlines from anterior end to aboral ciliary wreath		Silverlines from aboral ciliary wreath to scopula		Silverlines Ratio
	Extremes	Mean	Extremes	Mean	
<i>V. chlorellata</i>	35–40	39	19–24	21	0.54
<i>V. picta</i>	35–46	40	22–27	25	0.62
<i>V. chlorostigma</i>	101–118	107	41–55	50	0.47
<i>V. campanula</i>	69–77	72	27–33	29	0.40
<i>V. octava-complex</i>	24–39	30	9–16	11	0.37
<i>V. convallaria-complex</i>	70–90	80	19–27	22	0.27
<i>V. infusionum-complex</i>	28–40	34	6–13	9	0.26
<i>V. microstoma-complex</i>	43–65	51	10–14	11	0.22



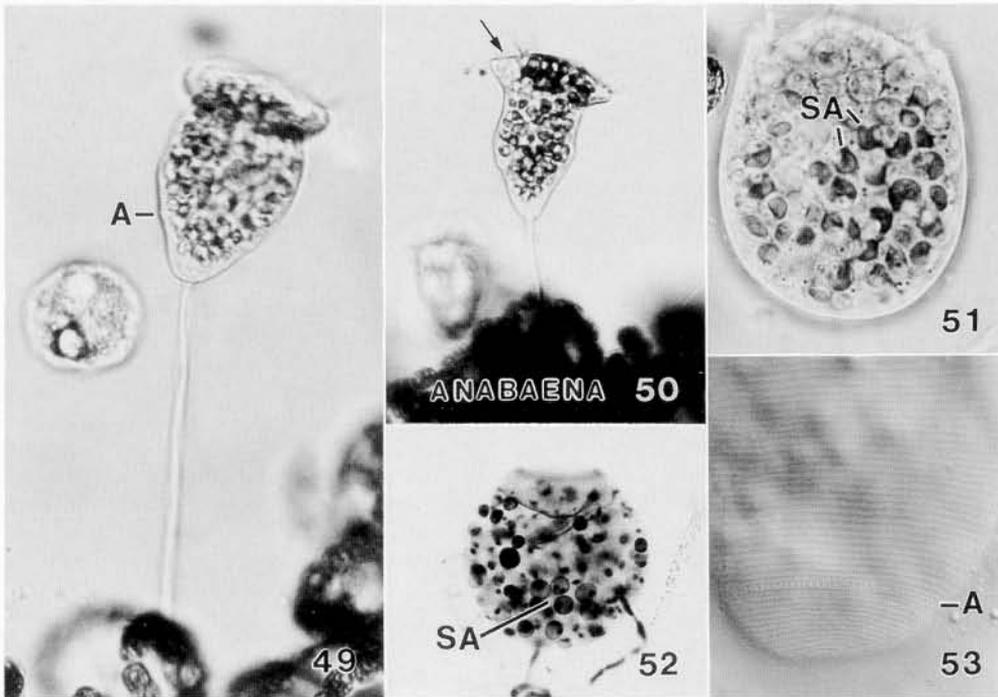
Figures 44–48. *Vorticella chlorellata* from life (44–46) and after protargol (47) and silver nitrate (48) impregnation. – Fig. 44: Typical specimen filled with symbiotic algae. Fig. 44a, b: *V. chlorellata* (from STILLER 1940), length 55–60 μm . – Fig. 45: Symbiotic algae, diameter about 5 μm . – Fig. 46: Cortical striation. – Fig. 47: Oral and somatic ciliary pattern of a swarmer, frontal view. Arrow marks epistomial membrane at vestibular entrance. – Fig. 48: Silverline system. A: anlage of aboral ciliary wreath, ACW: fully developed aboral ciliary wreath, CV: contractile vacuole, H: haplokinety (undulating membrane), M: body myonemes, MA: macronucleus, OO: contracted peristomial opening, P: polykinety (adoral zone of membranelles), SA: symbiotic algae (zoochlorellae). Bar division: 10 μm .

obliquely extending to body centre. Oral infraciliature (ciliary pattern; Fig. 47) quite similar to other members of genus, details, however, difficult to recognize due to heavily stained symbiotic algae. Haplokinety (undulating membrane) and polykinety (adoral ciliature) describe 1.5 turns (about 540°) at peristomial disc before plunging down into vestibulum and accomplishing a further turn. Epistomial membrane, at least its basal bodies, recognizable in both sessile specimens and swimmers, located at vestibular opening, i. e. far from distal end of adoral ciliary spiral (Fig. 47).

Swarmers observed only in stained preparations, disc-shaped with scopula in centre of aboral pole. Infraciliature as in sessile specimens, except for aboral ciliary wreath whose anlage develop to small kineties bearing long cilia (Fig. 47).

Occurrence and ecology: Attached to planktonic colonies of *Anabaena* sp. together with *P. infravacuolatus*, but much less numerous. Very likely occurring also on other planktonic algae (see "Identification and synonymy").

Identification and synonymy: Our population matched the original description of *V. chlorellata* quite nicely in habitat (on planktonic colonies of *Gloeotricha*), symbiotic algae, shape, and size (55–60 μm). The only significant difference concerns the location of the contractile vacuole, which STILLER (1940) illustrated (Fig. 44b) at the dorsal vestibular wall and described as follows: "The contractile vacuole is located at the level of the peristomial disc, rarely slightly underneath". However, STILLER (1940) mentioned that interior details were difficult to recognize due to the symbiotic algae; we can confirm this. Furthermore, STILLER illustrated the vestibulum plunging down vertically into the cell, which is unlikely for such a type of *Vorticella* usually having the vestibulum obliquely directed to the dorsal



Figures 49–53. *Vorticella chlorellata* from life (49–51, 53) and after protargol impregnation (52). – Figs. 49, 50: Typical specimens attached to *Anabaena* coenobia. Arrow marks vestibular entrance. – Figs. 51, 52: The cytoplasm contains many symbiotic algae. – Fig. 53: Cortical striation. A: anlage of aboral ciliary wreath, SA: symbiotic algae (zoochlorellae).

side (FOISSNER *et al.*, 1992). Thus, it is reasonable to assume that STILLER (1940) also misinterpreted the location of the contractile vacuole.

Vorticella chlorellata is distinctly different from *V. chlorostigma* (EHRENBERG, 1831), described below, in size, macronucleus, and silverline number. Thus, we refuse synonymization as suggested by WARREN (1986).

PRATT and ROSEN (1983) found a green *Vorticella* attached to planktonic *Anabaena*, *Microcystis*, and *Tabellaria*. They identified it as *Pseudovorticella margaritata* f. *chlorelligera* (now *P. fasciculata*, see below). Unfortunately, they did not provide any morphological details, and thus their determination cannot be confirmed or rejected. However, the habitats suggest that it was *V. chlorellata*.

Vorticella chlorellata is easily confused with *Vorticella fasciculata* MÜLLER, 1773, which is very similar in size, shape, location of contractile vacuole, and colour, i. e. bears symbiotic green algae, too. However, *V. fasciculata* has a reticulate silverline system and thus belongs to *Pseudovorticella* (see below and FOISSNER and SCHIFFMANN, 1975, WARREN, 1987). As concerns the number of silverlines, *V. chlorellata* is very close to *V. picta* (Table 3) which, however, lacks symbiotic algae and has two contractile vacuoles and very distinct stalk granules (FOISSNER *et al.*, 1992).

Vorticella chlorostigma (EHRENBERG, 1831) EHRENBERG, 1838 (Figs. 54–59, 62–68, Tables 1, 3)

Improved diagnosis: On average about 100×70 µm, conspicuously campanulate due to large, protruding peristomial collar, green by symbiotic algae. Macronucleus horseshoe-shaped near body centre. One contractile vacuole at dorsal wall of vestibulum. On average 107 silverlines (pellicular striae) between anterior end and aboral ciliary wreath and 50 silverlines between aboral ciliary wreath and scopula.

Neotype specimens: No type material of *V. chlorostigma* has been mentioned in the literature. Thus, we have deposited four neotype slides with silver nitrate prepared (dry method) specimens in the collection of microscope slides of the Oberösterreichische Landesmuseum in Linz (LI), Austria.

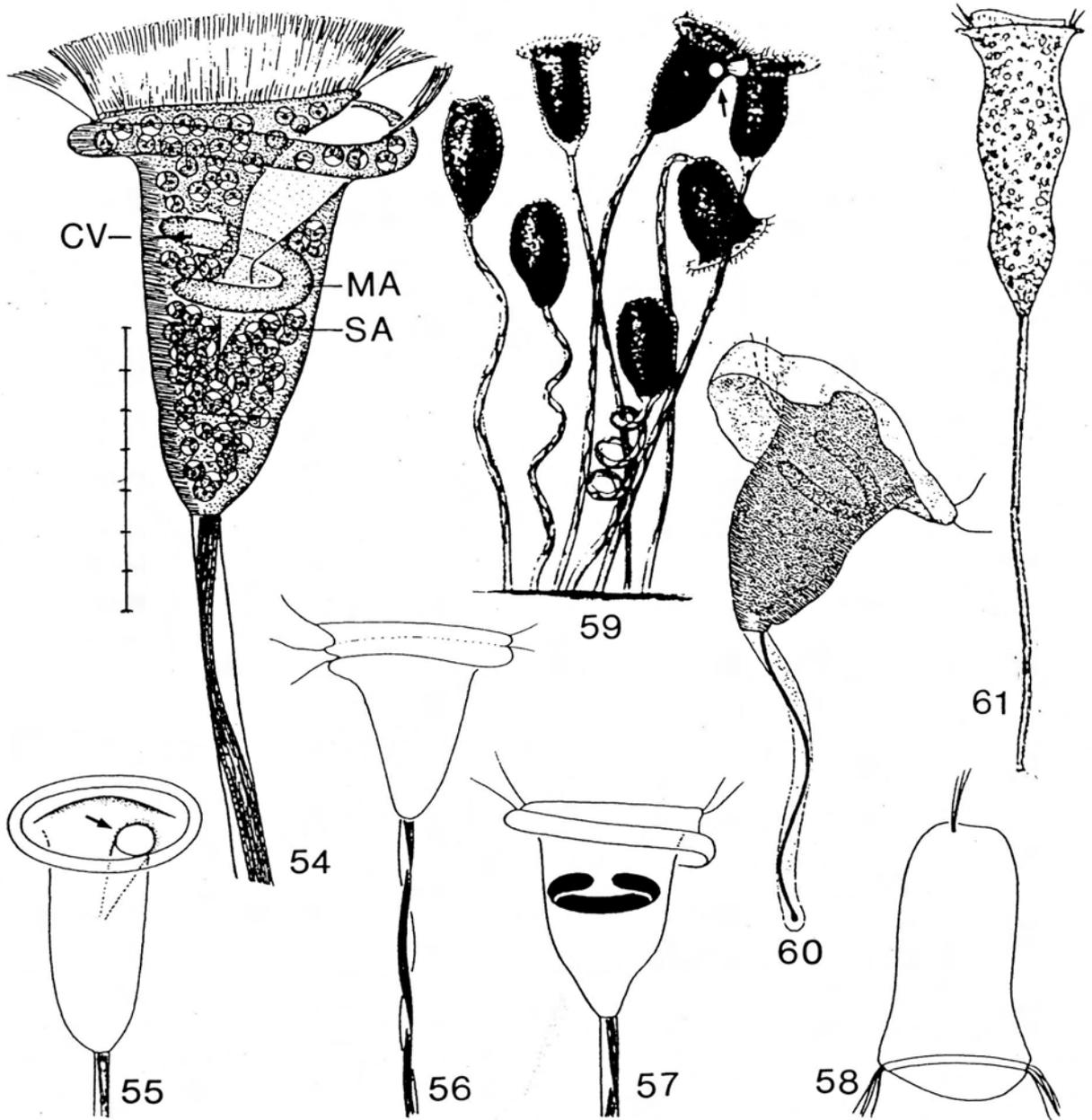
Redescription: The observations on this species are not as detailed as they should be because they were made 20 years ago when the senior author was still a beginner. However, the main characteristics were well documented and are thus described, so much the more as they prove the species status of *V. chlorellata* STILLER, described above.

Length *in vivo* about 85–110 µm. Distinctly campanulate due to widely protruding peristomial collar; body proper, however, calciform to almost cylindrical (Figs. 54, 56, 57, 64). Stalk up to 500 µm long, with distinct granules (Figs. 67), contracts helicoidally. Contracted specimens pyriform, usually with bulged anterior region due to withdrawn peristomial collar. Macronucleus in transverse axis of cell, almost circular ("horseshoe-shaped"; controled in hematoxilin stained silver nitrate slides). One contractile vacuole at dorsal wall near proximal end of vestibulum. Cells packed with symbiotic algae about 5 µm in diameter, with bowl-shaped chloroplast containing distinct pyrenoid, thus very likely belonging to genus *Chlorella*.

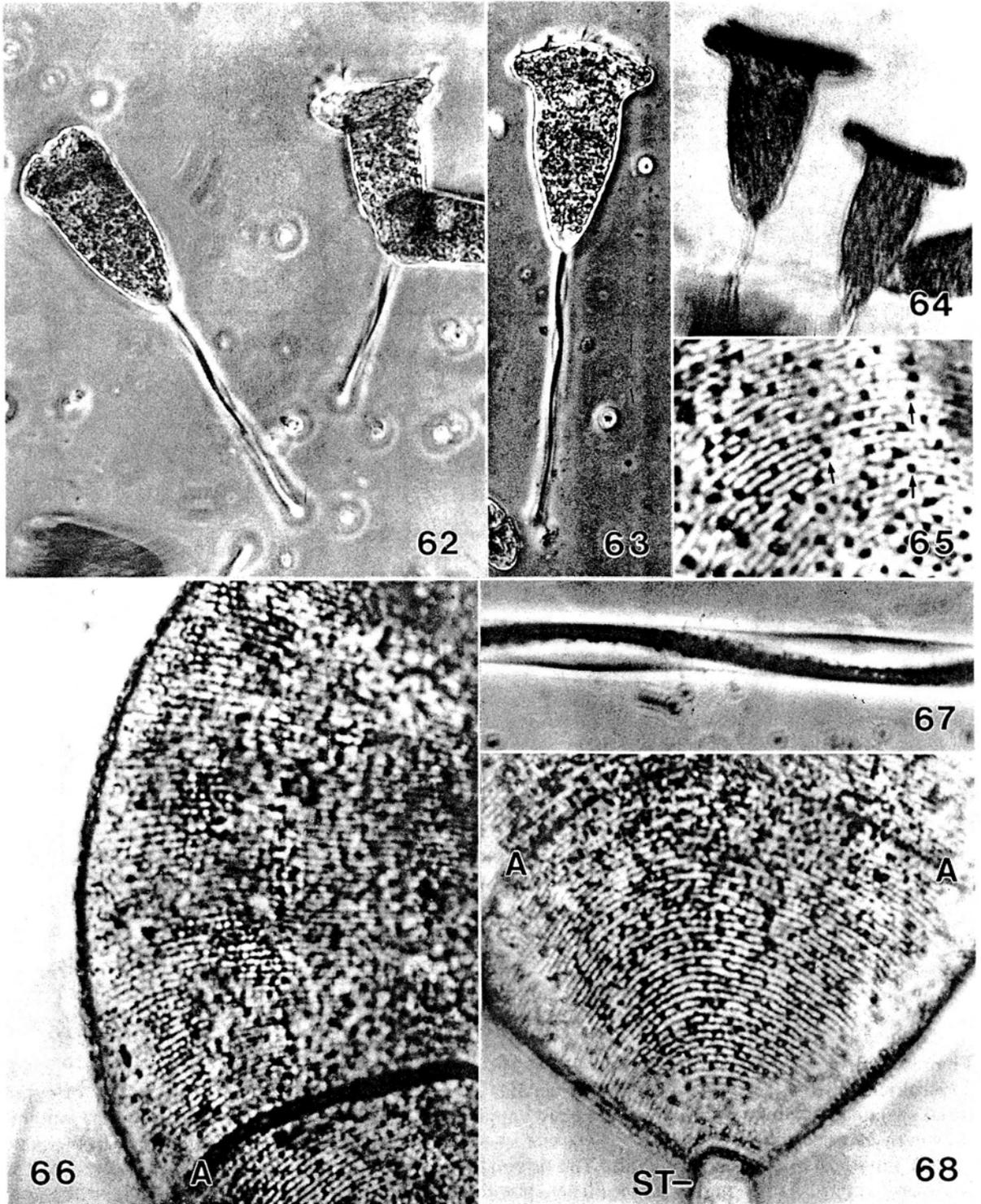
Pellicle and silverline system as in other members of genus, transverse striation, however, extremely narrow and thus hardly recognizable in live specimens; 20–41 (\bar{x} 30, n. 6) distinct pellicular pores per 10 µm² (Fig. 65). Structure of inactive and active aboral ciliary wreath also as in other vorticellids. Scopula margin formed by rather widely spaced granules surrounding argyrophilic centre.

Oral apparatus of usual structure, peristomial collar, however, very flexible and distinctly projecting, in fully extended specimens brim-like and frequently slightly curved backwards. Peristomial disc flat, slightly convex or slightly concave. Vestibulum large, obliquely extending to body centre. Oral infraciliature not studied.

Swarmers slightly conical and asymmetrical, with broadly rounded aboral end and scopula in centre of aboral pole (Fig. 58).



Figures 54–61. *Vorticella chlorostigma* (54–59) and related species (60, 61) from life. – Fig. 54: Typical specimen filled with symbiotic algae. Bar division 10 μm . – Fig. 55: Oblique view of cylindrical specimen. The vestibular opening (arrow) appears as bright blister. – Figs. 56, 57: Shape variants drawn from micrographs. – Fig. 58: Swarmer. – Fig. 59: *Vorticella chlorostigma* from EHRENBERG (1838), length of zooids about 100 μm . The original figure is green coloured and thus appears black in the reproduction. Arrow marks bright blister, possibly the vestibular opening (cp. Fig. 55) or the contractile vacuole. – Fig. 60: *Vorticella marginata* (from STILLER 1931), length of zooids 70–90 μm . – Fig. 61: *Vorticella sinuata* (from ZACHARIAS 1903), length of zooids 125 μm . CV: contractile vacuole, MA: macronucleus, SA: symbiotic algae (zoochlorellae).



Figures 62–68. *Vorticella chlorostigma* from life (62–64, 67) and after silver nitrate (65, 66, 68) impregnation. – Fig. 62: Contracted and extended specimen. – Fig. 63: Extended, slightly squeezed specimen. – Fig. 64: Two fully extended, swirling specimens. Cells appear blackish in bright field due to symbiotic algae. – Fig. 65: Silverline system at high magnification. Note distinct pellicular pores (arrows). – Fig. 66: More than 100 silverlines extend between anterior body end and aboral ciliary wreath (A). – Fig. 67: The stalk myoneme is distinctly granulated. – Fig. 68: About 50 silverlines extend between anlage (A) of aboral ciliary wreath and stalk (ST).

Occurrence and ecology: Forms conspicuous, green lawns on a variety of solid substrates like roots of water plants and blades of grass. Occurs in small meadow ponds (EHRENBERG 1838), but also in peat-bogs (own observation) and in lakes (GRAHAM and GRAHAM 1980).

Identification and synonymy: Our population matched the original description, which is, understandably, rather incomplete (*V. corpore ovato-conico, campanulato, annulato, ovario viridi, frontis margine exserto*), in most main characters, *viz.* size (about 70–100 μm according to EHRENBERG 1831, 1838), shape, symbiotic algae, and habitat (attached to a variety of solid substrates like roots of water plants and blades of grass). One of the specimens illustrated by EHRENBERG (1838) shows a bright blister at the margin of the cell (Fig. 59), indicating that the contractile vacuole is at the ventral wall of the vestibulum, which would be different to our specimens (Fig. 54). Alternatively, this blister can be interpreted as the vestibular opening, which appears, if specimens are observed in an oblique angle, as a roundish, bright spot (Fig. 55). In the absence of any other controversial data, it seems reasonable to identify our population as *V. chlorostigma* (EHRENBERG, 1831).

GRAHAM and GRAHAM (1980) provided some beautiful micrographs from a zoochlorellae-bearing *Vorticella* attached to small pieces of debris in Lake Wingra, USA. The specimens shown look very similar to those we investigated and have the same size, *viz.* 75–108 \times 58–85 μm (\bar{x} 93 \times 68, n 10). Thus, these populations are very likely conspecific. Unfortunately, GRAHAM and GRAHAM (1980) did not provide any details as to the nucleus, contractile vacuole, and number of pellicular striae.

At first glance, *V. chlorostigma* highly resembles *V. chlorellata* STILLER, 1940, described above. However, size, nucleus, and especially the number of silverlines are totally different (Table 1). Thus, both are distinct species. Certainly, *V. chlorostigma* is also easily confused with the green *V. fasciculata* MÜLLER, 1773 (see below) which, however, has a reticulate silverline system and thus belongs to the genus *Pseudovorticella* (FOISSNER and SCHIFFMANN 1974; WARREN 1987). *Vorticella sinuata* ZACHARIAS, 1903 also resembles *V. chlorostigma* in size (125 \times 60 μm), habitat (*Utricularia* pond), symbiotic green algae, and macronucleus shape. However, *V. sinuata* has a different, highly characteristic shape (Fig. 61) and is thus very likely another distinct, green species.

Vorticella chlorostigma is unusual not only by the symbiotic green algae but also by the horseshoe-shaped macronucleus. Usually, *Vorticellas* of this size and shape have a long, J-shaped nucleus (FOISSNER *et al.* 1992, WARREN 1986). However, *V. marginata* STILLER, 1931, which highly resembles *V. chlorostigma* in size, shape and extremely fine pellicular striation, has the same type of macronucleus (Fig. 60); and *V. sinuata*, mentioned above, very likely has a horseshoe-shaped macronucleus too. Obviously, these species form a particular group within the genus, as also indicated by the high number of silverlines, which distinguishes *V. chlorostigma* from all other species investigated so far (Table 3).

4. Taxonomic Innovations

Genus Pseudohaplocaulus

WARREN (1988) established the genus *Pseudohaplocaulus* “for *Haplocaulus*-like peritrichs which possess rows of regularly aligned pellicular tubercles and, therefore, reticulate silverline systems”. However, WARREN (1988) did not prove whether the species he assigned to the new genus actually have a reticulate silverline system. Our study shows that this is the case, and thus we recognize *Pseudohaplocaulus* as a distinct genus. *Pseudohaplocaulus* and *Haplocaulus* very likely differ only in this character like, e. g., *Vorticella* and *Pseudovorticella*. The evolutionary significance of this peculiarity is still not known. In spite of this, a

generic distinction appears warranted because it structures the "difficult" peritrichs more clearly.

Haplocaulus rhabdostyloides (KELLICOTT, 1885) *nov. comb.*
(*basionym*: *Vorticella rhabdostyloides* KELLICOTT, 1885)

This species was synonymized with *Vorticella striata* var. *octava* by NOLAND and FINLEY (1931), possibly because KELLICOTT (1885) did not provide a figure. Thus, WARREN (1986) excluded it from his annotated list of nominal species. However, a careful examination of KELLICOTT's rather detailed description revealed that *V. rhabdostyloides* is very likely a distinct species with characters, however, perfectly matching those of *Haplocaulus*. Because KELLICOTT's paper is difficult to obtain, we provide his description: "Body nearly globular, cuticular surface smooth, peristome border thickened, narrow, cilia relatively stout, endoplast thick, short and but slightly curved. When contracted the body becomes more nearly globular or even depressed until it is napiform. The pedicle is filiform, length about equaling that of the body; length of body 1/900 to 1/800 of an inch.

This vorticellid is plentiful during the winter months attached singly to floating diatoms in Niagara-water. It appears to prefer *Stephanodiscus niagarae*, which support, if it may be so called, it tows about by the activity of its cilia. I have called it *Rhabdostyloides*, from the fact that the shorter-stalked examples are so reluctant to contract their pedicles; sharp blows upon the cover glass do not always induce this movement; it then has much the appearance of a species of *Rhabdostyla*. The pedicle when contracted is thrown more or less into a zigzag than into a coil, as is usual with members of the genus.

The animal is not unlike *R. ovum*, but is more nearly spherical and very different when contracted with the contractile vesicle more nearly in the center of the body. The peristome-border and pedicle separate it with sufficient sharpness from the only spherical form which it approaches in size."

Of the *Haplocaulus* species recognized by WARREN (1988), *H. kahlii* (STILLER) and especially *H. epizoicus* (ŠRÁMEK-HUŠEK), a species attached to *Megacyclops viridis* and *Gammarus pulex*, resemble KELLICOTT's species. However, synonymization would be premature in the absence of detailed data for all species mentioned and the different hosts.

Pseudovorticella fasciculata (MÜLLER, 1773) *nov. comb.*

1773 *Vorticella fasciculata* MÜLLER, Vermium Terrestrium et Fluviatilium: 121 (without figures).

1786 *Vorticella fasciculata* MÜLLER, 1773 – MÜLLER, Animalcula Infusoria: 320 (with figures).

1881 *Vorticella fasciculata*, MÜLL. – KENT, Manual infusoria II: 681.

1885 *Vorticella smaragdina* STOKES, Am. Nat., 19: 21.

1935 *Vorticella margaritata f. chlorelligera* KAHL, Tierwelt Dtl., 30: 730.

1975 *Pseudovorticella margaritata f. chlorelligera* (KAHL, 1930–35) – FOISSNER and SCHIFFMANN, Protistologica, 11: 420.

1976 *Pseudovorticella chlorelligera* (KAHL) *comb. n.* – JANKOWSKI, Mat. II All-Union Cong. Protozool., 1: 169.

1987 *Pseudovorticella chlorelligera* (KAHL, 1935) JANKOWSKI, 1976 – WARREN, Bull. Br. Mus. nat. Hist., 52: 2.

WARREN (1986) suggested *V. fasciculata* MÜLLER, 1773 as *nomen dubium* and recognized *V. margaritata f. chlorelligera* KAHL, 1935 as valid species (WARREN, 1987). In our opinion this is not justified, because MÜLLER's description is rather detailed and KAHL (1935), when founding *V. margaritata f. chlorelligera*, definitely stated: "very likely identical with *V. fasciculata* O. F. MÜLLER, but hardly with the more slender *V. chlorostigma*

EHRENBERG." It is thus difficult to understand why KAHL established the new *forma* at all. Anyhow, his procedure should be not credited.

Vorticella smaragdina STOKES, 1885, rather superficially described and thus classified as *nomen dubium* by WARREN (1986), is very likely another synonym of *V. fasciculata*. This is not only indicated by distinct similarities in size and shape but also by the symbiotic green algae and the irregular distribution of cortical granules mentioned by STOKES. Such a granulation typically occurs in *Pseudovorticella* species, e. g. *P. monilata* (FOISSNER *et al.*, 1992).

5. Summary

Pseudohaplocaulus infravacuolatus nov. spec. and *Vorticella chlorellata* STILLER, 1940, two stalked peritrich ciliates, were discovered in Lake Grabensee (Salzburg, Austria) attached to planktonic coenobia of a cyanobacterium, *Anabaena* sp. *Vorticella chlorostigma* (EHRENBERG, 1831) EHRENBERG, 1838 occurred in a peat-bog in Upper Austria, attached to blades of grass. The morphology and infraciliature of these three species were studied in live cells, with the scanning electron microscope, and in specimens impregnated with protargol and silver nitrate. The genus *Pseudohaplocaulus* is confirmed. It has a tuberculate pellicle and, as supposed by WARREN (1988), a reticulate silverline system. *Pseudohaplocaulus infravacuolatus* is a campanulate species with an average size of 60×40 µm. It has a J-shaped macronucleus, two contractile vacuoles at the ventral wall of the vestibulum, and an average of 24 silverlines (mesh rows) between the anterior end and the aboral ciliary wreath and 20 silverlines between the ciliary wreath and the stalk (scopula). The new species is distinguished from its nearest relative, *P. anabaenae* (STILLER, 1940), mainly by the location of the anterior contractile vacuole. The number of silverline mesh rows is close to those of *Pseudovorticella monilata* and *P. chlamydophora*. *Vorticella chlorellata* and *V. chlorostigma* are redescribed. *Vorticella chlorellata* has symbiotic green algae, a J-shaped macronucleus, a single contractile vacuole at the ventral wall of the vestibulum, and a striated silverline system consisting, similar as in *V. picta*, of an average of 39 silverlines between the anterior end and the aboral ciliary wreath and 20 silverlines between the ciliary wreath and the scopula. *Vorticella chlorostigma* has symbiotic green algae too, but an horseshoe-shaped macronucleus, a single contractile vacuole at the dorsal wall of the vestibulum, and an average of 107 silverlines between the anterior end and the aboral ciliary wreath and 50 silverlines between the ciliary wreath and the scopula. An attempt is made to assign to these species some insufficiently determined or misidentified peritrichs from the ecological literature. *Vorticella rhabdostyloides* KELLICOTT, 1885 is recognized as a distinct species, but transferred to *Haplocaulus*: *H. rhabdostyloides* (KELLICOTT, 1885) nov. comb. Likewise, *Vorticella fasciculata* MÜLLER, 1773 is considered as a distinct species and transferred to *Pseudovorticella*: *P. fasciculata* (MÜLLER, 1773) nov. comb. *Vorticella smaragdina* STOKES, 1885 and *V. margaritata* f. *chlorelligera* KAHL, 1935 are very likely junior synonyms of *P. fasciculata* (MÜLLER, 1773).

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