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Biometric and Morphogenetic Comparison of the Sibling Species *Stylonychia mytilus* and *S. lemnae*, including a Phylogenetic System for the Oxytrichids (Ciliophora, Hypotrichida)[1])

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With 17 Figures

Key words: *Stylonychia mytilus* EHRENBERG, 1838; *S. lemnae* AMMERMANN and SCHLEGEL, 1983; biometry; morphogenesis; phylogenetic systematics

Summary

Stylonychia mytilus only differs from *S. lemnae* by its dorsal kineties 1—4, which are more bent apically and have a significantly greater number of cilia. These characters are difficult to recognize in vivo. Thus, we suggest that field biologists ought to employ the designation "member of the *Stylonychia mytilus* complex". The cortical divisional morphogenesis is the same in the 4 clones investigated and described in detail for *S. lemnae*. The development of the dorsal ciliature and the division of the nuclear apparatus do not differ from those known of other *Stylonychia* species. The stomatogenesis begins with a proliferation of basal bodies close to the uppermost transverse cirrus. Three frontal-ventral-transverse (FVT) anlagen of the opisthe separate from the oral primordium and 3 from the right postoral ventral cirrus. In the proter anlage 1 originates from the parental undulating membranes, anlage 2 from the oral primordium of the opisthe, anlage 3 from the left posterior frontal cirrus, anlage 4 from the right posterior frontal cirrus, and anlagen 5 and 6 evolve from the right postoral ventral cirrus. The anlagen 1—6 generate 1—3—3—3—4—4 FVT-cirri.

The phylogenetic sequence of the oxytrichous genera *Paraurostyla* (Pa), *Amphisiella* (Am), *Gastrostyla* (Ga), *Histriculus* (Hi), *Stylonychia* (St), *Oxytricha* (Ox), *Tachysoma* (Ta), *Urosoma* (Ur), *Urosomoida* (Ua), and *Gonostomum* (Go) is reconstructed using the method of HENNIG. For this proposal, 8 morphological and morphogenetic characters were selected. Their ancestral and derived states are discussed. The monophyletic origin of the oxytrichous ciliates is assumed for their longitudinal, fan-like FVT-anlagen, which evolve during the formation of the ventral ciliature. Synapomorphies show the close relationship of oxytrichids "sensu lato" (Pa, Am, Ga) and oxytrichids "sensu stricto" (Hi, St, Ox, Ta, Ur, Ua, Go). Only *Urosomoida* and *Gonostomum* can be justified to be "true" sister groups by autapomorphies at the present state of knowledge. This method furnishes additional arguments for the validity of questionable genera, like *Urosoma* and *Urosomoida*, and for the transfer of *Amphisiella* to the Oxytrichidae. The loss of caudal cirri in *Amphisiella* and *Tachysoma* is interpreted as parallelism. Synapomorphies relate *Histriculus* CORLISS, 1960 to *Stylonychia* EHRENBERG, 1838, but their lack of autapomorphies suggests an invalidity of *Histriculus*. However, the 17 FVT-cirri of "*Histriculus*" *muscorum* imply a slightly distant position, as compared with "typical" *Stylonychia* species, which possess 18 FVT-cirri. *Stylonychia mytilus* and *S. lemnae* are probably more evolved than *S. vorax* and *S. pustulata*, because of their more numerous synapomorphies. The scheme only proves *S. mytilus* and *S. lemnae* to be "true" sister species.

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Introduction

Numerous clones of *Stylonychia mytilus* were shown to belong to 2 varieties (syngens) by AMMERMANN (1965) using the mating type reactivity. But he hesitated to give them species status, because of the variable shape and size of the cells depending on the culture conditions. Recently, STEINBRÜCK and SCHLEGEL (1983) separated these syngens on the basis of their different isoenzyme pattern and DNA content. The assignment of the proper binomen *Stylonychia lemnae* AMMERMANN and SCHLEGEL, 1983 for the variety 1 was confirmed by the discovery of *Podophrya grelli*, a host-specific suctorian, never parasiting *S. mytilus* EHRENBERG, 1838 (variety 2; DIECKMANN 1985).

AMMERMANN and SCHLEGEL (1983) stated that the only morphological features discriminating these species are the shape and the size of the cells, despite the observation of AMMERMANN (1965). However, they did not prove their statement by biometric analyses. In addition, there is a lack of morphogenetic data, which are often useful in separating closely related species (WIRNSBERGER et al. 1985b). The present study was undertaken to fill the gaps left by WALLENGREN (1900), FRICK (1967, 1968), HEMBERGER (1982), and AMMERMANN and SCHLEGEL (1983).

The classification of the oxytrichids is extremely difficult, because of their rather uniform infraciliature and their similar morphogenesis. Thus, the systems and ideas presented by BORROR (1972), CORLISS (1979), MARTIN (1982), and FLEURY and FRYD-VERSAVEL (1984) based on conventional taxonomic procedures are very different. These problems encouraged us to try the method of phylogenetic systematics (HENNIG 1982), which is used more and more in protozoology (LIPSCOMB 1984; EISLER and BARDELE 1983).

Material and Methods

We obtained both species from Dr. SCHLEGEL, University of Tuebingen (FRG). The sources of the 4 strains are given in Table 1. We isolated single specimens for cloning. As a culture medium, tap water was used, with yeast, the flagellate *Chlorogonium elongatum*, and a species of the *Tetrahymena pyriformis* complex added as the food supply. All stocks were maintained at room temperature.

Ciliates were examined carefully in vivo (bright field). The protargol staining method according to FOISSNER (1982) was used to reveal the infraciliature. All measurements were taken by an ocular micrometer. With an oil immersion objective 1 scale mark corresponded to 1.3 μm. Since different statistical procedures were used in order to solve different problems, relevant information will be given in the corresponding section of the chapter "Results". The calculations were performed on a TI-59 minicomputer of Texas Instruments. To make plain the changes during the morphogenetic processes, old cirri were depicted only by contour, whereas the new ones were filled in. The terminology is according to WALLENGREN (1900), KAHL (1932), and BORROR (1972).

All measurements were performed on normal fed individuals from exponentially growing cultures.

Table 1. Sources of *Stylonychia mytilus* and *S. lemnae*

Species	Source and clon number according to SCHLEGEL (personal communication)	Our designation
S. mytilus	lake near Reutlingen-Gönningen (5)	C1
S. mytilus	valley of the Kirnbach, Olgahein (1)	C2
S. lemnae	gardening of Schilde in Wendelsheim (6)	C3
S. lemnae	Spitzberg near Tuebingen (1, mating type 7)	C4

Results

Morphology and biometry (Figs. 1—4, 17; Table 2)

The specimens, cloned from the different strains of *Stylonychia mytilus* and *S. lemnae*, show transitions of the body shape, from more or less parallel margins (Fig. 1) to the striking bulge in the region of the peristome (Fig. 2). They are flattened dorsoventrally about 2 : 1, with a very thin first and last quarter of the cell. Both species constantly possess 2 macronuclear segments (sometimes connected by a fine strand), 18 cirri on the ventral face (except the marginal cirri), and 3 unfringed caudal cirri, very stiff projecting laterally. The dorsal kineties are much more bent apically in *S. mytilus* than in *S. lemnae* (Figs. 3, 4). Dorsal cilia in vivo measure 5 μm, only the anterior basal body is ciliated.

Biometric analyses show that the coefficients of variation of the tested characters are in the same order of magnitude among the 4 clones (Table 2). To discover significant differences, we examined the data by the distribution-free multiple comparison of NEMENY (described in SACHS 1974). This method indicates a highly significant heterogeneity among the 4 clones (see the right column in Table 2). Only the number of the right marginal cirri, the total number of the dorsal cilia, and those within the dorsal kineties 1—4 allow a definite separation. But taking into consideration the extreme values, the unique feature without overlap is the number of dorsal cilia (Table 2). This is the best criterion to discriminate *Stylonychia mytilus* and *S. lemnae* in protargol slides.

The morphological relations among clones can be visualized in the form of a phenogram (Fig. 17). It was constructed from the data of Table 2 by the "Unweighted Pair-Group Method with arithmetic Averages" based on the "Coefficient of Racial Likeness" (SNEATH and SOKAL 1973). *Stylonychia mytilus* collected near Gönningen (C1) contrasts strikingly with *S. mytilus* (C2) and *S. lemnae* (C4) and is more like *S. lemnae* (C3).

Cortical development during cell division (Figs. 5—14)

We did not find any differences in the morphogenesis of *Stylonychia mytilus* and *S. lemnae*. Therefore the statements and drawings are valid for both species.

Stomatogenesis. Small groups of basal bodies evolve very close to the 1st (and sometimes the 2nd too) uppermost transverse cirrus, which remains unchanged (Fig. 5). The number of basal bodies increases and forms a longish anarchic field (Fig. 6). Only the 1st third of the parental undulating membranes is reorganized, because no further dispersal of basal bodies occurs (Figs. 12, 13). The primordium for the undulating membranes of the opisthe evolves from the oral anarchic field (Figs. 9, 10, 11). At this time also the first new adoral membranelles arrange themselves (Figs. 10, 11).

Development of the cirral primordia. In the opisthe the frontal-ventral-transverse (FVT) anlagen 1, 2, and 3 originate from the oral primordium (Figs. 10, 11). The anlagen 4, 5, and 6 are produced by the right postoral ventral cirrus (Figs. 8, 9, 10, 11). In the proter anlage 1 evolves from the parental undulating membranes (Figs. 11, 12, 13); anlage 2 from the oral primordium of the opisthe (Figs. 8, 9, 11); anlage 3 from the left posterior frontal cirrus (Figs. 8, 10, 11); anlage 4 from the right posterior frontal cirrus (Figs. 8, 10); and the anlagen 5 and 6 originate from the right postoral ventral cirrus (Figs. 8, 9, 10). Uniformly 6 FVT-anlagen are produced in each filial product (Figs. 11, 12).

The development of the marginal primordia always starts within the right row and proceeds more rapidly there than in the left row (Fig. 12). Later the events in the

Table 2. Biometric characterization and multiple comparison of 4 clones of *Stylonychia mytilus* EHRENBERG, 1838 and *S. lemnae* AMMERMANN and SCHLEGEL, 1983. All data are based on protargol impregnated specimens. All measurements in μm. C1 = *S. mytilus* (Gönningen); C2 = *S. mytilus* (Olgahein); C3 = *S. lemnae* (Schilde); C4 = *S. lemnae* (Spitzberg); Min = minimum; Max = maximum; n = sample size; ns = non significant; SD = standard deviation; V = coefficient of variation in %; $\bar{x}$ = mean; x = $0.1 \geq P > 0.05$; * = $0.05 \geq P > 0.01$; ** = $P \leq 0.01$

Character	$\bar{x}$	SD	V	Min	Max	n	multiple comparison			
								C2	C3	C4
Body, length	222.4	14.0	6.3	195	256	25	C1	**	**	**
	166.1	14.4	8.8	147	203	15	C2		*	*
	186.3	11.5	6.2	168	211	25	C3			**
	154.9	11.0	7.1	139	180	15	C4			
Body, width at the level of the buccal cirrus	110.9	8.9	8.1	96	127	25	C1	**	**	**
	69.7	9.2	13.1	57	87	15	C2		x	*
	78.7	5.4	6.8	70	95	25	C3			**
	60.1	4.2	7.0	52	68	15	C4			
Body, width at the level of the 3rd transverse cirrus	66.6	9.3	13.9	45	86	25	C1	**	ns	**
	42.1	7.7	18.2	25	58	15	C2		**	ns
	60.2	7.7	12.9	40	78	25	C3			**
	46.6	6.7	14.5	36	61	15	C4			
Distance between the first and the 3rd caudal cirrus	35.3	3.8	10.7	26	42	25	C1	**	**	**
	26.9	4.3	15.9	17	35	15	C2		ns	x
	27.2	4.0	14.8	19	34	25	C3			ns
	24.7	2.1	8.5	21	27	15	C4			
Distance from the anterior end to the last adoral membranelle	118.6	7.7	6.5	102	131	25	C1	**	**	**
	92.3	7.6	8.2	82	112	15	C2		ns	**
	98.4	3.9	4.0	88	105	25	C3			**
	78.7	5.5	7.0	69	88	15	C4			
Paroral membrane, length	72.4	6.4	8.9	59	81	15	C1	ns	**	**
	72.8	6.6	9.1	65	85	15	C2		**	**
	61.2	4.9	8.0	55	71	15	C3			x
	65.4	9.8	15.0	47	84	15	C4			
Endoral membrane, length	62.4	4.3	6.9	56	70	15	C1	ns	**	*
	62.4	7.1	11.3	46	74	15	C2		**	x
	51.4	4.0	7.8	46	57	15	C3			**
	57.5	8.9	15.5	42	73	15	C4			
Macronuclear segment, length	38.5	4.9	12.7	31	45	25	C1	**	**	**
	27.7	2.5	9.1	23	32	15	C2		x	ns
	31.6	3.6	11.4	25	39	25	C3			**
	26.4	4.6	17.3	19	38	15	C4			
Macronuclear segment, width	13.7	1.5	11.0	11	17	25	C1	**	ns	**
	10.9	1.4	12.5	9	13	15	C2		**	ns
	13.2	1.3	10.2	10	15	25	C3			**
	9.6	0.8	8.6	9	11	15	C4			
Number of micronuclei	3.7	0.5	14.2	3	5	25	C1	ns	ns	ns
	3.9	1.0	24.4	3	6	15	C2		ns	ns
	3.4	0.6	18.9	2	5	25	C3			ns
	3.5	0.7	21.4	2	5	15	C4			
Number of adoral membranelles	76.3	2.5	3.3	71	81	25	C1	**	**	**
	68.1	6.1	9.0	52	76	15	C2		**	**
	61.4	2.3	3.7	57	65	25	C3			ns
	58.5	2.5	4.4	52	61	15	C4			

Table 2. (continued)

Character	$\bar{x}$	SD	V	Min	Max	n	multiple comparison			
								C2	C3	C4
Number of left marginal cirri	26.7	1.3	5.0	24	29	25	C1	ns	**	ns
	28.0	1.6	5.9	25	30	15	C2		**	**
	25.0	1.1	4.5	23	27	25	C3			**
	26.5	1.6	6.0	24	29	15	C4			
Number of right marginal cirri	37.4	1.9	5.2	33	42	25	C1	ns	**	x
	39.3	2.9	7.5	33	44	15	C2		**	**
	34.3	1.6	4.6	31	37	25	C3			ns
	35.5	3.1	8.7	31	41	15	C4			
Number of dorsal kineties	6.1	0.3	4.6	6	7	25	C1	ns	ns	ns
	6.3	0.5	7.3	6	7	15	C2		ns	ns
	6.2	0.4	7.0	6	7	25	C3			ns
	6.2	0.4	6.7	6	7	15	C4			
Number of cilia in dorsal kinety 1	97.2	7.1	7.3	88	106	5	C1	ns	*	**
	100.4	10.5	10.5	85	111	5	C2		**	**
	76.8	3.0	3.9	74	81	5	C3			ns
	72.0	5.1	7.2	65	78	5	C4			
Number of cilia in dorsal kinety 2	80.8	5.4	6.7	72	86	5	C1	ns	**	**
	71.2	6.7	9.3	65	81	5	C2		x	*
	54.2	1.9	3.5	51	56	5	C3			ns
	53.8	8.6	16.0	49	69	5	C4			
Number of cilia in dorsal kinety 3	64.0	13.8	21.6	44	66	5	C1	ns	**	**
	60.6	5.8	9.5	53	66	5	C2		**	**
	36.8	2.8	7.5	33	40	5	C3			ns
	37.6	0.9	2.4	37	39	5	C4			
Number of cilia in dorsal kinety 4	51.8	3.3	1.9	47	56	5	C1	ns	**	**
	47.8	6.8	14.3	40	55	5	C2		**	**
	33.6	3.5	10.4	30	39	5	C3			ns
	33.0	2.0	6.1	31	36	5	C4			
Number of cilia in dorsal kinety 5	49.4	9.3	18.9	34	58	5	C1	ns	ns	*
	51.0	6.6	13.0	41	57	5	C2		*	*
	39.6	11.0	27.7	21	49	5	C3			ns
	41.8	3.6	8.5	38	46	5	C4			
Number of cilia in dorsal kinety 6	32.4	2.1	6.4	31	36	5	C1	ns	ns	ns
	32.0	6.6	20.7	23	41	5	C2		ns	ns
	35.8	5.6	15.6	30	45	5	C3			ns
	30.2	6.5	21.6	23	39	5	C4			
Total number of dorsal cilia	369.6	11.8	3.2	358	389	5	C1	ns	**	**
	363.0	35.4	9.8	318	398	5	C2		**	**
	284.6	13.7	4.8	271	304	5	C3			ns
	271.8	10.9	4.0	258	286	5	C4			

marginal rows appear to be correlated (Fig. 13). Five frontal cirri, the buccal cirrus, the left postoral ventral cirrus, the posterior ventral and transverse cirri, and several marginal cirri do not participate in the formation of primordia. The left posterior frontal cirrus and the right postoral ventral cirrus proliferate basal bodies and are partly dissolved (Figs. 10, 11, 12). The rest is resorbed in the last stages of the division, together with the other cirri, which are not involved in building the anlagen.

Further events. The nuclear apparatus divides in the same manner as described in *Stylonychia mytilus* by WALLENGREN (1900) and FRICK (1967, 1968). The differentiation of new cirri (Figs. 12, 13) — the FVT-anlagen 1—6 always generate 1, 3, 3, 3, 4, and 4 cirri —, their migration (Figs. 13, 14), and the development of the dorsal primordia are indistinguishable from those of other members of the genus *Stylonychia* (HEMBERGER 1982; WIRNSBERGER et al. 1985b).

Discussion

Morphological and biometric comparison

AMMERMANN and SCHLEGEL (1983) did not specify from which of the numerous biochemically investigated strains the morphological data were obtained. Thus, a true comparison with their rather fragmentary data concerning the variability among the different stocks is impossible. However, our results (Table 2, Fig. 17) prove that neither the shape nor the size provide criteria for the separation of *Stylonychia mytilus* and *S. lemnae*, as AMMERMANN and SCHLEGEL (1983) suggest. In addition, a highly variable cell size of *S. mytilus* is reported in the literature too (KAHL 1932; DRAGESCO 1966).

In all European clones of *S. lemnae* a second small undulating membrane occurs, which should be absent in a clone of *S. lemnae* from the USA and in *S. mytilus*. This is obviously a misobservation of AMMERMANN and SCHLEGEL (1983), because all hypotrichs — and of course *S. mytilus* too (Fig. 2; Table 2) — show a paroral and an endoral membrane.

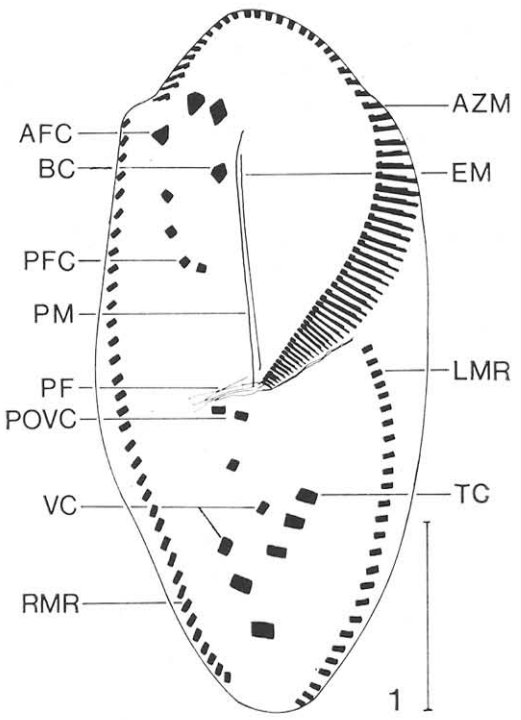
AMMERMANN and SCHLEGEL (1983) conclude from some REM-pictures that the arrangement of the dorsal cilia is the same in both species, which is disproved by our investigations. Indeed, the differences in the dorsal ciliature provide the unique criterion for the separation of *Stylonychia mytilus* and *S. lemnae* (Figs. 3, 4; Table 2).

Another interesting phenomenon is the host-specificity of the suctorian *Podophrya grelli*, which parasites only *S. lemnae*. Its mode of discrimination is unknown, but very effective (DIECKMANN 1985). Unfortunately, neither the dorsal pattern nor the association with *Podophrya grelli* are easily recognizable for field biologists. Thus, we suggest that they should designate these sibling species as "*Stylonychia* sp." or as a "member of the *Stylonychia mytilus* complex", as has recently been recommended by CORLISS and DAGGETT (1983) for the *Paramecium aurelia* and the *Tetrahymena pyriformis* complex.

Figs. 1—4. *Stylonychia lemnae* (1, 3) and *S. mytilus* (2, 4). Infraciliature after protargol impregnation. 1, 2: ventral view. AFC = anterior frontal cirri, AZM = adoral zone of membranelles, BC = buccal cirrus, EM = endoral membrane, LMR = left marginal row, PF = pharyngeal fibers, PFC = posterior frontal cirri, PM = paroral membrane, POVC = postoral ventral cirri, RMR = right marginal row, TC = transverse cirri, VC = ventral cirri. 3, 4: dorsal view. CC = caudal cirri, Ma = macronucleus, Mi = micronucleus, 1—6 number of dorsal kineties. Scales: 50 μm.

Figs. 5—10. *Stylonychia mytilus* complex. Morphogenetic stages in ventral view. 5—7: early events in *S. lemnae*. Arrows point to the oral primordium (OP). 8: detail of the development of cirral primordia in *S. mytilus*. 9, 10: intermediate morphogenetic stages in *S. lemnae*. Arrows point to the disintegrated right postoral ventral cirrus. The additional, unusual ventral cirrus in Fig. 10 is probably been left by the last cell division. Scales: 50 μm.

Figs. 11—14. *Stylonychia lemnae*. 11—13: late morphogenetic stages in ventral view. MP = marginal primordium. 14: ventral view of the opisthe immediately after cell division. Broken lines show the displacement of the frontal-ventral-transverse cirri. Scales: 50 μm.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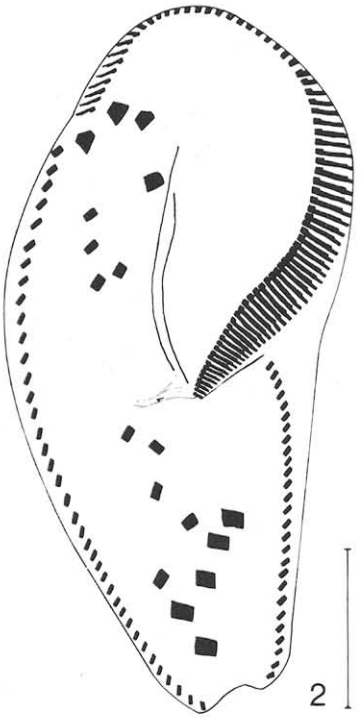
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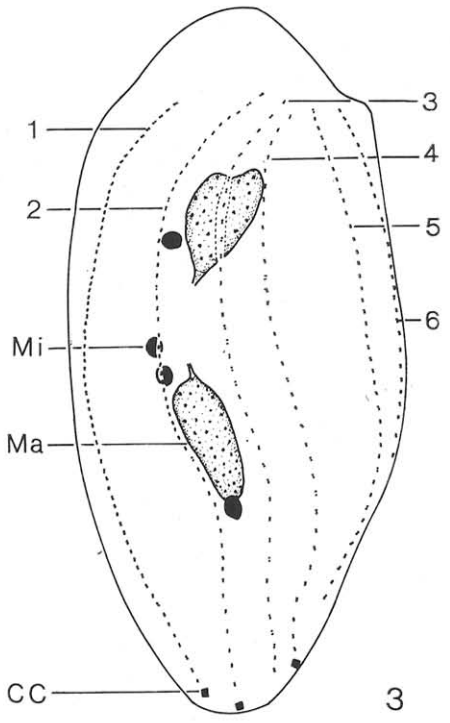
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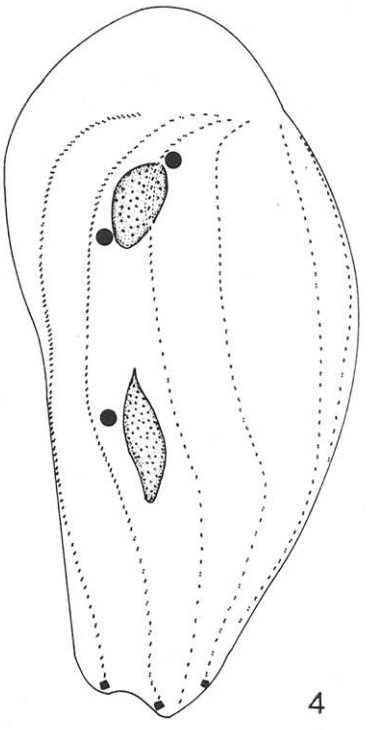
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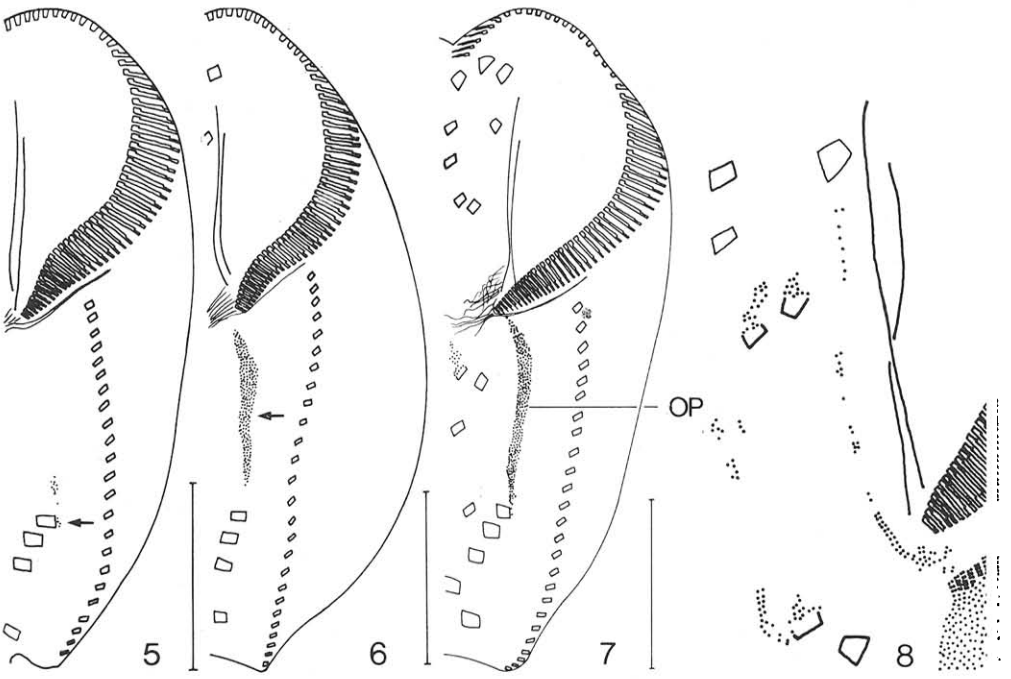
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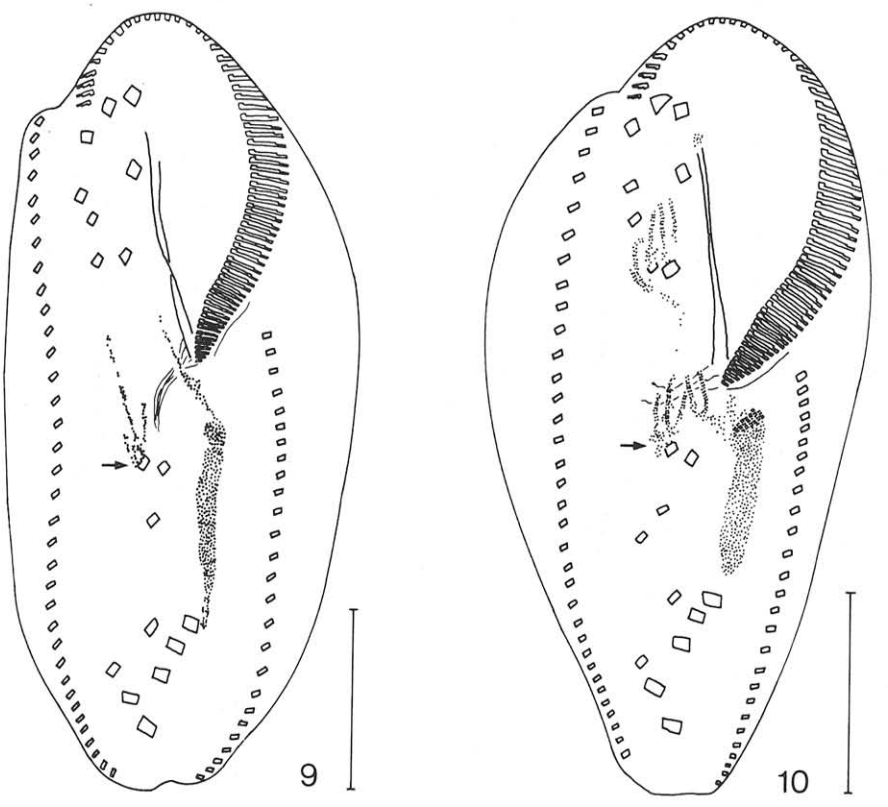
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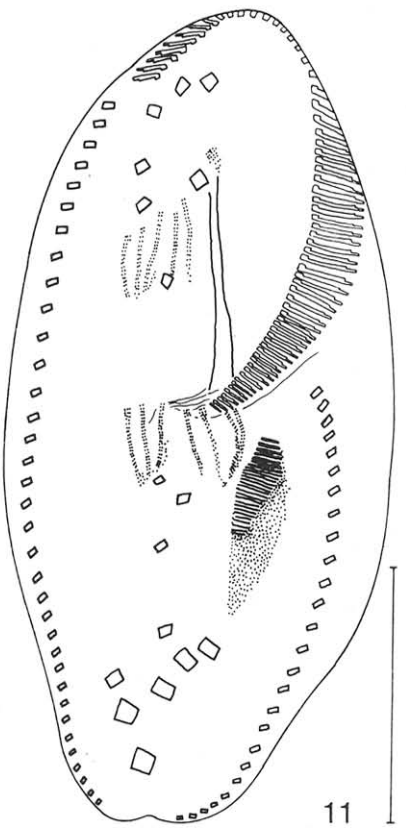
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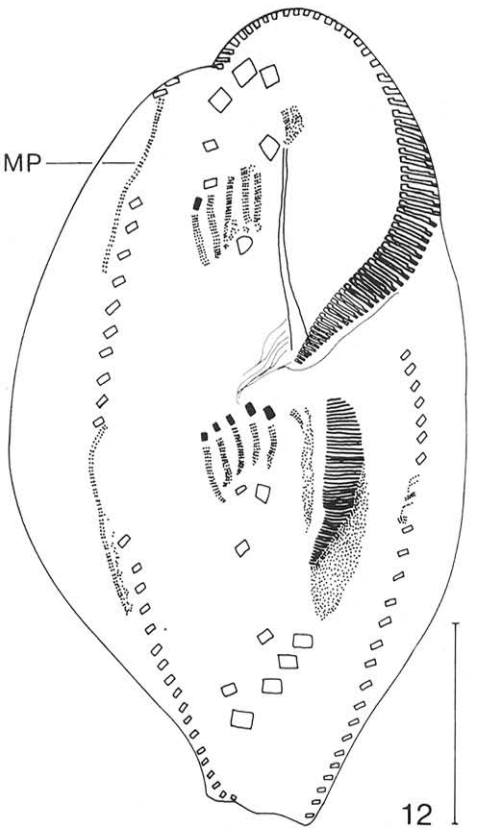
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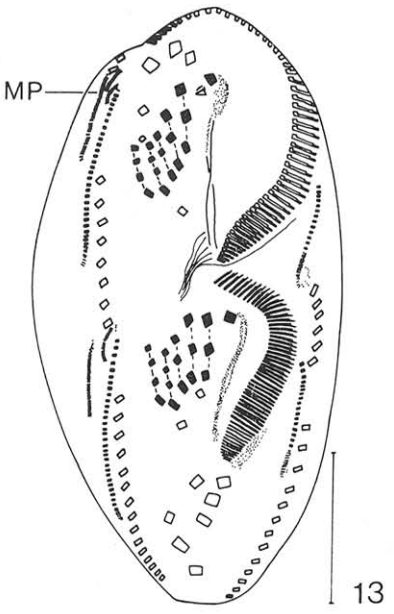
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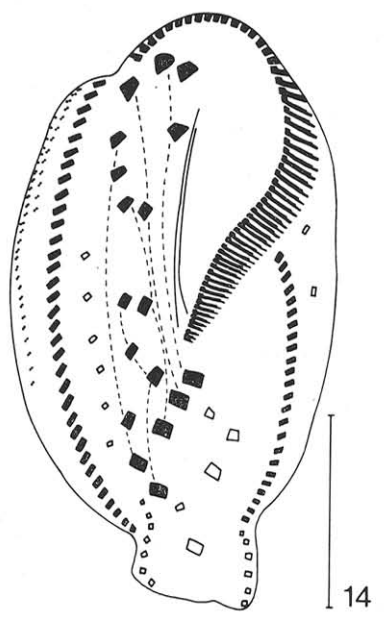
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Our attempt to separate *Stylonychia mytilus* and *S. lemnae* by UPGMA clustering was unsuccessful (Fig. 17). However, other examples demonstrate that numerical taxonomy can be useful to show racial differences (BERGER et al. 1985; SCHÖNBORN et al. 1983).

Divisional morphogenesis

The only almost complete, but unfortunately unpublished, description of the infraciliature during cell division of a "member of the *Stylonychia mytilus* complex" is given by HEMBERGER (1982). Our comparative study of the morphogenetic processes in *S. mytilus* and *S. lemnae* reveals some additional information. We could not find "de novo" anlagen in the frontal area, as supposed by HEMBERGER (1982) (Figs. 8, 10). He believes that the left posterior frontal cirrus remains intact, which is disproved by our observations (Figs. 8, 10, 11). But the misinterpretation of HEMBERGER (1982) is understandable, because this cirrus proliferates basal bodies only in the first stages and remains partly undissolved for a long time (Figs. 11, 12, 13). He mentions correctly that neither the buccal cirrus nor the 3rd postoral ventral cirrus participates in the formation of primordia. We found this particularity applied to the left postoral ventral cirrus too (Figs. 10, 11, 12, 13). These differences and the lower number of dorsal cilia in the Fig. 42 of HEMBERGER (1982) could be explained by the assumption of a third sibling species within the "*Stylonychia mytilus* complex".

Phylogenetic relations among the oxytrichids

BORROR (1972, 1979), CORLISS (1979), and others argue for the use of morphogenetic data in constructing ciliate phylogeny. FLEURY and FRYD-VERSAVEL (1984) suppose that the cirral pattern of the hypotrichs originates from many convergent evolutionary lines. Thus, they also favour morphogenetic characters. We point out that some types of stomatogenesis may have evolved by convergence too. For instance, the oral primordium appears "de novo" in more than 1 family. Similarly, within a genus, there are species with an apokinetal and a parakinetal stomatogenesis (WIRNSBERGER et al. 1985b; BUITKAMP 1975). In contrast, all other morphogenetic events are sometimes the same, for example in *Stylonychia vorax* and *S. pustulata*, although both species are clearly separable by their infraciliary pattern during the interphase (WIRNSBERGER et al. 1985b). For these reasons, we use selected morphological features and the way of building the FVT and dorsal primordia in our "scheme of argumentation of phylogenetic systematics".

Hypotrichs with many meridional cirral rows and an inconspicuous frontal ciliature, for instance *Kahliella*, are generally considered to be "primitive" (TUFFRAU 1979; CORLISS 1979; FLEURY and FRYD-VERSAVEL 1984; WICKLOW 1982). An increase of ciliary organelles (polymerization) is probably associated with early ciliate evolution, whereas their decrease (oligomerization by reduction or fusion) is associated with recent evolutionary events (WICKLOW 1981, 1982). There are certain degrees of oligomerization in all of the selected 8 characters. Thus, we decide they are derived traits (Table 3; exemplified for the characters 1 and 7 in Table 4).

We assume the monophyletic origin of the oxytrichids, because of their longitudinal, fan-like FVT-anlagen. This is probably the derived state of the development of cirri from a longitudinal series of oblique streaks (BORROR 1972; CORLISS 1979; WICKLOW 1981, 1982; FLEURY 1983).

We propose that the ancestral character state is probably represented by a *Paraurostyla*-like taxon, where the old ciliature participates extensively in the formation of the primordia of new organelles (characters 6 and 8; comp. JERKA-DZIADOSZ 1980).

Table 3. Ancestral and derived characters in the phylogeny of oxytrichids. BC = buccal cirrus; DK = dorsal kinety; FC = frontal cirrus; FVT = frontal-ventral-transverse; POVC = postoral ventral cirrus; RMP = right marginal primordium

Character		Character state	
		Ancestral	Derived
1	Number of FVT-cirri	high (36—100)	reduced (30—20) ′: 18—17 ″: 16—15 ‴: 14
2	Arrangement of cirri on the ventral side	at least 2 long ventral rows, frontal cirri, transverse cirri, 1 right and 1 left marginal row	1 long, 1 short ventral row ′: no ventral rows, 3 POVC close behind the peristomial lip ″: 3rd POVC displaced posteriorly ‴: POVC displaced to the frontal area
3	Number of dorsal kineties	7—9	6—5 ′: 4 ″: 3
4	Number and site of caudal cirri	10—18 in DK 1, 2, 4	3 in DK 1, 2, 4 ′: 3 in DK 1, 2, 3 ″: absent
5	Number of FVT-anlagen	6—9	always 6
6	Participation of old FVT-cirri in the formation of anlagen	many (variable number)	few (1 BC, 1—2 FC, 3 POVC) ′: (1 BC), 2 FC, 2 POVC
7	Number of new cirri formed in FVT-anlagen	highly variable	constant (1, 2—3, 3, 3, 4, 4) ′: 1, 2, 2, 2, 4, 4—5 ″: 1, 2, 2, 2, 3, 4
8	Development of dorsal primordia	fragmentation of DK 3 3—6 DK from RMP	1—2 from RMP ′: no fragmentation ″: no DK from RMP

Martin (1982) and Martin et al. (1983) suggest that *Laurentiella acuminata* is a primitive member of the Oxytrichidae and related to the Stichotrichina through the genera *Pleurotricha* and *Paraurostyla*. They consider *Paraurostyla* to be an evolved group within the stichotrichids. On the contrary, we agree with Borror (1979), Tuffrau (1979), and Jerka-Dziadosz (1980) that *Paraurostyla* is an oxytrichid, because it does not possess midventral cirri developing from a longitudinal series of oblique streaks. Martin (1982) and Martin et al. (1983) present some photographs of the morphogenetic events in *Laurentiella acuminata*, but their description of the development of some ventral and dorsal primordia is rather unclear. In fact, their observation of sometimes more than 6 FVT-anlagen relate this species to *Paraurostyla weissei* (comp. Wirnsberger et al. 1985a). Because of the still fragmentary data concerning the morphogenesis, we do not include the genera *Pleurotricha* and *Laurentiella* in our "scheme of argumentation".

Table 4. Available data for the differentiation of new cirri in oxytrichous species. FVT = frontal-ventral-transverse

Species (Literature)	Cirri in FVT-anlage						Number of FVT-cirri
	1	2	3	4	5	6	
Paraurostyla weissei (WIRNSBERGER et al. 1985a)	1 (anlagen	2—3 7—9)	2—8 7—22	9—18 7—27	4—24 19—22	4—23	89—121
Laurentiella acuminata (MARTIN et al. 1983)	1	4—6	7	7—8	6—8	6—11	36—46
Amphisiella marioni (WICKLOW 1982)	1	3	3	3—4	18—23	7—10	35—44
Gastrostyla steini (HEMBERGER 1982)	1	2	3	3—4	9	7	25—26
Oxytricha granulifera (FOISSNER and ADAM 1983a)	1	3	3	3	4	4	18
O. fennica (HEMBERGER 1982)	1	3	3	3	4	4	18
O. pseudosimilis (HEMBERGER 1982)	1	3	3	3	4	4	18
O. crassistillata (HEMBERGER 1982)	1	3	3	3	4	4	18
O. longa (HEMBERGER 1982)	1	2	3	3	4	4	17
O. terrestris (HEMBERGER 1982)	1	2	3	3	4	4	17
Histriculus muscorum (BERGER et al. 1985)	1	2—3	3	3	4	4	17—18
Stylonychia grandis (HEMBERGER 1982)	1	2—3	3	3	4	4	17—18
S. mytilus (present paper)	1	3	3	3	4	4	18
S. lemnae (present paper)	1	3	3	3	4	4	18
S. vorax (WIRNSBERGER et al. 1985b)	1	3	3	3	4	4	18
S. pustulata (WIRNSBERGER et al. 1985b)	1	3	3	3	4	4	18
Tachysoma pellionella (HEMBERGER 1982)	1	3	3	3	4	4	18
T. terricola (HEMBERGER 1981)	1	3	3	3	4	4	18
Urosoma macrostyla (FOISSNER 1983)	1	3	3	3	4	4	18
Gonostomum affine (HEMBERGER 1985)	1	2	2	2	4	4—5	15—16
Urosomoida agilis (BUITKAMP 1975)	1	2	2	2	3	4	14
U. agiliformis (FOISSNER and ADAM 1983b)	1	2	2	2	3	4	14

In *Amphisiella marioni* neither caudal cirri nor postoral ventral cirri are differentiated (WICKLOW 1982). In *Gastrostyla steinii*, *G. setifera*, and *G. minima* there is a further reduction of FVT-cirri, especially of the ventral cirri, which are produced by the anlagen 5 and 6 (Table 4). This reduction causes a "groupening" of the cirri (characters 1 and 2 in Table 3; HEMBERGER 1982). Two cirri in the posterior frontal region and 2 cirri near the pharynx are enlarged in *G. steinii* announcing the marked FVT-cirri of the "typical" oxytrichids.

The most widely distributed character states among protists are considered to be ancestral (LYNN and SMALL 1981). Transferring this to the oxytrichids "sensu stricto" — those showing 18—14 FVT-cirri grouped in special regions — and remembering the cirral pattern of *Gastrostyla*, we propose a derived trait to more "grouped" cirri (character 2′). Especially the relative position of the postoral ventral cirri (POVC) seems to deserve more attention. Numerous species of the genera *Oxytricha*, *Tachysoma*, *Urosoma*, and *Urosomoida* show a row of 3 POVC, close behind the peristomial lip (character 2′), which are also involved in the formation of the primordia (character 6; FOISSNER 1982; FOISSNER and ADAM 1983a, b; HEMBERGER 1982). In *Gonostomum*, where the morphogenesis has been described by HEMBERGER (1982), no POVC are recognizable during the interphase, but in the course of cell division the posteriormost cirri in the frontal area behave like the POVC of the above mentioned genera. In the species of the genera *Stylonychia* and *Histriculus* the 3rd POVC is separated by a gap and seems to migrate posteriad (character 2″). In addition, it does not participate in the formation of primordia (character 6′; WIRNSBERGER et al. 1985b; BERGER et al. 1985).

One of the arguments of MARTIN et al. (1983) for a common evolutionary origin of the hypotrich suborders Stichotrichina and Sporadotrichina is their share of dorsomarginal kineties. They exemplify their reduction and consider *Oxytricha agilis*, which is now transferred to the genus *Urosomoida* HEMBERGER, 1985, to be the last derived state. In our concept further derived states are the development of dorsal primordia only within the existing kineties (characters 3′ and 8′) and the loss of the dorsomarginal rows (characters 3″ and 8″).

From our "scheme of argumentation" (Fig. 15) the following testable hypotheses can be derived:

1. Synapomorphies show the close relationship of the investigated genera, but only *Urosomoida* and *Gonostomum* can be justified to be "true" sister groups by autapomorphies at the present state of knowledge.
2. Oxytrichids "sensu lato" possess ventral cirral rows and a variable number of cirri participate in the formation of usually more than 6 longitudinal, fan-like FVT-anlagen.
3. Oxytrichids "sensu stricto" have FVT-cirri restricted to special regions and a certain number of FVT-cirri evolving anlagen which generate at most 1—3—3—3—4—4 FVT-cirri.
4. Our scheme confirms BORROR's (1979) suggestion that the genus *Amphisiella* should be transferred to the Oxytrichidae. In addition, WICKLOW (1982) refers to the homologous morphogenetic pattern of *Amphisiella marioni* and *Gastrostyla*.
5. The lack of caudal cirri in the genera *Amphisiella* and *Tachysoma* is a true case of parallelism, because of the closely related ancestors. Whereas in convergence, the 2 forms with similarities have come from different ancestral types with basically different patterns of organization (HENNIG 1982).
6. The genus *Urosomoida* is defined by HEMBERGER (1985) refering to the beginning of the stomatogenesis at the level of the 3 POVC. As already discussed (p. 176), this

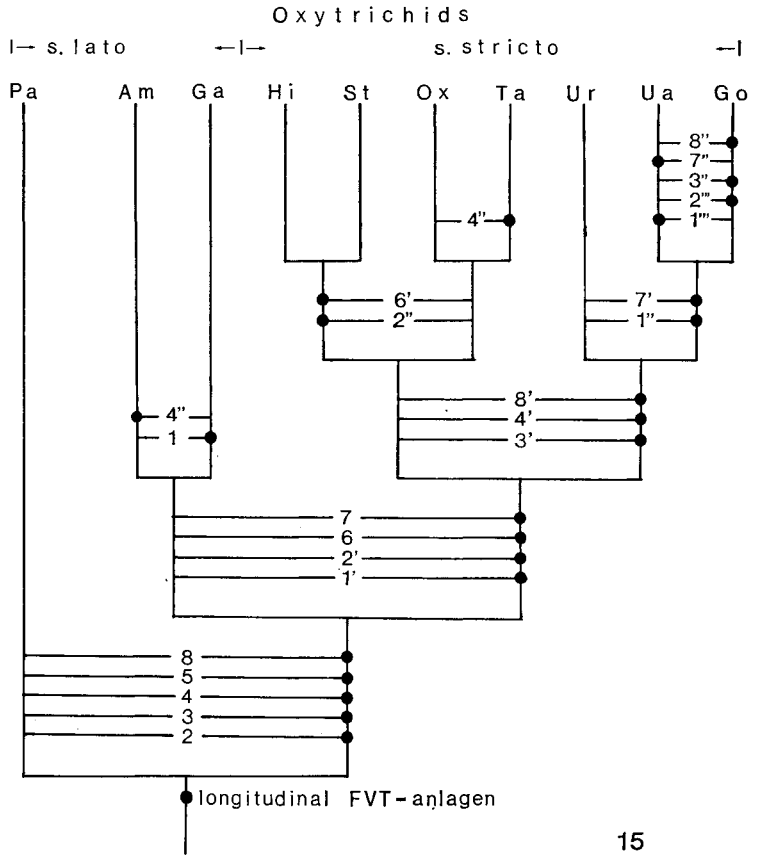

Fig. 15. "Scheme of argumentation of phylogenetic systematics" (cladogram) for 10 oxytrichous genera. The filled circle represents the apomorphy, which applies to the complete originating group. The number refers to the character shown in Table 3. Am = *Amphisiella*, FVT = frontal-ventral-transverse, Ga = *Gastrostyla*, Go = *Gonostomum*, Hi = *Histriculus*, Ox = *Oxytricha*, Pa = *Paraurostyla*, St = *Stylonychia*, Ta = *Tachysoma*, Ua = *Urosomoida*, Ur = *Urosoma*.

character is of no importance at the genus level. However, the cladistic method furnishes other apomorphies which strongly argue for the preservation of this genus. The same is true of *Urosoma*. But within the oxytrichids "sensu stricto" the *Urosoma-Urosomoida-Gonostomum*-group has a special position because their species evolve the oral primordium either "de novo" or with participation of the POVC (BUITKAMP 1975; FOISSNER 1983; FOISSNER and ADAM 1983b; HEMBERGER 1985). The latter mode of stomatogenesis is unusual in species of the genera *Stylonychia*, *Oxytricha*, and *Tachysoma*.

FOISSNER (1983) suggests *Urosoma* and *Gonostomum* are sister groups using other apomorphies. Further studies are necessary to clear the very complicated relations among the *Urosoma-Urosomoida-Gonostomum*-group.

7. The genus *Histriculus* shows more synapomorphies with *Stylonychia* than with the *Oxytricha-Tachysoma*-group. But as far as we know, no autapomorphy justifies the validity of itself. Thus, we consider *Histriculus* CORLISS, 1960 to be a synonym

of *Stylonychia* EHRENBERG, 1838. However, the scheme at the species level (Fig. 16) presents a slightly separate position of "*Histriculus*" *muscorum* if compared with "typical" species of the genus *Stylonychia*.

Very recently, FLEURY and FRYD-VERSAVEL (1984) re-defined the Oxytrichoïdea and introduced the term "monogéne", which means that the cirri of the same ventral anlage appear generally in the same row. We cannot accept this term and consequently the definition for the following reason: FLEURY (1983; Fig. 1) obviously misinterprets the migration of cirri. In the "typical" (means generally accepted and most widely known) oxytrichids the arrangement of the FVT-cirri in the interphase does not reflect in any way the primordial streaks from which they arise (WALLENGREN 1900; BERGER et al. 1985; WIRNSBERGER et al. 1985b). Even in *Paraurostyla weissei*, which shows clear ventral cirral rows, the farthestright ventral row is of composite origin from two FVT-streaks (WIRNSBERGER et al. 1985a). HEMBERGER (1981) shows the same for *Gastrostyla steinii*.

We shall not add a new, new diagnosis for the oxytrichids, because many genera have been left for detailed investigations. For instance, BORROR (1972), CORLISS (1979), HEMBERGER (1982), and FOISSNER (1982) disagree about the systematic position of the following taxa: *Trachelochaeta*, *Hemisincirra*, *Actinotricha*, *Opisthotricha*, *Steinia*, *Amphisiella*, *Engelmanniella*, *Urosoma*, and *Urosomoida*.

Phylogenetic relations among species of the genus *Stylonychia*

For the species level we use the additional characters 3, 4, 5, 6, 7, and 8 (Table 5). The remaining characters are based on the considerations explained above. We do not alter the binomen "*Histriculus*" *muscorum* (Fig. 16), because of the arising problem of homonyms, which is beyond the scope of this paper.

Table 5. Ancestral and derived characters in species of the genus *Stylonychia*. BC = buccal cirrus; FC = frontal cirrus; FVT = frontal-ventral-transverse; LMR = left marginal row; n = sample size; POVC = postoral ventral cirri; $\bar{x}$ = mean

Character		Character state	
		Ancestral	Derived
1	Number of FVT-cirri	constantly 18	sometimes 18, often 17
2	Arrangement of POVC	1st above the 2nd	1st and 2nd side by side
3	Marginal rows	LMR posteriorly J-shaped ("closed")	straight ("open")
4	Number of cilia in each of dorsal kineties 1—4	low ($\bar{x}$ = 18.5, n = 18)	increased ($\bar{x}$ = 49.7, n = 10) ': $\bar{x}$ = 71.7, n = 10)
5	Number of adoral membranelles	low (16—42)	increased (52—81)
6	Special feature	absent	host-specific parasite
7	Begin of the stomatogenesis	close to 1—2 transverse cirri	"de novo"
8	Origin of FVT-anlage 2 in the proter	buccal cirrus	oral primordium
9	Participation of old FVT-cirri in the formation of anlagen	5 (1 BC, 2 FC, 2 POVC)	3 (2 FC, 1 POVC)

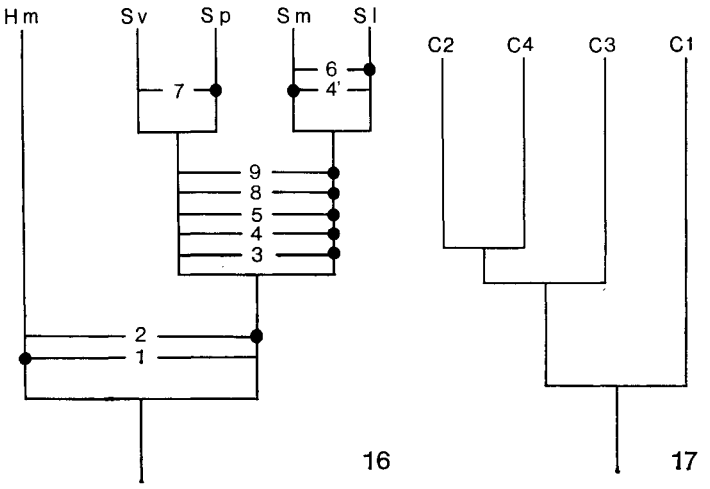

Fig. 16. "Scheme of argumentation" (cladogram) for 5 species of the genus *Stylonychia*. The filled circle represents the apomorphy, which applies to the complete originating group. The number refers to the character shown in Table 5. Hm = "*Histriculus*" *muscorum*, Sl = *Stylonychia lemnae*, Sm = *S. mytilus*, Sp = *S. pustulata*, Sv = *S. vorax*.

Fig. 17. Phenogram of 4 clones of *Stylonychia mytilus* (C1, C2) and *S. lemnae* (C3, C4). UPGMA (Unweighted Pair-Group Method with arithmetic Averages) cluster analysis of the coefficient of racial likeness based on the data of 21 characters presented in Table 2.

Within the genus *Stylonychia* there is one group constantly showing 18 FVT-cirri (character 1; Fig. 16) and a second group, which often lacks the transverse cirrus, generally produced in the FVT-anlage 2 (comp. Table 4). This derived state is described for *Stylonychia grandis*, *Oxytricha terrestris*, and "*Histriculus*" *muscorum* by HEMBERGER (1982) and BERGER et al. (1985). In addition, *Oxytricha terrestris* shows the synapomorphies of *Stylonychia* and should be transfered to it.

A phylogenetic size increase, for instance reported by LYNN (1978) within the genus *Colpoda*, is necessarily accompanied by the development of further cortical elements. In the Sporadotrichina a drastic increase of the portion adoral zone of membranelles size/body size results partly from the increase of the number of adoral organelles (MARTIN 1982). This is certainly true for *Stylonychia mytilus* and *S. lemnae* (character 5) and confirmed by the investigations of FOISSNER (1982) that show a very low uniformity of the number of adoral membranelles in hypotrichs. He mentiones the same for the number of dorsal kineties and we extend this to the number of dorsal cilia too (character 4).

The "de novo" origin of the oral primordium is generally accepted to be a derived trait (character 7; BUITKAMP 1975; CORLISS 1979). Remembering the reduction of cirri which participate in the formation of the FVT-anlagen (character 6 in Table 3), further derived states are recognizable at the species level (characters 8 and 9 in Table 5). Similarily, the widely open marginal rows can be interpreted as an apomorphy (character 3).

The scheme, presented in Fig. 16, does not only show a slightly distant position of "*Histriculus*" *muscorum*, but also the clear separability of the selected species of *Stylonychia* — some of them were often mixed up formerly (AMMERMANN 1965; WIRNSBERGER et al. 1985b). *S. mytilus* and *S. lemnae* are probably more evolved than

S. vorax and *S. pustulata*, because of their more numerous synapomorphies. The scheme only proves *S. mytilus* and *S. lemnae* to be "true" sister species.

Zusammenfassung

Stylonychia mytilus unterscheidet sich von *S. lemnae* nur durch die vorne stärker gekrümmten Dorsalkineten 1—4 und die signifikant höhere Anzahl von Cilien innerhalb derselben. Da diese geringen morphologischen Unterschiede in vivo sehr schwer erkennbar sind, empfehlen wir bei Feldbestimmungen diese Arten als „Mitglied des *Stylonychia mytilus*-Komplexes" zu führen. Die Morphogenese der corticalen Elemente verläuft in den 4 untersuchten Klonen gleich und wird für *S. lemnae* im Detail beschrieben. Jene der Dorsalciliatur und die Kernteilung unterscheiden sich nicht von anderen *Stylonychia*-Arten. Die Stomatogenese beginnt mit der Proliferation von Basalkörpern beim vordersten Transversalcirrus. Drei Frontal-Ventral-Transversal- (FVT-) Anlagen des Opisthen entstehen aus dem Oralprimordium und 3 aus dem rechten postoralen Ventralcirrus. Im Proter entwickelt sich die Anlage 1 aus den parentalen undulierenden Membranen, die Anlage 2 aus dem Oralprimordium des Opisthen, die Anlage 3 aus dem linken hinteren Frontalcirrus, die Anlage 4 aus dem rechten hinteren Frontalcirrus und die Anlagen 5 und 6 stammen aus dem rechten postoralen Ventralcirrus. Die Anlagen 1—6 bringen 1—3—3—3—4—4 Cirren hervor. Mit der Hennigschen Methode der phylogenetischen Systematik wurde versucht, die Verwandtschaft der oxytrichiden Gattungen *Paraurostyla* (Pa), *Amphisiella* (Am), *Gastrostyla* (Ga), *Histriculus* (Hi), *Stylonychia* (St), *Oxytricha* (Ox), *Tachysoma* (Ta), *Urosoma* (Ur), *Urosomoida* (Ua) und *Gonostomum* (Go) zu rekonstruieren. Ihr monophyletischer Ursprung wird wegen der Ausbildung von longitudinalen, fächerförmigen FVT-Anlagen während der Morphogenese angenommen. Acht morphologische und morphogenetische Kriterien werden in das Argumentationsschema einbezogen und ihre ursprünglichen und abgeleiteten Zustände diskutiert. Zahlreiche Synapomorphien begründen die enge Verwandtschaft der Oxytrichiden „sensu lato" (Pa, Am, Ga) und der Oxytrichiden „sensu stricto" (Hi, St, Ox, Ta, Ur, Ua, Go). Ein „echtes" Schwestergruppen-Verhältnis aufgrund von Autapomorphien kann jedoch nur für *Urosomoida* und *Gonostomum* wahrscheinlich gemacht werden. Ferner liefert das Schema Argumente für die Gültigkeit der fragwürdig gewesenen Gattungen *Urosoma* und *Urosomoida* sowie für den Einschluß von *Amphisiella* in die Oxytrichidae. Der Verlust der Caudalcirren bei *Amphisiella* und *Tachysoma* muß als Parallelismus interpretiert werden. *Histriculus* Corliss, 1960 und *Stylonychia* Ehrenberg, 1838 weisen Synapomorphien, aber keine Autapomorphien auf. *Histriculus* könnte daher aufgelöst werden. Die Reduktion der FVT-Cirren auf 17 hebt jedoch „*Histriculus*" *muscorum* von den „typischen" *Stylonychia*-Arten mit 18 Cirren ab. *S. mytilus* und *S. lemnae* sind vermutlich höher evolviert als *S. vorax* und *S. pustulata*, da sie mehr Synapomorphien besitzen. Das Argumentationsschema weist nur *S. mytilus* und *S. lemnae* als „echte" Schwesterarten aus.

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