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A Redescription of *Remanella multinucleata* (Kahl, 1933) nov. gen., nov. comb. (Ciliophora, Karyorelictea), Emphasizing the Infraciliature and Extrusomes

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

SUMMARY

The morphology, infraciliature, and extrusomes of *Remanella multinucleata* (Kahl, 1933) nov. comb. were studied in live cells, in protargol impregnated specimens, and with the scanning electron microscope. The entire somatic and oral infraciliature consists of dikinetids which have both basal bodies ciliated or only the anterior or posterior ones, depending on the region of the cell. The right side is densely ciliated. Its most remarkable specialization is a kinety which extends on the dorsolateral margin from mid-body to the tail, where the kinetids become condensed and associated with conspicuous fibres originating from the ciliated anterior basal bodies. The left side seemingly has two ciliary rows extending along the cell margins. However, detailed analysis showed that these rows are very likely a single kinety curving around the cell. The oral infraciliature of *Remanella* is very similar to that of *Loxodes* spp., i.e. consists of four highly specialized and specifically arranged kineties, whose structure is described in detail. Previous investigations could not determine whether or how the nematocyst-like extrusomes of *Remanella* are extruded. The present study shows that they are discharged, thereby assuming a unique, drumstick-like shape because the roundish extrusome capsule remains attached to the despiralized filament. The data emphasize the close relationship between *Remanella* and *Loxodes*, earlier proposed by Kahl, and suggest that they emerged from a common ancestor which looked similar to a present day *Loxodes*. *Remanella* Kahl, 1933 is a nomen nudum because Kahl, when founding the genus with five new species and one new variety, failed to designate any as type. I thus reinstall *Remanella* nov. gen. for the species assigned to Kahl's invalid taxon and fix *R. multinucleata* as type species. Correct names, dates, and authorships are provided for all species described.

Introduction

Species of the karyorelictid ciliate genus *Remanella* are common in marine interstitial and intertidal environments [10, 17, 26, 27]. Ultrastructural studies [37, 40] on the somatic cortical organization confirmed the close relationship with *Loxodes*, the sole freshwater karyorelictean genus, proposed by Kahl [26], the founder of the genus. However, a detailed study of the somatic and oral ciliary pattern of *Remanella* was never performed, possibly because it was difficult to reveal with the preparation methods available. Published figures are highly schematic and hardly show the details required for a proper comparison with *Loxodes* and related genera [1, 3, 10–12]. Using a new fixative, invented by Jean Dragesco, and Wilbert's protargol technique, I got some excellent preparations showing many previously unrecognized details, which are reported in this study, together with some speculations on evolution in loxodid ciliates. Furthermore, a detailed redescription of *R. multinucleata* is provided because previous studies do not meet the present standard of ciliate alpha-taxonomy. Last not least, extensive nomenclatural changes are required because Kahl, when

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founding the genus with five new species and a new variety, unfortunately failed to designate any as type. Thus, the genus is illegitimate according to the International Code of Zoological Nomenclature [25].

Material and Methods, Type specimens, Terminology

Remanella multinucleata occurred in considerable number in the mesopsammon of the French Atlantic coast at Roscoff. Samples were collected and treated exactly as described by Fauré-Fremiet [14], i.e. the specimens were detached from the sand grains by adding about 5 ml of a 12% $MgCl_2$ solution to about 20 ml sand and sea water. The mixture was then gently rotated in a petri dish so that the sand collected in the center and the ciliates could be picked up individually with a capillary pipette from the clear supernatant.

Cells were studied in vivo using a high-power oil immersion objective and differential interference contrast [19]. The infraciliature was revealed by protargol impregnation [19; protocol 2, Wilbert's method], using a special fixative invented by Jean Dragesco (pers. comm.): 5 ml glutaraldehyde (25%), 5 ml saturated, aqueous mercuric chloride, 3 ml aqueous osmium tetroxide (2%), and 1 ml glacial acetic acid are mixed just before use. Specimens are fixed for 15–30 min. and washed three times in distilled water. Preparation for scanning electron microscopy (SEM) was performed as described by Foissner [19], using the fixative mentioned above.

Counts and measurements on silvered specimens were performed at a magnification of X 1000. In vivo measurements were conducted at a magnification of X 40–1000. Although these provide only rough estimates, it is worth giving such data as specimens usually shrink in preparations or contract during fixation. Standard deviation and coefficient of variation were calculated according to statistics textbooks. Drawings of live specimens are based on free-hand sketches and micrographs, those of impregnated cells were made with a camera lucida.

No type slides of *R. multinucleata* are mentioned in the literature. Thus, I have deposited two neotype slides with specimens prepared as described in the Oberösterreichische Landesmuseum in Linz (LI), Austria. Relevant specimens are marked by a black ink circle on the cover glass.

Terminology is according to Corliss [6] and Foissner & Rieder [21], with slight modifications, and strictly descriptive because ontogenetic data are incomplete and conflicting [28, 30, 42].

All figures are oriented, if not stated otherwise, with the anterior end of the organism directed to top of page.

Results

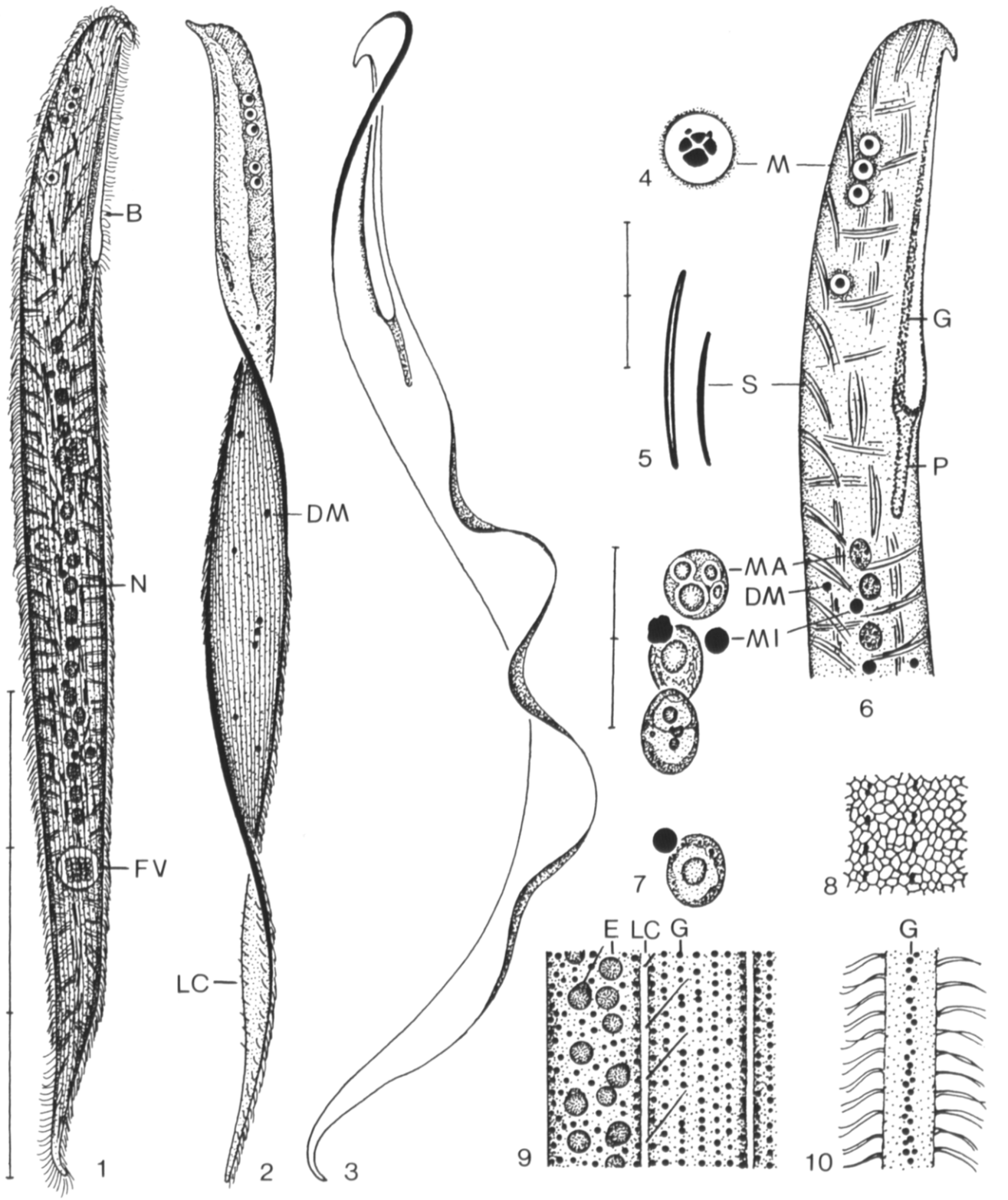
Remanella Kahl, 1933 is Invalid under Article 13b of the ICZN [25]

Kahl [26] founded *Remanella* with five new species and one new variety, none of which, unfortunately, he designated as type. The genus is thus invalid according to the ICZN. This was overlooked not only by Kahl [27] but also by the first reviser of the genus [10] and later monographers [5, 6]. I thus declare *Remanella* Kahl, 1933 to be a nomen nudum, but reinstall *Remanella* as new genus to avoid an inflation of names. Furthermore, I fix *R. multinucleata* (Kahl, 1933) nov. comb. as type species of the new genus, for which an improved diagnosis is provided in the discussion.

All *Remanella* species described need to be combined with the new genus. Note that Carey [5], without giving any reason, quotes Dragesco [10] as combining author of Kahl's [26] and Dragesco's [8, 9] species although he accepts Kahl [26] as founder of the genus and Dragesco [10] did not recognize Kahl's [26] mistake. Carey's [5] species citation is difficult to understand; possibly, he simply did not know that international rules exist. There are also several other nomenclatural mistakes. Thus, I decided to revise the nomenclature of the whole genus for the benefit of stability, the present paper, and future workers.

The genus name is derived from Adolf Remane (1898–1976), famous German zoologist and one of the discoverers of the marine interstitial fauna. *Remanella* has feminine gender according to article 30b of the ICZN [25].

1. *Remanella brunnea* (Kahl, 1933) nov. comb. (published by Kahl [26, 27] without figure; well redescribed in [12]);
2. *Remanella caudata* (Dragesco, 1954b) nov. comb. (misdated by Carey [5] as 1953 although the journal clearly states "paru en décember 1954");
3. *Remanella dragescoi* (Agamaliev, 1966) nov. comb.;
4. *Remanella faurei* (Dragesco, 1954a) nov. comb.;
5. *Remanella gigas* (Dragesco, 1954a) nov. comb.;
6. *Remanella granulosa* (Kahl, 1933) nov. comb.;
7. *Remanella levii* (Dragesco, 1960) nov. comb.;
8. *Remanella margaritifera* (Kahl, 1933) nov. comb.;
9. *Remanella microstoma* (Dragesco, 1954b) nov. comb. (misdated by Carey [5]; see above);
10. *Remanella minuta* (Dragesco, 1954a) nov. comb.;
11. *Remanella multicorpusculata* (Vacelet, 1961) nov. comb.;
12. *Remanella multinucleata* (Kahl, 1933), type of genus (see above);
13. *Remanella obtusa* (Fauré-Fremiet, 1951) nov. comb. (very likely does not belong to this genus; see discussion);
14. *Remanella rugosa* (Kahl, 1933) nov. comb.;
15. *Remanella rugosa* var. *unicorpusculata* (Kahl, 1933) nov. comb. (established as "species nova" by Dragesco [12] due to misinterpretation of article 45g of the ICZN);
16. *Remanella swedmarki* (Dragesco, 1954a) nov. comb.;
17. *Remanella trichocysta* (Dragesco, 1954a) nov. comb. (nom. em.; the original spelling "trichocystus" cannot be a Greek or latinized noun in apposition, as Dragesco possibly had in mind, because the noun is "trichocystis". Thus, the species name has to be treated as latinized adjective and coordinated with the gender of genus; article 31 of the ICZN);
18. *Remanella unirugosa* (Hartwig, 1973) nov. comb.



Figs. 1–10. *Remanella multinucleata* from life (Figs. 1–6, 9, 10) and after protargol (Fig. 7) and wet silver nitrate impregnation (Fig. 8). – Fig. 1. Right lateral view of typical specimen. – Figs. 2, 3. Spiralized and undulating specimens. – Figs. 4–7. Internal structures. – Fig. 8. Silverline system at ventrolateral margin. – Figs. 9, 10. Surface views of left and right side. B = buccal overture, DM = developing Müller vesicle, E = extrusomes, FV = food vacuole, G = cortical pigment granules, LC = left lateral ciliary row, M = Müller vesicle, MA = macronuclei, MI = micronuclei, N = nuclear chain, P = pharyngeal tube, S = spicules. Scale bar division = 100 μm (Figs. 1–3) and 10 μm (Figs. 4, 5, 7).

Redescription of Remanella multinucleata

Remanella multinucleata is a large and slender ciliate with a complicated and beautiful morphology. Accordingly, a reasonable general view of its ciliary pattern (infraciliature) is practically impossible (Figs. 1, 2), and even the figures from certain parts of the ciliate had to be greatly reduced to suffice the journal's space limit. Thus, not all details described could be figured.

Morphometric data shown in Tables 1 and 2 are repeated in this section only as needed for clarity. As usual with large ciliates, many characters are highly variable, i. e. have coefficients of variation greater than 15%.

The interpretation of cortical fine structures is partially based on previous transmission electron microscope studies [34, 37, 40].

General morphology. Live specimens of *R. multinucleata* are about 500–1000 × 40–80 μm in size and extremely flattened, i.e. less than 10 μm thick (Figs. 3, 15, 19). The shape is thus more slender than figured by most previous authors. The species is highly flexible, slightly contractile and often spirally contorted (Figs. 2, 12, 19). The anterior end is evenly rounded and has a snout-like ventral process usually directed posteriorly (Figs. 1, 6, 14), rarely anteriorly (Figs. 2, 23, 30). The posterior region is gradually narrowed and elongated tail-like with the end directed ventrally, as mentioned also by Kahl [26, 27]. The arrangement of the ciliary rows shows that the caudalisation is due to a narrowing of the ventral side (Figs. 35, 40). The right side is densely ciliated, the left bears a single kinety curving around the cell and several non-ciliated furrows which lack cortical granules (Figs. 1, 2, 9, 13, 19). The oral apparatus is located in the anterior region of the cell and, although very narrow, easily recognized because its margins are studded with ochre-coloured granules (Figs. 1, 6, 11, 14–16, 19).

Remanella multinucleata has many macronuclei forming a chain in the central third of the cell (Fig. 1). Micronuclei are scattered near and between the macronuclei. Morphometric (Tables 1, 2) and morphological data (Figs. 7, 18) agree well with the detailed investigations by Raikov [35, 38] to which the reader is referred. No contractile vacuole was found.

Remanella multinucleata appears yellowish at low magnification (X 50) due to many rows of ochre-coloured, highly refractile cortical granules. As first noticed by Dragesco [10], two size classes of pigment granules are distinguishable, viz. ones having a diameter of about 0.3–0.5 μm, and others with a size of about 1 μm. Both types are intermixed without any regularity and are possibly developmental stages of a single sort, as indicated by transmission electron microscopic investigations [37]. On the right side, the granules form distinct stripes between the ciliary rows (Figs. 10, 13), on the non-ciliated left side they are arranged in broad ribbons, interrupted by narrow stripes devoid of granules, corresponding to the furrows recognizable in the scanning electron microscope (Figs. 9, 13, 19, 42). The margins of the buccal cavity and the pharyngeal tube are studded with these pigment granules and thus appear conspicuously dark under bright field illumination (Figs. 1, 2, 6, 11, 14–16); frequently, the oral granules are impregnated with protargol, even if the somatic granules, which look the same in the light microscope, are not. This indicates that they have a slightly different chemical composition.

Like *Loxodes* [18, 21], *Remanella* has special organelles, the Müller vesicles, for gravity reception. The Müller vesicles of *R. multinucleata* are restricted to the anterior dorsal margin of the left side, where the cell is slightly thickened and the cytoplasm appears more gelatinous. The number and arrangement of the Müller vesicles are highly variable, but postoral vesicles have never been observed (Tables 1, 2, Figs. 2, 6, 11, 12, 14, 16). However, many immature Müller bodies, i.e. the globular mineral content of the vesicles are scattered through the organism (Figs. 2, 11, 17). The vesicles have a diameter of about 10 μm, the globular mineral content measures about 5 μm and is composed of 2–5 large and some small granules (Figs. 4, 14, 43). The Müller vesicles are associated with the left lateral kinety ([2] and section on left lateral somatic infraciliature), as in *Loxodes* [18, 21].

Remanella species have many spicules forming a unique cytoskeleton. My data matches previous investigations [10, 16, 37] to which the reader is referred. Morphometric analysis showed that two size classes (developmental stages?) can be distinguished (Table 1, Figs. 43, 45). The spicules rarely impregnate with protargol (Fig. 44). X-ray microanalysis showed that they do not contain any inorganic cations, as previously supposed [10, 16, 37], but are purely organic [41].

Remanella multinucleata feeds on various food items, especially on diatoms [17] and coccal cyanobacteria-plates (Fig. 1). It glides very elegantly between the sand grains and on the bottom of the petri dish, sometimes undulating beautifully (Fig. 3).

Right lateral somatic infraciliature. The right surface of *R. multinucleata* is densely ciliated. The cilia are about 12 μm long and arranged in slightly oblique rows which extend in distinct cortical furrows (Figs. 1, 13). The ciliary rows are gradually shortened anteriorly at the postoral dorsal margin of the cell and especially posteriorly at the ventral margin, where the body narrows to the tail. In the oral region the kineties encroach upon the left side dorsally and anteriorly (Figs. 1, 14, 19, 23, 24, 30, 31).

The entire infraciliature consists of dikinetids which, however, have a highly specialized ciliation. The dikinetids are slightly obliquely oriented, i.e. rotated about 10–20° counter-clockwise to the kinety axis, and are associated with prominent, overlapping postciliary microtubule ribbons [37, 40], which form a thick fibre right of each ciliary row (Fig. 35). Both basal bodies of the dikinetids are ciliated in the main portion of the cell. The posterior cilium is lacking in 3–20 dikinetids

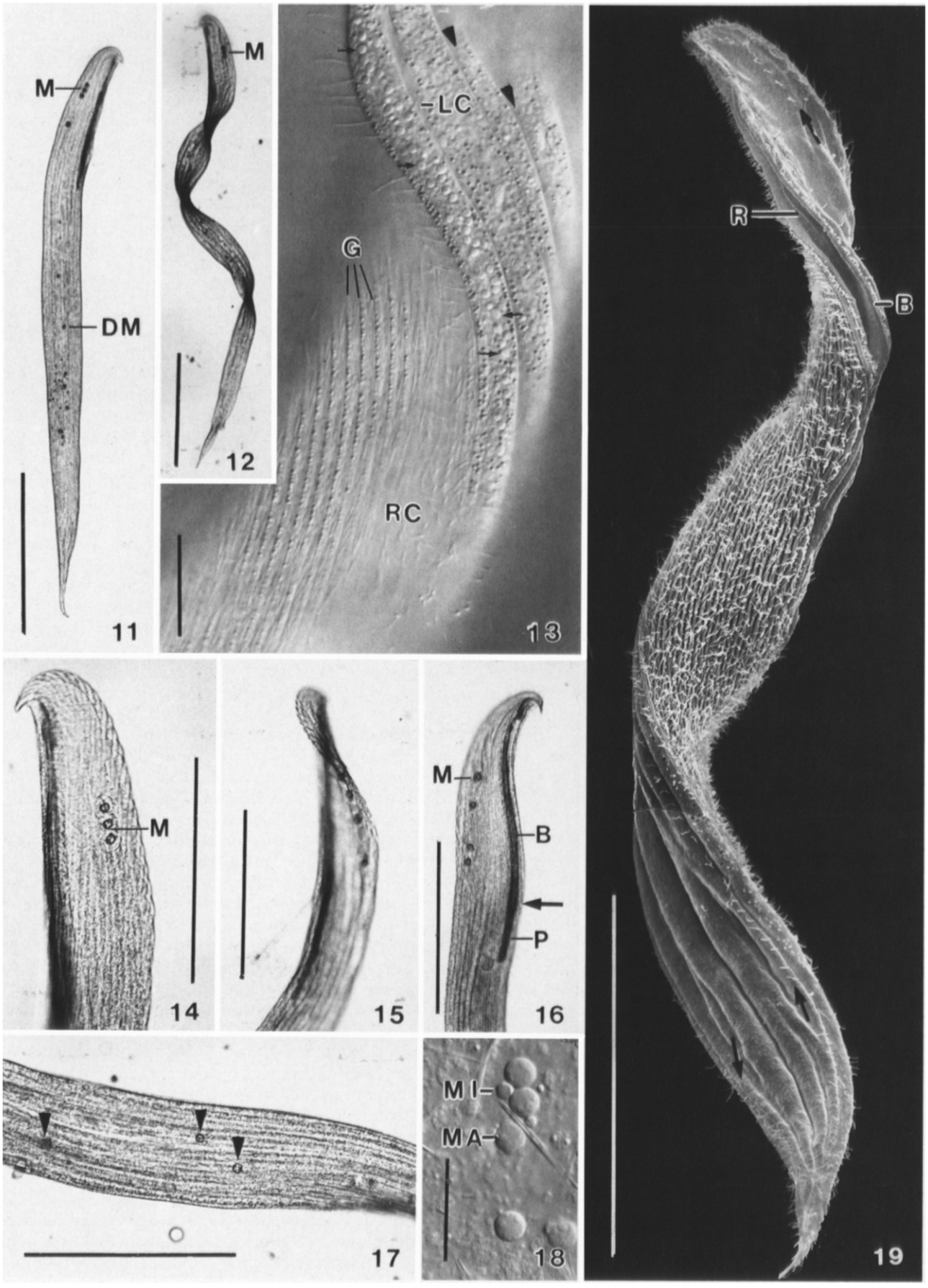

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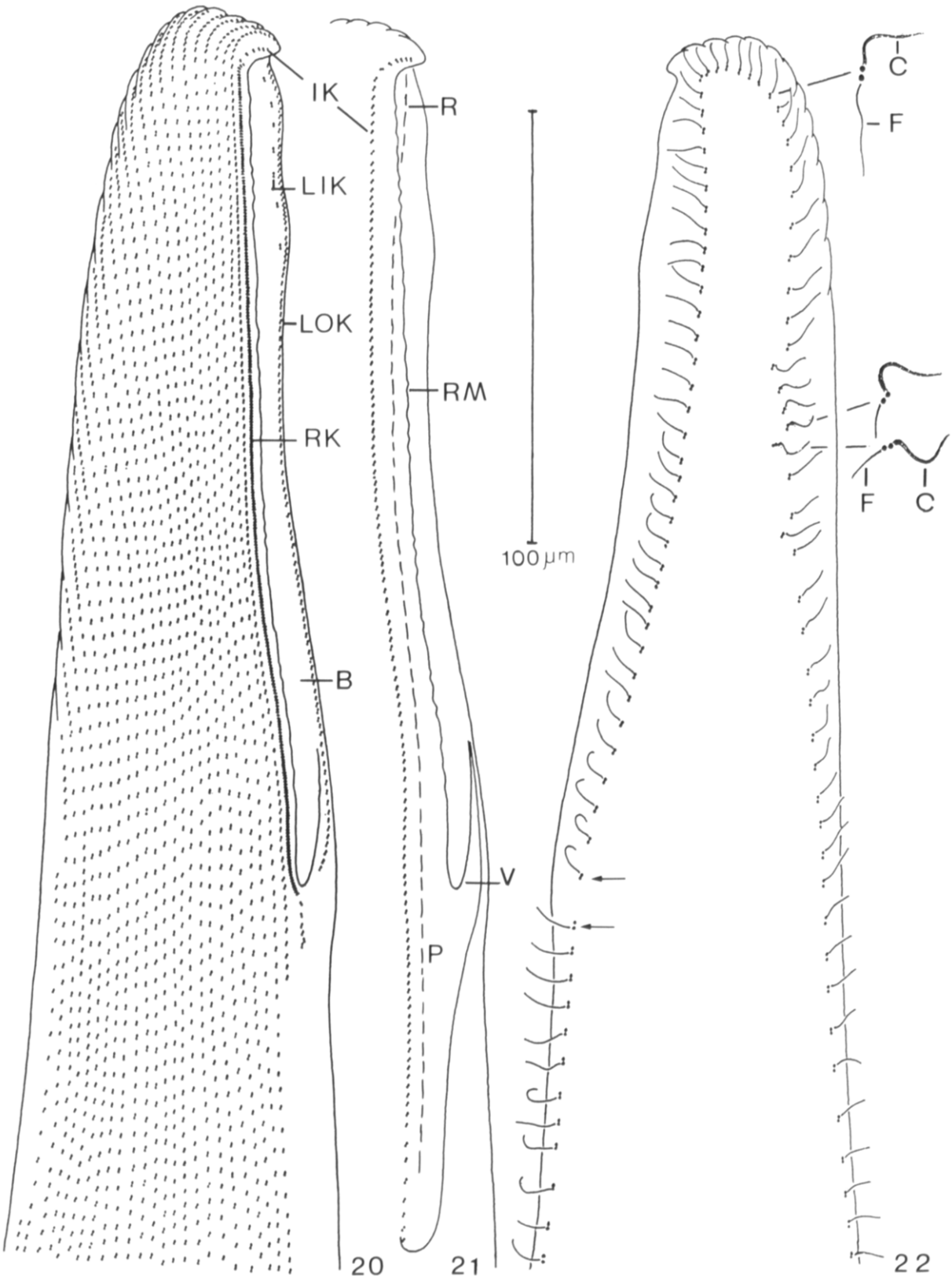
Table 1. Morphometric data from *Remanella multinucleata*

Character[1]	$\bar{x}$	M	SD	$SD_{\bar{x}}$	CV	Min	Max	n
Body, length	705.3	750.0	162.9	39.5	23.1	450	1000	17
Anterior end to proximal vertex of buccal overture, distance	164.1	165.0	34.8	2.7	21.2	100	230	17
Anterior end to proximal end of pharyngeal tube, distance	219.6	220.0	39.0	9.4	17.7	164	300	17
Anterior end to first macronucleus, distance	219.9	216.0	37.2	9.0	16.9	175	320	17
Body, width at proximal vertex of buccal overture	57.8	50.0	26.6	6.4	45.9	34	150	17
Body, maximum postoral width	64.6	60.0	17.6	4.3	27.3	37	100	17
Nuclear chain, length	212.8	190.0	69.2	16.8	32.5	136	360	17
Macronucleus, length	10.1	10.0	1.7	0.4	17.3	6	13	17
Macronucleus, width	7.8	8.0	1.2	0.3	15.6	6	11	17
Micronucleus, length	4.7	5.0	0.7	0.2	14.1	4	6	17
Micronucleus, width	4.5	4.5	0.7	0.2	14.9	3	6	17
Macronuclei, number	16.8	16.0	4.8	1.2	28.6	7	24	17
Micronuclei, number	5.6	6.0	1.9	0.5	34.6	3	9	17
Somatic kineties, number in mid-body	22.5	23.0	3.0	0.7	13.3	18	27	17
Left outer buccal kinety, number of dikinetids	92.6	90.0	23.9	5.8	25.8	43	140	17
Left inner buccal kinety, number of dikinetids	5.7	6.0	2.1	0.6	36.1	3	11	12
Intrabuccal kinety, number of dikinetids	111.3	110.0	21.9	8.9	19.7	75	135	6
Müller vesicles, number (in vivo)	3.1	3.0	1.1	0.3	36.6	1	4	11
Long skeleton needles, length (in vivo)	24.1	24.5	1.1	0.3	4.6	22	25	10
Short skeleton needles, length (in vivo)	15.7	16.0	0.8	0.2	5.0	14	17	11

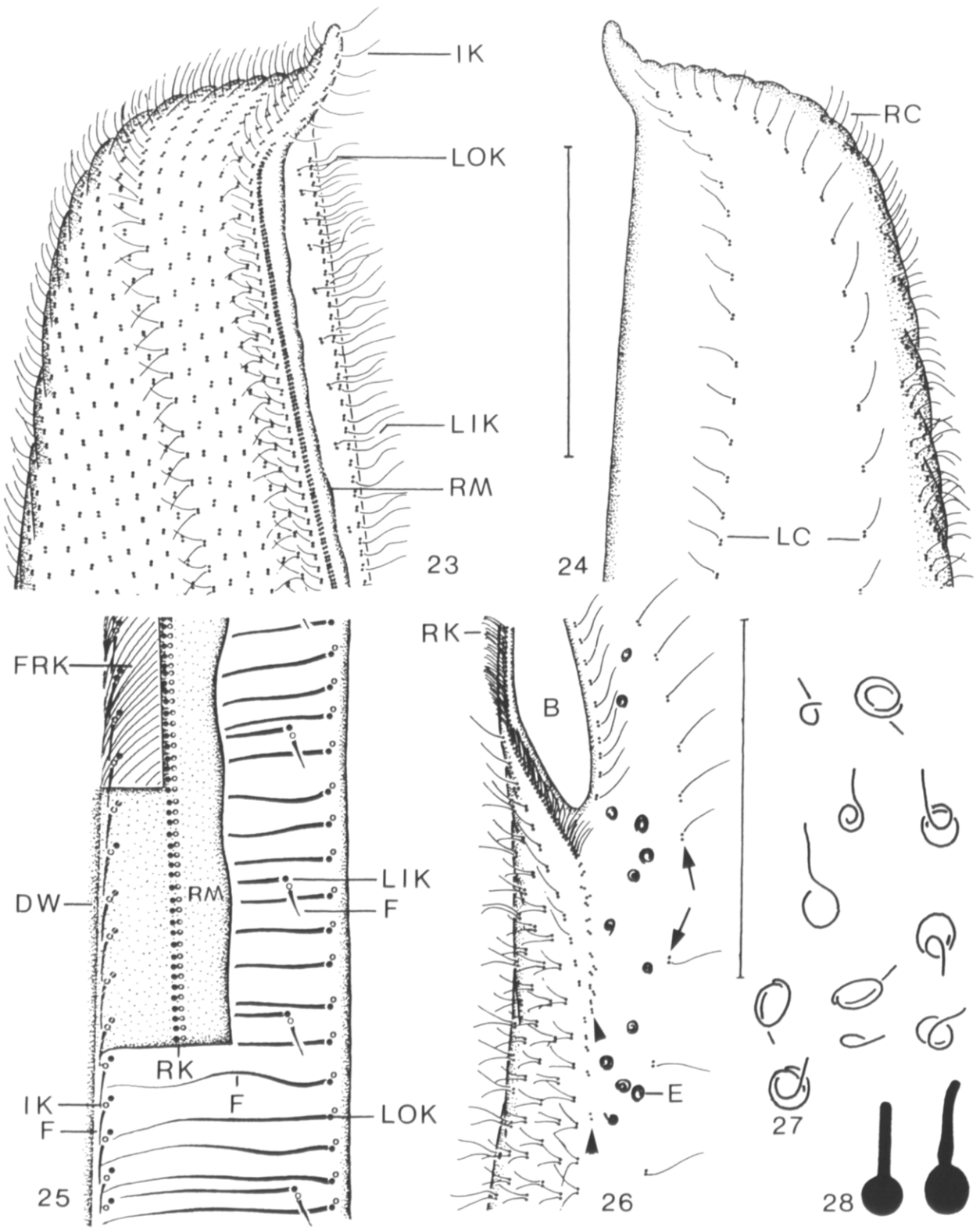
[1]Data are based, if not stated otherwise, on the investigation of protargol impregnated and mounted specimens from field. Measurements in μm. CV = coefficient of variation in %; M = median; Max = maximum; Min = minimum; n = number of specimens investigated; SD = standard deviation; $SD_{\bar{x}}$ =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

at both ends of all ciliary rows and in all dikinetids of the first "true" somatic kinety, which extends along the right buccal kinety and ends closely underneath the buccal overture, where the dikinetids also lose the anterior cilium, i.e. become barren (Figs, 20, 23, 24, 26, 29–31, 34, 35, 39, 40). The most conspicuous specializations are found in the rightmost kinety, which commences in mid-body and extends to the tail-end. This ciliary row is termed "dorsolateral kinety" and only has the anterior basal bodies of the dikinetids ciliated, which are more closely spaced (condensed) in the tail region, where they become associated with conspicu-

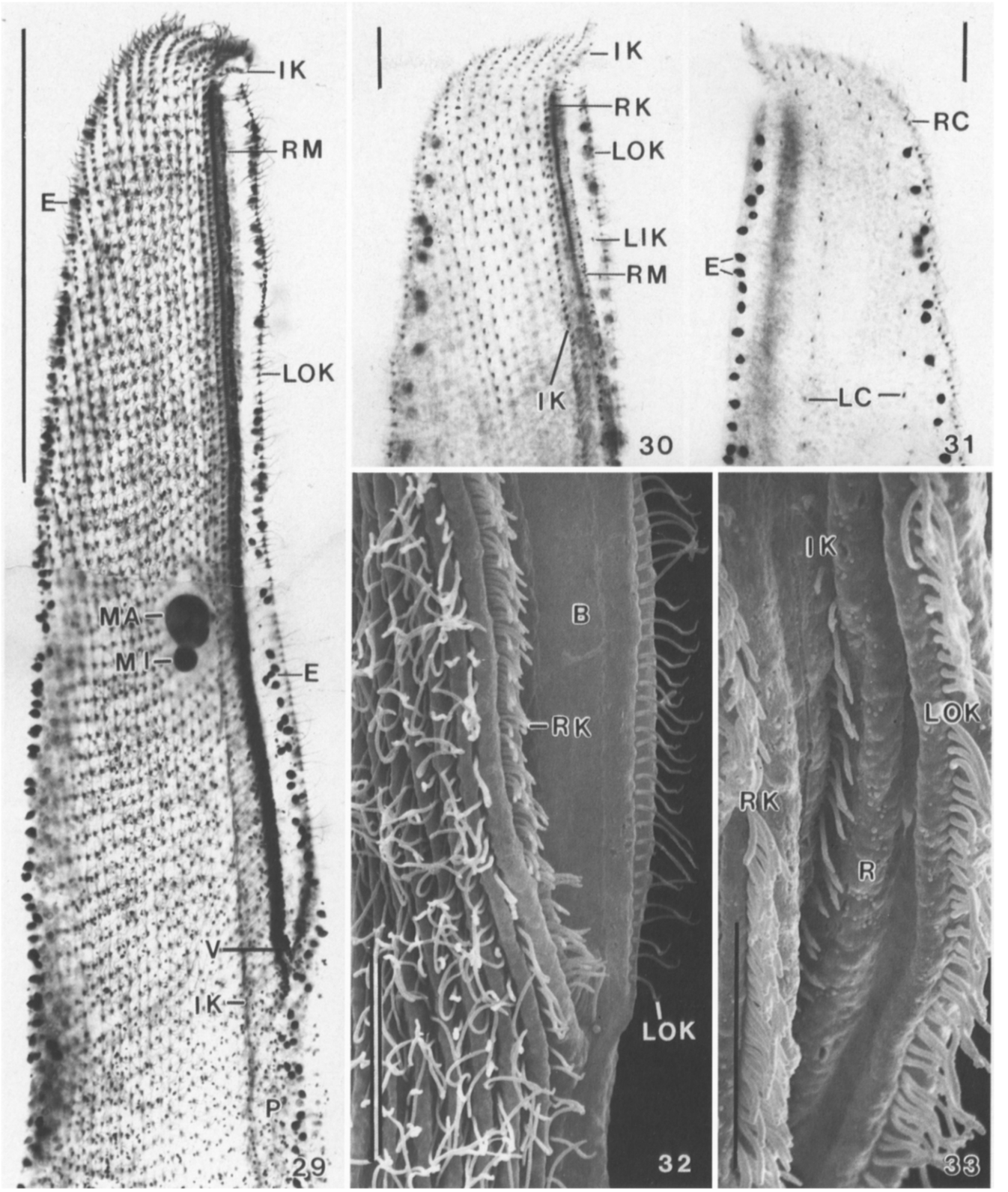
◀ Figs. 11–19. *Remanella multinucleata* from life (Figs. 11–18) and in the scanning electron microscope (Fig. 19). – Figs. 11, 12, 19. Flat and spiralized specimens. The right side is densely ciliated, the left is barren except for the marginal kinety (arrows). – Fig. 13. Mid-body region at higher magnification. The right side is densely ciliated and a ribbon of refractile, ochre-coloured cortical granules extends between each two ciliary rows. Many globular extrusomes (arrows) are in the left lateral margins of the cell. Arrowheads mark non-ciliated furrows on left side. – Figs. 14–16. Left lateral, dorsal, and right lateral views of oral area of three specimens. Note variability in number and arrangement of Müller vesicles and leaf-like flattening of cell (Fig. 15). The margins of the buccal overture and the pharyngeal tube are studded with pigment granules and thus appear black. Arrow in Fig. 16 marks proximal vertex of buccal overture. – Fig. 17. Mid-body region with developing Müller vesicles (arrowheads). – Fig. 18. Part of nuclear apparatus. B = buccal overture, DM = developing Müller vesicle, G = cortical pigment granules, LC = left lateral ciliary row, M = Müller vesicles, MA = macronuclei, MI = micronucleus, P = pharyngeal tube, R = buccal ridge, RC = right lateral ciliary rows. Bars = 200 μm (Figs. 11, 12), 100 μm (Figs. 14–17, 19), 20 μm (Figs. 13, 18).



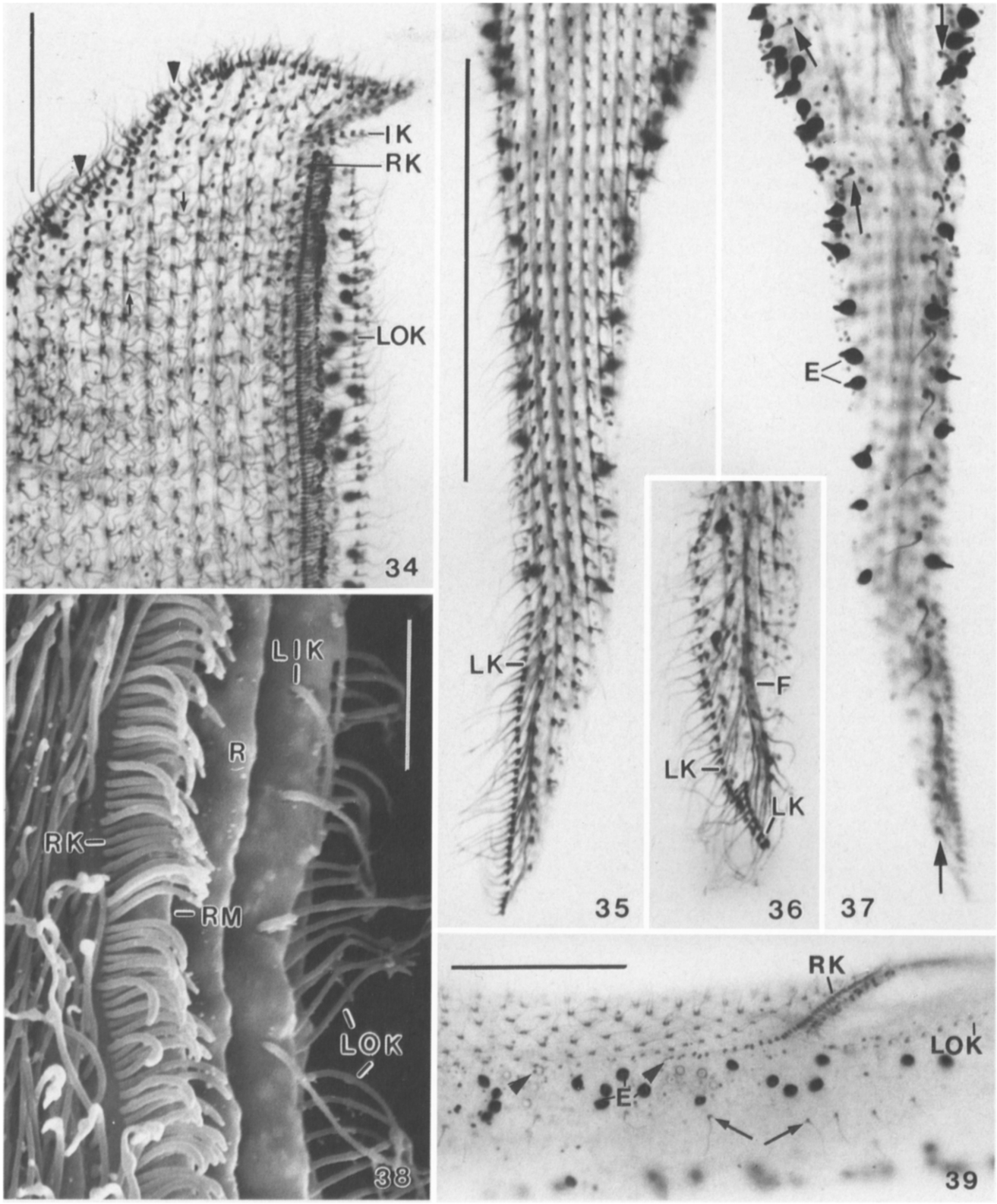
Figs. 20–22. *Remanella multinucleata*, right and left view of oral area after protargol impregnation. Fine structure of anterior left lateral dikinetids is shown in upper right corner. Arrows mark region where ciliation of dikinetids changes, i.e. the ends of the left lateral kinety meet. B = buccal overture, C = cilium, F = fibre, IK = intrabuccal kinety, LIK = left inner buccal kinety, LOK = left outer buccal kinety, P = pharyngeal tube, R = buccal ridge, RK = right buccal kinety, RM = right margin of buccal overture, V = proximal vertex of buccal overture.



Figs. 23–28. *Remanella multinucleata* after protargol impregnation (Figs. 23–27) and in the SEM (Fig. 28). – Figs. 23–26. Right lateral, left lateral, and ventral views of anterior body region. Arrows in Fig. 26 mark region where ciliation of dikinetids changes. Arrowheads mark barren dikinetids at ends of right buccal kinety and first somatic ciliary row. Full circles in Fig. 25 symbolize ciliated basal bodies, open circles non-ciliated. – Figs. 27, 28. Resting, exploding and discharged nematocysts. B = buccal overture, DW = dorsal wall of buccal cavity, E = extrusome, F = fibres, FRK = fibres originating from right buccal kinety, IK = intrabuccal kinety, LC = left lateral ciliary row, LIK = left inner buccal kinety, LOK = left outer buccal kinety, RC = right lateral ciliary rows, RK = right buccal kinety, RM = right margin of buccal overture. Bars = 40 μm.



Figs. 29–33. *Remanella multinucleata*, oral and somatic infraciliature after protargol impregnation (Figs. 29–31) and in the SEM (Figs. 32, 33). – Figs. 29, 30, 32. Right lateral views. – Fig. 31. Left lateral view of specimen shown in Fig. 30. – Fig. 33. Ventral view in mid-oral region. B = buccal overture, E = extrusomes, IK = intrabuccal kinety, LC = left lateral ciliary row, LIK = left inner buccal kinety, LOK = left outer buccal kinety, MA = macronucleus, MI = micronucleus, R = buccal ridge, RC = right lateral ciliary rows, RK = right buccal kinety, RM = right margin of buccal overture, P = pharyngeal tube, V = proximal vertex of buccal overture. Bars = 100 μm (Fig. 29) and 10 μm (Figs. 30–33).



Figs. 34–39. *Remanella multinucleata*, oral and somatic infraciliature after protargol impregnation (Figs. 34–37, 39) and in the SEM (Fig. 38). – Figs. 34, 38. Right lateral views of oral region. Arrows indicate ciliated dikinetids, arrowheads mark dikinetids with only anterior basal bodies ciliated. – Figs. 35–37. Right and left lateral views of posterior body region. Arrows mark left lateral kinety (cp. Fig. 41). – Fig. 39. Buccal vertex (anterior end of cell right). Arrows mark ends of left lateral kinety, arrowheads indicate non-ciliated tails of right buccal kinety and first somatic kinety (cp. Fig. 26). E = extrusomes, F = fibres, IK = intrabuccal kinety, LK = dorsolateral kinety, LIK = left inner buccal kinety, LOK = left outer buccal kinety, R = buccal ridge, RK = right buccal kinety, RM = right margin of buccal overture. Bars = 50 µm (Figs. 35, 37), 25 µm (Figs. 34, 39), and 5 µm (Fig. 38).

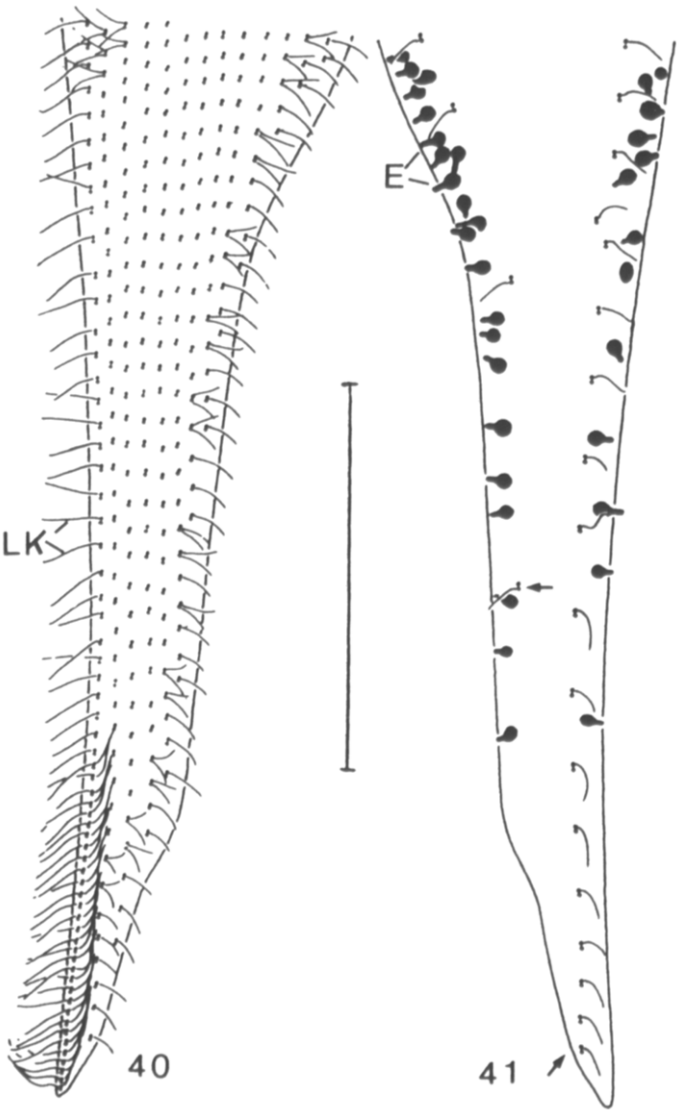
ous fibres originating from the ciliated anterior basal bodies; the fibres are about 10 µm long and extend in acute angles anteriorly forming more or less pronounced bundles (Figs. 35, 40). A second, smaller dorsolateral kinety is found in about half of the specimens (Fig. 36).

Left lateral somatic infraciliature. The left side of *R. multinucleata* is barren, except for the body margins, where seemingly two kineties composed of dikinetids extend. However, a detailed analysis indicates that these ciliary rows are very likely a single kinety curving around the cell or, alternatively, two kineties with opposed kinetids. Both ends of this kinety are near the proximal vertex of the buccal overture, frequently separate by a slightly enlarged distance between the dikinetids (Figs. 19, 22–24, 26, 31, 37, 39, 41). One end, possibly the anterior, extends along the left margin of the buccal overture to the anterior end of the cell, where it curves dorsally and backwards to the posterior end of the organism. The *anterior* basal body of the dikinetids is ciliated in this portion, whereas in the other, which extends between the posterior end and the postoral ventral margin, the *posterior* basal body of the dikinetids is ciliated. Thus, the orientation of the dikinetids appears inverted by 180° with respect to the ciliation where the two ends meet, viz. near the proximal vertex of the buccal overture (Figs. 22, 26, 39).

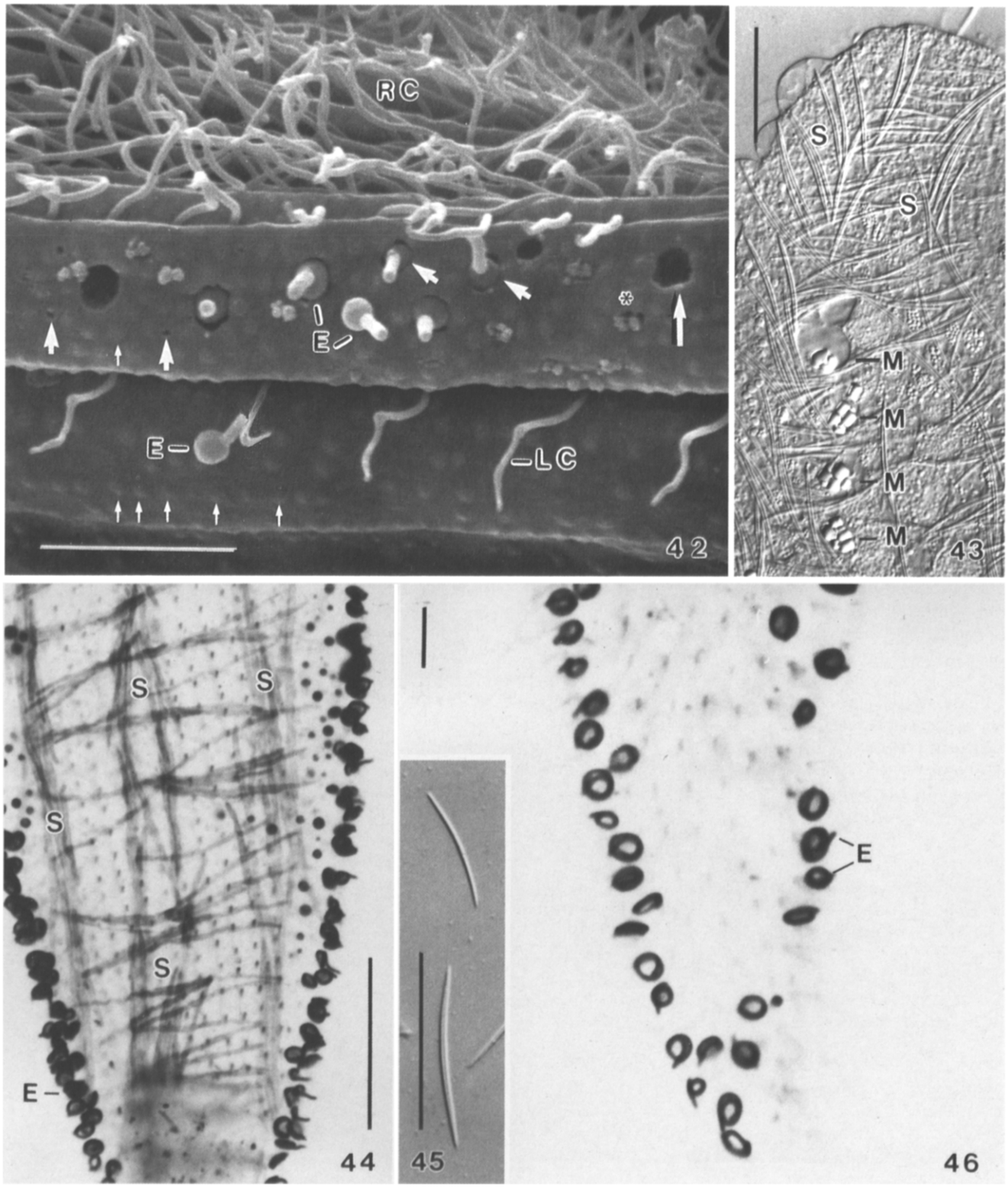
The left lateral kinety extends in a rather deep furrow along the extrusome stripe (Figs. 9, 13, 19, 31, 37, 41). Its kinetids are slightly more narrowly spaced in the oral and posterior dorsal region than in mid-body; in the posterior ventral region, where the body narrows to the tail, they are more widely spaced. The cilia have about the same length as those of the right lateral kineties, but are stiffer, and arise from deep and narrow cortical pits (Fig. 42). Usually, there are a few dikinetids out of line, i.e. displaced to the median of the cell in the anterior dorsal region (Fig. 22). These kinetids are, as in *Loxodes* [18, 21], obviously associated with the Müller vesicles, as indicated by the more obliquely extending (postciliary [18]) fibre associated with the posterior basal body (Figs. 6, 22).

Oral infraciliature. The oral apparatus of *R. multinucleata* occupies the anterior fourth to fifth of the cell. The buccal overture widens slightly to the proximal vertex, but is very narrow (about 5 µm) due to the strong flattening of the organism (Figs. 1–3, 6, 11, 16, 19, 20, 29). The buccal cavity is also comparatively small (if the intrabuccal kinety is taken as dorsal margin) and bipartitioned by a flat ridge which extends obliquely on the inner surface of the left buccal wall from the left anterior end of the cell to the dorsal wall of the pharyngeal tube (Figs. 19, 21, 33, 38). This ridge separates the intrabuccal kinety from the left inner and outer buccal kinety.

The oral infraciliature is complex and composed of four differently organized kineties (Figs. 20, 21, 23, 25, 26, 29, 30, 32, 33, 34, 38, 39). The left outer buccal kinety extends along the left margin of the buccal overture and consists of closely spaced, slightly counterclockwise rotated dikinetids having the posterior basal body ciliated. Thick, long fibres (nematodesmata according to [34]) originate from the ciliated basal bodies and extend horizontally to the dorsal wall of the buccal cavity, forming a ladder-like structure in the left buccal wall (Fig. 25).



Figs. 40, 41. *Remanella multinucleata,* right and left lateral view of posterior body portion after protargol impregnation. Arrows mark left lateral kinety whose dikinetids have the posterior (right) or anterior (left) basal body ciliated, respectively. Distinct fibres originate from the basal bodies of the condensed, posteriormost portion of the dorsolateral kinety. The dikinetids of this kinety have only the anterior basal body ciliated, like the posteriormost dikinetids of the normal somatic kineties. E = extrusomes, LK = dorsolateral kinety. Bar = 40 µm.



Figs. 42–46. *Remanella multinucleata* in the SEM (Fig. 42), from life (Figs. 43, 45), and after protargol impregnation (Figs. 44, 46). – Figs. 42, 44, 46. Arrangement and shape of extrusomes and pigment granules (short, thin arrows). Extrusomes are found exclusively along the cell margins (Fig. 44) and contain a spiralized filament (Fig. 46). Released extrusomes are drumstick-shaped (Fig. 42) and emerge through gradually extending cortical openings (short, thick arrows and asterisks). Conspicuous cavities (long, thick arrows) remain in the cortex when extrusomes have been released. – Fig. 43. Anterior dorsal region of squeezed specimen showing Müller vesicles and spicules. – Fig. 45. Long and short spicule at higher magnification. E = extrusomes, LC = left lateral ciliary row, M = Müller bodies composed of large and smoll granules, RC = right lateral ciliary rows, S = spicules. Bars = 5 μm (Figs. 42, 46) and 25 μm (Figs. 43–45).

The left inner buccal kinety extends to the right of and along the anterior quarter of the outer buccal kinety. It consists of widely spaced, slightly clockwise rotated dikinetids, the anterior basal bodies of which are ciliated and associated with a thick, long fibre, possibly a nematodesma, extending horizontally to the dorsal buccal wall. The posterior basal bodies are barren, but are associated with a short fibre extending obliquely posteriad (Fig. 25).

The right buccal kinety extends along the right margin of the buccal overture. It is located in a rather deep furrow about 5 μm apart from the overture margin which forms some kind of buccal lip (Figs. 23, 25, 29, 38). The right buccal kinety consists of very tightly spaced, inverted [28] and thus transversely oriented somatic dikinetids which have, as in *Loxodes* [34], very likely only the right basal body ciliated (Fig. 38). The dikinetids are associated with long, delicate fibres (nematodesmata according to [34]) extending closely underneath the ciliate's surface obliquely posteriad to the median of the cell, i.e. far beyond the intrabuccal kinety. The posterior region of the right buccal kinety extends beyond the vertex of the buccal overture, forming a specialized tail consisting of about 5–20 dikinetids, which are rather widely spaced, irregularly arranged and lack cilia (Figs. 20, 26, 32, 39).

Finally, there is an intrabuccal kinety which extends tight of the buccal ridge obliquely from the anterior end of the cell, i.e. from the tip of the snout, into the buccal cavity, and to the posterior dorsal end of the pharyngeal tube (Figs. 21, 29, 30, 33, 34). The intrabuccal kinety consists of comparatively widely spaced, slightly counter-clockwise rotated dikinetids having the anterior basal bodies ciliated and short, posteriorly directed fibres associated with the anterior or posterior basal body or both as in *Loxodes* [34].

Silverline system. Silver nitrate (wet method as described in [19]) reveals, as in *Loxodes* [21], a very fine-meshed (≤ 1 μm) lattice extending throughout the cortex (Fig. 8).

Extrusomes. Remanella species have unique, nematocyst-like extrusomes, i.e. capsules associated with a coiled or straight filament [37, 39]. Previous investigations could not determine whether or how these organelles are extruded [37, 39]. Fortunately, I found many exploding and (probably almost) completely discharged nematocysts in the protargol slides and in SEM preparations (Figs. 27, 28–31, 37, 41, 42, 44, 46). Thus, I shall treat this matter in some detail; the schematic figure 49 summarizes the observations.

The extrusomes are confined to a stripe each in the ventral and dorsal margin of the left side; in the anterior and posterior region they are less numerous (Figs. 13, 29–31, 37, 41), contrary to previous transmission electron microscope investigations [37]. In life specimens the extrusomes have a diameter of 1.5–2 μm and look like oviform fat droplets (Fig. 13); no structures are recognizable inside. Depending on the intensity of the impregnation, the capsule and the filament or only the filament are revealed with protargol (Figs. 44. 46). The filament forms a flat spiral with 1.5–2 turns in the resting extrusomes, which matches Raikov's [37] observations. It despiralizes to a straight rod when the organelle is extruded and penetrates the pellicle (Figs. 44, 46, 49). Some granular material is recognizable on the tip of the penetrating extrusomes (Fig. 42); whether these granules are remnants of the pellicle and/or extrusome envelope or released contents of the extrusome, as observed in toxicysts [24], could not be determined; in *Paramecium,* which has trichocysts, such structures have not been observed [32]. Next, the pellicle widens gradually and the extrusome leaves the cell

Table 2. Comparison of main characters of *Remanella multinucleata* populations

Character[1]	Kahl [26]	Dragesco [10, 11]	Hartwig [23]	Raikov [35]	This study
Body, length in μm (fixed & stained)	400–700[2]	500–800 (700)	450–620[2]	450–600	450–1000 (705)
Right lateral kineties, number	?	16	?	25–30	18–27 (23)
Müller vesicles, number	2–5	4–6	3–6	2–10 (4)	1–4 (3)
Macronuclei, number	many	12–23 (17)	10–14	7–35 (20)	7–24 (17)
Micronuclei, number	?	3–8 (6)	?	2–16 (5)	3–9 (6)

[1]Arithmetic means, where available, in brackets.
[2]in vivo.

together with the capsule. Thus, the discharged, up to 10 µm long extrusomes have a unique, drumstick-like shape (Figs. 28, 42), highly reminiscent of certain hydrozoan cnidocysts [29]. The relatively large, spherical cavity which the discharged extrusome leaves behind obviously gradually closes (Fig. 42).

Discussion

Identification and Synonymy

The gross morphology of the population studied matches the original description [26] and several more or less detailed redescriptions [10, 11, 23, 27, 35] of *R. multinucleata* (Table 2). However, all observations are from field material. Thus, it cannot be excluded that the material contained single specimens from other similar species. As concerns the present study, the normal (usual) coefficient of variation (13,3%, Table 1) of the somatic kinety number indicates that all specimens studied were from the same species despite the high variability of most other characters.

18 *Remanella* species have been described [5]. Of these, *R. faurei* (350–500 µm, 6–8 macronuclei, body without tendency to spiralize or undulate, [10]), *R. gigas* (length 1000 µm and more, 10 or more macronuclei and micronuclei, 7–9 Müller vesicles, [10]), and *R. levii* (600–700 µm, 4 macronuclei in two groups, each with single micronucleus in between, 2 Müller vesicles, [10]) partially or completely match the variability range of *R. multinucleata* (Tables 1, 2). In the absence of detailed morphometric and morphological data for these species, it is reasonable to consider them as junior synonyms of *R. multinucleata* or at least as species inquirendae.

Comparison of Remanella, Loxodes, and Kentrophoros

The ciliary pattern described for *R. multinucleata* perfectly matches that of *R. rugosa*, a much smaller and binucleate species found at the same locality (Fig. 47). It is also very similar to that of *Loxodes*, with some differences, however, which must be verified by a detailed reinvestigation of *Loxodes*. Possibly, most differences mentioned below are caused by incomplete data although the descriptions of the infraciliature of *Loxodes* agree surprisingly well [13, 21, 30, 34]. Unfortunately, my own slides from *Loxodes* are too poor for a reliable reinvestigation and the few electron microscope studies on *Loxodes* [34] and *Remanella* [37, 40] are also rather crude. A reinvestigation of *Loxodes* should thus specifically address the following uncertainties:

(1) Are both basal bodies of all somatic dikinetids ciliated? The ciliature of *Remanella* (Figs. 23, 40) and *Kentrophoros* [20] is much more differentiated;

(2) Are the posterior dikinetids of the dorsolateral kinety associated with special fibres as in *Remanella* (Fig. 40) and *Kentrophoros* [20]? The dorsolateral kinety of *Loxodes*, first described by Foissner & Rieder [21], has been widely overlooked [e.g. 34], even in recent descriptions [13, 18];

(3) Does the left outer buccal kinety really consist of monokinetids as light [13, 34] and electron microscopic [34] studies have suggested? Foissner & Rieder [21] figured it, at least in *L. magnus*, to be composed of dikinetids as in *Remanella*.

(4) How is the ciliation of the left lateral kineties organized? The *Remanella* data and a detailed analysis of *Kentrophoros* [20] indicate that the left marginal kineties are a single ciliary row. The most convincing argument for this interpretation comes from a reinvestigation of *Cryptopharynx* (Foissner, manuscript in preparation), another loxodid, which clearly shows a single kinety curving around the cell margin (Fig. 48).

The infraciliature of *Kentrophoros* has been recently described in great detail [20]. The somatic pattern matches those of *Remanella* and *Loxodes* well, especially in having the peculiar left lateral ciliature, and conspicuous fibres at the posterior end originating from specialized dikinetids obviously homologous to the dorsolateral kinety of *Remanella* and *Loxodes*. However, *Kentrophoros* has both basal bodies ciliated at the ends of the kineties and only the anterior ones in the centre of the body. This pattern is dissimilar to that of *Remanella* but possibly similar to that of *Loxodes*. Unfortunately, a more detailed comparison of the oral infraciliatures is impossible because the oral apparatus of *Kentrophoros* is reduced to inconspicuous vestiges [20]. Possibly, morphogenetic studies will provide deeper insights.

Remanella, a Junior Synonym of Loxodes?

The present study confirms the close relationship between *Loxodes* and *Remanella* proposed by Kahl [26, 27]. In fact, their somatic and oral infraciliatures and fine structures are almost identical (see preceding section). This raises the question whether or not *Remanella* should be synonymized with *Loxodes* because most ciliate genera are distinguished by differences in the somatic and/or oral ciliary pattern (infraciliature). Dragesco [10], the first reviser of *Remanella*, did not address this problem because details of the infraciliatures of *Loxodes* and *Remanella* were not yet known; on the contrary, he emphasized the homogeneity of the genus using the characters mentioned in Kahl [26].

Kahl [26] provided *Remanella* with a detailed diagnosis (translated from German): "An interesting genus differing from the closely related freshwater genus *Loxodes* mainly by the following characteristics: 1) beneath the ciliated broader side extends a complicated skeleton made of fusiform fibres; 2) the Müller vesicles contain only a single or few (4–8) granules (many tiny granules in *Loxodes*); 3) the posterior body portion is tailed and the end is bent ventrally; however, frequently it is symmetrical in teratological specimens". Note that this diagnosis contains a fourth character, viz. the different environments, marine or

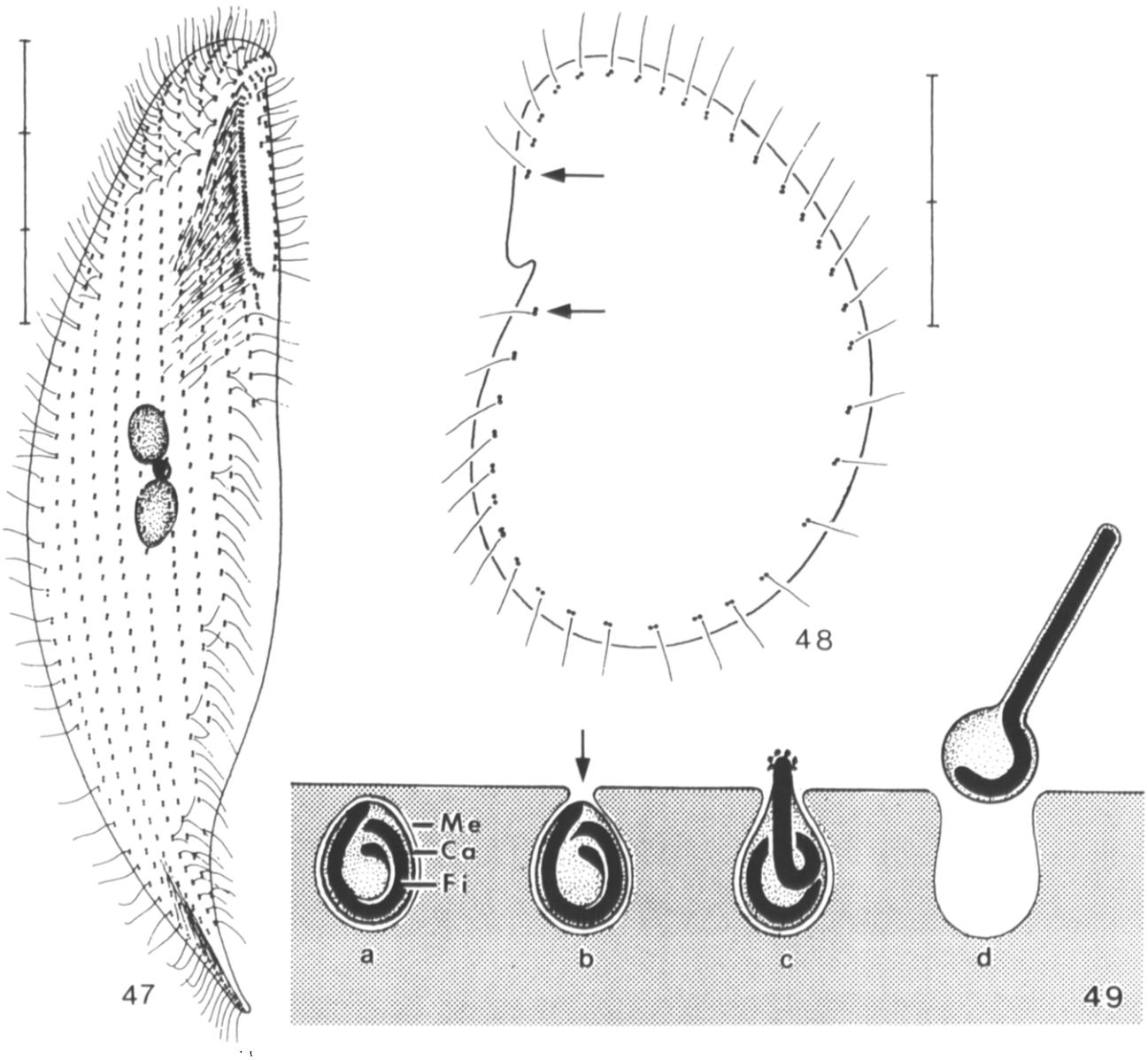


Fig. 47. *Remanella rugosa*, right lateral view after protargol impregnation. This small-sized, binucleate species has the same ciliary and fibrillar pattern as the large-sized *R. multinucleata*. Scale bar division = 10 μm.

Fig. 48. *Cryptopharynx* sp., infraciliature of left side after protargol impregnation. Arrows mark ends of kinety surrounding cell. The circular shape of the kinety results in the anterior ventral portion having the anterior basal body of the dikinetids ciliated, whereas the postoral portion has the posterior basal bodies ciliated. Scale bar division = 10 μm.

Fig. 49a–d. Interpretative scheme of extrusome discharge in *R. multinucleata*, based on live observations, protargol impregnation, and scanning electron microscopy (cp. Figs. 13, 27, 28, 37, 42, 46). – a. The resting extrusome is oviform and surrounded by a membrane (Me). The extrusome capsule (Ca) contains a coiled filament (Fi). – b, c. After stimulation, a small opening originates in the pellicle (b, arrow) through which the despiralizing filament emerges (c). The tip of the discharging extrusome is covered by granular material. – d. A large cavity remains in the ciliate cortex after the extrusome has been discharged.

freshwater, colonized by *Remanella* and *Loxodes*. A fifth attribute is the peculiar extrusomes (nematocysts; Figs. 27, 28, 42, 46) lacking in *Loxodes* [34] and, possibly, in some *Remanella* species [40]. Furthermore, the granules in the Müller vesicles of *Loxodes* and *Remanella* are different in chemical composition, i.e. contain barium and strontium, respectively [41].

The attributes mentioned by Kahl apply not only to the species discovered by himself, but also to most species described later [5, 10]. There is only one excep-

tion, viz *R. obtusa* [14], which apparently lacks a skeleton and is broadly rounded posteriorly. This species also lacks the pharyngeal prolongation so typical for *Loxodes* and *Remanella*. It thus very likely belongs to another genus (*Ciliofaurea?*) or family.

In my opinion the characters used by Kahl for distinguishing *Remanella* from *Loxodes* are still appropriate. There is no evolutionary or general constraint that ciliate genera must differ in the infraciliature although this is common. Other examples for this are found, e.g., in suctorians (*Podophrya* with resting cysts, *Sphaerophrya* without resting cysts), peritrichs (*Vorticella* with stalk, *Astylozoon* without stalk) and haptorids (*Fuscheria* and *Actinorhabdos* with nail-shaped and graver-shaped extrusomes, respectively).

I thus recognize *Remanella* as a valid genus and provide it with an improved diagnosis, including the new findings discussed above: Marine Loxodidae Bütschli, 1889 with organic spicules forming a cytoplasmic skeleton, cnidocyst-like extrusomes (nematocysts), one or several Müller vesicles containing a single or compound strontium granule, and narrowed or tailed posterior end. Type species: *R. multinucleata* (Kahl, 1933) nov. comb.

The main character of *Remanella* is the unique organic spicules. Whether all *Remanella* species have nematocysts and strontium in the Müller body needs further investigations. Possibly, differences in the structure of the extrusomes and the fibrillar associates of the dikinetids may be used at some time to split *Remanella* into two or more genera or subgenera. The small, binucleate *R. granulosa,* for instance, lacks typical nematocysts and bifurcated or double kinetodesmal fibres found in large, multinucleate species of *Loxodes* and *Remanella* [34, 40]. Again, this contrasts with the infraciliature which is identical in large, multinucleate (*R. multinucleata*) and small, binucleate species (*R. rugosa*, Fig. 47).

Evolution in Loxodid Ciliates

Remanella and *Loxodes* are two of few well-documented examples that generic differentiation did not occur at somatic and oral infraciliature but at cytoplasmic level. This provides an excellent opportunity of getting some insight into the evolution of the Loxodidae and to estimate the influence of biotope constraints.

Both *Remanella* and *Loxodes,* although restricted, respectively, to marine and freshwater biotopes, belong to the karyorelictids, i.e. have diploid, never dividing macronuclei [6, 7, 33]. All other karyorelictids live in the marine interstitial [6]. It is thus reasonable to assume that the Loxodidae evolved in the marine environment. Then, the freshwater genus *Loxodes* could be considered a derived branch which lost the specific traits (organic spicules, tail....) of *Remanella*. Although this possibility cannot be excluded (see discussion in [6]), I agree with Corliss & Hartwig [7] that *Remanella* and *Loxodes* evolved from a common ancestor, because the specific characters of *Remanella* look very much like adaptations evolved to withstand the particular physical constraints of the interstitial and intertidal environment (see [31] for a comprehensive review). This suggests a loxodid ancestor which was not restricted to the interstitial but lived in the Aufwuchs or on the mud surface, as *Loxodes* still does [22]. Furthermore, the ancestor very likely looked rather similar to a present day *Loxodes,* as indicated by the identical infraciliatures of *Loxodes* and *Remanella*. This pattern is obviously highly conserved.

Loxodes ceased generic diversification when it entered the more stable freshwater biotopes, while *Remanella* possibly gave rise to *Kentrophoros,* whose somatic infraciliature is strikingly similar to that of *Loxodes* and *Remanella* [20]. *Kentrophoros* reduced the oral apparatus to inconspicuous vestiges [20] due to its symbiosis with sulphur bacteria, which are phagocytosed through the left lateral surface [36].

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Key words: Infraciliature – Evolution – Loxodidae – *Remanella* nov. gen. – *Remanella multinucleata* nov. comb.

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