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Cortical Pattern in Non-dividers, Dividers and Reorganizers of an Austrian Population of *Paraurostyla weissei* (Ciliophora, Hypotrichida): A Comparative Morphological and Biometrical Study

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The morphology and the regulation of cortical pattern associated with the cell size, division, and reorganization of *Paraurostyla weissei* (Stein, 1859) were investigated. The ranges of variation of the Austrian, Polish, and American strains were compared by biometrical analyses. The Austrian population most frequently shows 4 frontal cirri in the anteriormost and 2 in the posterior row, 4 ventral rows, 8 transverse cirri, and 7 dorsal kineties. The oral primordium originates next to the postoral ventral row. The undulating membrane field and 3 frontal-ventral-transverse(FVT)-streaks for the opisthe develop as a result of the dispersion of the basal bodies of 1 or 2 cirri of the 1st ventral row. The farthest-right ventral row is of composite origin from 2 FVT-streaks. Three short dorsal bristle rows originating beside the right marginal row are a constant feature. In reorganizers the oral primordium characteristically possesses a group of kinetosomes extending toward the anterior right, fusing with the undulating membrane field. The development of dorsal primordia always starts in the 3rd dorsal kinety. These results provide important criteria for future species discrimination, if the examination of non-morphological characters supplies evidence that *P. weissei* is a complex of sibling species.

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Introduction

Biometrical analyses of protozoan morphology are on the incrase (Jerka-Dziadosz 1976, 1977; Gates 1978; Berger & Hatzidimitriou 1978; Kazubski 1980; Bakowska 1980, 1981; Foissner & Schubert 1983). However, it is very rare for morphometrical data to be combined with morphogenetical studies, as in the valuable paper of Jerka-Dziadosz & Frankel (1969) on *Paraurostyla weissei* (Stein, 1859). Our work presents a biometrical and morphogenetical study of an Austrian population of this species and a comparison with data available from Polish (Jerka-Dziadosz 1965, 1976; Bakowska 1980; Jerka-Dziadosz & Banaczyk 1983) and American stocks (Jerka-Dziadosz & Frankel 1969). This could contribute towards a resolution of the bewildering taxonomic problems in the genus *Paraurostyla* Borror, 1972.

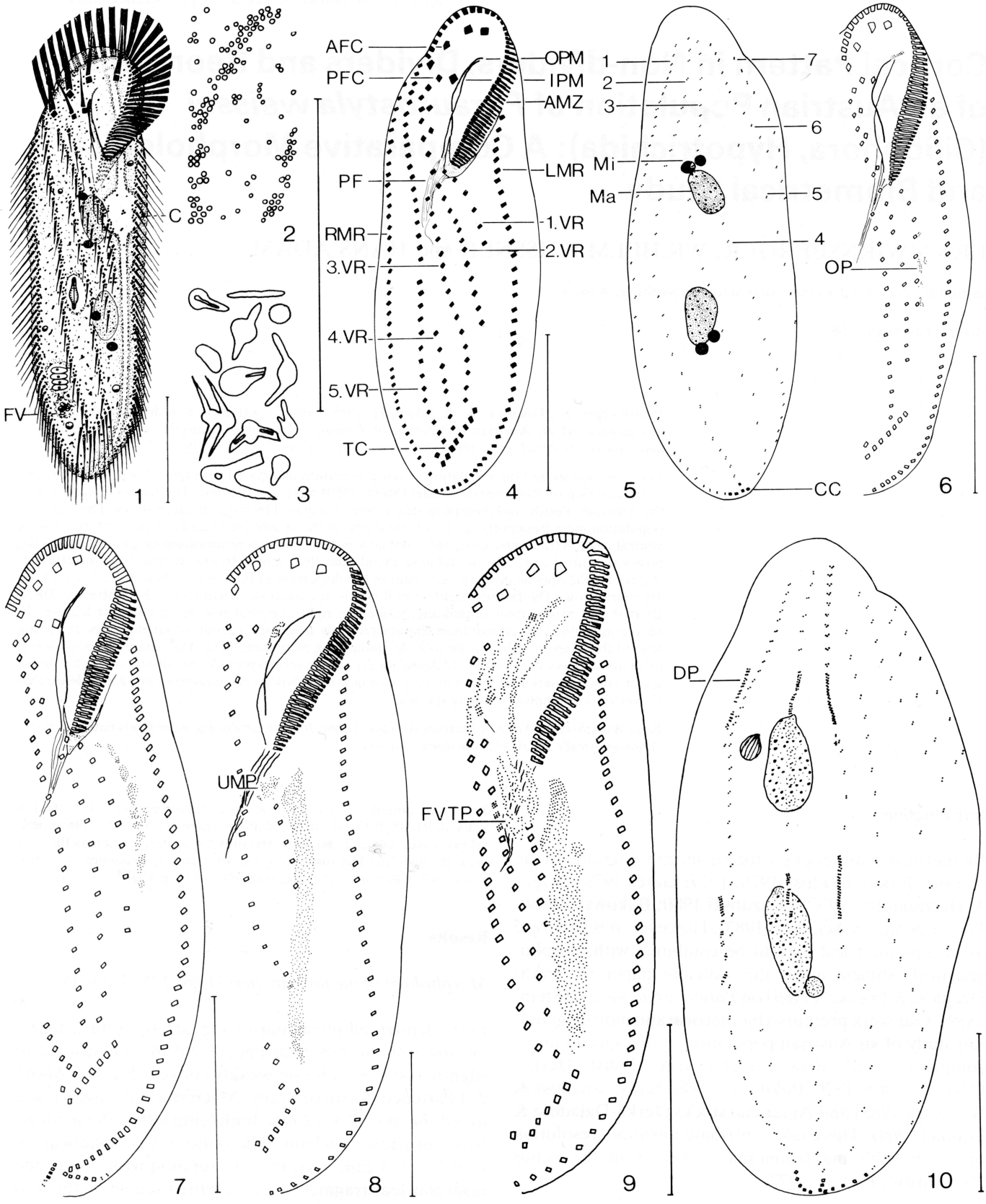
Material, methods and terminology

Paraurostyla weissei was collected in April 1983 from Mondsee (Salzburg, Austria). It was found upon sediment on the shore. As a culture medium, tap water was used, with yeast and a species of the "*Tetrahymena pyriformis*" complex, grown on dry egg yolk, added as the food supply. Ciliates were examined carefully *in vivo*. To reveal the infraciliature, the protargol silver staining method according to Foissner (1982) was used. All measurements were performed with an ocular micrometer. All data in the tables are based on protargol-impregnated specimens. Calculations were performed by a TI-59 minicomputer of Texas Instruments. Statistical procedures follow methods described in Sokal & Rohlf (1981). To make plain the changes during morphogenetical processes, old cirri are depicted only by contour, whereas the new ones are filled in. The terminology is according to Wallengren (1900), Kahl (1932), Borror (1972) and Jerka-Dziadosz & Frankel (1969).

Results

Morphology of the non-dividers (Figs. 1–5; Table I)

Body slender, elliptical, narrowing, and sometimes tapering towards the posterior end. Right margin straight to slightly concave, left one weakly convex (Fig. 1). About 2:1 flattened dorso-ventrally. Macronuclear fragments 2, ovoid, *in vivo* 20 × 12 μm, both lying left of the median, numerous little nucleoli. Micronuclei 3–6, spherical, *in vivo* 6.5 × 5 μm, each in close relation with one of the macronuclear fragments. Contractile vacuole on the left-hand border above the middle of the body, during diastole with 2 channels, which nearly reach the ends of the cell. Pellicula soft, flexible, with underlying yellow-greenish granules (about 1 μm diameter, certainly not symbiotic algae), which are grouped along the cirral rows and dorsal kinetics (Figs. 1, 2). They are extrusomes of the mucocyst type (Jerka-Dziadosz, personal communication). Their green colour is conspicuous even with low magnification. Subpellicular granules turn pale when the cover glass exerts pressure for a while and water enters the cell.



Figs. 1–10. Morphology and morphogenesis of *Paraurostyla weissei* (Stein, 1859) from life (*1–3*) and after protargol impregnation (*4–10*).—*1.* Ventral view.—*2.* Subpellicular granules.—*3.* Characteristic inclusions.—*4, 5.* Ventral and dorsal view of non-dividing specimens.—*6–10.* Early morphogenetical stages in ventral and dorsal view.
Each scale mark is equivalent to 50 μm.

Endoplasm full of numerous intensely yellow shining inclusions, which are of different shape (Fig. 3) and often aggregated in the posterior part of the body. Food vacuoles, *in vivo* 8–26 μm in diameter, include green algae, diatoms and flagellates. Movement moderately rapid, nestling close to particles of mud. Total isogamontic conjugation was observed very infrequently.

The infraciliature is described in Jerka-Dziadosz (1965). Here and in Table I we give some additional information. Right marginal row extends onto the dorsal

Table I. *Biometrical characterization of* Paraurostyla weissei

Character	$\bar{x}$	$\tilde{x}$	*SD*	*CV*	*Min–max*	*n*
Body length (μm)	126.80	120	34.27	27.10	73–198	28
Body width (μm)	47.80	45.5	13.39	28.00	26–73	28
Number of Ma-fragments	2.03	2	0.19	9.28	2–3	28
Macronucleus length (μm)	17.20	17	2.34	13.63	13–22	28
Macronucleus width (μm)	8.53	8	1.10	12.94	6–11	28
Number of micronuclei	4.03	4	0.88	21.83	3–6	28
Micronucleus length (μm)	5.00	5	0.00	0.00	5–5	28
Micronucleus width (μm)	4.00	4	0.00	0.00	4–4	28
Number of adoral membranelles	45.39	44	9.32	20.55	28–63	28
Distance from the anterior end of the body to the end of the AZM	47.10	46	10.19	21.69	30–66	28
Number of cirri in the LMR	34.82	35.5	7.17	20.59	20–59	28
Number of cirri in the RMR	34.96	35	6.10	17.44	24–46	28
Number of VR between MR	3.92	4	0.54	13.73	3–5	28
Number of cirri in VR 1	8.96	9	2.13	23.77	5–12	28
Number of cirri in VR 2	15.03	15	2.39	15.93	10–19	28
Number of cirri in VR 3	14.39	15	4.44	30.86	6–27	28
Number of cirri in VR 4	25.17	26	7.21	28.66	8–35	23
Number of cirri in VR 5	24.33	20	7.50	30.80	20–33	3
Total number of ventral cirri	61.90	63	14.29	23.07	34–86	28
Number of AFC	3.93	4	0.26	6.67	3–4	28
Number of PFC	2.00	2	0.00	0.00	2–2	28
Number of transverse cirri	7.75	8	0.70	9.03	6–9	28
Number of dorsal kinetics	7.17	7	0.86	12.02	6–8	28
Number of caudal cirri	13.52	13	1.83	13.53	10–18	23

side anteriorly (Fig. 4). Left marginal row bends posteriorly like a J and approaches more or less the dorsal side. Frontal cirri *in vivo* 23 μm long, bases about 2.6 μm wide, 4 in an anterior and 2 in a posterior row. Cirri of ventral rows *in vivo* about 10 μm long, bases 1.5 μm wide. First ventral row is separated in 3 slightly enlarged cirri in the frontal area and a short arched segment, which extends left to the pharynx until it reaches the posterior part of the body (originates from a single streak!). Second ventral row from frontal area to the left quarter of the body. Third ventral row from pharynx to the leftmost transverse cirri. Sometimes a very short ventral row follows (in this case counted as 4th ventral row). The typical 4th ventral row extends from the adoral zone of membranelles to the transverse cirri. This row can be interrupted in the middle of the cell, the resulting gap or overlap of 2 segments is the consequence of incomplete morphogenesis. Transverse cirri *in vivo* about 19 μm long, arranged in an oblique, J-shaped row, seldom reaching the posterior end of the body. Caudal cirri *in vivo* about 11 μm long, often hardly distinguishable from the cirri of the left marginal row (Fig. 5). Dorsal cilia *in vivo* 3 μm.

Cortical development during cell division (Figs. 6–22; Tables II, III)

Because of the pronounced similarities to the population described by Jerka-Dziadosz & Frankel (1969), we point out only differing and complementary observations. For further detailed comparison we refer to the drawings (Figs. 6–22). According to Wallengren (1900), we count the UM-primordium as streak 1, because it produces the 1st frontal cirrus (Fig. 13). Jerka-Dziadosz & Frankel (1969) do not number this streak, therefore their streak 1 is our streak 2, and so on.

Stomatogenesis. (a) In the earliest stage of development small groups of kinetosomes appear very close to the left cirri of the 1st ventral row ($n = 6$; Fig. 6). Jerka-Dziadosz & Frankel (1969) show only stages with a greater number of basal bodies. They are similar to our stage 2 (Fig. 7), where the anarchic field migrates away from the ventral row ($n = 4$).

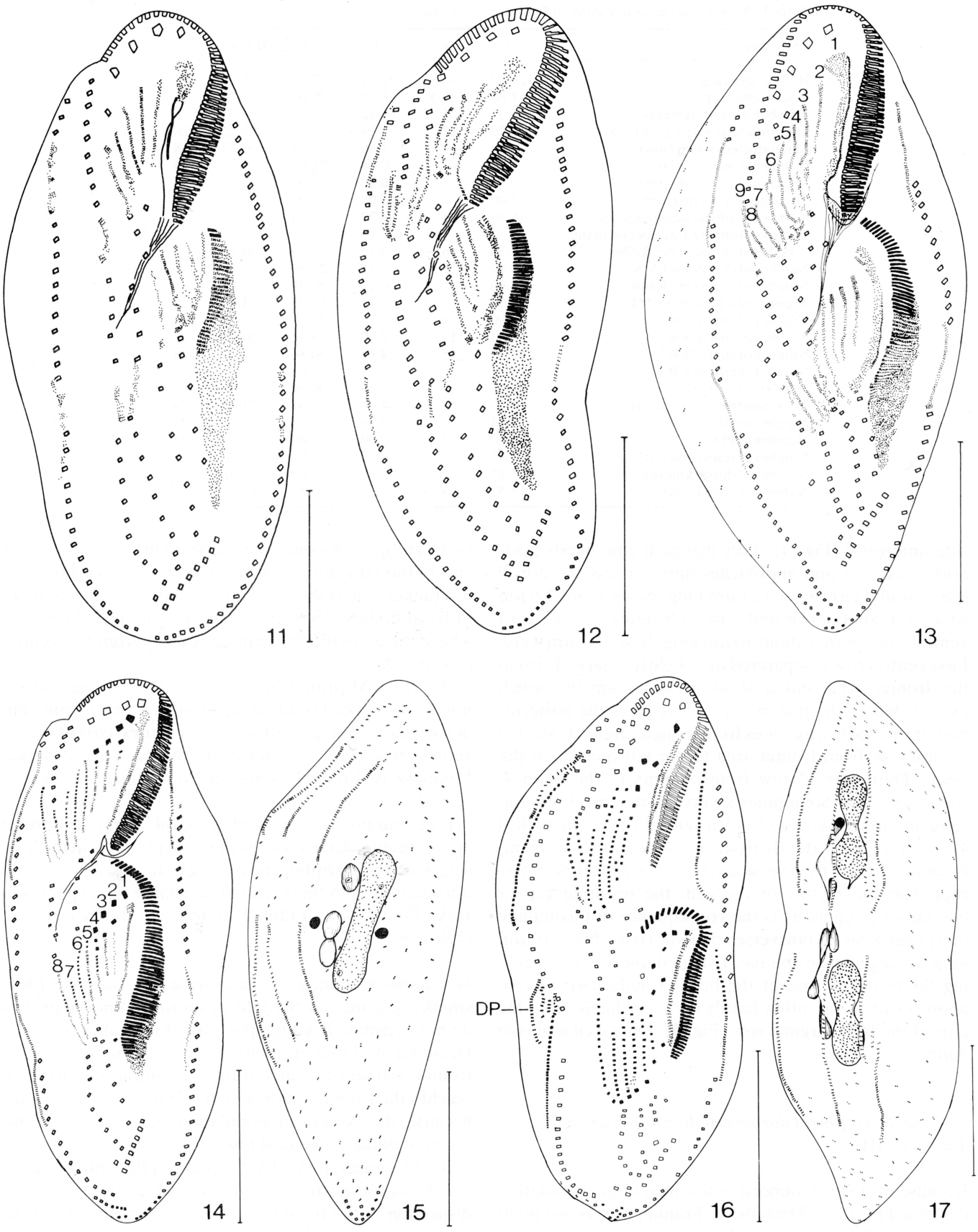
(b) The UM-primordium of opisthes is not formed "*de novo*", as Jerka-Dziadosz & Frankel (1969) state, but derives from disaggregation of 1–2 postoral cirri of the 1st ventral row (Fig. 8). However, the pictures of Jerka-Dziadosz & Frankel (1969) are not conclusive in this regard.

(c) In our population the pharyngeal fibers of the proter are reorganized, because they are not provable in the later stages of the morphogenesis (Figs. 16, 18, 20, 21). No information as to this feature is available in the papers of Jerka-Dziadosz & Frankel (1969) and Jerka-Dziadosz (1981*a*,*b*).

Development of the cirral primordia. (a) The 1st 3 FVT-streaks (leaving out the UM-primordium) in the proters do not originate from the posterior 3 frontal cirri (Jerka-Dziadosz & Frankel 1969), but from the posterior 2 frontal cirri and 1–2 cirri of the 1st ventral row, where it reaches the frontal sector (Fig. 9, arrow). This is obvious, because the American population does not show this segment of the 1st ventral row.

(b) The equivalent 3 FVT-streaks in the opisthes separate from the posterior UM-field, which develops from dispersion of the basal bodies of 1–2 postoral cirri of the 1st ventral row (Figs. 8, 9, 11). Later they migrate anteriorly (Figs. 12, 13). Jerka-Dziadosz & Frankel (1969) supposed that the streaks were apparently formed *de novo*, although involvement of some old cirri cannot be completely ruled out.

(c) The remaining streaks develop from portions of the pre-existing cirral rows (Figs. 11, 12). Typically, one streak forms within each row, except the 2 overlapping streaks associated with the farthest right ventral row in the



Figs. 11–17. Intermediate morphogenetical stages of *Paraurostyla weissei* (Stein, 1859) in ventral and dorsal view (after protargol impregnation) Each scale mark is equivalent to 50 μm.

anterior region (Jerka-Dziadosz & Frankel 1969). In our population the rule is that streaks are built 2 at a time in the 2 right ventral rows, in both proters and opisthes (Figs. 13, 14). We do not observe spatial continuity of the streaks with the old cirral row, one in the anterior and the other in the posterior direction, as Jerka-Dziadosz & Frankel (1969) did (Figs. 13, 14, 16).

(d) In general, 8 seldom 9, streaks are formed, whereas Jerka-Dziadosz & Frankel (1969) report a greater variation of 5–9, mostly 6 or 7 (Figs. 13, 14, 16).

Table II. *Differentiation of new cirri in dividing* Paraurostyla weissei

Character	$\bar{x}$	$\tilde{x}$	*SD*	*SE*	*CV*	*Min–max*	*n*
P-streak 1*	1.00	1	0.00	0.00	0.00	1–1	15
O-streak 1*	1.00	1	0.00	0.00	0.00	1–1	15
P-streak 2*	2.60	3	0.51	0.13	19.60	2–3	15
O-streak 2*	2.40	2	0.51	0.13	21.25	2–3	15
P-streak 3*	3.66	3	1.63	0.42	44.53	2–6	15
O-streak 3*	3.87	3	1.85	0.48	47.80	3–8	15
P-streak 4*	14.80	16	3.23	0.83	21.82	9–19	15
O-streak 4*	14.20	14	2.65	0.68	18.66	10–18	15
P-streak 5*	20.66	21	2.10	0.54	10.16	17–24	15
O-streak 5*	16.81	17	4.81	1.24	28.63	4–23	15
P-streak 6*	18.53	19	2.69	0.69	14.51	13–23	15
O-streak 6*	16.60	18	5.16	1.33	31.08	4–21	15
P-streak 7*	14.00	15	2.72	0.70	19.42	7–18	15
O-streak 7*	17.40	18	3.10	0.80	17.81	13–22	15
P-streak 8*	22.40	23	4.50	1.16	20.08	11–27	15
O-streak 8*	18.50	20	3.79	1.01	20.48	7–22	14
P-streak 9*		24					1
O-streak 9*	20.50					19–22	2
Total number of cirri (except MC)							
P	100.13	107	28.76	7.43	28.72	89–121	15
O	101.20	99	7.44	1.92	7.35	92–118	15
Total number of streaks							
P	8.10	8	0.35	0.09	4.32	8–9	15
O	8.00	8	0.37	0.09	4.72	7–9	15
Number of transverse cirri							
P	8.47	8	0.64	0.16	7.55	8–10	15
O	8.00	8	0.75	0.19	9.37	7–9	15
old	8.13	8	0.35	0.09	4.30	8–9	15

* Number of cirri in each streak.

(e) In our population the development of marginal streaks always begins within the right row and for some time here proceeds more rapidly than that of the left marginal streaks (Figs. 11, 12). Such a difference is not depicted or mentioned by Jerka-Dziadosz & Frankel (1969).

Differentiation of new cirri. In the Austrian population 4 streaks are involved in the formation of the anterior frontal cirri (Fig. 14). In the farthest right streak, uniformly 2 transverse cirri are produced (Figs. 18, 20). In contrast, in the American population of Jerka-Dziadosz & Frankel (1969), 3 streaks form the anterior frontal cirri and 1 transverse cirrus is built at the posterior tip of 6 or 7 streaks. We do not find the highly significant correlation between the number of old transverse cirri and the number of new ones for the opisthes, described by Jerka-Dziadosz & Frankel (1969) (compare our Table III with their table 4).

Table III. *Relationship between the number of old and new transverse cirri in dividing* Paraurostyla weissei

Number of new transverse cirri	Number of old transverse cirri		*n*
	8	9	
Proter			
8	8	1	9
9	5		5
10		1	1
Opisthe			
7	3		3
8	7	2	9
9	3		3
n	13	2	

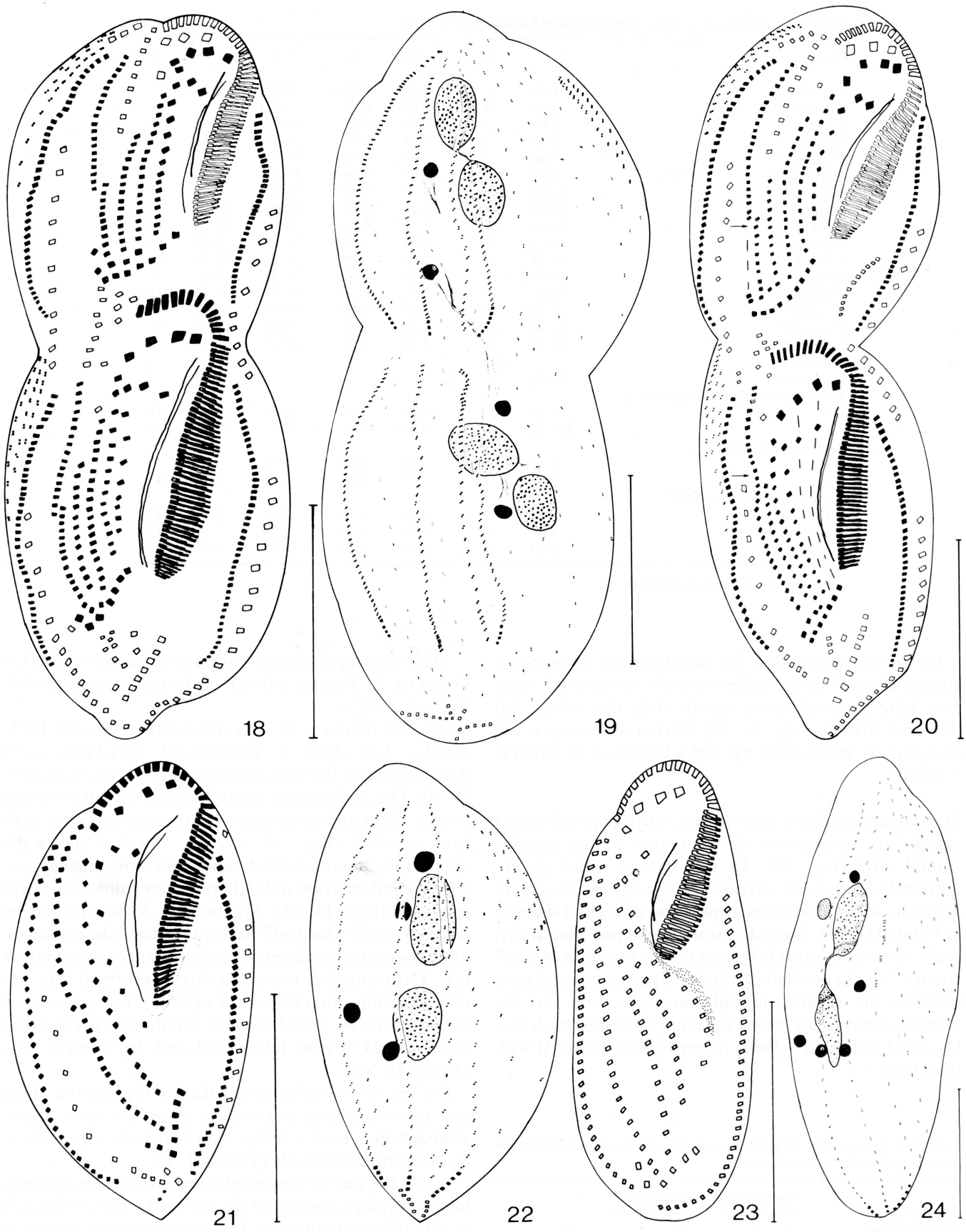
The following particulars are not mentioned by Jerka-Dziadosz & Frankel (1969) or Jerka-Dziadosz (1980, 1981*a*,*b*, 1982).

(a) The numbers of cirri differentiated in the FVT-streaks 2–9 show a pronounced variability, well documented by the high coefficients of variation (Tables II, V). The 2nd anterior frontal cirrus, the left posterior frontal cirrus and sometimes 1 transverse cirrus are built from streak 2 (Figs. 14, 18, 20). Streak 3 shows the greatest variation in both dividing and reorganizing cells: here the 3rd anterior and right posterior frontal cirrus are produced (Figs. 18, 20). Additionally, some cirri may be differentiated, which will be resorbed until the end of the morphogenetic processes or remain as a very short ventral row. Occasionally 1 transverse cirrus is formed (Fig. 20; note the connection line in the opisthe). For proters and reorganizers, we find the lowest variation in streak 5 and partly streak 6 (the future 2nd and 3rd ventral row) (Tables II, V).

(b) The total number of streaks and the number of old and new transverse cirri nearly show the same mean, although they have a rather high variation, especially in reorganizing individuals (Tables II, V).

(c) At the end of the morphogenesis and subsequently in non-dividers, the cirri of the 1st ventral row are located at very different intervals. Three enlarged cirri remain in a loose arrangement in the frontal area, while the posterior cirri of this streak migrate and extend left to the pharynx, back to the posterior part of the body, in an arc (Figs. 4, 6, 7, 20).

(d) The farthest right ventral row is in all cases composed of 2 FVT-streaks, because the cirri of the rightmost FVT-streak (except the 2 transverse cirri) carry out an extreme migration and fuse with the cirral row of the last



Figs. 18–24. Paraurostyla weissei (Stein, 1859) (after protargol impregnation).—*18–20.* Late morphogenetical stages in ventral and dorsal view.—*21, 22.* Ventral and dorsal view of the opisthe after division.—*23, 24.* Early morphogenetical stages of reorganizing specimens in ventral and dorsal view. Each scale mark is equivalent to 50 μm.

but one FVT-streak (Figs. 18, 20, *arrows*). If this considerable shift is not completed, the non-dividing cell shows 2 overlapping ventral rows, which Heckmann (1965) regards as an identifying characteristic of *Urostyla hologama* (Fig. 21).

(e) The total number of cirri varies much more in proters than in opisthes (Table II).

Development of the dorsal primordia. (a) Concerning the beginning of dorsal development, we do not have clear

results. However, we observe 2 individuals forming their primordia on the right of the pre-existing 1st kinety (Fig. 10), which was never observed by Jerka-Dziadosz & Frankel (1969) and Jerka-Dziadosz (1982). They state that new dorsal rows originate within the old ones. We get the same impression from our later stages.

(b) Our population generally possesses 3 short dorsal bristle rows (Figs. 16, 18, 20), whereas Jerka-Dziadosz & Frankel (1969) and Jerka-Dziadosz (1982) observe that 2 such rows remain in the filial products. Although Jerka-Dziadosz & Frankel (1969) sometimes found 2 or 3 short rows in certain stages of the morphogenesis, at the end of the dividing processes only 2 kineties remained. Whether the 3rd row is resorbed or 2 rows fuse was not clear to them.

(c) In contrast to the Polish and American strains, in our material there is an unequal number (3–7) of caudal cirri in each of the dorsal kineties 1, 2 and 4. In kinety 1 we always find fewer caudal cirri than in kinety 4 (Figs. 22, 24).

Reorganization (Figs. 23, 24; Tables IV, V)

The development of the cirral primordia and the arrangement of new cirri show the same peculiarities mentioned in dividing cells. Additional observations are as follows.

(a) Jerka-Dziadosz & Frankel (1969) state that the UM-primordium is of composite origin, partly "*de novo*" and partly from the old UM's, while our reorganizers possess a group of kinetosomes extending in the form of a streak toward the anterior-right (Fig. 23) and fusing with the anterior UM-field later.

(b) Development of the dorsal primordia always starts in kinety 3 and proceeds more rapidly for some time than in the case of kineties 1 and 2 (Fig. 24).

(c) We do not find the correlation between numbers of old and new transverse cirri described by Jerka-Dziadosz & Frankel (1969) (compare our Table IV with their table 5). Eight transverse cirri are formed irrespective of the number of old transverse cirri (Table V).

(d) Often cells with a higher number of micronuclei, reduced cell size and fewer cortical elements appear (compare Tables II and V). This phenomenon also occurs in well-fed cultures with numerous dividing individuals.

Table IV. *Relationship between the number of old and new transverse cirri in reorganizing* Paraurostyla weissei

Number of new transverse cirri	Number of old transverse cirri			
	7	8	9	*n*
7	2	5	1	8
8	6	10		16
9		1		1
n	8	16	1	

Discussion

Morphological and morphometrical comparison of different populations

The differences between known species of the genus *Paraurostyla* are very insignificant. For that reason Borror (1972) considers numerous species to be synonymous. To restrict the ranges of variation, we have re-examined previous morphometrical data and compared them to those of the Austrian population of *Paraurostyla weissei*. Here we consider only the differences.

(a) The infraciliature of the interphase individual of the Austrian population is more similar to the strains of *Paraurostyla weissei* collected in Poland than to those from Swan Lake (Johnson County, Iowa). The former most frequently have 4 frontal cirri in the anteriormost row, 4 ventral rows and 8 transverse cirri. Jerka-Dziadosz (personal communication) crossed American strains obtained from Iowa City and Hempstead (Long Island) with some mating types collected in different locations in Poland. The American strains conjugated with each other, but did not mate with the Polish strains. Therefore we expect that *Paraurostyla weissei* is a complex of sibling species.

(b) A remarkable feature of the Austrian population is its 7 dorsal kineties, since the dorsal ciliary pattern is considered to be a conservative and stable character (Frankel 1975; Foissner 1982; Foissner & Adam 1983). In contrast, the Polish and the American population have 2 short and 3 long kineties, of which the 3rd kinety is discontinuous, composed of an anterior and a posterior segment.

(c) The relation between length and width of the body

Table V. *Differentiation of new cirri in reorganizing* Paraurostyla weissei

Character	$\bar{x}$	$\tilde{x}$	*SD*	*SE*	*CV*	*Min–max*	*n*
Streak 1*	1.00	1	0.00	0.00	0.00	1–1	26
Streak 2*	2.23	2	0.81	0.16	36.55	1–5	26
Streak 3*	4.42	3	2.80	0.55	63.40	2–11	26
Streak 4*	11.80	12.5	3.36	0.66	28.42	3–18	26
Streak 5*	16.40	17	2.81	0.55	17.11	9–22	26
Streak 6*	14.60	14.5	2.88	0.56	19.68	9–19	26
Streak 7*	13.00	12	3.06	0.61	23.60	9–18	25
Streak 8*	16.10	16.5	3.64	0.85	22.60	9–23	18
Streak 9*	15.50	16.5	4.04	2.02	26.07	10–19	4
Total number of streaks	7.80	8	0.75	0.14	9.59	6–9	26
Total number of cirri (except MC)	77.60	77	12.66	2.48	16.52	55–100	26
Number of TC							
new	7.69	8	0.61	0.12	8.00	7–8	26
old	7.65	8	0.62	0.12	8.20	6–8	26

* Number of cirri in each streak.

is nearly the same (C-12 3.26:1; AP 2.65:1), but all values for our species are lower (Table VI; Jerka-Dziadosz & Banaczyk 1983, table 3).

(d) In tiny cells the number of left marginal cirri is larger than that of adoral membranelles (Bakowska 1980). We also find that reduction of the cell size causes a decrease in the number of adoral membranelles and left marginal cirri (Table VII), although our species differs in that the adoral zone of membranelles always contains a greater number of elements than the left marginal row. Nevertheless, statistical analysis yields the same high correlation between the number of LMC and the number of AM (r = 0.94, in the Polish strain r = 0.84). Our regression line is described by the equation: LMC = 4.206 + 0.66254 AM. Bakowska (1980) obtained for the Polish strain: LMC = 18.332 + 0.40352 AM.

(e) Table VIII shows a similar correlation of the Polish and Austrian strains. In both cases there is a clear correlation between the length of a cell and the number of left marginal cirri and adoral membranelles (Jerka-Dziadosz 1976, table 8).

(f) Jerka-Dziadosz & Frankel (1969, table 2) observed 108 individuals of an American stock, of which about 75% had 6 transverse cirri, while 25% had 7. Moreover they state that cells with 4 ventral rows almost invariably have 6 transverse cirri, while cells with 5 rows have either 6 or 7 transverse cirri. We have counted 126 individuals, of which 66% possessed 8 transverse cirri, 19% 7; 76% had 4 ventral rows, 17% 5 (Table IX).

(g) In both populations the total number of ventral cirri was found to be significantly correlated both with the number of ventral rows and with the number of transverse cirri (Table X; Jerka-Dziadosz & Frankel 1969, table 3). A striking feature is the lower total number of ventral cirri of the Austrian population. However, Student's t-test reveals no significant (at the 0.01 level) difference from the American stock.

(h) In our strain 4 large frontal cirri in the anteriormost row and 2 enlarged frontal cirri in a posterior row occur; in the Polish stocks there are also 4 anterior, but 3 or 4 posterior frontal cirri (Jerka-Dziadosz 1965, 1976). In the American strains there are always 6 frontal cirri arranged in 2 rows of 3 cirri each (Jerka-Dziadosz & Frankel 1969).

(i) The Austrian population frequently possesses 8 transverse cirri (Tables I, II, V, IX), just like the Polish stock (Jerka-Dziadosz 1965, 1976), whereas the American has 6 or 7 (Jerka-Dziadosz & Frankel 1969).

(j) According to a suggestion of Jerka-Dziadosz (personal communication), we tried to find relationships between the number of cirri within the streaks or ventral rows. But all coefficients of correlation were insignificant (r varies from 0.10 to 0.61).

(k) Although our species was cultured for 10 months, we never observed either double forms (Jerka-Dziadosz 1977) or the naturally occurring variant with an increased number of left marginal rows (Jerka-Dziadosz & Banaczyk 1983)

Morphogenetical processes

Only 2 species of *Paraurostyla* Borror, 1972 have been

Table VI. *Morphometrical data of different strains of* Paraurostyla weissei

Strain	n	Length (μm)	Width (μm)	Number of AM	Number of LMC
C-12†	20	162–243 (204.2)*	54–84 (62.6)	54–69 (62.6)	41–55 (49.7)
Ap	28	73–198 (126.8)	26–73 (47.8)	28–63 (45.4)	20–59 (34.8)

* Arithmetic means in parentheses.
† Data are from Jerka-Dziadosz & Banaczyk (1983).

Table VII. *The number of adoral membranelles and left marginal cirri in cells of different size of* P. weissei

Group of cells	Number of AM	Number of LMC	n
173–211 μm	47–63 (50–61)* 58.2 (56)	36–47 (36–49) 42.5 (41)	16 (11)
123–172 μm	35–58 (30–49) 49.9 (37)	26–44 (28–42) 37.7 (33)	19 (24)
73–122 μm	28–48 (19–23) 39.1 (26)	20–38 (23–34) 30.0 (29)	26 (13)

* Values in parentheses are from Bakowska (1980). The mean numbers are given on the second lines.

Table VIII. *The correlation coefficients for the length of a cell versus the number of elements in* P. weissei

	Correlation coefficient	
Cell length versus	Polish strain*	Austrian strain
LMC	0.769	0.893†
AM	0.837	0.919†
RMC	—	0.753†

* Data for the Polish strain are from Jerka-Dziadosz (1976).
† Significant at the 0.001 level.

Table IX. *Relation between the number of ventral rows and the number of transverse cirri in* P. weissei

Number of ventral rows	Number of transverse cirri 6	7	8	9	Total	%
3	2	7			9	6.9
4	1	18	73	6	98	75.9
5	1		12	9	22	17.0
Total	4	25	85	15	129	
%	3.1	19.3	65.9	11.6		

Table X. *Relation of the number of ventral rows and transverse cirri to the total number of ventral cirri of* P. weissei

	Average number of ventral cirri ± *SE*			
Number of ventral rows	Cells with 7 TC	Cells with 8 TC	Cells with 9 TC	Total
3	47.8 ± 2.83 (n = 10)	48.7 ± 3.76 (n = 9)		44.9 ± 0.92* (n = 23)
4	61.0 ± 1.15 (n = 3)	67.7 ± 2.32 (n = 23)	73.0 ± 0.99 (n = 2)	67.2 ± 1.13 (n = 28)
5	75 (n = 1)	73 (n = 1)	86.8 ± 1.55 (n = 8)	84.1 ± 2.08 (n = 10)
Total	61.2 ± 3.63	63.1 ± 2.22	79.0 ± 3.08	

* The means for categories containing only one or two cells are not shown, except as a part of the overall totals given on the bottom and on the right of the table. For this reason, the numbers of cells on which these totals are based are somewhat greater than the sum of the numbers within the table.

morphogenetically characterized. They differ clearly in the mode of formation of the oral primordium. In *P. hymenophora* (Stokes, 1886) partial deciliation at the anterior margin of the 6 transverse cirri precedes initiation of the oral primordium near transverse cirrus 6 (Grimes & L'Hernault 1978), whereas the anarchic field originates presumably "*de novo*" in the American strains of *P. weissei* (Jerka-Dziadosz 1969). In contrast, our population develops its oral primordium in the same way as *Kahliella* Corliss, 1960 and *Hypotrichidium* Ilowaisky, 1921 (Tuffrau 1969, 1972; Jerka-Dziadosz 1974).

Many other details are also slightly different. For instance, the Austrian population generally shows 3 short dorsal kineties and the farthest right ventral row is composed of 2 FVT-streaks. It is obvious that we need much more information about morphogenetical features on the species level to decide whether such characters are useful in discriminating species, as has recently been stressed by Foissner & Adam (1983).

Conclusions

The most important outcome of the present investigation is the distinct demonstration that species boundaries are extremely fluid in this genus. At this state the differences between the various populations of *Paraurostyla weissei* do not provide enough reasons for considering these strains as separate species. The taxonomic problem of species discrimination requires further study of morphological, biometrical, biochemical and physiological variation. Modern techniques, such as enzyme electrophoresis, characterization on the basis of mating-type reactivity and macronuclear DNA patterns, could also help to justify a new species assignment (Allen *et al.* 1983; Aufderheide *et al.* 1983; Steinbrück & Schlegel 1983).

So far, we suggest that attention should be paid to further identification of presumed sibling species. In our opinion the present results vindicate the establishment of 2 groups within the *Paraurostyla weissei* complex.

(a) Individuals possessing green subpellicular granules, 4 anterior frontal cirri, generally 4 ventral rows, and 8 transverse cirri arranged like a J. These are probably: *Urostyla polymicronucleata* Merriman, 1937; *U. hologama* Heckmann, 1965; *U. weissei* Stein, 1859 (*sensu* Dragesco 1970; Jerka-Dziadosz 1965); our *Paraurostyla weissei*.

(b) Individuals probably without subpellicular granules, but with 6 frontal cirri arranged in 2 rows of 3 cirri each, 6 or 7 transverse cirri in a straight row, and a number of ventral rows varying from 4 to 7. These are probably: *Urostyla weissei* Stein, 1859; *U. flavicans* Wrześniowski, 1870; *U. vernalis* Stokes, 1894; *U. paragrandis* Wang, 1930; *U. coei* Turner, 1939; *U. weissei* Stein, 1859 (*sensu* Kahl 1932; Dragesco 1966; Jerka-Dziadosz & Frankel 1969).

If this distinction should be accepted in future, we propose for the first group the most informative name *Paraurostyla hologama* (Heckmann, 1965).

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Abbreviations used in the figures and tables

AFC	anterior frontal cirri
AM	adoral membranelles
AP	Austrian population
AZM	adoral zone of membranelles
C	contractile vacuole
CC	caudal cirri
CV	coefficient of variation in %
C-12	Polish clone, wild type
DP	dorsal primordium
FV	food vacuole
FVTP	frontal-ventral-transverse-primordium
IPM	inner paroral membrane
LMC	left marginal cirri
LMR	left marginal row
Ma	macronucleus
Max	maximum
MC	marginal cirri
Mi	micronucleus
Min	minimum
n	sample size
O	opisthe
OP	oral primordium
OPM	outer paroral membrane
P	proter
PF	pharyngeal fibers
PFC	posterior frontal cirri
RMC	right marginal cirri
RMR	right marginal row
r	coefficient of correlation
SD	standard deviation
SE	standard error of the mean
TC	transverse cirri
UMP	primordium of the undulating membranes
VC	ventral cirri
VR	ventral row
$\bar{x}$	mean
$\tilde{x}$	median
1–9	number of dorsal kineties or FVT-streaks

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