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Morphology and morphogenesis of *Parakahliella haideri* nov. spec. (Ciliophora, Hypotrichida)

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CONTENTS

Synopsis. A description of the morphology and the morphogenesis of the hypotrichous soil ciliate *Parakahliella haideri* nov. spec. is given. This species differs from its congeners by its possession of a single left marginal row. The morphogenesis of both the ventral and dorsal infraciliature proceeds in a very similar way to that of the type-species *P. macrostoma*, indicating congenerity of these species. Thus, the diagnosis of *Parakahliella* is emended to include species with only 1 left marginal row.

INTRODUCTION

Recently, the kahliellid genus *Parakahliella* with *P. macrostoma* (Foissner, 1982) as type-species and *P. terricola* (Buitkamp, 1977) as congener was established (Berger *et al.*, 1985). The diagnosis excludes, among others, taxa with a single left marginal cirral row. However, recently we found a very similar population with only 1 left marginal row. The morphogenesis of cell division was studied and compared with that of the type-species (Berger *et al.*, 1985) in order to decide whether or not the new population should be separated at the genus level.

MATERIAL AND METHODS

The population of hypotrichs was found on 2 May 1985 in the lower part of a bundle of straw which was in contact with the soil of a meadow in the city of Salzburg, Austria. The culture method and the protargol staining technique according to Foissner (1982) were used. All counts and measurements were performed at a magnification of 1000 × (1 unit = 1 μm).

The body shape of the living specimens was drawn from slides without cover slips. Details were studied on slightly to strongly squeezed individuals using an oil immersion objective (100 ×; eyepiece, 10 ×) and bright field illumination. Drawings of the impregnated specimens were made with a camera lucida. For clarity, parental cirri are shown in Figures 10–22 only by outline, whereas new ones are shaded.

The terminology is according to Kahl (1932), Borror (1972), and Corliss & Lom (1985).

RESULTS

Parakahliella haideri nov. spec.

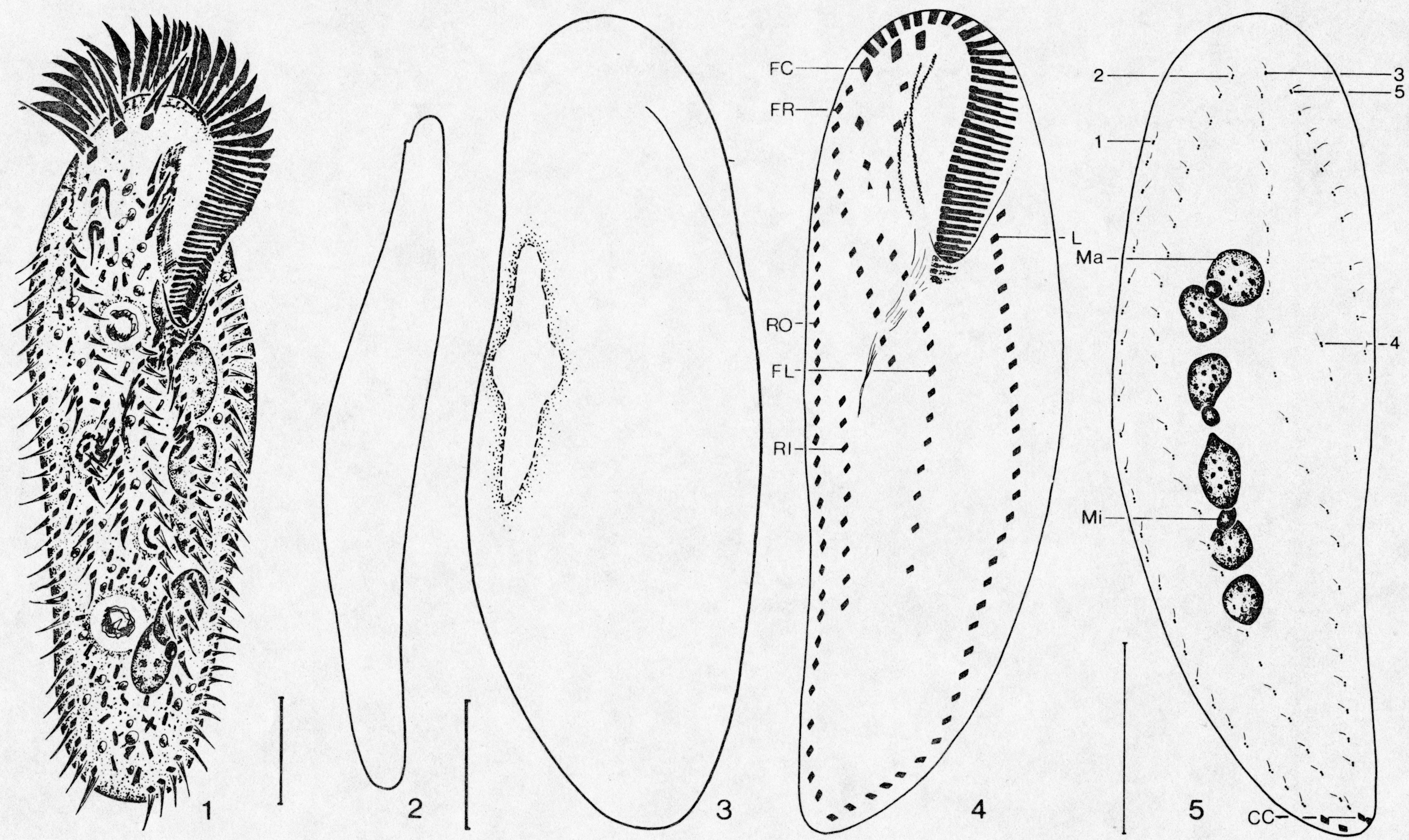
Diagnosis. *In vivo* about 150 × 50 μm. 1 long and 1 short (sometimes absent) right and 1 left marginal row. 48 adoral membranelles and 6 macronuclear segments on average.

Type location. Frequent in a bundle of straw, which was in contact with the soil of a meadow in Salzburg, Austria.

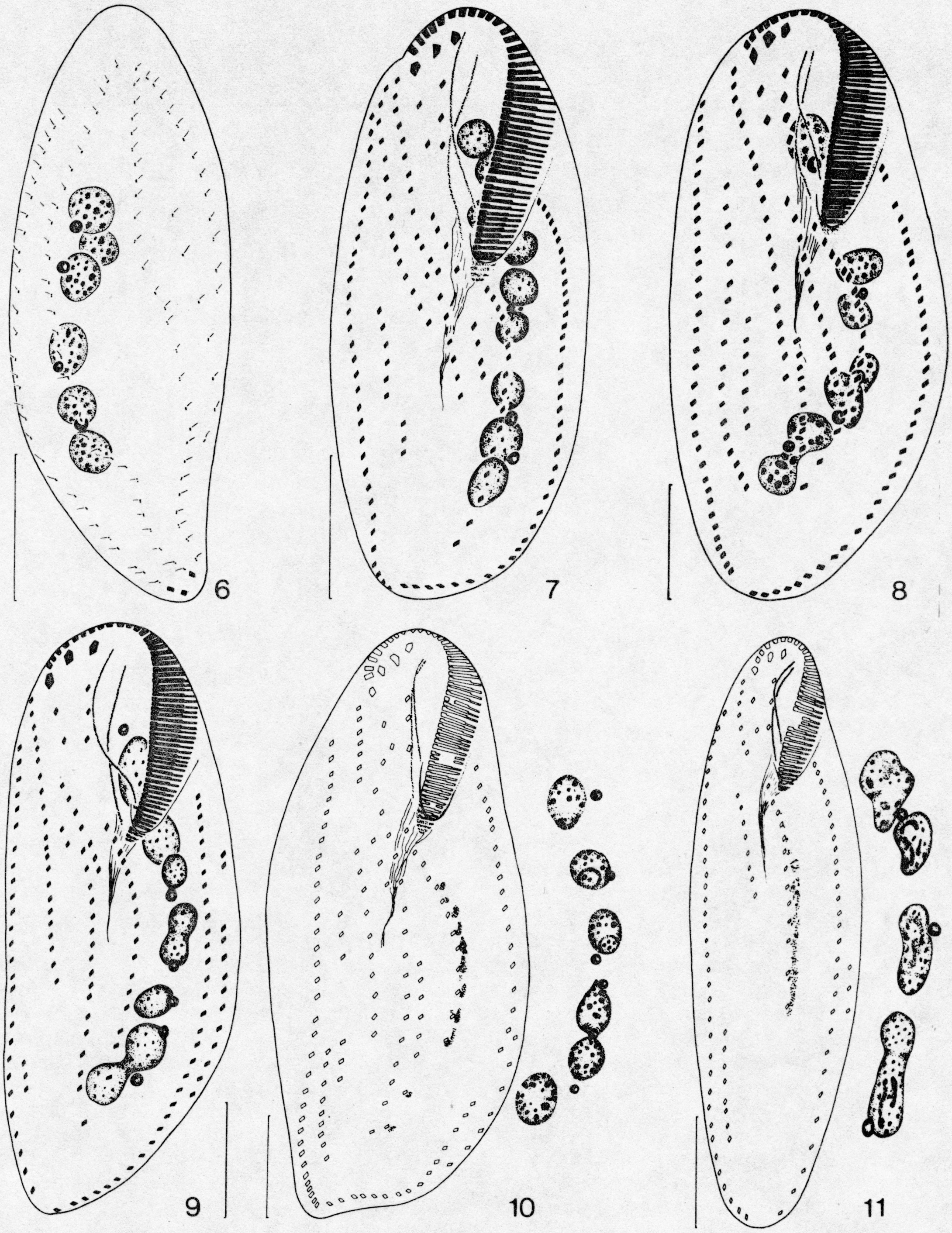
Type material. A slide of holotype specimens and 1 slide of paratype specimens are deposited in the British Museum (Natural History): holotype *N* 1987: 3: 19: 1; paratype *N* 1987: 3: 19: 2.

Dedication. This species is named in honour of Dipl.-Ing. Reinhold Haider, director of the Hydrologische Untersuchungsstelle Salzburg, as a small token of appreciation of his continuous support of our work.

Description (Figs 1–9, Table 1). Body usually S-shaped, sometimes distinctly converging posteriad, very flexible but not contractile. Both ends rounded, about 2 : 1 flattened dorso-ventrally (Figs 1–3). Macronuclear segments ovoid, lying left of the median. Contractile vacuole on the left-hand border, above the middle of the cell, during diastole with



Figs 1–5 *Parakahliella haideri* from life (Figs 1–3) and after protargol impregnation (Figs 4, 5). **1–3**, ventral, lateral, and dorsal view. **4**, infraciliature in ventral view. Arrow, buccal row; arrow head, frontal row. **5**, infraciliature in dorsal view. Note the short kinety 4 of this specimen. Scale marks = 30 µm. CC, caudal cirri; FC, right frontal cirrus; FL, FR, left and right fronto-ventral row; L, left marginal row; Ma, macronuclear segment; Mi, micronucleus; RI,RO, inner and outer right marginal row; 1–5, dorsal kineties.



Figs 6–11 *Parakahliella haideri* after protargol impregnation. 6–9 Non-dividing specimens. 10, 11 Morphogenetical stages. **6**, dorsal view of a specimen with a dorsal kinety 4 of average length. **7**, **8**, ventral view of specimens with additional cirral rows. **9**, ventral view of a specimen with a second left marginal row. **10**, **11**, very early morphogenetic stages. Scale marks = 30 μm.

Table 1. Biometrical characterization of *Parakahliella haideri*[1]

Character	x̄	M	SD	SE	CV	Min	Max	n
Body, length	127.1	125.5	12.5	1.978	9.8	105	160	40
Body, width	52.5	51.5	8.4	1.323	15.9	35	73	40
Adoral membranelles, No.	47.7	47.0	6.8	1.110	14.2	34	62	37
Adoral zone of membranelles, length	48.3	48.0	6.6	1.051	13.8	33	60	40
Macronuclear segments, No.	6.2	6.0	0.6	0.102	10.5	5	9	40
Posterior Ma, length	11.6	10.0	4.6	0.762	39.5	7	25	40
Posterior Ma, width	8.2	8.0	1.4	0.223	17.3	6	12	40
Micronuclei, No.	4.0	4.0	1.3	0.199	31.9	2	7	40
Posterior micronucleus, diameter	2.6	3.0	0.5	0.079	19.4	2	3	40
Enlarged frontal cirri, No.	3.0	3.0	0.4	0.063	13.2	2	5	39
Buccal row, No. cirri	3.0	3.0	0.7	0.104	22.2	1	4	40
Frontal row, No. cirri[2]	2.2	2.0	0.4	0.067	19.8	1	3	40
Left fronto-ventral row, No. cirri	13.6	13.0	3.4	0.563	25.2	4	20	37
Right fronto-ventral row, No. cirri	16.3	16.0	2.7	0.444	16.6	10	22	37
Left marginal row, No. cirri	32.3	32.0	3.9	0.613	12.0	23	40	40
Outer right marginal row, No. cirri	32.6	33.0	4.0	0.654	12.4	25	43	38
Inner right marginal row, No. cirri	9.3	8.0	4.7	0.798	50.9	2	18	35
Additional cirral rows, No.[3]	1.1	1.0	0.8	0.146	77.3	0	3	33
Dorsal kineties, No.	5.0	5.0	0	0	0	5	5	24
Dk 1, No. basal body pairs	28.5	28.0	3.5	0.653	12.4	21	34	29
Dk 2, No. basal body pairs	29.7	30.0	3.6	0.729	12.3	22	38	25
Dk 3, No. basal body pairs	26.4	27.0	3.4	0.686	12.7	19	33	24
Dk 4, No. basal body pairs	8.2	8.0	1.9	0.437	22.7	4	11	18
Dk 5, No. basal body pairs	12.1	12.0	1.9	0.359	15.4	9	16	27
Caudal cirri on Dk 1, No.	2.7	3.0	0.5	0.089	19.7	2	4	35
Caudal cirri on Dk 2, No.	1.1	1.0	0.3	0.056	29.3	1	2	34

[1] The data are based on protargol impregnated specimens. All measurements in µm. Legend: CV, coefficient of variation in %; Dk 1 – Dk 5; dorsal kinety 1–5, for the designation see Fig. 5; M, median; Ma, macronuclear segment; Max, maximum value; Min, minimum value; n, sample size; SD, standard deviation; SE, standard error of the arithmetic mean; x̄, arithmetic mean.
[2] The right enlarged frontal cirrus is not included.
[3] Single cirri and rows with only 2 or 3 cirri are not included.

short channels. Pellicle without subpellicular granules, cytoplasm colourless, filled with many yellow shining 2–4 µm large crystals and some food vacuoles with flagellates and ciliates (peritrichs, *Gonostomum* sp.). Movement moderately rapid gliding.

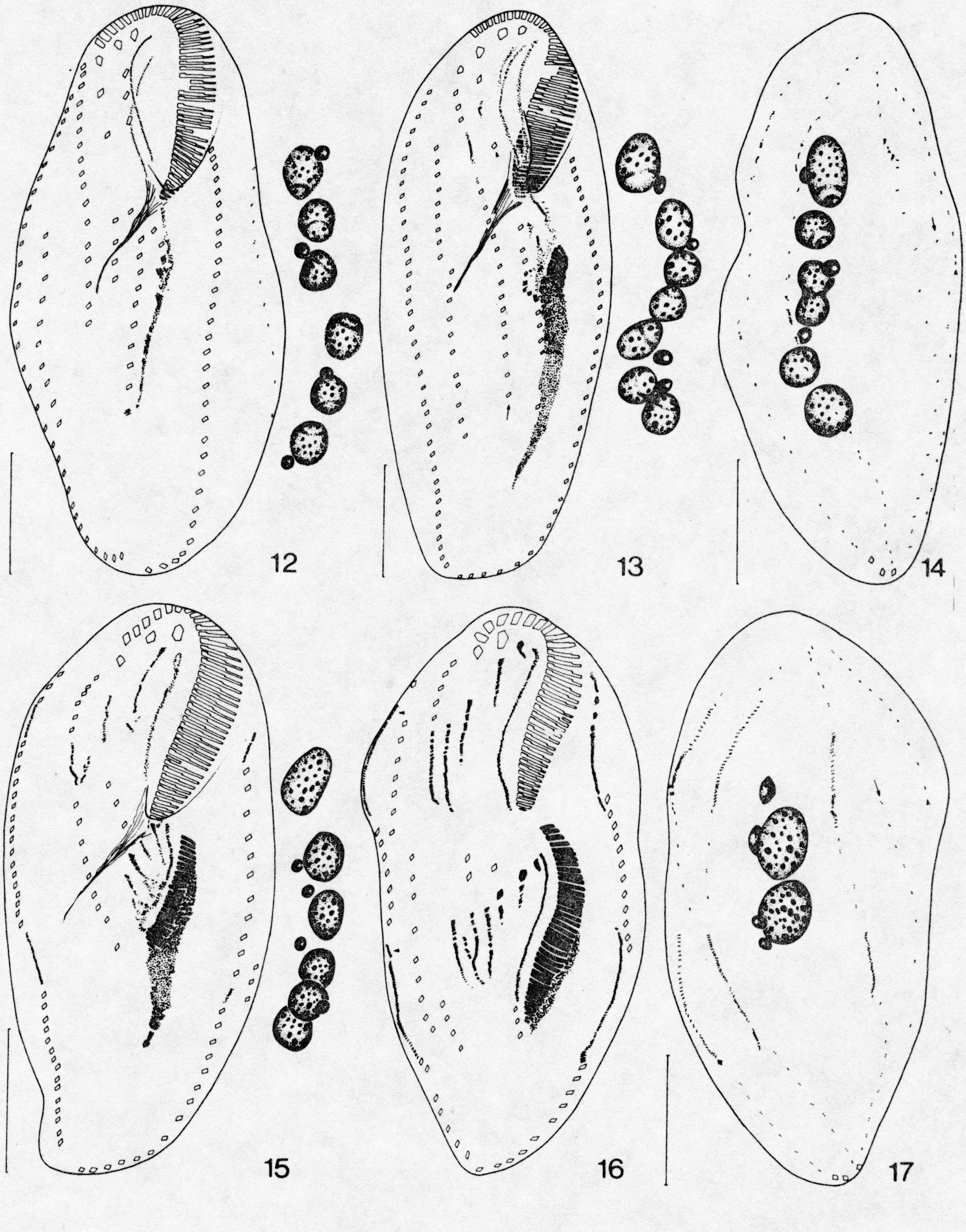
Adoral zone of membranelles usually formed like a question mark, about 40 % of body length, bases of the largest membranelles *in vivo* about 10 µm wide. Buccal area deep, undulating membranes slightly bent. Bases of the 3 frontal cirri distinctly enlarged. Cirri of the buccal row and the frontal row only slightly larger than the ventral and marginal cirri. Left fronto-ventral row usually in a line, but clearly separated from the short frontal row, begins anteriorly at about the level of the cytostome, terminates in the posterior half of the body. Right fronto-ventral row begins at the level of the right frontal cirrus, terminates usually in the middle of the cell. Rather frequent additional fronto-ventral rows occur, causing a great variability in the appearance of the ventral cirral pattern (Figs 7–9). Marginal rows inconspicuously separated posteriorly, cirri in vivo about 15 µm long. Very rarely (*c.* 1 of 50 specimens) a short second left marginal row occurs (Fig. 9). Dorsal cilia in vivo 2–3 µm long. Kinety 1 slightly shortened anteriorly, kineties 2 and 3 unshortened, kinety 4 shortened at both ends, and kinety 5 terminates in the middle of the cell. Dorsal rows 1 and 2 with caudal cirri.

MORPHOGENESIS OF CELL DIVISION (Figs 10–22). The earliest cortical morphogenetic event is the proliferation of basal bodies immediately left of the middle and posterior part of the left fronto-ventral row (Figs 10, 11). Subsequently a long and narrow oral primordium is formed (Fig. 12). The membranelles of the opisthe's adoral zone organize in a posterior direction. The buccal cirri, the second cirrus behind the right hypertrophied frontal cirrus, and some cirri in the anterior part of the right fronto-ventral row are modified to primordia. The parental undulating membranes commence with reorganization (Fig. 13). At about the same time the proliferation of new basal bodies occurs at 2 levels in the dorsal kineties 1, 2 and 3 (Fig. 14).

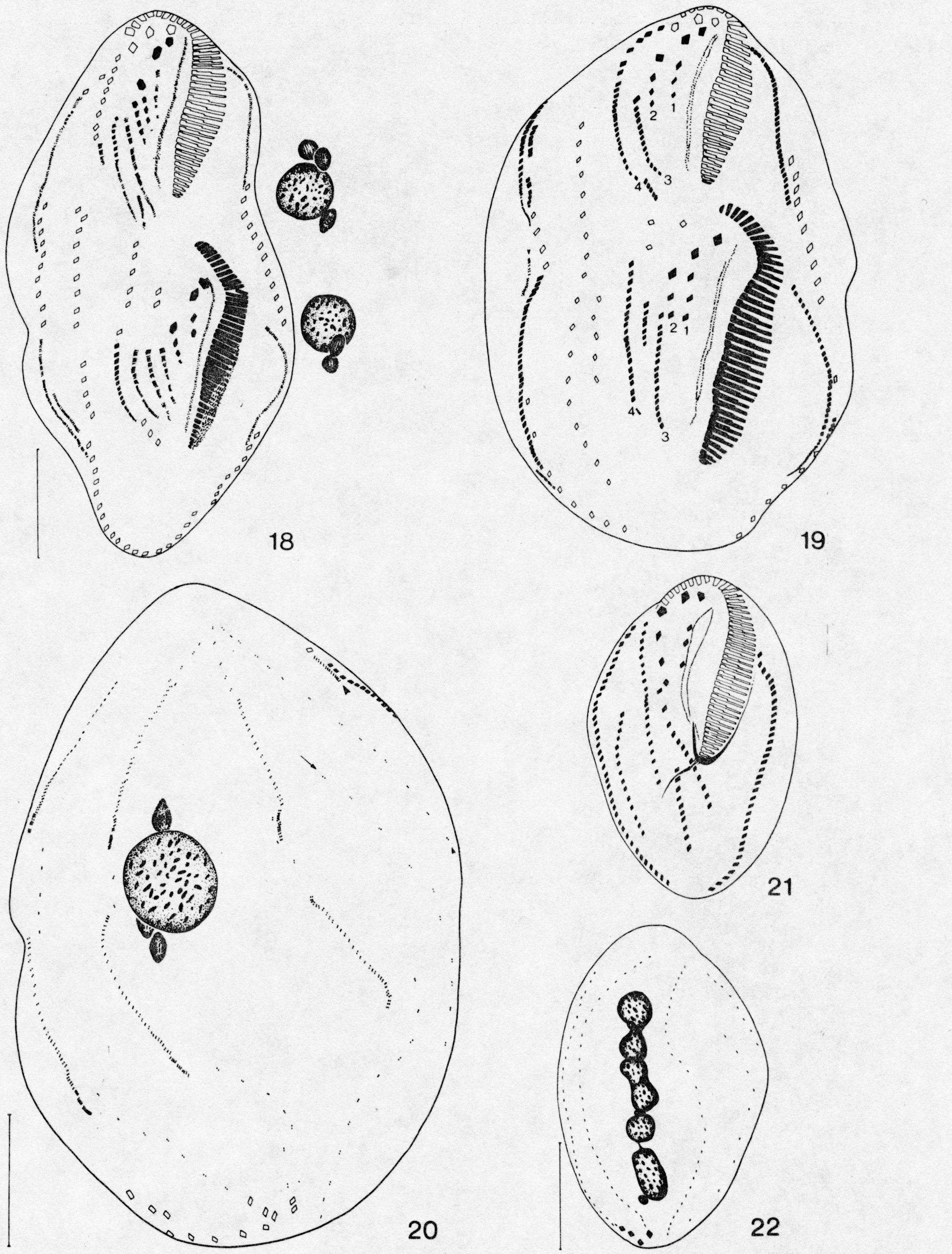
Division continues with the formation of the proter's and opisthe's marginal primordia and the further development of the fronto-ventral streaks. Usually 5 such streaks are formed, occasionally 6–9 occur (Fig. 15). Cortical morphogenesis proceeds with the cirral segregation from these streaks. At the anterior end of each right marginal primordium, 1 primordium of a dorsal kinety is separated and migrates onto the dorsal surface (Figs 16, 20). The primordia in the dorsal kineties 1–3 are elongated. The fusion of the macronuclear segments is almost completed (Fig. 17).

Figure 18 shows a late morphogenetic stage, where a large part of the opisthe's adoral zone is organized and the final number of membranelles recognizable. Many parental fronto-ventral and marginal cirri are still preserved. Parallel to the right marginal row of the opisthe there is a short marginal streak in this specimen which forms the inner right marginal row.

When the segregation of the fronto-ventral cirri is finished, the new left fronto-ventral rows become displaced in a posterior direction. At this stage the undulating membranes of both the proter and the opisthe are separated (Fig. 19).



Figs 12–17 Morphogenetical stages of *Parakahliella haideri* after protargol impregnation. **12**, early stage in ventral view. **13**, early stage in ventral view. Arrow, right fronto-ventral row; arrow head, frontal row. **14**, early stage in dorsal view. Arrow, parental dorsal kinety 4; arrow head, parental dorsal kinety 5. **15**, **16**, middle stages in ventral view. Arrow head, primordium of the new dorsal kinety 5. **17**, middle stage in dorsal view. Arrow, parental dorsal kinety 4; arrow head, parental dorsal kinety 5. Scale marks = 30 μm.



Figs 18–22 Morphogenetical stages of *Parakahliella haideri* after protargol impregnation. **18**, late stage in ventral view. **19**, very late stage in ventral view. 1, buccal row; 2, frontal row; 3, left frontoventral row; 4, right fronto-ventral row; arrow head, new dorsal kinety 5 of the opisthe. **20**, very late stage in dorsal view. Arrow, parental dorsal kinety 4; small arrow head, parental dorsal kinety 5; large arrow head, new dorsal kinety 5 of the proter. **21**, **22**, post divider in ventral and dorsal view. Scale marks = 30 μm.

The formation of the new dorsal kineties 1, 2 and 3 continues. Caudal cirri differentiate at the posterior end of the dorsal kineties 1 and 2. The parental kineties 4 and 5 are completely maintained. They form the new kinety 4 of the filial products (Figs 20, 22). After the separation of the proter and the opisthe the formation of the final cortical pattern is continued (Fig. 21).

DISCUSSION

SPECIES COMPARISON. *Parakahliella haideri* differs from both congeners in the possession of only 1 left marginal row. It can be further separated from *P. terricola* by the higher number of adoral membranelles (*P. haideri* $\bar{x}$ = 48, 34–62; *P. terricola* 28). All other biometrical and morphological characters overlap considerably (Buitkamp, 1977; Foissner, 1982; Berger *et al.*, 1985).

There is some evidence which suggests that there is a small variation in the number of the left marginal rows, even in species with normally only 1 row (Jeffries & Mellott, 1968; Grim, 1970; Walker & Grim, 1973; Borrow & Wicklow, 1983; Jerka-Dziadosz & Banaczyk, 1983). However, in many biometrical investigations this character was shown to be very stable in natural populations (e.g. Foissner, 1982, 1984; Berger *et al.*, 1985; Berger & Foissner, 1987; Wirnsberger *et al.*, 1985*a*, *b*). Thus, some variation might be caused by prolonged or suboptimal culture conditions and should not be included in species diagnosis.

Redefinition of the Genus *Parakahliella* Berger, Foissner & Adam, 1985

Parakahliella was originally characterized as 'Kahliellidae with caudal cirri and more than 1 right and 1 left marginal cirral row. Some parts of the parental left marginal infraciliature are preserved in the post-dividers' (Berger *et al.*, 1985). The species described in this paper agrees with the type-species *P. macrostoma* (Foissner, 1982) and *P. terricola* (Buitkamp, 1977) in the number and the arrangement of the fronto-ventral cirral rows and in particular with *P. macrostoma* in the formation of the fronto-ventral rows and the special morphogenetic pattern of the dorsal kineties. The conservation of the parental dorsal kineties 4 and 5 as new kinety 4 is a unique type of dorsal morphogenesis and a strong apomorphic character, which indicates the congenerity of the 3 species now included and separates *Parakahliella* from the other members of this family (Tuffrau, 1979; Foissner & Adam, 1983; Berger *et al.*, 1985). However, the diagnostic characters—'increased number of left marginal rows and preservation of some parts of the parental left marginal infraciliature'—would exclude *P. haideri* from this genus. Hence, we suggest a slight modification of the generic diagnosis of *Parakahliella*: Kahliellidae with caudal cirri and 1 or more right and left marginal rows. During morphogenesis some parental dorsal rows are conserved as new kinety in the filial products.

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