Acta Protozoologica (1996) 35: 257 - 280

ACTA
PROTOZOOLOGICA

Morphology and Morphogenesis of *Lamtostyla edaphoni* Berger and Foissner and *Onychodromopsis flexilis* Stokes, Two Hypotrichs (Protozoa: Ciliophora) from Antarctic Soils

Wolfgang PETZ and Wilhelm FOISSNER

Universität Salzburg, Institut für Zoologie, Salzburg, Austria

Summary. The morphology and morphogenesis of *Lamtostyla edaphoni* Berger and Foissner, 1987 and *Onychodromopsis flexilis* Stokes, 1887 were investigated using silver impregnation and scanning electron microscopy. Stomatogenesis of *L. edaphoni* commences apokinetally near the leftmost transverse cirrus, like in *L. perisincirra*, *L. hyalina* and *L. australis* nov. comb. This distinguishes *Lamtostyla* from *Amphisiella*, whose oral primordium originates parakinetally from the amphisiellid median cirral row (ACR). Five cirral anlagen develop. In the proter, the undulating membranes, the buccal cirrus and the cirrus left of the ACR each provides one streak, two anlagen derive from the ACR. In the opisthe, the oral primordium produces the anlage for the undulating membranes and very likely three cirral streaks; one anlage develops at the posterior end of the ACR. The new ACR is formed by alignment of the two rightmost cirral anlagen, proving that *Lamtostyla* belongs to the Amphisiellidae. Based on these data, improved definitions are given for all amphisiellid genera. *Onychodromopsis flexilis* is redescribed emphasizing somatic variation and the fine structure of the oral apparatus. It has cortical granules and an oxytrichid FVT-cirral pattern but two to three right and one to two left marginal rows. The morphogenetic processes are very similar to those of *Oxytricha granulifera*. In the opisthe, cirrus IV/2, V/3 and V/4 each provides one streak (anlagen 4-6), and three streaks (anlagen 1-3) originate from the oral primordium and/or the posterior ends of anlagen 4-6. The anlagen of the proter originate from the paroral membrane, cirri II/2, III/2 and IV/3, and by splitting of the opisthe's anlagen 5 and 6. Two marginal anlagen each develop in the outer right and inner left marginal row; the inner right and outer left row remain unchanged and are later resorbed. Physiological regeneration resembles development in the proter. However, cirrus V/3 is inactive and the anlagen 5 and 6 originate from cirri IV/2 and V/4, respectively. The data show that *O. flexilis* belongs to the Oxytrichidae and is closely related to *Oxytricha*.

Key words: *Amphisiella*, Antarctica, *Lamtostyla*, morphogenesis, *Onychodromopsis*, soil ciliates.

INTRODUCTION

The interphasic cirral pattern is a rather ambiguous character for the generic classification of hypotrichs because similar patterns may originate by different ontogenetic processes (Eigner and Foissner 1994, Eigner 1995). Therefore, morphogenetic features are increasingly used for distinguishing genera, families and orders (e.g. Borror 1972, 1979; Wicklow 1982; Eigner and Foissner 1994; Eigner 1995). In the present study, we describe the morphogenesis of *Lamtostyla edaphoni*, an amphisiellid hypotrich formerly assigned to the

Address for correspondence: Wolfgang Petz, Universität Salzburg, Institut für Zoologie, Hellbrunnerstrasse 34, A-5020 Salzburg, Austria; FAX: +43 (0) 662 8044 5698; E-mail: WOLFGANG.PETZ@MH.SBG.AC.AT

oxytrichids, and *Onychodromopsis flexilis*, a rather poorly known oxytrichid ciliate.

MATERIALS AND METHODS, TYPE SLIDES

Lamtostyla edaphoni, population I, was collected on 14.11.1993 in the 0-0.5 cm soil layer at Casey Station, Budd Coast, Wilkes Land, continental Antarctica, 66°17'S, 110°32'E, *ca.* 40 m NN. The ice-free surface is a cold-desert soil consisting of weathered charnockitic, granitic and gneissic debris (feelfield) containing very little organic material, mainly from epilithic algae and lichens; macroscopic vegetation is almost lacking. Daytime temperature is generally distinctly higher in soil than in air, i.e. often above freezing; it is usually below zero at night. In winter the area is covered with snow and ice.

Immediately after collection, the soil was saturated with deionized water in glass Petri dishes of 20 cm diameter, providing raw cultures. Morphogenesis was studied in pure cultures initiated with a few specimens from the raw cultures; a mixture of indigenous bacteria and snow algae (*Parmellopsis* sp., *Stichococcus* sp., *Macrochloris* sp.) from cultures was used as food.

Population II was found in moss collected by Dr R. I. L. Smith (British Antarctic Survey) on 23.03.1981 at Charlotte Bay, Andrée Island, maritime Antarctic, 64°31'S, 61°30'W. The air-dried sample was treated with the non-flooded Petri dish method (Foissner 1987).

Onychodromopsis flexilis was found on 18.01.1993 in moss collected by Dr J. Cooper (University of Cape Town) at the coast of Core Bay, Prince Edward Island, Prince Edward Islands, Subantarctic, 46°35'S, 37°56'E (Foissner 1996). A raw culture was established following the non-flooded Petri dish method (Foissner 1987). Morphogenesis was studied in pure cultures using a few crushed wheat grains to support growth of bacteria and small ciliates which served as food organisms.

Live observations and measurements are mostly from field material (*L. edaphoni*) and raw cultures (*O. flexilis*). The live measurements provide only rough estimates but are valuable because specimens usually shrink or contract during fixation and preparation. Biomass was estimated from biovolume using a conversion factor of 1 μm^3 = 1 pg protoplasm (Finlay 1982); volume was calculated using *in vivo* dimensions and applying standard geometric figures to cells. Specimens from raw and/or pure cultures were impregnated with protargol according to Wilbert (1975) or Foissner's Protocol A (1991; population II of *L. edaphoni*), and used for morphometry; counts and measurements were performed at x 1000 magnification (1 measuring unit = 1.3 µm). Drawings were made using a camera lucida. Statistics were calculated according to textbooks. Terminology mainly follows Kahl (1932), Wallengren (1900) and Eigner and Foissner (1994).

Soil pH (in deionized water) was measured using an electrode, humidity and loss-on-ignition (unsifted soil) were assessed after air-drying and heating to 550°C, respectively.

Neotype slides of *O. flexilis* and voucher slides of *L. edaphoni* are deposited in the collection of microscopic slides of the Oberösterreichische Landesmuseum in Linz (LI), Austria.

RESULTS

Morphology and morphogenesis of *Lamtostyla edaphoni* Berger and Foissner, 1987

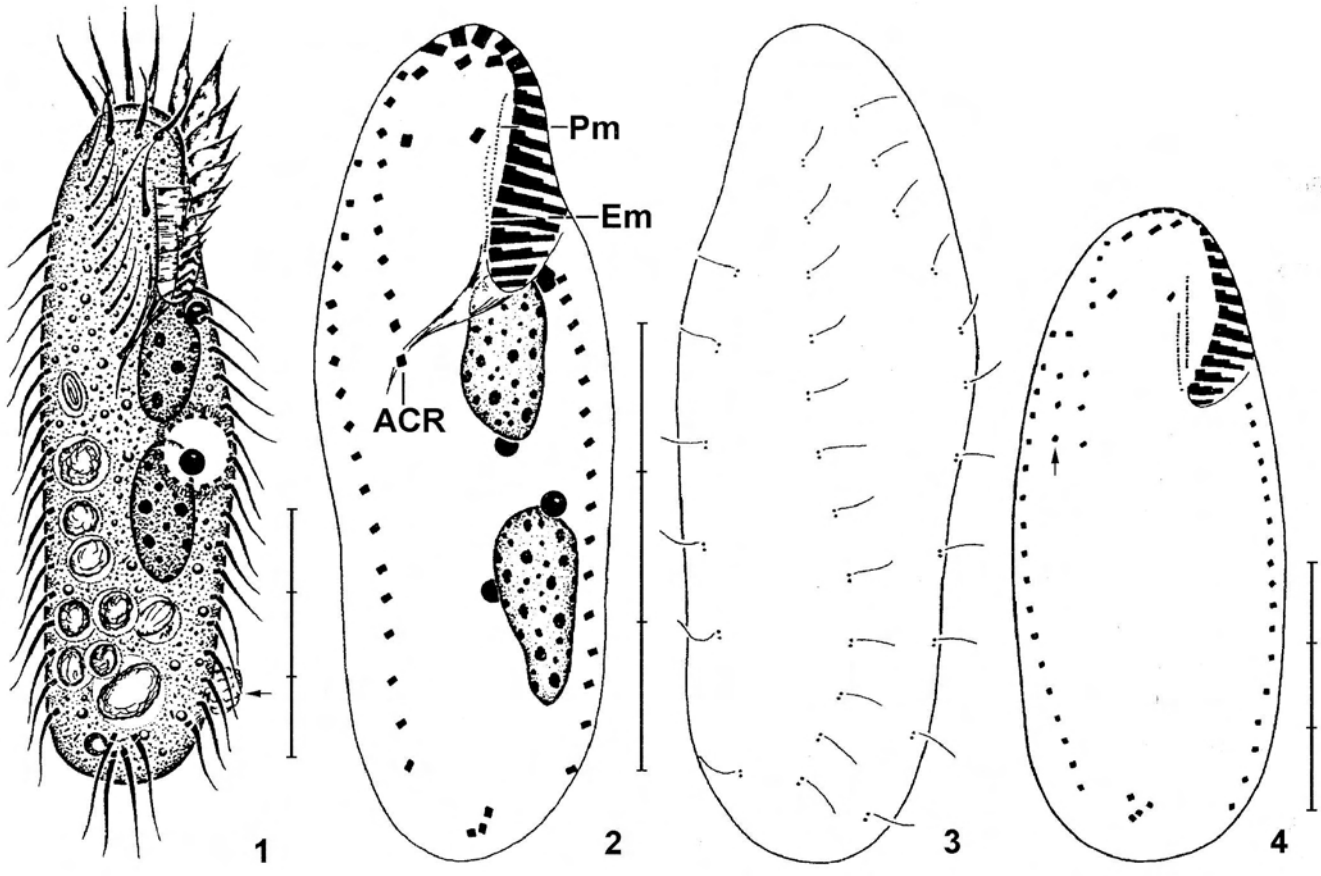
Morphology (Figs. 1-4, Table 1)

The Antarctic populations are very similar to the type specimens found in a bundle of straw in Austria. Thus, only supplementary observations of population I and a comprehensive morphometric characterization are provided. *In vivo* 55-80 (rarely up to 120) x 18-25 µm, flexible, usually rather transparent at low magnification. Macronuclear nodules *in vivo* 15-18 x 7-8 µm. One to four micronuclei, 2.5-3 µm across *in vivo*, in variable position attached to macronuclear nodules. Contractile vacuole slightly anterior to or in mid-body, on left margin, without collecting canals (Fig. 1). Food vacuoles contained dark and bright green debris (flagellates, algae), rarely fungi. Crawls moderately fast, quickly going back and forth; thigmotactic, i.e. not easy to take with pipette.

Frontal cirri composed of 2-3, all other cirri of 2 basal body rows; however, bases of frontal cirri, buccal cirrus and cirrus left of amphisiellid median cirral row (ACR, Eigner and Foissner 1994; formerly frontal row) slightly elongated and thus also larger (Fig. 2). Very rarely (in 2 out of about 70 specimens), a short second row of 3-4 cirri left of ACR's posterior portion, possibly remnants from last division (Fig. 4). Number of marginal cirri distinctly higher in cultured specimens, but other characters similar to field material (Table 1).

Buccal field very narrow. Adoral zone of membranelles about 30% of body length, cilia about 16 µm long. Undulating membranes often almost parallel, posterior portions rarely optically intersecting; each membrane possibly composed of single basal body row, cilia *in vivo* 5-6 µm long. Pharyngeal fibres 9-12 µm long in protargol impregnated specimens (Fig. 2).

Occurrence and ecology: *Lamtostyla edaphoni* was found at two sites of the Budd Coast, viz. in mineral debris overgrown with *Usnea sphacelata* (lichen) at Casey Station and in mineral debris covered with *Prasiola crispa* (alga) at the margin of a small melt pool on Shirley Island (Windmill Islands, 66°17'S, 110°29'E, about 15 m NN). At these sites, *L. edaphoni* occurred together with nematodes, rotifers, tardigrades, green flagellates and ciliates, viz. *Colpoda cucullus*, *Colpoda inflata*, *Euplotes* sp.,



Figs. 1-4. *Lamtostyla edaphoni* from life (1) and after protargol impregnation (2-4). 1 - ventral view of a typical specimen. Arrow marks cytopyge; 2, 3 - infraciliature of ventral and dorsal side of same specimen; 4 - ventral view showing surplus cirral row (arrow) adjacent to ACR. ACR - amphisiellid median cirral row, Em - endoral membrane, Pm - paroral membrane. Scale bar division 10 µm

Holosticha sigmoidea, *Keronopsis muscicola*, *Leptopharynx costatus*, *Odontochlamys* sp., *Pseudochilodonopsis mutabilis*, *Pseudoholophrya terricola*, *Pseudoplatyophrya nana*, *Sathrophilus muscorum*, *Spathidium* sp n. and *S. claviforme*. Environmental parameters in soil: humidity up to 26.6% of wet mass, loss-on-ignition <1-7.8% of dry mass, pH 5.1-6.6. Biomass of 10^6 individuals: 16 mg.

Population II was associated with the moss *Brachythecium austro-salebrosum*.

Comparison with type specimens and related species: The Antarctic specimens are very similar to those of the type population (Berger and Foissner 1987). The most conspicuous difference is the slightly higher number of cirri composing the median cirral row in population I ($\bar{x}$ = 9.5 vs. 8.0), which thus extends slightly beyond the proximal buccal vertex. This number matches that of *L. lamottei* Buitkamp, 1977 which has, however, three cirri left of the ACR, suggesting that it develops six frontoventral anlagen. Other minor differences to the type specimens concern the size of the macronuclear nodules (about 16-17 vs. 9-10 µm) and the position of the contractile vacuole, viz. on left margin vs. displaced towards the midline (Berger and Foissner 1987, 1988).

These differences are considered to be site-specific variations insufficient for separating population I as a distinct taxon. This is sustained by the significantly changed numbers of marginal cirri in specimens from pure cultures (Table 1). Furthermore, the ACR of population II also extends slightly beyond the proximal buccal vertex although its cirral number is the same as in the type specimens (Table 1).

Morphogenesis (Figs. 5-16)

Ontogenesis is very difficult to study in *L. edaphoni* because it is small and all cirri and primordia are very

Table 1. Morphometric characteristics from *Lamtostyla edaphoni*[1]. First line: raw culture of population I; second line: pure culture of population I; third line: raw culture of population II

Character	$\bar{X}$	M	SD	SE	CV	Min	Max	n
Body, length	76.8	78.0	10.4	1.87	13.5	55.0	109.0	31
	79.8	81.0	7.4	2.05	9.3	62.0	92.0	13
	57.5	56.0	3.5	1.06	6.1	52.0	63.0	11
Body, width	27.4	27.0	5.0	0.90	18.3	20.0	39.0	31
	30.8	30.0	4.0	1.12	13.1	25.0	38.0	13
	17.3	17.0	1.9	0.56	10.7	15.0	20.0	11
Anterior macronuclear nodule, length	16.4	16.0	3.6	0.65	22.2	11.0	25.0	31
	18.1	17.8	2.2	0.59	12.2	13.0	22.5	14
	11.8[2]	12.0	1.2	0.35	9.9	9.0	13.0	11
Anterior macronuclear nodule, width	7.4	7.5	1.3	0.22	16.8	5.0	10.0	31
	9.2	9.0	0.9	0.24	9.7	8.0	11.0	14
	4.8[2]	5.0	0.8	0.23	15.6	4.0	6.0	11
Posterior macronuclear nodule, length	17.4	16.0	3.8	0.68	21.7	12.0	26.0	31
	18.5	18.8	3.9	1.03	21.0	11.5	26.0	14
	-[3]	-	-	-	-	-	-	-
Posterior macronuclear nodule, width	7.5	7.0	1.8	0.33	24.6	4.5	12.0	31
	9.4	9.0	1.8	0.47	18.7	7.0	13.0	14
	-[3]	-	-	-	-	-	-	-
Micronucleus, length	2.9	3.0	0.4	0.08	12.9	2.0	4.0	31
	2.6	2.5	0.4	0.09	14.5	2.0	3.0	16
	2.1	2.0	0.3	0.10	15.1	2.0	3.0	11
Micronucleus, width	2.9	3.0	0.4	0.08	12.9	2.0	4.0	31
	2.4	2.5	0.4	0.10	16.3	2.0	3.0	16
	1.6	1.5	0.2	0.06	12.9	1.5	2.0	11
Adoral zone, length	23.2	24.0	3.0	0.55	13.1	16.0	29.0	31
	20.9	21.0	1.8	0.44	8.4	18.0	25.0	16
	17.0	17.0	1.3	0.40	7.9	16.0	20.0	11
Paroral membrane, length	10.3	10.0	1.8	0.33	17.5	7.0	13.5	30
	9.0	9.0	0.9	0.24	10.5	7.0	10.0	15
	-[3]	-	-	-	-	-	-	-
Endoral membrane, length	9.2	9.0	1.1	0.21	12.3	7.0	11.0	28
	7.8	8.0	0.9	0.24	11.4	6.5	9.0	14
	-[3]	-	-	-	-	-	-	-
Apex to posterior end of ACR, distance	29.2	30.0	6.0	1.07	20.4	19.0	38.0	31
	28.0	27.5	3.4	0.88	12.2	23.0	35.0	15
	19.5	19.0	1.6	0.49	8.4	17.0	22.0	11
Macronuclear nodules, number	2.0	2.0	0.2	0.03	8.8	2.0	3.0	31
	2.0	2.0	0	0	0	2.0	2.0	18
	2.0	2.0	0	0	0	2.0	2.0	11
Micronuclei, number	2.0	2.0	0.5	0.09	25.8	1.0	4.0	31
	1.9	2.0	0.5	0.12	25.8	1.0	3.0	17
	2.3	2.0	0.6	0.19	28.5	1.0	3.0	11
Adoral membranelles, number	16.8	17.0	1.0	0.18	6.0	14.0	19.0	31
	17.4	17.0	0.7	0.13	4.1	16.0	19.0	31
	16.1	16.0	0.5	0.16	3.4	15.0	17.0	11
Left marginal cirri, number	17.7	18.0	2.9	0.52	16.4	13.0	26.0	31
	25.4	24.5	3.6	1.05	14.3	20.0	31.0	12
	15.3	15.0	1.9	0.57	12.5	13.0	20.0	11
Right marginal cirri, number	18.2	18.0	1.7	0.31	9.6	15.0	21.0	31
	24.4	24.5	1.7	0.47	7.1	21.0	27.0	14
	15.5	16.0	1.6	0.49	10.5	13.0	18.0	11
Frontal cirri, number	3.0	3.0	0.2	0.03	6.1	2.0	3.0	31
	3.0	3.0	0	0	0	3.0	3.0	18
	3.0	3.0	0	0	0	3.0	3.0	11
Buccal cirri, number	1.0	1.0	0.2	0.03	17.4	1.0	2.0	31
	1.0	1.0	0	0	0	1.0	1.0	20
	1.0	1.0	0	0	0	1.0	1.0	11

Table 1 (con.)

Cirri in ACR, number[4]	9.5	9.0	1.3	0.21	13.3	7.0	13.0	35
	9.9	10.0	1.2	0.32	12.2	8.0	12.0	14
	7.8	7.0	1.1	0.33	13.8	7.0	10.0	11
Transverse cirri, number[5]	4.3	4.0	0.7	0.12	15.1	3.0	6.0	31
	4.4	4.0	0.8	0.19	18.1	3.0	6.0	17
	4.0	4.0	0.6	0.19	15.8	3.0	5.0	11
Dorsal kineties, number	3.0	3.0	0	0	0	3.0	3.0	30
	3.0	3.0	0	0	0	3.0	3.0	15
	3.0	3.0	0	0	0	3.0	3.0	11

[1] Based on randomly selected, protargol impregnated and mounted non-dividers. Measurements in µm. Abbreviations: CV - coefficcient of variation in %, M - median, Max - maximum, Min - minimum, SD - standard deviation, SE - standard error of arithmetic mean, $\bar{x}$ - arithmetic mean. [2] Not discriminated between anterior and posterior nodule. [3] Not determined. [4] Without cirrus left of it. [5] Including ventral cirri ahead of transverse cirri

close together. Thus, the origin of some anlagen could not be clarified unambiguously.

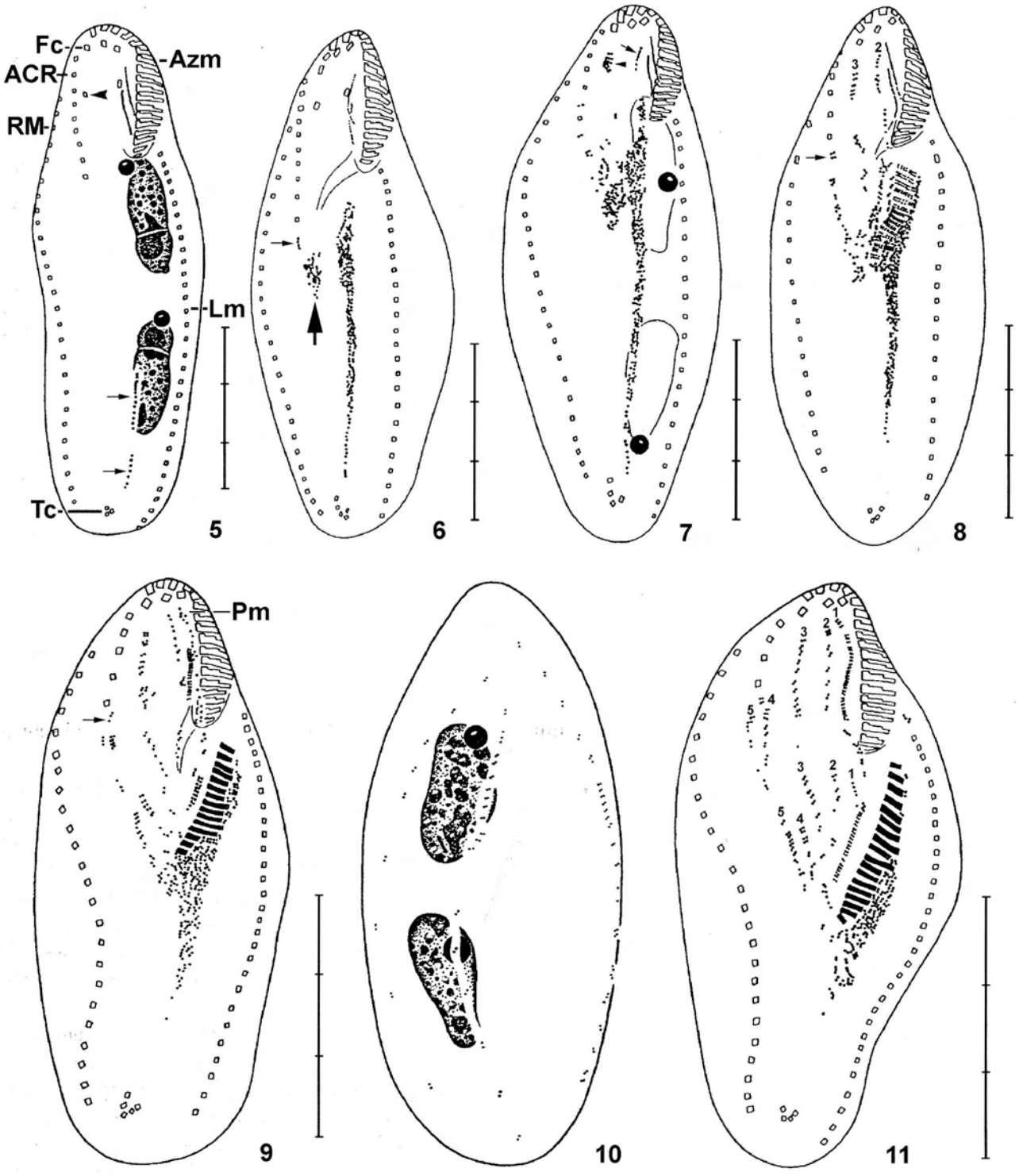
Oral primordium and cirral streaks (Figs. 5-9, 11-13, 15): Stomatogenesis commences with the apokinetal proliferation of basal bodies close above the left transverse cirrus (four cases observed; Fig. 5). The anarchic field then elongates anteriorly to the parental adoral zone. Simultaneously, the posteriormost cirrus of the amphisiellid median cirral row (ACR) disintegrates and a small patch of basal bodies develops posteriorly (Fig. 6). Whether this patch derives from a dedifferentiated ACR-cirrus or originates de novo could not be clarified. Furthermore, we could not determine whether this field is incorporated into the oral primordium or remains independent, forming only cirral anlagen (Figs. 6, 7). The same problems exist in *L. australis* and *L. perisincirra* (Berger et al. 1984, Voss 1992).

Subsequently, the buccal cirrus and the cirrus left of the ACR disaggregate, becoming proter's anlagen 2 and 3, respectively (Figs. 7, 8). Simultaneously, additional cirri dedifferentiate at the posterior end of the ACR, forming opisthe's anlage 5, which terminates near the oral primordium and, respectively, the basal body patch mentioned above (Figs. 7, 8). A further ACR-cirrus then disintegrates anterior to anlage 5, providing streak 4 of the proter (Fig. 8, arrow). The oral anarchic field differentiates membranelles from right to left in a posteriad direction (Fig. 8). Basal bodies right of these align to the primordium for the undulating membranes (anlage 1) and also form cirral anlagen 2 and 3 of the opisthe; some of the anlagen occasionally contact the posterior end of the proter's corresponding streaks (Figs. 8, 9, 11). The origin of the opisthe's anlage 4 could not be clarified unambiguously; very likely, it evolves from the oral primordium as stated in *L. australis* (Voss 1992).

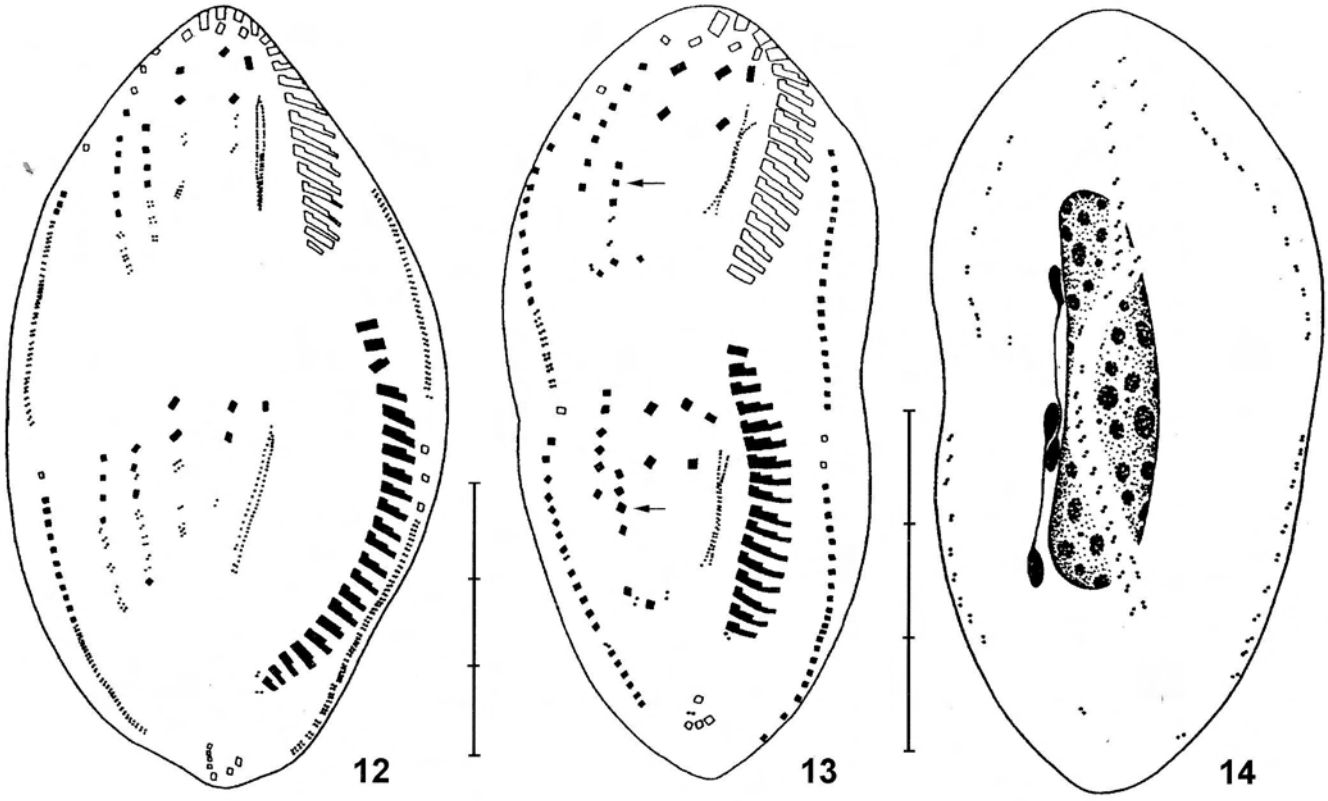
The parental paroral membrane dedifferentiates next and the endoral very likely becomes double-rowed, possibly incorporating basal bodies from the disaggregating paroral, which appears as a loose row extending to the opisthe's oral primordium. Finally, a conspicuous, double-rowed anlage is recognizable, the anterior portion of which becomes the leftmost frontal cirrus, while the posterior portion develops to the new undulating membranes (Figs. 9, 11, 12). Streak 5 of the proter develops anterior to anlage 4, very likely from a dissolving cirrus of the parental ACR (Figs. 9, 11). The streaks subsequently elongate by basal body proliferation and five anlagen each are recognizable in the proter and opisthe (Fig. 11). Cirri differentiate in a posteriad direction as follows (Fig. 12): left frontal cirrus and undulating membranes from anlage 1; middle frontal, buccal and sometimes also one transverse cirrus from anlage 2; right frontal, enlarged cirrus (rarely two) left of ACR and one transverse cirrus from anlage 3; a variable number of ACR-cirri and usually one, respectively, two transverse cirri from anlagen 4 and 5.

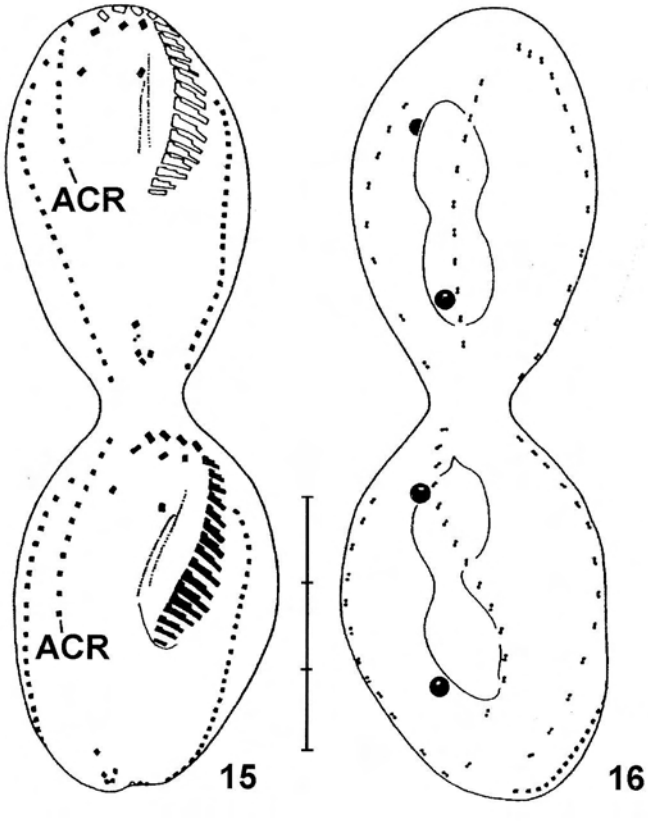
When the new transverse cirri organize, anlage 4 migrates backwards and aligns behind streak 5, both forming the new ACR (Figs. 12, 13, 15). Some surplus basal body pairs in the anlagen are apparently resorbed, as are all parental cirri not involved in primordia formation. However, we cannot exclude that some cirri at the anterior end of the old ACR remain because these are always very close to anlage 5 (Figs. 12, 13, 15). The parental adoral zone is apparently not renewed, but the pharyngeal fibres are resorbed and rebuilt during cytokinesis and in postdividers.

Marginal and dorsal anlagen (Figs. 10, 12-16): Most marginal cirri dissolve, forming two separate anlagen in



Figs. 5-11. Morphogenesis of *Lamtostyla edaphoni*, protargol impregnation. 5 - very early divider showing origin of oral primordium (arrows). Arrowhead marks cirrus left of ACR; 6, 7 - early dividers showing basal body patch (thick arrow) right of oral primordium. Thin arrows mark disintegrating ACR- and buccal cirrus, respectively; arrowhead denotes disaggregating cirrus left of ACR; 8, 9 - early dividers showing organization of cirral anlagen. Arrows mark anlagen for proter's streak 4 (Fig. 8) and 5 (Fig. 9); 10 - dorsal view of specimen shown in Fig. 9; 11 - middle divider showing five streaks each in proter and opisthe. ACR - amphisiellid median cirral row, Azm - adoral zone of membranelles, Fc - frontal cirri, Lm - left marginal row, Pm - disintegrated paroral membrane, Rm - right marginal row, Tc - transverse cirri; numbers denote cirral anlagen. Scale bar division 10µm





Figs. 12-16. Morphogenesis of *Lamtostyla edaphoni*, protargol impregnation. 12 - middle divider showing segregation of cirri and development of marginal primordia; 13, 14 - ventral and dorsal view of a late divider. Arrows mark migrating anlage 4; 15, 16 - ventral and dorsal view of a very late divider. Anlagen 4 and 5 have aligned one behind the other, producing the amphisiellid median cirral row (ACR). Scale bar division 10μm

each row (Figs. 12, 13). The dorsal kineties develop by intrakinetal basal body proliferation, i.e. according to type 1 of Foissner and Adam (1983), commencing in the anterior portions of rows 2 and 3 (Figs. 10, 14, 16). The anlagen in dorsal kinety 1 appear distinctly later. No caudal cirri are formed.

Nuclear division (Figs. 14, 16): This proceeds as usual, i.e. the micronuclei split once, very rarely twice; the macronuclear nodules first fuse and then divide twice, the second fission being completed after cytokinesis, i.e. in postdividers.

Morphology and morphogenesis of *Onychodromopsis flexilis* Stokes, 1887

Improved diagnosis of *Onychodromopsis* Stokes, 1887: Flexible Oxytrichidae with 18 frontal, ventral and transverse cirri; caudal cirri present. Undulating membranes side by side. Several right and left marginal cirral rows developing from at least two anlagen in a single right and left row each; parental rows completely resorbed during morphogenesis.

Redescription of *Onychodromopsis flexilis* Stokes, 1887 (Figs. 17-32, 70a, Table 2)

Improved diagnosis: Field populations *in vivo* about 90-125 x 40-70 µm, cultured stocks 100-200 x 40-80 µm. Cortical granules colourless, arranged in longitudinal rows. 2-3 right and 1-2 left marginal cirral rows. On average 33 adoral membranelles, 5 transverse cirri, 3 caudal cirri, 6 dorsal kineties, 2 macronuclei and 2 micronuclei. In freshwater and soil.

Redescription (Figs. 17-32, 70a, Table 2): Specimens in pure culture on average 24% larger than in raw culture (mean length 112.8 µm, SD 7.8, CV 6.9, extremes 98, 127 µm; mean width 55.4 µm, SD 6.0, CV 10.8, extremes 41, 70 µm; n = 30). Body very flexible, broadly elliptical and dorsoventrally flattened up to 2:1 (Figs. 17, 20, 21). Macronuclear nodules ellipsoidal; nucleoli spherical to ellipsoidal, 1-4 µm across in protargol slides. Micronuclei almost globular, usually one each in variable position in indentation of macronuclear nodules. Contractile vacuole with two collecting canals in mid-body near left margin. Cortical granules 0.8-1µm across, arranged in rather narrowly spaced rows underneath entire cell surface as in *Oxytricha granulifera* Foissner and Adam, 1983, colourless and rather compact, stain blue but become not extruded when methyl green-pyronin is added (Figs. 22, 70a), impregnate faintly to intensely with protargol depending on method and bleaching time (Fig. 30). A second type of granules, minute (≤ 0.2 µm) and invisible in live specimens, occurs in great numbers between the larger granules and stains red with methyl green-pyronin (Fig. 22); when the stain is added, many of them become extruded and adhere to cirri and adoral membranelles. Cytoplasm colourless, in field populations with many about 1-4 µm sized lipid droplets and 3-5 µm long, colourless crystals mainly in posterior portion (Fig. 23). Food vacuoles 15-20 µm across, often contain *Colpoda steinii* and *Polytoma* sp.; in cultures feeding also on *Cyclidium glaucoma*, starch and up to 45 µm long, slender bacteria carried over from raw culture. Glides moderately fast.

All cirri of field population about 13 µm long *in vivo*, insert in shallow cortical pits (Fig. 31). Cirral composition as shown in Fig. 18, only slightly variable, i.e. one basal body row more or less may occur in most FVT-cirri; first cirrus of inner left marginal row usually composed of three kineties. Transverse cirri only slightly projecting beyond posterior body margin. Marginal cirral rows open at posterior end, gap occupied by caudal cirri. Usually two left (81%, n = 31) and two right marginal rows (86%, n = 80); left outer row, however, frequently much less conspicuous than right inner row because consisting on average of five cirri only, in 19% of specimens even lacking, one cell with short third row (Figs. 17, 18, 26-28). Rarely, a very short third right marginal row is present, namely 1-7 cirri left of inner row (6%) or 2-3 cirri between inner and outer row (8%); very likely, these are remnants from last generation and/or young postdividers with parental cirri still in resorption (Figs. 28, 57, Table 2).

Dorsal cilia 3-5 µm long, insert in shallow cortical pits, arranged in six kineties (Fig. 19): kineties 1-3 almost as long as body, kinety 4 curved and commencing subequatorially, kinety 5 extends from anterior to mid-body, kinety 6 consists of 4-5 bristles only; frequently, some irregularly arranged cilia between kineties 3 and 4, very likely remnants from last generation. Three (4-5 in six out of 34 specimens) caudal cirri attached to dorsal kineties 1, 2 and 4, inconspicuous because not elongated and composed of four, rarely six cilia only (Fig. 18).

Adoral zone of membranelles conspicuous, about 40% of body length, distal portion ventrally covered by frontal scutum, cilia gradually shortened from distal to proximal end of zone; widest bases about 10 µm *in vivo*. Buccal cavity occupying about one third of cell width, anteriorly slightly curved and merging into frontal scutum, posteriorly gradually deepened and covered by buccal lip. Buccal lip hyaline, bent upright to and continuous with frontal cell surface, commences at level of buccal cirrus, gradually widened posteriorly to form wedge-shaped structure obliquely merging into posterior buccal ver-

Table 2. Morphometric characteristics from *Onychodromopsis flexilis* in pure culture[1]

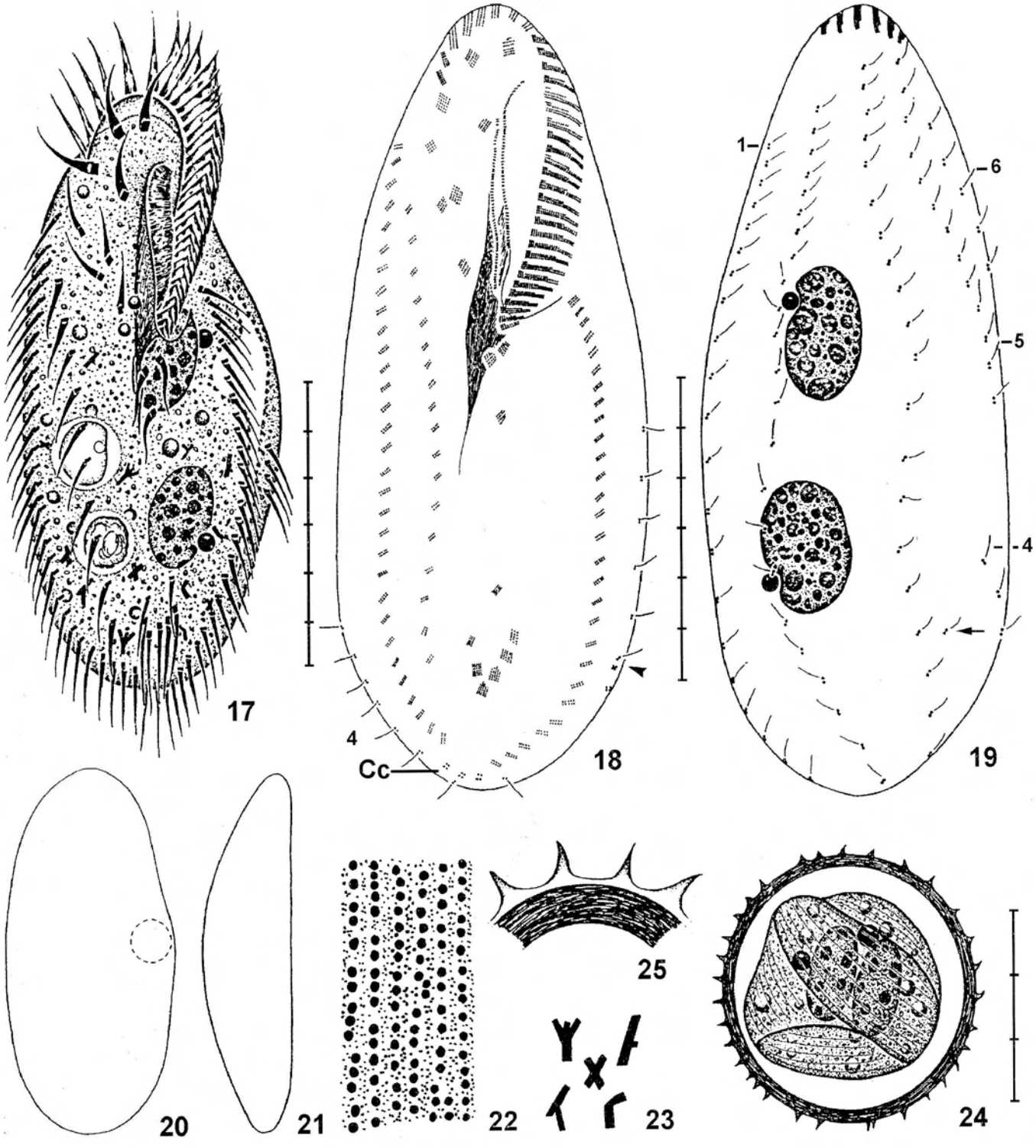
Character	$\bar{x}$	M	SD	SE	CV	Min	Max
Body, length	139.6	139.0	16.2	2.92	11.6	105	194.0
Body, width	63.1	62.0	9.2	1.65	14.6	43	83.0
Anterior macronuclear nodule,							
length	28.2	27.0	4.8	0.86	17.0	22	38.0
width	15.1	15.0	1.4	0.26	9.5	12	17.5
Posterior macronuclear nodule,							
length	26.8	25.0	4.5	0.8	16.7	22	39.0
width	16.6	17.0	2.0	0.36	11.9	13	22.0
Micronucleus, length	4.4	4.5	0.4	0.07	9.5	4	5.0
Micronucleus, width	4.1	4.0	0.4	0.06	8.4	3	5.0
Adoral zone, length	54.0	54.0	3.3	0.60	6.2	47	61.0
Paroral membrane, length	28.3	29.0	2.2	0.39	7.7	25	32.0
Endoral membrane, length	29.2	29.0	2.6	0.47	9.0	25	35.0
Apex to posterior end of inner							
right marginal row, distance	111.1	109.0	14.9	2.68	13.4	72	152.0
Distance between macronuclear nodules	15.5	16.0	5.1	0.92	33.1	4	27.0
Macronuclear nodules, number	2.0	2.0	0	0	0	2	2.0
Micronuclei, number	2.3	2.0	0.6	0.1	25.3	1	4.0
Adoral membranelles, number	33.0	33.0	1.7	0.3	5.0	30	37.0
Marginal cirri, number in							
outer right row	28.8	29.0	2.2	0.39	7.6	24	33.0
inner right row	17.1	17.0	3.5	0.62	20.3	10	25.0
inner left row	25.6	26.0	2.6	0.46	10.1	20	31.0
outer left row	4.6	5.0	3.7	0.65	79.5	0	13.0
Frontal cirri, number	3.0	3.0	0.2	0.03	6.1	2	3.0
Buccal cirri, number	1.0	1.0	0	0	0	1	1.0
Frontoventral cirri, number[2]	4.0	4.0	0	0	0	4	4.0
Ventral cirri, number	5.0	5.0	0	0	0	5	5.0
Transverse cirri, number	5.0	5.0	0	0	0	5	5.0
Caudal cirri, number	3.2	3.0	0.5	0.08	14.9	3	5.0
Dorsal kineties, number	6.1	6.0	0.2	0.05	3.7	6	7.0
Resting cysts, length[3]	41.0	41.0	2.9	0.65	7.1	36	48.0
Resting cysts, width[3]	39.7	40.0	2.9	0.64	7.2	34	44.0

[1] Based on 31 randomly selected, protargol impregnated and mounted non-dividers. Measurements in µm. Abbreviations: CV - coefficient of variation in %, M - median, Max - maximum, Min - minimum, SD - standard deviation, SE - standard error of arithmetic mean, $\bar{x}$ - arithmetic mean. [2] Excluding frontal and buccal cirri. [3] From three-week-old pure culture, measured *in vivo*

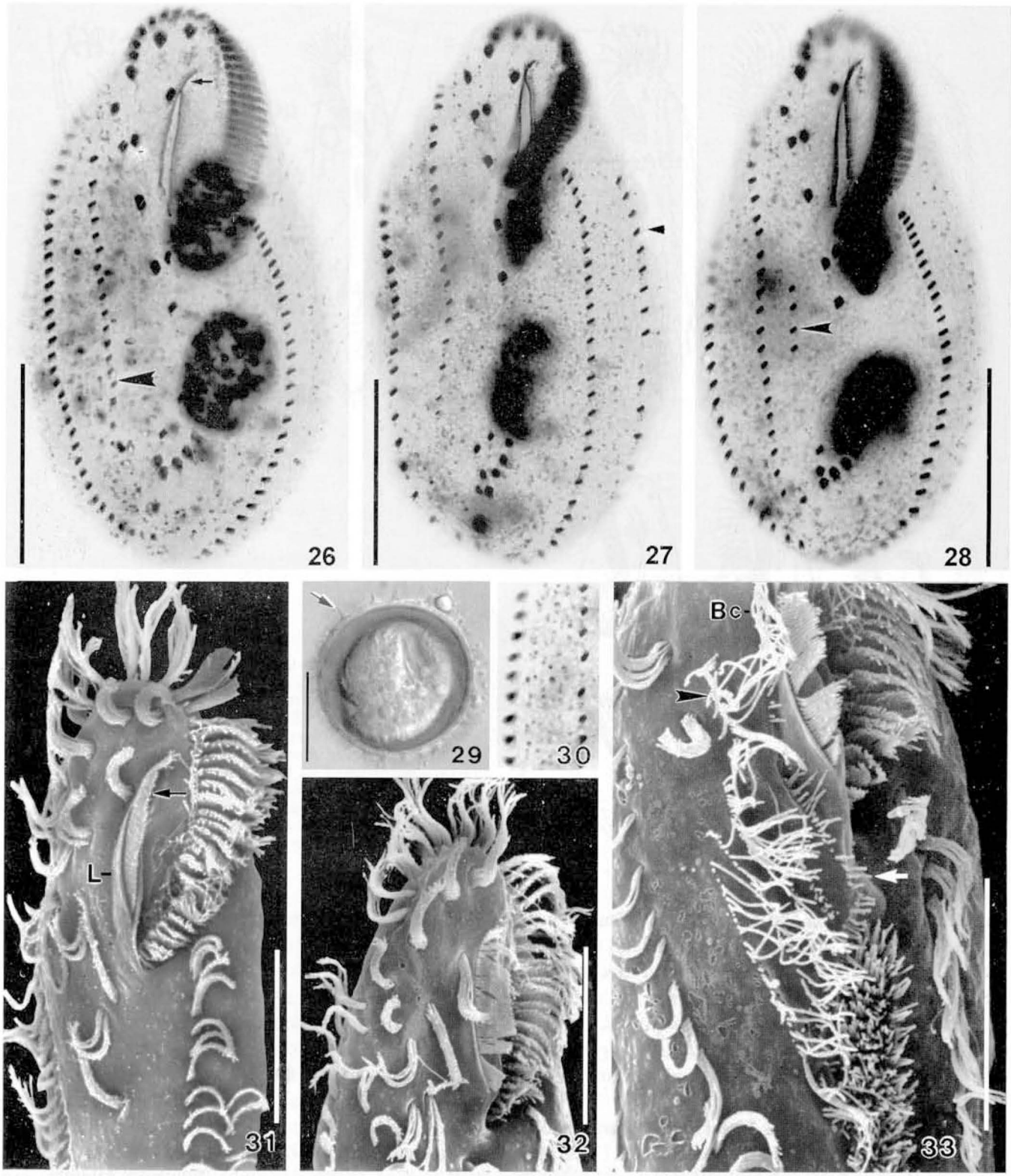
tex; longitudinally bipartite by deep cleft containing proximal two thirds of paroral membrane, right sheet narrower than left (Figs. 31, 32). Paroral membrane anteriorly slightly curved, cilia about 8 µm long. Endoral membrane straight, inserts on right wall of buccal cavity, not recognizable in scanning electron micrographs because underneath buccal lip. Paroral and endoral usually side by side in silvered specimens, posterior portions rarely slightly intersecting in surface view of cell, both very likely composed of dikinetids (Fig. 18). Pharyngeal fibres 30-55 µm long in protargol slides, originate from adoral membranelles and paroral and endoral membrane.

Resting cysts globular to slightly ellipsoidal (Figs. 24, 29; Table 2). Cyst wall colourless, about 2 µm thick, compact; surface studded with about 2 µm long, hyaline spines and sometimes separated by narrow, transparent layer from compact part of wall (Figs. 24, 25, 29). Cyst contents (cell) usually conspicuously lobed, does not occupy entire cyst volume (Fig. 29); however, when cyst is slightly pressed, its contents expand, completely filling interior. Cortex distinctly striated. Cytoplasm contains many 1-3 µm sized, colourless globules. Macronuclear nodules and micronuclei do not fuse (Fig. 24).

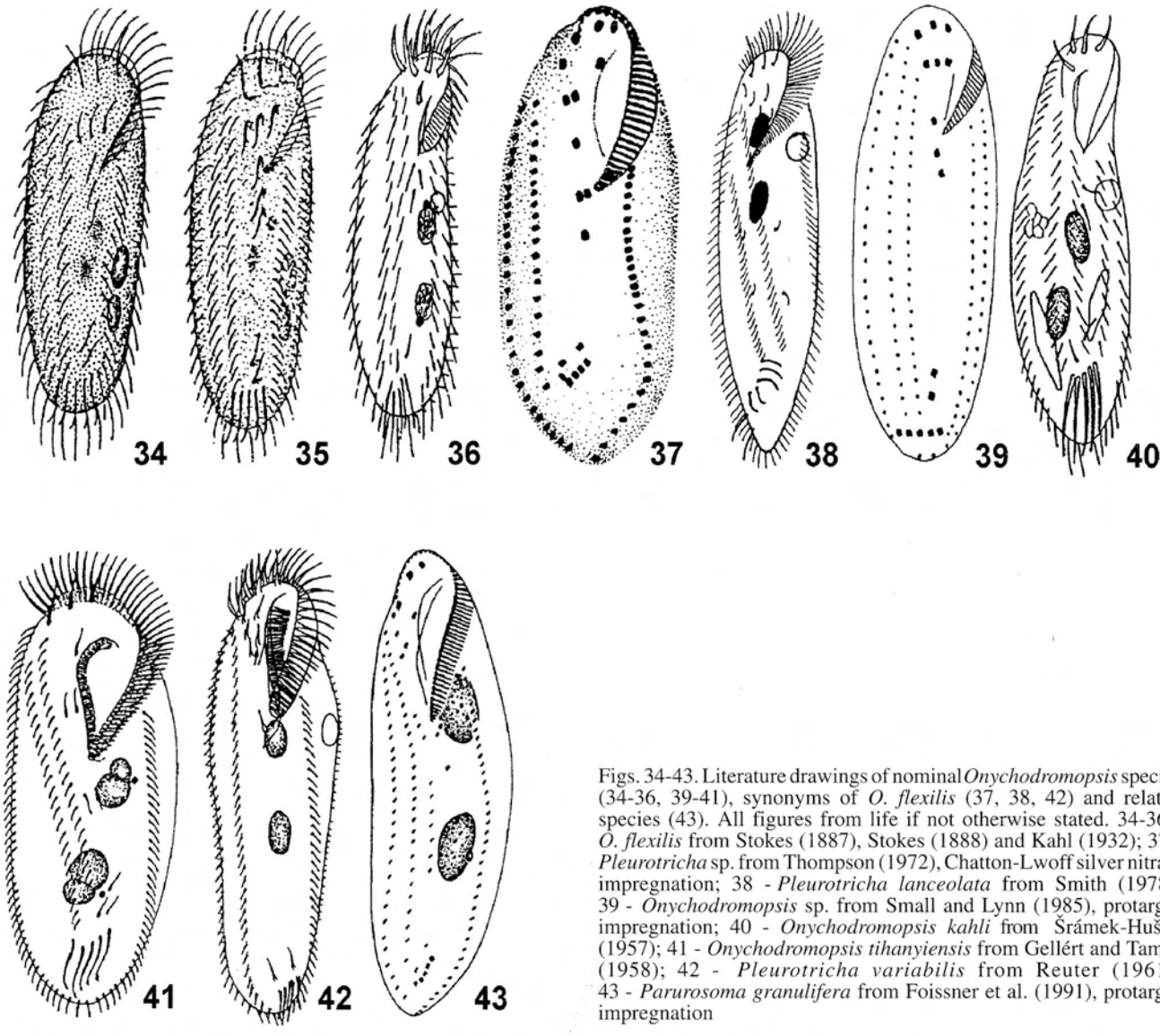
Occurrence and ecology: *Onychodromopsis flexilis* was found at two sites of the Prince Edward Islands, viz. in a slightly saline and acidic (pH 6.1) grass sward on rock at the seaward limit of vegetation on Marion Island and in a slightly saline and acidic (pH 6.3) moss sample



Figs. 17-25. *Onychodromopsis flexilis* from life (17, 20-25) and after protargol impregnation (18, 19). 17 - ventral view of a typical specimen; 18, 19 - infraciliature of ventral and dorsal side of same specimen. Arrowhead marks surplus dorsal kinety seen only in this specimen, arrow denotes interkinetal dorsal dikinetid; 20 - broad specimen; 21 - lateral view; 22 - cortical granulation consisting of small and large granules; 23 - cytoplasmic crystals; 24 - optical section of resting cyst; 25 - detail of cyst wall. Cc - caudal cirri; numbers denote dorsal kineties. Scale bar division 10 μm



Figs. 26-33. *Onychodromopsis flexilis* from life (29), after protargol impregnation (26-28, 30) and in the scanning electron microscope (31-33). 26, 27, 28 - ventral views. Arrow denotes paroral membrane, black arrowheads mark inner right and outer left marginal row, respectively; white arrowhead indicates surplus right marginal row; 29 - resting cyst, differential interference contrast; 30 - cortical granulation; 31, 32 - ventral views of oral area. Arrow marks paroral membrane inserted in deep furrow of buccal lip; 33 - early divider showing organizing cirral streaks. Opisthe's anlage 2 (arrow) extends anteriad from oral primordium not contacting parental paroral membrane. Arrowhead marks disaggregating cirrus III/2. Bc - dissolving buccal cirrus, L - buccal lip. Bars - 50 µm (Figs. 26-28), 20 µm (Figs. 29, 31-33)

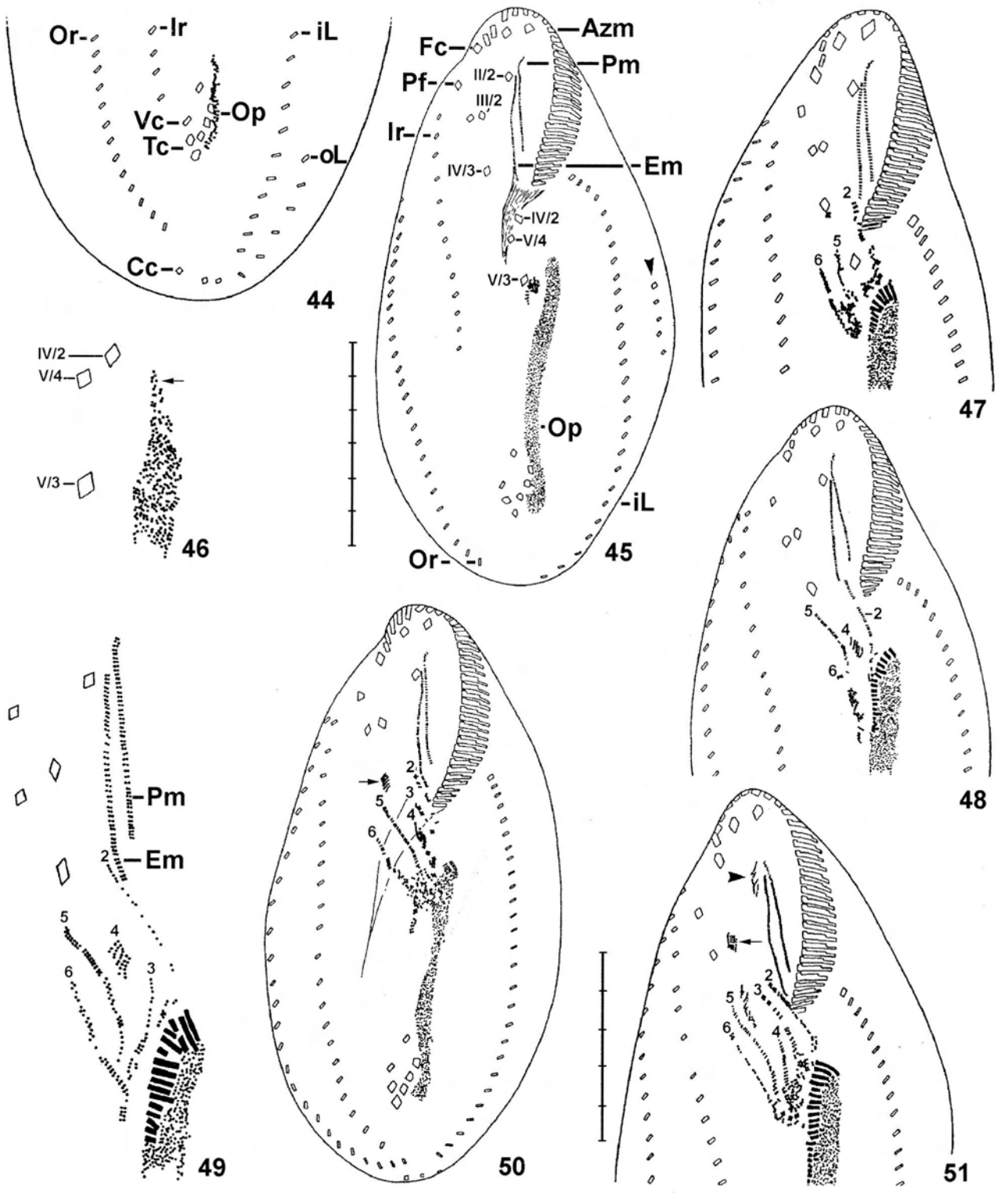


Figs. 34-43. Literature drawings of nominal *Onychodromopsis* species (34-36, 39-41), synonyms of *O. flexilis* (37, 38, 42) and related species (43). All figures from life if not otherwise stated. 34-36 - *O. flexilis* from Stokes (1887), Stokes (1888) and Kahl (1932); 37 - *Pleurotricha* sp. from Thompson (1972), Chatton-Lwoff silver nitrate impregnation; 38 - *Pleurotricha lanceolata* from Smith (1978); 39 - *Onychodromopsis* sp. from Small and Lynn (1985), protargol impregnation; 40 - *Onychodromopsis kahli* from Šrámek-Hušek (1957); 41 - *Onychodromopsis tihanyiensis* from Gellért and Tamás (1958); 42 - *Pleurotricha variabilis* from Reuter (1961); 43 - *Parurosoma granulifera* from Foissner et al. (1991), protargol impregnation

collected between *Poa* and *Callitricha* vegetation near a penguin rookery on Prince Edward Island (Foissner 1996). At these sites, *O. flexilis* occurred together with *Acineria uncinata*, *Colpoda aspera*, *C. cucullus*, *C. inflata*, *C. steinii*, *Cyrtolophosis mucicola*, *Haplocaulus terrenus*, *Leptopharynx costatus*, *Nivaliella plana*, *Platyophrya vorax* and *Pseudoplatyophrya nana*. Biomass of 10^6 individuals: 80 mg.

The type population was found in a freshwater pond with *Lemna* sp. (Stokes 1887). Later, Kahl (1932) reported *O. flexilis* from a sapropelic site near Hamburg together with rhodobacteria and flagellates. Other populations or very similar species were found in a variety of Antarctic and temperate freshwater and brackish habitats (see comparison with related species). Thompson (1972), for instance, described and illustrated (Fig. 37) a *Pleurotricha* sp. from an Antarctic tidal pool with freshwater dilution. However, size and infraciliature of this hypotrich are very similar to those of our specimens. Likewise, Smith (1978) reported a *Pleurotricha lanceolata* (Fig. 38), which is, according to the arrangement of the transverse cirri, very likely *O. flexilis*, too, from Subantarctic (South Georgia) and maritime Antarctic (South Orkney Islands, Elephant Island) moss peats and soils. Sandon and Cutler (1924) mentioned a *Pleurotricha* sp. from soils of Tristan da Cunha (Southern Atlantic), but did not provide a description or figure.

Comparison with related species: The Subantarctic specimens were rather similar to the original description by Stokes (1887), who mentioned, however, three right



Figs. 44-51. Morphogenesis of *Onychodromopsis flexilis*, protargol impregnation. 44 - very early divider with oral primordium close to the transverse cirri; 45 - early divider showing basal body patch close to postoral cirrus V/3. Arrowhead denotes outer left marginal row; 46 - anlage 2 (arrow) extending anteriorly from oral primordium; 47-49 - early dividers showing development of opisthe's anlagen 2-6; 50, 51 - early dividers. Arrows mark disaggregating cirrus IV/3 (Fig. 50) and III/2 (Fig. 51); arrowhead denotes dedifferentiating buccal cirrus II/2. Azm - adoral zone of membranelles, Cc - caudal cirri, Em - endoral membrane, Fc - anterior frontal cirri, iL, oL - inner and outer left marginal row, respectively, Ir, Or - inner and outer right marginal row, respectively, Op - oral primordium, Pf - posterior frontal cirri, Pm - paroral membrane, Tc - transverse cirri, Vc - ventral cirri; designation of cirri in Figs. 45, 46 according to Wallengren (1900), other numbers denote cirral anlagen. Scale bar division 10 μm

marginal rows (Fig. 34). Nevertheless, we consider our populations to be conspecific because 14% of the specimens (including postdividers) had three right marginal rows, too, and Stokes (1887), not having the advantage of silver impregnation, could not provide data on variability. Furthermore, he did not recognize the cortical granules, very likely because they are colourless.

The subsequent illustration by Stokes (1888) differs from the original in showing a straight row of transverse cirri at right-angles to the main body axis (Fig. 35). This difference appears to be an inaccuracy by Stokes (1888). However, *Onychodromopsis* sp. in Small and Lynn (1985) matches Stokes' (1888) figure of *O. flexilis* in every detail (Fig. 39). Compared with other populations of *O. flexilis* [Thompson 1972 (Fig. 37), Smith 1978 (Fig. 38), Lundin and West 1963], Stokes' (1887, 1888), Kahl's (1932), and Small and Lynn's (1985) drawings (Figs. 34-36, 39) lack some frontal cirri and are thus very likely incomplete or, more likely, influenced by Stokes' (1887) figure. Thus and in the absence of any type material, we fix our population as neotype.

Onychodromopsis kahli Šrámek-Hušek, 1957 (Fig. 40) is obviously based upon his own and Kahl's (1932) incomplete observations of *O. flexilis* and thus cannot be recognized as distinct species.

Onychodromopsis tihanyiensis Gellért and Tamás, 1958 (Fig. 41), the third nominal species, has two obliquely arranged ventral rows indicating that it belongs to another genus.

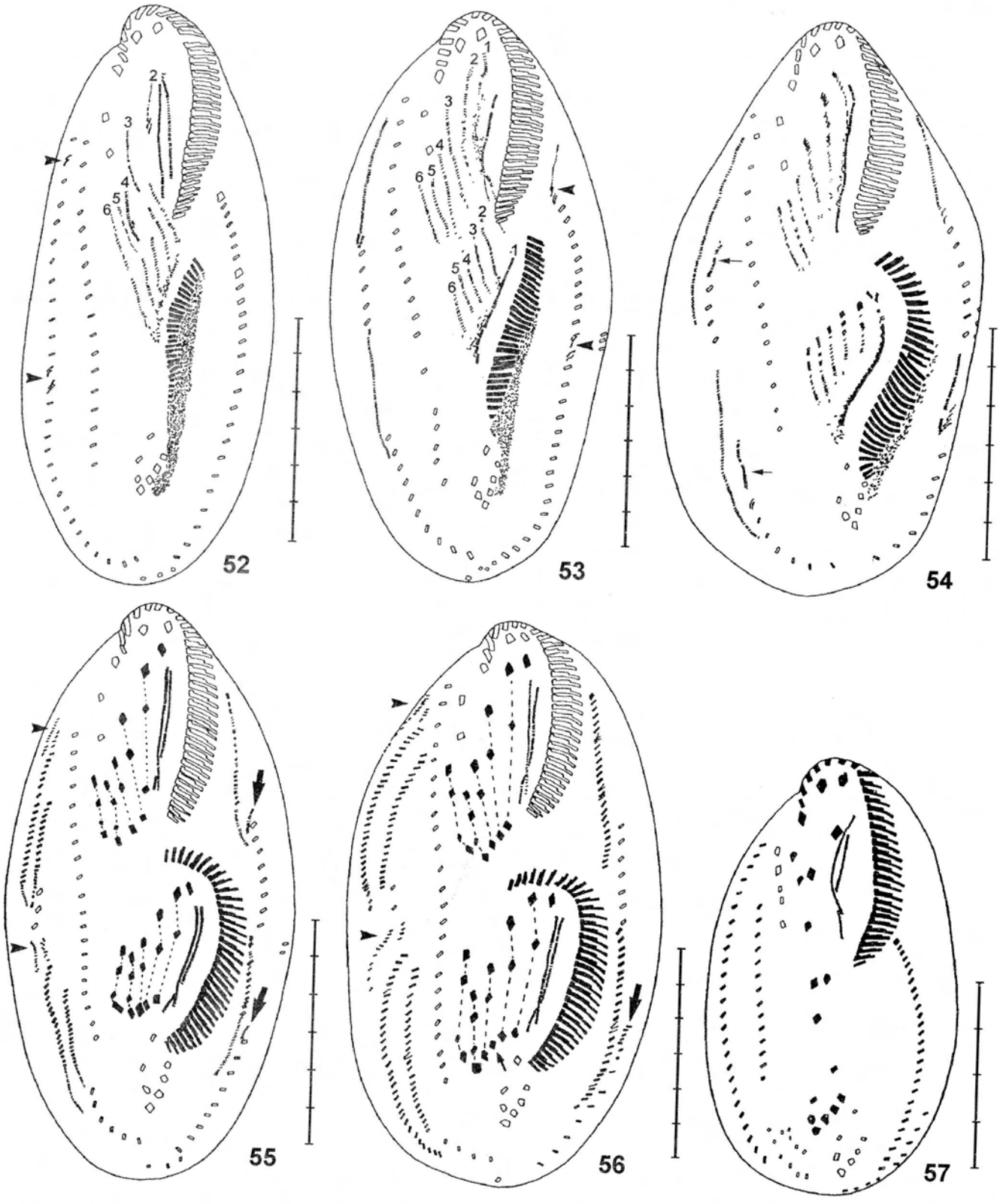
Pleurotricha variabilis Reuter, 1961 (Fig. 42) has, unlike the type of the genus, a flexible body and transverse cirri not separated into two groups. These characters match those of *Onychodromopsis*, to which Reuter's species is thus transferred: *O. variabilis* (Reuter, 1961) nov. comb. According to Reuter's rather detailed live observations on four cultured clones, his species differs from *O. flexilis* in size (200-220 μm), position of contractile vacuole (in anterior third of body) and in having only a single left marginal row. However, these are weak differences considering the high variability of *O. flexilis* (Table 2). *Parurosoma granulifera* (Fig. 43), a nomen nudum species in Foissner et al. (1991), very likely also belongs to *Onychodromopsis*, although it has distinctly curved and intersecting undulating membranes.

Morphogenesis (Figs. 33, 44-74)

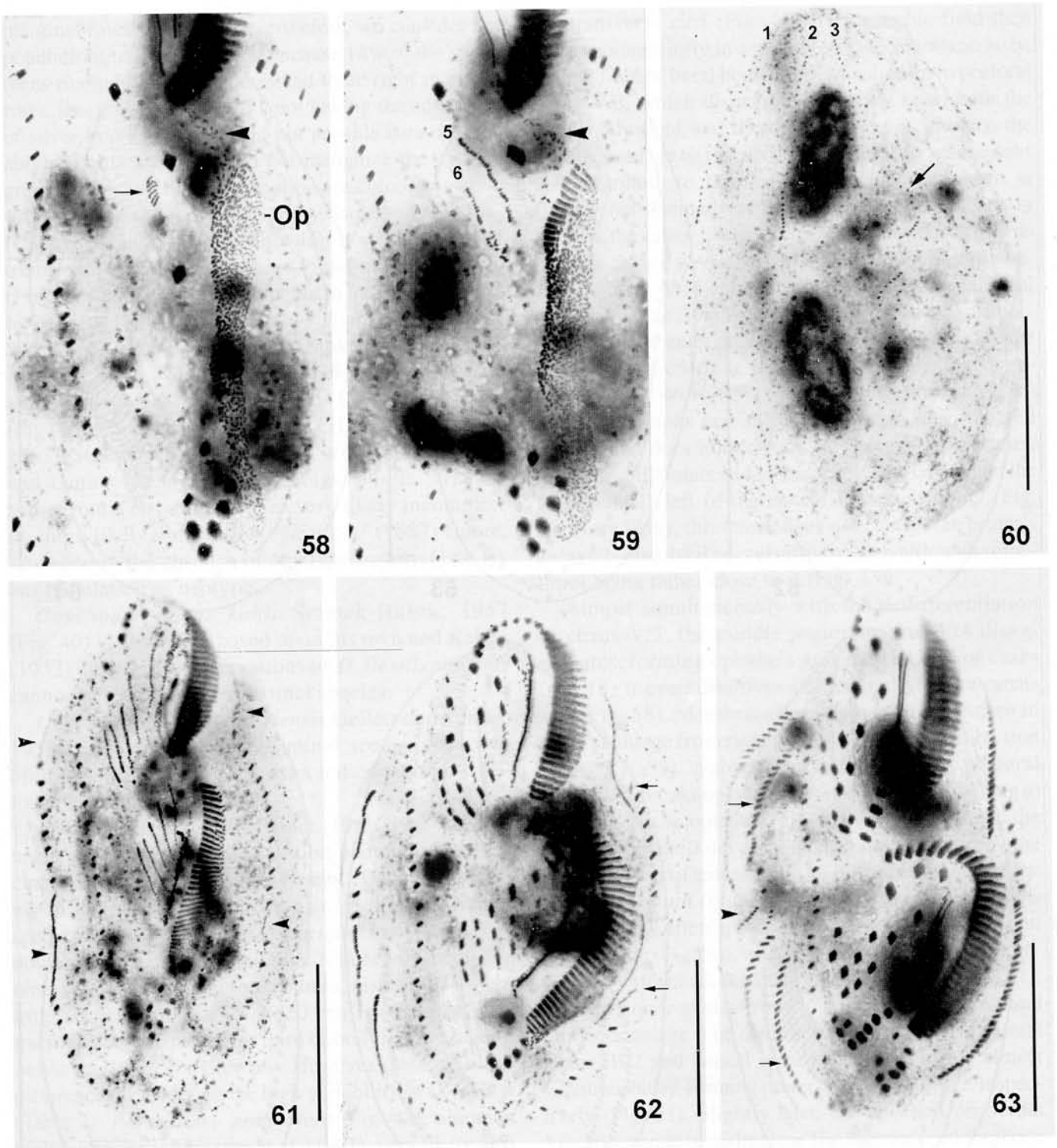
Oral primordium and cirral streaks (Figs. 33, 44-63, 70): Stomatogenesis commences with the apokinetal (?) proliferation of basal bodies close to the left transverse cirri (Fig. 44). The anarchic field then elongates anteriorly in a narrow streak. Simultaneously, a small field of basal bodies appears adjacent to postoral cirrus V/3, which disintegrates slightly later; both the basal body field and the dissolved cirrus produce the opisthe's anlage 6 (Fig. 45). Very likely, this anlage does not contribute to the oral primordium because it is slightly but distinctly separate from the oral anlage in 81% of the cases observed (n = 16) and cirrus V/3 is inactive during physiological regeneration. Slightly before or after disintegration of cirrus V/3, some basal bodies separate from the anterior end of the oral primordium, migrate anteriad and become the opisthe's anlage 2, seemingly touching the parental undulating membranes (Figs. 46, 47, 58, 59). However, scanning electron micrographs reveal that this streak is on the cell surface and does not contact the parental membranes, which are still intact and within the buccal cavity and the longitudinal cleft of the buccal lip, respectively (Fig. 33); very likely, this streak does not contact the proter's anlage 2 (dissolved buccal cirrus) either, although sometimes being rather close to it (Fig. 33).

Almost simultaneously with the dedifferentiation of cirrus V/3, the middle postoral cirrus V/4 disaggregates, forming opisthe's anlage 5; in 28% of cases (n = 18) it even dissolves immediately before cirrus V/3 (Fig. 58). Membranelles begin to differentiate in the oral anlage from right to left in a posteriad direction (Figs. 47, 59). Subsequently, the anterior postoral cirrus IV/2 breaks up into files of basal bodies aligning to anlage 4 of the opisthe (Fig. 48). Simultaneously, the opisthe's anlage 3 develops near, and possibly from, the posterior ends of anlagen 5 and 6 or from remnants of the oral primordium (Fig. 49). At this stage, the opisthe's cirral streaks often appear to be connected with the oral primordium (Fig. 50), which has, however, usually commenced to form adoral membranelles (Figs. 48, 49, 51).

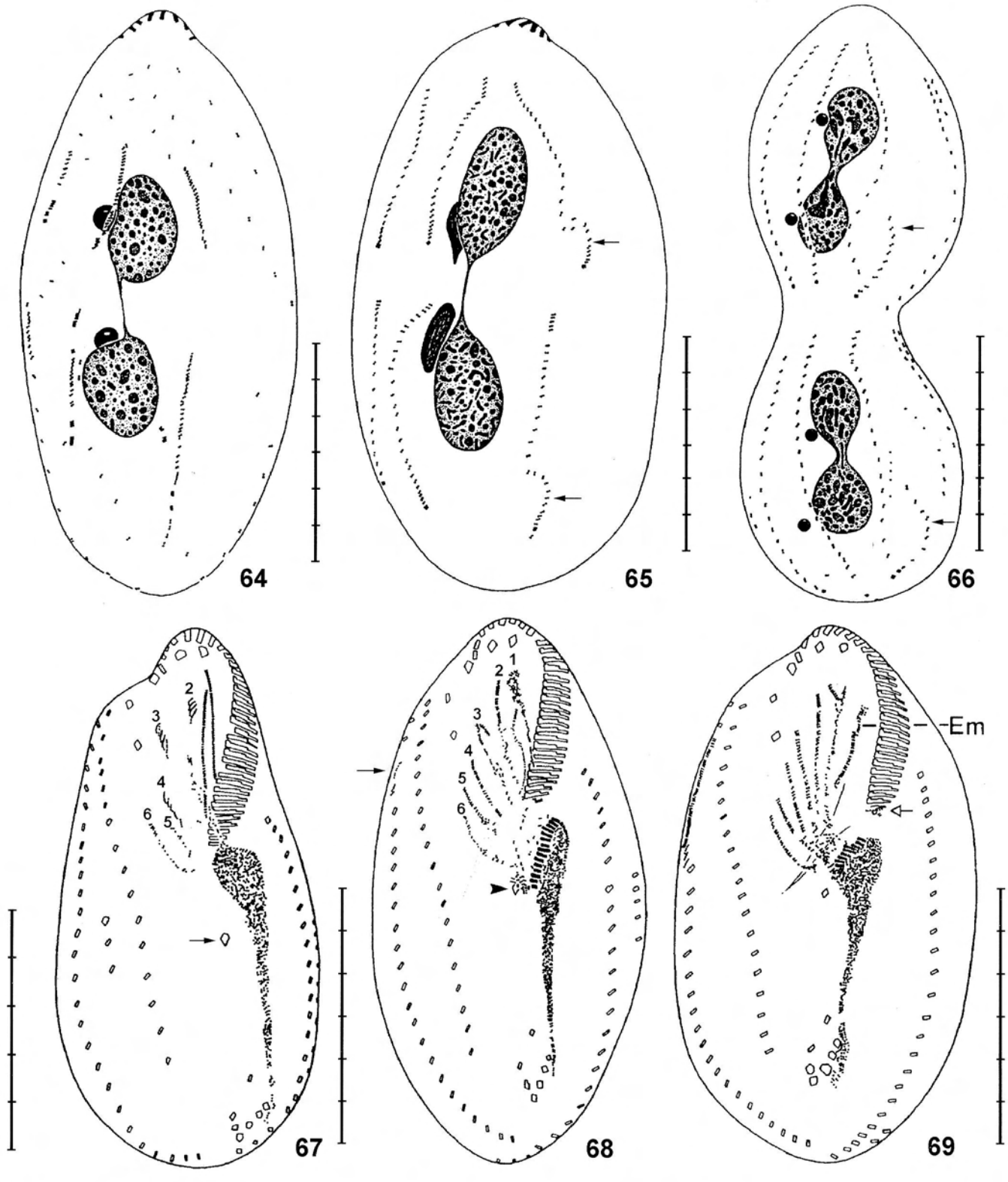
Posterior frontal cirrus IV/3 disintegrates next and produces anlage 4 of the proter (Fig. 50). Then, frontal cirrus III/2 and buccal cirrus II/2 disaggregate almost simultaneously, forming proter's anlagen 3 and 2, respectively (Fig. 51). Slightly later, the opisthe's primordia 5 and 6 separate in midregion. The anterior portions move forward, as indicated by the decreased distance to frontal cirrus VI/3, becoming proter's anlagen 5 and 6 (Figs. 33, 51-53). The origin of the opisthe's anlage 1 (undulating membranes) could not be clarified. It develops rather late from anarchic basal bodies located between the oral primordium and the posterior ends of the cirral streaks. Finally, all primordia of the opisthe



Figs. 52-57. Morphogenesis of *Onychodromopsis flexilis*, protargol impregnation. 52-54 - middle dividers showing separation of cirral streaks 5 and 6 and marginal anlagen formation. Arrowheads denote primordia for outer right and inner left marginal row, respectively; arrows mark anlage for inner right marginal row; 55, 56 - middle dividers showing migration of cirri, development of dorsal kineties 5 and 6 (arrowheads) and origin of outer left marginal row (large arrows). Small arrow marks surplus cirrus; 57 - postdivider (opisthe) still having some parental cirri. Scale bar division 10 μm



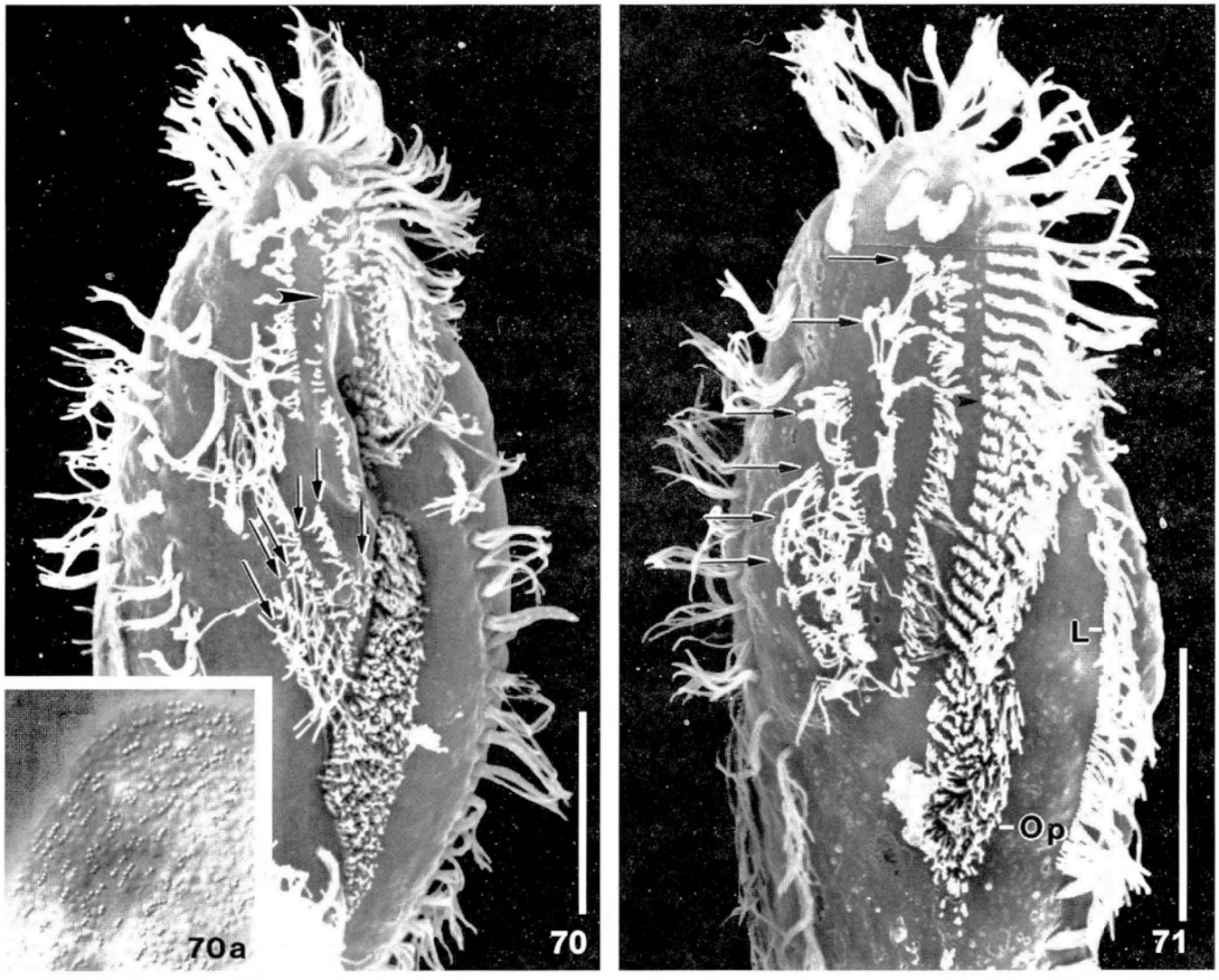
Figs. 58-63. Protargol impregnated dividers of *Onychodromopsis flexilis*. 58 - early divider showing dedifferentiating cirrus V/4 (arrow). Arrowhead marks anlage 2; 59 - early divider showing organizing anlagen 2 (arrowhead), 5 and 6 (compare Fig. 47); 60 - dorsal view of a middle divider showing new kineties 1-3 and separation of kinety 4 (arrow; compare Fig. 65); 61 - middle divider showing marginal primordia (arrowheads) and six cirral anlagen each in proter and opisthe; 62 - middle divider showing segregation of cirri. Arrows mark anlage for outer left marginal row; 63 - late divider showing anlagen for inner right marginal row (arrows) and new dorsal kineties 5 and 6 (arrowhead). Op - oral primordium; numbers denote cirral streaks (Fig. 59) and dorsal kineties (Fig. 60). Bars - 50 µm



Figs. 64-69. Morphogenesis of dorsal infraciliature (64-66) and physiological regeneration (67-69) of *Onychodromopsis flexilis*, protargol impregnation. 64-66 - middle and late dividers. Dorsal kinety 4 (arrows) splits from kinety 3; 67 - early reorganizer showing organization of cirral anlagen. Arrow marks inactive cirrus V/3; 68, 69 - early reorganizers showing dedifferentiation of undulating membranes and development of outer right marginal primordium (arrow). Arrowhead marks disintegrating cirrus V/3 seen only in this specimen, open arrow marks dissolving adoral membranelles. Em - reorganizing endoral membrane; numbers denote cirral anlagen. Scale bar division 10 μm

distinctly separate from those of the proter due to cell elongation and/or anlagen movement (Figs. 52, 53, 61, 70).

right ventral and one transverse cirrus from anlage 6. Subsequently, the cirri move to their specific positions and surplus cirri, which sometimes occur in the streaks,



Figs. 70-71. *Onychodromopsis flexilis* from life (70a) and in the scanning electron microscope (70, 71). 70 - middle divider showing evagination of buccal cavity, invagination of oral primordium and reorganizing paroral membrane (arrowhead). Arrows mark opisthe's cirral anlagen; 70a - cortical granulation; 71 - late reorganizer showing evaginated buccal cavity and reorganizing undulating membranes. Arrows mark cirral anlagen, arrowhead denotes reorganizing adoral membranelles. L - left marginal anlage, Op - oral primordium. Bars - 20 µm

In the broadened middle dividers, six cirral streaks each are recognizable in proter and opisthe (Figs. 54-56, 62). Cirri differentiate from anterior to posterior in the classical oxytrichid pattern: leftmost frontal cirrus and paroral membrane from anlage 1; one frontal, the buccal and one transverse cirrus from anlage 2; two frontal and one transverse cirrus from anlage 3; one frontal, one postoral (anteriormost) and one transverse cirrus from anlage 4; two postoral cirri, the left ventral and one transverse cirrus from anlage 5; two frontal cirri, the

are resorbed as are all cirri not involved in anlagen formation (Figs. 56, 63). These processes are completed in early postdividers (Fig. 57).

Concomitant with cirral streak separation, distinct changes occur in the daughters' oral structures. The opisthe's oral primordium invaginates, while the parental adoral zone and buccal cavity evaginate (Fig. 70). The evagination is accompanied by a dedifferentiation of the parental paroral membrane, which proliferates basal bodies at least at its anterior end (Figs. 53, 54, 61,

62). This anlage forms the leftmost frontal cirrus. The endoral membrane, which is always separate from the paroral anlage, is very likely also partially or completely reorganized as indicated by its slightly loosened kinetids; a special primordium is, however, not formed. When the buccal cavity evaginates, the undulating membranes become more narrowly spaced and optically intersect in their posterior third. When the buccal field invaginates in early postdividers, the membranes move apart and thus do not intersect any longer (Figs. 55-57). While the buccal cavity is restored, the pharyngeal fibres are resorbed and rebuilt.

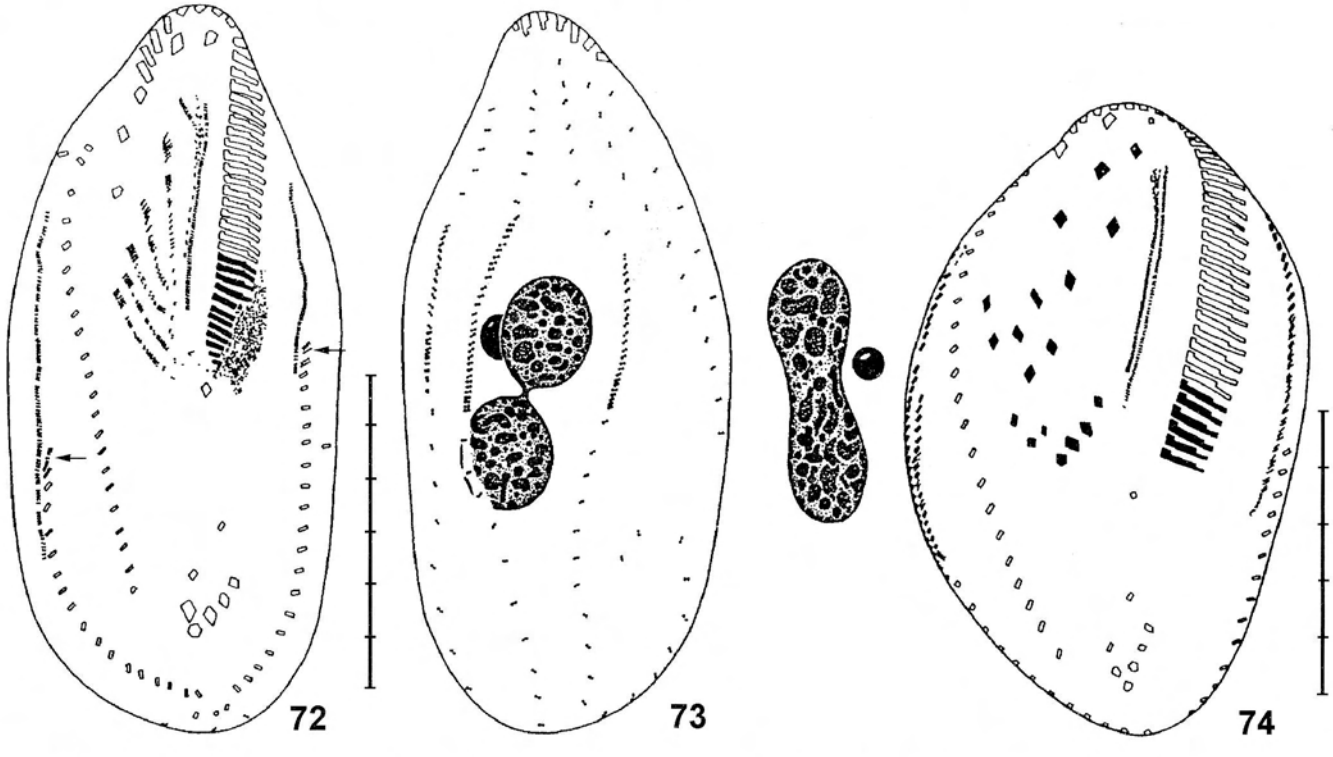
Marginal anlagen (Figs. 52-57, 61-63): Differentiation commences in middle dividers. The second (47% of cases), third (35%) or, rarely, first (18%) cirrus of the outer right row and, slightly later, invariably the first cirrus of the inner left row commence anlagen formation in the proter; the primordia for the opisthe originate from parental cirri at about mid-body (Figs. 52, 53). A few cirri each disintegrate into files of basal bodies which align longitudinally to form a row. These primordia subsequently become double-rowed and elongate by basal body proliferation and incorporation of additional cirri at their posterior ends (Figs. 53, 54, 61). The inner right and outer left marginal row are morphogenetically inactive but originate from primordia formed at the anterior ends of the remaining parental outer right and inner left marginal rows, respectively (Figs. 54, 62). The primordia in the left marginal row are distinctly smaller than those in the right row and thus produce fewer cirri.

The parental inner right marginal row is completely resorbed only after cytokinesis. Therefore, specimens having three right marginal kineties are very likely postdividers (Fig. 57).

Dorsal anlagen (Figs. 60, 64-66): The dorsal ciliature forms according to type 4 of Foissner and Adam (1983). Kineties 1-3 develop anlagen anterior and posterior to the prospective division furrow. Kineties 5 and 6 originate very close to or from the anterior end of the primordium for the outer right marginal row. Kinety 4 forms by posterior fragmentation of the new dorsal kinety 3 (Figs. 60, 65). Usually one, rarely two, caudal cirri each differentiate at the posterior ends of kineties 1, 2 and 4 (Fig. 66).

Nuclear division (Figs. 64-66): This proceeds as usual, i.e. the macronuclear nodules first fuse and then split twice, the last macronuclear division being completed in the postdividers.

Reorganization (Figs. 67-69, 71-74): Physiological regeneration largely resembles the development of the



Figs. 72-74. Physiological regeneration of *Onychodromopsis flexilis*, protargol impregnation. 72, 73 - ventral and dorsal view of a middle reorganizer. The adoral zone is partially renewed. Arrows mark anlagen for inner right and outer left marginal row, respectively; 74 - late reorganizer. Scale bar division 10μm

proter. Very early reorganizers cannot be distinguished from early dividers because the oral primordium originates in a similar way. Reorganizers are distinguishable from dividers only after the first and second postoral cirrus IV/2 and V/4 have disintegrated and, in contrast to division, the third postoral cirrus V/3 has remained unchanged (Fig. 67). In one specimen however, cirrus V/3 probably proliferated some basal bodies (Figs. 67, 68).

Unlike in fission, cirri IV/2 and V/4 develop anlagen 5 and 6, respectively. As in division, frontal cirri IV/3 and III/2 produce anlagen 4 and 3, respectively. An inconspicuous streak of basal bodies extends anteriorly at the frontal end of the oral primordium. Later, this streak very likely contacts anlage 2 produced by the dedifferentiated buccal cirrus II/2 (Fig. 67).

The cirral streaks elongate by basal body proliferation, seemingly contacting the oral primordium (Figs. 68, 69). The paroral and endoral membrane lose integrity and are reorganized (Figs. 68, 69, 71). As in division, this process is accompanied by an evagination of the buccal cavity and the resorption of the buccal lip (Fig. 71).

Only few adoral membranelles differentiate at the anterior portion of the oral primordium. They become attached to the proximal end of the parental adoral zone where some membranelles have been resorbed (Figs. 68, 69, 71, 72). In spite of this resorption, the total number of adoral membranelles is slightly increased temporarily ($\overline{X}$ = 37.5, n = 11; Table 2). Subsequently, membranelles at the posterior end of the adoral zone disintegrate and the usual number is again attained (Figs. 71, 72, 74). The midportion of the parental adoral zone is very likely also reorganized, as indicated by shortened cilia, but without a special primordium; we could not determine whether or not the foremost membranelles are renewed (Fig. 71). The elongate posterior portion of the oral primordium, which is composed of unorganized basal bodies, is obviously resorbed (Figs. 69, 71, 72).

Cirral differentiation in the FVT, marginal and dorsal anlagen occurs as described in division (Figs. 68, 69, 72-74). The macro- and micronuclei fuse and redivide (Figs. 73, 74).

DISCUSSION

Morphogenesis and systematic position of *Lamtostyla* and improved characterization of amphisiellid genera

Eigner and Foissner (1994) redefined the Amphisiellidae emphasizing morphogenetic characters. According to their diagnosis, *L. edaphoni* undoubtedly belongs to this family. The pattern of ACR and transverse cirri formation even suggests transferring *L. edaphoni* to the genus *Amphisiella*, i.e. to liquidate *Lamtostyla*. However, the type of *Amphisiella*, *A. marioni* Gourret and Roeser, 1888, differs considerably in the origin of the oral primordium, which derives from, or at least develops in close contact with the ACR (Wicklow 1982). This applies also to most other genera assigned to the Amphisiellidae by Eigner and Foissner (1994). Only *Gastrostyla* develops the oral primordium apokinetally (Walker and Grim 1973) like *L. edaphoni* (Fig. 5), *L. hyalina* and *L. perisincirra* (Berger et al. 1984), and *L. australis* (Voss 1992). However, *Gastrostyla* is distinguished from *Lamtostyla* by having caudal cirri, at least one postperistomial cirrus and two dorsal kineties developing from right marginal cirri (Walker and Grim 1973, Eigner and Foissner 1994).

Thus, there are obviously two groups of amphisiellids, one developing the oral primordium in close contact with the ACR (*Amphisiella*, *Amphisiellides*, *Hemiamphisiella*, *Paragastrostyla*, *Paramphisiella*, *Pseudouroleptus*) and another forming it apokinetally near the left transverse cirrus, viz. *Gastrostyla* and *Lamtostyla* (Walker and Grim 1973, Hemberger 1982, Wicklow 1982, Berger et al. 1984, Voss 1992, Eigner and Foissner 1994). Furthermore, genera having a rather short ACR (*Amphisiellides*, *Lamtostyla*, *Paragastrostyla*) commence anlagen formation at the posterior end of the ACR, whereas those having a long ACR (*Amphisiella*, *Gastrostyla*, *Hemiamphisiella*, *Paramphisiella*, *Pseudouroleptus*) develop them within-row. This pattern is independent of the number of anlagen composing the ACR, which is formed by three primordia in *Paragastrostyla* and by two in *Amphisiellides* and *Lamtostyla*. In addition, *Hemiamphisiella*, *Lamtostyla*, *Paramphisiella*, *Pseudouroleptus* and *Amphisiellides atypicus* agree in the close contact of daughters' anlagen 1, which appear as a single primordium in certain divisional stages (Fig. 9; Hemberger 1982, Eigner and Foissner 1994); in *Amphisiella*, the anlagen are distinctly separate (Wicklow 1982). However, the significance of this character remains obscure since the anlagen 1 are also clearly separate in *Amphisiellides illuvialis*, and this detail is insufficiently known in *Gastrostyla* and *Paragastrostyla* (Walker and Grim 1973, Hemberger 1982, Eigner and Foissner 1994).

Based on these data, amphisiellid genera can be more precisely characterized using the following 10 characters: origin of oral primordium, site of anlagen formation in the ACR and origin of the new ACR, origin of dorsal

kineties, number of cirri left and right of ACR, arrangement and origin of transverse cirri, presence/absence of postperistomial and caudal cirri.

Genus *Amphisiella* Gourret and Roeser, 1888: The oral primordium originates in close contact with the ACR. The ACR commences anlagen formation within-row and originates from two rightmost anlagen. All dorsal kineties develop intrakinetally. More than one cirrus left of ACR. Transverse cirri obliquely arranged, originate from more than one anlage. Caudal cirri lacking.

This diagnosis does not match *Amphisiella terricola* Gellért, 1955, which develops the oral primordium apokinetally and the new ACR possibly from a single anlage within the parental ACR (Hemberger 1982). This pattern is quite similar to that of *Orthoamphisiella* Eigner and Foissner, 1991, which lacks, however, transverse cirri (Eigner and Foissner 1991, 1993). Thus, a proper classification of *A. terricola* must await more detailed investigations.

Genus *Lamtostyla* Buitkamp, 1977: The oral primordium originates apokinetally near the transverse cirri. The ACR commences anlagen formation at its posterior end and originates from two rightmost anlagen. All dorsal kineties develop intrakinetally. At least one cirrus left of ACR. Transverse cirri obliquely arranged, originate from more than one anlage. Caudal cirri lacking.

This pattern is also found in *Amphisiella australis* (Foissner 1988, Voss 1992), which is thus transferred to *Lamtostyla*: *L. australis* (Blatterer and Foissner, 1988) nov. comb. Likewise, *Tachysoma perisincirra* Hemberger, 1985, included in *Amphisiella* by Eigner and Foissner (1994), belongs to *Lamtostyla* as previously proposed by Berger and Foissner (1987). Other *Amphisiella* species might also belong to *Lamtostyla*. However, their proper classification must await morphogenetic investigations because interphasic characters are identical in both genera.

The ontogenesis of *L. australis* and *L. perisincirra* differs slightly from that of *L. edaphoni* in developing a sixth cirral streak which results in the higher number of cirri left of the ACR (Berger et al. 1984, Berger and Foissner 1987, Foissner 1988, Voss 1992); furthermore, the oral primordium of *L. australis* may originate either parakinetally from, or apokinetally close to the transverse cirri, and the proter's and opisthe's cirral anlagen are more distinctly connected (Voss 1992).

It should be mentioned that the morphogenesis of *L. lamottei*, type of *Lamtostyla*, is still unknown. However, the interphasic cirral pattern of *L. lamottei* is very similar to that of *L. perisincirra* whose morphogenesis nicely matches that described for *L. edaphoni*. Thus, *L. edaphoni*, *L. perisincirra* and *L. australis* are very likely congeneric with *L. lamottei*.

Genus *Amphisiellides* Foissner, 1988: The oral primordium originates in close contact with the ACR. The ACR commences anlagen formation at its posterior end and originates from two rightmost anlagen. One dorsal kinety develops from the right marginal row. More than one cirrus left of ACR. Usually two cirri right of ACR. Transverse cirri longitudinally arranged, usually originate from single anlage. Caudal cirri present.

Genus *Gastrostyla* Engelmann, 1862: The oral primordium originates apokinetally near the transverse cirri. The ACR commences anlagen formation within-row and originates from three rightmost anlagen. Two dorsal kineties develop from the right marginal row. One or two postperistomial cirri originating from third anlage from right. One cirrus left of ACR. Transverse cirri obliquely arranged, originate from more than two anlagen. Caudal cirri present.

Genus *Hemiamphisiella* Foissner, 1988: The oral primordium originates in close contact with the ACR. The ACR commences anlagen formation within-row and originates from three rightmost anlagen. All dorsal kineties develop intrakinetally. Usually one postperistomial cirrus developing from third anlage from right. One cirrus left of ACR. Transverse cirri longitudinally arranged, originate from single anlage. Caudal cirri present.

Genus *Paragastrostyla* Hemberger, 1985: The oral primordium originates in close contact with the ACR. The ACR commences anlagen formation at its posterior end and originates from three rightmost anlagen. All dorsal kineties develop intrakinetally. More than one cirrus left of ACR. Caudal cirri present, transverse cirri absent.

Genus *Paramphisiella* Foissner, 1988: The oral primordium originates in close contact with the ACR. The ACR commences anlagen formation within-row and originates from two rightmost anlagen. All dorsal kineties develop intrakinetally. One cirrus left of ACR. Transverse cirri longitudinally arranged, originate from single anlage. Caudal cirri present.

Genus *Pseudouroleptus* Hemberger, 1985: The oral primordium originates in close contact with the ACR. The ACR commences anlagen formation within-row and originates from three rightmost anlagen. All dorsal kineties develop intrakinetally. Usually one postperistomial cirrus developing from third anlage from right. One cirrus left of ACR. Transverse cirral row almost as long as body, parallels ACR, originates from single anlage. Caudal cirri present.

Key to amphisiellid genera using interphasic (non-morphogenetic) characters recognizable in protargol slides.

1 With (1 or 2) postperistomial cirri 2
- without postperistomial cirri 4
2 Few or no cirri right of ACR 3
- cirral row right of ACR, extending almost over entire body length ..... *Pseudouroleptus*
3 Posterior end broadly rounded, transverse cirri conspicuous and obliquely arranged ..... *Gastrostyla*
- posterior end pointed and/or elongate tail-like, transverse cirri inconspicuous and longitudinally arranged ..... *Hemiamphisiella*
4 With transverse cirri 5
- without transverse cirri ..... *Paragastrostyla*
5 With caudal cirri 6
- without caudal cirri ..... *Amphisiella*, *Lamtostyla*
6 Few cirri right of ACR ..... *Amphisiellides*
- without cirri right of ACR ..... *Paramphisiella*

Morphogenesis and systematic position of *Onychodromopsis*

The main characteristics of *Onychodromopsis* clearly match those of oxytrichid hypotrichs. The FVT-cirral pattern is identical with that of, e.g., *Oxytricha*, *Sterkiella* and *Stylonychia* (Foissner and Adam 1983, Berger et al. 1985, Wirnsberger et al. 1985a, 1986). Even the origin of the pattern is highly similar, particularly to *Oxytricha granulifera* Foissner and Adam, 1983 and *O. pseudosimilis* Hemberger, 1985, which also develop anlagen 5 and 6 of both, proter and opisthe, from cirri V/4 and V/3, respectively (Hemberger 1982, Foissner and Adam 1983). Most other oxytrichids produce proter's anlagen 5 and 6 de novo or either from cirrus IV/3 or V/4, and those of the opisthe either from cirrus V/4 or V/3 (Berger et al. 1985, Wirnsberger et al. 1985a, 1986, Voss 1991a,b, Voss and Foissner 1996).

However, interphasic specimens of *Onychodromopsis* are rather dissimilar to "typical" oxytrichids, for instance *Oxytricha* and *Stylonychia*, due to their doubled marginal rows. In this respect, *Onychodromopsis* resembles *Pleurotricha* Stein, 1859, which is most similar to *O. flexilis* not only in the ventral cirral pattern but also in the macronucleus, whose nodules, unlike in some other oxytrichids (Grimes 1973, Walker et al. 1975, Jareno 1984, Ricci et al. 1985), do not fuse in the resting cyst (see above; Jeffries 1956, Matsusaka 1976). Unfortunately, the morphogenesis of *Pleurotricha* is still unknown. However, it is distinguished from *Onychodromopsis* by the lack of caudal cirri, the rigidity of the body and the separation of the transverse cirri into two distinct groups (Kahl 1932, Jeffries and Mellott 1968, Martín-González et al. 1984). Thus, we do not follow Bütschli (1889), Borror (1972) and others, who synonymized *Onychodromopsis* with *Pleurotricha*.

Another genus matching the main characters of *Onychodromopsis* is *Parurosoma* Gelei, 1954, originally established as subgenus of *Holosticha*. However, its frontal cirri are arranged as in *Urosoma* (Foissner 1982) and the posterior body portion is narrowed tail-like. Thus, it might be a distinct genus within the oxytrichids; *Holosticha mononucleata* Gelei, 1954, which was found together with *Parurosoma dubium* Gelei, 1954, is very likely a reorganizer of *P. dubium*.

Allotricha Sterki, 1878 (single species *A. mollis*) has, like *Onychodromopsis*, doubled marginal rows and a metabolic body. Thus, *Onychodromopsis* could be a junior synonym of *Allotricha*. However, the description of *Allotricha* lacks any other details and also a figure. We thus suggest considering *A. mollis* as genus and species indeterminata.

Coniculostomum Njiné, 1979, usually also included in the Oxytrichidae, develops, unlike *Onychodromopsis*, only a single right marginal primordium and retains most of the parental marginal and some dorsal kineties (Kamra and Sapra 1990, Kamra et al. 1994). Based upon the mode of marginal row formation, Eigner (1995) transferred *Coniculostomum* to Kahliellidae.

Other genera very likely closely related to *Onychodromopsis* are *Laurentiella* Dragesco and Njiné, 1971 and *Onychodromus* Stein, 1859. The former is distinguished from *O. flexilis* by having only one right and left marginal row, an increased number of FVT-cirri and some dorsal kineties originating by multiple fragmentation of at least two primordia (Dragesco and Njiné 1971, Martin et al. 1983, Foissner et al. 1987). The latter differs from *Onychodromopsis* by having ventral cirral rows and dorsal kineties also formed by multiple fragmentation (Foissner et al. 1987, Kamra and Sapra 1993, Szabó and Wilbert 1995). Due to their peculiar marginal row development, *Laurentiella acuminata* and *Onychodromus quadricornutus* were recently also transferred to the Kahliellidae (Eigner 1995).

Several other genera, e.g. *Paraurostyla* Borror, 1972 and *Parakahliella* Berger et al., 1985, also have more than two marginal cirral rows and/or a few ventral cirral rows and are thus superficially rather similar to *Onychodromopsis*. However, they lack the typical oxytrichid FVT-cirral pattern and develop the ventral ciliature differently (Borror 1972, Grimes and L'Hernault 1978, Berger et al. 1985, Wirnsberger et al. 1985b, Berger and Foissner 1989, Eigner 1995).

Acknowledgments. Supported by Australian Antarctic Division, Kingston, Tasmania (Australia), Fonds zur Förderung der Wissenschaftlichen Forschung (Austria), project P10264-BIO, and Stiftungs- und Förderungsgesellschaft der Paris-Lodron-Universität Salzburg. Many thanks to Drs R. D. Seppelt and D. R. Melick (Australian Antarctic Division) and the 1993/94 crew of Casey Station for logistic support, to Dr A. Jackson (CSIRO, Hobart, Tasmania) for providing algal cultures and to Mag. E. Strobl for linguistic improvements.

REFERENCES

Berger H., Foissner W. (1987) Morphology and biometry of some soil hypotrichs (Protozoa: Ciliophora). *Zool. Jb. Syst.* **114:** 193-239

Berger H., Foissner W. (1988) Revision of *Lamtostyla* Buitkamp, 1977 and description of *Territricha* nov. gen. (Ciliophora: Hypotrichida). *Zool. Anz.* **220:** 113-134

Berger H., Foissner W. (1989) Morphology and morphogenesis of *Parakahliella haideri* nov. spec. (Ciliophora, Hypotrichida). *Bull. Br. Mus. nat. Hist. (Zool.)* **55:** 11-17

Berger H., Foissner W., Adam H. (1984) Taxonomie, Biometrie und Morphogenese einiger terricoler Ciliaten (Protozoa: Ciliophora). *Zool. Jb. Syst.* **111:** 339-367

Berger H., Foissner W., Adam H. (1985) Morphological variation and comparative analysis of morphogenesis in *Parakahliella macrostoma* (Foissner, 1982) nov. gen. and *Histriculus muscorum* (Kahl, 1932), (Ciliophora, Hypotrichida). *Protistologica* **21:** 295-311

Blatterer H., Foissner W. (1988) Beitrag zur terricolen Ciliatenfauna (Protozoa: Ciliophora) Australiens. *Stapfia* (Linz) **17:** 1-84

Borror A. C. (1972) Revision of the order Hypotrichida (Ciliophora, Protozoa). *J. Protozool.* **19:** 1-23

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

Buitkamp U. (1977) Die Ciliatenfauna der Savanne von Lamto (Elfenbeinküste). *Acta Protozool.* **16:** 249-276

Bütschli O. (1889) Protozoa. III. Abt.: Infusoria und System der Radiolaria. In: Klassen und Ordnungen des Thier-Reichs, (Ed. H. G. Bronn). Winter'sche Verlagshandlung, Leipzig, **I:** 1585-2035

Dragesco J., Njiné T. (1971) Compléments à la connaissance des Ciliés libres du Cameroun. *Annls Fac. Sci. Univ. féd. Cameroun* **7-8:** 97-140

Eigner P. (1995) Divisional morphogenesis in *Deviata abbrevescens* nov. gen., nov. spec., *Neogeneia hortualis* nov. gen., nov. spec., and *Kahliella simplex* (Horváth) Corliss and redefinition of the Kahliellidae (Ciliophora, Hypotrichida). *Europ. J. Protistol.* **31:** 341-366

Eigner P., Foissner W. (1991) *Orthoamphisiella stramenticola* nov. gen., nov. spec., a new hypotrichous ciliate (Ciliophora: Hypotrichida) occurring in walnut leaf litter. *Acta Protozool.* **30:** 129-133

Eigner P., Foissner W. (1993) Divisional morphogenesis in *Orthoamphisiella stramenticola* Eigner and Foissner, 1991 and *O. grelli* nov. spec. (Ciliophora, Hypotrichida). *Arch. Protistenk.* **143:** 337-345

Eigner P., Foissner W. (1994) Divisional morphogenesis in *Amphisiellides illuvialis* n. sp., *Paramphisiella caudata* (Hemberger) and *Hemiamphisiella terricola* Foissner, and redefinition of the Amphisiellidae (Ciliophora, Hypotrichida). *J. Euk. Microbiol.* **41:** 243-261

Engelmann T. W. (1862) Zur Naturgeschichte der Infusionsthiere. *Z. wiss. Zool.* **11:** 347-393

Finlay B. J. (1982) Procedures for the isolation, cultivation and identification of protozoa. In: Experimental Microbial Ecology, (Eds. R. G. Burns, J. H. Slater). Blackwell, Oxford, 44-65

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

Foissner W. (1987) Soil protozoa: fundamental problems, ecological significance, adaptations in ciliates and testaceans, bioindicators, and guide to the literature. *Progr. Protistol.* **2:** 69-212

Foissner W. (1988) Gemeinsame Arten in der terricolen Ciliatenfauna (Protozoa: Ciliophora) von Australien und Afrika. *Stapfia* (Linz) **17:** 85-133

Foissner W. (1991) Basic light and scanning electron microscopic methods for taxonomic studies of ciliated protozoa. *Europ. J. Protistol.* **27:** 313-330

Foissner W. (1996) Terrestrial ciliates (Protozoa, Ciliophora) from two islands (Gough, Marion) in the Southern Ocean, with description of two new species, *Arcuospathidium cooperi* and *Oxytricha ottowi*. *Biol. Fertil. Soils* (in press)

Foissner W., Adam H. (1983) Morphologie und Morphogenese des Bodenciliaten *Oxytricha granulifera* sp. n. (Ciliophora, Oxytrichidae). *Zool. Scr.* **12:** 1-11

Foissner W., Schlegel M., Prescott D. M. (1987) Morphology and morphogenesis of *Onychodromus quadricornutus* n. sp. (Ciliophora, Hypotrichida), an extraordinarily large ciliate with dorsal horns. *J. Protozool.* **34:** 150-159

Foissner W., Blatterer H., Berger H., Kohmann F. (1991) Taxonomische und ökologische Revision der Ciliaten des Saprobiensystems. - Band I: Cyrtophorida, Oligotrichida, Hypotrichia, Colpodea. *Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft* **1/91:** 1-478

Gelei J. (1954) Über die Lebensgemeinschaft einiger temporärer Tümpel auf einer Bergwiese im Börzsönygebirge (Oberungarn). III. Ciliaten. *Acta biol. hung.* **5:** 259-343

Gellért J. (1955) Die Ciliaten des sich unter der Flechte *Parmelia saxatilis* Mass. gebildeten Humus. *Acta biol. hung.* **6:** 77-111

Gellért J., Tamás G. (1958) Detritusz-turzások kovamoszatainak és csillósainak ökológiai vizsgálata a tihanyi-félsziget keleti partján. *Annls Inst. biol. Tihany* **25:** 217-240

Gourret P., Roeser P. (1888) Contribution á l'etude des protozoaires de la Corse. *Archs Biol., Paris* **8:** 139-204

Grimes G. W. (1973) Differentiation during encystment and excystment in *Oxytricha fallax*. *J. Protozool.* **20:** 92-104

Grimes G. W., L'Hernault S. W. (1978) The structure and morphogenesis of the ventral ciliature in *Paraurostyla hymenophora*. *J. Protozool.* **25:** 65-74

Hemberger H. (1982) Revision der Ordnung Hypotrichida Stein (Ciliophora, Protozoa) an Hand von Protargolpräparaten und Morphogenesedarstellungen. Diss. Math.-Naturwiss. Fak. Univ. Bonn

Hemberger H. (1985) Neue Gattungen und Arten hypotricher Ciliaten. *Arch. Protistenk.* **130:** 397-417

Jareno M. A. (1984) Macronuclear events and some morphogenetic details during the excystment of *Onychodromus acuminatus* (Ciliophora, Hypotrichida). *J. Protozool.* **31:** 489-492

Jeffries W. B. (1956) Studies on excystment in the hypotrichous ciliate *Pleurotricha lanceolata*. *J. Protozool.* **3:** 136-144

Jeffries W. B., Mellott J. L. (1968) New observations on the anatomy of *Pleurotricha lanceolata*. *J. Protozool.* **15:** 741-747

Kahl A. (1932) Urtiere oder Protozoa I: Wimpertiere oder Ciliata (Infusoria). 3. Spirotricha. *Tierwelt Dtl.* **25:** 399-650

Kamra K., Sapra G. R. (1990) Partial retention of parental ciliature during morphogenesis of the ciliate *Coniculostomum monilata* (Dragesco & Njiné, 1971) Njiné, 1978 (Oxytrichidae, Hypotrichida). *Europ. J. Protistol.* **25:**264-278

Kamra K., Sapra G. R. (1993) Morphometric and morphogenetic comparisons between *Onychodromus indica* n. sp. and *O. quadricornutus* Foissner, Schlegel et Prescott, 1987; phylogenetic note on *Onychodromus* and related genera. *Acta Protozool.* **32:** 107-121

Kamra K., Sapra G. R., Ammermann D. (1994) *Coniculostomum bimarginata* n. sp., a new hypotrich ciliate: description and systematic relationships. *Europ. J. Protistol.* **30:** 55-67

Lundin F. C., West L. S. (1963) The free-living protozoa of the Upper Peninsula of Michigan. Northern Michigan College Press, Marquette

Martin J., Fedriani C., Perez-Silva J. (1983) Morphogenetic pattern in *Laurentiella acuminata* (Ciliophora, Hypotrichida): its significance for the comprehension of ontogeny and phylogeny of hypotrichous ciliates. *J. Protozool.* **30:** 519-529

Martín-González A., Serrano S., Fernández-Galiano D. (1984) New aspects of the morphology of *Pleurotricha lanceolata* (Ciliophora, Hypotrichida): cirral and membranellar patterns and fibrillar systems. *J. Protozool.* **31:** 347-351

Matsusaka T. (1976) An ultrastructural study of excystment in the hypotrichous ciliate *Pleurotricha* sp. *Kumamoto J. Sci.* **13:** 13-26

Njiné T. (1979) Compléments a l'étude des Ciliés libres du Cameroun. *Protistologica* **15:** 343-354

Reuter J. (1961) Einige faunistische und ökologische Beobachtungen über Felsentümpel-Ziliaten. *Acta zool. fenn.* **99:** 4-42

Ricci N., Verni F., Rosati G. (1985) The cyst of *Oxytricha bifaria* (Ciliata: Hypotrichida). I. Morphology and significance. *Trans. Am. microsc. Soc.* **104:** 70-78

Sandon H., Cutler D. W. (1924) Some Protozoa from the soils collected by the 'Quest' expedition (1921-1922). *J. Linn. Soc.* **36:** 1-12

Small E. B., Lynn D. H. (1985) Phylum Ciliophora Doflein, 1901. In: An Illustrated Guide to the Protozoa, (Eds. J. J. Lee, S. H. Hutner, E. C. Bovee). Allen Press, Lawrence, Kansas, 393-575

Smith H. G. (1978) The distribution and ecology of terrestrial protozoa of sub-Antarctic and maritime Antarctic islands. *Br. Antarct. Surv. Sci. Rep.* **95:** 1-104

Šrámek-Hušek R. (1957) K poznáni nálevníkú ostravského kraje. *Věst. čsl. zool. Spol.* **21:** 1-24

Stein F. (1859) Wissenschaftliche Mittheilungen. Charakteristik neuer Infusorien-Gattungen. *Lotos* **9:** 2-5, 57-60

Sterki V. (1878) Beiträge zur Morphologie der Oxytrichinen. *Z. wiss. Zool.* **31:** 29-58

Stokes A. C. (1887) Some new hypotrichous infusoria from American fresh waters. *Ann. Mag. nat. Hist. (Serie 5)* **20:** 104-114

Stokes A. C. (1888) A preliminary contribution toward a history of the fresh-water infusoria of the United States. *J. Trenton nat. Hist. Soc.* **1:** 71-319

Szabó A., Wilbert N. (1995) A redescription of the morphology of *Onychodromus grandis* Stein 1859 and the systematic implications of its morphogenesis. *J. Euk. Microbiol.* **42:** 50-60

Thompson J. C., Jr. (1972) Ciliated protozoa of the Antarctic Peninsula. *Antarctic Res. Ser.* **20:** 261-288

Voss H.-J. (1991a) Die Morphogenese von *Cyrtohymena muscorum* (Kahl, 1932) Foissner, 1989 (Ciliophora, Oxytrichidae). *Arch. Protistenk.* **140:** 67-81

Voss H.-J. (1991b) Die Morphogenese von *Notohymena rubescens* Blatterer & Foissner, 1988 (Ciliophora, Oxytrichidae). *Arch. Protistenk.* **140:** 219-236

Voss H.-J. (1992) Morphogenesis in *Amphisiella australis* Blatterer and Foissner, 1988 (Ciliophora, Hypotrichida). *Europ. J. Protistol.* **28:** 405-414

Voss H.-J., Foissner W. (1995) Divisional morphogenesis in *Steinia sphagnicola* (Ciliophora, Hypotrichida): a comparative light and scanning electron microscopic study. *Europ. J. Protistol.* **32:** 31-46

Walker G. K., Grim J. N. (1973) Morphogenesis and polymorphism in *Gastrostyla steinii*. *J. Protozool.* **20:** 566-573

Walker G. K., Maugel T. K., Goode D. (1975) Some ultrastructural observations on encystment in *Stylonychia mytilus* (Ciliophora; Hypotrichida). *Trans. Am. microsc. Soc.* **94:** 147-154

Wallengren H. (1900) Zur Kenntnis der vergleichenden Morphologie der hypotrichen Infusorien. *Bih. K. svenska VetenskAkad. Handl.* **26:** 1-31

Wicklow B. J. (1982) The Discocephalina (n. subord.): ultrastructure, morphogenesis and evolutionary implications of a group of endemic marine interstitial hypotrichs (Ciliophora, Protozoa). *Protistologica* **18:** 299-330

Wilbert N. (1975) Eine verbesserte Technik der Protargolimprägnation für Ciliaten. *Mikrokosmos* **64:** 171-179

Wirnsberger E., Foissner W., Adam H. (1985a) Morphological, biometric, and morphogenetic comparison of two closely related species, *Stylonychia vorax* and *S. pustulata* (Ciliophora: Oxytrichidae). *J. Protozool.* **32:** 261-268

Wirnsberger E., Foissner W., Adam H. (1985b) 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.* **14:** 1-10

Wirnsberger E., Foissner W., Adam H. (1986) Biometric and morphogenetic comparison of the sibling species *Stylonychia mytilus* and *S. lemnae*, including a phylogenetic system for the oxytrichids (Ciliophora, Hypotrichida). *Arch. Protistenk.* **132:** 167-185

Received on 8th January, 1996; accepted on 1st March 1996