Arch. Protistenkd. **138** (1990): 29–49
VEB Gustav Fischer Verlag Jena

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Natural and Cultured Variability of *Engelmanniella mobilis* (Ciliophora, Hypotrichida); with Notes on the Ultrastructure of its Resting Cyst

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With 27 Figures

Key words: *Engelmanniella mobilis;* Ciliophora, Hypotrichida; Morphometry; Morphogenesis; Cysts; Ultrastructure

Summary

The variability of 2 Austrian populations (Gn, Bn), one Turkish (Tn), and one Japanese population (Jn) of the hypotrich ciliate *Engelmanniella mobilis* (Engelmann, 1862) Foissner, 1982 is compared by morphological and morphogenetic analyses. These populations were isolated from soils and represent 2 groups (Gn, Bn, Tn; Jn) concerning some quantitative characters of the infraciliature, the morphology of the resting cyst, and some nuclear features during division. However, in cultures maintained for 3 months the variability of the Turkish population (Tc) increased markedly closing this gap. This demonstrates that morphological differences originating during cultivation might be greater than those observed in natural populations. The variability of our populations embraces *E. halseyi* (Calkins, 1929) and *E. mobilis americanus* (Kahl, 1932), which thus fall as junior synonyms of *E. mobilis*. During division and physiological reorganization the cortical events are identical in all populations, while the micronuclear processes may be slightly modified. Divisional and reorganizational morphogenesis differ in the origin of the frontal anlagen. The characterization of *Engelmanniella* Foissner, 1982 is improved.

Young resting cysts of Bn, Tn, and Tc are characterized by a mucus layer originating from the extruded subpellicular granules. This layer is absent in older cysts and in the resting cyst of the Japanese population, although the subpellicular granules are released too. Oxytrichid (4-layered cyst wall, fused macronuclear segments) and urostylid (cortical microtubules) characters are mixed up in the resting cyst of *E. mobilis, Kahliella simplex,* and *Paraurostyla weissei* suggesting that the proposed classification of hypotrich resting cysts is premature.

Introduction

At the beginning of the century, *Uroleptus mobilis* (basionym of *Engelmanniella mobilis*) has been designated as "the most satisfactory organism for experimental work" by Calkins (1919a). Subsequently numerous papers on basic biological subjects have been published (Calkins 1919b, 1920a, b, 1921, 1925; Austin 1927; Gregory 1925, 1926, 1928; Delamater 1936; Tittler 1938). Unfortunately, the "simple morphology" of *E. mobilis* (Engelmann, 1862) remained largely unknown, until Foissner (1982) gave a detailed lightmicroscopical and morphometric description. Recently, the divisional morphogenesis and the ultrastructure have been described in detail (Wirnsberger-Aescht et al. 1989).

In the present paper, we focus on the problem of natural and cultured variability of different populations of *E. mobilis*. In addition, the light and electron microscopical morphology of the resting cyst has been studied, since data on resting cyst morphology in the "primitive" hypotrichs are scarce (Foissner & Foissner 1987).

Material and Methods

FOISSNER (1982) collected *Engelmanniella mobilis* from the top soil (0−10 cm) of a wet fertile plain grown with willow-trees near Grafenwörth (Lower Austria) in 1980. From this paper we took the morphometric data for our comparison and refer to it as Austrian population (Gn). No cultures of this population were established. A second population was found in 1981 in a beach forest (0−2 cm; *Fagus, Pinus, Betula, Quercus*) near Baumgarten (Lower Austria), thus it is named Austrian population (Bn). This population was cultured for about 3 years and has been used for the electron microscopy of interphasic cells (WIRNSBERGER-AESCHT et al. 1989) and cysts. A detailed description of the collection sites and the autecology of the Austrian populations is given by FOISSNER et al. (1985). The Japanese population (Jn) was isolated in February 1988 from the soil of a rice field near Kumamoto. The Turkish population (Tn) occurred in the rhizosphere of marsh plants in Anatolien in 1988. Living cells and cysts of the Japanese and Turkish population are still alive. Raw cultures of all populations originated from air-dried soil remoistened with distilled water for about 6 days.

These 4 populations were morphometrically characterized soon after their appearance in the remoistened soil samples. It is assumed that cells of these populations represent the "natural variability". Due to some striking variation observed in cultures, we investigated the Japanese and Turkish population (the Austrian ones were no more alive) after 3 months of culturing ("cultured variability"). Cells were maintained at room temperature in petri dishes containing salad medium and Eau de Volvic (1:1) and a few wheat grains to stimulate bacterial growth. Usually, medium was changed every 2 weeks. These "cultured" populations are referred to as Japanese (Jc) and Turkish (Tc) population, respectively. The Japanese population was completely encysted in July 1988 and was revitalized, when we got the Turkish population in August 1988. Consequently, the sum of generations (1−2 per d) is different. However, this is of minor interest, since the morphology of the "older" Japanese population is quite stable, in contrast of that of the "younger" Turkish population.

Protargol silver staining and morphometric methods are described in FOISSNER (1982) and BERGER et al. (1985). All countings and measurements were performed on normal fed individuals at a magnification of 1.000× with different instruments (1 unit = 1 µm and 1.4 µm, respectively). Drawings were made with a camera lucida. The terminology is according to KAHL (1932) and WIRNSBERGER-AESCHT et al. (1989). Cysts of Bn were processed for transmission electron microscopy as described in WIRNSBERGER-AESCHT et al. (1989).

Summary of designations and origins of the populations:

Bn = Austria, Baumgarten, natural population;
Gn = Austria, Grafenwörth, natural population;
Jc = Japan, cultured population;
Jn = Japan, natural population;
Tc = Turkey, cultured population;
Tn = Turkey, natural population.

Results

The in vivo aspect of the 4 investigated populations of *Engelmanniella mobilis* is almost identical, although their soil habitats are quite dissimilar (fertile plain, forest, rice field). Its morphology is characterized as follows: slender, cylindrical shape, posterior end more or less pointed and curved (Figs. 1, 2, 3, 5, 19); in vivo c. 120−300 × 18−30 µm; small oral area (Figs. 1, 19); particularly short endoral membrane in front of the paroral membrane (Figs. 3, 5); many rows of spherical (0.5−1 µm in diameter), colourless to yellowish subpellicular granules (Fig. 2); somatic cirri consist of 2 basal bodies on the lateral sides and the posterior third of the cell and 4−10 basal bodies in the anterior part (Figs. 3−6; comp. WIRNBERGER-AESCHT et al. 1989). The following data are arithmetic means of all impregnated cells measured from the raw cultures (4 populations; n = 68): 22 adoral membranelles; 3 frontal cirri; 1 buccal cirrus; 4 parabuccal cirri; 3 left marginal rows comprising 29, 9, 6 cirri; 3 right marginal rows consisting of 33, 12, 37 cirri; 1 long and 1 very short dorsal kinety; 8 macronuclear segments; 3 micronuclei.

Morphometric analyses

All populations constantly have a single buccal cirrus and 3 frontal cirri (Figs. 1, 3, 5). The number of dorsal kineties − usually showing a low variability (FOISSNER 1982) − varies from 1 to

3 in certain cases: In Gn rarely a third dorsal kinety occurs (comp. FOISSNER 1982 and Fig. 14e therein). The short dorsal kinety (3–6 pairs of basal bodies; Figs. 4, 6) is frequently reduced to a single pair or even lost in 2/3 of the cells in Jc. This was never observed in the Austrian and Turkish populations. Thus, these particular characters are excluded from Table 1 and all calculations. The length of the adoral zone of membranelles, the number of adoral membranelles, and the number of cirri in the last generation of marginal rows (comp. morphogenetic section) are rather stable characters, apart from Gn. Concerning the other morphological parameters, the coefficients of variation are usually higher in Gn, Tn, and Tc than in Bn, Jn, and Jc (Table 1).

Analyses of variance prove the variability to be greater among than within the populations originating from raw cultures. Therefore, we examined 12 of the most important characters by the multiple comparison of NEMENY (see BERGER et al. 1985). Gn, Bn, and Tn are very similar, while Jn separates at 80 % dissimilarity (Table 2, Fig. 17). The Japanese population is characterized by a greater body width, a larger adoral zone of membranelles, and more numerous cirri in the first left and right marginal row and the rightmost marginal row (Table 1). However, if we include the cells of Tc and Jc, the 2 Austrian populations and Tn became indistinguishable, whereas the Japanese populations and Tc are different from this group in 63 % of the selected characters (Table 2, Fig. 17). Moreover, the cultured Japanese and Turkish population are morphologically identical. Obviously Tc links the Gn-Bn-Tn morphotype with Jn-Jc. Remarkably, the extreme values of some features of the adoral zone of membranelles (length and number) and the number of cirri in the first right marginal row do not overlap in Tn and Tc coming from the same site (Table 1). The size of the cultured cells (Tc) is about 50 % as large as that from the raw material (Tn). A similar situation exists in the number of micronuclei. About 30 % of the Tn cells shows only a single micronucleus (Fig. 4), while Tc cells have about 4 micronuclei like the Japanese population (Fig. 6, Table 1).

Cell division

The morphogenetic pattern of the Turkish and the Japanese population is nearly identical to that described in the Austrian one (WIRNSBERGER-AESCHT et al. 1989). In the meantime, the composite origin of the frontal anlagen II and III – partly de novo, partly from the buccal cirrus and the posterior parabuccal cirri (comp. Bn in WIRNSBERGER-AESCHT et al. 1989) – could be proved in Tn, Tc, Jn, and Jc. This detail may be of significance in phylogenetic considerations.

Some slight modifications should be mentioned. The first one refers to the conservation of the grandparental generation of cirri. Grandparental cirri are constantly present on the left margins of Bn, Jn, and Jc, while they are absent in about 10 % of the individuals of Tn (Fig. 4), Tc, and Gn (Table 1; re-examination of FOISSNER's slides showed that he has frequently overlooked them). In addition to those on the left margin, grandparental cirri frequently occur on the right lateral area too in Jn (Fig. 5), Jc, Tn, and Tc, whereas they were never observed on the right margins of Gn and Bn (Tables 1, 2). Therefore, this strain-specific ability to retain marginal cirri results in a continuous sequence of morphotypes; i.e. 2–3 marginal rows on the left side and 3–4 rows on the right side.

The second modification concerns the nuclear cycle. A "single micronucleus stage" – characteristic for Bn (WIRNSBERGER-AESCHT et al. 1989) – was only observed in 2 % of 153 relevant stages analyzed in Jn. In addition, no "micronucleus-chain" enclosed in a single envelope (WIRNSBERGER-AESCHT et al. 1989) was found in 178 dividing Japanese specimens, but 37 % of 238 dividers contain 1–3 interphasic micronuclei, even in the latest stages of the morphogenesis they were found in 23 % of the Jn cells. This may indicate that, contrary to Bn, some of them might be transferred to the post-dividers of Jn. This would explain the higher number of micronuclei in the Jn and Jc (Table 1). With exception of the "chain" the Turkish population shows a nuclear cycle similar to Bn.

Table 1. Morphometric characterization of 4 natural and 2 cultured populations of *Engelmanniella mobilis*. All data are based on protargol impregnated specimens. All measurements in µm. Bn = natural Austrian population, Baumgarten; Gn = natural Austrian population, Grafenwörth; CV = coefficient of variation in %; Jc = cultured Japanese population; Jn = natural Japanese population; M = median; Max = maximum value; Min = minimum value; n = sample size; No. = number; SD = standard deviation; SE = standard error of the arithmetic mean; Tc = cultured Turkish population; Tn = natural Turkish population; $\bar{x}$ = arithmetic mean.

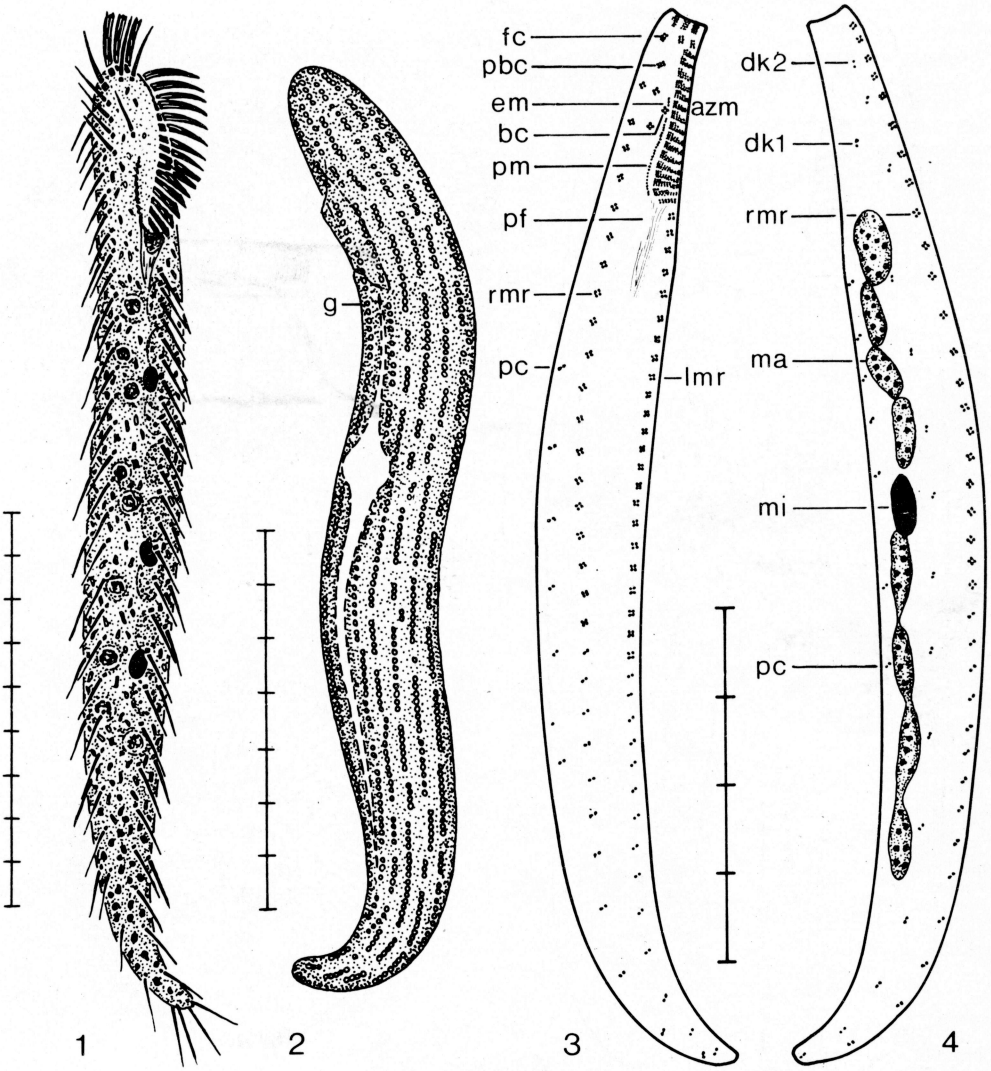
Character		$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	Gn	136.5	135	25.1	7.0	18.4	94	196	13
	Bn	121.2	120	10.3	2.1	8.5	96	143	25
	Tn	134.7	128	23.3	6.0	17.3	107	193	15
	Tc	221.7	229	32.4	8.4	14.6	177	283	15
	Jn	146.0	145	9.3	2.4	6.3	130	161	15
	Jc	187.3	190	16.6	4.3	8.8	153	218	15
Body, width	Gn	14.7	15	1.7	0.5	11.3	13	17	13
	Bn	17.1	17	2.1	0.4	12.2	13	21	25
	Tn	15.3	16	2.1	0.5	13.6	12	19	15
	Tc	21.0	20	4.2	1.1	20.0	16	31	15
	Jn	23.8	24	2.4	0.6	10.0	20	29	15
	Jc	17.9	17	2.7	0.7	14.8	14	22	15
Adoral zone of membranelles, length	Gn	22.1	23	3.7	1.0	16.6	14	26	13
	Bn	22.4	22	1.2	0.2	5.3	21	25	25
	Tn	25.2	25	2.1	0.6	8.5	22	29	15
	Tc	35.6	35	3.0	0.8	8.3	31	42	15
	Jn	35.2	35	2.2	0.6	6.3	30	39	15
	Jc	33.3	32	2.2	0.6	6.6	31	37	15
Macronuclear segments, No.	Gn	8.1	8	–	–	–	8	9	13
	Bn	7.2	8	1.2	0.2	16.6	5	8	25
	Tn	8.4	8	0.7	0.2	8.8	8	10	15
	Tc	10.9	10	2.3	0.6	20.9	8	15	15
	Jn	7.1	7	0.8	0.2	11.3	5	8	15
	Jc	12.8	13	2.2	0.6	17.5	8	16	15
Median macronuclear segment, length	Gn	8.3	8	1.7	0.5	20.8	6	12	13
	Bn	10.4	10	2.1	0.4	20.5	7	15	25
	Tn	8.4	8	1.8	0.5	21.9	6	13	15
	Tc	10.5	9	4.3	1.1	40.5	5	20	15
	Jn	10.5	10	3.0	0.8	28.9	7	20	15
	Jc	9.9	10	2.1	0.5	21.3	6	14	15
Median macronuclear segment, width	Gn	3.2	3	0.9	0.2	28.5	2	4	13
	Bn	3.8	4	0.7	0.1	18.3	3	6	25
	Tn	3.2	3	0.7	0.2	21.3	2	4	15
	Tc	3.6	3	0.6	0.2	17.6	3	5	15
	Jn	5.0	5	0.4	0.1	8.1	4	6	15
	Jc	2.9	3	0.7	0.2	22.2	2	4	15
Micronuclei, No.	Gn	2.4	2	–	–	–	2	3	13
	Bn	3.1	3	0.8	0.2	26.3	2	4	25
	Tn	1.6	2	0.6	0.2	39.4	1	3	15
	Tc	3.5	4	0.8	0.2	23.5	2	5	15
	Jn	3.4	4	1.2	0.3	34.7	2	6	15
	Jc	5.3	5	1.2	0.3	23.1	3	8	15
Micronucleus, length	Gn	3.7	4	0.7	0.2	18.6	3	5	13
	Bn	2.0	2	0.4	0.1	20.2	2	3	25
	Tn	4.7	5	1.1	0.3	23.8	3	7	15
	Tc	4.4	4	1.2	0.3	26.1	3	7	15
	Jn	2.0	2	0.1	0.0	6.4	2	3	15
	Jc	2.4	3	0.4	0.1	17.3	2	3	15

Character		x̄	M	SD	SE	CV	Min	Max	n
Micronucleus, width	Gn	2.3	2	0.3	0.1	14.2	2	3	13
	Bn	1.9	2	0.4	0.1	18.1	2	3	25
	Tn	2.2	2	0.5	0.1	22.4	2	3	15
	Tc	2.8	3	0.4	0.1	13.4	2	3	15
	Jn	1.8	2	0.2	0.1	13.1	2	2	15
	Jc	2.0	2	0.1	0.0	6.4	2	3	15
Adoral membranelles, No.	Gn	21.5	22	2.4	0.7	11.0	16	25	13
	Bn	20.6	20	0.9	0.2	4.2	19	22	25
	Tn	19.8	19	1.2	0.3	5.8	18	22	15
	Tc	25.3	25	1.5	0.4	6.1	23	28	15
	Jn	24.8	25	1.0	0.3	4.1	23	27	15
	Jc	23.4	23	1.4	0.4	6.0	21	26	15
Parabuccal cirri, No.	Gn	3.5	4	0.9	0.2	25.4	2	5	13
	Bn	3.7	4	0.6	0.1	16.4	3	5	25
	Tn	4.0	4	0.9	0.2	21.3	3	6	15
	Tc	4.9	5	0.7	0.2	15.2	4	6	15
	Jn	5.4	5	0.8	0.2	15.4	4	7	15
	Jc	4.2	4	–	–	–	4	5	15
1st left marginal row, No. cirri	Gn	27.0	27	4.8	1.3	17.7	17	35	13
	Bn	29.0	29	4.1	0.8	14.2	21	37	25
	Tn	26.2	25	3.7	1.0	14.2	22	37	15
	Tc	38.9	41	6.9	1.8	17.6	26	52	15
	Jn	34.9	35	3.6	0.9	10.2	30	43	15
	Jc	34.6	35	4.5	1.2	12.9	26	44	15
2nd left marginal row, No. cirri	Gn	10.8	8	5.3	1.5	49.3	6	23	13
	Bn	6.5	6	3.4	0.7	52.0	3	19	25
	Tn	8.6	7	3.3	0.8	38.0	5	14	15
	Tc	16.7	14	6.9	1.8	41.2	9	28	15
	Jn	13.5	12	5.8	1.5	43.0	7	23	15
	Jc	16.7	17	3.5	0.9	21.1	11	21	15
3rd left marginal row, No. cirri	Gn	5.5	6	–	–	–	5	6	2
	Bn	6.1	6	1.9	0.4	31.1	3	11	25
	Tn	3.8	4	2.9	0.8	76.6	1	11	13
	Tc	5.6	5	4.5	1.2	80.9	1	14	14
	Jn	6.6	6	2.3	0.6	35.2	3	11	15
	Jc	9.0	9	2.5	0.6	27.9	5	13	15
1st right marginal row, No. cirri	Gn	33.8	36	5.3	1.5	15.7	24	43	13
	Bn	31.1	31	2.6	0.5	8.3	26	38	25
	Tn	30.8	31	2.5	0.6	8.1	26	35	15
	Tc	46.0	47	5.3	1.4	11.4	36	55	15
	Jn	38.5	38	2.7	0.7	7.1	35	44	15
	Jc	40.3	41	3.8	1.0	9.3	34	48	15
2nd right marginal row, No. cirri	Gn	0.0	0	0.0	0.0	0.0	0	0	13
	Bn	0.0	0	0.0	0.0	0.0	0	0	25
	Tn	1.7	1	2.0	0.7	119.4	1	7	9
	Tc	1.6	4	3.9	1.8	245.0	2	15	5
	Jn	5.1	5	1.6	0.4	31.4	2	8	14
	Jc	1.0	1	0.0	0.0	0.0	1	1	3
3rd right marginal row, No. cirri	Gn	14.4	15	5.9	1.6	41.3	5	25	13
	Bn	11.6	10	3.6	0.7	30.8	5	20	25
	Tn	9.5	10	2.6	0.7	27.2	5	13	15
	Tc	17.9	16	6.7	1.7	37.5	9	30	15
	Jn	14.7	15	3.6	0.9	24.3	7	24	15
	Jc	20.7	21	4.3	1.1	20.7	12	28	15
Rightmost marginal row, No. cirri	Gn	34.6	35	5.3	1.5	15.4	26	48	13
	Bn	37.4	38	3.8	0.8	10.2	26	46	25
	Tn	34.5	34	2.6	0.7	7.7	30	40	15
	Tc	47.3	49	6.0	1.6	12.7	36	58	15
	Jn	42.5	43	2.0	0.5	4.8	39	46	15
	Jc	44.9	46	4.5	1.2	10.1	35	53	15

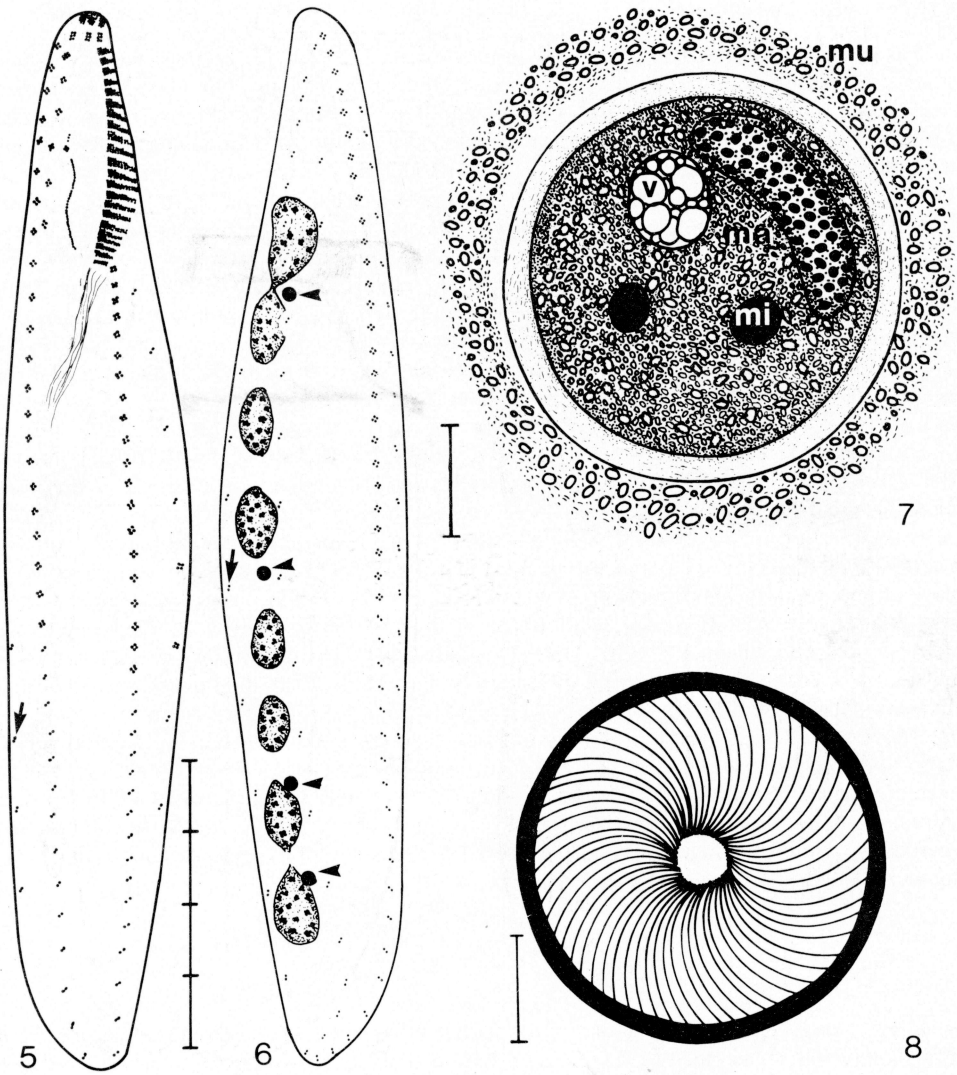
Table 2. Distribution-free multiple comparison of different populations of *Engelmanniella mobilis* (sample size = 13 for each population). For designation of populations see Table 1. ns = on significant; x = $0.10 \geq P > 0.05$; * = $0.05 \geq P > 0.01$; ** = $P \leq 0.01$.

Character	Natural populations				Natural and cultured populations					
		Gn	Bn	Tn		Gn	Bn	Tn	Jn	Tc
Body, length	Bn	x			Bn	ns				
	Tn	ns	ns		Tn	ns	ns			
	Jn	x	**	**	Jn	ns	x	ns		
					Tc	**	**	**	**	
					Jc	**	**	**	ns	ns
Body, width	Bn	x			Bn	ns				
	Tn	ns	ns		Gn	ns	ns			
	Jn	**	**	**	Jn	**	**	**		
					Tc	**	ns	**	ns	
					Jc	ns	ns	ns	**	ns
Adoral zone of	Bn	*			Bn	ns				
membranelles,	Tn	ns	ns		Tn	ns	ns			
length	Jn	**	**	**	Jn	**	**	**		
					Tc	**	**	**	ns	
					Jc	**	**	*	ns	ns
Adoral	Bn	ns			Bn	ns				
membranelles,	Tn	x	ns		Tn	ns	ns			
No.	Jn	**	**	**	Jn	**	**	**		
					Tc	**	**	**	ns	
					Jc	ns	x	**	ns	ns
Macronuclear	Bn	ns			Bn	ns				
segments, No.	Tn	ns	ns		Tn	ns	ns			
	Jn	**	ns	**	Jn	ns	ns	ns		
					Tc	x	**	ns	**	
					Jc	**	**	**	**	ns
Micronuclei,	Bn	ns			Bn	ns				
No.	Tn	**	ns		Tn	ns	ns			
	Jn	**	ns	**	Jn	ns	ns	**		
					Tc	ns	ns	**	ns	
					Jc	**	**	**	ns	ns

Character	Natural populations				Natural and cultured populations					
		Gn	Bn	Tn		Gn	Bn	Tn	Jn	Tc
Left marginal	Bn	**			Bn	ns				
rows, No.	Tn	*	ns		Tn	ns	ns			
	Jn	**	ns	ns	Jn	**	ns	ns		
					Tc	**	ns	ns	ns	
					Jc	**	ns	ns	ns	ns
Right marginal	Bn	ns			Bn	ns				
rows, No.	Tn	ns	ns		Tn	ns	ns			
	Jn	**	**	ns	Jn	**	**	ns		
					Tc	ns	ns	ns	*	
					Jc	ns	ns	ns	**	ns
Parabuccal	Bn	ns			Bn	ns				
cirri, No.	Tn	ns	ns		Tn	ns	ns			
	Jn	**	**	*	Jn	**	**	**		
					Tc	**	**	ns	ns	
					Jc	ns	ns	ns	*	ns
1st left	Bn	ns			Bn	ns				
marginal	Tn	ns	ns		Tn	ns	ns			
row, No. cirri	Jn	**	**	**	Jn	**	*	**		
					Tc	**	**	**	ns	
					Jc	**	**	**	ns	ns
1st right	Bn	ns			Bn	ns				
marginal row,	Tn	ns	ns		Tn	ns	ns			
No. cirri	Jn	x	**	**	Jn	ns	**	**		
					Tc	**	**	**	ns	
					Jc	x	**	**	ns	ns
Rightmost	Bn	ns			Bn	ns				
marginal row,	Tn	ns	ns		Tn	ns	ns			
No. cirri	Jn	**	**	**	Jn	**	ns	**		
					Tc	**	**	**	ns	
					Jc	**	**	**	ns	ns



Figs. 1–4. *Engelmanniella mobilis*. Figs. 1, 2. Ventral and dorsal view of the Austrian population (Gn) from life. Note the cilia-like cirri, the rows of subpellicular granules (g), and the contractile vacuole. Figs. 3, 4. Infraciliature of the Turkish population (Tn) in ventral and dorsal view; protargol impregnation. Parental cirri (pc) are present on the right and left margin; grandparental cirri are absent (comp. Figs. 5, 6). Note the single micronucleus (mi) which is nearly as large as a macronuclear segment (ma). azm = adoral zone of membranelles, bc = buccal cirrus, dk = dorsal kinety, em = endoral membrane, fc = frontal cirri, g = subpellicular granules, lmr = left marginal row, ma = macronuclear segment, mi = micronucleus, pbc = parabuccal cirri, pc = parental cirri, pf = pharyngeal fibers, pm = paroral membrane, rmr = right marginal row. Scale bar divisions = 10 μm.



Figs. 5–8. *Engelmanniella mobilis*. Figs. 5, 6. Infraciliature of the Japanese population (Jn) in ventral and dorsal view; protargol impregnation. Note the grandparental cirri at the right and left margin (arrows). The 4 micronuclei (arrowheads) are spherical and small (comp. Fig. 4). Fig. 7. The resting cyst of the Turkish population (Tn) is characterized by a mucus layer (mu) which contains released subpellicular granules and adhering bacterial endospores. The cyst wall measures about 2 µm. The cytoplasm contains a kidney-shaped macronucleus (ma), some micronuclei (mi), and a single vacuole (v) filled with opaque inclusions. Fig. 8. Radially stripes are visible on old and young cysts (comp. Fig. 21). Scale bar divisions = 10 µm.

Reorganization

Physiological reorganization has been studied in Bn, Jn, Tn, Jc, and Tc and was generally observed in well-fed cultures and to a less extent in the raw material. Only one set of primordia originates in a manner combining the development of anlagen in the opisthe and the proter during division. While the oral primordium arises apokinetally like in the ophiste, the frontal primordia are built mainly from parental structures (endoral membrane, buccal cirrus, parabuccal cirri) as in the proter (Fig. 9). Unlike in dividers, proliferation occurs nearer to the adoral zone of membranelles and the anarchic field is shorter and forms a small streak of new basal bodies extending onto the frontal area (Fig. 9). This extending streak probably contributes to the formation of the frontal anlagen. Remarkably, in the proter of dividing cells an additional anlage arises de novo beside the parental paroral membrane (see above). In contrast to the undulating membranes which are completely replaced in reorganizers, only 6–8 new adoral membranelles join with the posterior part of the membranellar band, where several adoral membranelles have been resorbed (Figs. 10, 11). The somatic ciliature is replaced as in dividers (WIRNSBERGER-AESCHT et al. 1989).

Contrary to the dividers, the nuclear cycle of reorganizers is correlated with cortical processes. The development of cirral primordia is generally finished until major changes of the nuclear apparatus are discernible (comp. WIRNSBERGER-AESCHT et al. 1989). In 28 stages of physiological reorganization we rarely (in 2 or 3 cases) discovered a single replication band in one of the macronuclear segments. This indicates that no reorganisation of the macronuclear material takes place as supposed by JERKA-DZIADOSZ & FRANKEL (1970). The macronuclear segments merely fuse to a lengthy mass (Fig. 13), while those of dividers became elliptical. This lengthy mass often disconnects unequally (Figs. 14, 15), obviously giving rise to an odd number of macronuclear segments in interphase specimens (comp. Table 1). In the Japanese population (Jn) characteristically (96.5%, n = 115) only a single micronucleus undergoes the mitotic cycle (Figs. 12–15). In 4 cases (3.5%) 2 prophasic micronuclei were found, whereas in the relatively few stages examined in Bn all micronuclei became prophasic. The Tn and Tc cells resemble the Japanese population in this respect. Most of the 1–5 interphasic micronuclei of Jn and Jc are present until the latest reorganizational stages (Figs. 14, 15). Due to the few reorganizing micronuclei, some of them must be transferred to the interphasic cell to explain the average number of 4–5 micronuclei (Table 1).

Conjugation

Several stages of sexual processes were found in all populations. The nuclear cycle largely corresponds to that described by CALKINS (1919a, b, 1930a, b), with exception of the number of pronuclei. CALKINS noted that in *Engelmanniella mobilis* 8–16 (mainly 3–4) micronuclei became prophasic, while in *E. halseyi* typically never more than 2 micronuclei enter the mitotic cycle. We observed 2–5 pronuclei in the Japanese and 1–3 in the Turkish population. The oral primordium originates de novo in each member of the pair and forms all frontal anlagen like the

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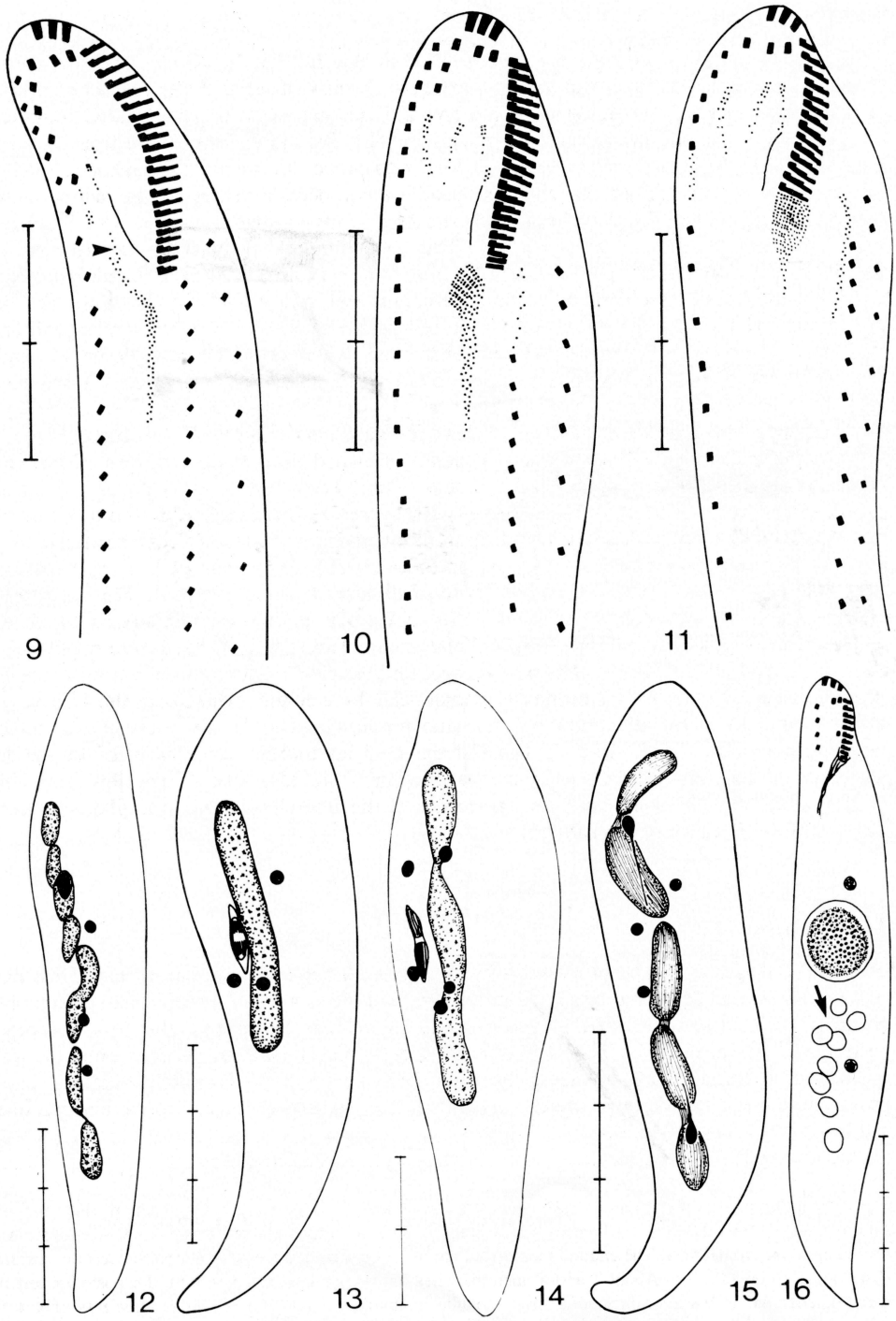
Figs. 9–16. *Engelmanniella mobilis*. Reorganizing cells (Figs. 9–15) and an exconjugant (Fig. 16) of the Japanese population (Jn); protargol impregnation. Fig. 9. The oral primordium forms a small streak (arrowhead) extending to the frontal area. The endoral membrane, the buccal cirrus, and the posterior parabuccal cirri proliferate basal bodies. Figs. 10, 11. About 7 adoral membranelles are reorganized and join with the posterior part of the membranellar band. Marginal primordia originate like in dividers. Figs. 12–15. In reorganizers only a single micronucleus undergoes the mitosis, the lengthy macronuclear mass divides unequally. Fig. 16. Oral area and nuclear apparatus of an exconjugant. Note the absent undulating membrans, the synkaryon, and the resorbing macronuclear segments (arrow). Scale bar divisions = 10μm.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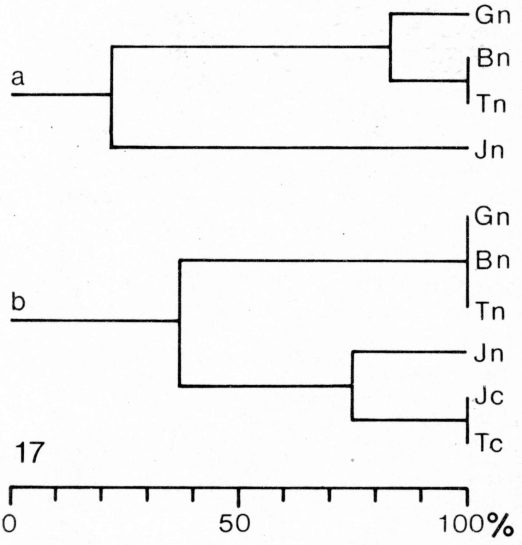
opisthe in dividers. Only a small adoral zone of membranelles is reorganized (Figs. 16, 18) and the undulating membranes are absent in the exconjugants (Fig. 16). A subsequent physiological reorganization is followed by encystation.

We tried to determine the mating-type reactivity of the Turkish and Japanese populations by mixing about one dozen different clones in pairs. In one case, conjugation took place, however, we suppose that it was an intraclonal conjugation which repeatedly occurred in one of this definite clones later.

Formation and structure of the resting cyst

Encystation was studied in the Turkish and the Japanese population. In general, the processes are similar; however, the populations differ in their capability to encyst and to excyst: Tn and Tc cells immediately form cysts after the transfer into fresh medium without food; encystation lasts about 2d. Contrary, the resting cysts of the Japanese population are difficult to obtain. Starved cells round up, but many to them fail to generate the cyst wall and die. Encystation of this population needs 3–4d. Air-dried cysts (about 1 month) of both populations can be reactivated by adding fresh culture medium and food. Remarkably, the Turkish population excysts more quickly than the Japanese population.



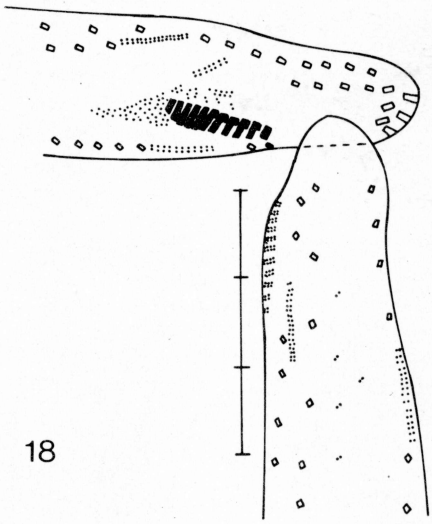


Fig. 17. *Engelmanniella mobilis*. Phenograms of the natural populations (a) and the natural *and* cultured populations (b). UPGMA clustering of the number of not significantly different characters in % obtained by multiple comparison procedures of the 12 characters (= 100%) presented in Table 2. Significance level for multiple comparison procedures $\alpha = 0.01$. Bn = natural Austrian population, Baumgarten, Gn = natural Austrian population, Grafenwörth, Jc = cultured Japanese population, Jn = natural Japanese population, Tc = cultured Turkish population, Tn = natural Turkish population.

Fig. 18. Intraclonal conjugants of the Japanese population (Jc) of *Engelmanniella mobilis*; protargol impregnation. The frontal anlagen originate from the oral primordium like in the opisthe during division. Scale bar divisions = 10 μm.

At the beginning of encystaion cells round up, resorb their ciliary structures, built up the cyst wall, and release the subpellicular granules (Figs. 24, 25). In some electron micrographs of young cysts considerable amounts of cytoplasmic material were found outside the cell suggesting

cytoplasma extrusion during encystation (Fig. 24). Soon, 50–60 stripes appear on the cell surface showing a radial symmetry (Figs. 8, 21). They are also evident in protargol preparations of old resting cysts of both, the Japanese and Turkish, populations. Their origin could not be clarified (comp. HASHIMOTO 1963; GRIMES 1973).

Apart from the different capability to encyst and to excyst, the populations differ by the appearance of the cyst wall. In Jn and Jc the wall is smooth, with exception of sometimes adhering detritus (Figs. 20, 21). Contrary, Bn, Tn, and Tc typically display a considerable mucus envelope with released granules and adherent bacterial endospores (Figs. 7, 22, 24). Frequently, the cyst wall becomes smooth in cultures kept for several months. Then, they are indistinguishable from the cysts of the Japanese population. Fully differentiated resting cysts have a single kidney-shaped macronucleus and some yellow opaque inclusions, mostly included in a single vacuole (Figs. 7, 20). The morphometric characters of the resting cysts of the Turkish and Japanese population are summarized in Table 3.

The peripheral zone of the fully differentiated resting cyst is characterized by the absence of subpellicular granules indicating that all have been discharged (Fig. 27). The granules obviously traverse the plasma membrane and the developing cyst wall (Figs. 23–27). Partly, their structure is still compact and identically to that of the interphasic cell (Figs. 24, 25), but most of them appear swollen and spongious (Figs. 23, 26, 27). The fibrils of the "mucus" (Fig. 26) are strongly reminiscent to that material which has been observed during the various developmental stages of the subpellicular granules (WIRNSBERGER-AESCHT et al. 1989). The structural alteration of the released granules is very likely not an artifact, because they are also enlarged in vivo. The granules accumulate more or less distant from the cyst wall and very likely form the thin dark layer which separates the granules from the mucus (Figs. 23, 24, 26, 27). Probably, the mucilaginous material scales away from this dense boundary.

A few sections of developing cysts and young resting cysts of the Bn reveal that the cyst wall has a rather usual equipment: a thin ectocyst, a filamentous mesocyst, an endocyst, and an inner granular layer, filling the rims of the cytoplasmic surface (Fig. 27). The different types of precursors could not be specified, with exception of the mesocyst precursor (Fig. 25). A single layer of microtubules is located beneath the cell membrane (Figs. 25, 27). Mitoribosomes were observed like in the interphasic cells (comp. WIRNSBERGER-AESCHT et al. 1989).

Discussion

Natural and cultured variability

Obviously the 4 populations investigated display a continuous sequence in many characters commonly used to distinguish species: body size, number and size of nuclei, length of the adoral zone of membranelles, and number of left and right marginal rows. Nonetheless, most characters of *Engelmanniella mobilis* show coefficients of variation in the same order of magnitude as other hypotrichs (comp. Table 1 and FOISSNER 1982). Exceptional is the highly instabile number of cirri comprising the parental and grandparental cirral rows. This instability and the uneven distances among the cirri comprising these rows are caused by the partition of different cirral generations on 2 cells (WIRNSBERGER-AESCHT et al. 1989).

The morphological (morphometry, occasionally loss of the second dorsal kinety in Jc, cysts) and ontogenetic (nuclear behaviour) analyses of the cells from the raw cultures reveal at least 2 groups of populations (Fig. 17). Each assemblage may represent a "stability range" defined by FRANKEL (1973) as the range of common and repeatedly observed corticotypes or even a "stability center" according to HECKMANN & FRANKEL (1968), the average corticotype at equilibrium. However, a considerable extent of morphometric and morphogenetic variation among different populations of the same species is probably widespread among ciliates (WIRNSBERGER et al. 1985a). Thus, we do not separate these groups at species level. This decision is strengthened by

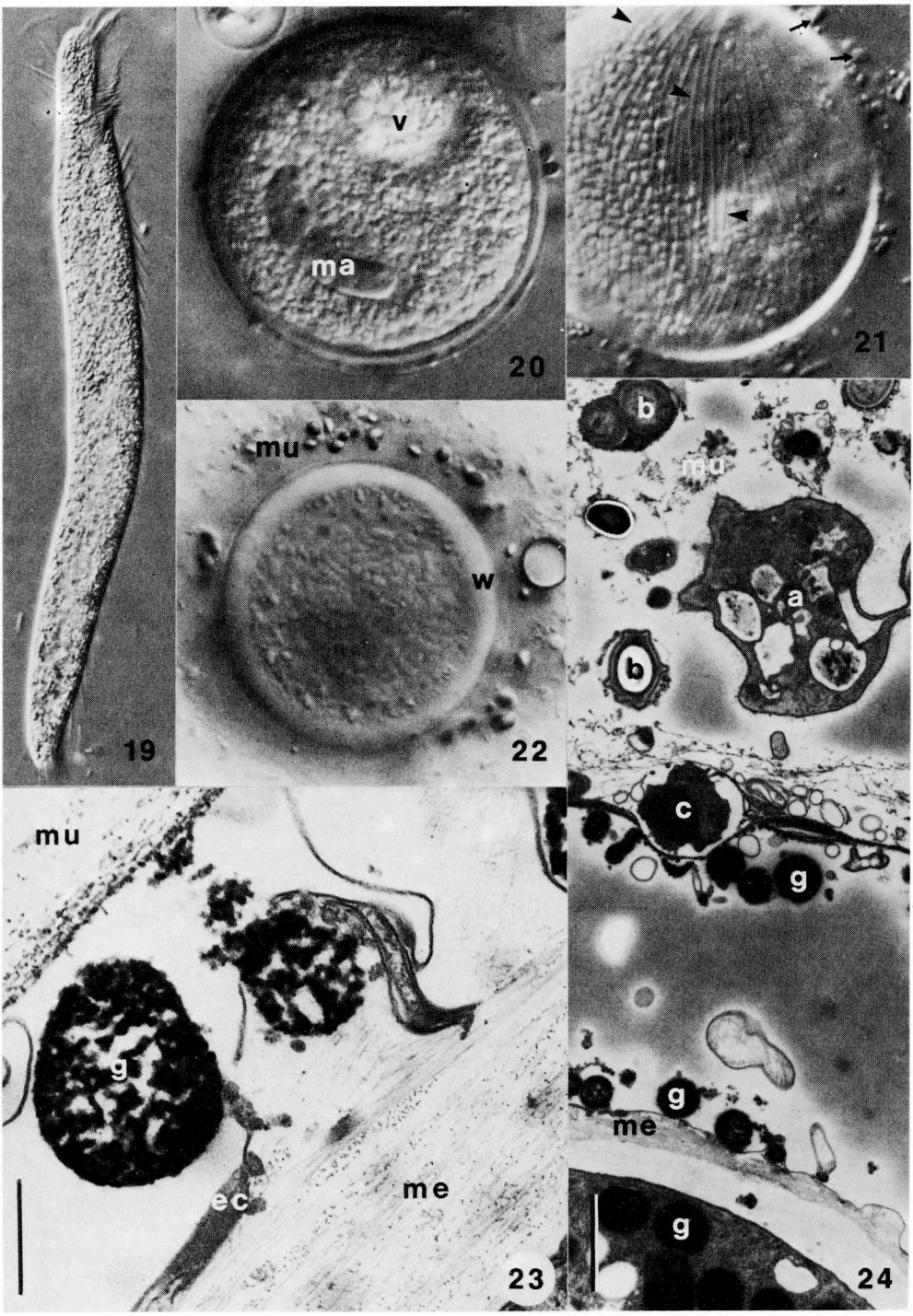
Table 3. Morphology of resting cysts of the Turkish (T) and Japanese (J) population of *Engelmanniella mobilis*. In vivo measurements embrace values from natural and cultured cells, other are from cultured cells. Legend see Table 1.

Character		$\bar{x}$	M	SD	SE	CV	Min	Max	n
Mucus layer (in vivo)	T	6.2	6	1.7	0.4	26.5	4	10	21
	J	–	–	–	–	–	–	–	–
Diameter (in vivo)	T	35.5	35	3.9	0.7	10.9	29	44	29
	J	33.4	33	3.0	0.5	8.9	26	41	33
Cyst wall (in vivo)	T	2.4	2.5	0.6	0.1	26.3	2	4	23
	J	1.8	2	0.4	0.1	21.0	1.3	3	17
Opaque vacuole, diameter (in vivo)	T	11.9	12.5	1.3	0.4	10.9	10	14	10
	J	10.5	7.5	1.9	0.5	18.1	7	15	14
Macronuclear segments, No.	T	1.0	1	–	–	–	1	1	15
	J	1.0	1	–	–	–	1	1	15
Micronuclei, No.	T	2.7	3	1.2	0.3	43.0	2	5	15
	J	2.5	3	1.1	0.3	42.4	1	4	15
Micronuclei, length	T	4.1	4	1.3	0.3	32.3	3	6	15
	J	2.9	3	1.0	0.3	34.5	2	5	15
Micronuclei, width	T	3.8	4	1.1	0.3	30.0	3	5	15
	J	2.1	2	0.6	0.2	30.7	2	3	15

the increasing variability of the Turkish population with culture age resulting in a transitional taxon between the both assemblages (Tables 1, 2, Fig. 17). Contrary, the Japanese population exhibits relatively stable morphological characters, even if cultured for several months (Table 1). A different extent of stability has also been observed in certain freshwater species of the genus *Stylonychia* (WIRNSBERGER et al. 1985b).

The present investigations have been performed on populations and not as widely done on clones. This proceeding is justified, in our opinion, because the population is the fundamental unit of each biological species. Moreover, ecologists are confronted with populations and not clones. In this connection a significant outcome of our study is that morphological differences originating in cells during some months of culturing might be greater than those observed in natural populations.

Figs. 19–24. *Engelmanniella mobilis*. Light (Figs. 19–22) and transmission electron micrographs (Figs. 23, 24). For designation of populations see Material and Methods or Fig. 17. Fig. 19. In vivo aspect of Tn. Fig. 20. The resting cyst of Jn has no mucus layer, a condensed macronucleus (ma), and a vacuole with opaque inclusions (v). Fig. 21. Stripes (arrowheads) and extruded subpellicular granules (arrows) of Jn. Fig. 22. Resting cyst of Tc showing the wall (w) and the mucus layer (mu) containing extruded subpellicular granules and bacterial endospores. Figs. 23, 24. Young cysts of Bn have a mesocyst (me), but yet lack the endocyst and the granular layer. Some of the extruded subpellicular granules (g) are swollen and form the mucus sheet (mu) where bacterial endospores (b) and a small amoebae (a) adhere. Some cytoplasmic material (c) has been extruded from the encysting cell. Bars = 500 nm and 2 µm, respectively.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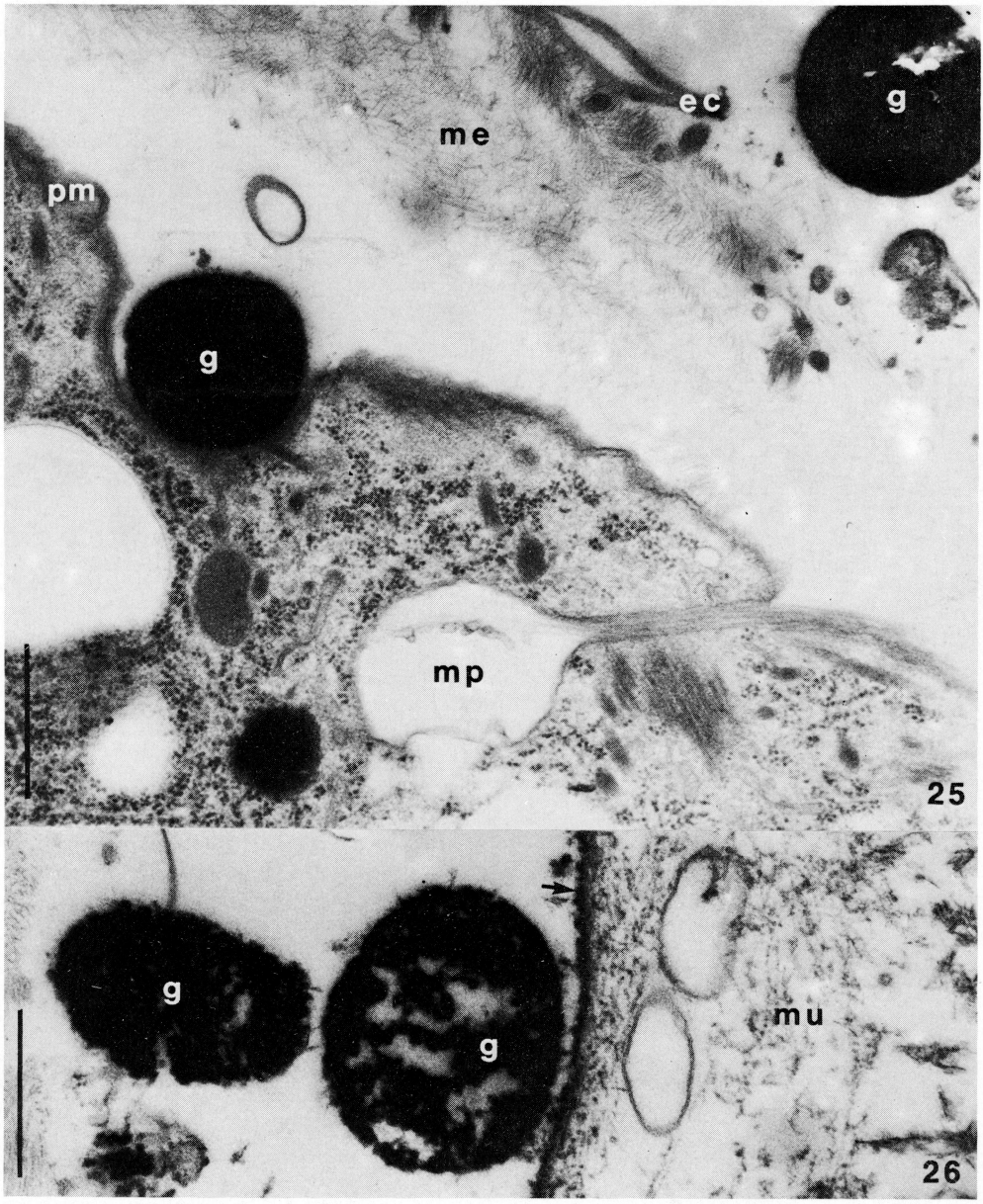

Figs. 25, 26. *Engelmanniella mobilis*. Young cysts of the Austrian population (Bn). Fig. 25. The subpellicular granules (g) traverse the plasma membrane (pm), the mesocyst (me), and the ectocyst (ec). A mesocyst precursor (mp) releases filaments. Fig. 26. The granules (g) are swollen and their spongious content forms the dark layer (arrow) which separates the granules from the mucus sheet (comp. Fig. 24). The fibrils of the mucus might scale away from this dense layer. Bars = 500nm.

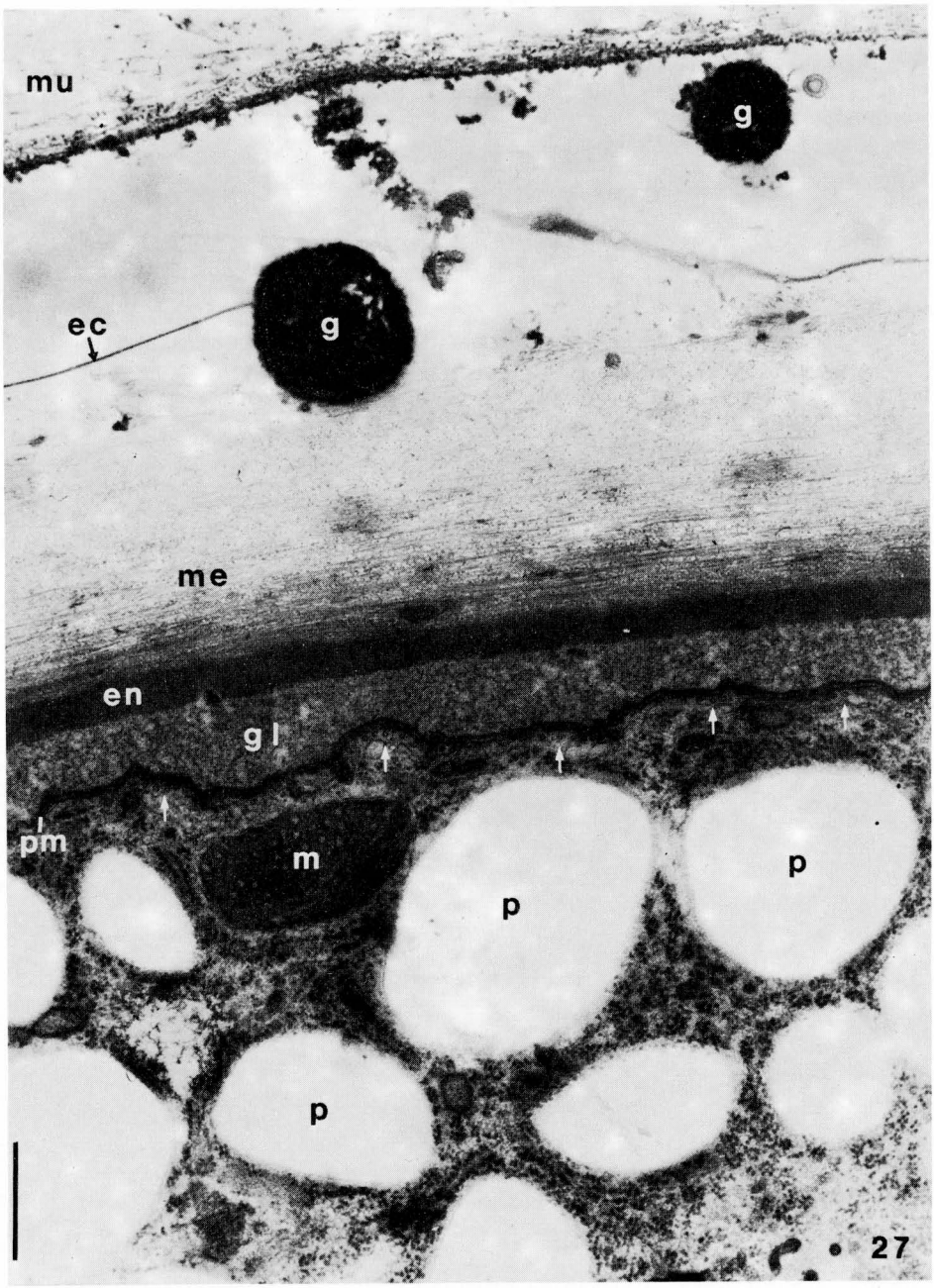

Fig. 27. *Engelmanniella mobilis*. Fully differentiated resting cyst of the Austrian population (Bn). Note the single layer of microtubules (arrows) underlining the plasma membrane (pm). ec = ectocyst, en = endocyst, g = released subpellicular granules, gl = granular layer, m = mitochondrion, me = mesocyst, mu = mucus layer, p = paraglycogen granules. Bar = 500 nm.

Resting cyst

The Austrian and Turkish populations differ from the Japanese population by their readiness to encyst and excyst quickly and the mucilaginous layer. The release of subpellicular granules was observed likewise in the Austrian, Japanese, and Turkish populations. However, these granules are obviously of somewhat different chemical nature, because they disappear soon in the Japanese population, while they produce the mucus envelope in Bn and the Turkish population. However, aged resting cysts of Bn, Tn, and Tc may get the smooth cyst wall typical for the Japanese population. Thus, the presence or absence of a mucus layer is not a reliable species criterion.

The transformation of subpellicular granules to a peculiar layer surrounding the cyst wall has yet not been observed in other hypotrichs. A mucus layer of unknown origin has been observed in *Oxytricha bifaria, Urosoma gigantea,* and *Kahliella simplex* (VERNI et al. 1984; BERGER & FOISSNER 1987; FOISSNER & FOISSNER 1987). At lightmicroscopical level, granules outside the cyst wall have been described in *Oxytricha granulifera* and *Urosoma gigantea* (FOISSNER & ADAM 1983; BERGER & FOISSNER 1987). It is unknown, whether these granules are used to built up the mucus envelope of the cysts or not. Granules may resist inside of resting cyst too, for instance in *Steinia muscorum, Urostyla grandis,* and *Paraurostyla weissei* (FOISSNER 1982; RIOS et al. 1985; DELGADO et al. 1987).

Cysts of dozen hypotrich species investigated ultrastructurally have been classified in 2 or 3 types (WALKER & MAUGEL 1980; RIOS et al. 1985). The resting cyst of *Engelmanniella mobilis* neither fits the oxytrichid (KR – kinetosome resorbing) type, nor the urostylid or euplotid type. Contrary to the KR cysts, cortical microtubules are maintained like in *Urostyla grandis,* the representative of the urostylid type, *Paraurostyla weissei,* and *Kahliella simplex* (RIOS et al. 1985; DELGADO et al. 1987; FOISSNER & FOISSNER 1987). This finding confirms the statement of FOISSNER & FOISSNER (1987) that the preservation of cortical microtubules cannot be used further as an euplotid character. Beside the preserved microtubules, the urostylid type is characterized by a 3-layered wall and macronuclei which do not fuse (RIOS et al. 1985). With exception of the conserved microtubules, these criteria are not shared by *Engelmanniella, Kahliella,* and *Paraurostyla,* because they have a 4-layered cyst wall and condensed macronuclear segments. The euplotid NKR (non kinetosome resorbing)-type was based on the study of a single species, *Diophrys scutum* (WALKER & MAUGEL 1980). However, recent data show that considerable parts of the ciliature are resorbed too in *Euplotes encysticus* (MATSUSAKA et al. 1989). Taking into account that *Engelmanniella mobilis* and *Kahliella simplex* (FOISSNER & FOISSNER 1987) are the only stichotrichid hypotrichs, the cyst of which have been seen at electron microscopical level, it is obviously premature to establish representative types.

The species problem

FOISSNER (1982) established the genus *Engelmanniella* with *Engelmanniella mobilis* (= *Uroleptus mobilis* ENGELMANN, 1862) as the type species. The original description of ENGELMANN is rather incomplete. Thus, FOISSNER based his identification on a paper of CALKINS (1919a) who studied a New York variety of this species. The Japanese population matches the American variety of CALKINS (1919a) better than the Austrian population (Gn) of FOISSNER (1982). CALKINS even mentioned smooth cysts of his form which was later designated by KAHL (1932) as *Uroleptus mobilis* var. *americanus.* FOISSNER (1982) included 2 additional species in this genus: *E. kahli* (GROLIERE) and *E. halseyi* (CALKINS, 1929). The former species is actually the type species of the genus *Perisincirra* JANKOWSKI and looks rather different from *Engelmanniella.* CALKINS (1929) distinguished *E. halseyi* from *E. mobilis* by its capability of stretching out until the length is sixteen times the diameter, the more pronounced pointed posterior end, the subpellicular granules, the 8–26 macronuclear segments, and the 1–2 very large micronuclei. However, particularly long cells usually develop in starved cultures, and highly

variable numbers of macronuclear segments occur in the cultured populations (Table 1). In contrast to cells of the Austrian populations, those of the Turkish population (Tn) often show a single, very large micronucleus (Fig. 4). However, smaller micronuclei of variable number were also observed, particularly in Tc (Table 1). CALKINS' description of subpellicular granules is valuable for identification, but these granules might have been overlooked in *E. mobilis* by ENGELMANN (1862) and by CALKINS himself, because he used different methods in earlier studies. The differences mentioned by CALKINS (1930a) in relation to the nuclear behaviour and the duration of conjugation are probably strain-specific (comp. above). Furthermore, CALKINS (1930b) mentioned that both forms are identically in their arrangement of the cirral rows. Considering the variability of different natural and cultured populations observed by us, the 2 forms described by CALKINS (1919a, 1929) are very likely only ecological or cultured variants of *E. mobilis* and are thus synonymized with this species.

Improved diagnosis of the genus *Engelmanniella*

Engelmanniella differs from all known hypotrich genera by the conservation of 3 generations of marginal cirri. During interphase the cirral pattern is rather undifferentiated, while frontal, parabuccal, buccal, and somatic cirri can be distinguished during the morphogenesis. Transverse, frontoterminal (migratory), and caudal cirri are absent.

Based on the previous morphogenetic results (WIRNSBERGER-AESCHT et al. 1989) and the data presented here, we improve the diagnosis of the genus *Engelmanniella* FOISSNER, 1982 as follows: Infraciliature consisting of frontal, parabuccal, buccal, and marginal cirri. Somatic cirral rows comprise 3 generations of cirri. A dorsal kinety develops de novo in the opisthe.

The systematic position of the genus is still unclear, it might have some relations to kahliellids and cladotrichids (WIRNSBERGER-AESCHT et al. 1989).

Zusammenfassung

Es wird die morphologische und morphogenetische Variabilität des hypotrichen Ciliaten *Engelmanniella mobilis* (ENGELMANN, 1862) FOISSNER, 1982 untersucht. Die aus dem Boden isolierten Populationen stammen aus Österreich (Bn, Gn), der Türkei (Tn) und aus Japan (Jn). Sie bilden hinsichtlich einiger quantitativer Merkmale der Infraciliatur, der Morphologie der Ruhecyste und dem Kernzyklus während der Teilung 2 Gruppen: Gn, Bn, Tn und Jn. Die Variabilität der türkischen Population (Tc) erhöht sich nach dreimonatiger Kultur jedoch so stark, daß diese Gruppierung undeutlich wurde. Merkmalsunterschiede, die durch Kultivierung entstehen, können demnach größer sein als jene, die sich zwischen natürlichen Populationen finden. Die von uns festgestellte Varibilität umfaßt *E. halseyi* (CALKINS, 1929) und *E. mobilis americanus* (KAHL, 1932), die deshalb mit *E. mobilis* synonymisiert werden. Während der Teilung und der Reorganisation sind bei allen Populationen die corticalen Prozesse sehr ähnlich, das Verhalten der Mikronuclei ist etwas unterschiedlich. Teilung und physiologische Reorganisation unterscheiden sich in der Entstehung der Frontalanlagen. Die Genusdiagnose von *Engelmanniella* FOISSNER, 1982 wird verbessert.

Die jungen Ruhecysten von Bn, Tn und Tc haben eine schleimartige Hülle, die von den ausgestoßenen subpelliculären Granula gebildet wird. Bei den älteren Cysten und den Ruhecysten der japanischen Population fehlt diese Hülle, obwohl auch sie alle subpelliculären Granula ausstoßen. Die Ruhecysten von *E. mobilis, Kahliella simplex* und *Paraurostyla weissei* besitzen oxytrichide (vierschichtige Wand, fusionierte Makronucleus-Segmente) und urostylide (corticale Mikrotubuli) Merkmale. Die derzeitige Klassifikation von Ruhecysten hypotricher Ciliaten ist daher offensichtlich nicht aufrecht zu erhalten.

Acknowledgements

The soil samples of Japan and Turkey were kindly provided by Dr. MATSUSAKA, Kumamoto University, and Univ.-Doz. Dr. SPETA, Landesmuseum Linz. We thank Prof. ADAM, the head of the Institute of Zoology,

University of Salzburg, for his institutional support. The photographical assistance of Mrs. BERNATZKY is greatly acknowledged. This study was supported by the "Fonds zur Förderung der wissenschaftlichen Forschung, Projekt Nr. P 5889" and the Oberösterreichische Landesregierung (Talentförderungsprämie).

Literature

AUSTIN, M. L. (1927): Studies on *Uroleptus mobilis* I. An attempt to profong the life-cycle II. The conditions necessary for conjugation. J. exp. Zool. **49**: 149–216.

BERGER, H., FOISSNER, W., & ADAM, H. (1985): Morphological variation and comparative analysis of morphogenesis in *Parakahliella macrostoma* (FOISSNER, 1982) nov. gen. and *Histriculus muscorum* (KAHL, 1932), (Ciliophora, Hypotrichida). Protistologica **21**: 295–311.

– & FOISSNER, W. (1987): Morphology and biometry of some soil hypotrichs (Protozoa: Ciliophora). Zool. Jb. Syst. **114**: 193–239.

CALKINS, G. N. (1919a): *Uroleptus mobilis,* ENGELM. I. History of the nuclei during division and conjugation. J. exp. Zool. **27**: 293–357.

– (1919b): *Uroleptus mobilis* ENGELM. II. Renewal of vitality through conjugation. J. exp. Zool. **29**: 121–156.

– (1920a): *Uroleptus mobilis* ENGELM. III. A study in vitality. J. exp. Zool. **31**: 287–305.

– (1920b): Age of parents and vitality in *Uroleptus mobilis.* Proc. Soc. exp. Biol. Med. **17**: 72–74.

– (1921): *Uroleptus mobilis* ENGELM. IV. Effect of cutting during conjugation. J. exp. Zool. **34**: 449–470.

– (1925): *Uroleptus mobilis* V. The history of a double organism. J. exp. Zool. **41**: 191–213.

– (1929): *Uroleptus halseyi,* n. sp. I. The effect of ultra-violet rays. Biol. Bull. Woods Hole **57**: 59–68.

– (1930a): *Uroleptus halseyi* CALKINS. II. The origin and fate of the macronuclear chromatin. Arch. Protistenkd. **69**: 151–174.

– (1930b): *Uroleptus halseyi* CALKINS. III. The kinetic elements and the micronucleus. Arch. Protistenkd. **72**: 49–70.

DELGADO, P., CALVO, P., & TORRES, A. (1987): Encystment in the hypotrichous ciliate *Paraurostyla weissei:* ultrastructure and cytochemistry. J. Protozool. **34**: 104–110.

DELAMATER, A. J. (1936): The effects of heavy water upon the fission rate and the life cycle of the cilicate, *Uroleptus mobilis.* Biol. Bull. Woods Hole **71**: 199–216.

ENGELMANN, T. W. (1862): Zur Naturgeschichte der Infusionsthiere. Z. wiss. Zool. **11**: 347–393.

FOISSNER, W. (1982): Ökologie und Taxonomie der Hypotrichida (Protozoa: Ciliophora) einiger österreichischer Böden. Arch. Protistenkd. **126**: 19–143.

– & ADAM, H. (1983): Morphologie und Morphogenese des Bodenciliaten *Oxytricha granulifera* sp. n. (Ciliophora, Oxytrichidae). Zool. Scr. **12**: 1–11.

– PEER, T., & ADAM, H. (1985): Pedologische und protozoologische Untersuchungen einiger Böden des Tullnerfeldes (Niederösterreich). Mitt. öst. bodenk. Ges. **30**: 77–117.

FOISSNER, I., & FOISSNER, W. (1987): The fine structure of the resting cysts of *Kahliella simplex* (Ciliata, Hypotrichida). Zool. Anz. **218**: 65–74.

FRANKEL, J. (1973): Dimensions of control of cortical patterns in *Euplotes:* the role of pre-existing structure, the clonal life cycle, and the genotype. J. exp. Zool. **183**: 71–94.

GREGORY, L. H. (1925): Direct and after effects of changes in medium during different periods in the life history of *Uroleptus mobilis.* Biol. Bull. Woods Hole **48**: 200–208.

– (1926): Effects of changes in medium during different periods in the life history of *Uroleptus mobilis.* Biol. Bull. Woods Hole **51**: 179–188.

– (1928): The effects of changes in medium during different periods in the life history of *Uroleptus mobilis* and other protozoa. Biol. Bull. Woods Hole **55**: 386–394.

GRIMES, G. W. (1973): Differentiation during encystment and excystment in *Oxytricha fallax.* J. Protozool. **20**: 92–104.

HASHIMOTO, K. (1963): Formation of ciliature in excystment and induced reencystment of *Oxytricha fallax* STEIN. J. Protozool. **10**: 156–166.

HECKMANN, K., & FRANKEL, J. (1968): Genetic control of cortical pattern in *Euplotes.* J. exp. Zool. **168**: 11–38.

JERKA-DZIADOSZ, M., & FRANKEL, J. (1970): The control of DNA synthesis in macronuclei and micronuclei of a hypotrich ciliate: a comparison of normal and regenerating cells. J. exp. Zool. **173**: 1–22.

KAHL, A. (1932): Urtiere oder Protozoa I: Wimpertiere oder Ciliata (Infusoria) 3. Spirotricha. Tierwelt Dtl. **25**: 399–650.

MATSUSAKA, T., NOGUCHI, O., & YONEZAWA, F. (1989): Cortical morphogenesis during encystment in a ciliate, *Euplotes encysticus* YONEZAWA. 1985. Europ. J. Protistol. **24**: 133–137.

Rios, R. M., Torres, A., Calvo, P., & Fedriani, C. (1985): The cyst of *Urostyla grandis* (Hypotrichida: Urostylidae): ultrastructure and evolutionary implications. Protistologica **21**: 481–485.

Tittler, I. A. (1938): Regeneration and reorganization in *Uroleptus mobilis* following injury by induced electric currents. Biol. Bull. Woods Hole **75**: 533–541.

Verni, F., Rosati, G., & Ricci, N. (1984): The cyst of *Oxytricha bifaria* (Ciliata Hypotrichida). II. The ultrastructure. Protistologica **20**: 87–95.

Walker, G. K., & Maugel, T. K. (1980): Encystment and excystment in hypotrich ciliates II. *Diophrys scutum* and remarks on comparative features. Protistologica **16**: 525–531.

Wirnsberger, E., Foissner, W., & Adam, H. (1985a): Cortical pattern in non-dividers, dividers and reorganizers of an Austrian population of *Paraurostyla weissei* (Ciliphora, Hypotrichida): a comparative morphological and biometrical study. Zool. Scr. **14**: 1–10.

– – – (1985b): Morphological, biometric, and morphogenetic comparison of two closely related species, *Stylonychia vorax* and *S. pustulata* (Ciliophora: Oxytrichidae). J. Protozool. **32**: 261–268.

Wirnsberger-Aescht, E., Foissner, W., & Foissner, I. (1989): Morphogenesis and ultrastructure of the soil ciliate *Engelmanniella mobilis* (Ciliophora, Hypotrichida). Europ. J. Protistol. **24:** 354–368.

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Arch. Protistenkd. **138** (1990): 50
VEB Gustav Fischer Verlag Jena

Buchbesprechung

MUNAWAR, M. (Ed.): **Proceedings of an International Symposium on the Phycology of Large Lakes of the World Held at the First International Congress, St. John's, Newfoundland, Canada.** In: Ergebnisse der Limnologie. Advances in Limnology. Edited by H.-J. ELSTER & W. OHLE. Heft 25 (Archiv für Hydrobiologie Beiheft 25). XI, 258 pages, 105 figures, 44 tables. E. Schweizerbart'sche Verlagsbuchhandlung (Nägele u. Obermiller), Stuttgart 1987. Price: DM 98.–; US $ 50.–.

The large lakes of the world represent one of the most undervalued resources on the surface of the globe. Much of human development has resulted from the very existence of these sweet water inland seas which have been rewarded by being turned into major receptacles for the waste by-products of this development. Over the past two decades the visible and often noxious deterioration in the world's large lakes has resulted in a developing interest and concern by both scientist and layman in these unique water bodies.

In 1982, the First International Phycological Congress focussed on the phycology of the large lakes on the world. Scientists from Canada, U.S.A., and U.S.S.R. contributed papers dealing with the large lakes of Africa, North America, Europe, and Asia. This symposium was unique since, firstly, it provided little-known world coverage of the large lakes that are distributed over a wide range of latidues and climatic regimes and, secondly, considerable information about the Russian Great Lakes was presented. Finally, phytoplankton from the ancient lakes of Africa were compared with algae from the relatively young lakes of North America, leading to a better understanding of the food chain dynamics of these lakes.

The phytoplankton of Great Bear and Great Slave Lakes in the Canadian subarctic are discussed (DUTHIE & HART), followed by studies of two northern European lakes, Ladoga and Onega, which include recent phycological successional changes (PETROVA). Structural and functional characteristics of Lake Baikal are then provided (OZHOVA). Coverage of Russian phycology continues with the evaluation of algal communities in reservoirs built on the Dnieper River which drains into the Black Sea (SIRENKO).

The symposium then focusses on the relatively young North American Great Lakes with case studies of mesoeutrophic Lake Ontario and oligotrophic Lake Superior (MUNAWAR, MUNAWAR & MCCARTHY) and on planktonic and physicochemical relationships in Lake Michigan (CLAFLIN). Some of the current research dealing with the toxicity of contaminants to size-fractionated natural phytoplankton by algal fractionation bioassays is discussed (MUNAWAR, MUNAWAR, ROSS & MAYFIELD), and the algal fractionation theme is further developed by the study of minute organisms (picoplankton) and their ultrasensitivity to contaminant stress (MUNAWAR, MUNAWAR, NORWOOD & MAYFIELD). Further studies relevant to the North American Great Lakes deal with the impact of algal size structure on the ecology of herbivorous zooplankton (ROSS & MUNAWAR), the invasion of marine algae into the Great Lakes (SHEATH), and statistical models developed to describe the association between phytoplankton biomass and chlorophyll **a** in Lake Huron and Georgian Bay (EL-SHAARAWI & MUNAWAR).

The symposium lastly deals with the large lakes of the lower latitudes which include the ancient great lakes of the rift valleys of Central and East Africa. This area contains both the second largest lake (Lake Victoria) and the longest lake (Lake Tanganyika) in the world. The phytoplankton ecology of Lakes Malawi (Nyasa), Tanganyika, Kivu, Edward, and Albert are compared (HECKY & KLING). Finally, the phytoplankton of equatorial Lake Victoria is treated in detail and comparisons are made with phytoplankton from other large lakes (TALLING).

It should be noted the recent increased interest of the scientific community towards the management of world lake environments as evidenced by the Shiga Conference in Otsu, Japan (1984); the World Conferences on Large Lakes in Mackinac, Michigan, U.S.A. (1986) and Keszthely, Hungary (1988) as well as the establishment of the International Lake Environment Committee (ILEC).

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(Text mostly adopted from M. MUNAWAR and R. L. THOMAS)