Europ. J. Protistol. 30, 156–170 (1994)
May 27, 1994

European Journal of
PROTISTOLOGY

Morphology and Morphogenesis of *Circinella arenicola* nov. gen., nov. spec., a Cephalized Hypotrich (Ciliophora, Hypotrichida) from Sand Dunes in Utah, USA

Wilhelm Foissner
Universität Salzburg, Institut für Zoologie, Salzburg, Austria

Summary

Circinella arenicola nov. gen., nov. spec. was discovered in a sand-litter mixture from the Coral Pink Sand Dunes in Utah, USA. Its morphology and morphogenesis were studied in live cells and in specimens impregnated with protargol. The new genus, *Circinella*, possibly belongs to the family Cladotrichidae and is unique by having a filiform body, a short row of ventral cirri developing apokinetally, 1 left and 1 right marginal row, and neither transverse nor caudal cirri. The opisthe's oral apparatus and frontoventral ciliature and the proter's ventral row originate and develop without participation of parental cirri. The new species, *C. arenicola*, measures about 400 × 22 µm and is the first cephalized, non-marine hypotrich. It shortens and broadens markedly during fission and resorbs some macronuclear nodules. Two species originally considered as belonging to the genera *Perisincirra* and *Hemisincirra* are newly combined with *Circinella: C. filiformis* (Foissner, 1982) nov. comb. (basionym: *Perisincirra filiformis*) and *C. vettersi* (Berger & Foissner, 1989) nov. comb. (basionym: *Hemisincirra vettersi*). An illustrated and morphometric key to the *Circinella* species is provided. The systematic position of *Circinella* and the adaptive value of the cephalization are discussed. 23 species of ciliates, most of which are new for the fauna of North America, occurred together with *C. arenicola* and are listed in the ecology section.

Introduction

About 100 new hypotrichs have been described from soils during the last decade [e.g., 1–3, 7–14, 17]. This is, however, only the tip of the iceberg. The unpublished material of our group includes more than 100 new hypotrichs found in terrestrial biotopes all over the world. This paper describes a strange, thread-like species from an inland sand dune of the USA. It has a cephalized anterior end like hypotrichs of the suborder Discocephalina living in the marine interstitial [21].

Inland sand dunes contain much plant debris, providing food for a remarkably diverse and rich protozoan fauna which is still poorly known. Blatterer & Foissner [3] listed 42 species (including two new and eight non-identified taxa) found in a sample from a dune in Australia. Some species have been reported from sand dunes of the Sahara desert in Africa [16, 20] and from the Kara-Kum desert in Asia [5]. However, these data are not very detailed and most identifications seem unreliable.

Material and Methods

Circinella arenicola was collected on June 23rd, 1989 from the Coral Pink Sand Dunes about 25 km west of Rockville, Zion National Park, Utah, USA (W 113°, N 37°). The sand contains much plant debris which was enriched by sieving. Dune vegetation is sparse, and restricted mainly to *Nerisyrenia camporum*.

In the laboratory, the dry litter-sand mixture was saturated with distilled water according to the non-flooded petri dish method [12]. The rewetted mixture had pH 5.6. *Circinella*

0932-4739/94/0030-0156$3.50/0

24 Uni S., Iseki M., Maekawa T., Moriya K. and Takada S. (1987): Ultrastructure of *Cryptosporidium muris* (strain RN66) parasitizing the murine stomach. Parasitol. Res., *74*, 123–132.
25 Upton S. J. and Current W. L. (1985): The species of *Cryptosporidium* (Apicomplexa: Cryptosporidiidae) infecting mammals. J. Parasitol., *71*, 625–629.
26 Wenyon C. M. (1926): Protozoology, a manual for medical men, veterinarians and zoologists, vol. II. London. Baillier, Tindall and Cox.
27 Yoshikawa H. and Iseki M. (1992): Freeze-fracture study of the site of attachment of *Cryptosporidium muris* in the gastric glands. J. Protozool., *39*, 539–544.

Key words: Cryptosporidium muris – Wild mice – Microscopy

Rachel M. Chalmers, School of Natural and Environmental Sciences, Coventry University, Priory Street, Coventry, CV1 5FB, UK

arenicola excysted 14 days after rewetting and became very abundant 4 days later when the culture was sampled destructively.

Cells were studied in vivo using a high-power oil immersion objective and differential interference contrast [15]. Protargol (protocol 1, [15]) was used to reveal the infraciliature.

Counts and measurements on silvered specimens were performed at a magnification of X 1,000. In vivo measurements were conducted at a magnification of X 250–1,000. Although these provide only rough estimates, it is convenient to give such data as specimens usually shrink in preparations or may even contract during fixation. Standard deviation and coefficient of variation were calculated according to statistics textbooks. Drawings of live specimens are based on photographic records, those of impregnated cells were made with a camera lucida.

Terminology is according to [6, 7].

Results

Circinella nov. gen.

Diagnosis. Filiform Cladotrichidae (?) with short, oblique row of ventral cirri longer than adoral zone of membranelles. 1 left and 1 right marginal row. No transverse and caudal cirri. The opisthe's oral apparatus and frontoventral ciliature and the proter's ventral row originate and develop without participation of parental cirri.

Type species. Circinella arenicola nov. spec.

Derivatio nominis. "circinella" (lat.), tiny, curled hair. Feminine.

Description of Circinella arenicola nov. spec. (Figs. 1–32, Table 1).

Diagnosis. Size in vivo about 400 × 22 μm. Filiform, anterior end (oral area) slightly broadened (cephalized). 78 macronuclear nodules on average, distributed throughout cell. Adoral zone of membranelles about 8 % of body length, bipartite, on average 7 membranelles in distal and 13 in proximal portion. Right and left row of marginal cirri composed of an average of 90 and 95 cirri, respectively. Ventral cirral row about 21 % of body length, consists of 24 cirri on average. Usually 1 buccal cirrus and 3 dorsal kineties.

Derivatio nominis. "arenicola" (lat.), living in sand.

Type location. In sand from the Coral Pink Sand Dunes near the Zion National Park, Utah, USA (W 113° N 37°).

Type specimens. A holotype and a paratype of *Circinella arenicola* as 2 slides of protargol impregnated cells have been deposited in the collection of microscope slides of the Oberösterreichische Landesmuseum in Linz.

Description (see Table 1 for additional morphometric data). Size, especially length, highly variable, possibly due to injury, in vivo 200–600 × 18–30 μm, normally about 400 × 22 μm. Shape very distinct, viz. extremely slender and anterior end slightly to distinctly broadened (cephalized), giving cells odd, spathidiform appearance (Figs. 1, 6–8, 10, 15, 16, 22, 23, 27, 28). Middle third of body widened, especially in well-nourished specimens, anterior third less attenuated than posterior and broadened in oral region, posterior end not tapered tail-like but rounded.

Table 1. Morphometric characterization of *Circinella arenicola* (Ca), *Circinella filiformis* (Cf; from [9]), and *Circinella vettersi* (Cv; from [2])

Character[1]	Species	$\bar{x}$	M	SD	$SD_{\bar{x}}$	CV	Min	Max	n
Body, length	Ca	331.3	330.0	85.1	13.1	25.7	180	540	42
	Cf	108.7	106.0	16.1	5.1	14.9	83	140	10
	Cv	143.6	145.0	18.6	5.2	13.0	112	180	13
Body, width	Ca	19.6	20.0	2.7	0.4	13.7	15	24	42
	Cf	7.2	6.8	1.3	0.4	18.1	5	11	10
	Cv	12.0	11.0	1.5	0.4	12.7	10	15	13
Adoral zone of membranelles, length	Ca	24.6	25.0	2.3	0.6	9.4	21	30	17
	Cf	7.8	8.0	0.6	0.2	8.0	6	9	10
	Cv	8.5	8.0	0.9	0.2	10.4	7	10	13
Distance anterior end to proximal end of ventral cirral row	Ca	76.1	70.0	17.6	4.3	23.1	50	107	17
	Cf	16.2	16.0	2.3	0.7	14.3	13	20	10
	Cv	16.5	16.0	1.7	0.4	10.1	14	20	13
Macronuclear nodule, length	Ca	7.2	7.0	2.1	0.5	28.7	4	11	17
	Cf	5.8	5.3	1.1	0.3	18.6	4	8	10
	Cv	9.2	7.0	4.9	1.4	54.0	3	22	13
Macronuclear nodule, width	Ca	3.0	3.0	1.7	0.4	55.4	2	9	17
	Cf	1.9	1.7	0.5	0.2	26.6	1.4	2.6	10
	Cv	1.8	1.7	0.4	0.1	21.0	1.2	2.5	13
Micronucleus, length	Ca	7.8	8.0	1.7	0.4	21.4	6	13	17
	Cf	1.6	1.5	0.2	0.1	12.8	1.4	1.9	10
	Cv	8.2	8.0	1.3	0.4	15.7	7	11	13
Micronucleus, width	Ca	2.5	2.5	0.5	0.1	18.9	2	3	17
	Cf	1.6	1.5	0.2	0.1	12.8	1.4	1.9	10
	Cv	2.0	2.0	0.5	0.1	24.4	1.4	2.8	13

Table 1 (to be continued)

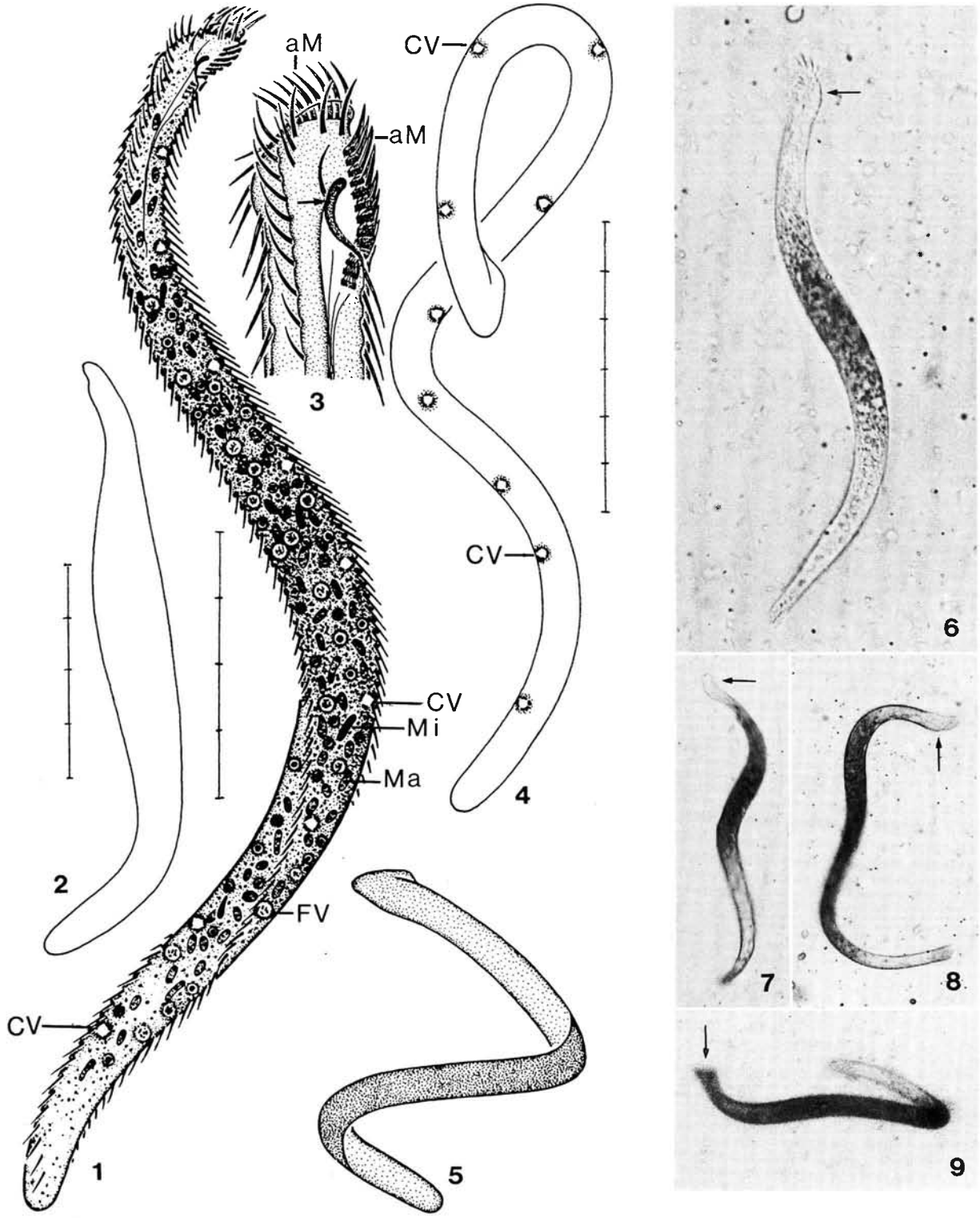
Character[1]	Species	$\bar{x}$	M	SD	$SD_{\bar{x}}$	CV	Min	Max	n
Adoral membranelles, total number	Ca	19.9	19.0	2.9	0.7	14.4	15	27	17
	Cf	9.8	10.0	0.9	0.3	8.9	9	12	10
	Cv	8.3	8.0	0.6	0.2	7.6	7	9	13
Adoral membranelles, number in distal portion	Ca	7.2	7.0	1.6	0.4	21.5	5	12	17
Adoral membranelles, number in proximal portion	Ca	12.8	13.0	1.8	0.4	13.7	9	16	17
Ventral row, number of cirri	Ca	25.2	24.0	5.8	1.4	23.0	18	37	17
	Cf	8.2	8.0	1.2	0.4	15.2	6	10	10
	Cv	8.2	8.0	1.4	0.4	17.2	6	11	13
Right marginal row, number of cirri	Ca	92.8	90.0	17.1	4.2	18.4	71	130	17
	Cf	52.9	50.0	8.8	2.8	16.6	44	74	10
	Cv	68.8	70.0	6.2	1.7	9.0	58	78	13
Left marginal row, number of cirri	Ca	102.8	95.0	19.2	4.7	18.7	84	156	17
	Cf	40.8	39.0	6.7	2.1	16.4	33	55	10
	Cv	52.1	53.0	4.7	1.3	9.1	43	60	13
Frontal cirri, number	Ca	3.0	3.0	0.0	0.0	0.0	3	3	17
	Cf	3.0	3.0	0.0	0.0	0.0	3	3	10
	Cv	3.0	3.0	0.0	0.0	0.0	3	3	13
Cirri below 3rd frontal cirrus, number	Ca	1.6	1.0	–	–	–	1	5	17
	Cf	0.0	0.0	–	–	–	0	0	10
	Cv	0.0	0.0	–	–	–	0	0	13
Buccal cirri, number	Ca	1.1	1.0	–	–	–	1	2	17
	Cf	1.0	1.0	0.0	0.0	0.0	1	1	10
	Cv	1.0	1.0	0.0	0.0	0.0	1	1	13
Dorsal kineties in anterior third of cell, number	Ca	3.4	3.0	–	–	–	3	4	17
	Cf	1.0	1.0	0.0	0.0	0.0	1	1	10
	Cv	3.0	3.0	0.0	0.0	0.0	3	3	13
Macronuclear nodules, number	Ca	77.8	78.0	14.5	3.6	18.8	46	102	17
	Cf	16.4	15.5	4.6	1.5	28.4	11	26	10
	Cv	27.5	27.0	7.5	2.1	27.2	20	50	13
Micronuclei, number	Ca	4.9	4.0	1.7	0.4	33.8	2	8	17
	Cf	2.0	2.0	0.0	0.0	0.0	2	2	10
	Cv	1.9	2.0	0.5	0.1	25.7	1	3	13
Dividing cells, length	Ca	171.6	160.0	34.1	7.5	19.9	124	245	21
Dividing cells, width	Ca	50.0	50.0	8.2	1.8	16.3	30	65	21

[1] All data are based, if not stated otherwise, on the investigation of randomly selected, protargol impregnated and mounted non-dividers. All measurements in µm. CV = coefficient of variation in %; M = median; Max = maximum; Min = minimum; n = number of investigated specimens; SD = standard deviation; $SD_{\bar{x}}$ = standard deviation of arithmetic mean; $\bar{x}$ = arithmetic mean.

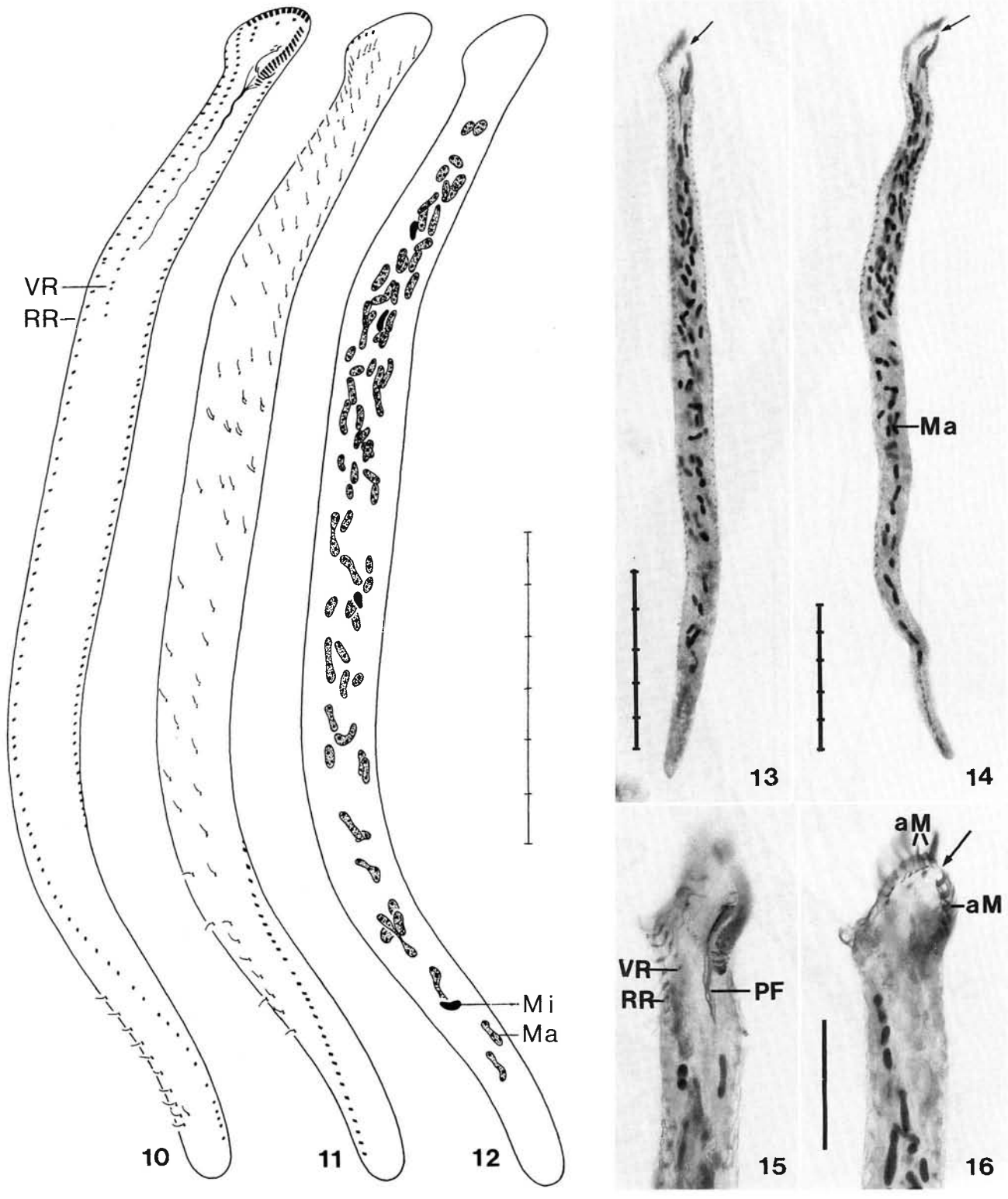
Oral area flattened about 2:1, postoral portion unflattened. Very flexible, slightly spiralized longitudinally and always more or less distinctly serpentine and coiled (Figs. 4, 5, 7–9, 22–24). Macronuclear nodules distributed throughout cell, ellipsoid. Micronuclei on average slightly larger (!) than individual macronuclear nodules, compact, usually comma-shaped, rarely ellipsoid (Figs. 12, 27, 32). About 10 contractile vacuoles along left body margin. Pellicle and cytoplasm colourless, no special cortical granules or cytoplasmic crystals. Middle third of trophonts filled with 3–4 µm sized food vacuoles and 0.2–2 µm sized silvery shining globules making cells dark at low magnification; anterior and posterior third usually hyaline because of missing or only few food vacuoles (Figs. 1, 6–8). Feeds on bacteria. Movement slow, sluggishly winding, rarely gliding; cells concentrated in a small drop of water look like a miniaturized worm community.

About 10 % of the specimens have a bulbous dilation in the anterior body half (Figs. 25, 26). Their infraciliature and nuclear apparatus look normal. In most specimens, this dilation is filled with food vacuoles.

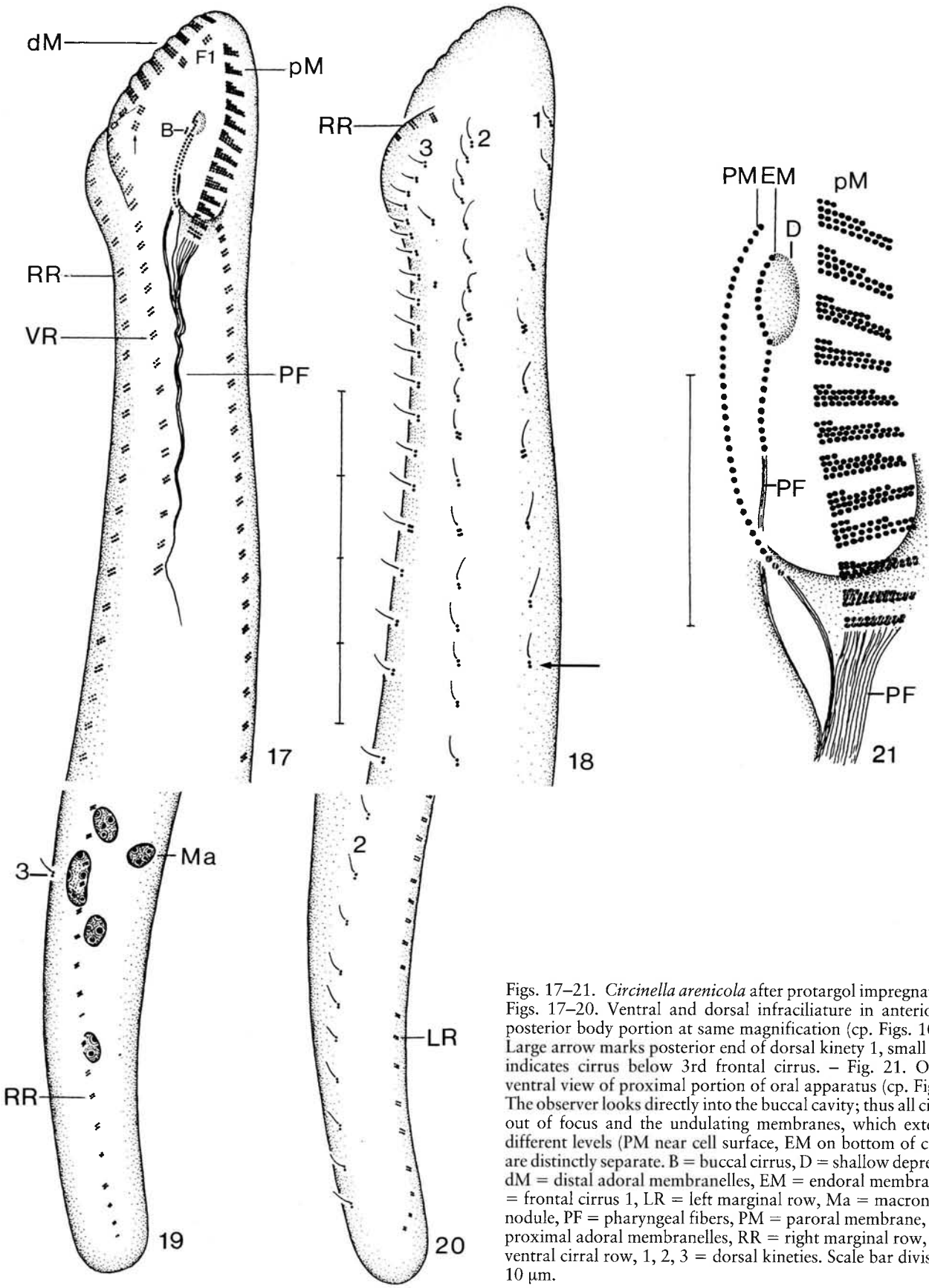
Oral apparatus very small compared to size of cell, viz. about 8 % of body length (Figs. 1, 6, 10, 13, 14, 22). Adoral zone of membranelles bipartitioned by more or less distinct gap, smaller distal portion at oblique anterior end, larger proximal portion slightly curved and extending obliquely from left anterior end to median of cell. Bases of largest membranelles about 5 µm long, of usual structure, i.e. composed of 4 rows of basal bodies of different length. Buccal cavity narrow but deep, right edge bordered by



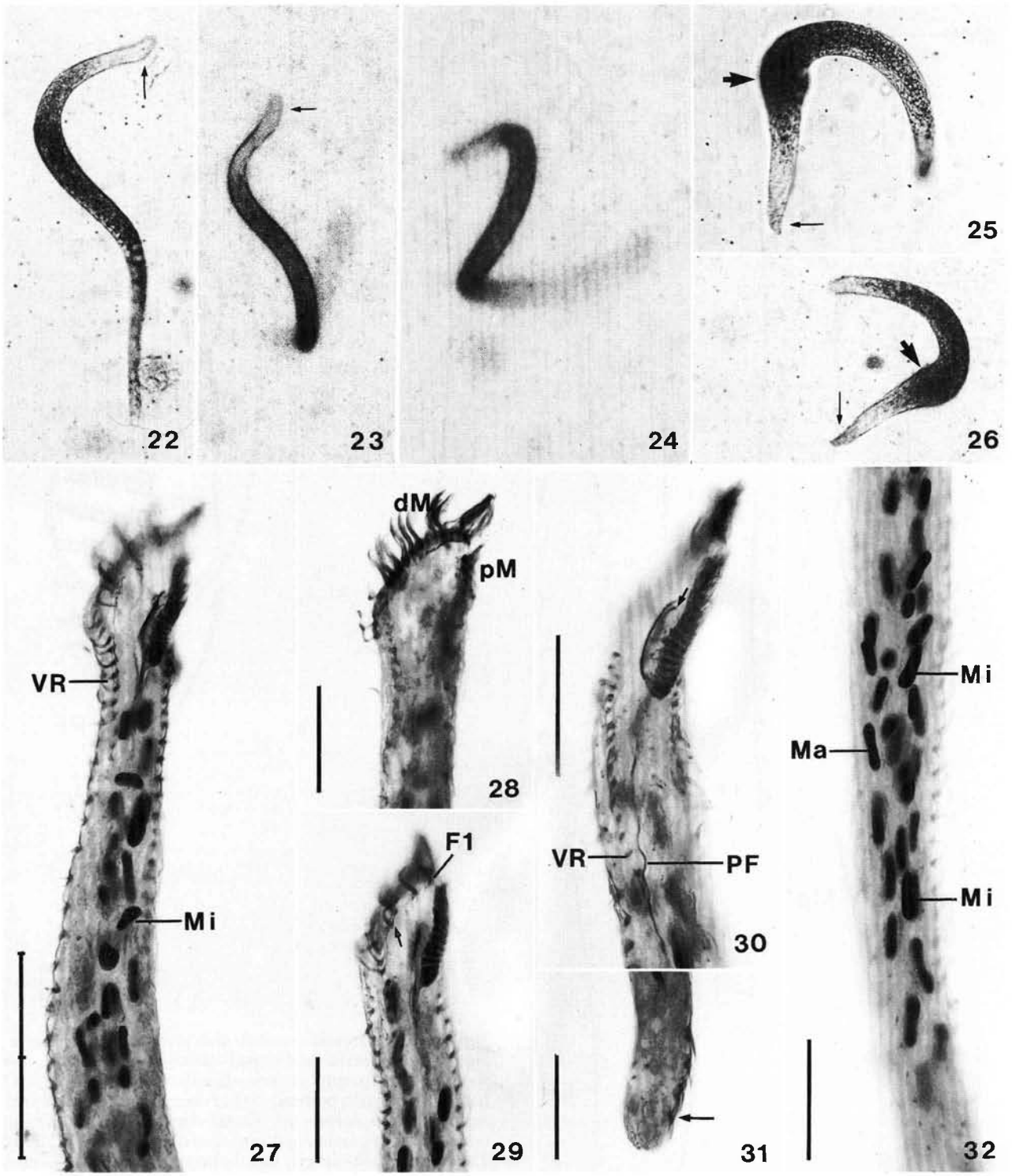
Figs. 1–9. *Circinella arenicola* from life. – Fig. 1. Ventral view of typical specimen. – Fig. 2. Lateral view of well-nourished trophont. – Fig. 3. Oral area of specimen with helmet-like anterior end. Arrow marks compact oral lip. – Figs. 4, 5. Slender theront and spiralized, slowly moving specimen. – Figs. 6–9. Bright field light micrographs of freely moving, typical specimens. Arrows mark broadened (cephalized) anterior end. The middle third of the cells contains many food vacuoles and thus appears dark. aM = adoral membranelles, CV = contractile vacuoles, FV = food vacuole, Ma = macronuclear nodule, Mi = micronucleus. Scale bar division = 20 μm.



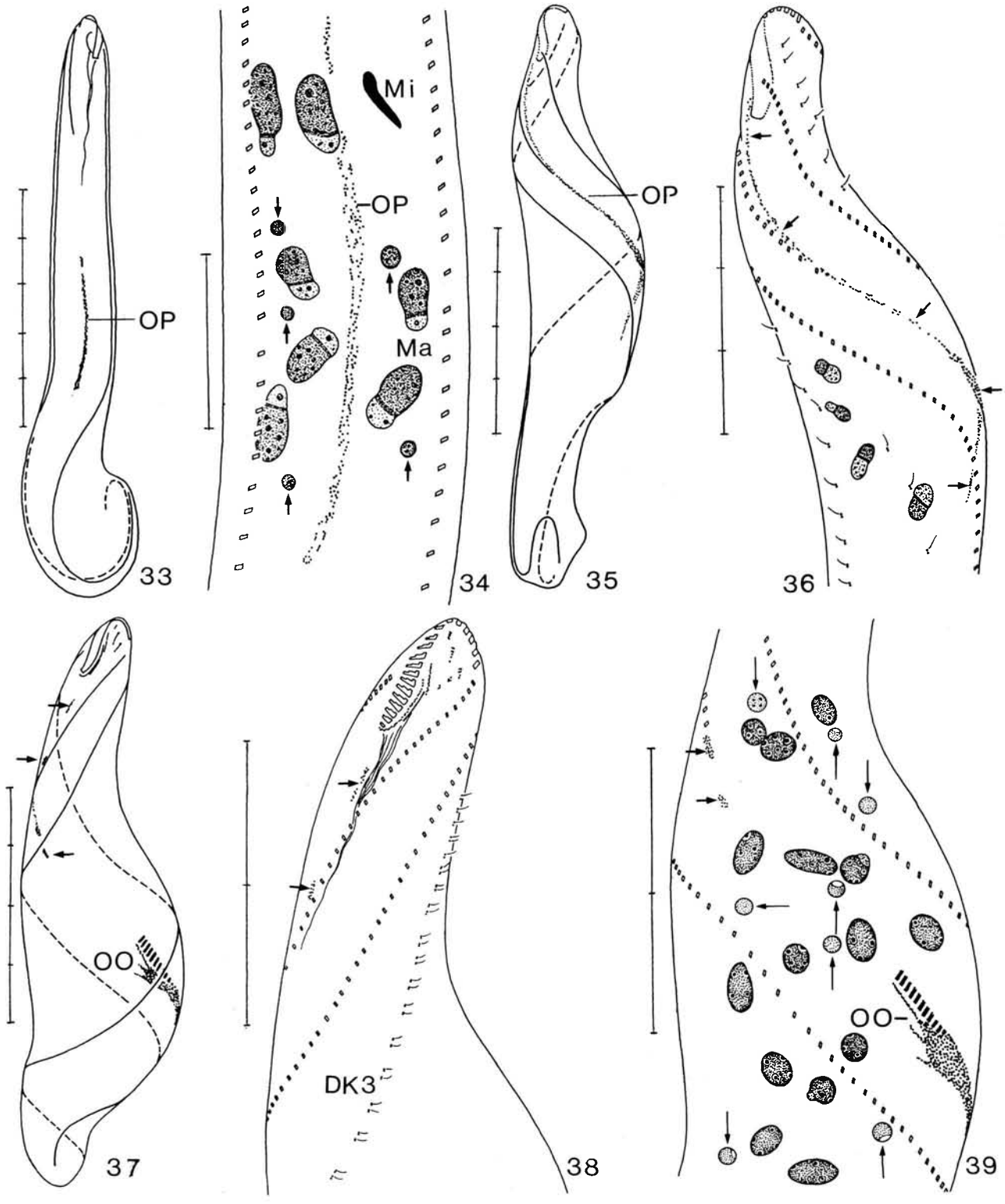
Figs. 10–16. *Circinella arenicola* after protargol impregnation. – Figs. 10–12. Infraciliature of ventral and dorsal side, and nuclear apparatus. – Figs. 13, 14. General morphology. Arrows mark break between distal and proximal adoral membranelles. – Figs. 15, 16. Anterior portion of single specimen photographed at two focus levels to show broadened (cephalized) oral area, ventral cirral row, and break between distal and proximal adoral membranelles (arrow). aM = adoral membranelles, Ma = macronuclear nodule, Mi = micronucleus, PF = pharyngeal fibers, RR = right marginal row, VR = ventral cirral row. Scale bar division = 20 μm.
Note: To save space, all figures are orientated as seen from the ventral side, i.e. the dorsal surface is shown by transparency. In the spiralized dividers the opisthe's oral apparatus always faces the observer.



Figs. 17–21. *Circinella arenicola* after protargol impregnation. – Figs. 17–20. Ventral and dorsal infraciliature in anterior and posterior body portion at same magnification (cp. Figs. 10–12). Large arrow marks posterior end of dorsal kinety 1, small arrow indicates cirrus below 3rd frontal cirrus. – Fig. 21. Oblique ventral view of proximal portion of oral apparatus (cp. Fig. 30). The observer looks directly into the buccal cavity; thus all cirri are out of focus and the undulating membranes, which extend at different levels (PM near cell surface, EM on bottom of cavity), are distinctly separate. B = buccal cirrus, D = shallow depression, dM = distal adoral membranelles, EM = endoral membrane, F1 = frontal cirrus 1, LR = left marginal row, Ma = macronuclear nodule, PF = pharyngeal fibers, PM = paroral membrane, pM = proximal adoral membranelles, RR = right marginal row, VR = ventral cirral row, 1, 2, 3 = dorsal kineties. Scale bar division = 10 μm.



Figs. 22–32. *Circinella arenicola* in vivo (Figs. 22–26) and after protargol impregnation (Figs. 27–32). – Figs. 22–24. Bright field light micrographs of freely moving, typical specimens. Arrows indicate anterior end of cells. – Figs. 25, 26. Lateral view of specimens with bulbous broadening (thick arrows). Thin arrows mark flattened anterior end. – Figs. 27, 28. Ventral views of broadened (cephalized) anterior body portion. – Fig. 29. Anterior end of indistinctly cephalized specimen. Arrow marks single cirrus below 3rd frontal cirrus. – Fig. 30. Oblique ventral view showing spoon-shaped endoral membrane and shallow depression nearby (arrow; cp. Fig. 21). – Fig. 31. The marginal cirral rows end subterminally (arrow). – Fig. 32. Middle portion of cell showing two comma-shaped micronuclei and many macronuclear nodules. dM = distal adoral membranelles, F1 = first frontal cirrus, Ma = macronuclear nodule, Mi = micronuclei, PF = pharyngeal fibers, pM = proximal adoral membranelles, VR = ventral cirral row. Scale bar division = 20 μm.



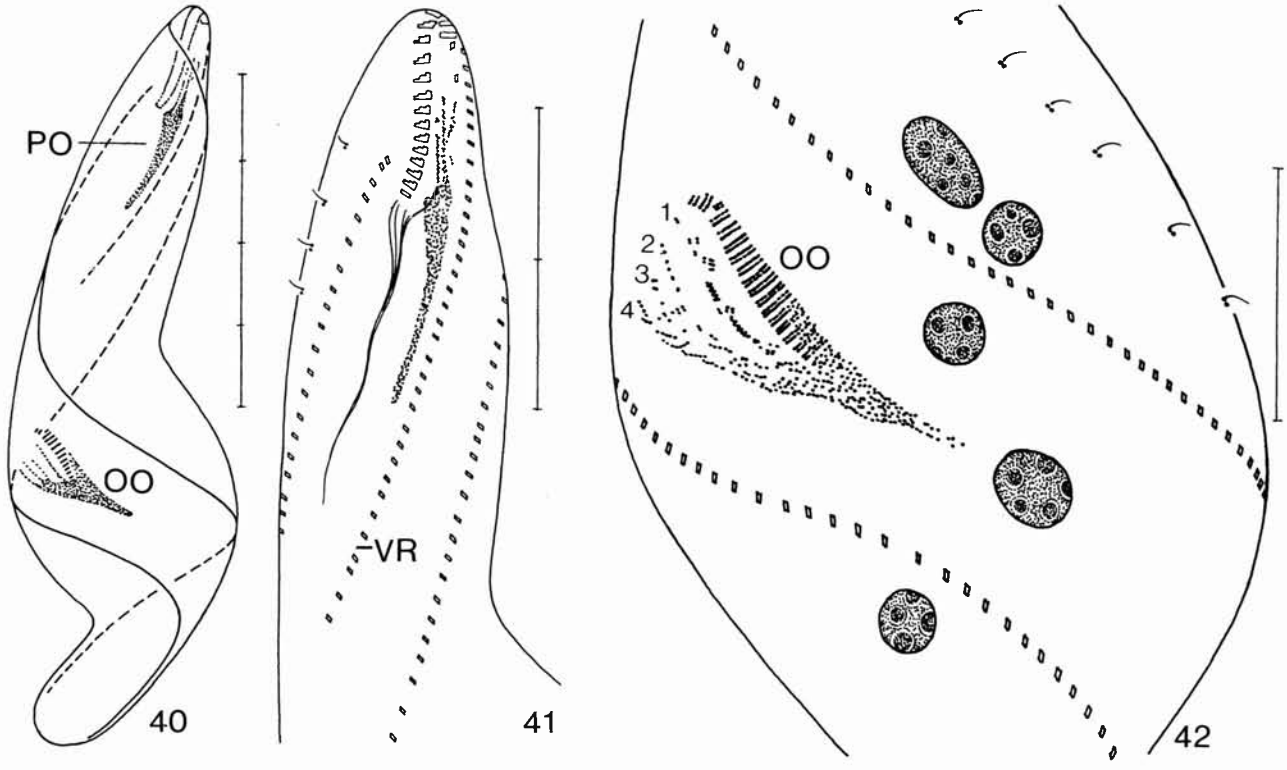
Figs. 33–39. *Circinella arenicola*, early morphogenetic stages, protargol impregnation. – Figs. 33, 34. Division commences with the apokinetal development of an oral primordium in mid-body. The posterior portion of the cell shortens and rounds up. Some macronuclear nodules degenerate (arrows). – Figs. 35, 36. The oral primordium develops to a long streak of basal bodies extending from mid-body to proter's oral apparatus (arrows). The middle portion of the cell broadens. – Figs. 37–39. The oral primordium divides into an anterior (thick arrows) and posterior portion (OO). The proter's frontal cirri and undulating membranes organize cirral anlagen. Many macronuclear nodules degenerate (thin arrows). DK3 = dorsal kinety 3, Ma = macronuclear nodule, Mi = micronucleus, OO = opisthe's oral apparatus, OP = oral primordium. Scale bar division = 20 µm.

distinct, compact lip (Figs. 3, 17, 21). Paroral membrane slightly curved, presumably composed of single row of basal bodies bearing 6 µm long cilia. Endoral membrane likewise composed of single row of basal bodies, shorter than paroral membrane, spoon-shaped, i.e. anterior end concave, right of small, ellipsoid depression slightly reminiscent of the larger cavity found in the oxytrichid genus *Steinia* [14]. Pharyngeal fibres long, originate at proximal end of paroral and endoral membrane and from adoral membranelles (Figs. 10, 15, 17, 21, 27–30).

All cirri remarkably short, i.e. about 7 µm long, and of similar structure, viz. composed of two rows of basal bodies each comprising three (mostly two in posterior third) cilia. Frontal cirrus 2 usually composed of 9 cilia, buccal cirrus of 2–3 cilia only. Marginal cirral rows distinctly separate at posterior end of cell, right row extends anteriorly on dorsal side. Ventral cirral row distinctly longer than adoral zone of membranelles, occupies about 21 % of body length, commences at right end of adoral zone of membranelles and extends slightly obliquely posteriad, never passing median of cell. No transverse and caudal cirri (Figs. 1, 10, 11, 13–20, 27–31). Dorsal kineties 2 and 3 almost as long as cell, kinety 1 (and, if present, neighbouring kinety) terminates in anterior third of cell or near mid-body. Kineties composed mainly of paired basal bodies, the anterior (rarely also the posterior) of which bears an about 4 µm long bristle (Figs. 11, 18, 20); usually, some complexes composed of 4 basal bodies interspersed between paired ones.

Occurrence and ecology. Circinella arenicola apparently excysted from resting cysts because the sample was completely dry when it was rewetted. As yet, it has been found only at the type location, together with the following species, most of which (marked by an asterisk) are new for the fauna of North America: *Bryophyllum* sp. (very likely a new species), * *Colpoda aspera* Kahl, 1926, * *C. edaphoni* Foissner, 1980, *C. inflata* (Stokes, 1885), *C. steinii* Maupas, 1883, * *Cyrtolophosis elongata* (Schewiakoff, 1892), * *Drepanomonas pauciciliata* Foissner, 1987, * *Enchelydium terrenum* Foissner, 1984, * *Fuscheria terricola* Berger, Foissner & Adam, 1983, *Gonostomum affine* (Stein, 1859), * *Grossglockneria acuta* Foissner, 1980, * *Hausmanniella discoidea* (Gellért, 1956), * *Hemisincirra gracilis* Foissner, 1982, * *H. wenzeli* Foissner, 1987, *Leptopharynx costatus* Mermod, 1914, * *Nivaliella plana* Foissner, 1980, * *Notoxoma parabryophryides* Foissner, 1993, * *Platyophrya macrostoma* Foissner, 1980, *P. vorax* Kahl, 1926, * *Pseudocyrtolophosis alpestris* Foissner, 1980, * *Pseudoplatyophrya nana* (Kahl, 1926), * *P. terricola* Foissner, 1985, * *Spathidium procerum* Kahl, 1930, * *Urosomoida agiliformis* Foissner, 1982.

The ciliate fauna in sand dunes is obviously dominated by *r* – selected colpodids (*Colpoda* spp., *Grossglockneria, Cyrtolophosis, Hausmanniella, Nivaliella, Platyophrya,*



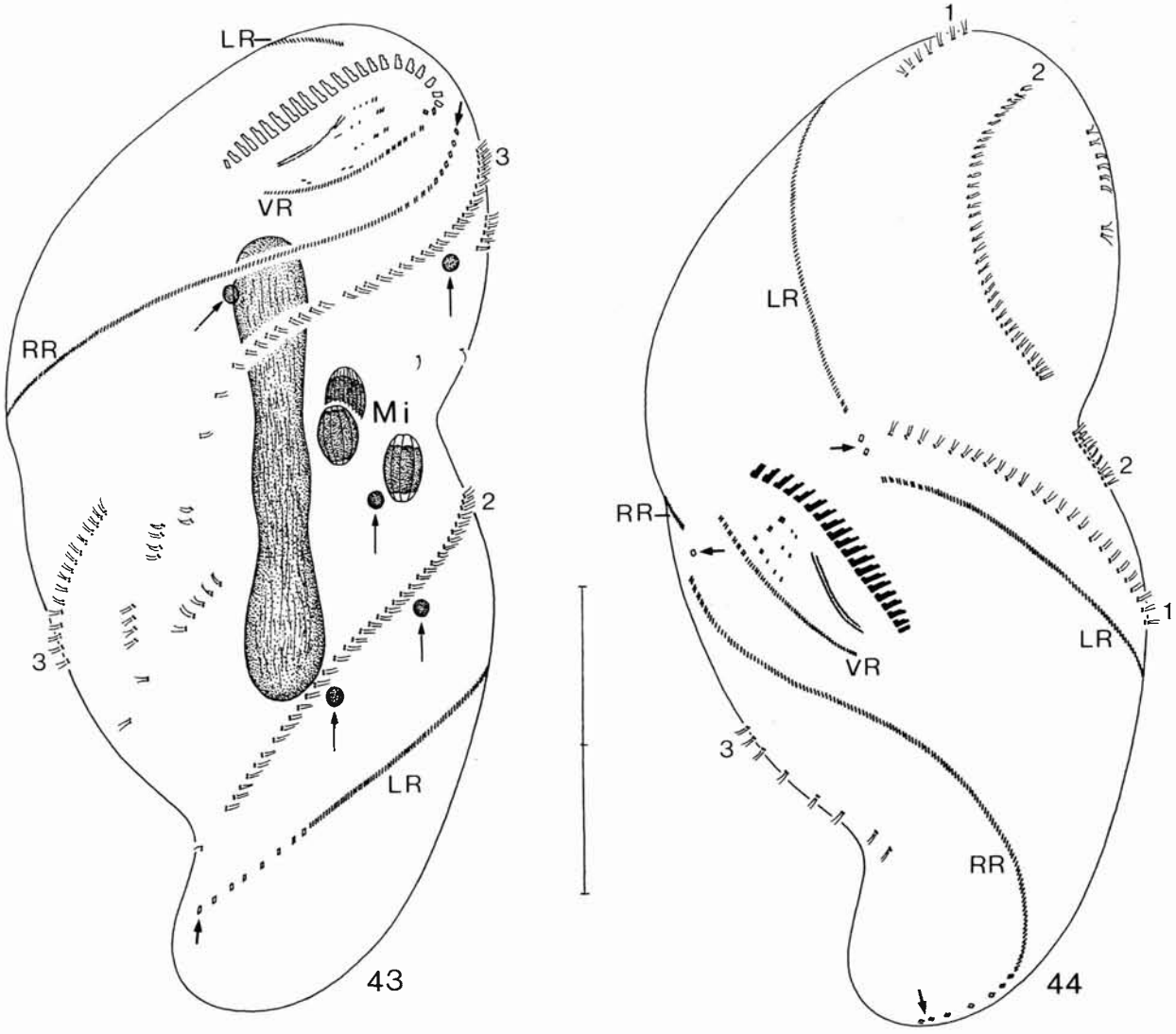
Figs. 40–42. *Circinella arenicola*, middle morphogenetic stage, protargol impregnation. The oral primordium of the proter (PO) unites with the anlagen organized by the frontal cirri and the undulating membranes. The oral primordium of the opisthe (OO) organizes adoral membranelles and four streaks of basal bodies (1–4). The parental ventral cirral row (VR) does not organize anlagen and thus appears unchanged. Scale bar division = 20 µm.

Pseudoplatyophrya spp., *Notoxoma, Pseudocyrtolophosis*), indicating the extreme nature of this environment. *Circinella arenicola* must be a rare species since I did not find it in about 1000 other soil and moss samples collected worldwide; it is probably restricted to sand dunes and sandy soils. The long and narrow body shows that it is well adapted to live in such an environment. *Circinella arenicola* became abundant when the water of the remoistened sample turned yellowish and slightly viscous by leached substances from the plant debris and the sand grains. This may indicate that it is active mainly after longer periods of rain.

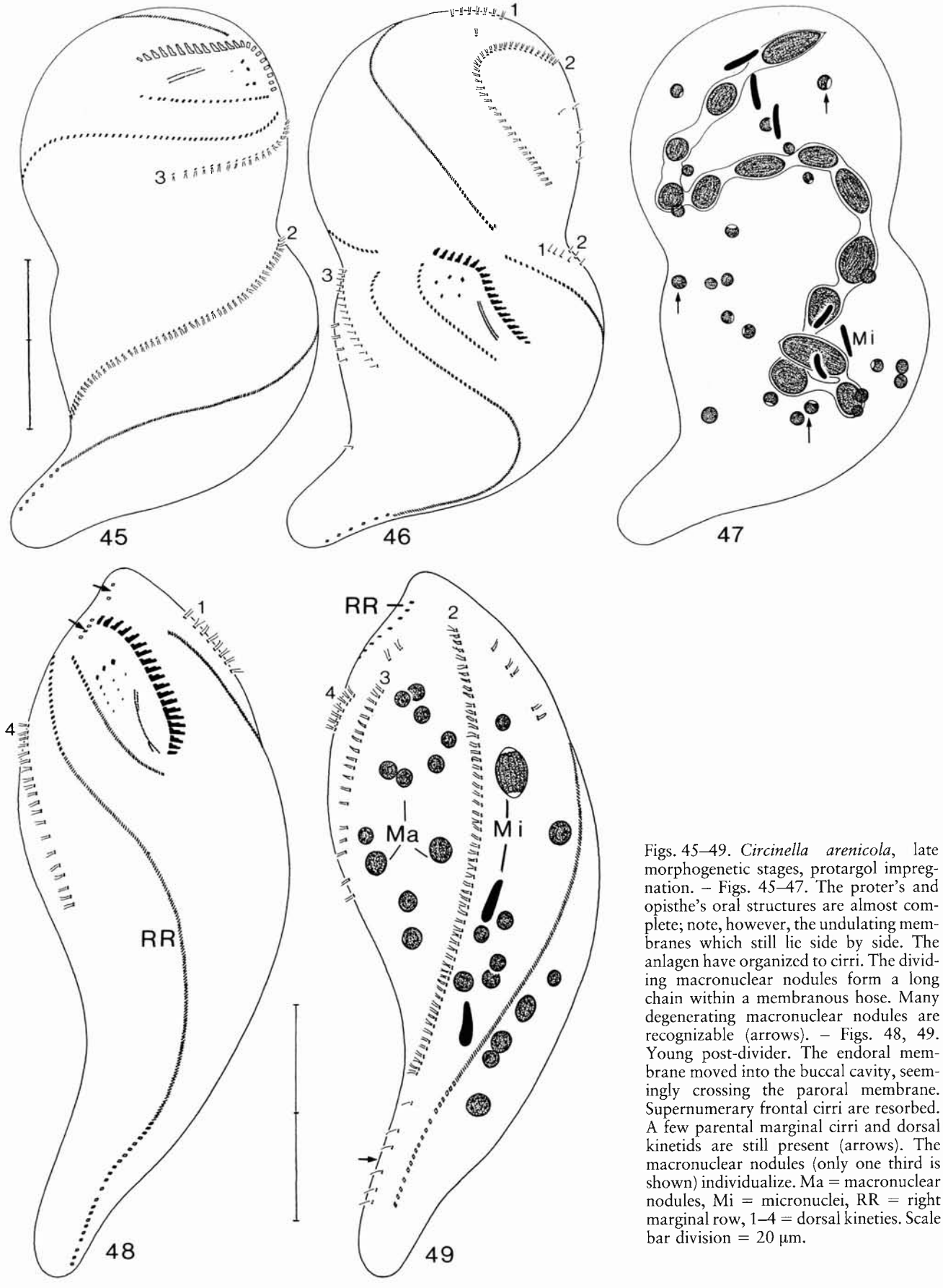
Morphogenesis in Circinella arenicola
(Figs. 33–49, Table 1)

About 50 dividers were found in the protargol slides. It was thus possible to reconstruct an almost complete sequence of the processes associated with divisional morphogenesis.

Body shape. Dividing cells of *C. arenicola* become markedly shorter and broader (Table 1). When division commences, i.e. when the opisthe's oral primordium appears, the posterior third becomes spheroidal, giving cells a drumstick-like appearance (Fig. 33). Next, the



Figs. 43, 44. *Circinella arenicola*, middle morphogenetic stage, protargol impregnation. The opisthe's oral apparatus is almost complete and the anlagen in the proter and opisthe organize cirri. The dorsal kineties reproduce by intrakinetal proliferation of kinetids. Thick arrows mark parental marginal cirri. The macronuclear nodules have fused to a roundish mass which elongates to a dumbbell-shaped structure; some degenerating macronuclear nodules are recognizable (thin arrows). The micronuclei commence division. LR = left marginal row, Mi = micronuclei, RR = right marginal row, VR = ventral cirral row, 1, 2, 3 = dorsal kineties. Scale bar division = 20 μm.

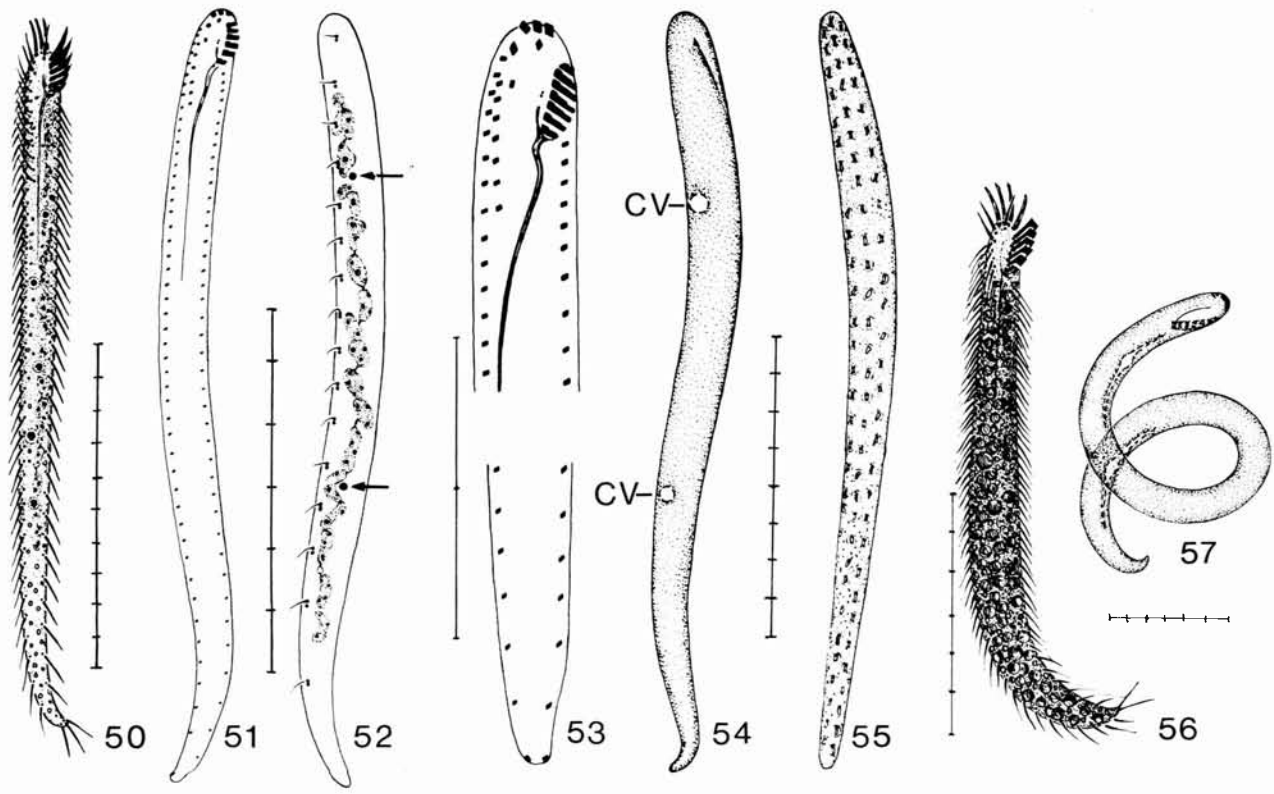


Figs. 45–49. *Circinella arenicola*, late morphogenetic stages, protargol impregnation. – Figs. 45–47. The proter's and opisthe's oral structures are almost complete; note, however, the undulating membranes which still lie side by side. The anlagen have organized to cirri. The dividing macronuclear nodules form a long chain within a membranous hose. Many degenerating macronuclear nodules are recognizable (arrows). – Figs. 48, 49. Young post-divider. The endoral membrane moved into the buccal cavity, seemingly crossing the paroral membrane. Supernumerary frontal cirri are resorbed. A few parental marginal cirri and dorsal kinetids are still present (arrows). The macronuclear nodules (only one third is shown) individualize. Ma = macronuclear nodules, Mi = micronuclei, RR = right marginal row, 1–4 = dorsal kineties. Scale bar division = 20 μm.

middle third of the cell broadens considerably, making early and middle dividers spindle-shaped (Figs. 35, 37, 40). Late dividers are almost ellipsoid (Figs. 43, 45); postdividers are pisciform (Fig. 48). These changes are caused, at least partially, by a slow spiral contraction of the cell because the proter's oral apparatus and the opisthe's oral primordium face opposite directions (180°) in middle and late dividers (Figs. 35, 37, 40, 43–46).

Nuclear apparatus. The general processes associated with nuclear fission in *C. arenicola* are very similar to those known from other multinucleate hypotrichs, i.e. most macronuclear nodules have a reorganization band in early dividers (Figs. 34, 36, 39), and the reorganized nodules fuse to a globular mass in middle dividers. This mass elongates and fragments during cytokinesis (Figs. 43, 47). The micronuclei divide in the usual way. Besides the normal macronuclear nodules, degenerating pieces were observed in almost all dividers (Figs. 34, 39, 43, 47). Such nodules are globular, smaller, and usually faintly stained; often they have a clear, unstained cap and/or a few sharply stained granules inside (Figs. 39, 47).

Oral apparatus and frontoventral cirri. The oral primordium of the opisthe develops apokinetally in mid-body between the marginal rows (Fig. 33) and elongates to a long streak extending to the proter's frontal area (Figs. 35, 36). Next, the streak splits (Figs. 37–39): the anterior portion fuses with the frontoventral anlagen of the proter, the left half of the posterior portion differentiates adoral membranelles, while the right half forms four streaks which organize the opisthe's frontoventral cirri. Thus, the oral apparatus and the frontoventral ciliature of the opisthe originate de novo, i.e. without any participation of parental cirri. In the opisthe, anlage 1 generates the undulating membranes and the first (left) frontal cirrus; anlage 2 the second frontal cirrus and, possibly, the buccal cirrus; anlage 3 the third frontal cirrus and 1–5 cirri below (in fact, a short row of ventral cirri); and anlage 4 produces the ventral cirral row (Figs. 40–46). In the proter, anlagen development is very similar to that in the opisthe. The frontal cirri produce short streaks (Figs. 37, 38) but remain intact and are still recognizable in middle dividers (Fig. 43). The parental ventral cirral row does not produce anlagen but is resorbed while the new row is generated from the anlagen of the frontal cirri and the opisthe's oral primordium (Figs. 36, 38, 41, 43). Supernumerary frontal cirri usually occur in the anlagen 1–3 of the proter and opisthe (Figs. 43, 44), frequently persisting in late dividers and in young postdividers (Fig. 48). Likewise, the undulating membranes, which develop side by side (Figs. 44–46), attain their final position only after completion of cytoki-



Figs. 50–57. *Circinella filiformis* from life (Figs. 50, 54–57) and after protargol impregnation (Figs. 51–53). – Figs. 50, 54. Ventral and dorsal view of theronts. – Figs. 51, 52. Infraciliature of the ventral and dorsal side of a theront. Arrows mark micronuclei. – Fig. 53. Ventral infraciliature at higher magnification. – Fig. 55. Lateral view of a theront. The cortex contains small crystals. – Figs. 56, 57. Ventral views of an extended and a spiralized trophont. CV = contractile vacuoles. Scale bar division = 10 µm. Reproduced from [9].

nesis. The endoral membrane migrates into the buccal cavity, seemingly crossing the paroral membrane (Fig. 48).

The bipartition of the adoral zone of membranelles disappears during the early morphogenetic stages, i.e. when the cell begins to contract (Figs. 36, 38). In both the proter and the opisthe the bipartition appears only in the postdividers when the shape is remodeled, i.e. the cell elongates and the anterior end cephalizes.

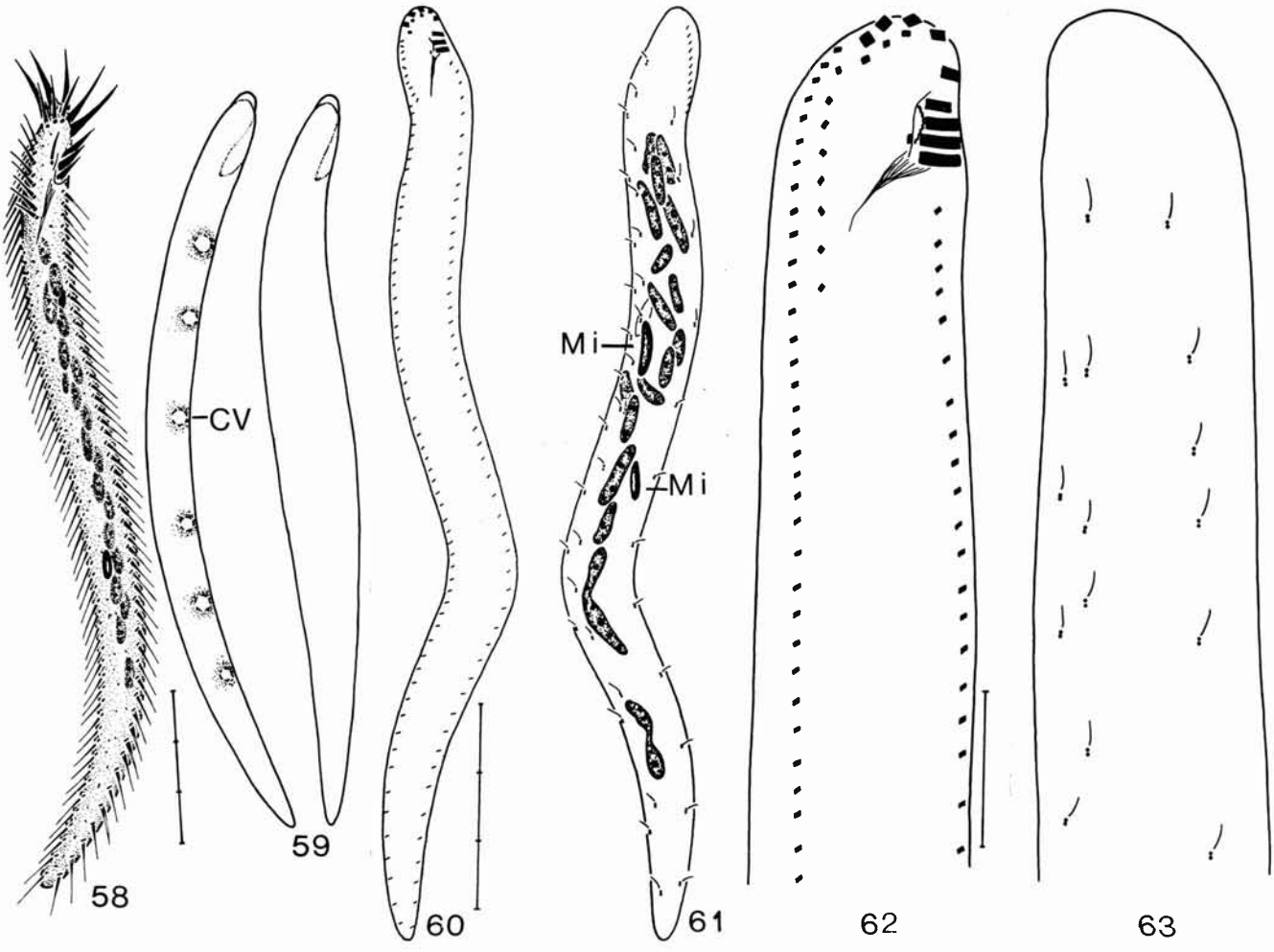
Marginal cirri and dorsal kineties. The marginal rows reproduce as is usual, i.e. an anlage originates in both proter and opisthe within the parental rows (Figs. 43–46).

The morphogenesis of the dorsal kineties could not be followed in all details. However, marginal cirri are clearly not involved, nor are caudal cirri formed. Kinety 1 probably develops de novo as in *Engelmanniella* [22]. The other kineties obviously reproduce by intrakinetal proliferation of kinetids. Both basal bodies become ciliated in developing and even in parental kinetids during reproduction (Figs. 43–49).

Discussion

Morphogenetic Comparison and Systematic Position of Circinella

The morphogenesis of *C. arenicola* shows several remarkable features: (1) dividing cells shorten markedly; (2) a considerable portion of the macronuclear nodules does not fuse but degenerates and is resorbed; (3) the oral apparatus and the frontoventral ciliature of the opisthe originate and develop apokinetally, i.e. without any participation of parental cirri; (4) the ventral row of the proter is formed by a branch of the opisthe's oral primordium because the parental row does not produce anlagen. These peculiarities are unexpected since the interphase infraciliature of *C. arenicola* is rather inconspicuous and highly reminiscent of cladotrichid and amphisiellid hypotrichs. However, amphisiellids compose the ventral row from several cirri at least two anlagen of which



Figs. 58–63. *Circinella vettersi* from life (Figs. 58, 59) and after protargol impregnation (Figs. 60–63). – Fig. 58. Ventral view of a theront. – Fig. 59. Ventral view of a theront and a trophont. – Figs. 60, 61. Infraciliature of the ventral and dorsal side of a theront. – Figs. 62, 63. Infraciliature of the anterior ventral and dorsal side at higher magnification. CV = contractile vacuole, Mi = micronuclei. Scale bar division = 10 µm. Reproduced from [2].

arrange one behind the other during and after cytokinesis, and the opisthe's oral apparatus develops from basal bodies proliferated by the parental ventral row [7]. Obviously, the morphogenetic pattern of *Circinella* is quite different and the genus cannot thus be assigned to the family Amphisiellidae.

The lack of frontoterminal (migratory), midventral, transverse, and caudal cirri as well as the apokinetal origin and development of the opisthe's oral apparatus and ventral ciliature relate *Circinella* to *Cladotricha* [4] and *Engelmanniella* [22]. However, the proter's ventral row of these genera is produced from anlagen developing within or at the proximal end of the parental ventral row. Although this is possibly an important difference, I relate *Circinella* to these genera to avoid a monotypic family. *Cladotricha, Engelmanniella, Uroleptoides, Lamtostyla*, and *Perisincirra* were united by Small & Lynn [19] to a new family, Cladotrichidae. The diagnosis provided is rather meagre "frontal file, on right, rarely extends past midbody; at least 1 left and 1 right marginal files", but matches *Circinella* which is thus provisionally assigned to this family.

A distinct shortening of the body during divisional morphogenesis, as found in *Circinella*, has not yet been reported in other hypotrichs. It might be related to the long and narrow body. Likewise, a resorption of macronuclear nodules was unknown in hypotrichs, but the process found in *Circinella* resembles the chromatin extrusion observed in various other ciliate groups [18].

The bipartition of the adoral zone of membranelles occurs only in postdividers, indicating that this speciality is a young evolutionary acquisition. Analogous processes are known from the oral structures of several oxytrichid hypotrichs (e.g., *Cyrtohymena, Notohymena*).

Comparison of Circinella with Related Genera

Circinella arenicola and the species combined with the genus later on are easily recognized by their long, filiform body. The interphase infraciliature, however, is rather similar to some other genera of the Cladotrichidae. A detailed comparison is thus appropriate.

Circinella differs from *Cladotricha* by the lack of a second row of right marginal cirri. The ventral cirral row of the proter originates from anlagen produced within the parental row in *Cladotricha* [4].

Circinella differs from *Engelmanniella* by the lack of parental and grandparental cirral rows. The ventral cirral row of the proter originates from anlagen produced at the proximal end of the parental row in *Engelmanniella* [22].

Circinella differs from *Hemisincirra* and *Perisincirra* by the length of the ventral row, which usually does not extend beyond the peristomial vertex in these genera, whose taxonomy and systematic position are rather uncertain [10]. The cirri composing the short ventral row are usually slightly disordered, often causing a midventral-like pattern; those of *Circinella* are very regularly spaced and arranged (Figs. 10, 17, 27, 30). The ventral cirral row of the proter of *Hemisincirra* originates from anlagen produced at the proximal end of the parental row [Hemberger 1982, thesis Univ. Bonn]. At least two *Perisincirra/Hemisincirra* species have the interphase characteristics of *Circinella* and should thus be combined with this genus: *C. filiformis* (Foissner, 1982) nov. comb. (basionym: *Perisincirra filiformis*) and *C. vettersi* (Berger & Foissner, 1989) nov. comb. (basionym: *Hemisincirra vettersi*).

Circinella differs from *Lamtostyla* by the lack of transverse cirri [1]. The morphogenesis in this genus is not known, because *Lamtostyla perisincirra* has been transferred to the genus *Amphisiella* [7]. *Uroleptoides* is a junior synonym of *Amphisiella* [13].

Circinella differs from *Orthoamphisiella*, a genus of unknown family affinity, by having fewer rows of ventral cirri, the rightmost of which originates from anlagen produced within the parental row [8].

Comparison of Circinella arenicola with Related Species

There is no species in the literature which possesses the characteristics of *Circinella arenicola*, especially the head-like broadening (cephalization) of the anterior body portion bearing the oral apparatus. This character also separates *C. arenicola* from the species combined with *Circinella* above.

Key to Circinella Species

Numbers are averages from at least 10 protargol impregnated specimens from natural populations (Table 1).

1. Length in vivo ≤ 250 µm. Anterior end slightly tapered 2
– Length in vivo > 250 µm. Anterior end broadened head-like. 18 adoral membranelles and 24 cirri in ventral row. 78 macronuclear nodules distributed throughout cell. 3 dorsal kineties . . . *C. arenicola* (Figs. 1–32, Table 1)
2. Length in vivo 150–250 µm. 10 adoral membranelles and 8 cirri in ventral row. Macronucleus moniliform, consists of 16 nodules. 1 dorsal kinety. *C. filiformis* (Figs. 50–57, Table 1)
– Length in vivo about 150 µm. 8 adoral membranelles and 8 cirri in ventral row. 27 macronuclear nodules distributed throughout cell. 3 dorsal kineties . . . . . *C. vettersi* (Figs. 58–63, Table 1)

Convergent Evolution in Soil and Marine Sand Ciliates

Cephalized ciliates, especially hypotrichs, are known from marine sands only [12, 21]. *Circinella arenicola* is the first distinctly cephalized hypotrich described from a non-marine biotope. However, cephalization in *C. arenicola* and marine sand hypotrichs is different: that of *Circinella* is produced by a broadening of the anterior end, whereas marine interstitial hypotrichs attenuate the anterior portion. This indicates different environmental or functional constraints, although there can hardly be any doubt that the sand environment favours cephalization in both the inland and marine sand biotopes.

The adaptive advantage of the cephalization is rather obscure. As concerns *Circinella*, it can be speculated that the broadening of the anterior end enlarges the oral area without relinquishing the advantages of a narrow body in a sand biotope.

Acknowledgements

I would like to thank Dr. Eva Herzog, Andreas Zankl, and Maria Waldhör for technical assistance, and Mag. Eric Strobl for improving the English.

References

1 Berger H. and Foissner W. (1988): Revision of *Lamtostyla* Buitkamp, 1977 and description of *Territricha* nov. gen. (Ciliophora: Hypotrichida). Zool. Anz., *220*, 113–134.
2 Berger H. and Foissner W. (1989): Morphology and biometry of some soil hypotrichs (Protozoa, Ciliophora) from Europe and Japan. Bull. Br. Mus. nat. Hist. (Zool.), *55*, 19–46.
3 Blatterer H. und Foissner W. (1988): Beitrag zur terricolen Ciliatenfauna (Protozoa, Ciliophora) Australiens. Stapfia (Linz), *17*, 1–84.
4 Borror A.C. and Evans F.R. (1979): *Cladotricha* and phylogeny in the suborder Stichotrichina (Ciliophora, Hypotrichida). J. Protozool., *26*, 51–55.
5 Brodsky A.L. and Yankowskaya A. (1929): Contribution for the study of soil-fauna in Central Asia. Part II. Soil-protofauna in the desert Kara-Kum. Acta Univ. Asiae médiae, *6*, 1–36 (in Russian with English summary).
6 Corliss J.O. (1979): The ciliated protozoa. Characterization, classification and guide to the literature. 2. ed. Pergamon Press, Oxford and Frankfurt.
7 Eigner P. and Foissner W. (1993a): A comparative study on divisional morphogenesis of amphisiellid hypotrichs (Ciliophora). J. Euk. Microbiol. (in press).
8 Eigner P. and Foissner W. (1993b): Divisional morphogenesis in *Orthoamphisiella stramenticola* Eigner & Foissner, 1991 and *O. grelli* nov. spec. (Ciliophora, Hypotrichida). Arch. Protistenk., *143*, 337–345.
9 Foissner W. (1982): Ökologie und Taxonomie der Hypotrichida (Protozoa: Ciliophora) einiger österreichischer Böden. Arch. Protistenk., *126*, 19–143.
10 Foissner W. (1984): Infraciliatur, Silberliniensystem und Biometrie einiger neuer und wenig bekannter terrestrischer, limnischer und mariner Ciliaten (Protozoa: Ciliophora) aus den Klassen Kinetofragminophora, Colpodea und Polyhymenophora. Stapfia (Linz), *12*, 1–165.
11 Foissner W. (1987a): Neue und wenig bekannte hypotriche und colpodide Ciliaten (Protozoa: Ciliophora) aus Böden und Moosen. Zool. Beitr. (N. F.), *31*, 187–282.
12 Foissner W. (1987b): Soil protozoa: fundamental problems, ecological significance, adaptations in ciliates and testaceans, bioindicators, and guide to the literature. Progr. Protistol., *2*, 69–212.
13 Foissner W. (1988): Gemeinsame Arten in der terricolen Ciliatenfauna (Protozoa: Ciliophora) von Australien und Afrika. Stapfia (Linz), *17*, 85–133.
14 Foissner W. (1989): Morphologie und Infraciliatur einiger neuer und wenig bekannter terrestrischer und limnischer Ciliaten (Protozoa, Ciliophora). Sber. Akad. Wiss. Wien, *196*, 173–247.
15 Foissner W. (1991): Basic light and scanning electron microscopic methods for taxonomic studies of ciliated protozoa. Europ. J. Protistol., *27*, 313–330.
16 FoissnerW. (1993): Colpodea (Ciliophora). G. Fischer, Stuttgart.
17 Hemberger H. (1985): Neue Gattungen und Arten hypotricher Ciliaten. Arch. Protistenk., *130*, 397–417.
18 Raikov I.B. (1982): The protozoan nucleus. Morphology and evolution. Cell Biol. Monogr., 9, XV + 474 pp.
19 Small E.B. and Lynn D.H. (1985): Phylum Ciliophora. In: Lee J.J., Hutner S.H. and Bovee E.C. (eds.): Illustrated guide to the protozoa, pp. 393–575. Society of Protozoologists, Allen Press, Lawrence, Kansas.
20 Varga L. (1936): Études sur la faune des protozoaires de quelques sols du Sahara et des hauts plateaux Algeriens. Annls. Inst. Pasteur, *56*, 101–123.
21 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.
22 Wirnsberger-Aescht E., Foissner W. and Foissner I. (1989): Morphogenesis and ultrastructure of the soil ciliate *Engelmanniella mobilis* (Ciliophora, Hypotrichida). Europ. J. Protistol., *24*, 354–368.

Key words: Hypotrichida – *Circinella* nov. gen. – *Circinella arenicola* nov. spec. – Morphogenesis – Cladotrichidae – Sand dunes

Wilhelm Foissner, Universität Salzburg, Institut für Zoologie, Hellbrunnerstrasse 34, A-5020 Salzburg, Austria