PROTISTOLOGICA, 1985, T. XXI, fasc. 3, p. 295-311

MORPHOLOGICAL VARIATION AND COMPARATIVE ANALYSIS OF MORPHOGENESIS IN *PARAKAHLIELLA MACROSTOMA* (FOISSNER, 1982) NOV. GEN. AND *HISTRICULUS MUSCORUM* (KAHL, 1932), (CILIOPHORA, HYPOTRICHIDA)

Helmut BERGER, Wilhelm FOISSNER
and Hans ADAM

Institut für Zoologie der Universität Salzburg,
Akademiestraße 26, A — 5020 Salzburg (Austria).

SUMMARY

A comparative analysis of the morphology and the morphogenesis of the kahliellid *Parakahliella macrostoma* nov. comb. and the oxytrichid *Histriculus muscorum* was performed. The morphogenesis of *P. macrostoma* reveals the following peculiarities : a) The primordium III originates from the third anteriormost cirrus of the short frontal row, sugggesting a homology with the cirrus III/2 of the oxytrichids. b) The cirri of the primordium IV migrate in a posteriad direction, forming the left fronto-ventral row of non-dividers. The conformities in pattern formation imply a rather close lineage of the Kahliellidae and Oxytrichidae. c) Each two right and left somatic ("marginal") cirral rows are developed and fragments of the parental dorsal kineties 4 and 5 are conserved as "new kinety 4". The homonomy of the dorsal kineties and marginal rows is proposed. Morphogenesis of *H. muscorum* is similar to that of *Stylonychia* and *Oxytricha*. The phenetic resemblance of 4 alpine populations of *H. muscorum* is assessed on the basis of 29 characters, by means of both a multiple comparison procedure and the coefficient of racial likeness. Both methods give a good reflection of the geographical distances of their sample sites. However, at present it is impossible to decide if the differences observed are due only to effects of the environment upon the phenotype or if they are determined genetically. The analysis of correlation yields only a few significant associations, suggesting a rather great taxonomic value of the selected characters. A comparative consideration of the morphogenetic processes in some species formerly assigned to *Kahliella* and *Paraurostyla* suggests the establishment of two new kahliellid genera. *Parakahliella* nov. gen. is characterized by the presence of caudal cirri and more than one right and one left selfreplicating somatic ("marginal") rows. Because of the conspicuous resemblance of *Parakahliella macrostoma* and *Paraurostyla terricola* the later species is also transferred into the new genus : *Parakahliella terricola* (BUITKAMP, 1977) nov. comb. The evolved frontal ciliature and the high dominance of the somatic cortical pattern in *Kahliella marina* FOISSNER *et al.*, 1982 justify the establishment of a further, presumably ancestral kahliellid genus, *Pseudokahliella* nov. gen. The first character separates it from *Parastrongylidium* and the second from the other related genera.

Key-words : Hypotrichs, *Parakahliella, Pseudokahliella, Histriculus,* morphogenesis, biometric analysis.

RÉSUMÉ

Cette étude est une analyse comparative de la morphologie et de la morphogenèse du Cilié kahliellidé *Parakahliella macrostoma* nov. comb. et du Cilié oxytrichidé *Histriculus muscorum*. La morphogenèse de *P. macrostoma* présente les particularités suivantes : a) le primordium III provient du troisième cirre (ceux-ci étant numérotés d'avant en arrière) de la rangée frontale courte; ceci indique une homologie avec le cirre III/2 des oxytrichidés. b) Les cirres issus du primordium IV tournent vers l'arrière, engendrant la rangée fronto-ventrale gauche des individus quiescents. Ces similitudes dans la formation de l'infraciliature indiquent une proche parenté entre Kahliellidae et Oxytrichidae. c) Les deux rangées, droites et gauches (« marginales ») se reforment, tandis que des fragments des rangées parentales dorsales 4 et 5 sont conservées, constituant les rangées 4 des deux tomites. Nous considérons les rangées dorsales et marginales comme homonomes. La morphogenèse de *H. muscorum* ressemble à celle de *Stylonychia* et *d'Oxytricha*. La ressemblance phénétique entre 4 populations alpines de *H. muscorum* est estimée d'une part par application d'une technique non paramétrique de comparaisons multiples

Manuscrit reçu le 26 décembre 1984, accepté par le Comité de lecture le 12 juin 1985.

et d'autre part à l'aide de ressemblance raciale sur la base de 29 caractères. Les deux méthodes rendent bien compte des distances géographiques de leurs provenances. Il reste cependant actuellement impossible de déterminer si les différences observées sont liées à l'influence de l'environnement sur le phénotype, ou attribuables à des facteurs génétiques. Les différents caractères choisis sont en général faiblement corrélés à la longueur cellulaire, ce qui permet de penser qu'ils ont une bonne valeur taxinomique. Une analyse comparative des stades morphogénétiques de quelques espèces, autrefois inclues dans les genres *Kahliella* et *Paraurostyla,* nécessite la création de deux genres nouveaux, proches de *Kahliella. Parakahliella* nov. gen. est caractérisé par la présence de cirres caudaux et de plusieurs rangées autonomes droites et gauches (rangées « marginales »). *Paraurostyla terricola* est transférée dans le nouveau genre *Parakahliella (Parakahliella terricola* (BUITKAMP, 1977) nov. comb.) en raison de sa ressemblance avec *Parakahliella macrostoma.* Par sa ciliature frontale évoluée et par la prépondérance des processus de type « somatique » dans la morphogenèse corticale, *Kahliella marina* FOISSNER *et al.,* 1982 se révèle suffisamment originale pour que cette espèce soit considérée comme appartenant à un genre nouveau, *Pseudokahliella* nov. gen., qui est probablement un Kahliellidae primitif : le premier caractère le sépare du genre *Parastrongyliduim* et le second des autres genres apparentés.

Mots-clés : Hypotriches, *Parakahliella, Pseudokahliella, Histriculus,* morphogenèse, analyse biométrique.

I. — INTRODUCTION

Hypotrichs with a uniform cortical pattern are considered to be less evolved than those with a differentiated and oligomerized pattern (BORROR and EVANS, 1979; CORLISS, 1979; TUFFRAU, 1979). In recent times several unusual soil species with an infraciliature between those of lower and higher hypotrichs have been described (BUITKAMP, 1977; FOISSNER, 1982). However, their positioning in the modern schemes was arbitrary, since no data were available about their ontogeny, the most appropriate criterion for homology of the structures usually used in classification of these animals (WALLENGREN, 1900; BORROR, 1979; CORLISS, 1979).

Fortunately, we have now been able to study the morphogenesis of one of these species, and the results allow a comparison with our own data on the evolved hypotrich *Histriculus muscorum* and with those on *Kahliella* published by TUFFRAU (1969) and FLEURY and FRYD-VERSAVEL (1982).

In addition, the present paper describes the first detailed investigation into the variability of different populations of a non-euplotine hypotrich (GATES, 1978).

II. — MATERIAL AND METHODS

Parakahliella macrostoma; 11.8.1982; graded ski trail (0-2 cm), Schloßalm, alt. 1 950 m, Bad Hofgastein, Salzburg. For a detailed description see "Taxotop H" in FOISSNER and PEER (1985).

Histriculus muscorum, population 1; 9.6.1978; wodland, Guttal, Glocknerarea, alt. 1 900 m, Kärnten. For a detailed description see "SO 9" in FOISSNER (1982). Population 2; 23.10.1980; see *P. macrostoma.* Population 3; 29.7.1981; alpine pasture (0-5 cm), Schloßalm, alt. 1 964 m, Bad Hofgastein, Salzburg. For detailed description see "Untersuchungsfläche 11" in BERGER *et al.* (1985). Population 4; 3.7.1982; see population 3.

Parakahliella macrostoma and the populations 1, 2, and 3 of *H. muscorum* were cultivated by the method of FOISSNER (1982). Population 4 was maintained in soil medium with *Colpoda aspera* and air-dried yolk added as the food supply. The protargol method to reveal the infraciliature is described in FOISSNER (1982).

All measurements were performed with an ocular micrometer with one unit = 1 µm at a magnification of 1 250 x. Statistical procedures follow methods described in SNEATH and SOKAL (1973), SOKAL and ROHLF (1981), and SACHS (1984). The populations of *H. muscorum* were compared by a nonparametric a posteriori testing procedure according to NEMENYI (SACHS, 1984) : There are k treatment groups with equal sample sizes n. In this study k = 4 (P 1, P 2, P 3, and P 4) and e.g. n = 15 for the character body length. Rank all (n × k) observations from smallest to largest when pooled together into a single sample. In case of ties, compute the average ranks. Sum the ranks separately for each treatment group and make all possible absolute differences of these sums. If an observed difference between two treatments is as great or greater than a critical value D (Table 180 in SACHS, 1984) then a real difference exists. The results for 29 traits are illustrated in the right column of Table 2. In order to discern geographical variation, we added the "*n*umber of *n*ot *s*ignificantly *d*ifferent *c*haracters" (NNSDC) for each pair of populations at 3 significance levels. These values were converted to percentages with 29 = 100 %, which denotes "total similarity". The same data set was used to calculate the coefficient of racial likeness (C.R.L.). This distance function was favoured over the taxonomic distance since it is scale-independent and considers the variances of the variables (SNEATH and SOKAL, 1973; ATCHLEY *et al.,* 1982). Phenograms were constructed by the unweighted pair-group method with arithmetic averages (UPGMA; SNEATH and SOKAL, 1973).

To make plain the changes during morphogenesis, parental cirri are depicted only by contour, whereas the new cirri are filled in. Terminology follows WALLENGREN (1900), KAHL (1932), and BORROR (1979). Considering the suggestion of the reviewer in the summary and the diagnosis the functional term "somatic ciliature" is used (BORROR, 1979). In the remaining text the more common terms "marginal row" and "dorsal kinety" are employed (KAHL, 1932).

III. — RESULTS

1. ***Parakahliella macrostoma*** (FOISSNER, 1982) nov. comb. (Figs. 1-12, Tables 1, 4).

1.1. *Non-dividing specimen* (Figs. 1, 2, Table 1).

The in vivo aspect of the alpine population (140-160 × 50-55 µm; n = 2) agrees largely with the type material (FOISSNER, 1982). However, during diastole the contractile vacuole possesses a posterior as well as an anterior channel, and the small crystals, which are dumb-bell-shaped, do not only occur close beneath the pellicule but also in the remaining cytoplasm. Feeds on Desmidiaceae (*Cylindrocystis* sp.), ciliates, etc. The ciliates were caught while *P. macrostoma* is swimming and ingested very rapidly.

The cortical pattern of this population is very similar to that of the type material. Nevertheless, we give a characterization, since study of morphogenesis reveals morphogenetically recognizable differences in the uniform infraciliature.

Adoral zone of membranelles usually formed like a question mark, about 1/3 of body length. Paroral membrane shorter than the endoral one. Three hypertrophied obliquely arranged frontal cirri. Cirri of the buccal and frontal row slightly enlarged. Left fronto-ventral row in a line, but clearly separated from the short frontal one, begins anteriorly at the level of the posterior region of the adoral zone of membranelles, usually terminates near the posterior end of the cell. Right fronto-ventral row arises at the level of the right frontal cirrus, usually terminates more anteriorly than the left one. Often, additional short rows occur to the right or to the left of the right fronto-ventral row. Posterior ends of marginal rows sometimes nearly confluent. Outer row of right marginal cirri usually longer than the inner one, often extending onto the dorso-lateral surface anteriorly. Inner left marginal row J-shaped, extends from the level of the posterior edge of the buccal cavity to the cell's end. Next row usually shorter. The outer marginal rows are most frequently parental fragments with enlarged distances between the cirri.

1.2. *Morphogenesis of cell division* (Figs. 3-12, Table 4).

The first morphogenetic event is the formation of an oral primordium just left of the middle and posterior region of the left fronto-ventral row (Fig. 3). At the right anterior part of this area the development of membranelles has already started. Just anteriorly a small heterogeneous anarchic field is formed. This and some disorganized cirri of the middle part of the left fronto-ventral row shape a ramified primordium (Fig. 4). The second cirrus behind the right hypertrophied frontal one also commences with the development of a primordium (Fig. 4, large arrow). From about this level posteriorly just to the end of the adoral zone of membranelles some cirri of the right fronto-ventral row are modified to a streak (Fig. 4, small arrows). Membranelles of the opisthe's adoral zone organize in a posteriad direction. Simultaneously, the proliferation of new basal bodies occurs at 2 levels in the dorsal kineties 1, 2, and 3. The nuclear apparatus is unchanged.

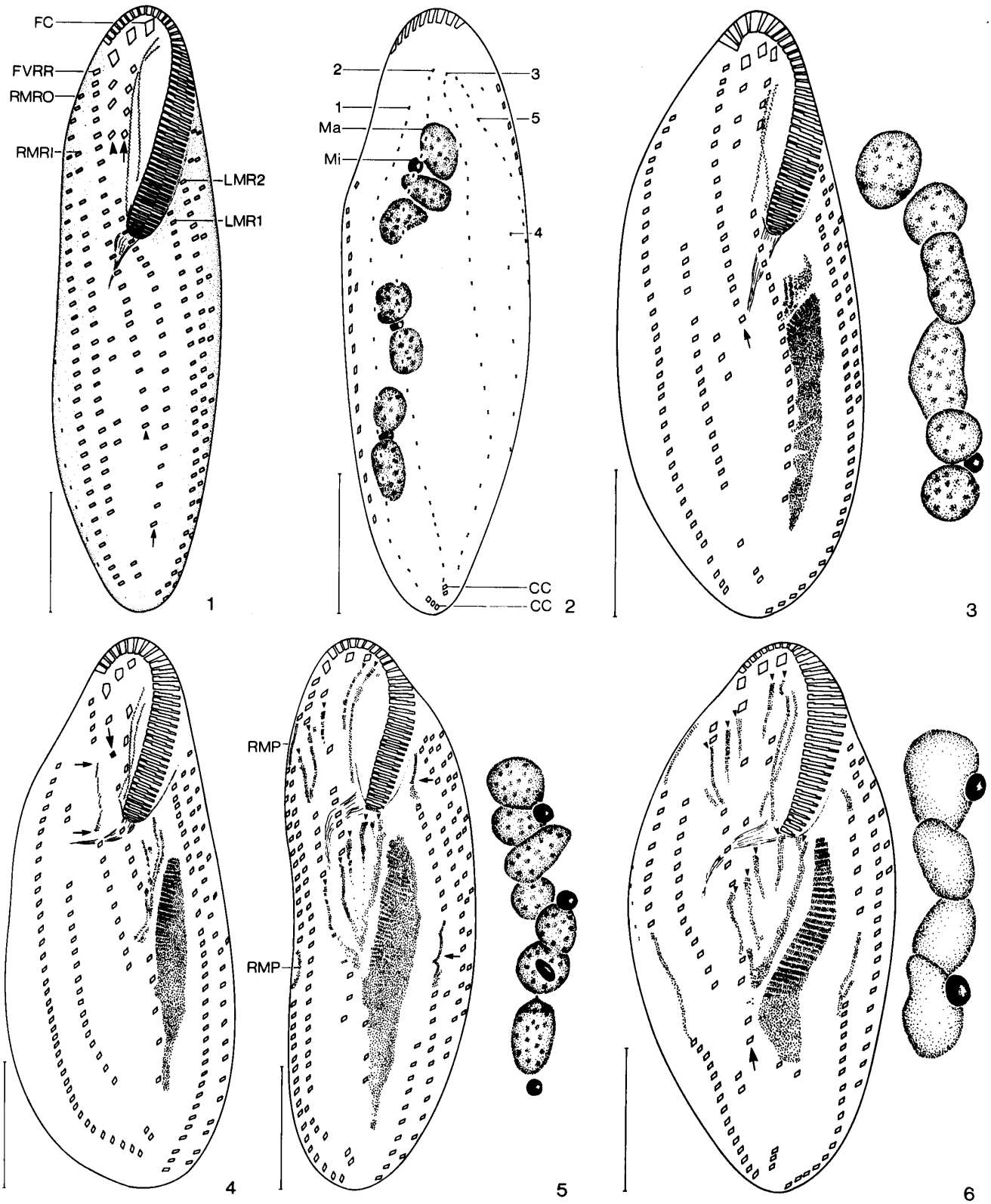
The origin of the fronto-ventral primordia of both the proter and the opisthe is shown in Table 4. Some cirri behind the anteriormost one of the outer right and the anteriormost cirri of the inner left marginal row are modified to the proter's marginal primordia (Fig. 5). The middle regions of the same rows are already incorporated in the primordia of the opisthe. The oral primordium is not far advanced in the formation of membranelles.

Division continues with the maturation of the primordia (Fig. 6). Both in the proter and in the opisthe 5 fronto-ventral anlagen are recognizable. Occasionally, an additional small streak occurs to the right or to the left of streak V (Figs. 4, 5, 6, 9). Presumably it forms those cirri that appear between or on the right of the ventral rows. The marginal primordia become longer due to incorporation of parental cirri. However, none originate within the inner right and the outer left marginal rows. The macronucleus fragments begin to fuse.

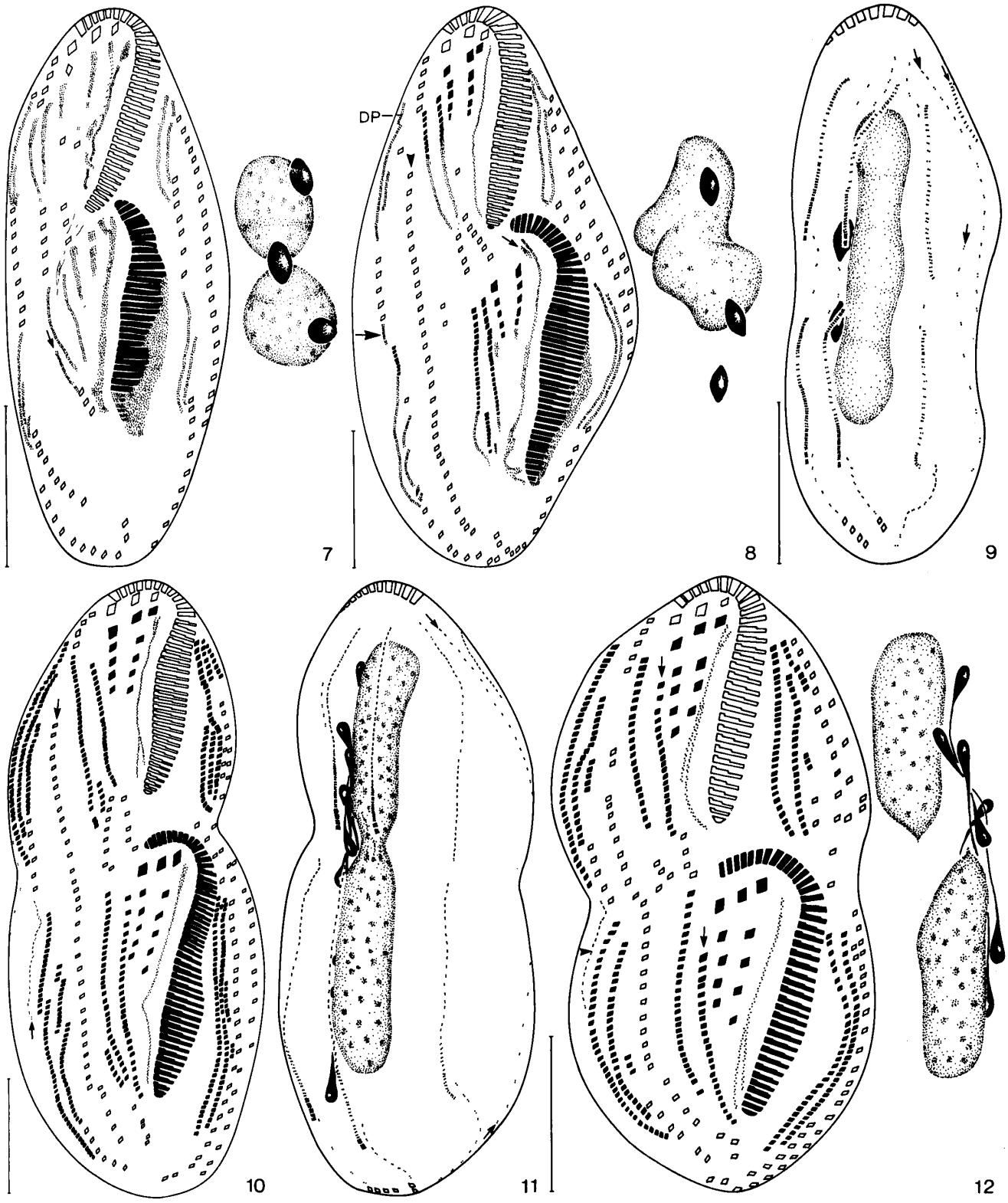
A conspicuous morphogenetic event is the occurrence of additional streaks within each marginal primordium (Fig. 7). They form the inner right and the outer left marginal row respectively. About a quarter of the opisthe's adoral zone of membranelles is still unstructured. The fusion of the macronucleus fragments is almost completed.

Cortical morphogenesis proceeds with the cirral segregation from the fronto-ventral and marginal primordia (Fig. 8). The undulating membranes are fused in both filial products. The right half of the primordium of the adoral zone is clearly modified to the final number of membranelles, while the posterior region of the left one is still undifferentiated. The anteriormost parental cirrus of the outer right marginal row and the one in front of the opisthe's right marginal primordium are modified to primordia of dorsal kineties; it is striking that no further dorsal anlagen can be observed (Fig. 8). Subsequently, these streaks migrate onto the dorsal surface while continuing with the proliferation of new basal bodies (Fig. 9). Caudal cirri develop from the posterior ends of dorsal kineties 1 and 2. The macronucleus and the micronuclei begin stretching (Figs. 8, 9).

By the time the segregation of new cirri is finished, the adoral zone of membranelles of the opisthe has its definitive shape (Fig. 10). The new cirral rows start the extension and migration to form the mature cortical pattern. Some of the new marginal rows are still fragmentary. The parental inner right and outer left marginal row(s) — they do not produce primordial ! — and short fragments of the parental ventral rows are still preserved. The old dorsal kineties 1, 2, and 3 are nearly completely resorbed, while the kineties 4 and 5 are fully maintained (Figs. 9, 11). Presumably they form the new kinety 4 of the opisthe and the proter respectively. Both the cell and the macronucleus are distinctly dumb-bell-shaped. The divided micronuclei are still connected by a thin filament (Fig. 11).



FIGS. 1-6. — *Parakahliella macrostoma* after protargol impregnation. 1, 2 : Non-dividing specimens. 3-6 : Morphogenetical stages in ventral view. 1 : Ventral view. *Large arrow,* buccal row; *large arrow head,* short fronto-ventral row; *small arrow,* left fronto-ventral row; *small arrow head,* right fronto-ventral row. 2 : Dorsal view and nucleus apparatus. 3 : Early stage. *Arrow,* right fronto-ventral row. 4 : Early stage. For explanation see text and Table 4. 5 : Middle stage. The *small arrow heads* point to the 5 fronto-ventral primordia of the proter and opisthe. *Large arrows,* left marginal primordia. 6 : Middle stage. *Small arrow heads,* fronto-ventral primordia; *large arrow,* right fronto-ventral row. Scale mark = 30 μm. CC, caudal cirri; FC, left frontal cirrus; FVRR, right fronto-ventral row; LMR 1, LMR 2, left marginal rows; Ma, macronucleus fragment; Mi, micronucleus; RMP, right marginal primordium; RMRI, RMRO, inner and outer right marginal row respectively; 1-5, dorsal kineties.



FIGS 7-12. — *Parakahliella macrostoma.* Morphogenetical stages in ventral (7, 8, 10, 12) and dorsal view (9, 11). 7 : Middle stage. *Arrow,* additional fronto-ventral streak. 8 : Late stage. *Small arrow,* left frontal cirrus of the opisthe; *arrow head,* inner right marginal row; *large arrow,* primordium of the dorsal kinety 5 of the opisthe. 9 : Late stage. *Small arrow,* dorsal kinety 5 of the proter; *anterior and posterior large arrow,* parental dorsal kinety 5 and 4. 10 : Late stage; *Small arrow,* dorsal kinety 5 of the opisthe; *large arrow,* inner right marginal row. 11 : Late stage. *Anterior and posterior arrow,* parental dorsal kinety 5 and 4. 12 : Late stage. *Arrow,* left fronto-ventral row; *arrow head,* dorsal kinety 5 of the opisthe. Scale mark = 30 μm. DP, primordium of dorsal kinety 5 of the proter.

TABLE 1

Biometrical characterization and comparison of 2 populations of *Parakahliella macrostoma* (1).

Character	$\bar{x}$	SD	CV	Min	Max	n	Test
Body,	127.4	20.12	15.8	98.0	171.0	25	t_s =
lenght (2)	106.4	13.27	12.5	86.0	130.0	10	3.035**
Body,	38.4	8.88	23.1	27.0	61.0	25	t_s =
width	40.3	7.06	17.5	28.0	53.0	10	0.588
No.	7.4 (4)	1.39	18.7	5.0	10.0	25	D_s =
Ma	10.6	1.51	14.2	8.0	13.0	10	180***
Posterior	13.1	2.72	20.7	8.0	19.0	25	t_s =
Ma, length	9.3	1.54	16.6	7.0	12.0	10	4.198***
Posterior	8.3 (4)	1.63	19.5	6.0	12.0	25	D_s =
Ma, width	5.4	1.59	29.2	4.0	8.0	10	190***
AZM,	44.5 (4)	11.29	25.2	32.0	76.0	21	D_s =
length	40.7	6.57	16.1	27.0	50.0	10	50
No.	50.8	12.61	24.8	40.0	75.0	8	t_s =
AM	52.5	6.22	11.9	38.0	61.0	10	0.572
No.	5.0	0.00	0.0	5.0	5.0	25	
DK	5.0	0.00	0.0	5.0	5.0	10	
No.	2.9 (4)	0.79	26.7	2.0	5.0	25	D_s =
LMR	4.2 (4)	0.42	10.0	4.0	5.0	10	200***
No.	4.4 (4)	0.87	19.7	4.0	8.0	25	D_s =
CRR	4.1 (4)	0.32	7.7	4.0	5.0	10	65
No. cirri	4.5 (4)	1.19	26.6	3.0	8.0	15	D_s =
FVRS (3)	4.3 (4)	0.71	16.3	3.0	5.0	9	24
No. cirri	17.3	3.24	18.8	13.0	24.0	15	t_s =
FVRL	22.0	4.96	22.5	15.0	30.0	8	2.753*
No. cirri	17.4 (4)	3.46	19.9	13.0	27.0	22	D_s =
FVRR	24.8	4.25	17.2	18.0	33.0	10	168***
No. cirri	16.3	4.2	25.7	8.0	25.0	25	t_s =
RMRI	22.8	5.25	23.0	18.0	35.0	10	3.829***
No. cirri	29.2 (4)	7.13	24.4	13.0	37.0	24	D_s =
RMRO	32.6	4.50	13.8	25.0	40.0	10	52
No. cirri	25.0	6.77	27.1	14.0	47.0	24	t_s =
LMR1	29.5	5.36	18.2	19.0	35.0	9	1.788
No. cirri	16.5	4.26	25.7	10.0	27.0	25	t_s =
LMR2	20.6	5.72	27.7	13.0	29.0	9	2.255*
No. cirri	8.7 (4)	5.55	63.8	3.0	29.0	23	D_s =
LMR3	15.3 (4)	3.74	24.3	7.0	20.0	8	113*
No. cirri	6.7	1.50	22.2	5.0	8.0	4	D_s =
LMR4	5.8 (4)	3.40	57.9	3.0	13.0	8	16
No.	3.0	0.00	0.0	3.0	3.0	25	
CF	3.0	0.00	0.0	3.0	3.0	10	
No.	3.0 (4)	0.84	27.7	2.0	5.0	25	D_s =
CB	3.9 (4)	1.10	28.2	3.0	6.0	10	75
No. basal body	10.6	1.97	18.6	7.0	13.0	12	
pairs in DK4	—	—	—	—	—	0	
No. basal body	14.5	2.43	16.7	11.0	19.0	12	
pairs in DK5	—	—	—	—	—	0	
No. all	4.8 (4)	0.80	16.5	3.0	7.0	25	D_s =
CC	5.0	0.91	18.9	4.0	6.0	10	70
No. CC	3.0 (4)	0.57	18.6	2.0	5.0	25	
in DK1	—	—	—	—	—	0	
No. CC	1.7 (4)	0.44	24.8	1.0	2.0	25	
in DK2	—	—	—	—	—	0	

(1) All data are based on protargol-impregnated specimens. All measurements in µm. Legend : AM, adoral membranelles; AZM, adoral zone of membranelles; CB, CC, CF, buccal, caudal, and frontal cirri; CRR, cirral rows right to the median; CV, coefficient of variation in %; DK, dorsal kineties; D_s, test statistic of the Kolmogorov-Smirnov two-sample test; FVRL, FVRR, FVRS, left, right, and short fronto-ventral row; LMR1-4, left marginal rows, LMR1 is the inner one; Ma, macronucleus fragment(s); Max, maximum value; Min, minimum value; n, sample size; RMRI, RMRO, inner and outer right marginal row, SD, standard deviation; t_s, test statistic of the t-test; $\bar{x}$, arithmetic mean; *, $0.05 \geqslant P > 0.01$; **, $0.01 \geqslant P > 0.001$; ***, $P \leqslant 0.001$; two-tailed.

(2) Upper line, alpine population; lower line, type material.

(3) Inclusive the right frontal cirrus.

(4) The values of this sample are not normally distributed (Kolmogorov-Smirnov one-sample test for intrinsic hypothesis; $\alpha = 0.05$; two-tailed).

TABLE 2

Biometrical characterization and comparison of 4 populations of *Histriculus muscorum* (5)

Character		x̄	SD	CV	Min.	Max.	n	Multiple Comparison (6) P1	P2	P3
Body, length	P1	81.7	4.46	5.5	72.0	88.0	15			
	P2	73.6 (7)	8.44	11.5	52.0	82.0	15	*		
	P3	71.5	6.24	8.7	61.0	82.0	15	**	ns	
	P4	64.9	5.38	8.3	57.0	75.0	15	**	*	ns
Body, width		42.8	5.75	13.4	33.0	50.0	15			
		40.7	6.28	15.4	26.0	50.0	15	ns		
		35.6	4.24	11.9	29.0	44.0	15	*	ns	
		32.7	3.97	12.1	28.0	42.0	15	**	**	ns
No. Ma		2.0	0.00	0.0	2.0	2.0	15			
		2.0	0.00	0.0	2.0	2.0	15	ns		
		2.0	0.00	0.0	2.0	2.0	15	ns	ns	
		2.0	0.00	0.0	2.0	2.0	15	ns	ns	ns
Anterior Ma, length		17.4	2.07	11.9	14.0	21.0	15			
		14.2	2.93	13.6	9.0	17.0	15	**		
		13.0 (7)	1.51	11.6	11.0	16.0	15	**	ns	
		14.8	1.28	8.6	13.0	17.0	15	×	ns	×
Anterior Ma, width		10.3 (7)	0.82	7.9	9.0	11.0	15			
		8.8	0.96	10.9	7.0	11.0	15	ns		
		7.1 (7)	0.72	10.1	6.0	8.5	15	**	**	
		7.2 (7)	0.53	7.3	6.5	8.0	15	**	**	ns
Ma, distance between		9.3 (7)	3.18	34.0	2.0	13.0	15			
		7.8	1.89	24.1	5.0	12.0	15	ns		
		7.6	3.73	48.9	3.0	15.0	15	ns	ns	
		5.9	2.12	35.7	2.0	10.0	15	**	ns	ns
Posterior Ma, length		17.1 (7)	2.19	12.8	14.0	21.0	15			
		15.1	2.19	14.5	9.0	18.0	15	ns		
		14.1	2.16	15.3	11.0	19.0	15	**	ns	
		15.2	3.09	20.4	11.5	20.0	15	×	ns	ns
Posterior Ma, width		10.2	0.92	9.0	9.0	12.0	15			
		8.2 (7)	1.03	12.5	7.0	10.0	15	*		
		7.2 (7)	0.65	9.0	6.0	8.0	15	**	ns	
		6.7 (7)	0.86	12.8	5.0	8.0	15	**	*	ns
Anterior Mi, greatest diameter		2.4	0.38	15.6	2.0	3.0	6			
		2.1 (7)	0.20	9.8	2.0	2.5	6	ns		
		2.1 (7)	0.20	9.8	2.0	2.5	6	ns	ns	
		2.3 (7)	0.27	12.2	2.0	2.5	6	ns	ns	ns
Posterior Mi, greatest diameter		2.2 (7)	0.26	11.9	2.0	2.5	6			
		2.2 (7)	0.26	11.9	2.0	2.5	6	ns		
		2.1 (7)	0.20	9.8	2.0	2.5	6	ns	ns	
		2.2 (7)	0.26	11.9	2.0	2.5	6	ns	ns	ns
AZM, length		31.1	2.55	8.2	27.0	37.0	15			
		29.4 (7)	2.77	9.4	22.0	33.0	15	ns		
		28.1	2.00	7.1	24.0	31.0	15	*	ns	
		27.5	1.88	6.9	25.0	32.0	15	**	*	ns
No. AM		31.0	2.29	7.4	26.0	34.0	9			
		31.2	1.39	4.5	29.0	33.0	9	ns		
		30.1	3.18	10.6	24.0	34.0	9	ns	ns	
		29.2	1.72	5.9	27.0	32.0	9	ns	ns	ns
No. cirri right MR		20.7	2.10	10.2	17.0	24.0	12			
		18.8 (7)	1.06	5.6	17.0	21.0	12	×		
		18.4 (7)	1.51	8.2	16.0	22.0	12	**	ns	
		19.0 (7)	1.04	5.5	17.0	21.0	12	ns	ns	ns
No. cirri left MR		19.0	1.10	5.8	17.0	21.0	11			
		17.5	1.57	9.0	15.0	20.0	11	ns		
		16.9 (7)	0.94	5.6	15.0	18.0	11	*	ns	
		15.9 (7)	1.64	10.3	12.0	18.0	11	**	ns	ns
No. frontal cirri		3.0	0.00	0.0	3.0	3.0	15			
		3.0	0.00	0.0	3.0	3.0	15	ns		
		3.0	0.00	0.0	3.0	3.0	15	ns	ns	
		3.0	0.00	0.0	3.0	3.0	15	ns	ns	ns
No. buccal cirri		1.0	0.00	0.0	1.0	1.0	15			
		1.0	0.00	0.0	1.0	1.0	15	ns		
		1.0	0.00	0.0	1.0	1.0	15	ns	ns	
		1.0	0.00	0.0	1.0	1.0	15	ns	ns	ns

TABLE 2 *(continued)*

Biometrical characterization and comparison of 4 populations of *Histriculus muscorum* (5)

Character		x̄	SD	CV	Min.	Max.	n	Multiple Comparison (6) P1	P2	P3
No. cirri beside AZM	P1	4.0	0.00	0.0	4.0	4.0	15			
	P2	4.0	0.00	0.0	4.0	4.0	15	ns		
	P3	4.0	0.00	0.0	4.0	4.0	15	ns	ns	
	P4	4.0	0.00	0.0	4.0	4.0	15	ns	ns	ns
No. postoral ventral cirri		5.1 (7)	0.32	6.2	5.0	6.0	10			
		5.0 (7)	0.00	0.0	5.0	5.0	10	ns		
		4.8 (7)	0.42	8.8	4.0	5.0	10	ns	ns	
		5.0 (7)	0.00	0.0	5.0	5.0	10	ns	ns	ns
No. transverse cirri		4.0 (7)	0.41	10.2	3.0	5.0	13			
		3.9 (7)	0.28	7.1	3.0	4.0	13	ns		
		3.9 (7)	0.28	7.1	3.0	4.0	13	ns	ns	
		4.2 (7)	0.38	9.0	4.0	5.0	13	ns	ns	ns
No. caudal cirri		3.0	0.00	0.0	3.0	3.0	14			
		3.0	0.00	0.0	3.0	3.0	14	ns		
		3.0	0.00	0.0	3.0	3.0	14	ns	ns	
		3.0	0.00	0.0	3.0	3.0	14	ns	ns	ns
No. DK		6.0	0.00	0.0	6.0	6.0	12			
		6.0	0.00	0.0	6.0	6.0	12	ns		
		6.0	0.00	0.0	6.0	6.0	12	ns	ns	
		6.0	0.00	0.0	6.0	6.0	12	ns	ns	ns
No. basal body pairs DK1		24.0	2.83	11.8	18.0	28.0	10			
		20.8	2.15	10.3	17.0	24.0	10	×		
		19.4	1.58	8.1	16.0	21.0	10	**	ns	
		21.2	1.14	5.4	19.0	23.0	10	ns	ns	ns
No. basal body pairs DK2		23.4	1.51	6.4	22.0	26.0	8			
		19.6 (7)	0.74	3.8	19.0	21.0	8	**		
		19.4	2.00	10.3	17.0	23.0	8	**	ns	
		20.3	1.39	6.9	19.0	22.0	8	*	ns	ns
No. basal body pairs DK3		16.6	1.41	8.5	14.0	19.0	8			
		13.1	1.73	13.2	11.0	16.0	8	**		
		14.9	1.64	11.0	13.0	18.0	8	ns	ns	
		15.5 (7)	1.20	7.7	13.0	17.0	8	ns	×	ns
No. basal body pairs DK4		16.3	1.73	10.6	13.0	19.0	9			
		14.2 (7)	1.09	7.7	12.0	15.0	9	×		
		12.8 (7)	3.49	27.3	7.0	17.0	9	*	ns	
		14.1	1.90	13.5	12.0	17.0	9	×	ns	ns
No. basal body pairs DK5		10.8	1.99	18.4	7.0	14.0	10			
		8.9 (7)	1.10	12.4	8.0	11.0	10	ns		
		8.2	0.79	9.6	7.0	9.0	10	*	ns	
		7.7	1.70	22.1	6.0	10.0	10	**	ns	ns
No. basal body pairs DK6		4.5	1.51	33.2	2.0	7.0	13			
		3.7 (7)	0.63	17.1	3.0	5.0	13	ns		
		4.0 (7)	0.71	17.7	3.0	5.0	13	ns	ns	
		4.4 (7)	0.77	17.5	3.0	5.0	13	ns	ns	ns
Body, width/body, length (8)		52.4	6.32	12.1	39.5	59.8	15			
		55.3	6.38	11.5	46.2	69.9	15	ns		
		50.0	6.46	12.8	42.7	67.5	15	ns	×	
		50.4	4.87	9.7	44.0	62.5	15	ns	ns	ns
AZM, length/body, length (8)		38.0 (7)	2.60	6.7	35.0	46.2	15			
		40.1	2.50	6.3	36.2	45.5	15	×		
		39.5	2.85	7.2	35.7	44.2	15	ns	ns	
		42.1	2.82	6.7	38.0	47.4	15	**	ns	×

(5) All data are based on protargol-impregnated specimens. All measurements in µm. Legend: AM, adoral membranelles; AZM, adoral zone of membranelles; CV, coefficient of variation in %; DK, dorsal kinety(ies); Ma, macronucleus fragment (s); Max, maximum value; Mi, micronucleus; Min, minimum value; MR, marginal row; n, sample size; P1, P2, P3, P4, population 1-4; SD, standard deviation; x̄, arithmetic mean.

(6) See materials and methods. ns, $P > 0.1$; ×, $0.1 \geq P > 0.05$; *, $0.05 \geq P > 0.01$; **, $P \leq 0.01$; two-tailed.

(7) The values of this sample are not normally distributed. Tested with the Kolmogorov-Smirnov one-sample test for intrinsic hypothesis ($\alpha = 0.05$; two-tailed).

(8) The values are given in %.

TABLE 3

Spearman's coefficient of rank correlation of 17 selected pairs of biometric characters of 4 populations of *Histriculus muscorum* (9).

Character Pair	P 1	n	P 2	n	P 3	n	P 4	n
L-W	0.627	10	0.385	10	0.437	10	0.738*	10
L-MCL	0.372	10	0.552	10	0.311	10	0.462	10
L-MCR	0.307	10	0.563	10	0.044	10	0.762*	10
L-DK 1	0.059	10	0.354	10	−0.152	10	0.629	10
L-DK 2	0.038	10	0.349	10	−0.714*	8	0.549	10
L-DK 3	0.000	9	0.349	10	−0.509	8	−0.209	10
L-DK 4	0.262	10	0.323	10	−0.585	9	0.477	10
L-DK 5	0.284	10	0.283	10	−0.282	10	−0.580	10
L-DK 6	0.370	10	−0.051	10	−0.031	10	0.624	10
MCR-DK 5	0.899**	7	0.249	10	−0.011	10	0.256	10
MCR-DK 6	0.203	8	0.212	10	0.457	10	0.369	10
DK 3 - DK 4	0.251	9	0.056	10	0.358	8	0.072	9
MCR-MCL	0.567	10	0.374	10	0.763*	10	0.502	10
L-AM	0.577	10	0.491	8	0.194	10	0.707*	10
L-AZM	0.608	10	0.677*	10	0.749*	10	0.585	10
AZM-AM	0.892**	10	0.325	8	0.672*	10	0.574	10
L-AMa	−0.202	10	0.752*	10	0.295	10	0.194	10

(9) Legend : AM, number of adoral membranelles; AMa, AZM, length of the anterior macronucleus fragment and of the adoral zone of membranelles respectively; DK 1 - DK 6, number of basal body pairs in dorsal kinety 1 - 6; L, body length; MCL, MCR, number of left and right marginal cirri respectively; n, sample size; P 1, P 2, P 3, P 4, population 1 - 4; W, body width; *, $0.05 \geqslant P > 0.01$; **, $P \leqslant 0.01$ (two-tailed; SACHS, 1984).

The last conspicuous process is the migration of the left fronto-ventral row to its definitive site behind the short frontal row of primordium III (Figs. 1, 12). In both filial products the streak of the undulating membranes begins to separate. A cytopharynx is not recognizable either in the proter or in the opisthe. Both possess 2 new right and 2 new left marginal rows. Occasionally, additional short new marginal rows can be observed. Most of the parental left marginal infraciliature is resorbed, but a variable fraction is preserved in the post-division specimens. The division of the macronucleus fragments and the mitosis of the micronuclei is still going on.

2. ***Histriculus muscorum*** (KAHL, 1932)
(Figs. 13-35, Tables 2-5).

2.1. *Non-dividing specimen* (Figs. 13, 14, Tables 2, 3).

Since there is a detailed description of the non-dividing pattern available (FOISSNER, 1982), we treat only the morphological variability. Six of 29 characters analyzed proved to be constant within and among populations (Table 2). At the $\alpha = 0.05$ significance level the multiple comparison procedure indicates that 7 attributes — number of adoral membranelles, postoral ventral cirri, etc. — are not significantly different between populations. In nearly all of the remaining 16 characters listed in Table 2 the arithmetic mean is distinctly higher in population 1. Hence, the tests reveal that most of the significant differences are between this population and the other ones. For $\alpha = 0.1$, 0.05, and 0.01 the phenograms of the NNSDC method show that population 1 is different from the cluster P 2, P 3, and P 4 in 27 %, 22 %, and 18 % respectively (Fig. 35 a-c). The UPGMA cluster analysis of the coefficient of racial likeness yields a phenogram similar to that given by the previous method (Fig. 35 d). The results of the analysis of correlation are presented in Table 3.

2.2. *Morphogenesis of cell division* (Figs. 15-34, Tables 4, 5).

Because of the pronounced resemblance to related species (see FOISSNER and ADAM, 1983 a; WIRNSBERGER *et al.*, 1985 a), we describe only important and deviating observations.

The stomatogenesis commences just left of the transverse cirrus III/1 and the proliferation of basal bodies yields a long and narrow oral primordium which subsequently enlarges and differentiates to adoral membranelles in a posteriad direction. The cytopharynx of the proter is reorganized (Figs. 15-28).

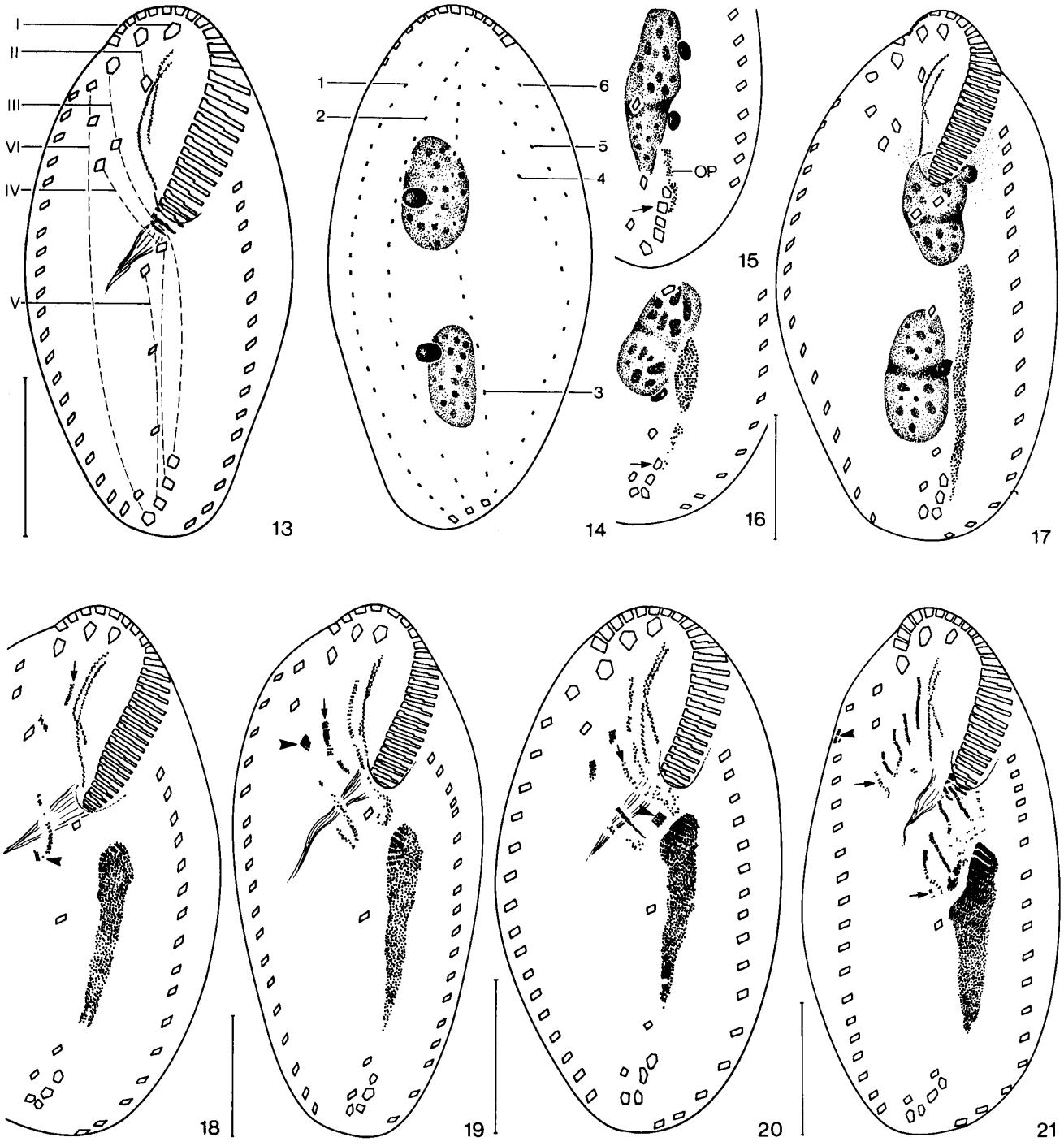
The origin and the order of the development of the 6 fronto-ventral-transverse primordia of both filial products are presented in Table 4 and Figures 18-22. About 88 % of the specimens analyzed biometrically (n = 52) possess 4 transverse cirri (6 % with 5 and 6 % with 3). The high dominant set of 17 cirri, of course without marginal and caudal ones, arises within the streaks as shown in Table 5 and their conspicuous migrations are illustrated in Figures 13, 25-33.

The formation of the new marginal and dorsal rows proceeds as in *Stylonychia vorax* and *S. pustulata* (WIRNSBERGER *et al.*, 1985 a). However, the right marginal primordium of the proter originates from the second anteriormost cirrus (Figs. 21-34).

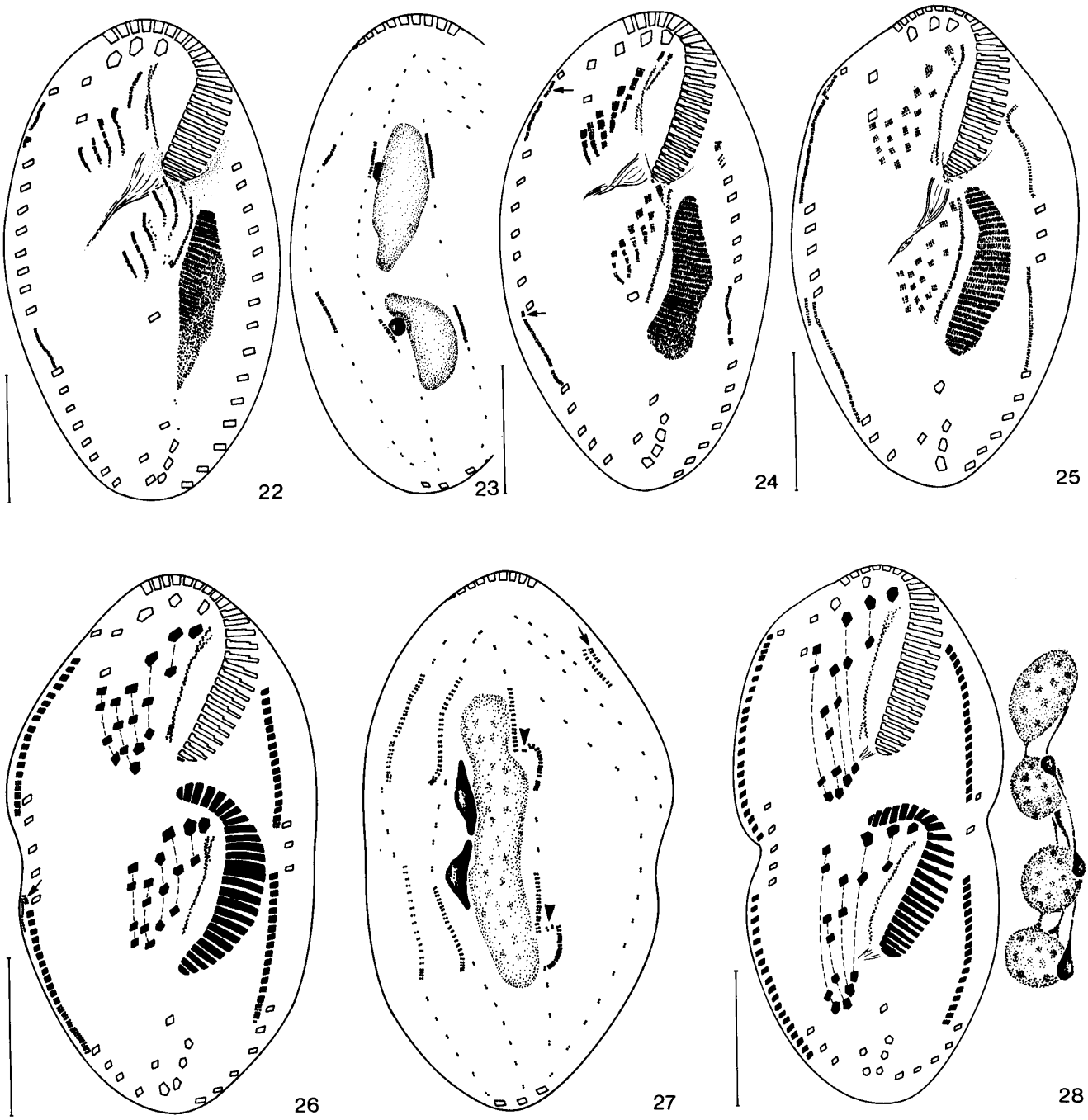
IV. — DISCUSSION

1. Intra- and interpopulation variation of *Parakahliella macrostoma* and *Histriculus muscorum*

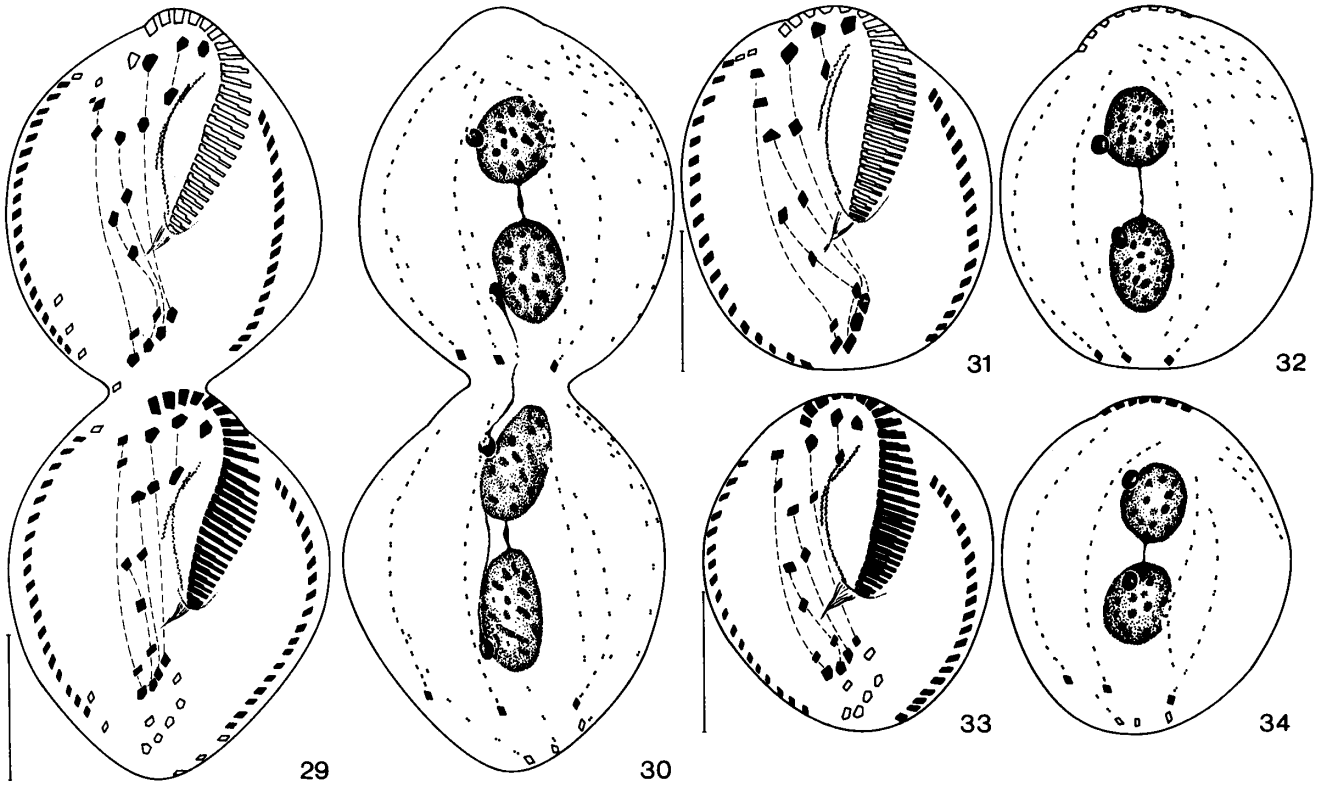
Morphometrical investigations of the alpine population and the type material of *P. macrostoma* shows that only 2 of 21 characters, the number of dorsal kineties and hypertrophied frontal cirri, do not vary within or among populations (Table 1; FOISSNER, 1982). Additionally, in *H. muscorum* the macronucleus fragments, buccal cirri, cirri beside the adoral zone of membranelles, and caudal cirri are constant (Table 2). This agrees with the results of FOISSNER (1982), who emphasizes the conspicuously low variability — and hence the applicability at the species level — of the feature "number of dorsal kineties". However, BORROR and WICKLOW (1983) avoid the employment of this character for species distinction within



FIGS. 13-21. — Morphology and morphogenesis of *Histriculus muscorum* after protargol impregnation. 13, 14 : Non-dividing specimen in ventral and dorsal view. Designation of primordia and cirri according to WALLENGREN (1900). 15-21 : Early and middle stages of morphogenesis in ventral view. 15-17 : Origin of the oral primordium (0P). *Arrow,* transverse cirrus III/1. 18 : The buccal cirrus II/2 *(arrow)* and the ventral cirrus V/4 *(arrow head)* are modified to primordia. 19 : The cirri III/2 *(arrow)* and IV/3 *(arrow head)* also commence with the modification to primordia. 20 : The postoral cirrus IV/3 *(arrow head)* starts with the disorganization. *Arrow,* primordium III. 21 : *Arrow,* primordium VI; *arrow head,* right marginal primordium of the proter. Scale mark = 20 μm. I-VI, fronto-ventral-transverse primordia; 1-6, dorsal kineties.



FIGS. 22-28. — Morphogenesis of *Histriculus muscorum*. 22, 23 : Middle stage in ventral and dorsal view. The dorsal kineties 1, 2, and 3 commence with the proliferation. 24 : Middle stage. *Arrow*, primordium of dorsal kinety 5. 25 : Late stage. The segregation of new fronto-ventral-transverse cirri is finished. 26, 27 : Late stage in ventral and dorsal view. *Arrow*, primordium of dorsal kinety 6; *arrow head*, separation of the dorsal primordia 3 and 4. 28 : Late stage. Scale mark = 20 μm. The cirri of a primordium are connected by a dotted line.



FIGS. 29-34. — Morphogenesis of *Histriculus muscorum*. 29, 30 : Very late stage in ventral and dorsal view. 31-34 : Proter (31, 32) and opisthe (33, 34) in dorsal and ventral view. Scale mark = 20 µm. The cirri of a primordium are connected by a dotted line.

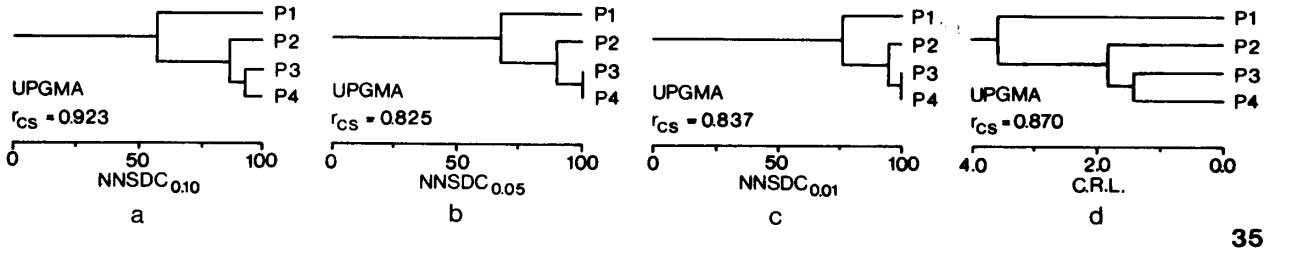


FIG. 35. — Phenograms of 4 populations (P 1 - P 4) of *Histriculus muscorum*. **a-c** : UPGMA clustering of the number of not significantly different characters (NNSDC) in % obtained by multiple comparison procedures on 29 characters (= 100 %) presented in Table 2. Significance levels for multiple comparison procedures $\alpha = 0.10$ **(a)**, $\alpha = 0.05$ **(b)**, and $\alpha = 0.01$ **(c)**. **d** : UPGMA cluster analysis of the coefficient of racial likeness (C.R.L.) basing on the data of 29 characters presented in Table 2. r_{cs}, cophenetic correlation coefficient.

the urostylines because they found some variation among populations. Recently, WIRNSBERGER *et al.* (1985 b) also reported some intra- and interpopulation variability of this character in cultured specimens of *Paraurostyla weissei*. However, there is the question if and how much the different and mostly sub-optimal culture conditions influence the variability of this attribute, which proves to be very stable in field samples (FOISSNER, 1982).

Other traits of *P. macrostoma*, — such as length of the adoral zone of membranelles, body width — show higher coefficients of variation in the alpine population than in the lowland one (Table 1). The differences among the populations, however, are not significant. The remaining characters are significantly different, but they always overlap considerably. This supports the assumption of conspecifity too (Table 1).

TABLE 4

Origin of the fronto-ventral-transverse primordia I-VI in the proter (above) and in the opisthe (below) in *Parakahliella macrostoma* and 6 typical oxytrichids (10).

Species	Primordium of the proter					
	I	II	III	IV	V	VI
Parakahliella macrostoma (11)	UM	some or all BC	2nd C behind RFC	some C of anterior part of FVRR		
Oxytricha granulifera	UM	II/2 and part of O II	III/2	IV/3	a part of O V	a part of O VI
Histriculus muscorum	UM	II/2 and part of O II	III/2	IV/3	IV/3	de novo or part of O V or VI
Stylonychia vorax	UM	II/2	III/2	IV/3	IV/3	IV/3
Stylonychia pustulata	UM	II/2	III/2	IV/3	IV/3	IV/3
Urosomoida agiliformis	UM	II/2	III/2	IV/3	de novo	de novo
Urosomoida agilis (12)	UM	II/2	III/2	IV/3	de novo	de novo

Species	Primordium of the opisthe					
	I	II	III	IV	V	VI
P. macrostoma (11)	OP and middle part of FVRL	OP	OP	middle part of FVRL	posterior part of FVRR	
O. granulifera	OP	OP	OP	IV/2	V/4	V/3
H. muscorum	OP	OP	OP	IV/2	V/4	V/4
S. vorax	OP	OP	OP	IV/2	V/4	V/4
S. pustulata	OP	OP	OP	IV/2	V/4	V/4
U. agiliformis	OP	OP	OP	IV/2	V/4	V/3
U. agilis	?	?	?	?	?	?

(10) References : BUITKAMP (1975), FOISSNER and ADAM (1983 a, b), WIRNSBERGER *et al.* (1985 a). Designation of primordia and cirri according to WALLENGREN (1900); see also Figs. 1-6 and 13-22. Legend : BC, buccal cirri; C, cirrus; FVRL, FVRR, left and right fronto-ventral row respectively; O, opisthe's; OP, oral primordium; RFC, right frontal cirrus; UM, undulating membranes of the parental cell.

(11) The primordia I-III of this species are very probable homologous with these of the oxytrichids. However, we could not decide which of the primordia IV-VI is "absent" in *P. macrostoma*. Hence, their designation IV and V is arbitrarily.

(12) The origin was ascertained from the Figures 3 and 4 in BUITKAMP (1975).

In contrast to the alpine population of *P. macrostoma*, the number of adoral membranelles of *H. muscorum* shows low coefficients of variation and insignificant differences among populations (Table 2). This result implies the likelihood of high selection pressure, which is said to stabilize characters (STEBBINS, 1980). LYNN and BERGER (1972) made similar observations in the scuticociliate *Plagiopyliella pacifica*.

Because of its low variability among populations, the cell width/length index proves to be an excellent attribute that supports the conspecifity of populations (Table 2). Recently, BORROR and WICKLOW (1983) also recommended the employment of this index for species identification.

The analysis of 4 alpine populations gives a good reflection of the geographical distances of their sample sites (Fig. 35). Both the NNSDC method and the coeffi-

TABLE 5

Differentiation of new cirri in 7 typical oxytrichids (13)

Species	Primordium						SUM FVT
	I	II	III	IV	V	VI	
Gastrostyla pulchra.....	1	3	3	4	5	5	21
Stylonychia pustulata	1	3	3	3	4	4	18
Oxytricha granulifera....	1	3	3	3	4	4	18
Urosoma macrostyla (14).....	1	3	3	3	4	4	18
Histriculus muscorum ..	1	2	3	3	4	4	17
Urosomoida agilis (15) ..	1	2	2	2	3	4	14
Urosomoida agiliformis (14).....	1	2	2	2	3	4	14

(13) References : WALLENGREN (1900), BUITKAMP (1975), FOISSNER (1983 a), FOISSNER and ADAM (1983 a, b), WIRNSBERGER *et al.* (1985 a). Legend : FVT, fronto-ventral-transverse cirri.

(14) The interpretation is different from that of FOISSNER (1983 a) and FOISSNER and ADAM (1983 b).

(15) The numbers were ascertained from the Figures 6 and 7 in BUITKAMP (1975).

cient of racial likeness (SNEATH and SOKAL, 1973) yield a high phenetic resemblance among the populations of the Schloßalm (P 2, P 3, and P 4), while population 1, which was collected at nearly the same altitude but 20 km away, forms a separated branch in the phenograms (Fig. 35). The populations 3 and 4 were sampled in 1981 and 1982 respectively at the same site in an alpine pasture. Population 2 occurred in the raw soil of a graded ski trail with a sparse vegetation cover and hence deviating edaphic factors (FOISSNER and PEER, 1985). This habitat is located about 500 m north of the sample site of population 3 and 4. Of course, we are unable to decide if the observed morphological differences are only due to effects of the environment upon the phenotype or if they are already determined genetically (SOKAL, 1965). Within the asexual testaceans, however, similar differences are now used to discriminate races (SCHÖNBORN *et al.*, 1983).

The aim of correlation analysis in *H. muscorum* was to obtain an estimate of the association of some variable characters used in Table 2 to ascertain the phenetic resemblance of the populations (Table 3). Most attributes prove to be not significantly correlated with body length, indicating that they do not comprise redundant information. This justifies their use in Table 2. LYNN and BERGER (1972) found in a scuticociliate that most of the attributes are independent of somatic length after protargol staining, but all are significantly correlated when the Chatton-Lwoff method is used. The results obtained with protargol-impregnated specimens of *Stylonychia pustulata*, however, suggest that at least in firm hypotrichs correlations remain unchanged (WIRNSBERGER *et al.*, 1985 a).

In *H. muscorum* and other hypotrichs the anterior parts of the right marginal primordia differentiate to dorsal kineties (Fig. 24; BUITKAMP, 1975; FOISSNER and ADAM, 1983 b; WIRNSBERGER *et al.*, 1985 a, b). Despite this close relationship the coefficient of correlation is significant only for the character pair "number of right marginal cirri/number of units in dorsal kinety 5" of population 1 (Table 3).

2. Morphogenesis of *Parakahliella macrostoma* and *Histriculus muscorum*.

The cortical morphogenesis of the frontal and somatic ciliature of *P. macrostoma* shows 4 remarkable features : a) The primordium III originates from the third anteriormost cirrus of the short frontal row (Figs. 4-7). It is evident from Table 4 that in *H. muscorum* and some other oxytrichids streak III arisis from cirrus III/2 (Figs. 13, 18-21), which has nearly the same position as that of *P. macrostoma*. This suggests a homology of these cirri. b) The migration of the cirri of primordium IV in a posteriad direction (Fig. 12) to form the left fronto-ventral row of non-dividers (Fig. 1). Row B_5 of *Kahliella* sp. (FLEURY and FRYD-VERSAVEL, 1982), but also the anlagen IV and especially V of *H. muscorum* show a similar displacement. The right frontal row of *P. macrostoma* and the rows B_6 of *Kahliella* sp. and the cirri of the anlage VI of *H. muscorum* commence uniformly at the level of the hypertrophied frontal cirri (Figs. 1, 13). These conformities in the formation of the frontal ciliature imply a close lineage of the Kahliellidae and Oxytrichidae. c) The formation of each 2 left and right marginal rows and the preservation of parts of the parental left marginal ciliature in the filial products. The latter feature explains the high variability of this character complex (Table 1). This interesting and apomorphic feature also occurs in species of *Kahliella* (HORVATH, 1932; TUFFRAU, 1969; FLEURY and FRYD-VERSAVEL, 1982) and *Engelmanniella* (FOISSNER unpubl.). d) The conservation of the parental dorsal kineties 4 and 5 as new kinety 4. To get the typical infraciliature of a non-dividing specimen both parental dorsal kineties have to migrate in a posteriad direction (Figs. 2, 9, 11). This is the only way we can explain the origin of the "new" dorsal kinety 4 in both filial products. The arithmetic mean of the number of basal body pairs in dorsal kinety 4 is significantly smaller ($P < 0.001$; one-sided t-test) than that of kinety 5. This indicates the resorption of some few units (Table 1). In many other species — e.g., *H. muscorum, O. granulifera,* and *P. weissei* — the kinety 4 arises by early fragmentation of the primordium of the leftmost unshortened row, in the middle stages of division (Fig. 27; FOISSNER and ADAM, 1983 a; WIRNSBERGER *et al.*, 1985 a, b). Thus the proter of *P. macrostoma* possesses 3 (adoral zone of membranelles, left marginal cirri, dorsal kinety 5) and the opisthe 2 (left marginal cirri, dorsal kinety 4) parts of the parental infraciliature. Previously *Euplotes* had been the only hypotrich in which fragments of the old dorsal kineties have been found to be preserved in post-dividers (FOISSNER and ADAM, 1983 a). However, the morphogenesis of the dorsal infraciliature of *Euplotes* proceeds very differently from that of *Parakahliella* (HECKMANN and FRANKEL, 1968).

Comparative analysis of some typical oxytrichids re-

veals that the origin of the 6 fronto-ventral-transverse primordia is very similar (Table 4). It is evident that *H. muscorum* is in the very close lineage of *Stylonychia* sp. Additionally, morphogenesis shows clearly that in *H. muscorum* caudal cirri originate at the posterior ends of the dorsal kineties 1, 2, and 4 (Figs. 13, 14, 30). Hence, the rows of left and right marginal cirri are not confluent posteriorly, as already supposed by FOISSNER (1982).

WALLENGREN (1900) stated that reduction of fronto-ventral-transverse cirri within the oxytrichids commences in the anterior part of the cell. This is true for the step *Gastrostyla — Stylonychia* or *Oxytricha*. However, a further decrease in the line *Stylonychia — Histriculus — Urosomoida* is due to the resorption of the left transverse cirri (II/1, III/1, IV/1) and the ventral cirrus V/2 (Fig. 13, Table 5; BUITKAMP, 1975; FOISSNER and ADAM, 1983 b, WIRNSBERGER *et al.*, 1985 a).

3. The homonomy of marginal and dorsal rows

Species of *Kahliella* possess rows the anterior part of which consists of basal body pairs whereas the posterior part is formed by cirri (HORVATH, 1932). FLEURY and FRYD-VERSAVEL (1982) observed that the ratio is rather variable. *Parakahliella macrostoma* possesses up to 5 cirri in kinety 1 (Table 1). We found no criterion by which to decide if such a row must be designated as a marginal row or as a dorsal kinety with a high number of caudal cirri. In the oxytrichid line *Gastrostyla — Stylonychia, Oxytricha, Histriculus — Tachysoma* there also exists the tendency to reduce the cirral contribution to the dorsal rows (FOISSNER, 1982; BERGER *et al.*, 1984). The equal development by "within proliferation" of marginal and dorsal rows (BORROR, 1979) and the ultrastructural identity of both marginal and caudal cirri (JERKA-DZIADOSZ, 1982) are further indications that these structures are homonomous. Thus it is reasonable to summarize marginal rows and dorsal kineties as somatic infraciliature (BORROR, 1979).

4. Comparative morphology of *Parakahliella macrostoma* and related species

Parakahliella macrostoma was originally described in *Paraurostyla*, which is now considered to be a member of the Oxytrichidae because of similarities in the morphogenetic pattern (BORROR, 1979; FOISSNER, 1982). The most closely related species is *Paraurostyla terricola* BUITKAMP, 1977, which must also be transferred into the new genus : *Parakahliella terricola* (BUITKAMP, 1977) nov. comb. Unfortunately, nothing is known about the variability of this soil hypotrich. Hence a modified t-test was used to compare the data (SOKAL and ROHLF, 1981). The only significant differences from both populations of *P. macrostoma* so found were in body width and number of cirri in the left fronto-ventral row; there were additional differences from the type-material in body length, number of adoral membranelles, and cirri in the right fronto-ventral row. Our criteria for the discrimination of the type species from its very similar congener are the mean number of adoral membranelles (nearly twice as high, and even the minimum value is considerably higher), the less fragmented fronto-ventral and right marginal rows, and the possession of small crystals (FOISSNER, 1982).

5. Characterization of two new kahliellid genera

- *Parakahliella* nov. gen.

Diagnosis : Kahliellidae with caudal cirri and more than one right and one left somatic ("marginal") cirral row. Some parts of the parental left somatic (marginal) infraciliature are preserved in the post-dividers.

Type-species : Parakahliella macrostoma (FOISSNER, 1982) nov. comb. (*Paraurostyla macrostoma* FOISSNER, 1982).

Recently, FOISSNER *et al.* (1982) described another peculiar lower hypotrich, *Kahliella marina,* with an evolved frontal ciliature but an apomorph morphogenetic pattern. A comparison with *Kahliella, Parakahliella, Psilotricha,* and *Parastrongylidium* (TUFFRAU, 1969; FLEURY and FRYD-VERSAVEL, 1982, 1984; FOISSNER, 1983 b) shows that this character pair justifies the establishment of a new genus.

- *Pseudokahliella* nov. gen.

Diagnosis : Kahliellidae with an evolved frontal ciliature and numerous self-replicating somatic ("right marginal") cirral rows.

Type-species : Pseudokahliella marina (FOISSNER *et al.*, 1982) nov. comb. (*Kahliella marina* FOISSNER *et al.*, 1982).

Both morphological and morphogenetic data demonstrate *Parakahliella* and *Pseudokahliella* to be in the kahliellid lineage "which includes all genera of the hypotrich suborder Stichotrichina the species of which lack transverse cirri and show an untwisted meridional arrangement of the somatic rows" (TUFFRAU, 1979). *Parakahliella* is easily distinguishable from all other genera of this family by the character pair "caudal cirri and two or more left and right marginal rows" (HORVATH, 1932; KAHL, 1932; CORLISS, 1979; FOISSNER, 1982, 1983 b).

JERKA-DZIADOSZ and BANACZYK (1983) described a variable number of left marginal rows in clones of *Paraurostyla weissei* crossed in the laboratory. This aberration could be an argument against the use of the diagnostic feature "number of marginal rows". However, the observations on the morphogenesis and the biometrical analyis show that this character is very stable in natural populations (Table 1).

The monotypical genus *Pseudokahliella* is characterized unequivocally by a clearly differentiated frontal ciliature and a high dominance of the somatic cortical pattern. The former attribute separates it from *Parastrongylidium* FLEURY and FRYD-VERSAVEL, 1984, and the latter one from other related genera. The plagiotomid morphogenetic pattern implies an ancestral position within the Kahliellidae and hence a close relationship to "non-hypotrichs".

ACKNOWLEDGEMENTS

This study was supported by the "Fonds zur Förderung der wissenschaftlichen Forschung, Projekt Nr. 5526" and the "Projekt 2794, Dynamik der Hochgebirgsböden". We thank Mrs. KARIN ANRATHER for technical assistance and Dr. ISLE FOISSNER for the translation of the french summary.

LITERATURE

ATCHLEY W.R., NORDHEIM E.V., GUNSETT F.C. and CRUMP P.L. (1982). — Geometric and probabilistic aspects of statistical distance functions. *Syst. Zool.*, **31,** 445-460.

BERGER H., FOISSNER W. und ADAM H. (1984). — Taxonomie, Biometrie und Morphogenese einiger terricoler Ciliaten (Protozoa : Ciliophora). *Zool. Jb. Syst.*, **111,** 339-367.

BERGER H., FOISSNER W. und ADAM H. (1985). — Protozoologische Untersuchungen an Almböden im Gasteiner Tal (Zentralalpen, Österreich). IV. Experimentelle Studien zur Wirkung der Bodenverdichtung auf die Struktur der Testaceen- und Ciliatentaxozönosen. *Veröff. Österr. MaB — Hochgebirgsprogramms Hohe Tauern,* **9,** 97-112.

BORROR A.C. (1979). — Redefinition of the Urostylidae (Ciliophora, Hypotrichida) on the basis of morphogenetic characters. *J. Protozool.*, **26,** 544-550.

BORROR A.C. and EVANS F.R. (1979). — *Cladotricha* and phylogeny in the suborder Stichotrichina (Ciliophora, Hypotrichida). *J. Protozool.*, **26,** 51-55.

BORROR A.C. and WICKLOW B.J. (1983). — The suborder Urostylina Jankowski (Ciliophora, Hypotrichida) : morphology, systematics and identification of species. *Acta Protozool.*, **22,** 97-126.

BUITKAMP U. (1975). — The morphogensis of *Oxytricha agilis* Engelmann (Ciliatea, Hypotrichida). *Acta Protozool.*, **14,** 67-74.

BUITKAMP U. (1977). — Über die Ciliatenfauna zweier mitteleuropäischer Bodenstandorte (Protozoa, Ciliata). *Decheniana,* **130,** 114-126.

CORLISS J.O. (1979). — The ciliated protozoa. Characterization, classification and guide to the literature. 2nd ed. Pergamon Press, Oxford, New York, Toronto, Sydney, Paris, Frankfurt, 455 p.

FLEURY A. et FRYD-VERSAVEL G. (1982). — Aspects de la morphogenèse chez *Kahliella* (Cilié hypotriche). *Protistologica,* **18,** 135-145.

FLEURY A. et FRYD-VERSAVEL G. (1984). — Unité et diversité chez les hypotriches (Protozoaires ciliés). I. — Approche morphogénétique par l'étude de quelques formes peu différencées. *Protistologica,* **20,** 525-546.

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

FOISSNER W. (1983 a). — Die Morphogenese von *Urosoma macrostyla* (WRZESNIOWSKI, 1870) (Ciliophora : Oxytrichidae). *Arch. Protistenk.*, **127,** 413-428.

FOISSNER W. (1983 b). — Morphologie und Morphogenese von *Psilotricha succisa* (O.F. MÜLLER, 1786) nov. comb. (Ciliophora, Hypotrichida). *Protistologica,* **19,** 479-493.

FOISSNER W. und ADAM H. (1983 a). — Morphologie und Morphogenese des Bodenciliaten *Oxytricha granulifera* sp. n. (Ciliophora, Oxytrichidae). *Zool. Scr.*, **12,** 1-11.

FOISSNER W. und ADAM H. (1983 b). — Die Morphogenese von *Urosomoida agiliformis* FOISSNER, 1982 (Ciliophora, Oxytrichidae). *Zool. Anz.*, **211,** 161-176.

FOISSNER W., ADAM H. und FOISSNER I. (1982). — Morphologie und Infraciliatur von *Bryometopus pseudochilodon* KAHL, 1932, *Balantidioides dragescoi* nov. spec. und *Kahliella marina* nov. spec. und Revision des Genus *Balantidioides* PENARD, 1930 (Protozoa, Ciliophora). *Protistologica,* **18,** 211-225.

FOISSNER W. und PEER T. (1985). — Protozoologische Untersuchungen an Almböden im Gasteiner Tal (Zentralalpen, Österreich). I. Charakteristik der Taxotope, Faunistik und Autökologie der Testacea und Ciliophora. *Veröff. Österr. MaB — Hochgebirgsprogramms Hohe Tauern,* **9,** 27-50.

GATES M.A. (1978). — Morphometric variation in the hypotrich ciliate genus *Euplotes. J. Protozool.*, **25,** 338-350.

HECKMANN K. and FRANKEL J. (1968). — Genic control of cortical pattern in *Euplotes. J. exp. Zool.*, **168,** 11-38.

HORVATH J. v. (1932). — Ein neues hypotriches Infusor, *Kahlia acrobates* nov. gen., nov. sp. *Arch. Protistenk.*, **77,** 424-433.

JERKA-DZIADOSZ M. (1982). — Ultrastructural study on the development of the hypotrich ciliate *Paraurostyla weissei.* IV. Morphogenesis of dorsal bristles and caudal cirri. *Protistologica,* **18,** 237-251.

JERKA-DZIADOSZ M. and BANACZYK I.A. (1983). — Cell shape, growth rate and cortical pattern aberrations in an abnormal strain of the hypotrich ciliate *Paraurostyla weissei. Acta Protozool.*, **22,** 139-156.

KAHL A. (1932). — Urtiere oder Protozoa I : Wimpertiere oder Ciliata (Infusoria), 3. Spirotricha. In : DAHL F. (ed.). — Die Tierwelt Deutschlands. Fischer Verlag, Jena.

LYNN D.H. and BERGER J. (1972). — Morphology, systematics, and demic variation of *Plagiopyliella pacifica* POLJANSKY, 1951 (Ciliatea : Philasterina), an entocommensal of strongylocentrodid echinoids. *Trans. Amer. Microsc. Soc.*, **91,** 310-336.

SACHS L. (1984). — Angewandte Statistik. 6th ed. Springer Verlag, Berlin, Heidelberg, New York. 552 p.

SCHÖNBORN W., FOISSNER W. und MEISTERFELD R. (1983). — Licht- und Rasterelektronenmikroskopische Untersuchungen zur Schalenmorphologie und Rassenbildung bodenbewohnender Testaceen (Protozoa : Rhizopoda)

sowie Vorschläge zur biometrischen Charakterisierung von Testaceen- Schalen. *Protistologica,* **19,** 553-566.

SNEATH P.H.A. and SOKAL R.R. (1973). — Numerical taxonomy. W.H. Freeman, San Francisco. 573 p.

SOKAL R.R. (1965). — Statistical methods in systematics. *Biol. Rev.,* **40,** 337-391.

SOKAL R.R. and ROHLF F.J. (1981). — Biometry. 2nd ed. W.H. Freeman, San Francisco. 859 p.

STEBBINS G.L. (1980). — Evolutionsprozesse. 2nd ed. Fischer Verlag, Stuttgart, New York. 229 p.

TUFFRAU M. (1969). — L'origine du primordium buccal chez les ciliés hypotriches. *Protistologica,* **5,** 227-237.

TUFFRAU M. (1979). — Une nouvelle famille d'hypotriches, Kahliellidae n. fam., et ses conséquences dans la répartition des Stichotrichina. *Trans. Amer. Microsc. Soc.,* **98,** 521-528.

WALLENGREN H. (1900). — Zur Kenntnis der vergleichenden Morphologie der hypotrichen Infusorien. *Bih. K. Svenska Vetensk. Akad. Handl.,* **26,** 1-31.

WIRNSBERGER E., FOISSNER W. and ADAM H. (1985 a). — Morphological, biometrical, and morphogenetical comparison of the closely related species *Stylonychia vorax* and *S. pustulata* (Ciliophora : Oxytrichidae). *J. Protozool.* **32,** 261-268.

WIRNSBERGER E., FOISSNER W. and ADAM H. (1985 b). — Cortical pattern in non-dividers, dividers, and reorganizers of an Austrian population of *Paraurostyla weissei* (Ciliophora, Hypotrichida) : a comparative morphological and biometrical study. *Zool. Scr.* (in press).