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The Myriokaryonidae fam. n., a New Family of Spathidiid Ciliates (Ciliophora: Gymnostomatea)

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Summary. The new family Myriokaryonidae is based on a thorough literature review and the (re) investigation of *Myriokaryon lieberkuehnii* (Bütschli, 1889) Jankowski, 1973 and *Cephalospatula brasiliensis*, a new genus and species discovered in soils of South America. The key features of the new family, which belongs to the order Spathidiida Foissner and Foissner, 1988, are the truncated anterior body end and the spoon-shaped oral bulge, respectively, circumoral kinety. The anterior truncation causes a highly characteristic bend of the oral bulge and circumoral kinety in the transition zone of spoon-shovel and spoon-handle, that is, subapically where the oral bulge and the circumoral kinety enter the ventral side of the cell. Based on literature data, *Holophrya emmae* Bergh, 1896 and *Pseudoprorodon armatus* Kahl, 1930a are classified as representatives of two further new myriokaryonid genera, viz., *Berghophrya* gen. n. and *Kahlophrya* gen. n. Genera within the Myriokaryonidae are distinguished by details of the dorsal brush and the arrangement of the somatic ciliary rows and extrusomes. *Pseudoprorodon emmae* (Bergh, 1896), as redescribed by Song and Wilbert (1989), is recognized as a new genus and species, *Songophrya armata* gen. n., sp. n., likely belonging to the gymnostomatous family Pseudoholophryidae.

Key words: biodiversity, Haptorida, infraciliature, Litostomatea, soil protozoa, South America.

INTRODUCTION

The haptorid gymnostomes ("Litostomatea") are a highly diverse ciliate assemblage, ranging from the simple *Enchelys* to the complex *Homalozoon* and from common freshwater and marine to highly specialized enterozooic species (Corliss 1979, Grain 1994). However, many gymnostomes are rather inconspicuous and thus attracted few specialists, most notably Kahl (1926, 1930a, b), Lipscomb and Riordan (1990), and myself (Foissner 1984, 1996; Foissner and Foissner 1988). Accordingly, the group contains a huge amount of undescribed taxa, as shown by a recent study on soil ciliates from Namibia, describing 10 new genera and many new species (Foissner *et al*. 2002). Detailed observations and much experience are necessary to unravel this hidden diversity. This is evident also from the present study, where a new family and four new genera will be established.

Large ciliates, such as *Myriokaryon lieberkuehnii* and *Cephalospatula brasiliensis*, are difficult to present by ordinary figures. Thus, I fragmented them into many details, which, however, strongly increased the number of pages. But this is the sole way to document such species, which tend to be misidentified, to an extent that detailed biogeographic comparisons of species and populations will be possible in future.

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MATERIALS AND METHODS

Myriokaryon lieberkuehnii was found in the microaerobic mud of a boggy drainage ditch at the margin of a small bog near the village of Franking (13°E 48°2'N), Upper Austria, in April 1990. Specimens were numerous and survived in the collecting jar for weeks, but did not reproduce.

Cephalospatula brasiliensis was discovered in soil samples from three sites of South America. The type population occurred in a sample, kindly collected by Dr. L. Felipe Machado Velho (Maringá State University) in May 2001, from the high Paraná River floodplain near the town of Maringá (53°15'W 22°40'S, altitude about 500 m), State of Mato Grosso do Sul, Brazil. The sample was taken from the Aurelio Lagoon, that is, a marginal lagoon associated with the Baia River, a tributary of the Paraná River. The dark, humic soil was mixed with much partially decomposed plant litter, had pH 5.1 (in water), was air-dried in the Salzburg laboratory for about one month, and stored in a plastic bag. In November 2001, the about 300g soil were put in a Petri dish and saturated, but not flooded with distilled water to obtain a "non-flooded Petri dish culture", as described in Foissner *et al*. (2002). About two weeks after rewetting, a small population of *C. brasiliensis* developed. The second population of *C. brasiliensis* occurred in the surroundings of Rio de Janeiro (43°W 23°S), that is, in the Restingha area about 100 m inshore the Atlantic Ocean, where the ground is partially covered by grass and an up to 1 cm high litter layer. The sample, which was taken on 16.11.1996 and treated as described above, contained sandy soil, surface litter, and plant residues sieved off the very sandy soil up to a depth of 10 cm. A weak population of *C. brasiliensis* developed 8 days after rewetting the sample, which had pH 5.2 (in water), in May 1997. The third population of *C. brasiliensis* was found near the airport of Puerto Ayacucho (68°W 5°N), Venezuela, on 28.5.1997. Here are large, granitic rocks (Lajas) with many pools. The sample comprised litter, mud and soil accumulated in a pool between the cushion-like root layer of a species of the endemic Velloziaceae family. The material, which was treated as described above and had pH 5.3 (in water), was rewetted in June 1997, when a small population of *C. brasiliensis* developed after 5 days.

Specimens were studied *in vivo* using a high-power, oil immersion objective and differential interference contrast optics. The ciliary pattern and various cytological structures were revealed by protargol impregnation, as described in Foissner (1991). Counts and measurements on prepared specimens were performed at a magnification of x1000. *In vivo* measurements were conducted at magnifications of x100-1000. Although these provide only rough estimates, it is worth giving such data as specimens may change in preparations. Illustrations of live specimens were based on free-hand sketches, while those of prepared cells were made with a camera lucida. Terminology is mainly according to Corliss (1979).

RESULTS

Genus *Myriokaryon* Jankowski, 1973

Improved diagnosis: vermiform Myriokaryonidae with long mouth on steeply slanted anterior body region and many (>3) isomorphic dorsal brush rows converging to an acute pattern anteriorly. Extrusomes scattered in oral bulge. At left side of circumoral kinety many transverse kinetofragments partially connected with left side ciliary rows (basically *Supraspathidium* pattern).

Type species (by monotypy): *Prorodon Lieberkühnii* Bütschli, 1889.

Redescription of *Myriokaryon lieberkuehnii* (Bütschli, 1889) Jankowski, 1973 (Figs 1-53; Table 1)

1859 *Enchelys gigas* Stein, Organismus der Infusionsthiere, p. 80 (a nomen nudum because too briefly described without figure).

1889 *Prorodon Lieberkühnii* Bütschli, Protozoa, explanation to figure 6 of plate LVII (single figure, here reproduced as figure 91; without description).

1914 *Spathidium gigas* (Stein 1859) - Cunha, *Mem. Inst. Osw. Cruz*, 6: 173 (synonymy doubtful; possibly a "true", large *Spathidium*/*Arcuospathidium*; Fig. 96).

1930 *Pseudoprorodon (Prorodon) lieberkühni* Bütschli, 1889 - Kahl, *Tierwelt Dtl*., 18: 71 (first reviser and important new observations; Figs 97, 99).

1972 *Pseudoprorodon lieberkühni* Bütschli - Dragesco, *Annls Fac. Sci. Univ. féd. Cameroun*, 11: 73 (redescription, mainly from life; Figs 92, 93, 95, 98).

1973 *Myriokaryon lieberkühnii* (Bütschli, 1889) Jankowski comb. n. - Jankowski, *Zool. Zh*., 52: 424 (solid redescription and transfer to the new genus *Myriokaryon*; in Russian with English summary; Fig. 101).

1986 *Myriokaryon lieberkühni* (Bütschli, 1889) Jankowski, 1973 - Dragesco and Dragesco-Kernéis, *Fauna tropicale*, 26: 169 (brief review and description of a Benin population; Fig. 94).

Material and types: Jankowski (1973) stored 29 neotype slides with 70 conventionally (various hematoxylin methods, Feulgen reaction, bromphenol) prepared specimens of *M. lieberkuehnii* at the marine biological laboratory of the Russian Academy of Sciences in St. Peterburg. Although these slides do not show all the details necessary for a reliable identification, I suggest to accept them as a neotype because the known data agree with my material. The specimens of Dragesco (1972) and Dragesco and Dragesco-Kernéis (1986) are likely still in the private collection of Prof. Jean Dragesco. Furthermore, they are poorly prepared, as obvious from the mistakes in the description (see discussion). My material is excellently prepared and fully described below. Five slides with protargol-impregnated

Table 1. Morphometric data on *Myriokaryon lieberkuehnii*.

Characteristics[a]	x	M	SD	SE	CV	Min	Max	n
Body, length	1321.0	1320.0	280.1	61.1	21.2	860.0	1800.0	21
Body, width about 100 µm posterior of anterior end	52.8	53.0	5.1	1.1	9.7	45.0	63.0	21
Body, maximum width	77.1	75.0	9.3	2.0	12.0	68.0	110.0	21
Body length:maximum width, ratio	17.3	16.9	3.9	0.8	22.5	9.1	24.3	21
Mouth, length (anterior end to proximal end of circumoral kinety, distance)	328.3	330.0	57.1	12.5	17.4	240.0	450.0	21
Body length:mouth length, ratio	4.1	3.9	0.9	0.2	21.4	3.0	6.3	21
Mouth, anterior width (distance between circumoral kinety in head area)	10.5	11.0	2.0	0.6	19.0	7.0	14.0	13
Mouth, mid-region width (distance between circumoral kinety)	6.9	7.0	1.3	0.3	18.6	5.0	10.0	18
Mouth, posterior width (distance between circumoral kinety)	11.2	10.0	2.2	0.5	19.5	8.0	15.0	17
Macronuclei, length	8.9	8.0	4.1	0.9	46.6	4.0	18.0	21
Macronuclei, width	3.6	4.0	0.6	0.1	16.7	3.0	5.0	21
Micronuclei, length	3.0	3.0	0.5	0.1	16.0	2.2	4.0	21
Micronuclei, width	3.0	3.0	0.5	0.1	16.0	2.2	4.0	21
Excretory pores, number per vacuole	2.3	2.0	0.6	0.1	28.2	1.0	3.0	21
Somatic kineties, number in mid-oral area[b]	82.8	82.0	-	-	-	73.0	100.0	21
Somatic kineties, number in mid-body[b]	94.3	95.0	-	-	-	83.0	110.0	21
Kinetids, number in 10 µm in oral area	6.1	6.0	1.0	0.2	15.7	5.0	9.0	21
Kinetids, number in 10 µm in mid-body	5.0	5.0	0.8	0.2	15.5	4.0	7.0	21
Kinetids, number in 10 µm near posterior end	3.1	3.0	0.2	0.1	7.2	3.0	4.0	21
Dorsal brush kineties, number near anterior body end	7.5	7.5	0.6	0.1	8.1	6.0	8.0	20
Anterior body end to end of dorsal brush, distance[b]	508.3	500.0	-	-	-	300.0	680.0	21

[a] Data based on protargol-impregnated (Wilbert's method; see Foissner 1991), mounted, morphostatic field specimens. Measurements in µm. CV - coefficient of variation in %, M - median, Max - maximum, Min - minimum, n - number of individuals investigated, SD - standard deviation, SE - standard error of arithmetic mean, x - arithmetic mean. [b] Approximate values.

(Wilbert's method) specimens have been deposited in the Biologiezentrum of the Oberösterreichische Landesmuseum in Linz (LI), Austria. Relevant specimens are marked with black ink on the cover glass.

Description of Austrian population: true size difficult to ascertain because contractile by about one third of body length and contraction, respectively, extension occur so slowly that is is impossible to recognize whether or not the cell is fully extended, as also mentioned by Engelmann in Bütschli (1889). Thus, size variability is high, viz., 900-2000 x 70-120 µm *in vivo*, usually near 1500 x 90 µm, with conspicuous length:width variation of 9-24:1 in protargol preparations, where cell width is rather distinctly shrunken (Table 1). Jankowski (1973), however, mentions that it does not contract when touched, but he might have overlooked the slow contraction described above. He measured 34 specimens and noted also a pronounced variability: length 625-1250 µm, usually 825-950 µm; width at anterior end 37-52 µm; width at proximal oral bulge end 47-62 µm; width in mid-body 100-175 µm, usually 100-125 µm.

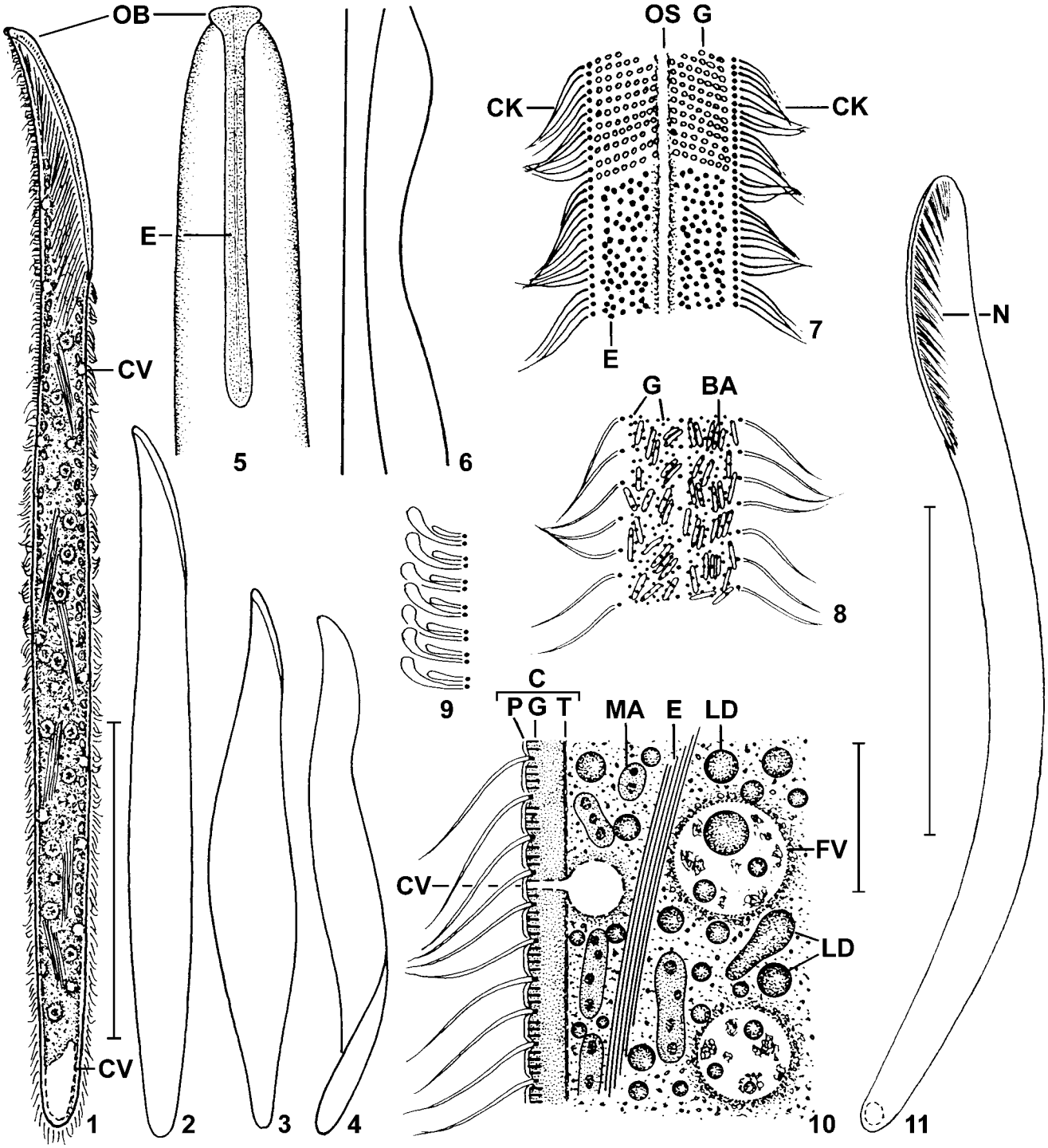
Basically elongate knife-shaped with blade (=oral area) occupying 25% of body length on average, handle thus much longer than blade; anterior and posterior quarter flattened laterally up to 2:1, anterior body end acute due to steeply slanted mouth area and indistinct oral bulge gradually merging into body proper proximally (Figs 1-4, 12, 20); usually widest in or near mid-body, rarely in blade-like oral area making specimens somewhat club-shaped (Fig. 11); contracted cells widened in mid-body (Figs 2, 3). Largest specimens with about 5000 (!) macronuclear nodules scattered throughout body in an about 15 µm thick, subcortical layer; individual nodules globular to elongate ellipsoidal with several minute and small nucleoli of various shape (Figs 1, 10, 14, 18, 33, 35, 40, 45, 46; Table 1). Micronuclei less numerous than macronuclear nodules, likely between 100-200, minute, that is 3-4 µm across. A large contractile vacuole with several excretory pores in rear end and about 60 small contractile vacuoles each with one to three intrakinetal excretory pores scattered throughout cortex (Figs 1, 10, 16, 19, 22-24, 33). Extrusomes (likely toxicysts) accumu-

lated in both sides of oral bulge and scattered throughout cytoplasm in conspicuous bundles; individual extrusomes rod-shaped and very flexible, straight to slightly curved, about 80 x 0,5 µm in size; those attached to oral bulge never impregnate with the protargol method used, while cytoplasmic bundles often stain deeply with individual rods frequently somewhat disordered and irregularly curved (Figs 1, 5-7, 10, 29, 30, 33-37, 42, 43). A second type of minute (about 1-1.5 x 0.4 µm), rod-shaped structures, likely mucocysts (Fauré-Fremiet and André 1968), forms oblique rows in the oral bulge and is scattered throughout the cortex and cytoplasm, where rods are up to 2 µm long and occasionally impregnated with protargol (Figs 7, 8, 10, 33, 36, 39, 46). Cortex conspicuous because 3-4 µm thick and sharply separated from granular cytoplasm by a distinct *tela corticalis* described by Fauré-Fremiet and André (1968); in most specimens rather densely covered with 2-4 µm long bacterial rods (Figs 1, 8, 10, 29, 31, 33, 39). Cytoplasm colourless, packed with lipid droplets 1-10 µm across and surprisingly small, viz., 10 µm-sized food vacuoles containing colourless, granular remnants and golden lipid droplets, indicating heterotrophic and autotrophic protists as main food source (Figs 1, 10, 30); unfortunately, definite food inclusions were neither found *in vivo* nor prepared cells, indicating that prey is rapidly lysed either outside the cell or in the food vacuoles. Swims and crawls worm-like in and on the sediment and microscope slide, showing great flexibility, viz., may curl-up and/or spiralize along main body axis (Fig. 4).

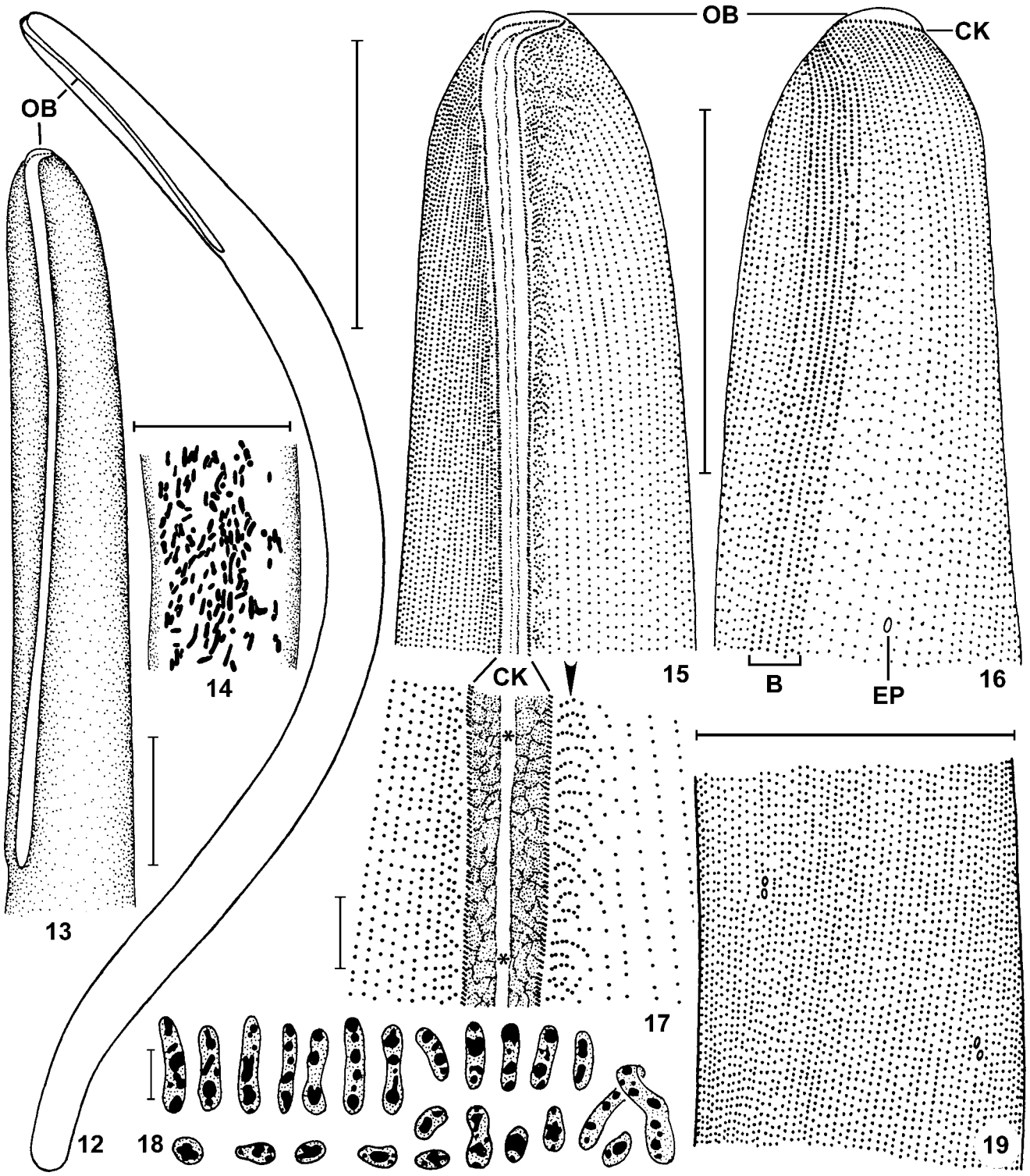
Cilia about 12 µm long *in vivo* and narrowly spaced, especially right of oral bulge, arranged in an average of 95 rows in mid-body and of only 82 rows in mid-oral area due to gradual shortening along circumoral kinety (Figs 15, 17, 25, 37, 40, 41, 44; Table 1), while some rows are added postorally and along left margin of dorsal brush (Figs 16, 48-53). Ciliary rows equidistantly and narrowly spaced (about 2 µm), extend meridionally; right side rows loosely ciliated anteriorly and shortened successively abutting on circumoral kinety in steep angles, while densely ciliated and strongly curved anterior end of left side ciliary rows abuts on circumoral kinety at almost right angles; furthermore, many additional, small kinetofragments of unknown origin occur along left side of circumoral kinety, a special feature also found in *Cephalospatula brasiliensis* (Figs 15, 17, 19, 25-28, 37, 38, 40, 41, 44). These fragments look like dileptid "adesmokineties", a term coined by Jankowski earlier than the American "paratenes". Kinetids of posterior body region associated with long fibres forming conspicuous, subcortical bundles extending anteriorly (Fig. 22). Dorsal brush at anterior portion of six to eight slightly left laterally located, ordinary somatic ciliary rows, longest brush kineties occupy 38% of body length on average (Table 1); composed of narrowly spaced dikinetids with posterior bristles up to 5 µm long and inflated distal end curved anteriorly (Figs 1, 9, 29, 39); kineties gradually shortened from left to right, except of the three rightmost rows, bristles mixed with ordinary cilia posteriorly, that is, before brush kineties extend as ciliary rows to rear body end; middle brush rows, additionally, slightly shortened anteriorly, where the unshortened marginal rows curve right and converge subapically near the circumoral kinety, providing the brush with an acute end, another unique feature of the somatic ciliary pattern of *Myriokaryon* (Figs 16, 20, 21, 23, 24, 26, 27, 29, 38, 39, 48-53; Table 1).

Mouth occupies steeply slanted and slightly convex anterior 25% of body, *in vivo* distinct due to the numerous and long extrusomes contained, basically, however, indistinct because oral bulge hardly set off from body proper, that is, only about 5 µm high and 12 µm wide. Oral bulge elongate dumbbell-shaped in frontal view, curved anterior portion slightly thicker (higher) and wider than straight proximal part; oral slit stands out as a whitish (unimpregnated) cleft from brownish impregnated bulge wall, containing a fibrous reticulum and innumerable extrusomes, as described above. Circumoral kinety composed of very narrowly spaced, oblique dikinetids having ciliated only one basal body, likely consists of many kinetofragments of varying length, as indicated by minute breaks making kinety somewhat irregular; of same shape as oral bulge, that is, elongate dumbbell-shaped with highly characteristic, sharp bend in the transition zone of transverse-truncate anterior body end and curved ventral portion. Oral basket rods originate from circumoral dikinetids, very fine and short (about 30 µm) as compared to size of cell, basket thus inconspicuous in protargol preparations and invisible *in vivo*, where it is easily confused with the more distinct and longer, rod-shaped extrusomes (Figs 1-5, 7, 11-13, 15, 17, 25-29, 32, 37, 40, 41, 43-45, 47; Table 1).

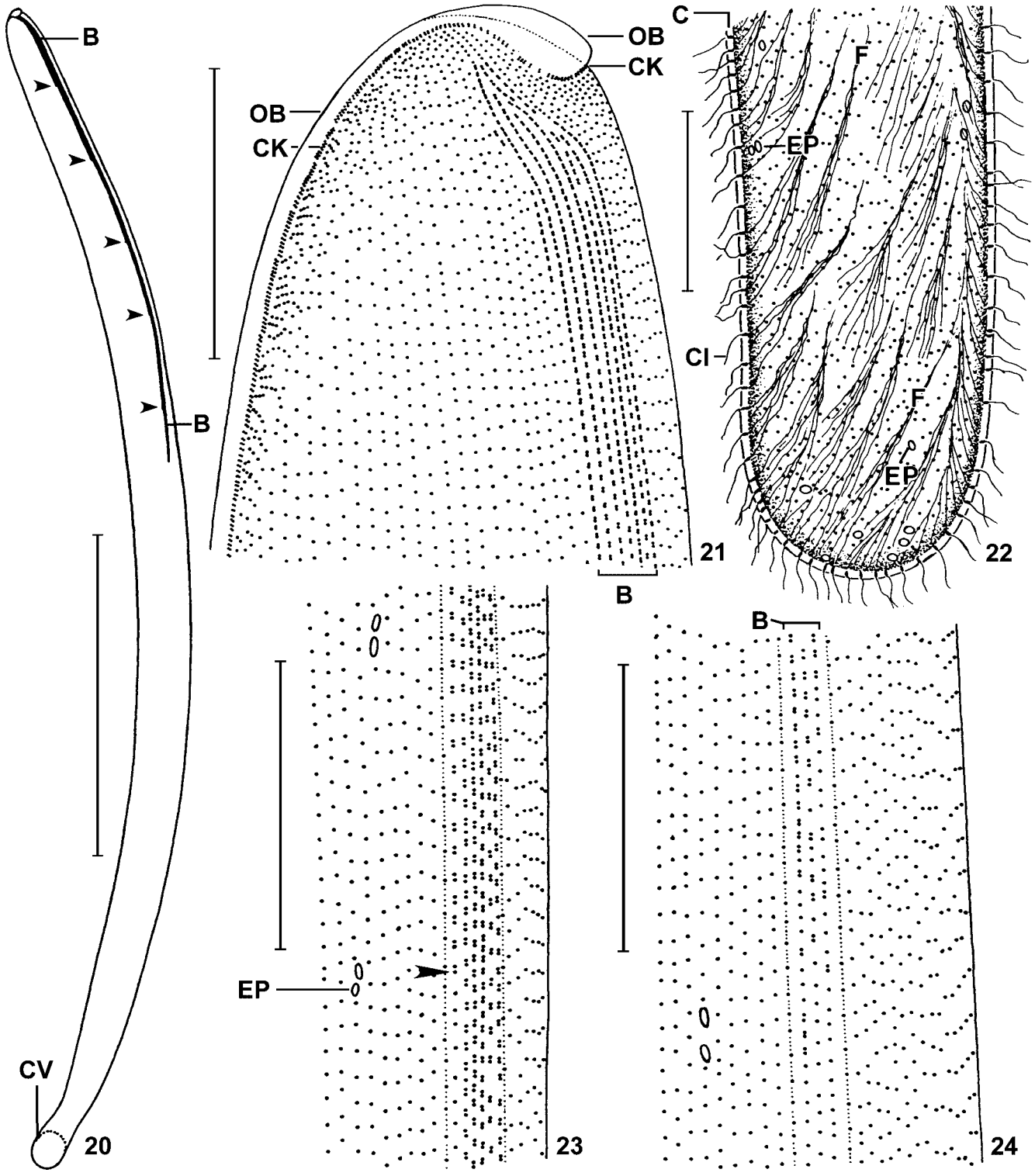
Distribution and ecology: all reliable records of *M. lieberkuehnii* are from the Holarctic and African region (Bütschli 1889, Kahl 1930a, Dragesco 1972, Jankowski 1973, Dragesco and Dragesco-Kernéis 1986, present study). Cunha (1914) reported it from freshwater in the surroundings of Manguinhos, Brazil, where it occurred only once, but in great numbers (Fig. 96). However, I agree with Kahl (1930a) that conspecificity



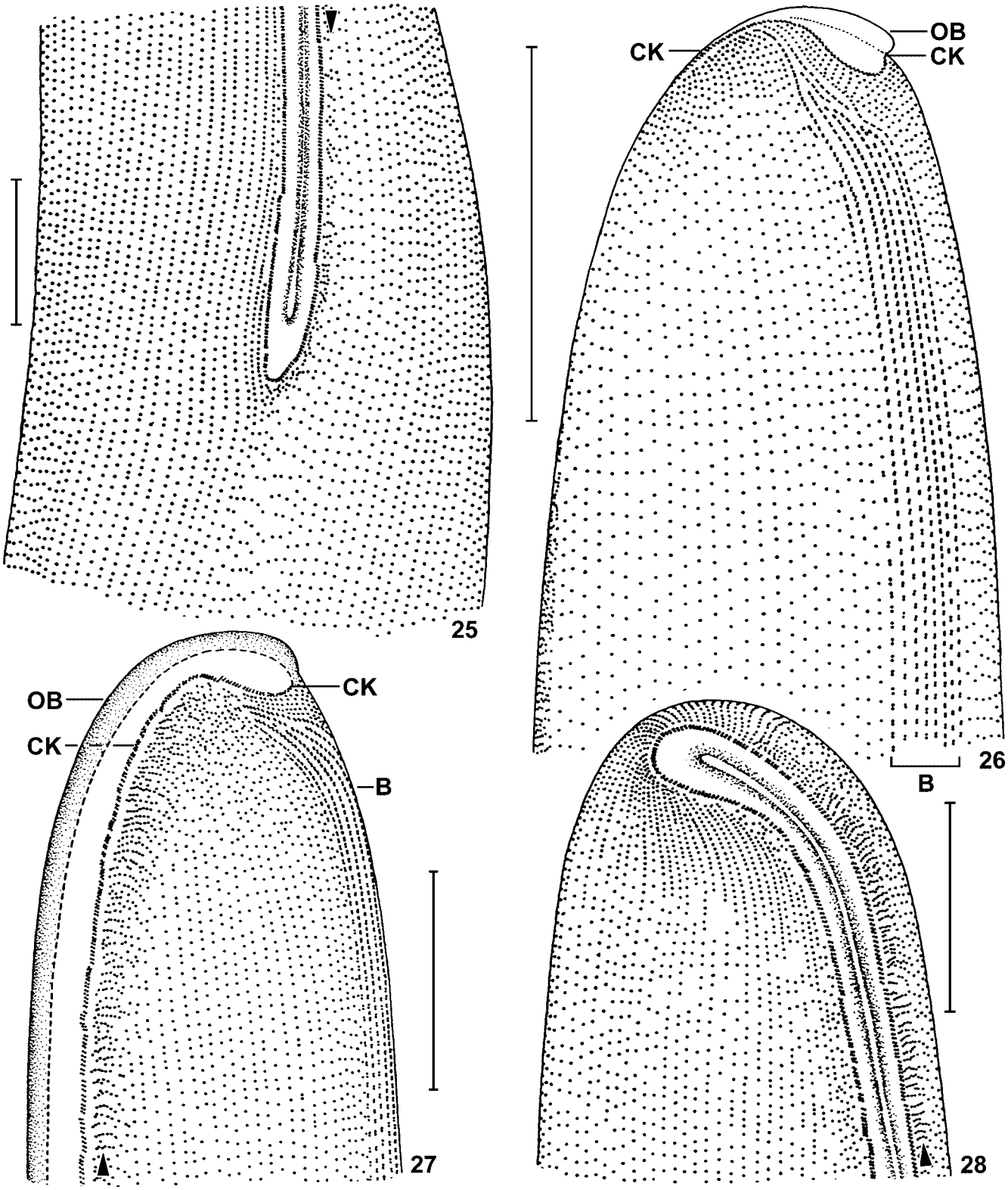
Figs 1-11. *Myriokaryon lieberkuehnii* from life (1-10) and after protargol impregnation (11). **1** - right side view of a representative specimen, length 1400 µm. For details, see figure 10; **2, 3** - a specimen extended and contracted; **4** - a slightly spiralized specimen; **5** - ventral view of oral area; **6** - oral bulge extrusomes, length 80 µm; **7** - ventral view of oral bulge showing cortical granules (upper half) and extrusomes underneath (lower half); **8** - surface view showing cortical granules and epicortical bacteria; **9** - part of a dorsal brush row with posterior bristles 5 µm long and inflated distally; **10** - optical section showing the 3-4 µm thick cortex and main cytoplasmic inclusions. Note that the extrusome bundle (80 µm) is not shown in full length; **11** - a specimen widest in oral area. B - dorsal brush; BA - epicortical bacteria; C - cortex; CK - circumoral kinety; CV - contractile vacuoles; E - extrusomes; FV - food vacuole; G - cortical granules; L - lipid droplets; MA - macronuclear nodule; N - nematodesmata; OB - oral bulge; OS - oral slit; P - pellicle; T - tela corticalis. Scale bars 10 µm (10); 400 µm (1, 11).



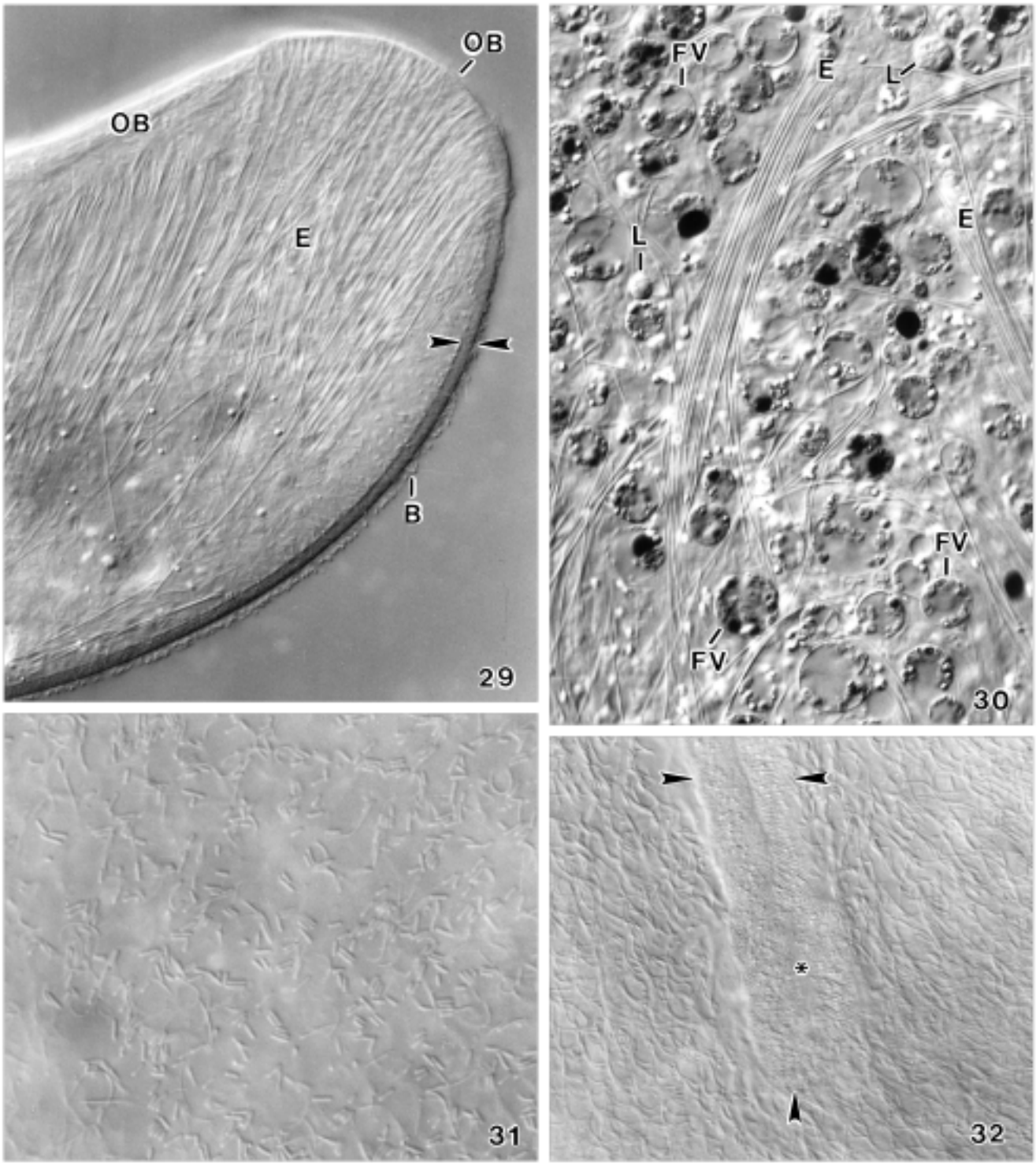
Figs 12-19. *Myriokaryon lieberkuehnii*, main voucher specimen after protargol impregnation. **12, 13** - ventrolateral overview (length 1800 µm) and oral area at higher magnification; **14** - upper layer of macronuclear nodules in mid-body; **15, 16** - oral and somatic ciliary pattern of ventral and dorsal anterior body portion; **17** - ciliary pattern of mid-oral area at high magnification. Arrowhead marks kinetofragments, some obviously connected with the ciliary rows, at left margin of circumoral kinety. Asterisks denote oral slit; **18** - variability of macronuclear nodules, drawn to scale (6 µm); **19** - ciliary pattern in mid-body. B - dorsal brush; CK - circumoral kinety; EP - excretory pore; OB - oral bulge. Scale bars 6 µm (17, 18); 70 µm (13, 14-16, 19); 400 µm (12).



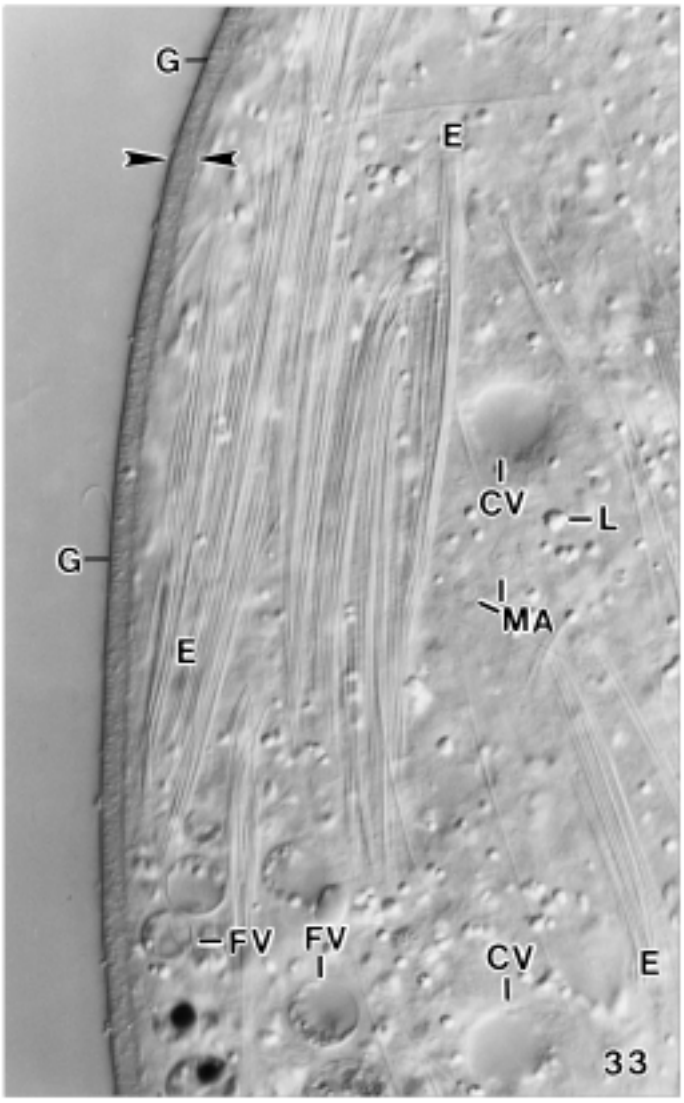
Figs 20-24. *Myriokaryon lieberkuehnii*, infraciliature after protargol impregnation. **20, 21, 23, 24** - dorsolateral overview (20) and details of dorsal brush in anterior (21), middle (23), and posterior (24) region. The brush rows gradually decrease in length from left to right (arrowheads) and continue posteriorly as ordinary somatic ciliary rows (24). Anteriorly, the middle brush rows are slightly shortened, while the marginal ones converge, forming a highly characteristic, pointed anterior brush end (21); **22** - posterior body region with subcortical fibre bundles originating from basal bodies of cilia. B - dorsal brush; C - cortex; CI - cilia; CK - circumoral kinety; CV - contractile vacuole; EP - excretory pores; F - fibre bundles; OB - oral bulge. Scale bars 30 µm (21-24); 400 µm (20).

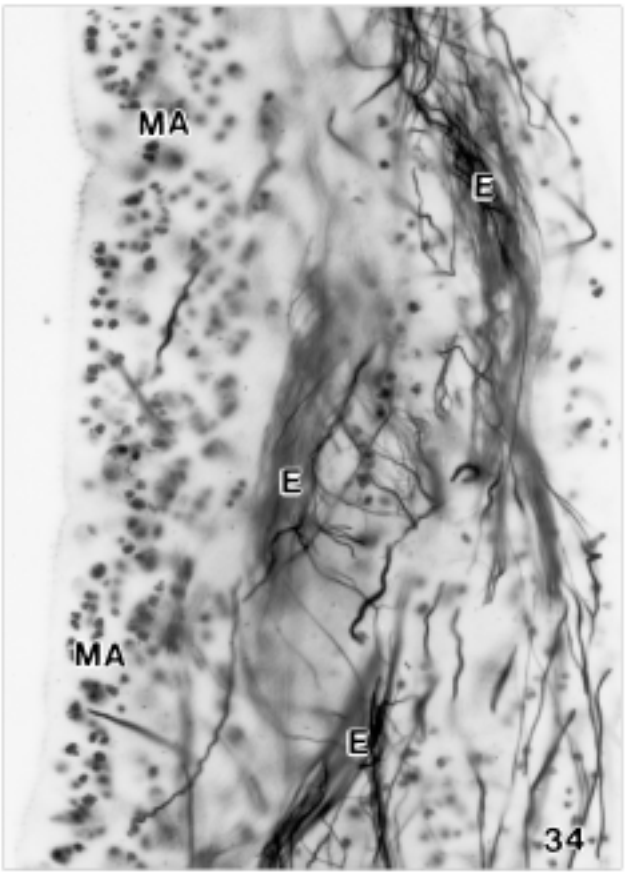


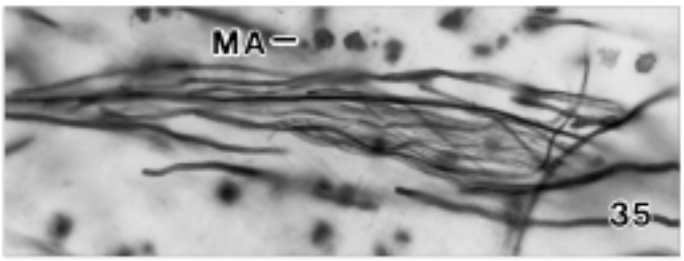
Figs 25-28. *Myriokaryon lieberkuehnii*, details of ciliary pattern after protargol impregnation. At right, the ciliary rows abut on the circumoral kinety in very steep angles, whereas at left many small kinetofragments, some obviously connected with the ciliary rows, occur and abut on the circumoral kinety at right angles (arrowheads). **25, 28** - ventral and frontal view showing the slightly widened posterior and anterior mouth end; **26, 27** - lateral views showing the main family features, viz., the strongly curved anterior portion of the oral bulge and circumoral kinety. Note the pointed anterior brush end. B - dorsal brush; CK - circumoral kinety; OB - oral bulge. Scale bars 30 µm.

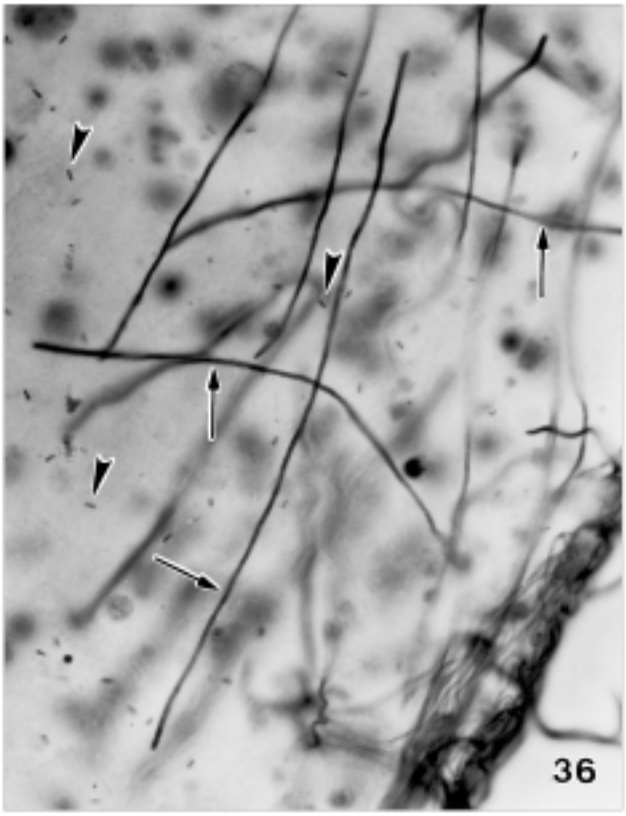


Figs 29-32. *Myriokaryon lieberkuehnii* from life (interference contrast). **29 -** anterior body portion of a slightly squashed specimen showing the 80 µm long extrusomes attached to the oral bulge. The opposed arrowheads mark the unusually thick cortex; **30 -** the cytoplasm is packed with extrusome bundles and about 10 µm-sized food vacuoles containing golden (and thus dark in the micrograph) lipid droplets, indicating that this specimen fed on autotrophic protists; **31 -** surface view showing the cortex covered with bacterial rods; **32 -** ventral view of posterior mouth end. The oral bulge, marked by arrowheads, is finely striated by rows of cortical granules, likely mucocysts; underneath are the extrusomes, whose anterior ends appear as minute granules (cp. figure 7). Asterisk denotes the mouth slit. B - dorsal brush; E - extrusomes; FV - food vacuoles; L - lipid droplets; OB - oral bulge.

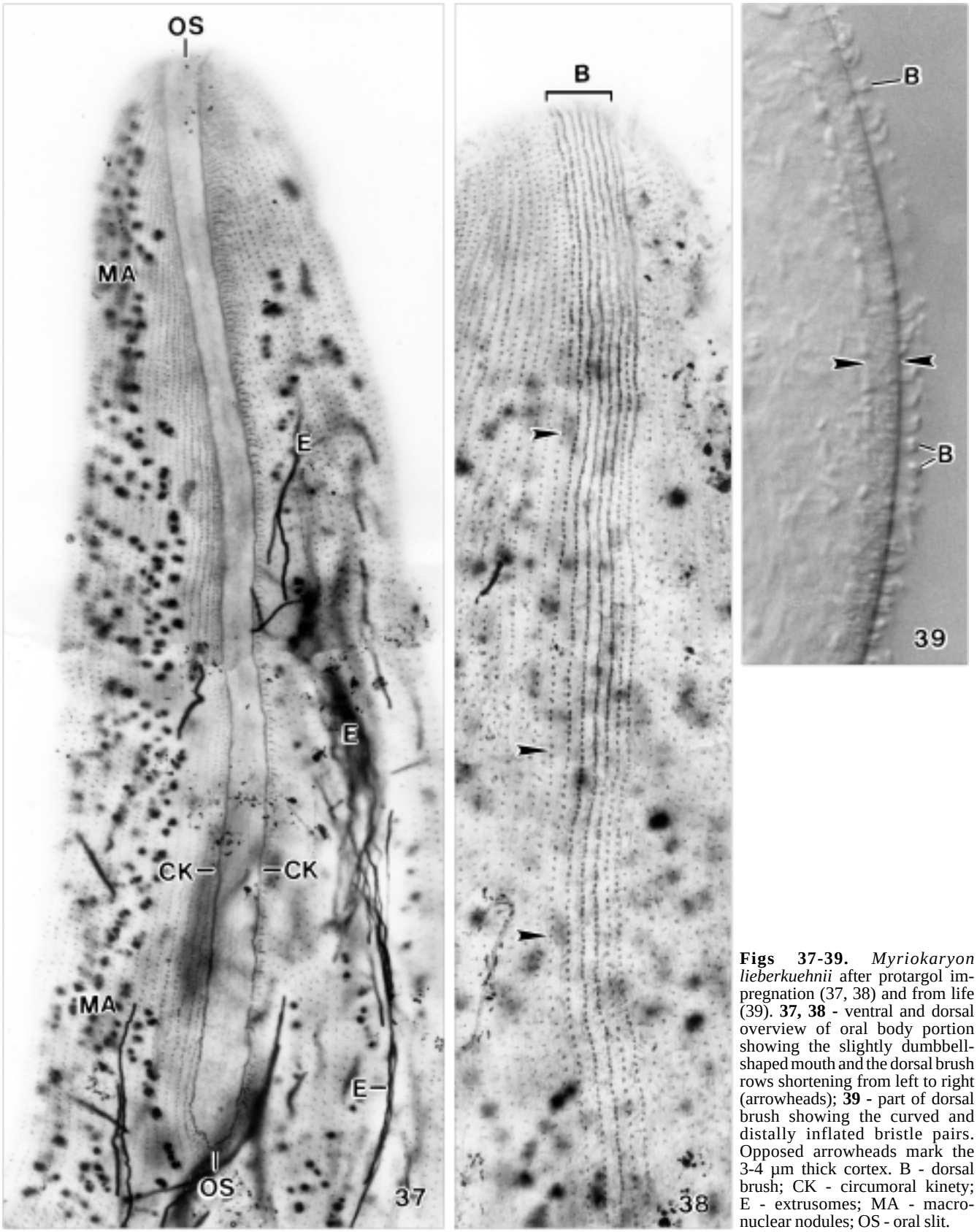




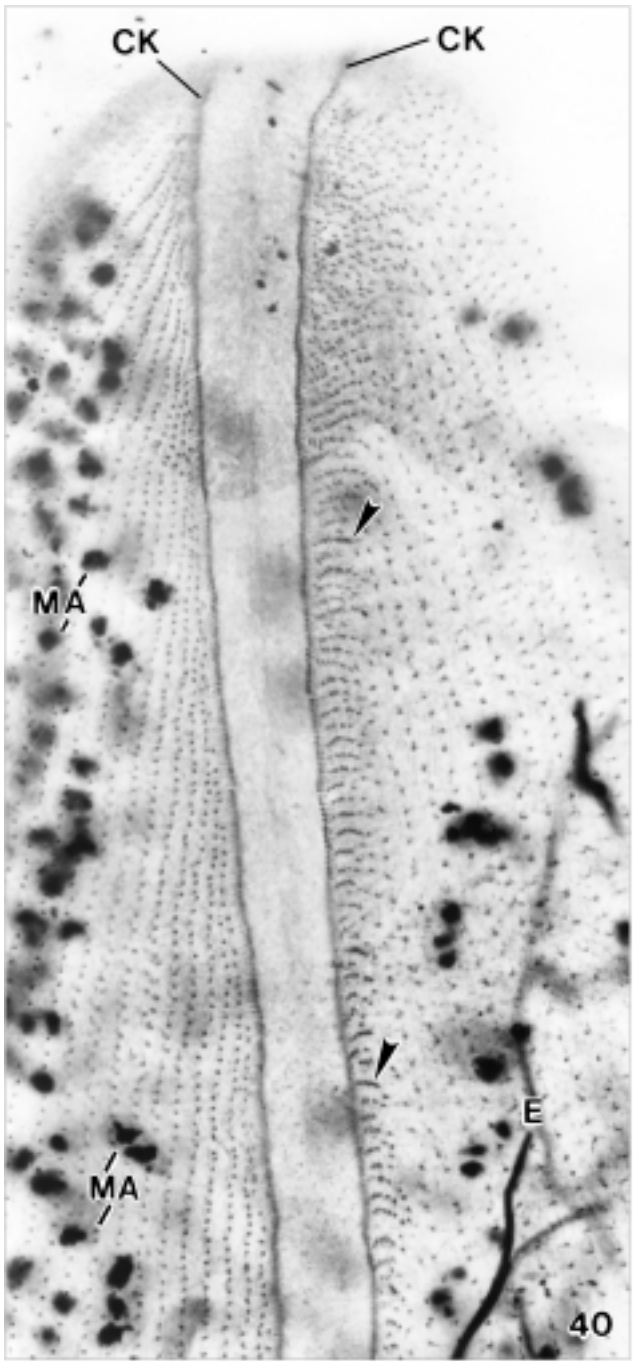


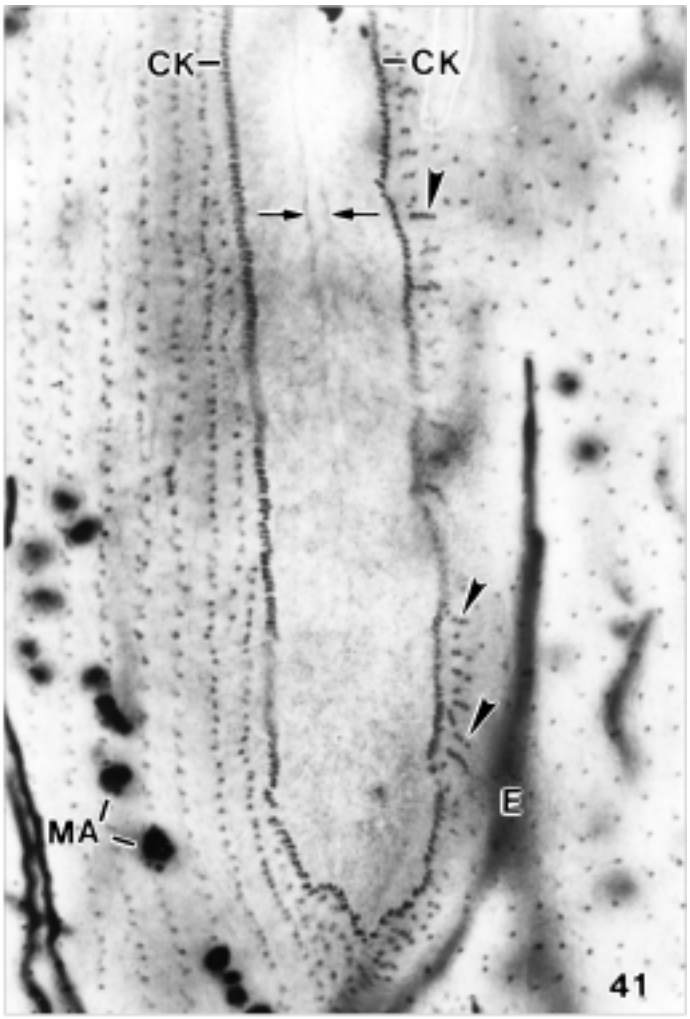


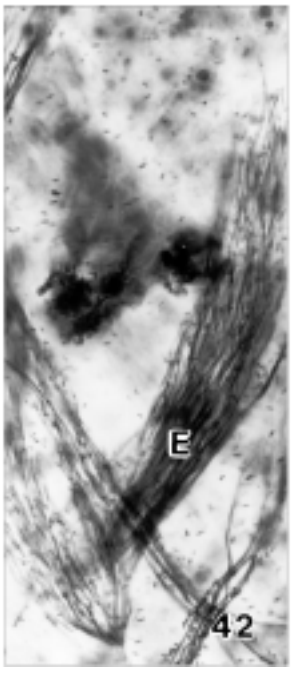
Figs 33-36. *Myriokaryon lieberkuehnii* from life (33) and after protargol impregnation (34-36). **33 -** optical section in mid-body showing the 3-4 µm thick cortex, marked by opposed arrowheads, and many about 80 µm long extrusome bundles; **34, 35** - overviews in mid-body, showing the cell packed with macronuclear nodules and extrusome bundles; **36 -** long (toxicysts, arrows) and short (likely mucocysts, arrowheads) extrusomes occur in the cytoplasm. CV - contractile vacuoles; E - extrusome bundles; FV - food vacuoles; G - cortical granules, likely mucocysts; L - lipid droplets; MA - macronuclear nodules.

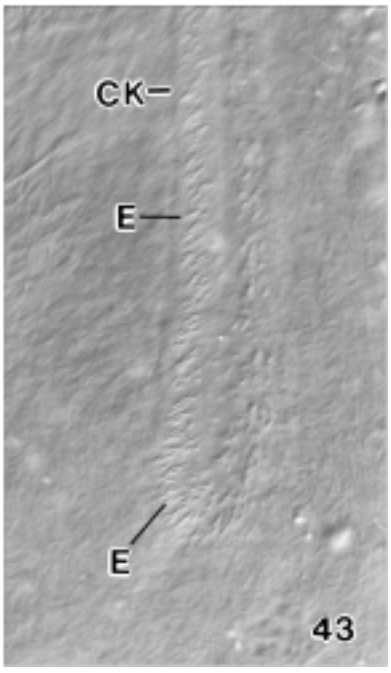


Figs 37-39. *Myriokaryon lieberkuehnii* after protargol impregnation (37, 38) and from life (39). **37, 38** - ventral and dorsal overview of oral body portion showing the slightly dumbbell-shaped mouth and the dorsal brush rows shortening from left to right (arrowheads); **39** - part of dorsal brush showing the curved and distally inflated bristle pairs. Opposed arrowheads mark the 3-4 µm thick cortex. B - dorsal brush; CK - circumoral kinety; E - extrusomes; MA - macronuclear nodules; OS - oral slit.

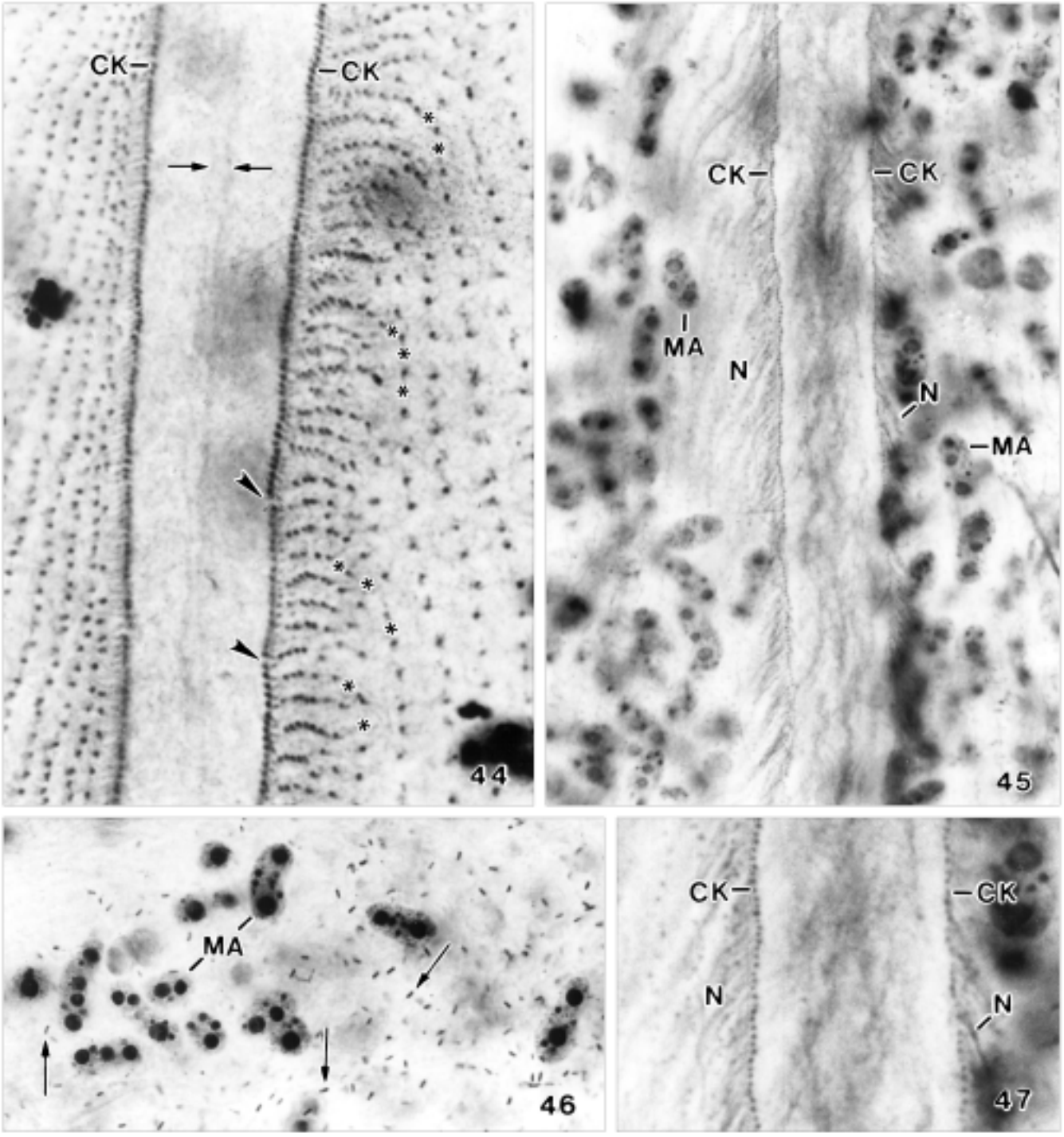




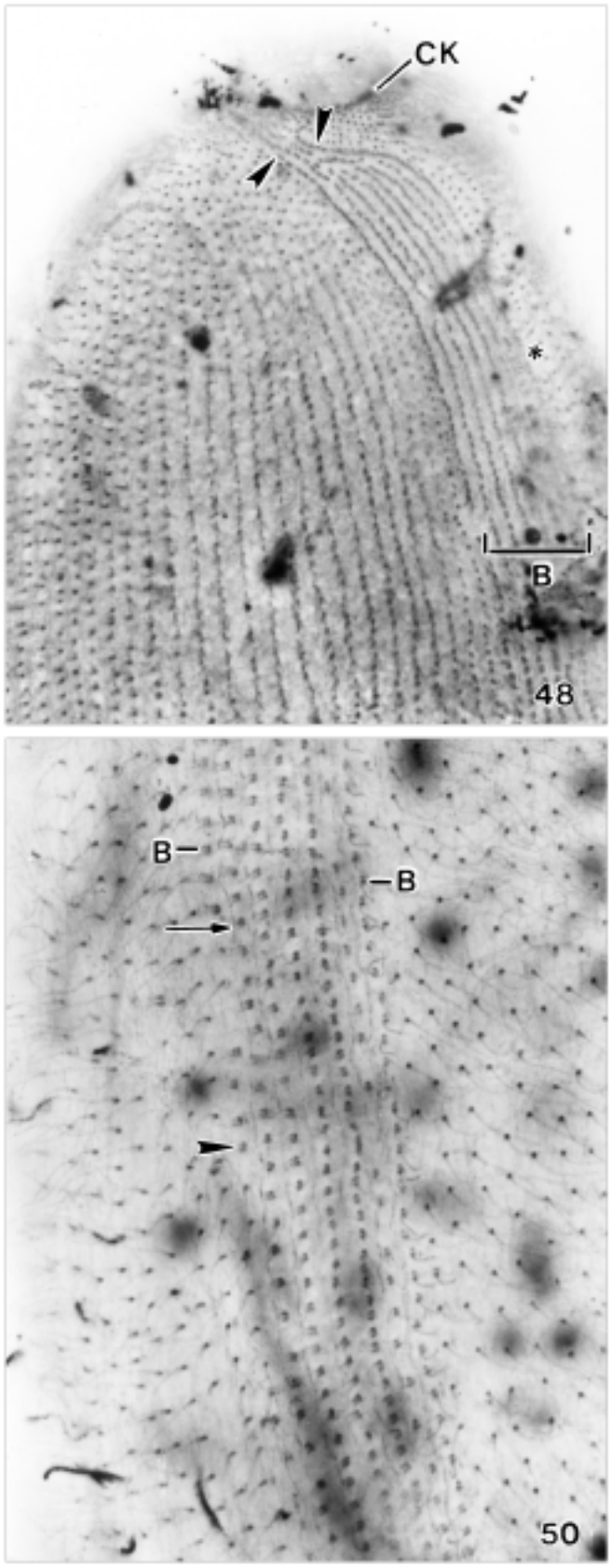


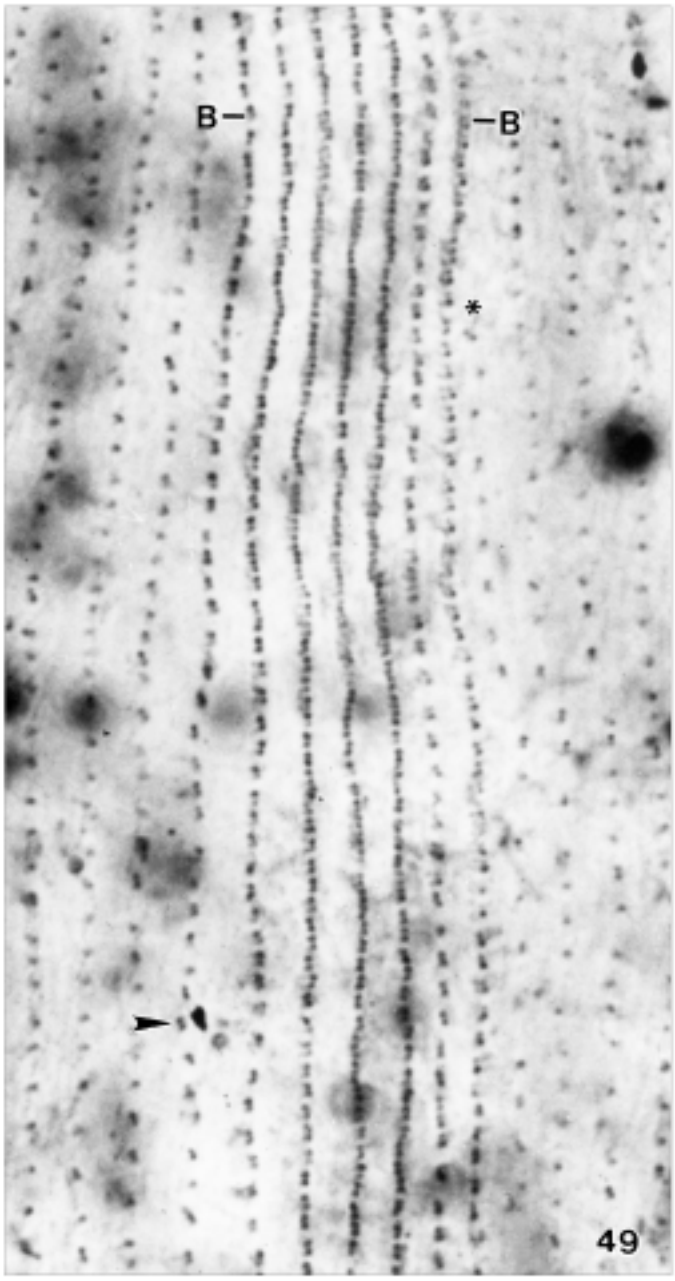


Figs 40-43. *Myriokaryon lieberkuehnii* after protargol impregnation (40-42) and from life (43). **40, 41** - anterior and posterior portion of mouth at high magnification (for an overview, see figure 37). At right, the somatic ciliary rows abut to the dikinetidal circumoral kinety in steep angles, while at left many transversely oriented, monokinetidal kinetofragments occur (some marked by arrowheads), some of which are obviously connected with the ciliary rows. Opposed arrows mark the mouth slit sensu stricto; **42** - extrusome bundles in the cytoplasm; **43** - surface view of posterior portion of oral bulge packed with extrusomes. CK - circumoral kinety; E - extrusomes; MA - macronuclear nodules.

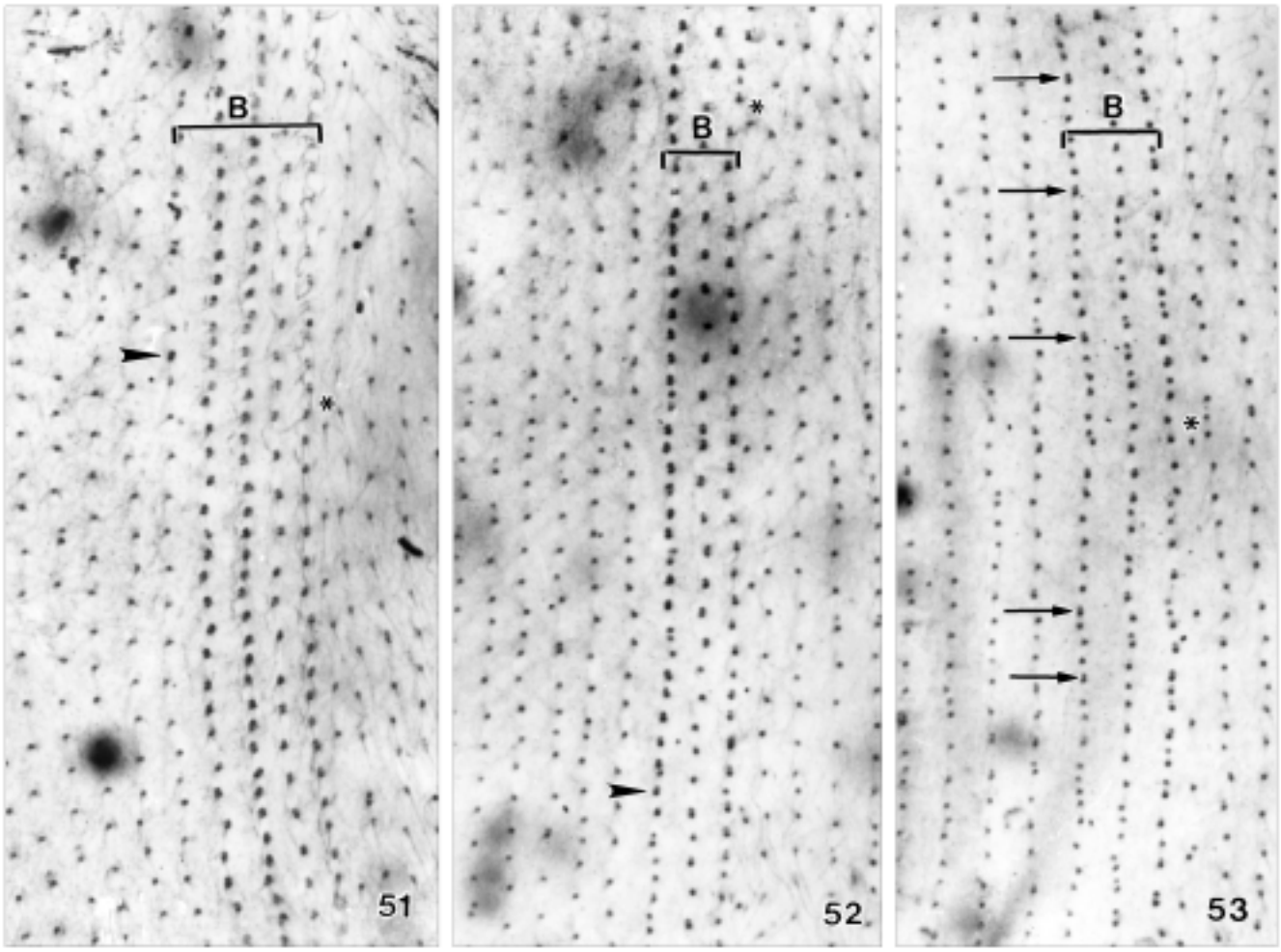


Figs 44-47. *Myriokaryon lieberkuehnii* after protargol impregnation. **44, 45, 47 -** oral infraciliature at high magnification and two focal planes, viz., at level of basal bodies (44) and tightly underneath (45, 47) to show the peripherically arranged macronuclear nodules and the very fine oral basket rods (nematodesmata) associated with the circumoral dikinetids (kinety). The circumoral kinety consists of dikinetidal kinetofragments, of which one is marked by arrowheads (44). Opposed arrows in figure 44 denote the faintly impregnated oral slit sensu stricto. At right, the somatic ciliary rows abut on the circumoral kinety at steep angles, while at left many transversely oriented, monokinetidal kinetofragments occur, some of which are obviously connected with the somatic ciliary rows (asterisks). This pattern reminds on *Spathidium* and *Supraspathidium*; **46 -** macronuclear nodules and 2 µm long rods (arrows), likely developing mucocysts, in subcortical layer. CK - circumoral kinety; MA - macronuclear nodules; N - nematodesmata.





Figs 48-50. *Myriokaryon lieberkuehnii*, dorsal brush after protargol impregnation. The brush consists of narrowly spaced dikinetids in the anterior third of six to eight dorsal ciliary rows (Table 1). Kineties (asterisks) are successively inserted left of the brush. Thus and due to successive addition of kineties along the right mouth margin, kinety number is higher in mid-body than in the oral area. **48 -** anteriorly, the middle brush rows are shortened, while the unshortened marginal rows converge (arrowheads) and produce a unique, pointed brush end; **49, 50 -** subapical brush region of two other specimens, showing that the brush rows are successively shortened from left to right (arrowheads) and continue as ordinary somatic kineties posteriorly (see also following figures). Arrow in figure 50 marks a fine fibre (?) between the brush rows. B - dorsal brush; CK - circumoral kinety.



Figs 51-53. *Myriokaryon lieberkuehnii*, dorsal brush after protargol impregnation. The figures are from the same specimen as shown in figure 49, but demonstrate the middle (51) and posterior (52) region, where the brush, due to successive shortening of the rows from left to right (arrowheads), consist of only five, respectively, three rows. Figure 53 shows the post-brush area, where kinetids are slightly narrower spaced and some dikinetids (arrows) are interspersed in the basically monokinetidal rows extending to rear body end as ordinary somatic kineties. Kineties are successively inserted along the left brush margin (asterisks). Thus and due to the successive addition of kineties along the right mouth margin (Figs 37, 40, 44), kinety number is higher in mid-body than in the oral area. B - dorsal brush.

must be confirmed by more detailed investigations. Indeed, *M. lieberkuehnii* has been confused with other large, likely not yet described species, for instance, by Kahl (1930a; the small form, Fig. 99) and Al-Rasheid (2000), whose identification did not withstand a thorough reinvestigation (slide kindly provided by Dr. K. Al-Rasheid). The specimen illustrated (Fig. 100) and some others contained in the slide are insufficiently impregnated, but observation with interference contrast optics reveals a three-rowed polykinetid along the long and narrow mouth, indicating that it might be a poorly preserved geleiid. These data suggest that misidentifications are common and several not yet described or recognized *Myriokaryon* or *Myriokaryon*-like ciliate species exist, such as *Cranotheridium elongatum* Penard, 1922 and the new genus described below.

Myriokaryon lieberkuehnii is likely restricted to freshwater, occurring in ponds and pond-like habitats (Kahl 1930a; present study) or the lentic zones of running waters (Buck 1961, Dragesco 1972). Only Jankowski (1973) found it in plankton of ponds and in a lake near Leningrad. He observed up to 10 specimens in 1l lake water, where they hanged vertically in the water

column, indicating negative geotaxis. The records available show that *M. lieberkuehnii* has a wide ecological range from clean lake water to microaerobic bog environment (present record); it is thus surprising that it is so rare.

Detailed data on food and environmental requirements are unknown, although Buck (1961) classified *M. lieberkuehnii* as a beta-mesosaprobic indicator species in rivers of Germany. Like me, Jankowski (1973) observed bacteria, organic debris, small diatoms, and chrysomonads in the food vacuoles. *Colpidium*, when added in mass, was not ingested; thus, pure cultures failed. Jankowski (1973) observed globular inclusions 3-6 µm across, possibly endosymbionts.

Cephalospatula gen. n.

Diagnosis: vermiform Myriokaryonidae with long mouth on golfclub-shaped anterior (oral) body portion and 3 isomorphic dorsal brush rows. Extrusomes bundled in inflated anterior portion of oral bulge. At left side of circumoral kinety few oblique kinetofragments more or less distinctly connected with left side ciliary rows (basically *Spathidium* pattern).

Type species: *Cephalospatula brasiliensis* sp. n.

Etymology: composite of the Greek noun *cephalo* (head) and the Latin generic name *Spathidium* (spatulate organism), referring to both, the inflated anterior end and the similarity with members of the family Spathidiidae. Feminine gender.

Description of *Cephalospatula brasiliensis* sp. n. (Figs 54-90; Table 2)

Diagnosis: size about 350 x 35 µm *in vivo*. Rod-shaped with flat, inconspicuous oral bulge extending about one third of body length. Macronucleus filiform. On average 4 contractile vacuoles in line with dorsal brush. Two types of extrusomes: type I acicular and about 10 x 1 µm *in vivo*; type II rod-shaped and 3 µm long. On average 37 ciliary rows and about 50 dikinetids in each brush row.

Type location: floodplain soil of Paraná River in Brazil, near the town of Maringá, 53°15'W 22°40'S.

Etymology: named after the native country.

Type material: 1 holotype slide and 4 paratype slides with protargol-impregnated specimens from type location and 6 voucher slides with protargol-impregnated specimens from the other populations have been deposited in the Biologiezentrum of the Oberösterreichische Landesmuseum in Linz (LI). Relevant specimens are marked by a black ink circle on the cover glass.

Description: I studied 3 populations of this species. However, only few specimens were found, altogether 16 cells. Thus, morphometry of the individual populations is incomplete (Table 2). A closer analysis of the data shows that the two Brazilian populations tend to be more similar to each other than to the Venezuelan specimens, indicating some biogeographic specialization. However, variability of most characters is high, as usual in long and slender ciliates, suggesting that morphometric differences should not be over-interpreted. Nonetheless, I base the diagnosis and description only on the two Brazilian populations. The Venezuelan specimens are considerably longer and thinner than the Brazilian ones (439 x 27 µm *vs*. 375 x 31 µm and 287 x 32 µm) and have also fewer ciliary rows (32 *vs.* 36-38). All other main features, viz., the nuclear apparatus and extrusome size, shape, and location are very similar.

Size 200-500 x 20-45 µm *in vivo*, depending on population, Brazilian specimens frequently near 250 x 35 µm and distinctly stouter than Venezuelan cells (Table 2). Usually rod-shaped and slightly curved, rarely vermiform; unflattened and acontractile. Anterior body end obliquely truncate and slightly inflated, especially in protargol preparations, inflation ("head") and oblique truncation difficult to recognize *in vivo* because specimens are very flexible and restless; posterior end narrowly rounded, widest near or in mid-body (Figs 54, 68, 78, 83, 86, 90). Nuclear apparatus usually in posterior two thirds of cell. Macronucleus filiform, tortuous, often somewhat spiralized and nodulated, ribbon-like flattened (2:1) in most specimens from type location and in some cells from the other populations, a conspicuous feature found also in several slender spathidiids (Foissner *et al*. 2002); nucleoli scattered, small, inconspicuous. On average 18 globular to broadly ellipsoidal micronuclei attached to or near macronuclear strand, some scattered (Figs 54, 67, 69, 80, 83, 86). Three to eight, usually three to five contractile vacuoles in line with dorsal brush, first vacuole, occasionally also second within brush rows; each vacuole with several closely spaced, interkinetal excretory pores in line, except of scattered pores of last vacuole in posterior body end (Figs 54, 57, 66, 68, 71). Cortex rather thick, contains about three rows of pale, 0.8-1 x 0,4 µm-sized granules between each two ciliary rows; granules form short, transverse rows (type location) or arrow-like pattern (other populations) in cortex of oral bulge (Figs 55, 56, 59, 60, 64). Two shape and size types of extrusomes scattered in cytoplasm and assembled to highly conspicuous bundle in inflated anterior portion of oral bulge, definitely lacking in ventral bulge

Table 2. Morphometric data on three populations of *Cephalospatula brasiliensis.*

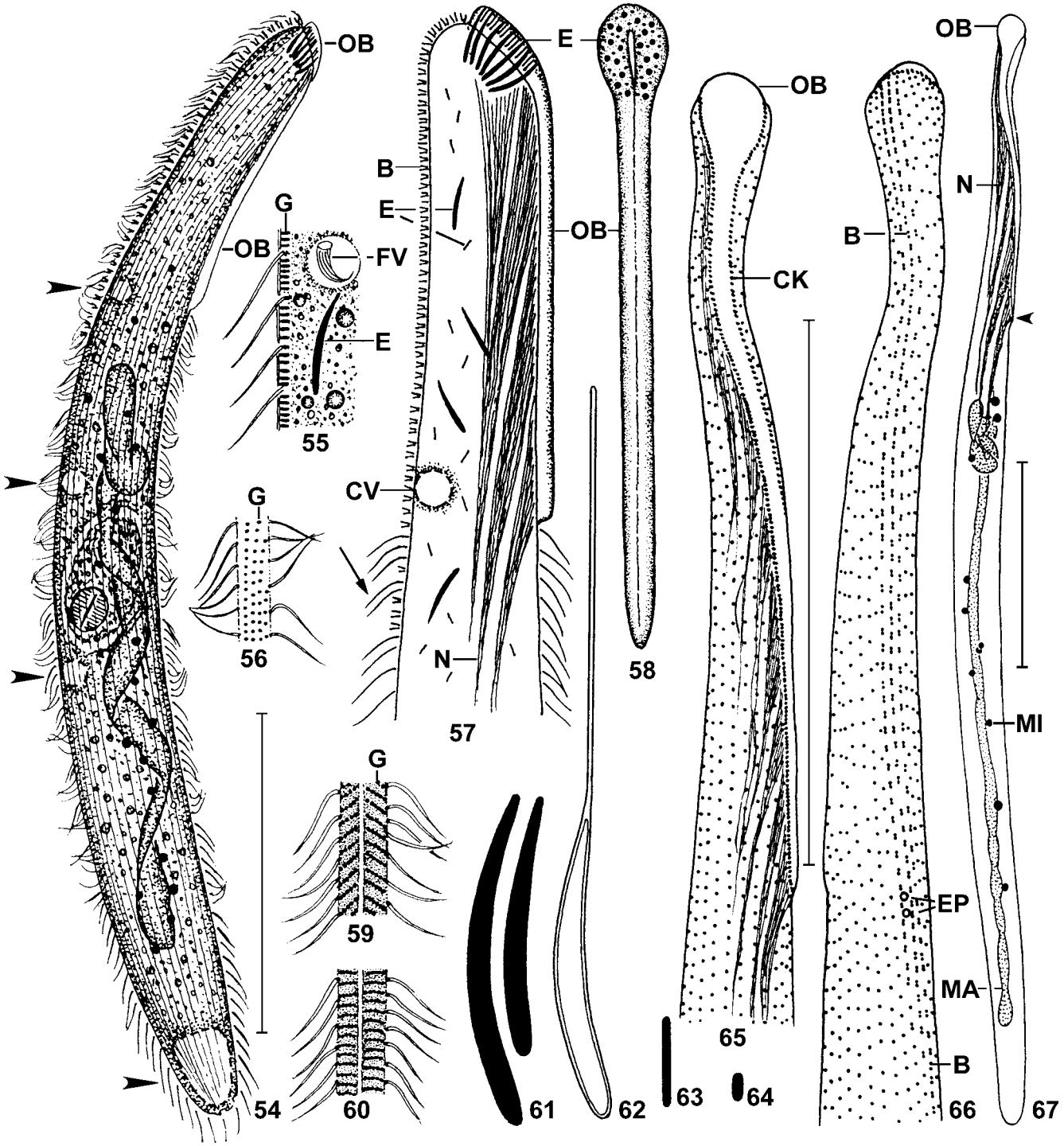
Characteristics[a]	Pop[b]	x	M	SD	SE	CV	Min	Max	n
Body, length	BRP	375.0	390.0	101.9	38.5	27.2	195.0	500.0	7
	BRR	287.5	310.0	59.7	29.8	20.8	200.0	330.0	4
	VEN	439.0	435.0	95.2	42.6	27.7	300.0	550.0	5
	TOT	373.1	380.0	103.4	25.8	21.7	195.0	550.0	16
Body, maximum width	BRP	31.0	31.0	5.0	1.9	16.1	22.0	36.0	7
	BRR	32.0	30.0	5.4	2.7	16.9	28.0	40.0	4
	VEN	26.8	28.0	4.4	2.0	16.6	20.0	31.0	5
	TOT	29.9	30.0	5.1	1.3	17.1	20.0	40.0	16
Body length:width, ratio	BRP	11.9	12.3	1.9	0.7	16.1	8.9	14.7	7
	BRR	9.2	9.3	2.4	1.2	26.2	6.7	11.4	4
	VEN	16.5	15.0	3.5	1.6	21.1	13.7	17.9	5
	TOT	12.7	12.6	3.8	0.9	29.9	6.7	22.0	16
Mouth, length (anterior body end to	BRP	108.0	115.0	29.0	11.0	26.9	55.0	140.0	7
proximal end of circumoral kinety, distance)	BRR	98.5	107.5	21.2	10.6	21.5	67.0	112.0	4
	VEN	128.2	125.0	42.4	19.0	33.1	70.0	180.0	5
	TOT	111.9	111.0	32.4	8.1	29.0	55.0	180.0	16
Body length:mouth length, ratio	BRP	3.5	3.5	0.2	0.1	5.6	3.1	3.7	7
	BRR	2.9	3.0	0.1	0.1	4.9	2.7	3.0	4
	VEN	3.6	3.5	0.5	0.2	15.1	2.8	4.3	5
	TOT	3.4	3.5	0.4	0.1	13.4	2.7	4.3	16
Mouth, anterior width (distance between	BRP	12.0	-	-	-	-	9.0	15.0	2
circumoral kinety in head area)	BRR	14.5	-	-	-	-	12.0	17.0	2
	VEN	12.5	-	-	-	-	12.0	13.0	2
	TOT	13.0	12.5	2.8	1.1	21.2	9.0	17.0	16
Mouth, mid-region width (distance between	BRP	4.7	5.0	-	-	-	4.0	5.0	6
circumoral kinety)	BRR	5.3	4.5	1.9	1.0	36.1	4.0	8.0	4
	VEN	4.0	4.0	-	-	-	4.0	4.0	3
	TOT	4.7	1.1	0.3	23.6	4.0	4.0	8.0	13
Anterior body end to macronucleus, distance	BRP	117.9	125.0	30.7	11.6	26.0	65.0	150.0	7
	BRR	110.5	122.5	34.4	17.2	31.1	60.0	137.0	4
	VEN	147.6	138.0	31.3	14.0	21.2	120.0	190.0	5
	TOT	125.3	125.0	33.5	8.4	26.8	60.0	190.0	16
Macronuclear figure, length	BRP	209.2	200.0	73.9	30.2	35.3	95.0	290.0	6
	BRR	143.0	147.5	38.8	19.4	27.1	92.0	185.0	4
	VEN	232.0	240.0	71.8	32.1	31.0	125.0	310.0	5
	TOT	199.1	190.0	71.3	18.4	35.8	92.0	310.0	15
Macronucleus spread, length (uncoiled but	BRP	270.0	270.0	-	-	-	110.0	400.0	7
not despiralized, very approximate values)	BRR	176.3	180.0	-	-	-	110.0	235.0	4
	VEN	266.0	295.0	-	-	-	125.0	360.0	5
	TOT	245.3	255.0	-	-	-	110.0	400.0	16
Macronucleus, width	BRP	8.7	9.0	1.4	0.5	15.8	7.0	10.0	7
	BRR	6.0	6.0	0.8	0.4	13.6	5.0	7.0	4
	VEN	7.6	8.0	1.5	0.7	20.0	5.0	9.0	5
	TOT	7.7	8.0	1.7	0.4	21.6	5.0	10.0	16
Macronucleus, number (in 2 out of 16	BRP	1.0	1.0	0.0	0.0	0.0	1.0	1.0	5
specimens broken into two long pieces)	BRR	1.0	1.0	0.0	0.0	0.0	1.0	1.0	4
	VEN	1.0	1.0	0.0	0.0	0.0	1.0	1.0	5
	TOT	1.0	1.0	0.0	0.0	0.0	1.0	1.0	14
Micronuclei, diameter	BRP	3.6	3.5	-	-	-	3.0	4.0	7
	BRR	3.5	3.5	-	-	-	3.0	4.0	3
	VEN	3.5	3.5	-	-	-	3.0	4.0	5
	TOT	3.6	3.5	-	-	-	3.0	4.0	16
Micronuclei, number	BRP	19.3	20.0	2.9	1.1	15.2	14.0	23.0	7
	BRR	17.8	17.5	5.7	2.8	32.0	12.0	24.0	4
	VEN	19.0	17.0	4.0	1.8	21.1	15.0	25.0	5
	TOT	18.8	19.0	3.8	1.0	20.3	12.0	25.0	16

Table 2. (contd)	Pop[b]	x	M	SD	SE	CV	Min	Max	n
Contractile vacuoles, number	BRP	5.3	5.0	1.8	0.7	34.0	3.0	8.0	7
	BRR	3.0	3.0	0.0	0.0	0.0	5.0	5.0	3
	VEN	5.0	5.0	1.2	0.6	24.5	3.0	6.0	5
	TOT	5.1	5.0	1.4	0.4	26.4	3.0	8.0	15
Somatic kineties, total number in mid-body	BRP	35.9	36.0	4.5	1.7	12.4	29.0	41.0	7
	BRR	37.8	38.0	2.9	1.4	7.6	34.0	41.0	4
	VEN	31.6	32.0	2.5	1.1	7.9	28.0	35.0	5
	TOT	35.0	34.5	4.2	1.0	11.9	28.0	41.0	16
Ciliated kinetids in a lateral kinety, number	BRP	121.4	130.0	33.0	12.5	27.2	60.0	155.0	7
	BRR	109.3	110.0	29.0	16.8	26.5	80.0	138.0	3
	VEN	154.0	170.0	36.0	16.1	23.4	95.0	183.0	5
	TOT	129.9	138.0	35.9	9.3	27.7	60.0	183.0	15
Dorsal brush rows, number	BRP	3.0	3.0	0.0	0.0	0.0	3.0	3.0	7
	BRR	3.0	3.0	0.0	0.0	0.0	3.0	3.0	3
	VEN	3.0	3.0	0.0	0.0	0.0	3.0	3.0	4
	TOT	3.0	3.0	0.0	0.0	0.0	3.0	3.0	14
Dorsal brush row 1, length (distance circumoral kinety to last dikinetid)	BRP	113.9	100.0	38.5	14.6	33.8	67.0	170.0	7
	BRR	113.3	115.0	2.9	1.7	2.6	110.0	115.0	3
	VEN	157.5	175.0	49.2	24.6	31.3	85.0	195.0	4
	TOT	126.2	115.0	40.8	10.9	32.4	67.0	195.0	14
Dorsal brush row 1, number of dikinetids	BRP	43.9	39.0	14.2	5.4	32.4	26.0	67.0	7
	BRR	40.7	42.0	10.1	5.8	24.8	30.0	50.0	3
	VEN	51.0	55.5	16.0	8.0	31.3	28.0	65.0	4
	TOT	45.2	46.0	13.6	3.6	30.0	26.0	67.0	14
Dorsal brush row 2, length (distance circumoral kinety to last dikinetid)	BRP	123.9	130.0	35.3	13.3	28.5	67.0	170.0	7
	BRR	121.7	120.0	7.6	4.4	6.3	115.0	130.0	3
	VEN	163.8	185.0	53.6	26.8	32.7	85.0	200.0	4
	TOT	134.8	130.0	40.1	10.7	29.8	67.0	200.0	14
Dorsal brush row 2, number of dikinetids	BRP	57.6	55.0	21.8	8.2	37.8	18.0	80.0	7
	BRR	54.0	55.0	13.5	7.8	25.1	40.0	67.0	3
	VEN	57.0	67.0	19.1	11.0	33.5	35.0	69.0	3
	TOT	56.6	55.0	18.2	5.0	32.1	18.0	80.0	13
Dorsal brush row 3, length (distance circumoral kinety to last dikinetid)	BRP	133.1	130.0	41.1	15.5	30.9	67.0	190.0	7
	BRR	125.0	125.0	5.0	2.9	4.0	120.0	130.0	3
	VEN	163.8	182.5	46.6	23.3	28.5	95.0	195.0	4
	TOT	140.1	130.0	39.2	10.5	28.0	67.0	195.0	14
Dorsal brush row 3, number of dikinetids	BRP	49.1	50.0	14.4	5.4	29.3	27.0	70.0	7
	BRR	49.0	50.0	10.5	6.1	21.5	38.0	59.0	3
	VEN	49.8	51.5	12.5	6.2	25.1	33.0	63.0	4
	TOT	49.3	50.0	12.2	3.3	24.7	27.0	70.0	14

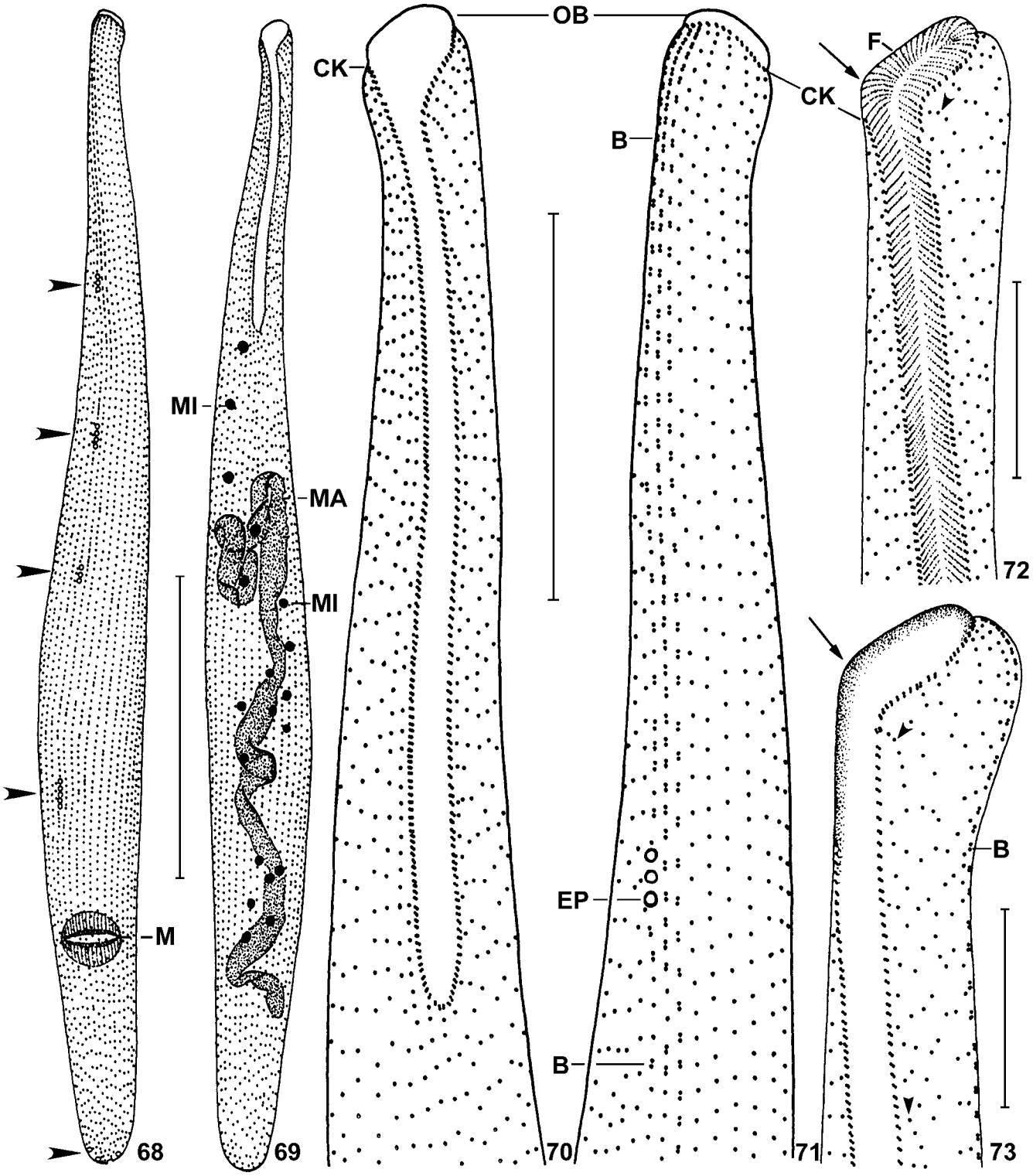
[a] Data based on mounted, protargol-impregnated (Foissner's method), morphostatic specimens from non-flooded Petri dish cultures. Measurements in µm. CV - coefficient of variation in %, M - median, Max - maximum, Min - minimum, n - number of individuals investigated, SD - standard deviation, SE - standard error of arithmetic mean, x - arithmetic mean. [b] Populations: BRP - Brazil, Paraná floodplain type population; BRR - Brazil, Restingha region (Mata Atlantica) near Rio de Janeiro; VEN - Venezuela, Laja (rock pool) at Puerto Ayacucho airport; TOT - all three populations combined.

portion of all populations and specimens investigated (Figs 54, 57, 58, 61-63, 79, 81, 82, 90): type I extrusomes conspicuous because acicular, slightly curved and 12 x 1 µm in size (9-11 x 1 µm in second Brazilian population, 12-14 x 1 µm in Venezuelan specimens), rarely faintly impregnate with the protargol method used; type II extrusomes rod-shaped, inconspicuous because fine and only 3-4 µm long. Exploded type I extrusomes 25-35 x 1 µm in size, of typical toxicyst structure (Figs 62, 79, 82). Cytoplasm colourless, usually crammed with lipid droplets 1-2 µm across and food vacuoles containing remnants of rotifers and oral baskets of small ciliates, likely *Drepanomonas* (Figs 54, 55, 68). Swims rather rapidly by rotation about main body axis, showing great flexibility.

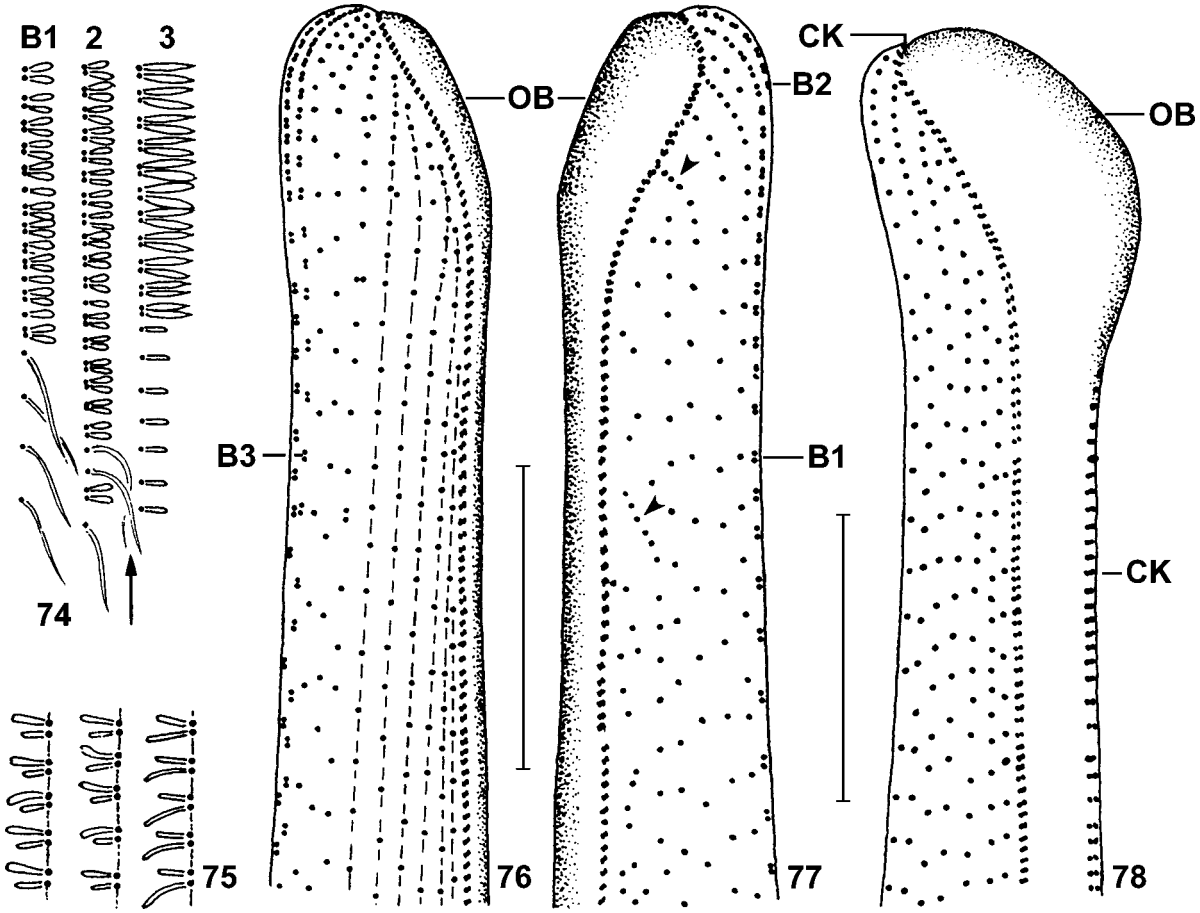
Cilia about 8 µm long *in vivo*, loosely spaced in oral area, arranged in an average of 37 (32 in Venezuelan specimens) ordinarily and equidistantly spaced rows abutting on circumoral kinety in *Spathidium* pattern, that is, in steep angles on right side and at almost right angles



Figs 54-67. *Cephalospatula brasiliensis* from life (54-64) and after protargol impregnation (65-67). **54 -** right side view of a representative specimen from type location. Note the large food vacuole with a decomposing rotifer in mid-body. Arrowheads mark contractile vacuoles; **55, 56 -** optical section and surface view of cortex. Note food vacuole with a decomposing oral basket of a microthoracid ciliate; **57, 58 -** lateral and frontal view of oral area, showing the conspicuous, spoon-shaped oral bulge containing extrusomes only in the anterior inflation. Arrow marks posterior brush region, where bristles and ordinary cilia alternate; **59, 60 -** cortical granulation of oral bulge in a Venezuelan (59) and Brazilian (60) specimen; **61-63 -** resting (61, 63) and exploded (62) type I (61, 62) and type II (63) oral bulge extrusomes, drawn to scale, length 9-12 µm, 25 µm, 3-4 µm; **64 -** cortical granule, about 0.8-1 x 0.4 µm; **65, 66 -** ventral and dorsal view of ciliary pattern in oral body portion of a Venezuelan specimen; **67 -** ventrolateral view of a Venezuelan specimen with almost straight macronucleus. Arrowhead marks end of oral bulge. B - dorsal brush; CK - circumoral kinety; CV - contractile vacuole; E - extrusomes; EP - excretory pores; FV - food vacuole; G - cortical granules; MA - macronucleus; MI - micronucleus; N - nematodesmata; OB - oral bulge. Scale bars 100 µm.



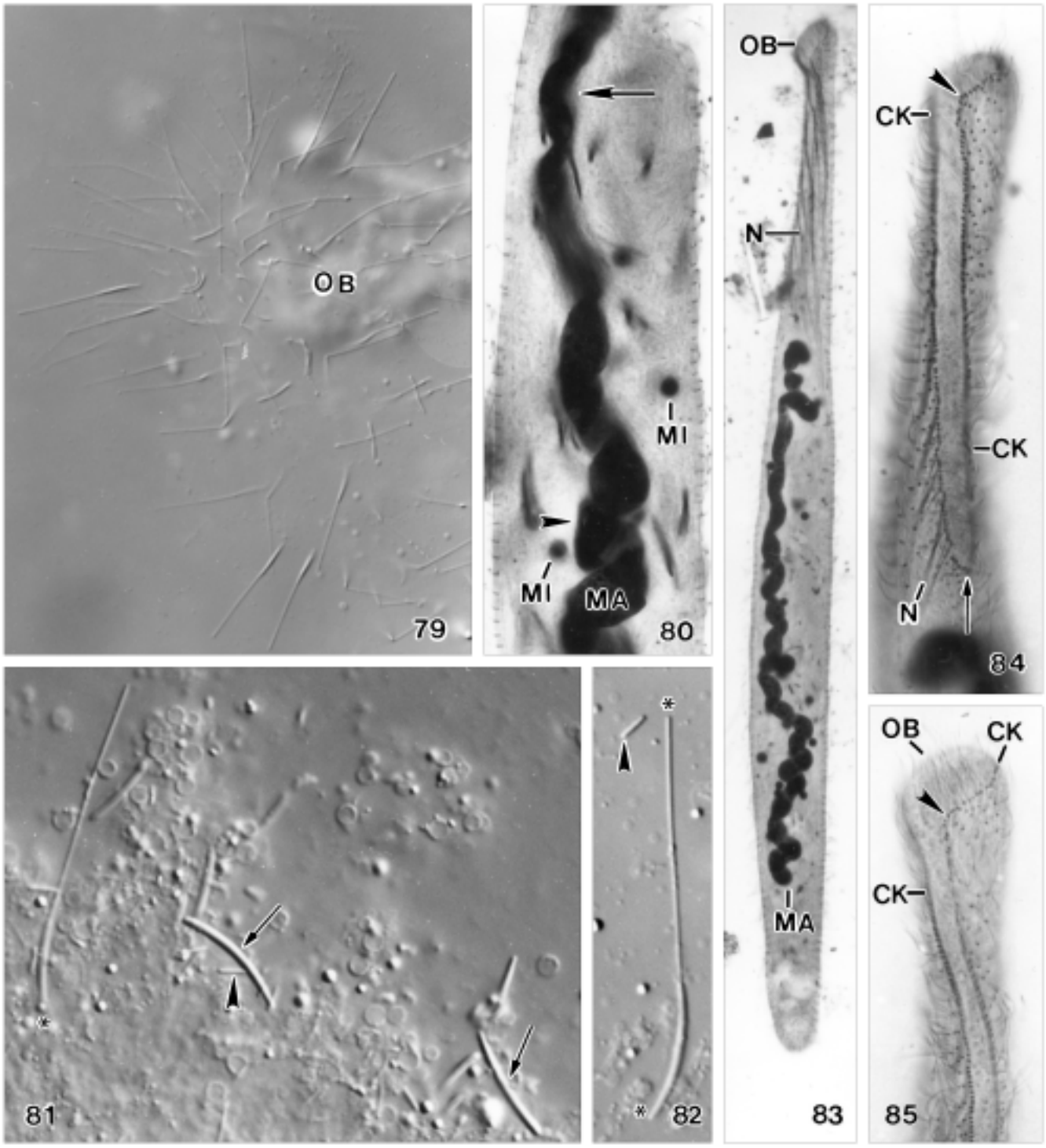
Figs 68-73. *Cephalospatula brasiliensis*, ciliary pattern after protargol impregnation. **68, 69** - dorsal and ventral view of holotype specimen. Arrowheads mark excretory pores of the contractile vacuoles; **70, 71** - ventral and dorsal view of oral body portion of holotype specimen; **72, 73** - left side view of anterior body portion of two other specimens from type location. Note the sharp angle in the oral bulge (arrows) and circumoral kinety caused by the oblique truncation of the body end. Arrowheads mark indistinct left side kinetofragments. B - dorsal brush; CK - circumoral kinety; EP - excretory pores; F - oral bulge fibres; M - mastax of a rotifer; MA - macronucleus; MI - micronuclei; OB - oral bulge. Scale bars 100 µm (68, 69); 40 µm (70, 71); 20 µm (72, 73).



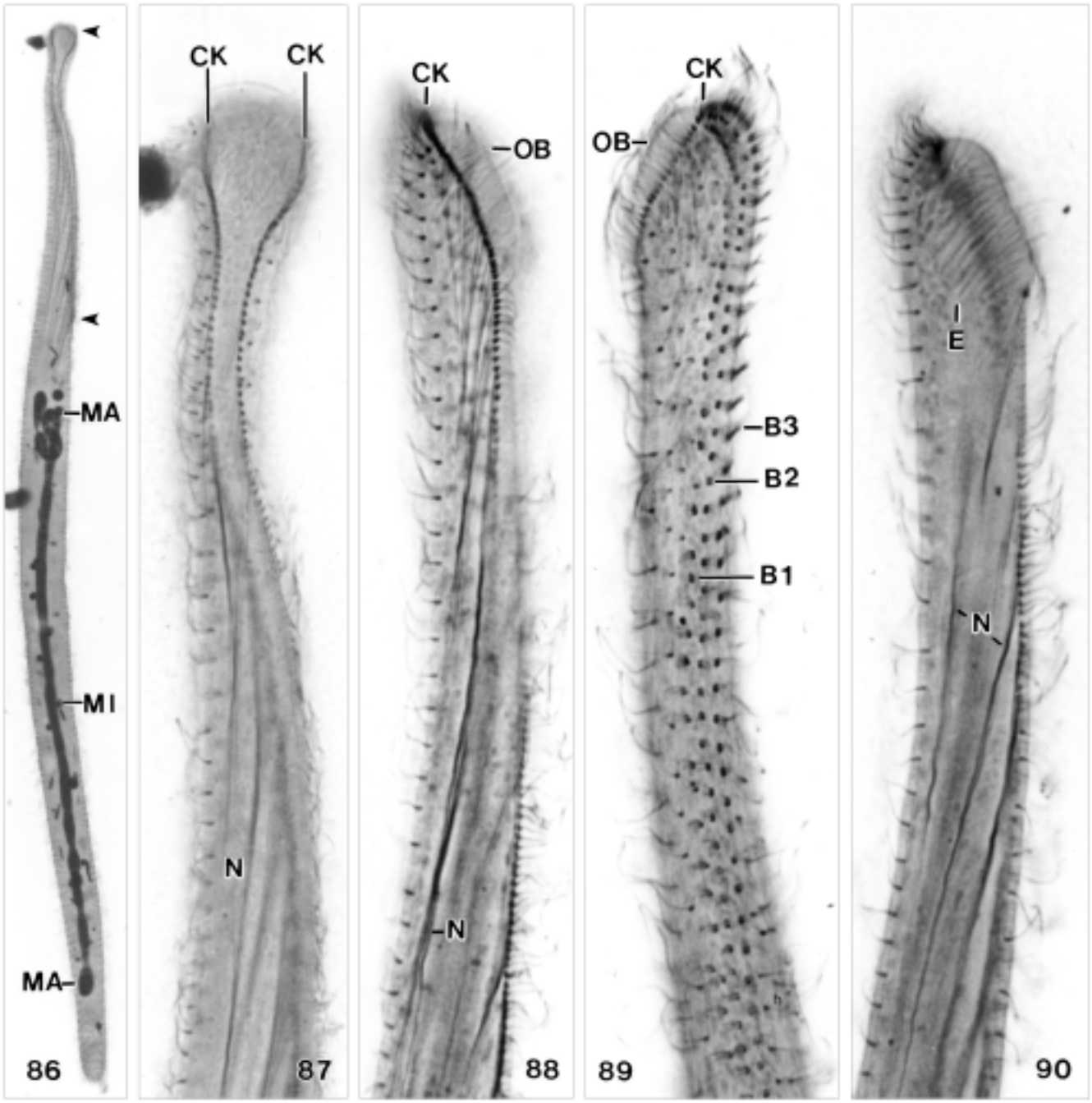
Figs 74-78. *Cephalospatula brasiliensis* from life (74) and after protargol impregnation (75-78). **74, 75 -** posterior portion of dorsal brush in a specimen from Brazilian type location *in vivo* (74) and middle brush region of a Venezuelan specimen after protargol impregnation. Arrow denotes ordinary cilia between brush bristles. Note monokinetidal bristle tail of row 3; **76, 77 -** right and left side ciliary pattern of anterior body portion in a Venezuelan specimen. The ciliary rows (basal bodies connected by lines) abut on the right branch of the circumoral kinety at very steep angles (*Arcuospathidium*/*Myriokaryon* pattern), while at left side an indistinct *Myriokaryon* pattern occurs, as indicated by some oblique kinetofragments (arrowheads); **78 -** ventrolateral view of anterior portion of a specimen from Brazilian population II. Note the strong inflation of the anterior body end, respectively, of the oral bulge. B1-3 - dorsal brush rows; CK - circumoral kinety; OB - oral bulge. Scale bars 20 µm.

on left; left side pattern, however, distinct only in apical region, where cilia form kinetofragment-like condensations (Figs 54, 65, 68-73, 76-78, 83-85, 87, 88; Table 2). Three dorsolateral ciliary rows anteriorly differentiated to dorsal brush occupying 35% of body length on average; brush, however, inconspicuous *in vivo* because bristles merely up to 4 µm long; dikinetidal and monokinetidal bristles irregularly alternate in posterior region of brush, and some monokinetids are interspersed in whole length of brush (Figs 54, 57, 66, 68, 71, 76, 77, 89; Table 2). Brush rows 1 and 2 of very similar structure, that is, composed of about 2 µm long, paired, inflated bristles, row 2 slightly longer than rows 1 and 3; row 3 composed of 3-4 µm long, fusiform bristles and a monokinetidal tail extending to second body third with about 3 µm long bristles; rarely, brush rows have a short, monokinetidal tail anteriorly (Figs 54, 57, 74, 75).

Mouth extends on anterior third of body, indistinct, except of inflated anterior portion containing the conspicuous extrusome bundle, due to the flat, hardly projecting oral bulge. Oral bulge distinctly spoon-shaped, conspicuous when viewed ventrally, both *in vivo* and protargol preparations, due to the anterior inflation; contains fine, short fibres originating from circumoral dikinetids and extending obliquely anteriorly. Circumoral kinety composed of comparatively widely spaced, oblique dikinetids having ciliated only one basal body; of same shape as oral bulge, shows highly characteristic,



Figs 79-85. *Cephalospatula brasiliensis* from life (79, 81, 82) and after protargol impregnation (80, 83-85). **79 -** anterior body (oral bulge) end of a squashed specimen with released type I extrusomes, which have typical toxicyst structure and are about 25 µm long; **80 -** middle portion of nuclear apparatus. The macronucleus is spiralized and ribbon-like flattened showing either the broad (arrowhead) or narrow (arrow) side; **81, 82 -** resting (arrows) and extruded (asterisks) type I extrusomes and resting type II extrusomes (arrowheads), which are 3-4 µm long; **83 -** overview showing some main features, such as the obliquely truncated anterior end and the spiralized macronucleus; **84, 85 -** ventral views of anterior body portion showing the sharp bend (arrowheads) in the oral bulge and circumoral kinety, a main feature of the family Myriokaryonidae. Arrow denotes proximal end of mouth (circumoral kinety). CK - circumoral kinety; MA - macronucleus; MI - micronuclei; N - nematodesmata; OB - oral bulge.



Figs 86-90. *Cephalospatula brasiliensis* after protargol impregnation. **86, 87 -** overview and oral detail of a slender specimen. Arrowheads mark the mouth, respectively, oral bulge, which is hardly set off from body proper proximally, and thus difficult to recognize *in vivo*. Note the conspicuous widening of oral bulge and circumoral kinety in the truncated anterior body end, a main feature of the family; extrusomes are contained only in the widened area, a main feature of the genus (Figs 57, 90); **88-90 -** right (88) and left (89) side view of ciliary pattern and optical section (90) of a laterally oriented specimen showing details of oral area, viz., the anteriorly distinctly curved dikinetidal circumoral kinety associated with conspicuous nematodesmata; the three-rowed dorsal brush; and the extrusomes in the anterior widening of the oral bulge. B1-3 - dorsal brush rows; CK - circumoral kinety; E - extrusomes; MA - macronucleus; MI - micronucleus; N - nematodesmata (oral basket rods); OB - oral bulge.

sharp bend subapically, that is, in the transition zone of oblique anterior and straight ventral portion. Oral basket conspicuous because of long nematodesma bundles originating from circumoral dikinetids (Figs 54, 57, 58, 65-73, 76-78, 83-90; Table 1).

Occurrence and ecology: as yet found only at three sites in South America, as described in the material and methods section, although I investigated similar biotopes worldwide (Foissner 1998, Foissner *et al*. 2002, and unpubl. data), suggesting that this conspicuous ciliate might be restricted to South America and/or Gondwana. Two of the three sites, and to a certain extent also the Restingha area, are definitely semiterrestrial (floodplain soil, mud and soil from a rock-pool), indicating that *C. brasiliensis* might occur also in ordinary freshwaters, although the slender shape suggests a preference for soil (Foissner 1987).

DISCUSSION

Myriokaryonidae fam. n.

Diagnosis: Spathidiina with spoon-shaped oral bulge (circumoral kinety) and oblique to transverse-truncate anterior body end, causing a more or less sharp bend in oral bulge and circumoral kinety.

Type genus: *Myriokaryon* Jankowski, 1973.

Nomenclature: Jankowski (1975) already erected a family Myriokaryonidae, but without any characterization. Thus, it is a nomen nudum.

Suprafamiliar classification: *Myriokaryon* and related genera belong to the gymnostomatous holotrichs, as defined by Corliss (1979), Grain (1994), and Lynn and Small (2002), because they have a holotrichous ciliature composed of monokinetids, a rhabdos-type oral ciliature, a dorsal brush, and toxicysts. Today, this assemblage is usually ranked as a class, viz., Litostomatea or Gymnostomatea (Foissner *et al*. 2002). Many distinct groups are recognizable within this large clade, which contains about 1000 described and many undescribed species (Foissner *et al*. 2002). Unfortunately, within-class classification differs considerably, likely because few detailed data are available on ultrastructure, character states (plesiomorphies, apomorphies), and gene sequences (Corliss 1979, Foissner and Foissner 1988, Grain 1994, Lynn and Small 2002). My own cladistic attempts (unpubl., Hennig's method) failed because I could not unequivocally determine the state of most characters. Similarly, the cladistic analysis by Lipscomb and Riordan (1990) obviously confused character states because spathidiids and pleurostomatids form a clade, which is, in my opinion, unlikely. Gene sequence data are available only from few species and thus cannot be used in the present context. Thus, my classification of the Myriokaryonidae follows the system of Foissner and Foissner (1988), which is based on light microscopical and ultrastructural data. However, I emphasize that any classification must be considered as preliminary at the present state of knowledge.

In spite of these problems, most recent authors agree that *Myriokaryon* belongs to the group which contains *Spathidium* and related genera. This is in accordance with the present results, which suggest that the Myriokaryonidae should be classified as a family of the order Spathidiida Foissner and Foissner (1988): "Cytostome apical, round or slit-like, in suborder Didiniina on top of cone-like proboscis; rhabdos made of three microtubular components: transverse ribbons originating from the nonciliated kinetosomes of the oral dikinetids, nematodesmal bundles originating exclusively from the same source, and bulge microtubules; somatic ciliation uniform or limited to dense bands which, however, rest within longitudinally running kineties composed of nonciliated kinetids; dorsal brush composed of two to many kineties; toxicysts localized, typically in or near oral area; free-living". Foissner and Foissner (1988) distinguish three suborders within the Spathidiida, viz., the Belonophryina (mainly *Actinobolina* and related genera), the Didiniina (*Didinium* and related genera), and the Spathidiina, which they define as follows: "Cytostome apical, round, oval or slit-like, in some genera covering the ventral body margin; somatic ciliation usually uniform". Obviously, the Myriokaryonidae match this definition.

Comparison with related families: the Myriokaryonidae are established to include *Myriokaryon* Jankowski, 1973 and three new genera, viz., *Cephalospatula*, *Berghophrya*, and *Kahlophrya*. The key features uniting these genera, viz., the transverse-truncate anterior body end and the spoon-like anterior widening of the circumoral kinety and oral bulge are, unfortunately, difficult to recognize because the truncated part, viz., the spoon-shovel, is small and the oral bulge flat (Figs 1, 5, 13, 20, 40, 48, 54, 57, 70, 76-78, 83-85). The truncation of the body end causes a highly characteristic bend of the oral bulge and circumoral kinety in the transition zone of spoon-shovel and spoon-handle, that is, the region where the oral bulge and the circumoral kinety enter the ventral side of the cell (Figs 15, 26-28, 57, 72, 73, 76, 84,

85, 87, 88); again, the bend is not easily recognized neither *in vivo* or silver preparations, especially in the elliptical species, viz., *Bergophrya* and *Kahlophrya* (Figs 102, 103, 107, 109-111).

As discussed above, the Myriokaryonidae match the diagnosis of the suborder Spathidiina, which contains the families Spathidiidae, Lacrymariidae, Homalozoonidae, and Trachelophyllidae; the latter family was raised to subordinal rank recently (Foissner *et al*. 2002). Within this assemblage, the Myriokaryonidae are obviously most closely related to the Spathidiidae, as shown by the general body plan and ciliary pattern, which basically match those of "classical" spathidiids, such as *Spathidium* and *Arcuospathidium*, as described by Foissner (1984) and Foissner *et al*. (2002). Interestingly, most generic patterns found in the Spathidiidae occur also in the Myriokaryonidae, indicating highly convergent evolution.

Admittedly, the features separating the Myriokaryonidae from the Spathidiidae (preliminary characterization: Spathidiina with roundish to elongate elliptical oral bulge and circumoral kinety) are rather inconspicuous. However, this must be considered under a more general view, viz., that haptorid gymnostomes have, compared with hypotrichs for instance, fewer distinct features, which, additionally, are more difficult to recognize and reveal.

Kahl (1930a) classified *Myriokaryon lieberkuehnii* in *Pseudoprorodon* (now *Prorodon* for nomenclatural reasons, see Aescht 2001 and Foissner *et al*. 1994), a still poorly known genus of unclear affinities. However, if the redescription of the type species, *P. niveus*, by Grolière (1977) is accepted, then *Prorodon* is highly different from *Myriokaryon* and, likely, also from the spathidiids. This is emphasized by *Pseudoprorodon* (now *Prorodon*) *arenicola*, which, at first glance, looks like a myriokaryonid (Dragesco 1960), but has a prorodontid oral basket (Kattar 1972).

Based on a reinvestigation, Jankowski (1973) classified *Prorodon lieberkuehnii* into a new genus, *Myriokaryon*, which he assigned to the Tracheliidae because of the supposed dileptid oral ciliary pattern. This was not accepted by Lynn and Small (2002), who classified *Myriokaryon* in the Spathidiidae, a relationship also discussed by Jankowski (1973). My investigations show that the short, transverse kineties at the left side of the circumoral kinety are not dileptid preoral ciliary rows, as supposed by Jankowski (1973), but the polymerized anterior end of the left side somatic kineties. Such polymerization is frequent in spathidiids (Foissner 1984, Foissner *et al*. 2002).

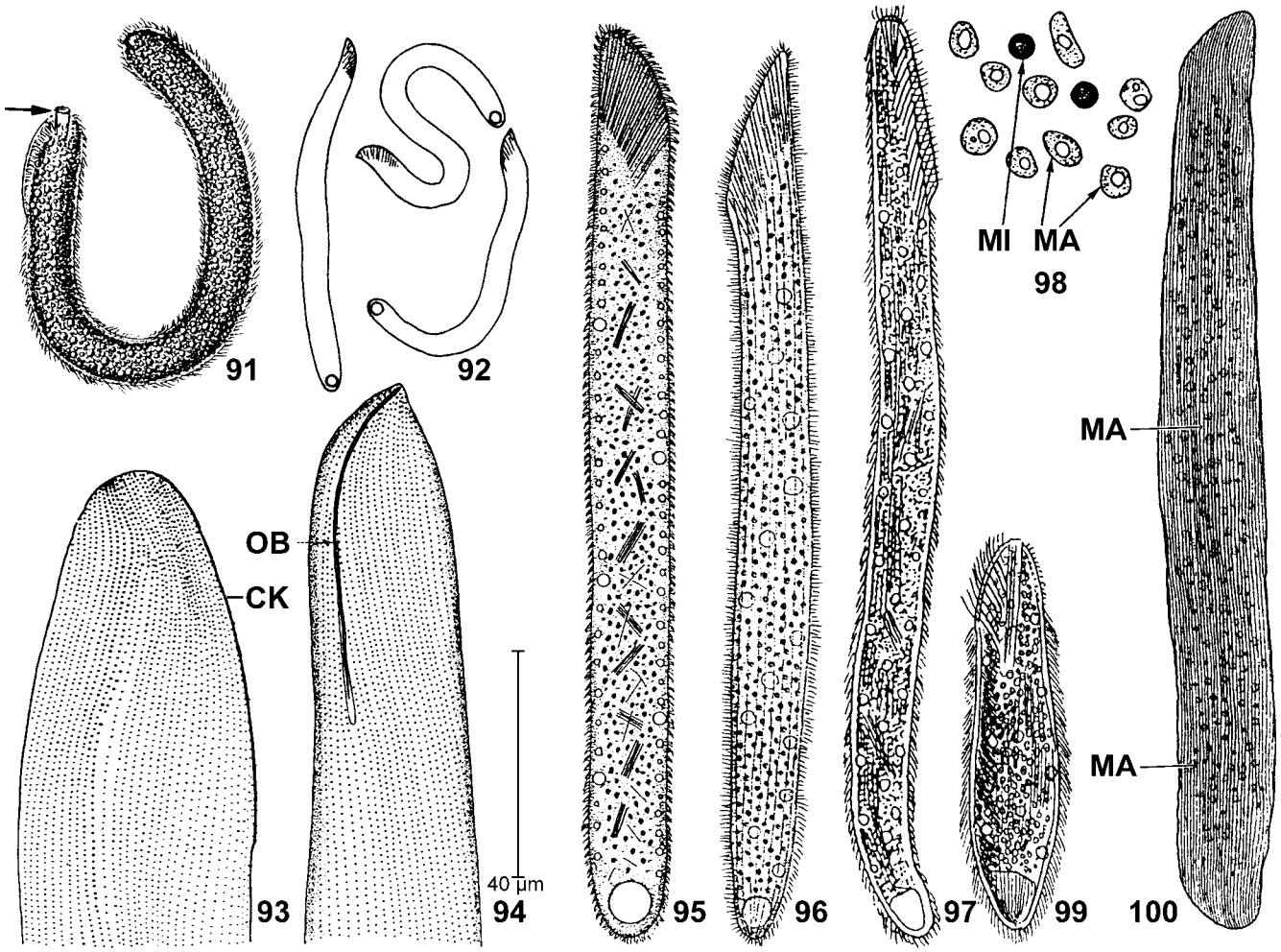
Cranotheridium foliosum (Foissner, 1983), as redescribed by Wirnsberger *et al*. (1984), has very similar generic features as *Myriokaryon*, viz., a slightly spoon-shaped oral bulge and many isomorphic dorsal brush rows. However, I hesitate to transfer it to *Myriokaryon* because it is a small (length near 80 µm), *Spathidium*-shaped species and thus quite dissimilar to *M. lieberkuehnii*. Possibly, *C. foliosum* evolved convergently and belongs to the Spathidiidae, as proposed by Wirnsberger *et al*. (1984). Unfortunately, details of the oral and somatic ciliary pattern of *Cranotheridium taeniatum*, type of the genus, are unknown. However, if the observations of Schewiakoff (1893) are correct, *Cranotheridium* likely neither belongs to the Myriokaryonidae nor Spathidiidae because it has a distinct, prostomatid or nassulid pharyngeal basket. Indeed, very recent observations on a *Cranotheridium foliosum*-like ciliate from soil suggest that such species represent a new spathidiid genus different from *Cranotheridium* Schewiakoff, 1893.

Myriokaryon lieberkuehnii

My population of *M. lieberkuehnii* basically matches the original figure by Bütschli (1889) and several redescriptions (Kahl 1930a, Dragesco 1972, Jankowski 1973, Dragesco and Dragesco-Kernéis 1986), especially in having a large, slender body with a minute, transverse truncation anteriorly; more than 2000 macronuclear nodules; many contractile vacuoles; long, fine extrusomes; and about 100 ciliary rows. Thus, identification is beyond reasonable doubts.

However, more or less pronounced differences are found in details, all likely caused by incomplete and/or incorrect observations of the above mentioned authors. I shall not discuss all these mistakes, but some must be mentioned for the sake of identification and taxonomic classification; a few doubtful identifications and synonymies are mentioned in Kahl (1930a) and the distribution and ecology section.

Bütschli (1889) and Kahl (1930a) illustrated a sort of conical oral basket at the anterior end of the organisms (Figs 91, 97, 99). Such basket is definitely absent in my specimens. I do not have any explanation for this difference, except of that these are different species, which is, however, unlikely considering that many other features match well. Jankowski (1973) suggests that previous authors misinterpreted the apical extrusome bundles ("trichites") as a nematodesmal apparatus. Dragesco (1972) and Dragesco and Dragesco-Kernéis (1986), whose *in vivo* observations match my data, did



Figs 91-100. *Myriokaryon lieberkuehnii*, figures from literature. **91** - from Bütschli (1889), length 1250 µm. Arrow marks tubular "mouth"; **92, 93, 95, 98** - from Dragesco (1972), shape variability from life (92), ciliary pattern in anterior body region after protargol impregnation (93), general *in vivo* view, length 1100 µm (95), and nuclear pattern after Feulgen reaction (98); **94** - from Dragesco and Dragesco-Kernéis (1986), ciliary pattern of ventral side after protargol impregnation; **96** - from Cunha (1914), general *in vivo* view, length 600-800 µm; **97** - from Kahl (1930a), general *in vivo* view of an ordinary specimen, length 1100 µm; **99** - from Kahl (1930a), general *in vivo* view of a small specimen, length 600 µm (likely a misidentification); **100** - from Al-Rasheid (2000), left lateral view after protargol impregnation, length 600-800 µm (misidentification, see discussion). CK - circumoral kinety; MA - macronuclear nodules; MI - micronucleus, OB - oral bulge.

not see the dorsal brush and the special ciliary pattern at the left side of the circumoral kinety, although they used protargol impregnation (Figs 92-95). Likely, their preparations were too weak. The data of Jankowski (1973) are much better than those of Dragesco, although he misinterpreted the whole mouth organization, possibly because he related *Myriokaryon* to the dileptids (Fig. 101). Specifically, he did not observe the circumoral kinety and the very fine nematodesmata. Thus, he interpreted the narrow, central mouth slit as "mouth free of any nematodesmal armature". Further, he misinterpreted the densely ciliated anterior end of the left side ciliary rows as tracheliid preoral kineties, and the long toxicysts as "trichites". On the other hand, Jankowski (1973) recognized, inter alia, the widened anterior end of the oral bulge, the polymerized anterior end of the left side kineties, and the high number (about 10) of dorsal brush rows (thigmotactic stripe).

Cephalospatula brasiliensis as a new genus and species

Cephalospatula is obviously related to *Myriokaryon*, as shown by distinct similarities in shape of body and oral bulge and the kinetofragments along the left margin of the circumoral kinety, although these are less conspicuous. On the other hand, there are also considerable differences, mainly in the number of dorsal brush rows (three *vs.* many) and the arrangement of the oral

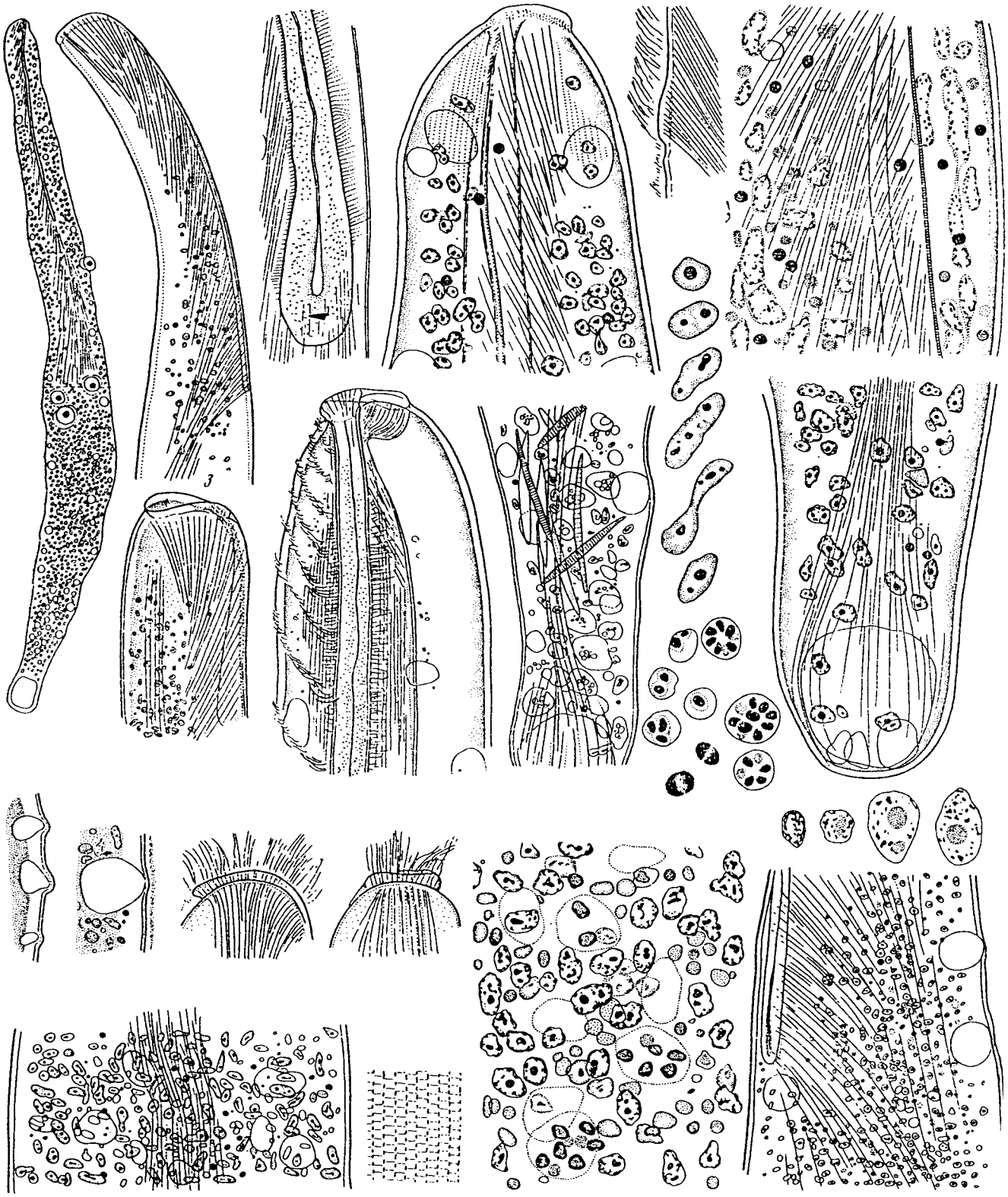


Fig. 101. *Myriokaryon lieberkuehnii*, Russian neotype population investigated by Jankowski (1973). Figures without scale bars and explained in text. Thus, the reader is referred to the original publication (English translation available from Foissner).

extrusomes (single apical bundle *vs.* scattered in whole bulge). Three brush rows are the usual brush pattern in haptorid gymnostomes and are thus likely the plesiomorphic state of this important specialization (Foissner and Foissner 1988, Foissner *et al*. 2002). Thus, any deviation from this pattern, as in *Myriokaryon*, should be rated rather high, viz., at genus level. Likewise, the extrusome pattern is widely used for separation of genera and even families, for instance, in the spathidiid genera *Legendrea* and *Cranotheridium* (see Kahl 1930a for literature), and the definition of the family Pleuroplitidae Foissner, 1996.

There is only one species in the literature, viz., *Spathidium vermiforme* Penard, 1922, bearing some resemblance to *C. brasiliensis*. However, *S. vermiforme* is leaf-like flattened and has the extrusomes scattered in the short, oblique oral bulge. Thus, *C. brasiliensis* is a very distinct species easy to recognize by the large, slender body; the extrusome bundle in the widened apical end; the filiform macronucleus; and the dorsal row of contractile vacuoles.

Berghophrya gen. n. (Figs 102-109)

Diagnosis: ellipsoidal Myriokaryonidae with short mouth on obliquely truncated anterior body end and 3 dorsal brush rows accompanied by 3 rows of papillae. Extrusomes scattered in oral bulge and postoral bundles. Infraciliature likely in *Arcuospathidium* pattern.

Type species: *Holophrya Emmae* Bergh, 1896.

Dedication: I dedicate this genus to Dr. R. S. Bergh, the Danish protozoologist who discovered and described the type species so well that the data are useful even today. *Berghophrya* is a composite of *Bergh* and the Greek noun *ophrya* (eyebrow ~ cilia ~ ciliate). Feminine gender.

Comparison with related genera: the excellent observations of Bergh (1896) were confirmed and supplemented by Kahl (1930a). They show that *Holophrya emmae* has the same main generic feature as *Myriokaryon lieberkuehnii* and *Cephalospatula brasiliensis*, viz., a spoon-like oral bulge (Figs 102-109). Kahl (1930a) even recognized the similarity with *M. lieberkuehnii* and classified both in *Pseudoprorodon*. Accordingly, the redescription of *H. emmae* by Song and Wilbert (1989), which shows a ciliate with a circular oral bulge, is based on a misidentification (see the new genus *Songophrya* below). *Holophrya emmae* is sufficiently different in details of the dorsal brush and extrusome pattern to be transferred to a new genus: *Berghophrya emmae* (Bergh, 1896) comb. n.

Details of the infraciliature from silver-impregnated *B. emmae* are not available. However, Kahl (1930a) shows that it likely has an *Arcuospathidium* pattern, like *Kahlophrya armata*, that is, the ciliary rows abut on the circumoral kinety at steep angles at both sides of the oral bulge (Fig 107).

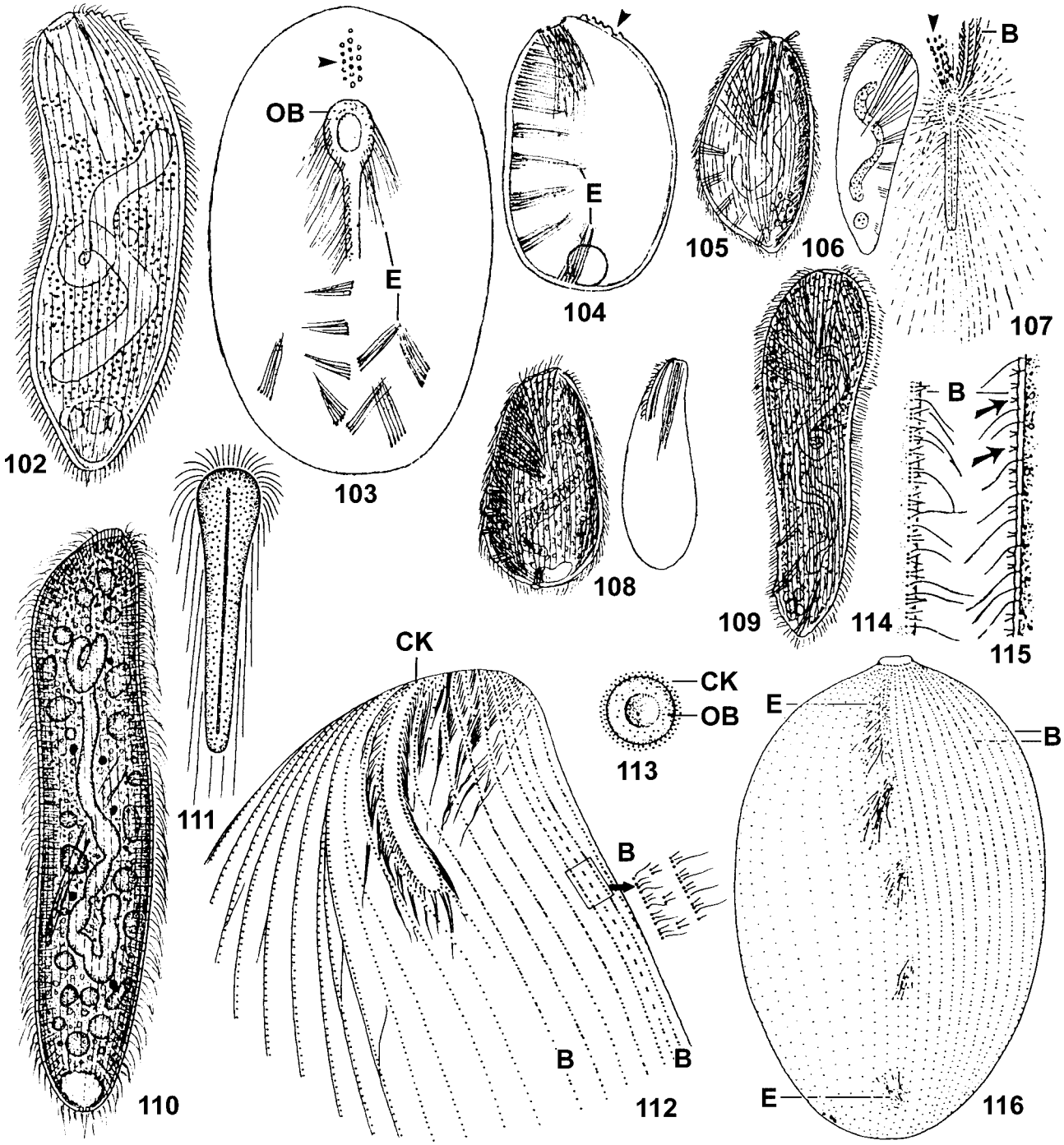
Kahlophrya gen. n. (Figs 110-112)

Diagnosis: elongate Myriokaryonidae with short mouth on obliquely truncated anterior body end and many (more than 3) dorsal brush rows, most of which are heteromorphic. Extrusomes scattered in oral bulge and equidistant body stripes. Infraciliature in *Arcuospathidium* pattern.

Type species: *Pseudoprorodon armatus* Kahl, 1930a.

Dedication: I dedicate this genus to Alfred Kahl (1877-1946), the famous German ciliate taxonomist, whose detailed observations greatly facilitated the present study. *Kahlophrya* is a composite of *Kahl* and the Greek noun *ophrya* (eyebrow ~ cilia ~ ciliate). Feminine gender.

Comparison with related genera: *Kahlophrya* is based on the redescription of *Pseudoprorodon armatus* Kahl, 1930a by Foissner (1997). This study shows the features mentioned in the genus diagnosis and the spoon-shaped oral bulge characteristic for the family (Figs 110-112). Thus, *Pseudoprorodon armatus* Kahl, 1930a and *Prorodon armatides* Foissner, 1997 are combined to *Kahlophrya armata* (Kahl, 1930a) comb. n. The main generic feature of *Kahlophrya* is the dorsal brush, which consists of about 20 rows. This resembles *Myriokaryon*, whose rows are, however, isomorphic, that is, consist of dikinetids with short cilia (bristles). *Kahlophrya* has only one isomorphic brush row, all others are heteromorphic, that is, composed of irregularly alternating monokinetids with ordinary cilia and dikinetids with short bristles. A tendency for heteromorphy is recognizable also in the posterior region of the brush rows of *Myriokaryon* and *Cephalospatula* (Figs 51-53, 57). Another important feature of *Kahlophrya* are the about 20 stripes of body extrusomes not found in any other genus of the family, although the genus *Berghophrya* shows such a tendency (see above); further, somatic extrusome stripes occur in several genera of related families, viz., in *Apospathidium* of the family Spathidiidae and in *Apobryophyllum* of the family Bryophyllidae (Foissner *et al*. 2002). The ciliary pattern of *Kahlophrya* is as in the spathidiid genus



Figs 102-109. *Berghophrya emmae* from life, according to Bergh 1896 (102-104) and Kahl 1930a (105-109). **102 -** general left side view, length up to 200 µm; **103, 104 -** ventral and lateral view of squashed specimens showing the spoon-shaped oral bulge, the dorsal papillae (arrowheads), and postoral extrusome bundles; **105-107 -** small variety (length 160 µm), lateral, dorsal, and frontal view of oral area with dorsal papillae marked by arrowhead; **108 -** medium-sized variety, length 300 µm; **109 -** vermiform variety, length 320 µm.

Figs 110-112. *Kahlophrya armata* from life (110, 111) and after protargol impregnation (112), according to Foissner (1997). **110-111 -** general left side view (length 210 µm) and frontal view of oral area; **112 -** ciliary pattern of anterior ventral side. Note the complicated dorsal brush composed of many rows with bristles and ordinary cilia.

Figs 113-116. *Songophrya armata* from life (114) and after protargol impregnation (113, 115, 116), according to Song and Wilbert (1989). This species has a circular oral bulge (113) and is thus highly different from *Berghophrya emmae*, which has a spoon-shaped oral bulge (103, 107). *Songophrya armata* has a size of 90-200 x 60-120 µm and the same brush type as *Kahlophrya armata*, that is, many rows composed of short, paired bristles (arrows) alternating with ordinary cilia (112, 114-116). B - dorsal brush; CK - circumoral kinety; E - extrusomes; OB - oral bulge.

Arcuospathidium and the myriokaryonid genus *Berghophrya* (see above), that is, the somatic ciliary rows abut on the circumoral kinety in steep angles at both sides of the oral bulge.

***Songophrya* gen. n. (Figs 113-116)**

Diagnosis: Pseudoholophryidae with circular oral opening and a row of extrusome bundles extending from anterior to posterior body end.

Type species: *Songophrya armata* sp. n.

Dedication: I dedicate this genus to Prof. Dr. Weibo Song (Ocean University of China), an eminent Chinese protozoologist, who significantly contributes to ciliate alpha-taxonomy since 15 years and discovered the type species. *Songophrya* is a composite of *Song* and the Greek noun *ophrya* (eyebrow ~ cilia ~ ciliate). Feminine gender.

Comparison with related genera: Foissner and Gschwind (1998) and Foissner *et al*. (2002) suggested that *Pseudoprorodon emmae* Bergh, 1896, as redescribed by Song and Wilbert (1989), is likely another species and the representative of a new genus belonging to the family Pseudoholophryidae, as redefined by Foissner *et al*. (2002). With the new knowledge available from *Myriokaryon* and *Cephalospatula*, it is evident that the species described by Song and Wilbert (1989) is not *Holophrya emmae* Bergh, 1896 because it has a simple, circular oral bulge, while that of *H. emmae* is conspicuously spoon-shaped (Figs 103, 113). Unfortunately, Song and Wilbert (1989) did not discuss this important difference, and thus their identification remains obscure; possibly, they did not know Bergh's original description. Within the family Pseudoholophryidae, which contains the genera *Pseudoholophrya*, *Paraenchelys*, and *Ovalorhabdos*, *Songophrya* is unique in having a row of extrusome bundles. Further, the ciliary rows extend almost meridionally, while distinctly spirally in the other genera. As concerns the oral bulge, it is circular in *Songophrya*, *Pseudoholophrya* and *Paraenchelys*, while distinctly elliptical in *Ovalorhabdos* (Foissner 1984, Foissner and Gschwind 1998, Foissner *et al*. 2002). The extrusomes, which distinguish the genera *Pseudoholophrya* and *Paraenchelys* (basically rod-shaped *vs.* basically drumstick-shaped), were not studied *in vivo* by Song and Wilbert (1989). Likely, they are filiform, but it cannot be excluded that a second fusiform type is present, which would be a further important genus character.

***Songophrya armata* sp. n.**

Diagnosis: size 90-200 x 60-120 µm *in vivo*; ellipsoidal. Macronucleus filiform. Extrusome row composed of 5-7 (x 5.3) bundles. On average 102 ciliary rows, more than 20 differentiated to dorsal brush in anterior half.

Type location: pond (Poppelsdorfer Weiher) in Bonn, Germany (7°E 51°N).

Etymology: the Latin adjective *armata* (armed) refers to the conspicuous extrusomes.

Description: see Song and Wilbert (1989) and figures 113-116.

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