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Divisional Morphogenesis in *Orthoamphisiella stramenticola* EIGNER & FOISSNER, 1991 and *O. grelli* nov. spec. (Ciliophora, Hypotrichida)

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Dedicated to Professor Dr. KARL G. GRELL on the occasion of his 80th birthday.

Summary: Divisional morphogenesis was investigated in *Orthoamphisiella stramenticola* EIGNER & FOISSNER, 1991 and *O. grelli* nov. spec. using protargol impregnation. *Orthoamphisiella grelli* nov. spec. differs from *O. stramenticola* mainly by having only 2 macronuclear segments. A Japanese population of *O. stramenticola* is also described. It differs from the type population mainly by the absence of a third short ventral row. Divisional morphogenesis is very similar in both species. The oral primordium originates apokinetally and develops the oral apparatus and the left frontal cirrus for the opisthe. All cirral anlagen originate in the frontal area of the proter and from parental cirri. Later, the anlagen (primary primordia) split and the proximal portions migrate posteriad forming the ventral ciliature of the opisthe. The long ventral (median) row develops from a single primordium within the central portion of the parental row. This anlage splits and proliferates basal bodies anteriad and posteriad. Dorsal kineties develop by intrakinetal proliferation; no caudal cirri are formed. Compared to other amphisiellid hypotrichs, *Orthoamphisiella* spp. are unique in having an apokinetal stomatogenesis and a long ventral (median) row originating from a single anlage. Further studies are needed to elucidate the phylogeny of amphisiellid hypotrichs.

Key Words: Ciliophora; Hypotrichida; Morphogenesis; *Orthoamphisiella stramenticola; Orthoamphisiella grelli* nov. spec.

Introduction

Hypotrichs have developed many specific cirral patterns. One of these includes species having at least one long ventral (median) row together with one row each of right and left marginal cirri (BORROR & WICKLOW 1982). Such species are presently assigned to several genera *(Orthoamphisiella, Amphisiella, Paramphisiella, Amphisiellides, Hemiamphisiella, Gastrostyla, Trachelochaeta, Gonostomum, Wallackia, Kahliella)* most of which belong to the rather vaguely defined family Amphisiellidae. Differences between genera are sometimes inconspicuous. Thus, morphogenetic data can often contribute considerably to a better definition. Three detailed morphogenetic studies from amphisiellid hypotrichs are available, viz. by Voss (1992) on *Amphisiella australis,* by WICKLOW (1982) on *Amphisiella marioni* and by HEMBERGER (1982) on *Paramphisiella caudata.*

Our paper represents a further contribution to the study of amphisiellid hypotrichs by providing a detailed description of the morphogenesis in *Orthoamphisiella stramenticola* and *O. grelli* nov. spec.

Material and Methods

Orthoamphisiella stramenticola was collected in July 1991 from the type location.

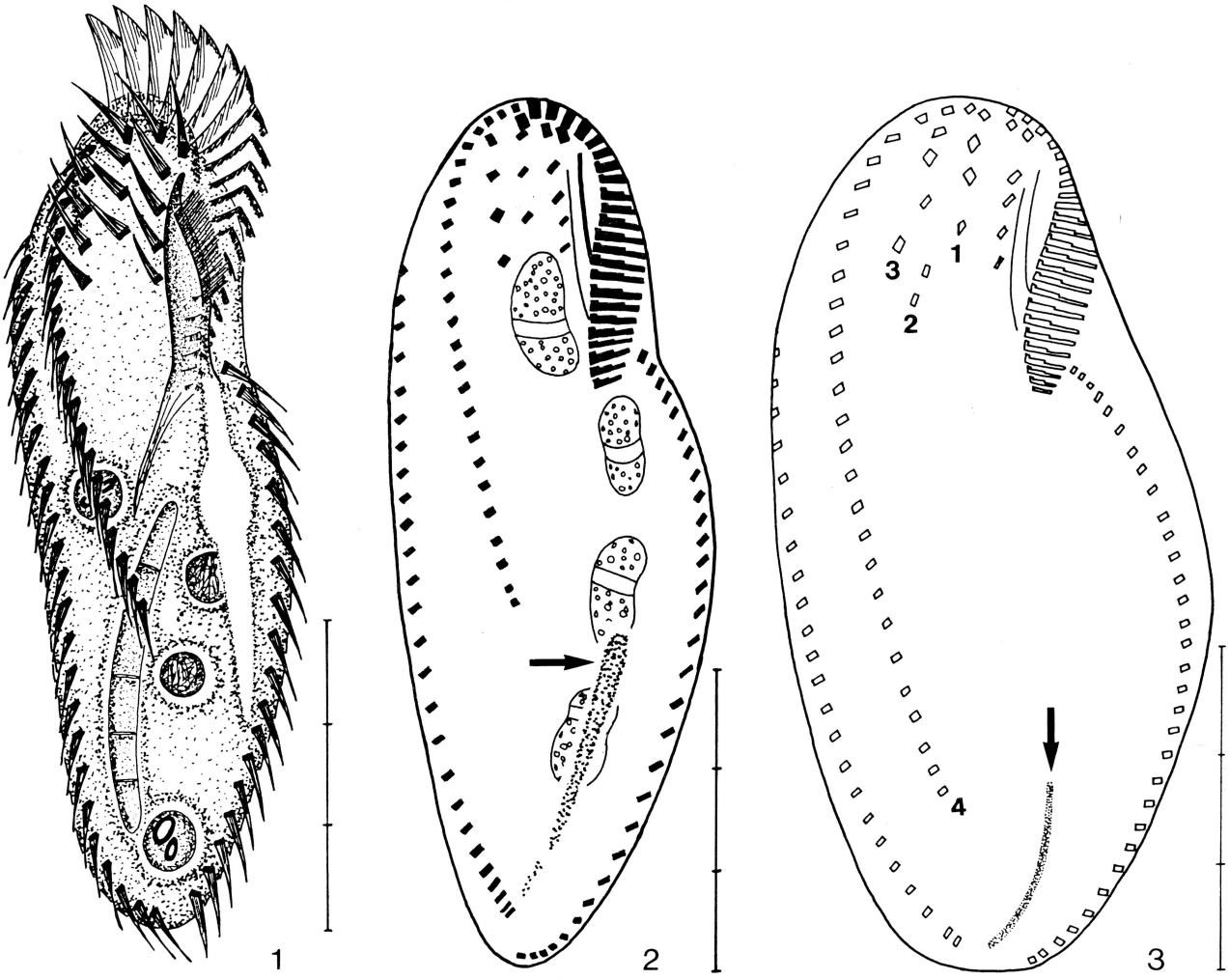
Another population of *O. stramenticola* was discovered on July 15th 1989 in a sample containing litter and roots from small bamboo and beech trees collected in Japan near the peak of the "Female" Tsukuba mountain (c. 800 m above sea-level).

Orthoamphisiella grelli nov. spec. was discovered in a sample of moss and soil (pH 4.3) collected on October 21st 1990 by Dr. J. COOPER (South Africa) from a river bank on Gough Island, Transvaal Bay, about 50 m above sea-level.

All populations were grown in raw cultures set up according to FOISSNER (1987). Body shapes of living specimens were drawn from slides without coverslip. Details were studied on slightly to heavily squeezed individuals using an oil immersion objective and interference contrast optics. The infraciliature was revealed by FOISSNER's (1991) protargol protocol. Drawings were made with the help of a camera lucida.

To illustrate the changes occurring during morphogenetic processes, old (parental) cirri are depicted by contour, whereas new cirri are shaded black.

Terminology is according to EIGNER & FOISSNER (1991). Statistical procedures follow SOKAL & ROHLF (1981).



Figs. 1–3. *Orthoamphisiella stramenticola.* Ventral views from life (Fig. 1) and after protargol impregnation (Figs. 2, 3). – 1, 2. Interphase specimen and early divider from Japanese population. – 3. Early divider from Austrian population. Numbers 1–4 designate ventral rows. Arrows in Figs. 2 and 3 mark oral primordium. Scale bar divisions = 10 μm.

Table 1. Morphometric characterization of *Orthoamphisiella stramenticola* (type population, 1st line; from EIGNER & FOISSNER 1991), *O. stramenticola* (Japanese population; 2nd line) and *O. grelli* (3rd line).

Character[1])	x̄	M	SD	SE	CV	Min	Max	n
Body, length	93.8	92.5	6.5	1.2	6.9	78.7	105.0	29
	80.7	79.0	12.4	2.5	15.4	57.0	102.0	25
	67.8	68.0	8.9	1.8	13.1	51.0	87.0	25
Body, width	28.8	27.5	6.6	1.2	22.9	18.7	50.0	29
	28.2	27.0	5.5	1.1	19.5	21.0	43.0	25
	23.0	21.0	3.8	0.8	16.5	16.0	31.0	25
Adoral zone of membranelles, length	27.5	27.5	4.6	0.8	16.7	22.5	37.5	29
	29.0	29.0	3.2	0.6	11.0	24.0	37.0	25
	22.8	22.0	1.8	0.4	7.9	19.0	27.0	25
Ventral row, length	46.2	48.7	8.9	1.7	19.2	41.2	83.7	27
	46.7	46.0	7.9	1.6	17.0	31.0	66.0	25
	41.0	42.0	12.0	2.4	29.2	27.0	74.0	25
Anterior macronuclear segment, length	10.9	11.3	1.7	0.4	15.2	6.8	13.8	22
	10.0	10.0	2.4	0.5	24.0	6.0	15.0	25
	13.0	12.0	3.2	0.6	24.6	9.0	20.0	25
Anterior macronuclear segment, width	5.9	6.3	0.9	0.2	15.2	3.8	7.5	22
	5.7	6.0	0.6	0.1	10.5	5.0	7.0	25
	6.0	6.0	1.2	0.2	20.0	4.0	9.0	25
Second anterior macronuclear segment, length	11.9	12.5	3.0	0.6	25.2	5.0	17.5	28
	7.5	6.5	2.2	0.4	29.3	5.0	15.0	25
	11.9	12.0	2.9	0.6	24.4	6.0	17.0	24
Second anterior macronuclear segment, width	5.3	5.0	0.9	0.2	16.9	3.7	7.5	29
	5.2	5.0	0.6	0.1	11.5	4.0	6.0	25
	5.9	6.0	1.0	0.2	16.9	4.0	9.0	24
Macronuclear segments, number	4.3	4.0	–	–	–	4.0	6.0	30
	4.0	4.0	0.0	0.0	0.0	4.0	4.0	25
	2.1	2.0	–	–	–	1.0	3.0	25
Micronuclei, number	5.1	5.0	1.3	0.2	25.4	3.0	7.0	28
	4.8	5.0	1.5	0.3	31.2	3.0	8.0	25
	2.5	2.0	1.2	0.3	48.0	1.0	6.0	23
Adoral membranelles, number	20.4	20.0	2.7	0.6	13.2	18.0	30.0	23
	23.2	24.0	1.9	0.4	8.2	19.0	26.0	25
	20.3	21.0	1.2	0.2	5.9	18.0	22.0	25
Right marginal row, number of cirri	40.7	41.0	2.1	0.5	5.1	36.0	44.0	19
	28.2	28.0	2.0	0.4	7.1	24.0	32.0	25
	26.4	26.0	2.4	0.5	9.1	20.0	31.0	25
Left marginal row, number of cirri	33.5	34.0	2.3	0.5	6.9	30.0	38.0	21
	24.3	24.0	2.6	0.5	10.7	18.0	30.0	25
	22.6	23.0	2.7	0.5	11.9	18.0	28.0	25
Buccal cirri, number	4.7	5.0	1.0	0.2	21.2	4.0	7.0	22
	3.5	3.0	–	–	–	3.0	4.0	25
	2.1	2.0	–	–	–	2.0	3.0	25
Fronto-ventral row 1, number of cirri	3.7	4.0	0.7	0.1	18.9	3.0	5.0	22
	3.0	3.0	0.5	0.1	16.6	2.0	4.0	25
	2.2	2.0	0.5	0.1	22.7	1.0	3.0	25
Fronto-ventral row 2, number of cirri	4.0	4.0	0.6	0.1	15.0	3.0	5.0	23
	3.6	4.0	0.6	0.1	16.7	3.0	5.0	25
	3.0	3.0	0.5	0.1	16.7	2.0	4.0	25
Fronto-ventral row 3, number of cirri	2.8	3.0	1.0	0.2	35.7	1.0	5.0	15
	0.0	0.0	0.0	0.0	0.0	0.0	0.0	25
	2.6	3.0	0.8	0.3	30.8	1.0	4.0	10
Long ventral (median) row, number of cirri	22.8	23.0	2.4	0.5	10.5	19.0	30.0	20
	19.7	20.0	1.6	0.3	8.1	16.0	22.0	25
	18.2	18.0	1.7	0.4	9.3	14.0	22.0	23
Dorsal kineties, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	20
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	20
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	20

[1]) Data are based on protargol impregnated specimens from a clone (*O. stramenticola*; type population) and from raw cultures (*O. s.* Japanese population and *O. grelli*). Measurements in μm. x̄ – arithmetic mean; M – median; SD – standard deviation; SE – standard error of arithmetic mean; CV – coefficient of variation; Min – minimum value; Max – maximum value; n – sample size.

Results

Morphology of *Orthoamphisiella stramenticola*, Japanese population (Figs. 1, 2; Table 1)

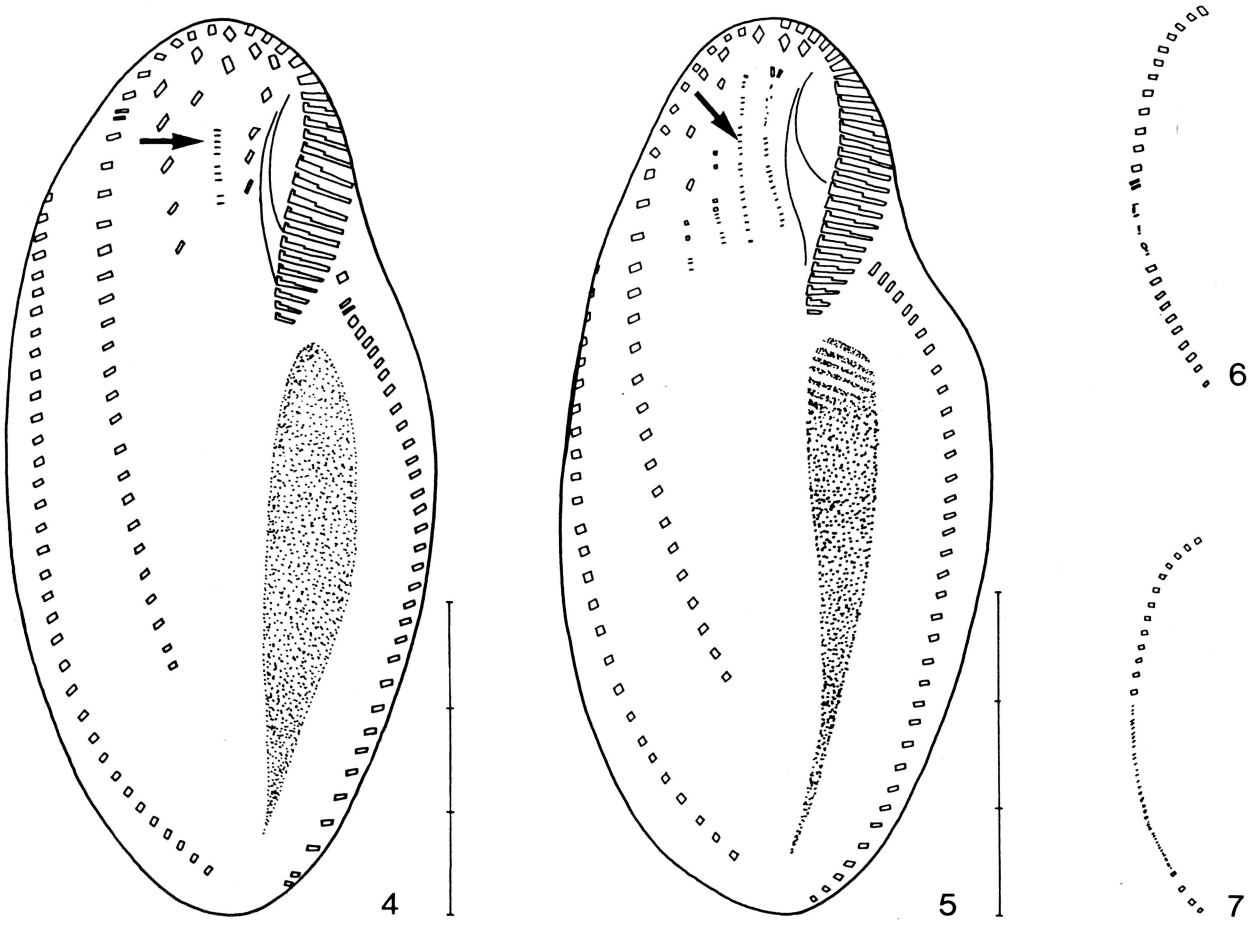
The Japanese population differs slightly from the Austrian type population and is thus briefly described below.

Size in vivo about 90 × 30 µm. Elliptical, right body margin slightly concave, left convex and slightly indented beneath adoral zone of membranelles. Posterior end slightly narrowed, both ends broadly rounded. Contractile vacuole in mid-body and with collecting canals. No cortical granules; loosely arranged, inconspicuous subpellicular granules were erroneously reported for the type population (EIGNER & FOISSNER 1991). A reinvestigation of material from the type location showed that these were actually mitochondria. Cytoplasm contains many colourless, fatty globules, 1–3 µm in diameter. Food vacuoles filled with fungal spores and filamentous and coccal (c. 4 × 3 µm) cyanobacteria.

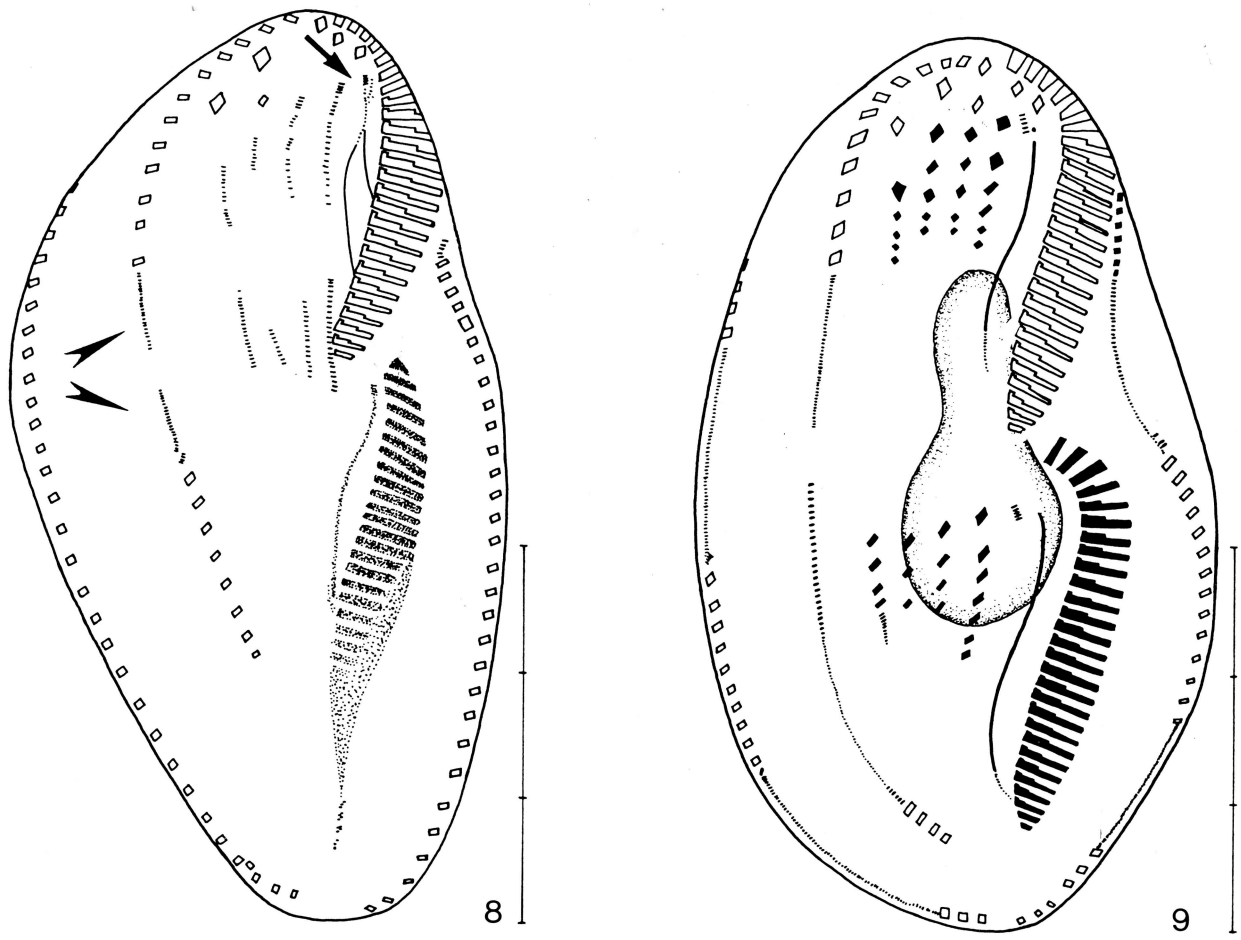
Adoral zone of membranelles 35 % of body length, bases of membranelles 7 µm in vivo. Oral lip extends lid-like across buccal cavity. Paroral membrane inserted in small fold on outer surface of lip, alongside more or less oblique left edge of anterior portion of oral lip. Endoral membrane slightly curved, on right inner surface of buccal cavity. All cirri c. 10 µm long. Right marginal row commencing on a level with 4th–6th cirrus of long ventral row, curves subterminally to median of cell almost contacting left marginal row. Long, rightmost ventral (median) row commences at distal end of adoral zone of membranelles and extends to centre of ventral surface. Buccal cirri almost in line with 2nd frontal cirrus. Fronto-ventral row 1 in line with 3rd frontal cirrus. A third short fronto-ventral row is absent, whereas it is present in 64 % of the type population individuals (Figs. 1, 2).

Dorsal cilia in vivo 3 µm long, arranged in 2 kineties. Caudal and transverse cirri absent.

The type population has a mean of 23 cirri in the long ventral (median) row (Table 1). The specimens used in this



Figs. 4–7. Early morphogenetic stages in *Orthoamphisiella stramenticola*. Austrian population (Figs. 4, 5, 6) and Japanese population (Fig. 7). Figs. 6 and 7 show development of the (4th, median) long ventral row from a single primordium. Arrows in Figs. 4 and 5 mark streaks derived from 1st ventral row. Scale bar divisions = 10 µm.



Figs. 8–9. Middle morphogenetic stages of *Orthoamphisiella stramenticola*. Austrian population. Arrow in Fig. 8 marks disorganizing undulating membranes, arrowheads mark the splitting of the anlage in the 4th, median) long ventral row. Scale bar divisions = 10 μm.

study, although originating from the type location, have 28 cirri (Min = 26; Max = 32; n = 12). This may be due to cloning of the (first) type population, whereas specimens from a raw culture were used in this study.

Divisional morphogenesis in *Orthoamphisiella stramenticola* (Figs. 2–12)

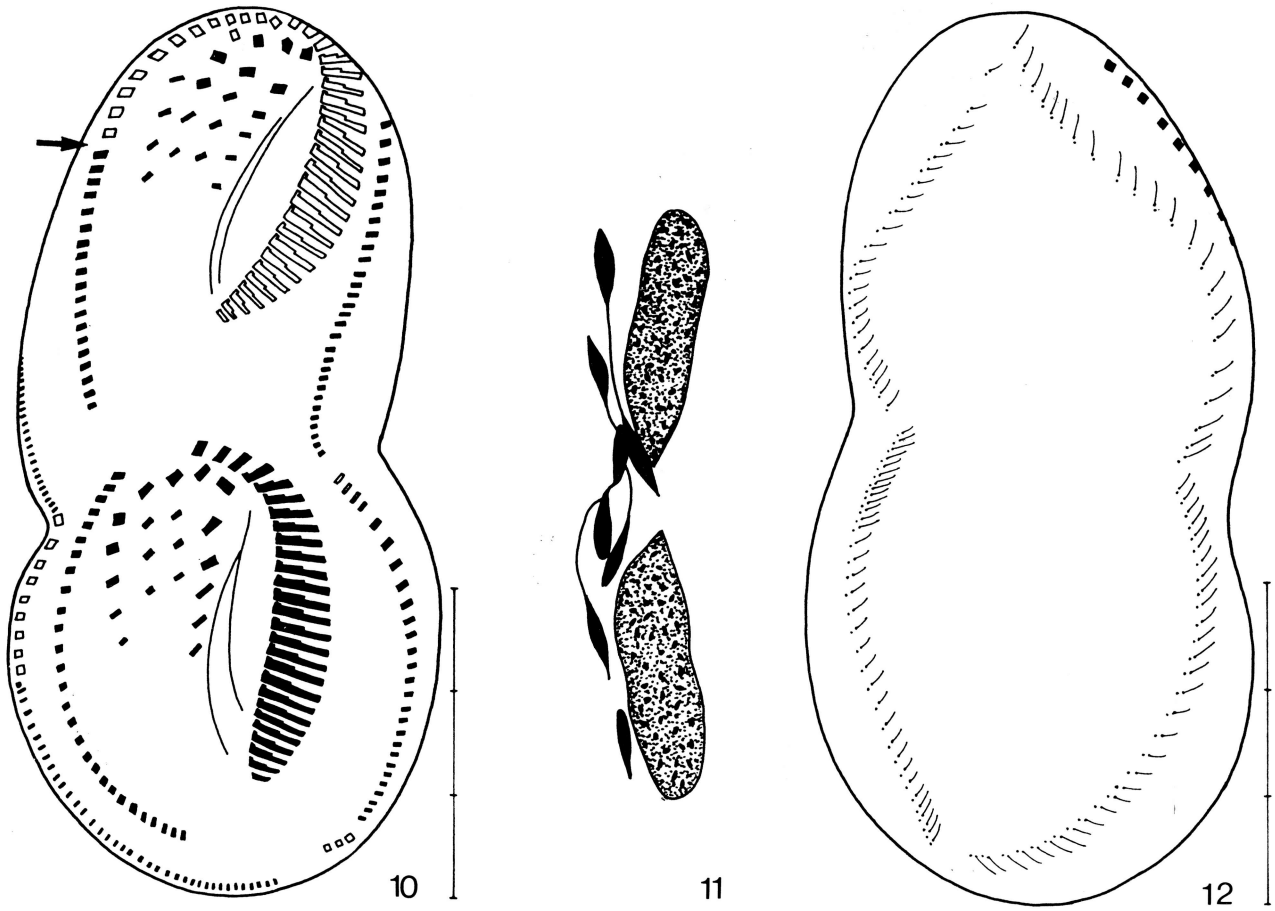
The nuclear apparatus and the marginal rows divide in the usual way (Figs. 9, 11). The dorsal infraciliature develops according to type 1 (FOISSNER & ADAM 1983). No caudal cirri are formed (Fig. 12). These processes therefore require no further comment.

Stage 1 (Figs. 2, 3): Stomatogenesis commences with the proliferation of basal bodies to form a narrow anarchic field near the open ends of the right and left marginal row (Figs. 2, 3, arrow).

Stage 2 (Fig. 4): The oral primordium grows to a large field of loosely arranged basal bodies extending between the adoral zone of membranelles and the posterior end of the cell. The posterior cirri of the 1st fronto-ventral row disaggregate to a short streak (Fig. 4, arrow).

Stage 3 (Fig. 5): The posterior portion of the oral primordium narrows, the anterior portion differentiates adoral membranelles. The 1st fronto-ventral row disorganizes completely and forms a long streak of basal bodies (Fig. 5, arrow; anlage 3 generating right frontal cirrus and 1st fronto-ventral row of proter and opisthe, respectively). Likewise, the buccal cirri disaggregate to a long streak of basal bodies (anlage 2 generating middle frontal cirrus and buccal cirri of proter and opisthe, respectively). The 2nd and 3rd fronto-ventral row also disaggregate and form short streaks of basal bodies (anlagen 4 and 5 for 2nd and 3rd fronto-ventral row of proter and opisthe, respectively).

Stage 4 (Figs. 6–8): Right of the developing adoral membranelles a streak of basal bodies separates from the oral primordium generating the 1st frontal cirrus and the undulating membranes for the opisthe. The proter's anlagen 2–5 split and their posterior portions migrate pos-



Figs. 10–12. Late morphogenetic stages of *Orthoamphisiella stramenticola* (Austrian population) in ventral (Fig. 10) and dorsal view (Figs. 11, 12). Fig. 11. shows the dividing macronuclear segments and micronuclei of the specimen shown in Fig. 10. Arrow in Fig. 10 marks border between old and new cirri in the (4th, median) long ventral row. Scale bar divisions = 10 μm.

teriad; the anterior ends of the anterior portions develop frontal cirri. The parental undulating membranes disaggregate forming the 1st frontal cirrus and a single, long and narrow streak of basal bodies (Fig. 8, arrow; anlage 1 of proter). An anlage develops within the middle portion of the long ventral (median) row (Fig. 6). The splitting of this anlage occurred slightly earlier in the Austrian population (Fig. 8, arrowheads) than in the Japanese one (Fig. 7). At this stage six anlagen are thus recognizable for each the proter and the opisthe. Individuals having only 2 short fronto-ventral rows possess five anlagen each.

Stage 5 (Fig. 9): The formation of the opisthe's adoral membranelles is complete. The anlagen for the undulating membranes are long, single streaks of basal bodies in both proter and opisthe. The fronto-ventral anlagen have organized to cirri.

Stage 6 (Figs. 10, 11): The anlagen for the undulating membranes split in both proter and opisthe to form the endoral and paroral membrane. The anlage within the long ventral row proliferates 28 cirri in the opisthe from disaggregated parental cirri, i.e. all cirri are new. In contrast, only 19 cirri ($\bar{x}$ = 19.3; n = 6) are formed in the proter; 11 parental cirri ($\bar{x}$ = 11.6; n = 18) remain or are renewed in post-dividers (Fig. 10, arrow).

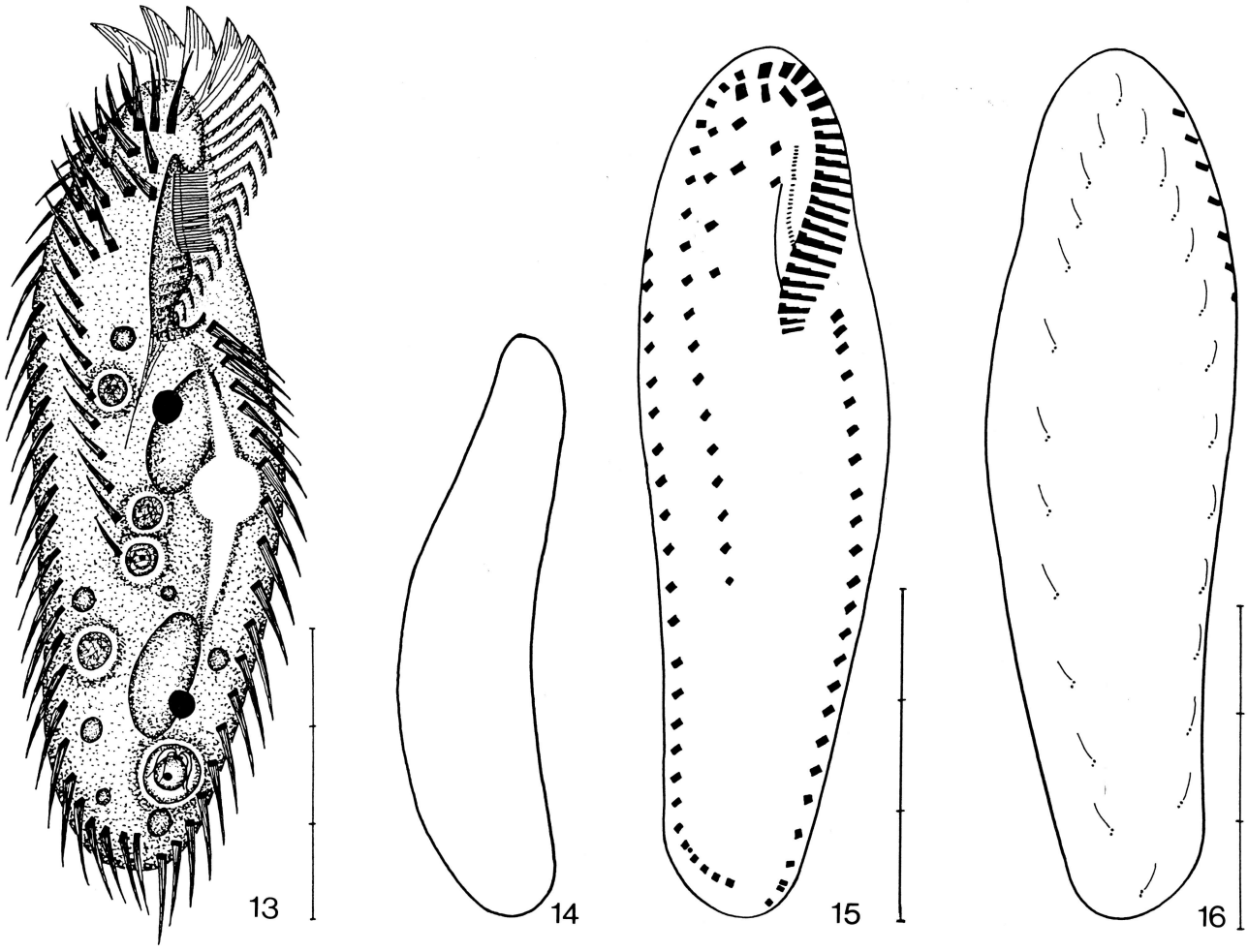
Orthoamphisiella grelli nov. spec. (Figs. 13–16; Table 1)

Diagnosis: Size in vivo 60–90 × 20–30 μm. 2 macronuclear segments, 20 adoral membranelles, 2 buccal cirri at anterior end of endoral membrane and 7 fronto-ventral cirri in 2–3 short rows on average.

Type location: In moss and soil from a river bank on Gough Island, Transvaal Bay (W 10° 00′, S 40° 20′).

Type specimens: A holotype and a paratype of *O. grelli* as 2 slides of protargol impregnated cells have been deposited in the collection of microscopic slides of the Oberösterreichisches Landesmuseum in Linz.

Dedication: This new species is named in honour of Professor Dr KARL G. GRELL (Tübingen), a tireless and



Figs. 13–16. *Orthoamphisiella grelli* nov. spec. from life (Figs. 13, 14) and after protargol impregnation (Figs. 15, 16). – 13, 15. Ventral views. – 14. Lateral view. – 16. Dorsal view. Scale bar divisions = 10 μm.

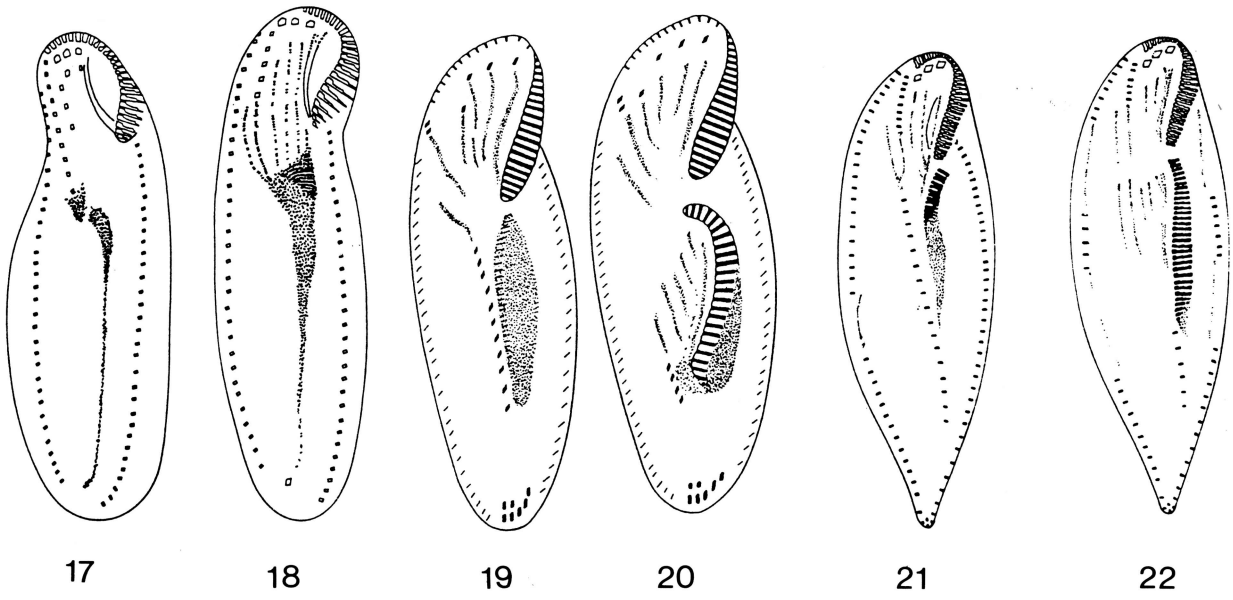
successfull investigator of marine and freshwater protists.

Description (morphometric data shown in Table 1 are not repeated): Long-elliptical, right body margin straight to slightly concave, left more or less convex. Anterior and posterior end slightly tapered. Dorso-ventrally inconspicuously flattened; highly flexible. Macronuclear segments ellipsoid, in vivo about 15 × 6 μm, left of cell median. Usually 2–3 micronuclei attached to macronuclear segments, in vivo about 3 μm in diameter. Contractile vacuole near left margin in mid-body, with 2 inconspicuous collecting canals. No cortical granules or cytoplasmic crystals. Cytoplasm with some fatty globules 2–4 μm in diameter and many small food vacoules 4–7 μm in diameter containing bacteria and heterotrophic flagellates (Figs. 13, 14).

Adoral zone of membranelles 30% of body length, commences in median of cell, i.e. at level of second frontal cirrus. Oral lip extends lid-like across buccal cavity. Paroral membrane straight, inserted in shallow fold on outer surface of lip, parallel to oblique left edge of anterior portion of oral lip. Endoral membrane slightly curved, inserted on right inner surface of buccal cavity. All cirri about 10 μm long. Right marginal row commences at level of 2nd–3rd cirrus of long ventral row, curves subterminally to median of cell, regularly terminating slightly above left marginal row. Long ventral (median) row commences at distal end of adoral zone of membranelles and usually extends to centre of ventral surface. Uppermost (frontal) 3 cirri distinctly enlarged. Buccal cirri in line with 2nd frontal cirrus. Fronto-ventral row 1 in line with 3rd frontal cirrus (Fig. 15).

Dorsal cilia in vivo 3 μm, arranged in 2 rows almost as long as cell. Caudal and transverse cirri absent (Fig. 16).

Comparison with related species: *Orthoamphisiella grelli* differs from the only congener, *O. stramenticola,* mainly in the number of macronuclear segments (4 in *O. stramenticola*). Minor differences concern the number



Figs. 17–22. Morphogenetic stages of *Amphisiella australis* (Figs. 17, 18, from Voss 1992). *A. marioni* (Figs. 19, 20, from WICKLOW 1982) and *Paramphisiella caudata* (Figs. 21, 22, from HEMBERGER 1982). In these species the long ventral (median) cirral row in each proter and opisthe develops from two streaks which later arrange one behind the other.

and location of the buccal cirri and the body size (Table 1).

Divisional morphogenesis: Divisional morphogenesis in *O. grelli* is very similar to that of *O. stramenticola.* However, the primordium for the long ventral row develops more anteriad, leaving only 3–7 ($\bar{x} = 4.5$; $n = 6$) parental cirri intact. *Orthoamphisiella stramenticola,* in contrast, has this anlage in the centre of the long ventral row. Thus, 9–14 ($\bar{x} = 11.6$; $n = 18$) parental cirri remain or are renewed in post-dividers (Fig. 10, arrow).

Discussion

Most hypotrichs can be assigned to one of three types of ventral cirral development. Type 1 generates the cirri from independent primordia, i.e. the proter and the opisthe each develop their own cirral anlagen. This type is common in oxytrichids s. str., e.g. *Stylonychia* spp. (WIRNSBERGER et al. 1986; cp. Table 4 in BERGER et al. 1985) and *Kahliella franzi* (BERGER & FOISSNER 1988). Type 2 develops long primary primordia, most of which originate in contact with the oral primordium and later split in the middle; the anterior portions form the new cirri for the proter, the posterior portions those for the opisthe. This type occurs in, e.g., *Tachysoma pellionellum* (HEMBERGER 1982), *Urosoma macrostyla* (FOISSNER 1983) and *Gonostomum strenua* (SONG WEIBO 1990). Type 3, represented by *Orthoamphisiella* spp., also develops long primary primordia but originating from parental cirri. In contrast to type 2, primary and oral primordia are not connected.

According to the descriptions of the divisional morphogenesis in 3 amphisiellid hypotrichs by Voss (1992), WICKLOW (1982) and HEMBERGER (1982), all cirral anlagen develop from, or are at least formed in connection with the oral primordium, i.e. develop according to type 2. We suggest, however, another interpretation based on our own detailed investigations of *Orthoamphisiella* spp. and the re-evaluation of the drawings by the above mentioned authors. These show rather clearly that *Amphisiella australis, A. marioni* and *Paramphisiella caudata* develop their cirral pattern like *Orthoamphisiella* spp., i.e. according to type 3 (Figs. 17–22). However, the drawings are not detailed enough to be fully conclusive, e.g. the decisive stage is not provided for *A. marioni.* Furthermore, the figures for *Paramphisiella caudata* are rather ambiguous; possibly some basal bodies of the oral primordium contribute in forming the primary primordia. The data on other amphisiellids, viz. *Amphisiella terricola, A. binucleata* and *Amphisiellides atypicus,* provided by HEMBERGER (1982) is too incomplete for a reliable interpretation.

Several evolutionary lines are recognizable within hypotrichs with a long ventral (median) row. *Orthoamphisiella* spp. develop the oral primordium apokinetally, *Amphisiella australis* parakinetally from the transverse cirri, and *A. marioni* and *Paramphisiella caudata* parakinetally from the long ventral row. In *Orthoamphisiella* the long ventral (median) row develops from a single

anlage in each proter and opisthe. In contrast, the long ventral (median) row of the species mentioned above and shown in Figs. 17–22 develops from two anlagen in each proter and opisthe. Further modes are known (BORROR & WICKLOW 1982) indicating non-homology of this pattern. This suggests that *Orthoamphisiella* is misclassified in the Amphisiellidae. Indeed, the development of its ventral cirral pattern resembles strongly to that known for *Trachelochaeta gonostomoida* HEMBERGER, 1982.

At present a profound definition of amphisiellid hypotrichs is not possible. More comparative morphogenetic data from hypotrichs with a median cirral row are needed to distinguish between analogies and homologies.

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