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Morphology and ontogenesis of some soil spathidiids (Ciliophora, Haptoria)

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A b s t r a c t : We describe two new bryophyllids from Africa, viz., *Bryophyllum longisetum* nov. spec. and *Apobryophyllum sulcatum* nov. spec. Supplementary observations are provided for *Neobryophyllum penardi* and *N. paucistriatum*. These observations and literature data are used to establish the new family Bryophyllidae FOISSNER nov. fam., comprising the genera *Bryophyllum* KAHL 1931, *Apobryophyllum* FOISSNER 1998, and *Neobryophyllum* FOISSNER nov. gen. The Bryophyllidae, which evolved from the Spathidiidae, are unique in that the oral bulge extends whole body length. The dorsal brush is isomorphic (*Bryophyllum*, *Neobryophyllum*) or heteromorphic (*Apobryophyllum*) and composed of three rows (*Bryophyllum*) or of more than three rows (*Apobryophyllum*, *Neobryophyllum*). The ontogenesis of *Arcuospathidium coemeterii* (KAHL 1943) shows several specific features, suggesting that spathidiid division patterns are more diverse than previously assumed.

K e y w o r d s : Africa, *Apobryophyllum sulcatum* nov. spec., *Arcuospathidium coemeterii*, Bryophyllidae nov. fam., *Bryophyllum longisetum* nov. spec., *Neobryophyllum* nov. gen., Protozoa, South America.

Introduction

The haptorid ciliates are a (sub)order of the class Gymnostomatea. The name refers to their ability to capture prey, usually other ciliates or heterotrophic flagellates, but also micrometazoans like rotifers (CORLISS 1974). However, the most characteristic features are the possession of toxicysts to paralyse the prey; the dorsal brush, a more or less large field of specialized (sensory?) cilia on the anterior dorsal and/or left side; and somatic monokinetids associated with conspicuous postciliary microtubules, forming a single layer between two ciliary rows each (CORLISS 1979, FOISSNER & FOISSNER 1988, LYNN 1981).

At first glance, many haptorids are inconspicuous. However, more detailed observations reveal a great diversity (FOISSNER 1984, 2003, FOISSNER et al. 2002). This is sustained by the present study, in which a new family, a new genus, and two new species are established. They are from tropical and subtropical Africa, emphasizing that equatorial and subequatorial Africa are centres of ciliate biodiversity (FOISSNER 1998, FOISSNER et al. 2002). Likewise, ontogenesis shows many specific traits, exemplified on *Arcuospathidium coemeterii*, a rediscovered species from KAHL'S forgotten publication in 1943 (FOISSNER et al. 2004).

This publication is part of the doctoral thesis of Y.-L. LEI. Unfortunately, she felt that the scientific level required is too high. Thus, she continued her studies with a less strict ecologist. For estimating the quality of the descriptions, I must emphasize that all life observations and preparations are from myself and that I checked LEI'S work against the preparations. Thus, the data are reliable. Idea generation was also done by myself because Mag. LEI could not read the German literature and was not familiar with the methods of phylogenetic systematics. Likewise, manuscript preparation was done by me. Miss LEI mainly did technical work, that is, morphometry, illustrations, a text draft based on my notes and the slides she studied, and stored my text in the computer. Nonetheless, she co-authors the paper and those new taxa for which she analyzed my preparations.

Materials and methods, type slides

The source of the species studied is provided in the individual descriptions. All species are from terrestrial habitats, that is, from the upper 5 cm litter and soil layer. The samples were collected and processed as described in FOISSNER et al. (2002), that is, with the non-flooded Petri dish method.

The cytological methods used are described in FOISSNER (1991). All populations were observed in vivo and in protargol preparations. Illustrations of prepared specimens were made with a camera lucida.

Two or more type slides (1 holotype and several paratypes) each of the new species described and several voucher slides of the species redescribed have been deposited in the Oberösterreichische Landesmuseum in Linz (LI), Biologiezentrum. The slides usually contain many protargol-impregnated cells, with relevant specimens marked by black ink circles on the cover glass.

Description of taxa

Bryophyllidae FOISSNER nov. fam.

Diagnosis: Spathidiida with oral bulge extending meridionally or spirally to posterior body end. Ciliary rows meridionally arranged, those of left side partially or entirely differentiated to dorsal brush anteriorly. Dorsal brush isomorphic (*Neobryophyllum*, *Bryophyllum*) or heteromorphic (*Apobryophyllum*), composed of three rows (*Bryophyllum*) or of more than three rows (*Neobryophyllum*).

Type genus: *Bryophyllum* KAHL 1931.

Nomenclature: JANKOWSKI (1967, p. 37) mentions a family Bryophyllidae, but without any characterization. Thus, it is a nomen nudum.

Comparison with related families: Traditionally, *Bryophyllum* is classified into the family Spathidiidae (CORLISS 1979). However, the spathidiids s. str. include now several families with more than 10 genera, all having an oral bulge distinctly shorter than the body and an isomorphic dorsal brush (FOISSNER 1984, FOISSNER et al. 2002, FOISSNER & XU 2005). The meridional body organization separates the Spathidiidae and

Bryophyllidae from the Perispiridae, whose ciliary rows spiral around the body. The Myriokaryonidae have a spoon-shaped oral bulge and transverse-truncate anterior body end, causing a more or less sharp bend in the oral bulge and circumoral kinety (for a revision, see FOISSNER 2003).

There are two main types of Bryophyllidae, viz., those with an ordinary (isomorphic) dorsal brush and others with a heteromorphic brush, that is, where bristles irregularly alternate with ordinary cilia. For the later, FOISSNER (1998) established the genus *Apobryophyllum*. A third genus is created here (see below). These three genera form a homogenous group clearly different from all other spathidiids, and are thus classified into a distinct family: Bryophyllidae FOISSNER nov. fam. Likely, a detailed reinvestigation of limnetic *Bryophyllum* species will further add to their generic diversity.

Within the Bryophyllidae, *Bryophyllum* is likely the ancestral genus because it has the usual, three-rowed dorsal brush. *Apobryophyllum* evolved from *Bryophyllum* by modifying further kineties to dorsal brush rows which, however, still contain ordinary cilia. The end of this process represents *Neobryophyllum*, which has more than three brush rows all entirely composed of bristles. The same process occurred in the Myriokaryonidae, where *Cephalospathula* represents the three-rowed plesiomorphic state, *Kahlophrya* the first derived state, and *Myriokaryon* the second derived state (FOISSNER 2003). In the Spathidiidae s.l., an *Apobryophyllum*-like dorsal brush has not yet described, if it exists at all (FOISSNER & XU 2005).

Possibly, *Apobryophyllum* is also biphyletic because it contains species with three brush rows (*A. vermiforme*) and with more than three rows (*A. terricola*, *A. etoschense*, *A. sulcatum*). However, *A. vermiforme* is a very slender and thus derived species which likely reduced the dorsal brush secondarily to three rows due to spatial constraints (FOISSNER et al. 2002).

The Bryophyllidae likely evolved from the Spathidiidae s.l., possibly from an *Arcuospathidium*- or *Spathidium*-like ancestor, by elongating the mouth to body end. This hypothesis is supported by several observations: (i) the ciliary pattern is as in *Arcuospathidium*, that is, the anterior end of the rows is directed dorsally on both sides of the cell; (ii) many *Arcuospathidium* species have a long and narrow oral bulge, for instance, *A. cultriforme megastoma*, where the bulge extends above body half; (iii) specimens with spathidiid/arcuospathidiid anterior bulge quarter occur in several *Bryophyllum*, *Neobryophyllum*, and *Apobryophyllum* species, including *Bryophyllum longisetum* described below; (iv) nematodesmata are often recognizable only in the anterior, "spathidiid" portion of the bulge, where the circumoral dikinetids and usually also the extrusomes are more narrowly spaced than posteriorly; our excellent preparations from *B. longisetum* strongly suggest that nematodesmata indeed occur only in the anterior, "spathidiid" quarter of the oral bulge.

Genus *Neobryophyllum* FOISSNER nov. gen.

Diagnosis: Bryophyllidae with more than three isomorphic dorsal brush rows.

Type species: *Bryophyllum penardi* KAHL 1931, as redescribed by FOISSNER et al. (2002).

Etymology: Composite of the Greek noun *neo* (new) and the generic name

Bryophyllum (mossleaf-like), referring to the more than three isomorphic dorsal brush rows and the similarity with the genus *Bryophyllum*. Neuter gender.

Comparison with related genera: *Neobryophyllum* differs from *Bryophyllum* in having more than the usual three dorsal brush rows. FOISSNER et al. (2002) already recognized that *Bryophyllum* is biphyletic, viz., comprises species with three and with more than three dorsal brush rows. This difference is more than a simple quantitative feature because (i) three dorsal brush rows is the usual number in many haptorids and likely an ancient feature, and (ii) the number of brush rows is independent of body size and number of ciliary rows, as shown by *B. tegularum*, *Neobryophyllum paucistriatum*, and *N. lingua multistriatum*.

Species assignable: *Neobryophyllum penardi* (KAHL 1931) nov. comb. (basionym: *Bryophyllum penardi* KAHL 1931), as redescribed by FOISSNER et al. (2002); *Neobryophyllum lingua* (GELEI 1934) nov. comb. (basionym: *Bryophyllum lingua* GELEI 1934); *Neobryophyllum lingua lingua* (GELEI 1934) nov. comb. (basionym: *Bryophyllum lingua lingua* GELEI 1934 as classified by FOISSNER et al. 2002); *Neobryophyllum lingua multistriatum* (FOISSNER, AGATHA & BERGER 2002) nov. comb. (basionym: *Bryophyllum lingua multistriatum* FOISSNER, AGATHA & BERGER 2002); *Neobryophyllum paucistriatum* (FOISSNER, AGATHA & BERGER 2002) nov. comb. (basionym: *Bryophyllum paucistriatum* FOISSNER, AGATHA & BERGER 2002); *Neobryophyllum caudatum* (GELEI 1934) nov. comb. (basionym: *Bryophyllum caudatum* GELEI 1934).

No detailed data are available for most other described *Bryophyllum* species, except of *B. loxophylliforme*, for which KAHL (1931) definitely states three dorsal brush rows, and for *B. tegularum* KAHL 1931, which has, according to the redescriptions of FRYD-VERSAVEL et al. (1975) and FOISSNER (1984), also three dorsal brush rows. A third, new species with three brush rows is described below. All poorly known species should remain in *Bryophyllum* until redescriptions become available showing their true generic home. *Bryophyllum carinatum* GELEI 1934 likely belongs to *Apobryophyllum* because GELEI mentions that bristles alternate with ordinary cilia in some brush rows, just as characteristic for *Apobryophyllum* FOISSNER 1998.

Neobryophyllum penardi (KAHL 1931) nov. comb. (Fig. 1a-e; Tables 1, 2)

1922 *Loxophyllum armatum* CLAP. et LACHM. 1859 – PENARD, Infusoires, p. 74.
1931 *Bryophyllum penardi* KAHL, Tierwelt Dtl. **21**:185.
1934 *Bryophyllum spathidioides* GELEI, Arch. Protistenk. **81**: 206 (synonym according to FOISSNER et al. 2002).
2002 *Bryophyllum penardi* KAHL, 1931 – FOISSNER, AGATHA & BERGER, Denisia **5**: 350 (neotypification; slides with protargol-impregnated specimens from neotype location are deposited in the Oberösterreichische Landesmuseum in Linz, Upper Austria).

Material: Moderately abundant in surface soil mixed with Banana plant litter from living plants and ground collected on the Isla de San Andrés, Caribbean Sea, 82°W 12°N. The sample, kindly provided by Dr. Wolfgang PETZ, was moderately saline (10‰-20‰) and had pH 7.0.

Supplementary observations from the San Andrés population and comparison with previous descriptions: The San Andrés specimens match the African populations in almost all main features (overall size and shape, nucleus pattern, shape of the extrusomes, brush details), but differ considerably in the number and

distribution of the somatic ciliary rows (Fig. 1a-e; Table 1): they have a higher number of rows (on average 31 vs. 25 in Madagascan and 28 in Namibian populations) and the number of rows is invariably considerably higher (20) on the right than left side (11). A reinvestigation of the Madagascan neotype population showed the same tendency (13 vs. 11 rows), but much less pronounced (Table 1).

Further differences and observations (Fig. 1a-e; Table 1): (i) Body length (149 µm) of protargol-impregnated specimens is in between those from Madagascar (118 µm) and Namibia (166 µm), but the San Andrés cells are more slender, that is, have a length:width ratio of about 3.2:1 (vs. 2.9:1 in Madagascan and 1.7:1 in Namibian specimens). (ii) Dorsal and anterior ventral body margin may slightly undulate both in vivo and in protargol preparations (not described in the African populations). (iii) Nuclear apparatus underneath mid-body (vs. in middle body third); in two thirds of 41 specimens analysed, the macronucleus strand is highly tortuous or coiled and distinctly nodulated (Fig. 1a, d), while it is more or less C-shaped or tortuous in the African populations, and nodulated in only a quarter of the (reinvestigated) Madagascan specimens. (iv) Excretory pores of contractile vacuole only on right side of cell in nine out of ten specimens analysed, on both sides in one specimen (Table 2). (v) Extrusomes slightly longer, viz.,

Table 1: Morphometric data on *Neobryophyllum penardi* from San Andrés (upper line) and Madagascar (lower line; reinvestigated).

Characteristics[1]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	148.8	151.0	15.2	3.5	10.2	115.0	172.0	19
Body, width	47.3	48.0	8.6	2.0	18.2	30.0	62.0	19
Body length:width, ratio	3.2	3.0	0.6	0.1	19.0	2.4	5.1	19
Posterior body end to dorsal end of oral bulge, distance	18.5	18.0	3.3	0.8	17.7	14.0	24.0	18
Anterior end to end of longest brush row, distance	36.5	35.8	3.9	0.9	10.8	32.0	44.5	18
Oral bulge, height	2.1	2.0	-	-	-	1.5	2.5	19
Macronucleus, length (spread; values thus	106.9	105.0	-	-	-	75.0	140.0	19
Macronucleus, width	5.9	6.0	1.0	0.2	16.9	5.0	8.0	19
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
Micronucleus, length	5.9	6.0	0.5	0.1	8.4	4.5	6.5	19
Micronucleus, width	2.9	3.0	0.5	0.1	17.8	2.0	3.5	19
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
Somatic kineties, total number	31.0	31.0	1.5	0.4	4.8	28.0	34.0	17
	24.6	24.0	2.1	0.6	8.4	21.0	28.0	14
Somatic kineties on right side, number	19.6	20.0	1.4	0.3	7.0	17.0	22.0	17
	13.4	13.0	1.8	0.5	13.3	11.0	16.0	14
Somatic kineties on left side, number	11.4	11.0	1.1	0.3	9.3	10.0	13.0	17
	11.3	11.0	0.8	0.2	7.3	10.0	13.0	14
Dorsal brush rows, number	5.9	6.0	0.5	0.1	8.0	5.0	7.0	18

[1] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected 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, $\bar{x}$ – arithmetic mean.

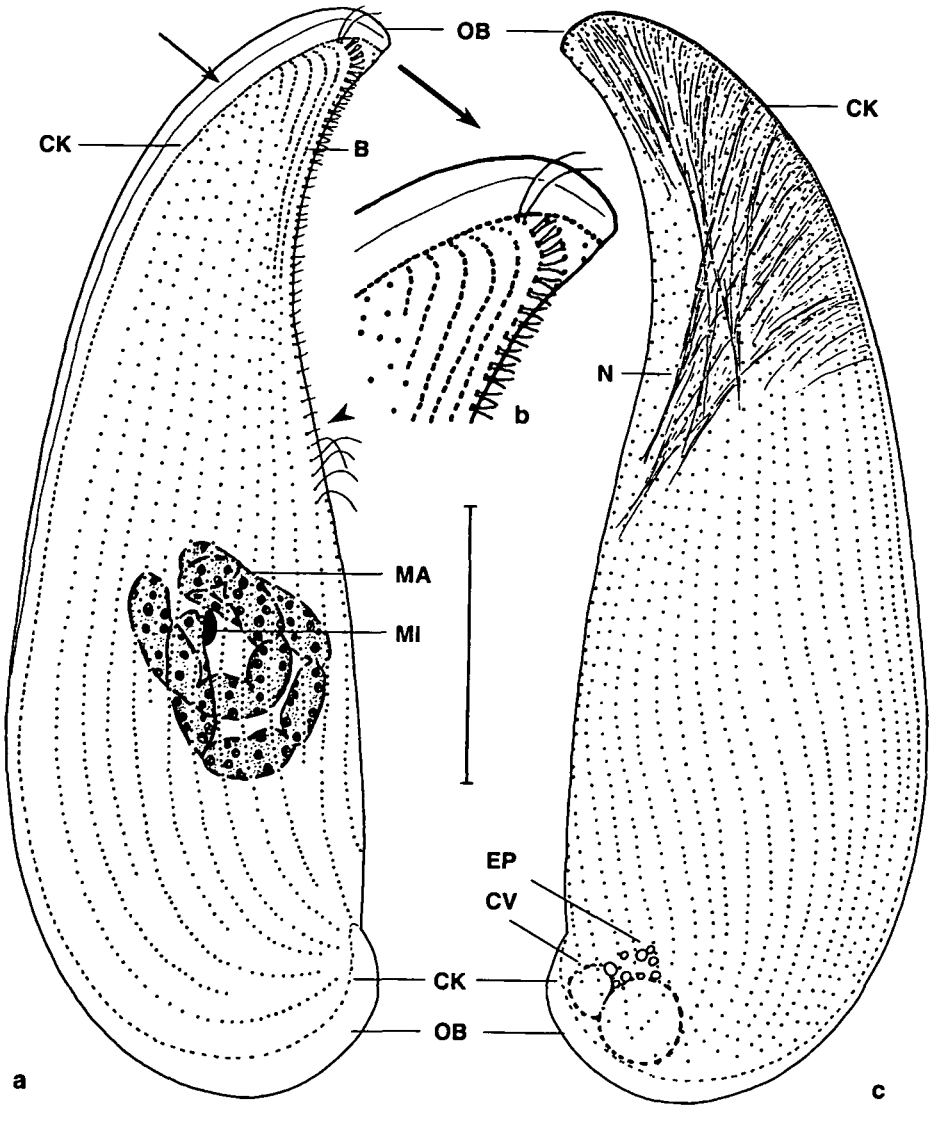


Fig. 1a-c: *Neobryophyllum penardi*, a San Andrés specimen after protargol impregnation, showing body shape, nuclear apparatus, and ciliary pattern of left (a) and right side (c), length 162 µm. The specimen has 18 ciliary rows on the right side, while only 12 on the left, where the first row left of the circumoral kinety is so strongly curved that it almost touches the dorsal end of the oral bulge. The dorsal brush is composed of six rows of dikinetids, and the last (leftmost) row is followed by a monokinetidal bristle tail extending to mid-body (arrowhead); most brush rows commence with some ordinary cilia. Arrow denotes bulge slit. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuole, EP – excretory pores, MA – macronucleus, MI – micronucleus, N – nematodesmata, OB – oral bulge. Scale bar 40 µm.

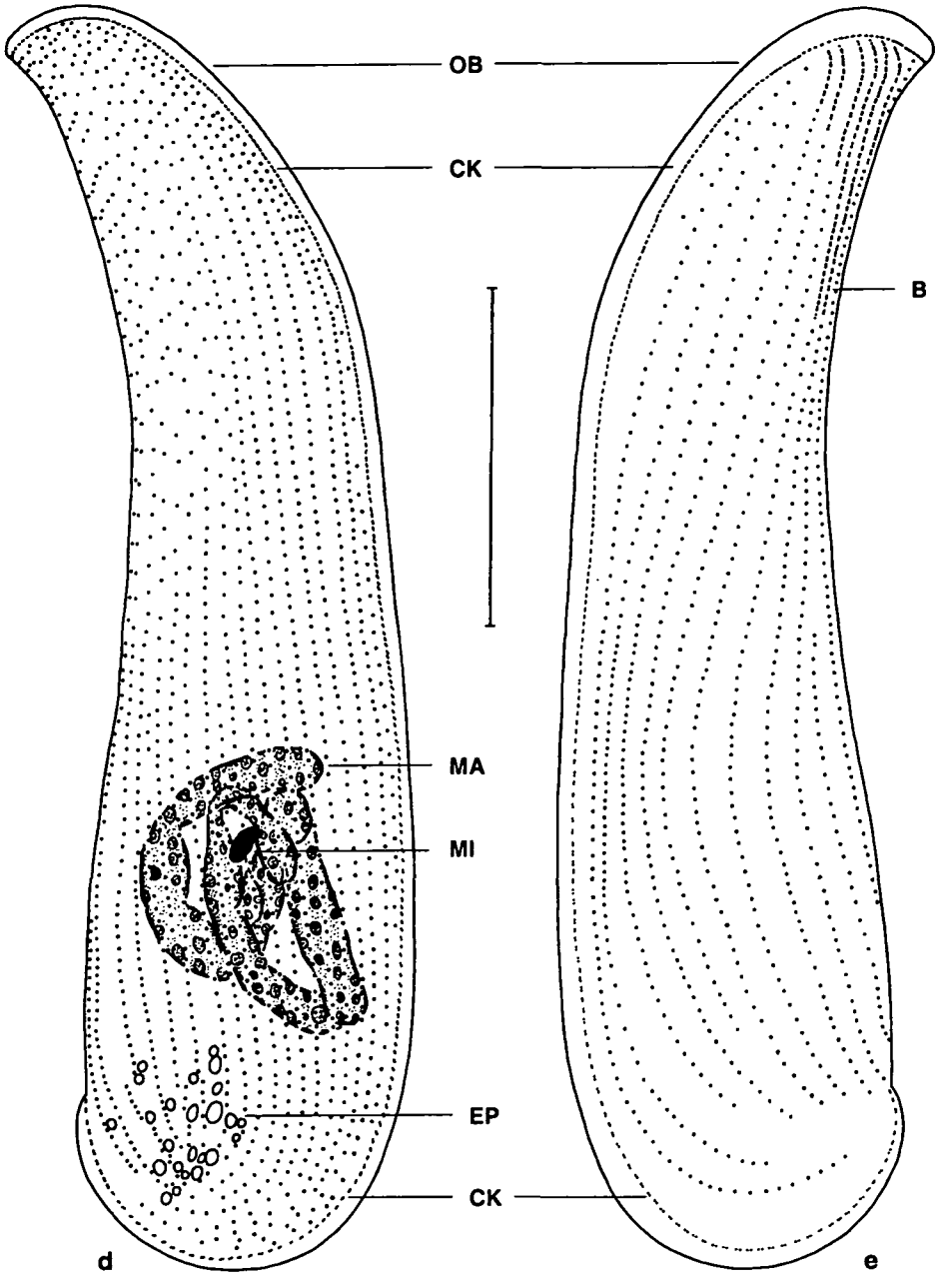


Fig. 1d, e: *Neobryophyllum penardi*, ciliary pattern and nuclear apparatus of a slender San Andrés specimen after protargol impregnation, length 150 µm. There are distinctly more ciliary rows on the right (19) than left (11) side. B – dorsal brush, CK – circumoral kinety, EP – excretory pores, MA – macronucleus, OB – oral bulge. Scale bar 40 µm.

type I distinctly acicular and about 9 × 1 µm (vs. 6 × 0.8 µm) in size; type II about 2 µm (vs. 1.5 µm) long, fine rods; only the short oral extrusomes and certain cytoplasmic developmental stages frequently intensely impregnate with the protargol method used. (vi) A 180 µm long food vacuole with a rotifer is recognizable in two specimens. (vii) Ciliary rows frequently strongly curved dorsally at posterior end, especially the leftmost kinety, which follows the curvature of the circumoral kinety and almost abuts to the posterior bulge end; anteriorly, several supernumerary basal bodies occur occasionally between the leftmost and circumoral kinety (Fig. 1a, c-e); in the (reinvestigated) Madagascan specimens, the posterior ciliary pattern varies from almost straight to distinctly curved. (viii) Brush rows usually commencing with some ordinary cilia anteriorly and occupying about 25% of body length (vs. 23% in Madagascan and 19% in Namibian populations); bristles clavate and about 3 µm long, the last row followed by 2-3 µm long bristles forming a monokinetidal tail extending to mid-body. (ix) Oral bulge studded with oblique rows of cortical granules forming an upward (vs. downward)-directed, arrowhead-like pattern.

Altogether, the differences between the Carribean and African populations are rather distinct, especially the number and distribution of the ciliary rows, indicating some biogeographic specialization. Noteably, GELEI (1934) already mentions that the number of ciliary rows is lower on the right than the left side (on left than right side in our specimens!), viz., ca. 40 vs. 100 in *Neobryophyllum caudatum* (GELEI 1934) and ca. 15-16 vs. 20 in the Hungarian population of *N. penardi* (*Bryophyllum spathidioides*, see synonymy above). Thus, the number and distribution of the ciliary rows are obviously highly variable and cannot be used to rank the populations as subspecies.

At first glance, the Carribean population of *Neobryophyllum penardi* highly resembles *Bryophyllum loxophylliforme* KAHL 1931, which, however, has only three dorsal brush rows, as definitely stated by KAHL (1931).

Occurrence and ecology: The literature shows that *N. penardi* prefers limnetic habitats, viz., a *Sphagnum* pond in Swiss (PENARD 1922), a eutrophic pond in Hungary (GELEI 1934), streamlet mud (pH 6.1) from a rain forest of Madagascar (FOISSNER et al. 2002), and astatic freshwater pools (pH 6.7) in Namibia (FOISSNER et al. 2002). Our record is in this line (plant litter) and shows that *N. penardi* occurs also in saline habitats and in Central America. Thus, it is likely a euryoecious cosmopolitan.

Table 2: Supplementary data on the location of excretory pores of the contractile vacuole in *Neobryophyllum paucistriatum* and *N. penardi*.

Species[1]	Only on right side of cell	Only on left side of cell	On both sides	n
N. paucistriatum	7	0	5	12
N. penardi	9	0	1	10

[1] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. n – number of specimens investigated.

Neobryophyllum paucistriatum **(FOISSNER, AGATHA & BERGER 2002) nov. comb. (Fig. 2a-e, 3-5; Tables 2, 3)**

2002 *Bryophyllum paucistriatum* FOISSNER, AGATHA & BERGER, Denisia 5: 340 (type and voucher slides with protargol-impregnated specimens from type location and a voucher location are deposited in the Oberösterreichische Landesmuseum in Linz, Upper Austria).

Material: Rare in leaf litter and blackbrown soil (pH 6.1 in water) from a *Notofagus* forest (southern beech) with bamboo undergrowth about 30 km south of the town of Pucon, Chile, W72° S39°13′. The sample was kindly provided by Dr. Michael BONKOWSKI (Göttingen University).

Supplementary observations from the Chilean population and comparison with original description: The Chilean specimens match the African populations in all main features (overall size and shape, nucleus and ciliary pattern, size and shape of the extrusomes), but differ in several details. (i) Size and length: width ratio of protargol-impregnated specimens match the Namibian population (130 × 36 µm, 3.9:1; Fig. 1a-d, 3; Table 3), while the Kenyan cells are, on average, considerably smaller and slimmer (123 × 37 µm vs. 87 × 41 µm, 3.4:1 vs. 2.2:1). (ii) The ventral body margin may slightly undulate, which was not observed in the Kenyan specimens. (iii) Macronucleus almost as long as in Namibian specimens (71 µm), but distinctly longer than in Kenyan type population (65 µm vs. 34 µm); conspicuously tortuous and nodulated in two thirds of specimens (Fig. 2b-d), while elongate reniform in Kenyan type and highly tortuous, but only rarely nodulated in (reinvestigated) Namibian specimens; micronucleus not recognizable in Chilean cells. (iv) Excretory pores of contractile vacuole only on right side of cell in seven specimens, while on both sides in five specimens (Table 2). (v) Extrusomes scattered in oral bulge (vs. in short, oblique rows in Kenyan type) and cytoplasm, shape and size very similar to that of Austrian specimens, viz., type I rod-like with narrowed ends and about 5-6 × 0.3 µm in size, impregnates more or less intensely, especially the posterior portion, with the protargol method used; type II about 2 µm long, fine rods. (vi) Invariably two to three ordinary somatic ciliary rows between circumoral kinety and dorsal brush rows (Fig. 2b, d), while all or most left side ciliary rows are differentiated to brush kineties anteriorly in the Kenyan specimens. (vii) Dorsal brush kineties curve sharply (vs. slightly) rightwards anteriorly and abut (vs. separate) on circumoral kinety with some (vs. none) ordinary cilia (Fig. 2b, d, e). Anterior brush dikinetids each with an about 3 µm long, rod-shaped anterior bristle and a 4-5 µm long, clavate posterior bristle; both bristles rod-shaped in mid and posterior region of brush, decreasing in length from 3-4 µm to 2 µm. (viii) Oral bulge in vivo about 3 µm (vs. 5 µm) high and studded with oblique rows of cortical granules, forming an arrowhead-like pattern; oral bulge and circumoral kinety rather distinctly (vs. indistinctly) inflated in anterior third, where the bulge contains an obconical depression in midline, likely marking the temporary cytostome (Fig. 2a-d, 3-5).

Altogether, the differences between the Chilean and African populations are rather pronounced, indicating some biogeographic specialization. However, *Bryophyllum* s. l. species are highly variable (FOISSNER et al. 2002 and present data), and thus it would be premature to split the populations at subspecies or species level without additional (molecular) data.

Occurrence and ecology: FOISSNER et al. (2002) found *Neobryophyllum paucistriatum* in oligo- to mesohaline, circumneutral (pH 6.5 – 7.8) soil samples from Spain and Austria (Europe), Utah (USA), and Kenya and Namibia (Africa). Our record is

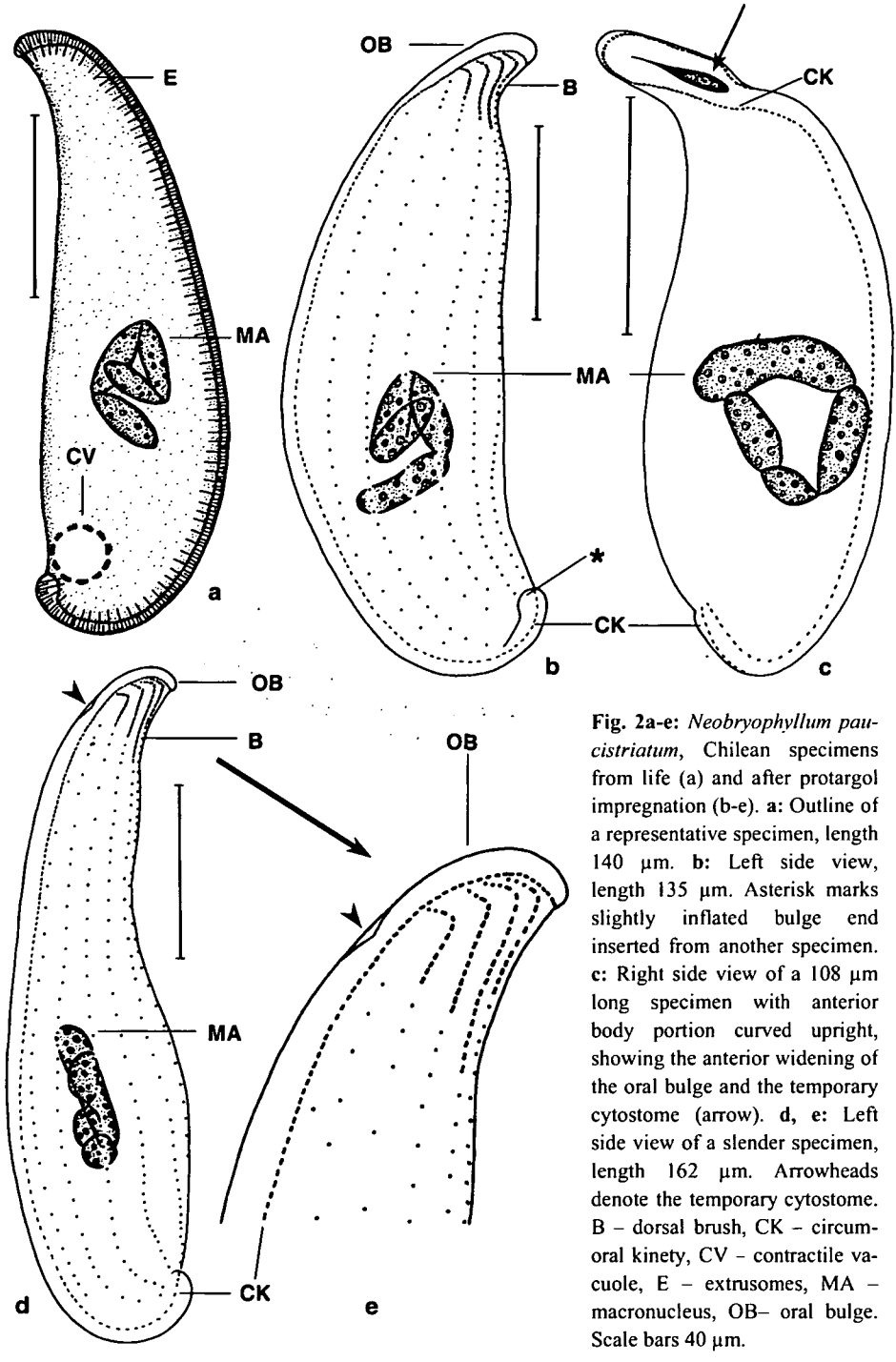
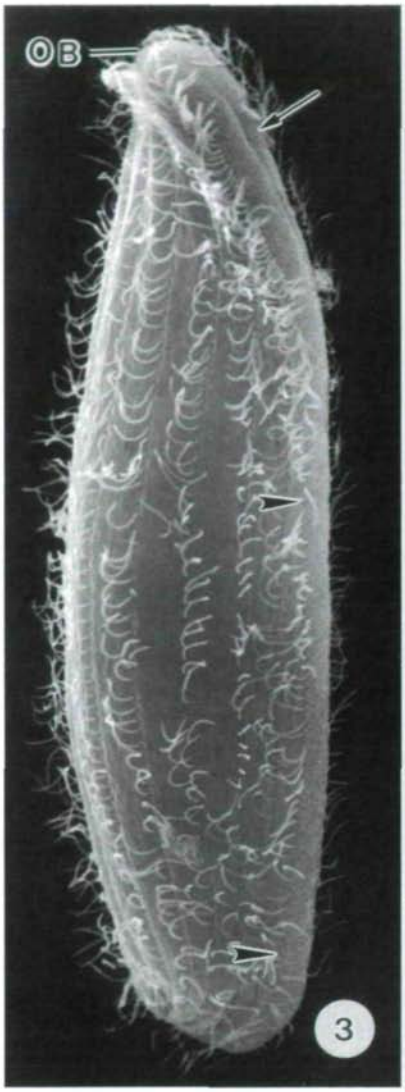
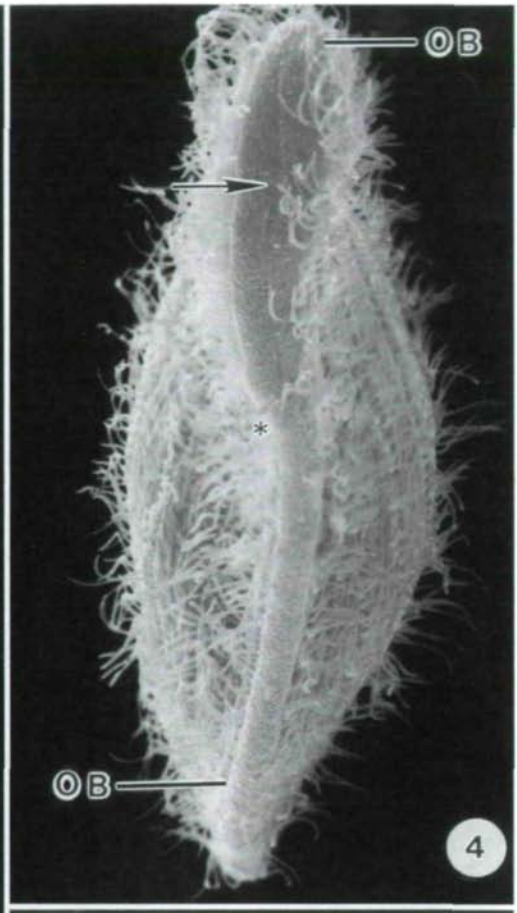


Fig. 2a-e: *Neobryophyllum paucistriatum*, Chilean specimens from life (a) and after protargol impregnation (b-e). **a:** Outline of a representative specimen, length 140 µm. **b:** Left side view, length 135 µm. Asterisk marks slightly inflated bulge end inserted from another specimen. **c:** Right side view of a 108 µm long specimen with anterior body portion curved upright, showing the anterior widening of the oral bulge and the temporary cytostome (arrow). **d, e:** Left side view of a slender specimen, length 162 µm. Arrowheads denote the temporary cytostome. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuole, E – extrusomes, MA – macronucleus, OB– oral bulge. Scale bars 40 µm.





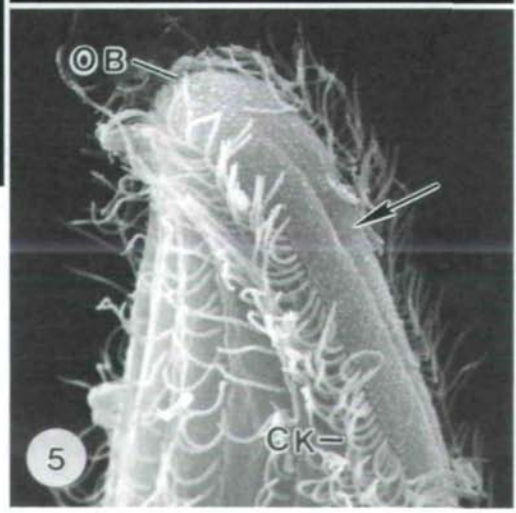


Fig. 3-5: *Neobryophyllum paucistriatum* in the scanning electron miscroscope, showing the meridionally extending ciliary rows, the temporary cytostome (arrows), the oral bulge extending to posterior body end (arrowheads), and the widening of the oral bulge in the anterior third (asterisk). CK – circumoral kinety, OB– oral bulge.

Table 3: Morphometric data on *Neobryophyllum paucistriatum* from Chile.

Characteristics[1]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	123.1	114.0	20.5	4.7	16.6	96.0	170.0	19
Body, width	37.2	38.0	5.8	1.3	15.6	23.0	47.0	19
Body length:width, ratio	3.4	3.2	0.8	0.2	24.7	2.3	5.1	19
Anterior body end to end of longest dorsal brush row, distance	17.2	18.0	1.9	0.4	11.2	14.0	20.0	19
Posterior body end to dorsal end of oral bulge, distance	12.7	12.0	2.1	0.5	16.5	9.0	18.0	19
Oral bulge, height	2.6	2.5	-	-	-	2.0	3.0	19
Macronucleus, length (spread; values thus approximate)	64.7	60.0	-	-	-	36.0	96.0	19
Macronucleus, width	7.2	7.0	1.3	0.3	18.2	5.0	10.0	19
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
Nodes in macronucleus, number	4.3	4.0	2.2	0.5	51.8	0.0	8.0	19
Somatic kineties on right side, number	6.5	6.0	0.7	0.1	10.5	5.0	8.0	21
Somatic kineties on left side, number	6.0	6.0	0.5	0.1	8.4	5.0	7.0	21
Somatic kineties, total number	12.4	12.0	0.9	0.2	7.4	11.0	14.0	21
Dorsal brush rows, number	4.2	4.0	-	-	-	4.0	5.0	19

[1] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. 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, $\bar{x}$ – arithmetic mean.

the first of South America, supporting the proposal of FOISSNER et al. (2002) that *N. paucistriatum* is an euryoecious cosmopolitan, though records form Asia, Australia and Antarctica are still lacking. Further, the Chilean specimens differ rather distinctly from the African populations, which might be an indication of biogeographic separation at subspecies level (see above).

Genus *Bryophyllum* KAHL 1931

Improved diagnosis: Bryophyllidae with three isomorphic dorsal brush rows.

Type species (by original designation): *Bryophyllum loxophylliforme* KAHL 1931.

Etymology: Not given in the original description. The name is a composite of the Greek words *bryo* (relating to mosses) and *phyllus* (leaved), obviously referring to the mossleaf-like shape of some of the species included.

Species assignable: *Bryophyllum loxophylliforme* KAHL 1931; *B. tegularum* KAHL 1931, as redescribed by FOISSNER (1984); *B. hyalinum* GELEI 1936; *B. longisetum* nov. spec.

Bryophyllum longisetum **FOISSNER & LEI nov. spec. (Fig. 6a-x, 7a-l, 8-24; Tables 4, 5)**

Diagnosis: Size about 180 × 20 µm in vivo. Slender with body and oral bulge slightly to distinctly twisted. Macronucleus in about 100 scattered nodules. Oral extrusomes indistinctly fusiform to acicular and 5-6 µm long; somatic extrusomes scattered between ciliary rows, rod-shaped and 2.5-3 µm long. On average nine ciliary rows, the three left side rows anteriorly differentiated to conspicuous dorsal brush with bristles of row 3 up to 10 µm long; all brush rows of similar length.

Type location: Soil from Kenyan part of the Kilimanjaro, about 2600 m above sea-level, 38°E 2°S.

Etymology: Composed of the Latin adjective *longus* (long) and the Latin noun *seta* (bristle), referring to the conspicuous brush bristles, a main feature of the species.

Description: Size 140-240 × 15-25 µm in vivo, usually about 180 × 20 µm, as calculated from some in vivo measurements and the morphometric data; length:width ratio 6.5-13.2:1 in protargol preparations, on average about 9:1 in vivo (n = 8) and 11:1 in silver slides, a rather distinct difference for which we have no explanation, except that specimen's width shrinks stronger than length (Table 5); highly flexible but acontractile. Usually slender with anterior quarter frequently slightly, in two out of 38 specimens analysed even distinctly projecting from body proper ventrally and thus more or less conspicuously spatulate; most specimens more or less twisted along main axis, rarely occur flat or almost flat cells; both ends narrowly rounded (Fig. 6a, k-o, p-r, t, u, x); 2:1 to 3:1 flattened in anterior quarter, where both body and oral bulge might be flat or twisted (≤ 90°), as shown by the course of the ciliary rows; widest in middle body portion, which is slightly flattened or unflattened in 13 out of 21 specimens analysed,

Table 4: *Bryophyllum longisetum*, body and oral bulge shape and course of kinety bearing brush row 3 in 20 specimens.

Characteristics[1]	Flat	Slightly spiral	Moderatel y spiral	Distinctly spiral (~90°)	Very distinctly spiral (~180°)	Meri-dional	Diag-onal
Oral bulge and body in anterior quarter	6	5	2	7	0		
Oral bulge in posterior body quarter	3	1	2	7	7		
Course of kinety bearing brush row 3						7	13[2]

[1] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture.

[2] Diagonal course, that is, from anterior dorsal to posterior ventral margin, occurs only in specimens with oral bulge spiraled ≥ 90° in posterior body quarter.

while more flattened on left than right side in seven cells, and more flattened on right than left side in one specimen (Fig. 7j-l); indistinctly flattened in narrow and thin posterior quarter, where we could not decide whether both body and oral bulge or only the oral bulge twists around the body. Considering that it is the body which twists in the anterior quarter, it is reasonable to assume that it does so in the posterior; however, figures 7a-h and the data compiled in table 4 indicate that indeed only or mainly the oral bulge twists by up to 180°.

Table 5: Morphometric data on *Bryophyllum longisetum*.

Characteristics[1]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	169.7	168.0	24.5	5.4	14.5	125.0	208.0	21
Body, width	15.6	16.0	2.4	0.5	15.6	13.0	22.0	21
Body length:width, ratio	11.0	11.5	1.6	0.4	14.8	6.5	13.2	21
Posterior body end to dorsal end of oral bulge, distance	3.5	3.0	1.0	0.2	27.8	2.5	6.0	21
Oral bulge, height at anterior body end[2]	1.9	2.0	0.4	0.1	21.0	1.5	2.5	20
Oral bulge, maximum height in middle body portion[3]	2.1	2.0	0.4	0.1	18.5	1.5	2.5	20
Oral bulge (circumoral kinety), width in anterior body portion	3.1	3.0	-	-	-	2.5	3.5	7
Oral bulge (circumoral kinety), width in posterior body portion	2.5	2.5	-	-	-	2.5	2.5	8
Anterior body end to end of longest dorsal brush row, distance	35.3	35.0	4.9	1.1	13.9	29.0	45.0	21
Dorsal brush row 1, length (first to last dikinetid)	25.2	25.0	3.6	0.8	14.4	18.0	34.0	19
Dorsal brush row 2, length (first to last dikinetid)	32.4	32.0	4.4	1.0	13.5	23.0	42.0	19
Dorsal brush row 3, length (first to last kinetid)	29.7	30.0	5.6	1.3	18.8	18.0	40.0	19
Macronucleus figure, length	93.1	95.0	16.4	3.6	17.6	68.0	120.0	21
Macronucleus nodules, length	4.4	4.0	1.4	0.3	31.0	2.5	7.0	21
Macronucleus nodules, width	2.1	2.0	0.3	0.1	16.2	1.0	2.5	21
Macronucleus nodules and micronuclei, number	121.9	100.0	51.6	11.3	42.4	64.0	256.0	21
Micronuclei, diameter	2.6	2.5	-	-	-	2.0	3.0	11
Somatic kineties, total number	9.1	9.0	0.7	0.2	8.0	8.0	11.0	21
Somatic kineties on left side, number	4.2	4.0	0.4	0.1	10.3	4.0	5.0	21
Somatic kineties on right side, number	5.1	5.0	0.5	0.1	10.6	4.0	6.0	21
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Dikinetids in brush row 1, number	18.2	18.0	3.6	0.8	19.6	12.0	27.0	19
Dikinetids in brush row 2, number	31.9	30.0	6.1	1.4	19.0	22.0	44.0	19
Dikinetids in brush row 3, number	20.9	20.0	5.1	1.2	24.3	12.0	35.0	19

[1] Data based on mounted, protargol-impregnated (FOISSNER's method), and randomly selected specimens from a non-flooded Petri dish culture. 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, $\bar{x}$ – arithmetic mean.

[2] Measured in laterally oriented cells as distance from margin of bulge to circumoral kinety over brush row 2.

[3] Measured from circumoral kinety to margin of bulge in laterally oriented cells.

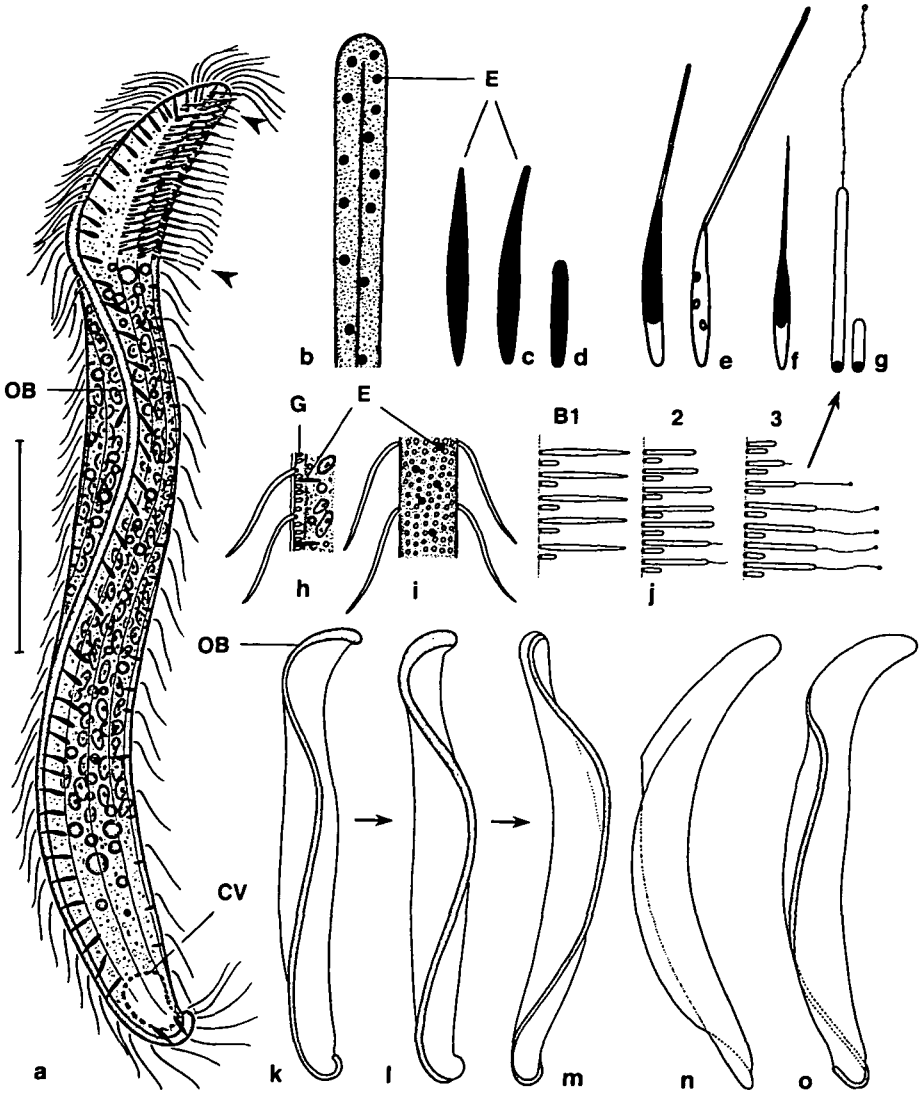


Fig. 6a-o: *Bryophyllum longisetum* from life (a, k-o; redrawn from video records). **a:** Left side view of a representative specimen, length 180 µm (bar 40 µm). Arrowheads denote bristles of brush row 3, an important character of this species. **b:** Frontal view of anterior portion of oral bulge. **c:** Oral extrusomes are 5-6 µm long. **d:** Somatic extrusome, length 3 µm. **e, f:** Exploded oral (e) and somatic (f) extrusomes, length 13 µm, 16 µm, 10 µm. Both types are toxicysts. **g, j:** Anterior portion of dorsal brush. The anterior bristles of row 3 have a 4-10 µm long, fragile process which degenerates granularly (g). Further details, see figure 12. **h, i:** Cortical granulation and extrusomes in optical section and surface view. **k-m:** Same specimen rotating from left to ventral side. **n, o:** *Spathidium*-shaped specimens. B1-3 – dorsal brush rows, CV - contractile vacuole, E – extrusomes, G – cortical granules, OB – oral bulge.

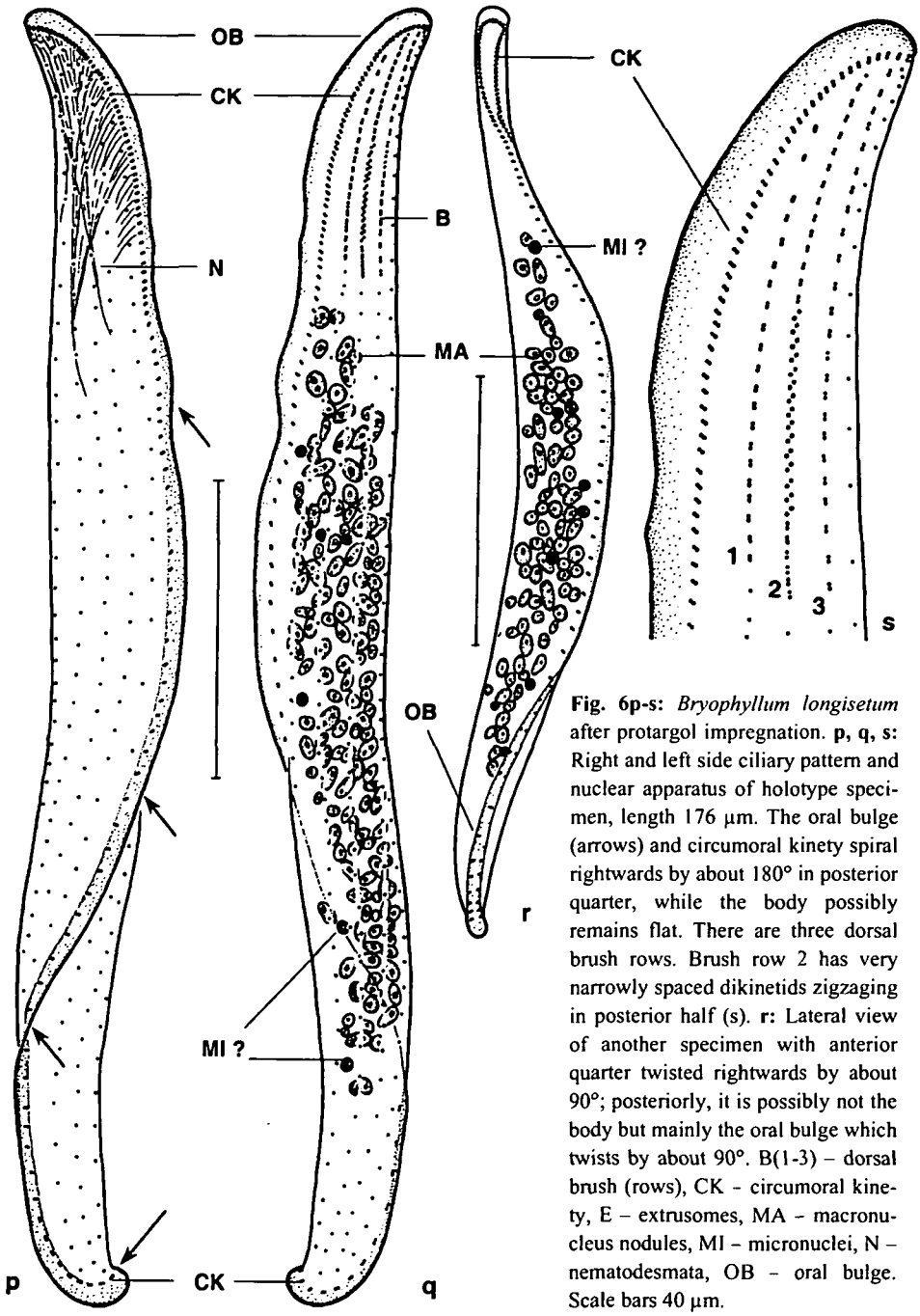


Fig. 6p-s: *Bryophyllum longisetum* after protargol impregnation. **p, q, s:** Right and left side ciliary pattern and nuclear apparatus of holotype specimen, length 176 µm. The oral bulge (arrows) and circumoral kinety spiral rightwards by about 180° in posterior quarter, while the body possibly remains flat. There are three dorsal brush rows. Brush row 2 has very narrowly spaced dikinetids zigzaging in posterior half (s). **r:** Lateral view of another specimen with anterior quarter twisted rightwards by about 90°; posteriorly, it is possibly not the body but mainly the oral bulge which twists by about 90°. B(1-3) – dorsal brush (rows), CK – circumoral kinety, E – extrusomes, MA – macronucleus nodules, MI – micronuclei, N – nematodesmata, OB – oral bulge. Scale bars 40 µm.

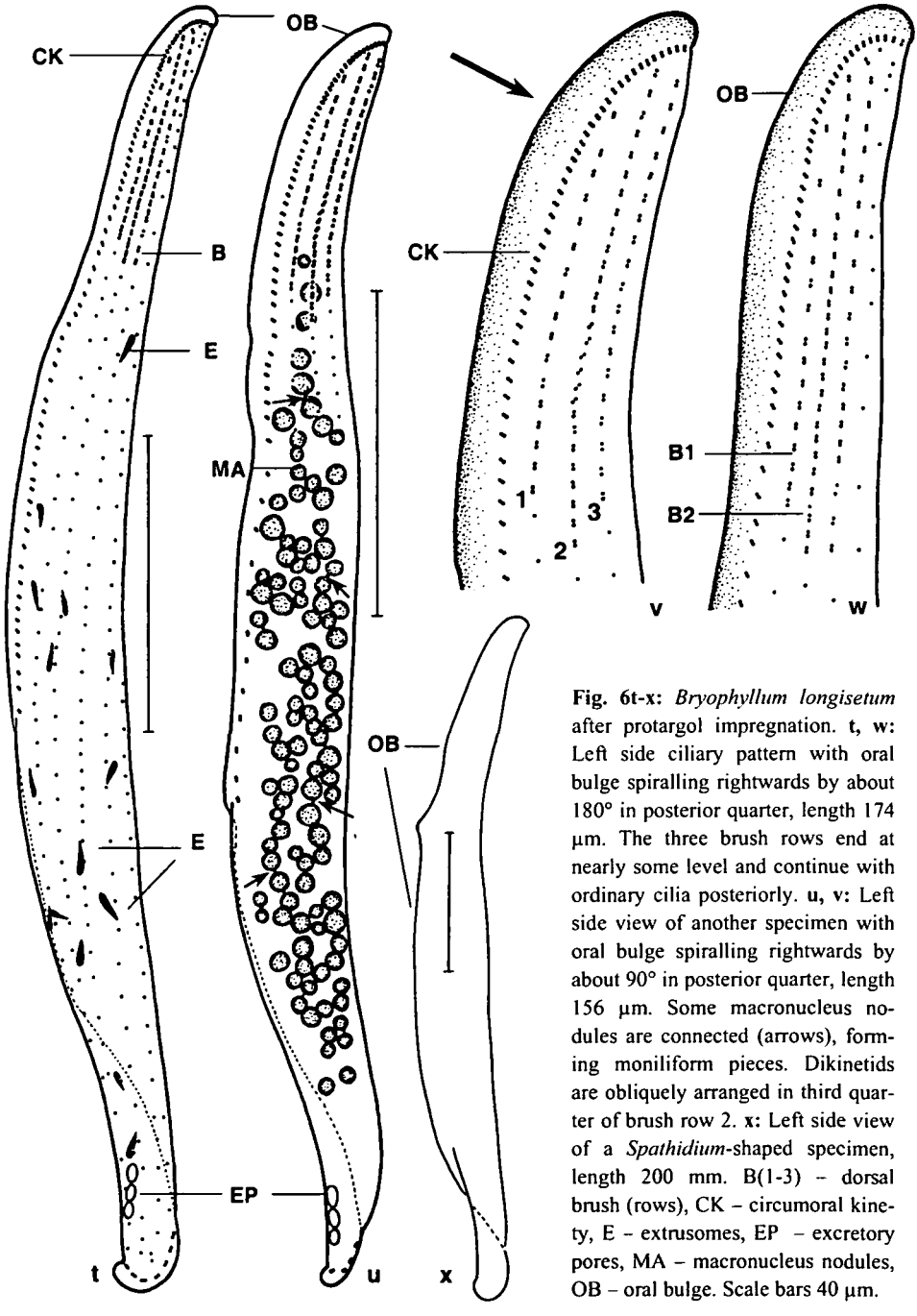
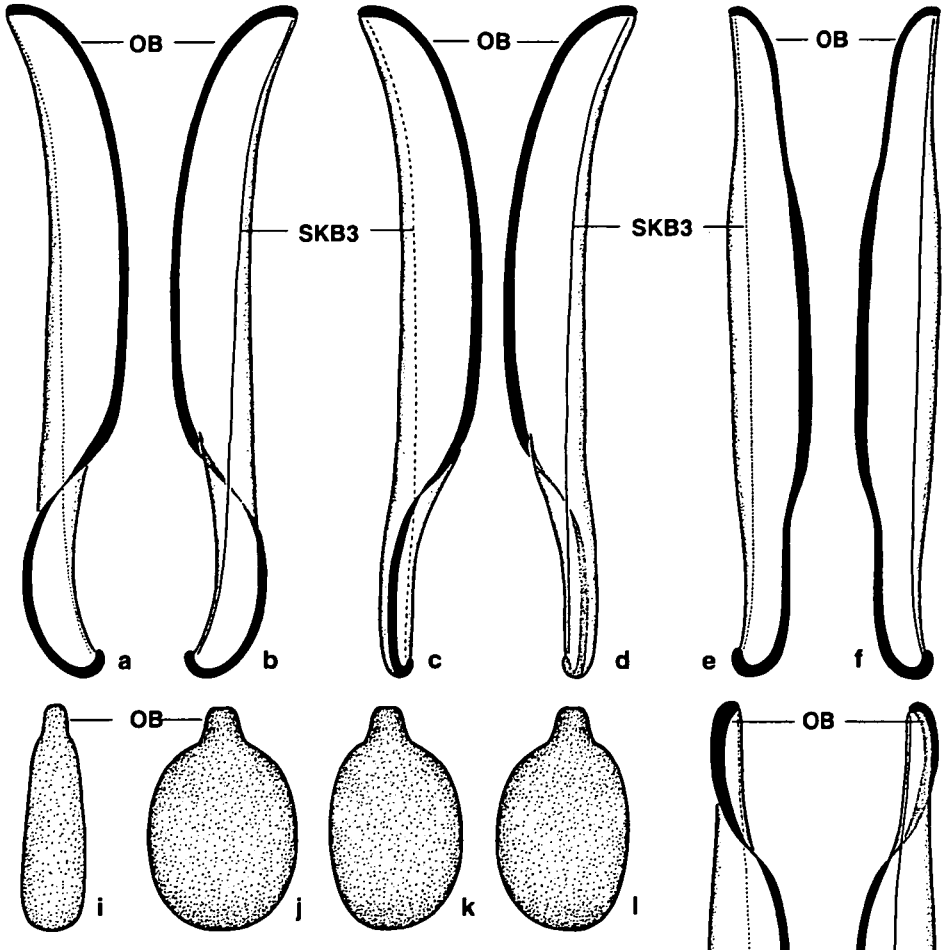


Fig. 6t-x: *Bryophyllum longisetum* after protargol impregnation. **t, w:** Left side ciliary pattern with oral bulge spiralling rightwards by about 180° in posterior quarter, length 174 µm. The three brush rows end at nearly some level and continue with ordinary cilia posteriorly. **u, v:** Left side view of another specimen with oral bulge spiralling rightwards by about 90° in posterior quarter, length 156 µm. Some macronucleus nodules are connected (arrows), forming moniliform pieces. Dikinetids are obliquely arranged in third quarter of brush row 2. **x:** Left side view of a *Spathidium*-shaped specimen, length 200 mm. B(1-3) – dorsal brush (rows), CK – circumoral kinety, E – extrusomes, EP – excretory pores, MA – macronucleus nodules, OB – oral bulge. Scale bars 40 µm.



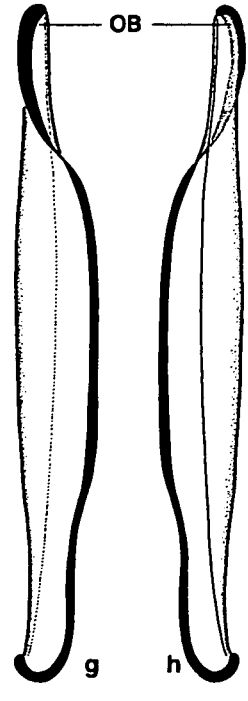


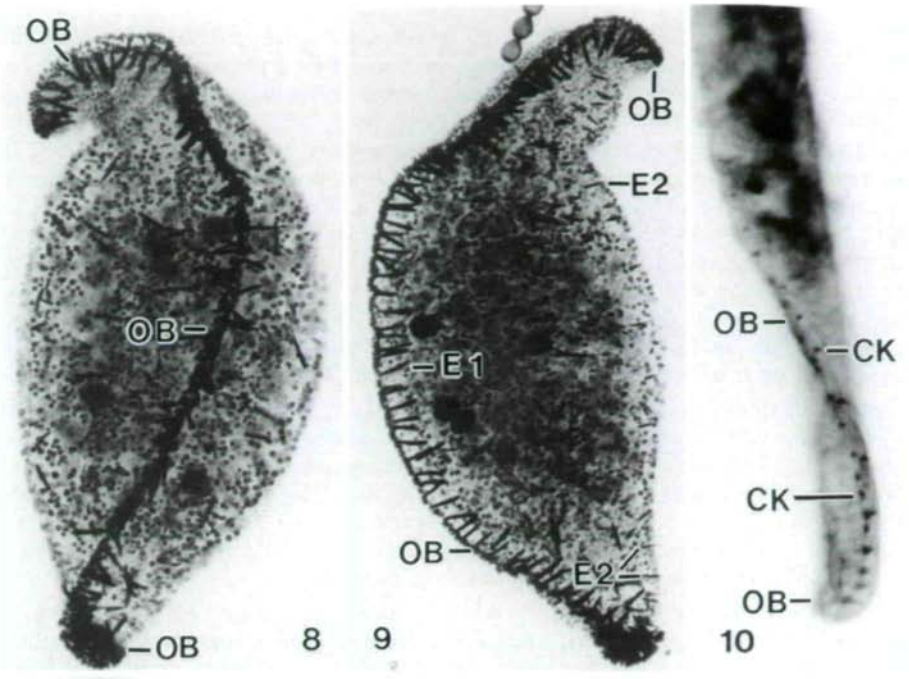
Fig. 7a-l: *Bryophyllum longisetum*, semi-schematic illustrations of protargol-impregnated specimens, showing the variability of the course of the oral bulge and the kinety associated with brush row 3 (a-h). In the anterior quarter, body and oral bulge are flat or twisted (a-h), while possibly mainly the oral bulge twists in the posterior quarter, as indicated by the straight course of the ciliary rows (SKB3; a-d). Rarely, cells are flat (e, f). **i-l:** Reconstructed transverse views. The anterior body portion is distinctly flattened (i). In mid-body, the trunk is usually slightly flattened or unflattened at both sides (j); sometimes it is more flattened on left than right side (k) or vice versa (l). OB – oral bulge, SKB3 – somatic kinety associated with brush row 3.

Most macronucleus nodules scattered in middle quarters of cell, occasionally some nodules connected by thin bridges forming short, moniliform pieces; individual nodules globular to ellipsoidal, about 4 × 2 µm in size, contain few globular nucleoli. Micronuclei about 2.5 µm across, exact number difficult to determine because hardly distinguishable from similar-sized and impregnated macronucleus nodules (Fig. 6q, r, u, 16, 17, 19, 23). Contractile vacuole in rear body end, three to ten excretory pores subterminal on dorsal side (Fig. 6t, u). Two types of extrusomes (Fig. 6a-d, h, i, 8, 9, 11, 13-15, 18, 21, 22): type I studded in oral bulge, indistinctly fusiform to acicular, straight or slightly curved and 5-6 µm long; type II attached to cortex, scattered between ciliary rows, rod-shaped and 2.5-3 µm long; both types heavily impregnate with silver carbonate, but not with the protargol method used, which impregnates only certain cytoplasmic developmental stages in eight out of 21 specimens analysed. Exploded oral and body extrusomes of typical toxicyst structure, 13-16 µm and about 10 µm long in vivo (Fig. 6e, f, 13-15, 18, 22).

Cortex very flexible, contains approximately six rows of granules about 0.5 × 0.2 µm in size between each two somatic kineties and scattered toxicysts, as described above (Fig. 6h, i, 18, 21). Cytoplasm studded with macronucleus nodules and few to many lipid droplets up to 5 µm across, indicating a predatory life style. Food vacuoles rarely recognizable in vivo and protargol preparations, occasionally an up to 8 µm-sized subterminal vacuole with indigestible prey remnants. Swims and creeps very slowly and serpentinously performing conspicuous undulations (Fig. 6a, k-o).

Cilia about 10 µm long in vivo, arranged in an average of nine equidistant, rather loosely ciliated rows, usually five on right side and four on left, some slightly shortened anteriorly and posteriorly, where they abut on circumoral kinety in acute angles; oral bulge usually stronger twisted (90-180° in two thirds of specimens) than body and ciliary rows extending meridionally or slightly obliquely (spirally) from anterior dorsal to posterior ventral margin of cell (Fig. 6p-r, t, u, 7a-h, 10, 17; Tables 4, 5). Dorsal brush dikinetidal, invariably in anterior portion of the three rightmost ciliary rows of the left side, commences at nearly same level and gradually shorten anteriorly when abutting on curved portion of circumoral kinety; conspicuous in vivo, though occupying only 19% of body length on average, due to the long bristles (Fig. 6a, j, p, q, s, t, v, w, 12, 16, 17, 19, 20, 24; Table 4). Brush row 1 slightly shorter than row 2, composed of an average of 18 dikinetids associated with 5-6 µm long, acicular anterior bristles and 1.5-2 µm long, rod-shaped posterior bristles. Brush row 2 slightly longer than rows 1 and 3, composed of an average of 32 dikinetids much more narrowly spaced than those of rows 1 and 3; some to many dikinetids obliquely arranged in subterminal row area, forming conspicuous zigzag pattern in 12 out of 21 specimens analysed; individual dikinetids associated with a 1.5-2 µm long, rod-shaped posterior bristle and a rod-shaped anterior bristle gradually increasing in length from 3 µm anteriorly to 5 µm posteriorly, where some bristles have a short, hair-like process. Brush row 3 almost as long as row 2, consists of an average of 21 dikinetids likely not followed by a monokinetidal bristle tail; individual dikinetids associated with a 1.5-2 µm long, rod-shaped posterior bristle and a rod-shaped anterior bristle with length gradually increasing from 3 µm anteriorly to 6 µm posteriorly; most anterior bristles of dikinetids associated with an up to 10 µm long, hair-like process soon degenerating granularly in disturbed specimens (Fig. 6a, g, j, p, q, s, t, v, w, 12, 16, 17, 19, 20, 24; Table 4).

Oral bulge occupies whole body length, fairly conspicuous because rather distinctly separate from body proper and usually more or less sigmoidal performing undulating movements, likely together with the body proper (Fig. 6a, k-o, 7a-l, 8-10, 16, 17; Tables 4, 5).



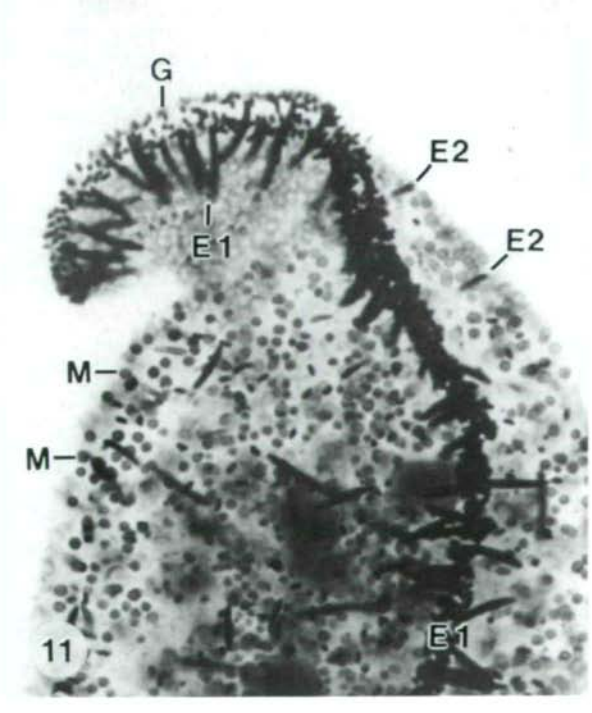
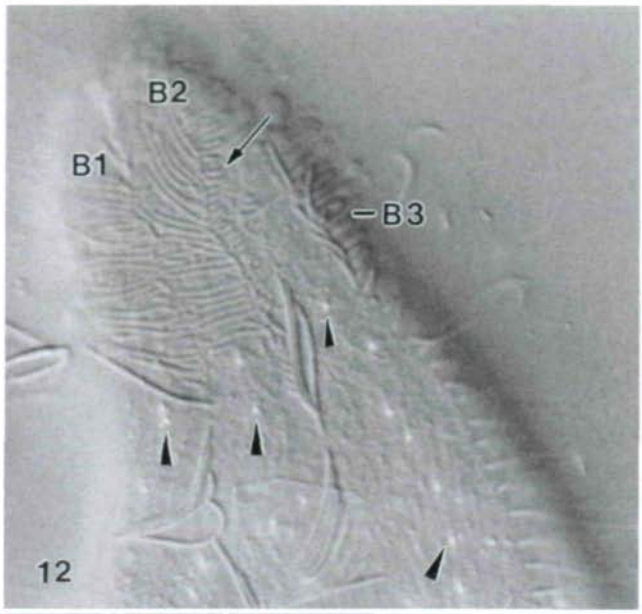
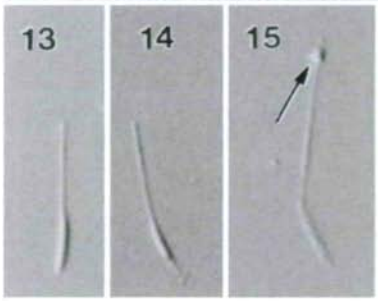
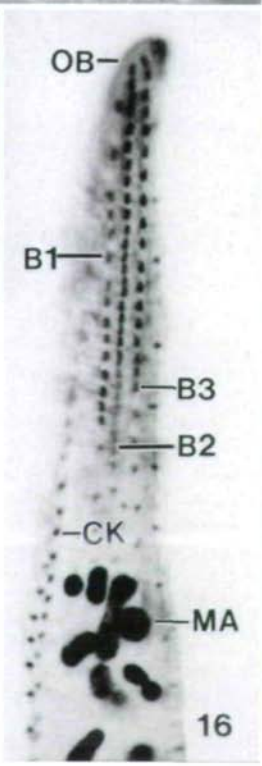


Fig. 8-11: *Bryophyllum longisetum* after silver carbonate (8, 9, 11) and protargol (10) impregnation. **8, 9, 11:** Strongly flattened (by cover glass pressure) specimens in ventral (8, 11) and lateral (9) view. The about 5 µm long oral (type 1) extrusomes impregnate intensely and mark the slightly spiral course of the oral bulge. The 3 µm long somatic extrusomes (type 2) are sparse and inconspicuous. **10:** Posterior body portion showing the spiral course of the oral bulge. CK – circumoral kinety, E1, 2 – type I and type II extrusomes, G – cortical granules, M – mitochondria, OB – oral bulge.







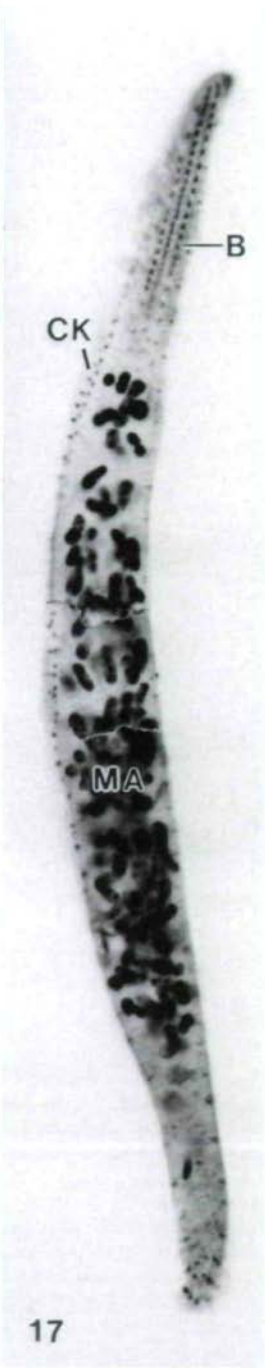
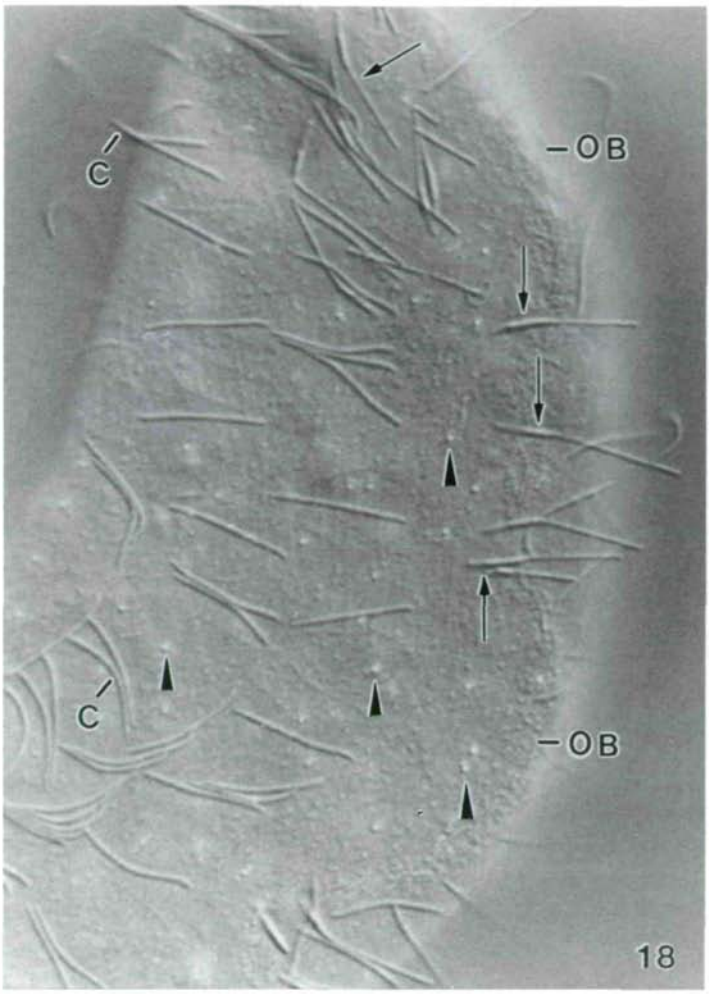
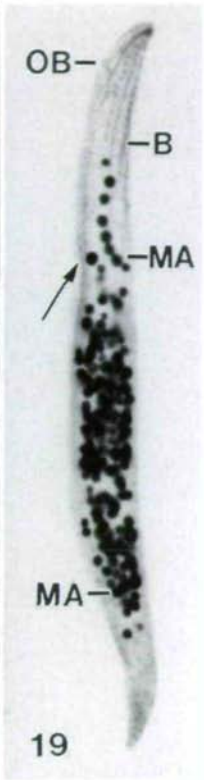


Fig. 12-17: *Bryophyllum longisetum* from life (12-15) and after protargol impregnation (16-17). **12**: Dorsal view showing the bright somatic extrusomes (arrowheads) and the long brush bristles, of which those of row 3 are partially destroyed. The arrow marks the minute posterior bristles of the brush dinkinetids. **13-15**: Exploded type I extrusomes. Arrow marks toxin drop leaving the organelle. **16, 17**: Ciliary pattern of dorsal side and nuclear apparatus. Note the very slender body. B (1-3) – dorsal brush (rows), CK – circumoral kinety, MA – macronucleus nodules, OB – oral bulge.





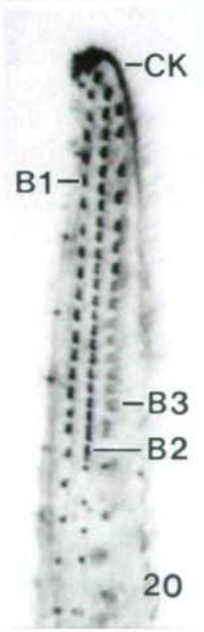
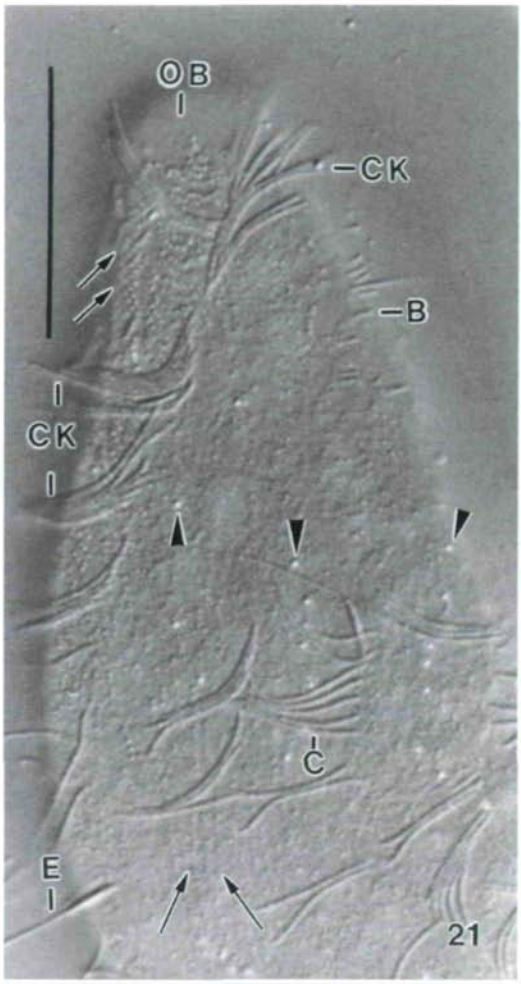
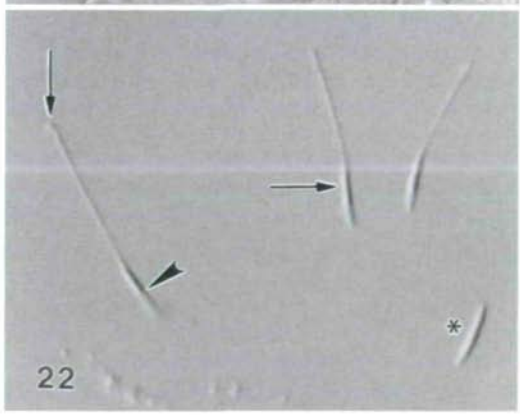


Fig. 18-20: *Bryophyllum longisetum* from life (18) and after protargol impregnation (19, 20). **18**: Middle portion of right side of a strongly flattened (by cover glass pressure) cell, showing exploded type I (oral) extrusomes (arrows) and the scattered, resting type II (somatic) extrusomes (arrowheads), which are seen "frontally" and thus appear as bright dots. **19**: Left side overview showing the slender body packed with macronucleus nodules. Arrow marks the proximal end of the "spathidiid" portion of the oral bulge. Only the spathidiid part of the oral bulge is associated with nematodesmata, suggesting that the Bryophyllidae evolved from a *Spathidium*-like ancestor (see also Fig. 23, 24). **20**: Dorsal view of anterior body region. The three dorsal brush rows have similar length and are composed of dikinetids with highly differentiated bristles (cp. figures 7j and 12). B(1-3) - dorsal brush (rows), C - ordinary somatic cilia, CK - circumoral kinety, MA - macronucleus nodules, OB - oral bulge.





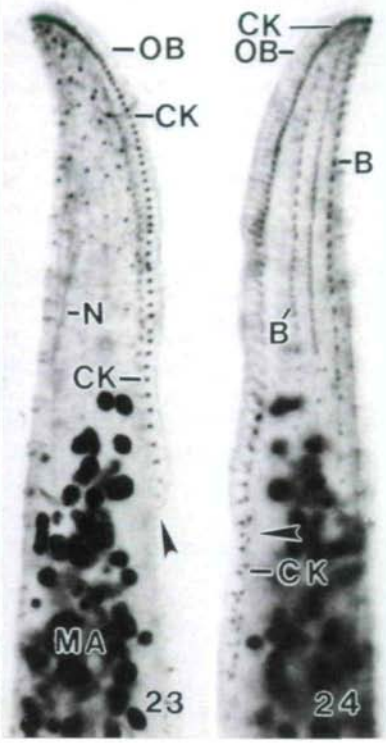


Fig. 21-24: *Bryophyllum longisetum* from life (21, 22) and after protargol impregnation (23, 24). **21:** Ventrolateral view of anterior body portion, showing somatic extrusomes (arrowheads) and rows of minute granules in oral and somatic cortex (arrows). The cilia of the circumoral kinety (CK) form a membrane-like structure. Dorsal brush (B) largely destroyed due to the cover glass pressure. **22:** Resting (asterisk) and exploded (arrows) oral toxicysts. The toxin of the left extrusome is just leaving the organelle (arrow and arrowhead). **23, 24:** Ciliary pattern of right and left side in anterior body portion of same specimen. Arrowheads mark proximal end of spathidiid part of oral bulge. B – dorsal brush, CK – circumoral kinety, E – extrusome, MA – macronucleus nodules, N – nematodesmata, OB – oral bulge.

Circumoral kinety at the base of oral bulge, composed of dikinetids much more closely spaced anteriorly than posteriorly; each dikinetid associated with an about 12 µm long cilium and a fine nematodesma present, however, only in anterior body quarter, viz., the spatulate "head" region. Oral basket inconspicuous and recognizable only in anterior portion of prepared specimens (Fig. 6p-w, t, u, 16, 17, 23, 24).

Occurrence and ecology: As yet found only at type location. *Bryophyllum longisetum* became abundant in the non-flooded Petri dish culture, but no dividers were found, indicating that most specimens originated from resting cysts. The sample, kindly provided by DI Georg ERTL (Linz), was an acidic (pH 5.4) mixture of soil and litter from a cloud forest with tree-like Ericaceae as understorey; it contained about 34 species of ciliates, of which several were undescribed.

Comparison with related species: The combination of slender body, sigmoidal oral bulge, hair-like brush bristles, numerous macronucleus nodules, and somatic toxicysts clearly distinguishes *B. longisetum* from all other members of the family. As concerns body shape, it is highly similar to that of *Apobryophyllum vermiforme*, which has a long macronucleus strand and very fine, rod-shaped extrusomes (FOISSNER et al. 2002). The curious bristles of brush row 3 are unique to the entire suborder.

Apobryophyllum sulcatum FOISSNER & LEI nov. spec. (Fig. 25a-n, 26-31; Table 6)

Diagnosis: Size about 180 × 25 µm in vivo. Slenderly ellipsoidal to indistinctly knife-shaped. Macronucleus a more or less tortuous strand; several lanceolate or fusiform micronuclei. Extrusomes rod-shaped and 5-6 µm long, in oral bulge and somatic cortex, where they form a longitudinal row each in the ridges of a deep furrow on left dorsolateral margin. On average 14 ciliary rows, about five leftmost rows differentiated to complex dorsal brush anteriorly.

Type location: Soil from margin of a flat pond (Sirkelsvlei) in the Cape Peninsula National Park, Republic of South Africa, E18°25' S33°53'.

Etymology: The Latin adjective *sulcatus* (furrowed) refers to the conspicuous furrow on the left dorsolateral margin of the cell, a main feature of the species.

Description: Few and only mediocre impregnated specimens were available. Nevertheless, the decisive features are recognizable in at least nine specimens. The details of the dorsal brush are perfectly revealed in the holotype and a paratype specimen.

Size 110-210 × 20-40 µm in vivo, usually about 180 × 25 µm, as calculated from some in vivo measurements and the morphometric data; length:width ratio 3.6-8.9:1, on average near 7:1 both in vivo and protargol preparations (Table 6); laterally flattened up to 2:1 in mid-body and up to 3:1 at body ends. Outline elongate elliptical to indistinctly knife-shaped, in one out of 17 specimens analysed distinctly spatulate; left dorsal margin duplicated by a rectangular furrow extending whole body length (Fig. 25a, f); ventral anterior quarter, likely the original mouth, more or less distinctly convex, rarely straight and slightly projecting from body proper proximally, dorsal anterior end bluntly pointed; posterior end narrowly rounded and usually slightly notched by the dorsolateral furrow and the oral bulge end (Fig. 25a, h-j, l, 29). Macronucleus in middle body third, on average 58 µm long, usually a tortuous and indistinctly nodulated strand, rarely helically coiled or rod-shaped; nucleoli lobate to globular. On average five micronuclei near or attached to macronucleus, individual micronuclei lanceolate or fusiform and about 5 × 2 µm in size (Fig. 25h-j, l, 26-28). Contractile vacuole in rear body end, some excretory

pores in pole area (Fig. 29). Extrusomes studded in oral bulge and the two ridges formed by the dorsolateral furrow; appear in two forms, viz., as slightly curved rods narrowed at both ends and as indistinctly acicular rods; intensely impregnate and appear as slightly curved rods with ends not narrowed in protargol preparations (Fig. 25b, c, f, h, i, 26-28, 30, 31). Cortex very flexible, contains about five rows of narrowly spaced, colourless granules less than 0.5 µm across between two ciliary rows each. Cytoplasm colourless, contains few to many lipid droplets up to 4 µm across and many only 2-4 µm-sized food vacuoles with loose content. Glides and wriggles slowly on microscope slide.

Cilia about 8 µm long in vivo, arranged in an average of 14 equidistant, meridional rows distinctly separate from circumoral kinety (Fig. 25j, k). Four (possibly only three in two out of 17 specimens analysed) to seven, on average five leftmost rows differentiated to complex dorsal brush occupying anterior third of body (Fig. 25a, d, k-n, 28; Table 6). All brush rows, except of leftmost row, composed of rather irregular fragments each consisting of very narrowly spaced kinetids with 3-5 µm long, acicular bristles irregularly alternating with ordinary cilia; leftmost row (rarely perhaps also anterior portion of penultimate row) of ordinary structure, that is, composed of narrowly spaced, lined up dikinetids each bearing an about 3 µm long, slightly clavate anterior bristle and a 1.5 µm long, rod-shaped posterior bristle (Fig. 25d, k-n, 28).

Table 6: Morphometric data on *Apobryophyllum sulcatum*.

Characteristics[1]	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	156.2	162.0	26.8	6.5	17.2	108.0	195.0	17
Body, width	25.6	24.0	5.8	1.4	22.6	20.0	38.0	17
Body length:width, ratio	6.3	6.6	1.5	0.4	24.2	3.6	8.9	17
Posterior body end to dorsal end of oral bulge, distance	2.8	2.3	1.8	0.7	61.8	1.0	6.0	6
Anterior body end to end of longest dorsal brush row, distance	49.0	52.0	9.9	3.7	20.2	36.0	60.0	7
Oral bulge, height	1.8	2.0	-	-	-	1.2	2.5	11
Macronucleus figure, length	58.0	54.0	15.5	3.8	26.7	31.0	86.0	17
Macronucleus, length (spread)	86.1	84.0	26.4	6.4	30.7	39.0	164.0	17
Macronucleus, width	7.6	8.0	1.3	0.3	17.3	5.0	10.0	17
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	17
Micronuclei, length	5.2	5.0	0.7	0.2	13.1	4.0	6.0	16
Micronuclei, width	2.3	2.0	0.3	0.1	14.1	2.0	3.0	16
Micronuclei, number	4.7	5.0	1.8	0.5	39.4	2.0	7.0	15
Somatic kineties, total number	13.7	14.0	1.1	0.4	8.2	12.0	15.0	9
Somatic kineties on left side, number	6.6	7.0	0.7	0.2	11.1	5.0	7.0	9
Somatic kineties on right side, number	7.1	7.0	0.6	0.2	8.5	6.0	8.0	9
Dorsal brush rows, number	5.1	5.0	1.1	0.3	21.6	4.0	7.0	10
Somatic extrusomes rows, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	17

[1] Data based on 17 specimens found in the preparations (FOISSNER's method) of the material from the non-flooded Petri dish culture. 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, $\bar{x}$ – arithmetic mean.

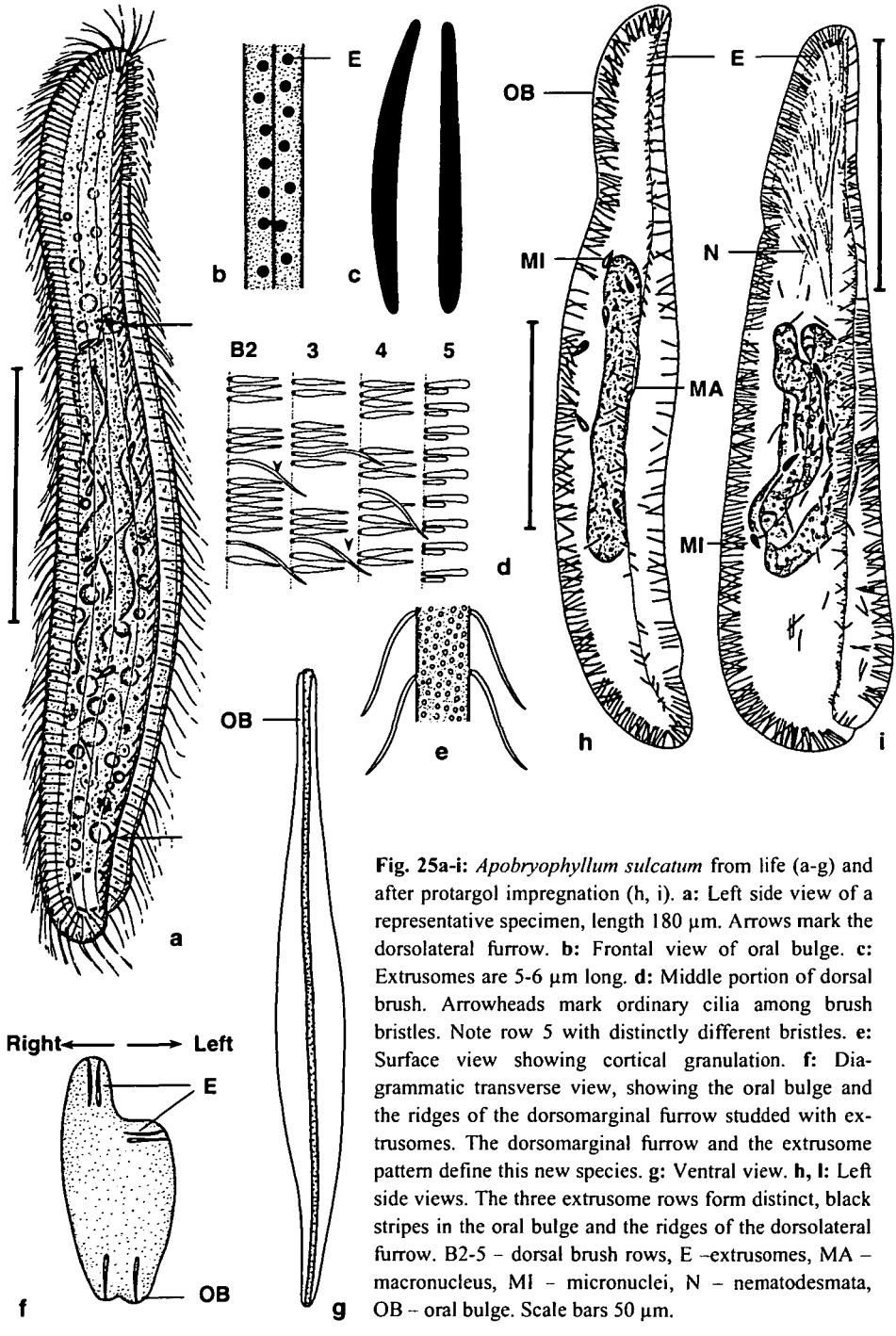


Fig. 25a-i: *Apobryophyllum sulcatum* from life (a-g) and after protargol impregnation (h, i). **a:** Left side view of a representative specimen, length 180 µm. Arrows mark the dorsolateral furrow. **b:** Frontal view of oral bulge. **c:** Extrusomes are 5-6 µm long. **d:** Middle portion of dorsal brush. Arrowheads mark ordinary cilia among brush bristles. Note row 5 with distinctly different bristles. **e:** Surface view showing cortical granulation. **f:** Diagrammatic transverse view, showing the oral bulge and the ridges of the dorsomarginal furrow studded with extrusomes. The dorsomarginal furrow and the extrusome pattern define this new species. **g:** Ventral view. **h, i:** Left side views. The three extrusome rows form distinct, black stripes in the oral bulge and the ridges of the dorsolateral furrow. B2-5 – dorsal brush rows, E –extrusomes, MA – macronucleus, MI – micronuclei, N – nematodesmata, OB – oral bulge. Scale bars 50 µm.

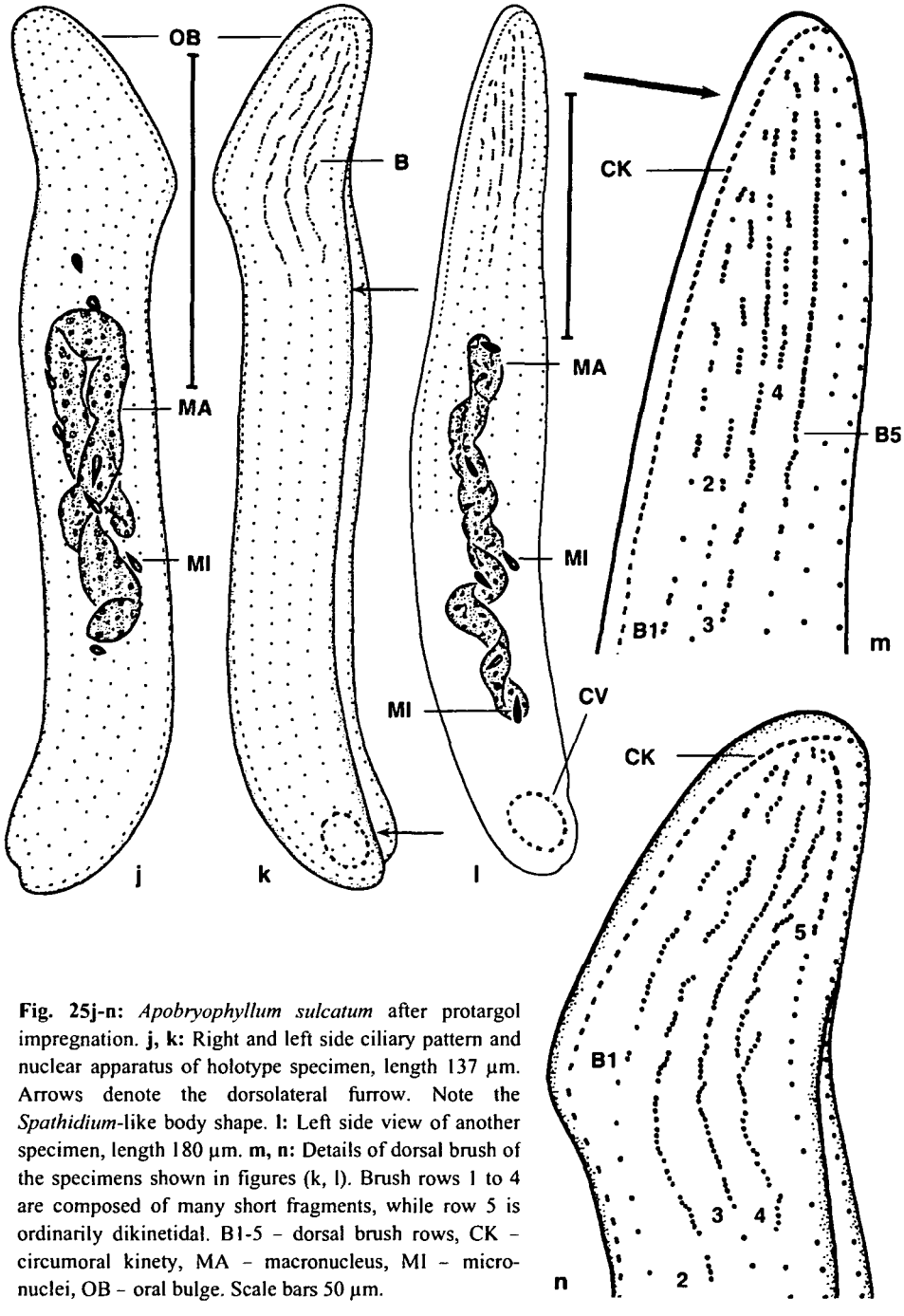


Fig. 25j-n: *Apobryophyllum sulcatum* after protargol impregnation. **j, k:** Right and left side ciliary pattern and nuclear apparatus of holotype specimen, length 137 µm. Arrows denote the dorsolateral furrow. Note the *Spathidium*-like body shape. **l:** Left side view of another specimen, length 180 µm. **m, n:** Details of dorsal brush of the specimens shown in figures (k, l). Brush rows 1 to 4 are composed of many short fragments, while row 5 is ordinarily dikinetidal. B1-5 – dorsal brush rows, CK – circumoral kinety, MA – macronucleus, MI – micronuclei, OB – oral bulge. Scale bars 50 µm.

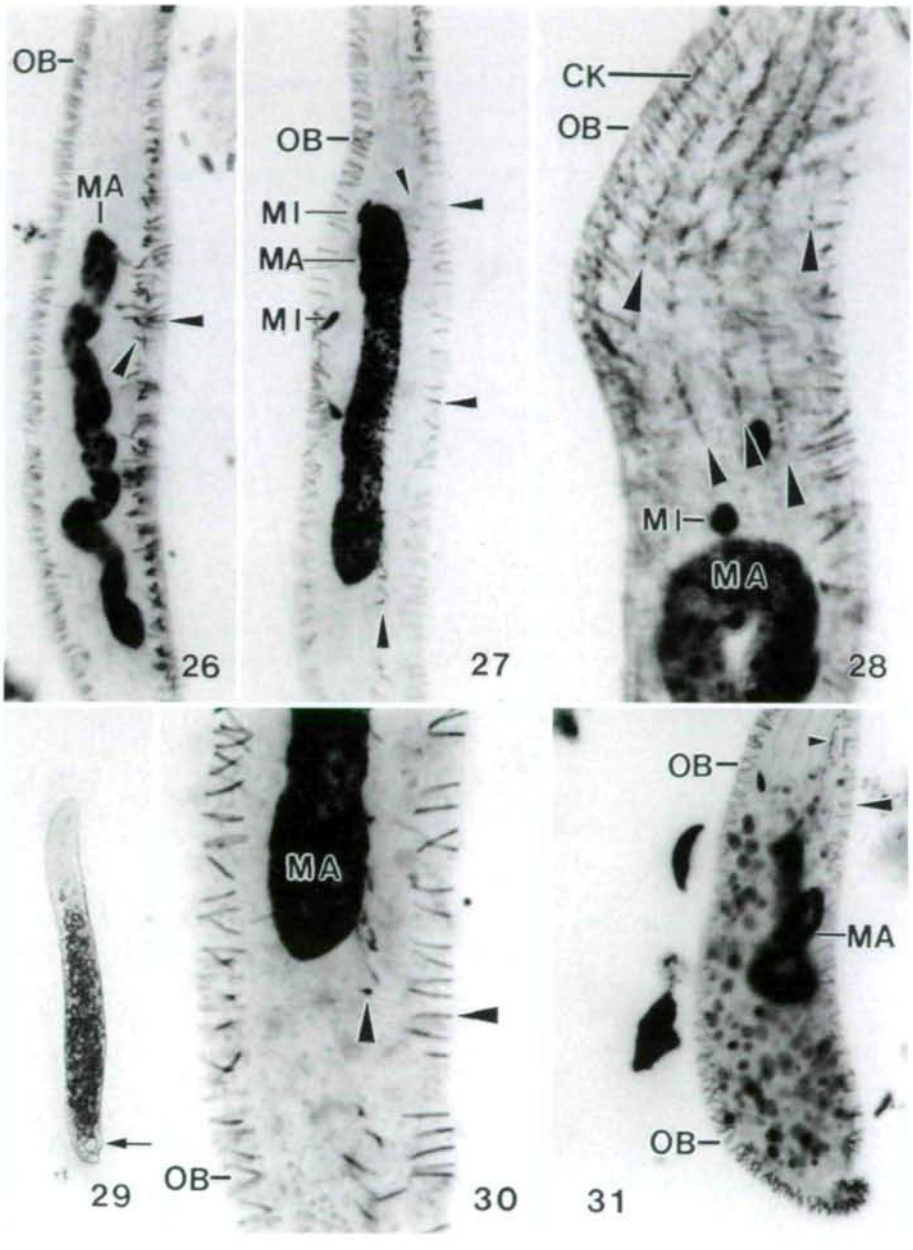


Fig. 26-31: *Apobryophyllum sulcatum* from life (29) and after protargol impregnation (26-28, 30, 31). **26, 27, 30, 31:** Left side views with the two dorsomarginal extrusome rows marked by arrowheads; a third row is formed by the extrusomes in the oral bulge (OB). **28:** Left side view with brush rows marked by arrowheads. **29:** Left side view with contractile vacuole marked by arrow. CK – circumoral kinety, MA – macronucleus, MI – micronuclei, OB – oral bulge.

Oral bulge extends whole body length, very inconspicuous because only about 2 µm high and hardly separate from body proper. Circumoral kinety at base of oral bulge, composed of very narrowly spaced dikinetids each associated with a cilium and a fine nematodesma in anterior body quarter, viz., the spathidiid "head" region; oral basket thus recognizable only in anterior portion of prepared specimens and likely lacking underneath (Fig. 25b, i-l, 28, 29).

Occurrence and ecology: As yet found only at type location. The sample, which contained about 45 species, of which 13 (!) were undescribed, was taken on 18. 02. 1995 and investigated on 31. 07. 1995. Few specimens of *A. sulcatum* developed six weeks after rewetting the sample, which was taken from a 10 m wide, grassy area (mainly short grass and sedges), flooded during periods of high water, around the pond, that is, about 10 m off the water margin. The sample, which had pH 5.4 in water, was composed of grass litter, dark, very sandy soil, and many fine roots. The sampling site and the late appearance and low abundance in the non-flooded Petri dish culture indicate that *A. sulcatum* prefers limnetic habitats, similar to *A. vermiforme* and *A. etoschense*.

Comparison with related species: *Apobryophyllum sulcatum* is a very distinct species, differing from the congeners (*A. etoschense* FOISSNER 1998; *A. terricola* FOISSNER 1998; *A. vermiforme* FOISSNER, AGATHA & BERGER 2002) by the distinct extrusome rows in the ridges produced by the dorsolateral furrow. *Apobryophyllum terricola*, possibly the nearest relative, has about six rows of somatic extrusomes and globular (vs. lanceolate or fusiform) micronuclei (FOISSNER 1998, FOISSNER et al. 2002).

Family Spathidiidae KAHL 1929

Ontogenesis of *Arcuospathidium coemeterii* (KAHL 1943) FOISSNER et al. 2004

Material: Division was studied in a population from soil of a *Hordelymo-Fagetum* (Woodruff-beech) forest in the surroundings of Vienna, Austria, viz., in the suburb Klausen-Leopoldsdorf (see FOISSNER et al. 2004 for detailed site description). Cultures were established in Eau de Volvic (French table water) enriched with some drops of percolate from the non-flooded Petri dish culture and a few crushed wheat grains to stimulate growth of bacteria and prey protozoa (*Colpoda inflata*).

The Klausen-Leopoldsdorf specimens match the neotype population in most main features (nuclear and ciliary pattern, extrusomes, brush details), but differ considerably in size and shape (64 × 20 µm vs. 87 × 21 µm, that is, 3.2:1 vs. 4.3:1 in protargol preparations) and, especially, in the shape of the circumoral kinety, which is distinctly cuneate, while elliptical to indistinctly cuneate in the neotype specimens (Fig. 32h-j, n, s; Table 7). These differences might support ranking the population as a distinct subspecies. However, when considering the rather pronounced overall variability and the agreement in all other main features, such split appears too progressive at the present stage of knowledge. As concerns shape, the Klausen-Leopoldsdorf specimens match almost perfectly KAHL's type specimen (length: width ratio 2.75:1), further supporting the identification of FOISSNER et al. (2004). Further differences and observations (Fig. 32a, 33a-d; Table 7): (i) frequently, the macronucleus is in the middle body third (vs. beneath mid-body); (ii) usually, the micronucleus (possibly two in some specimens) is rather distant from (vs.

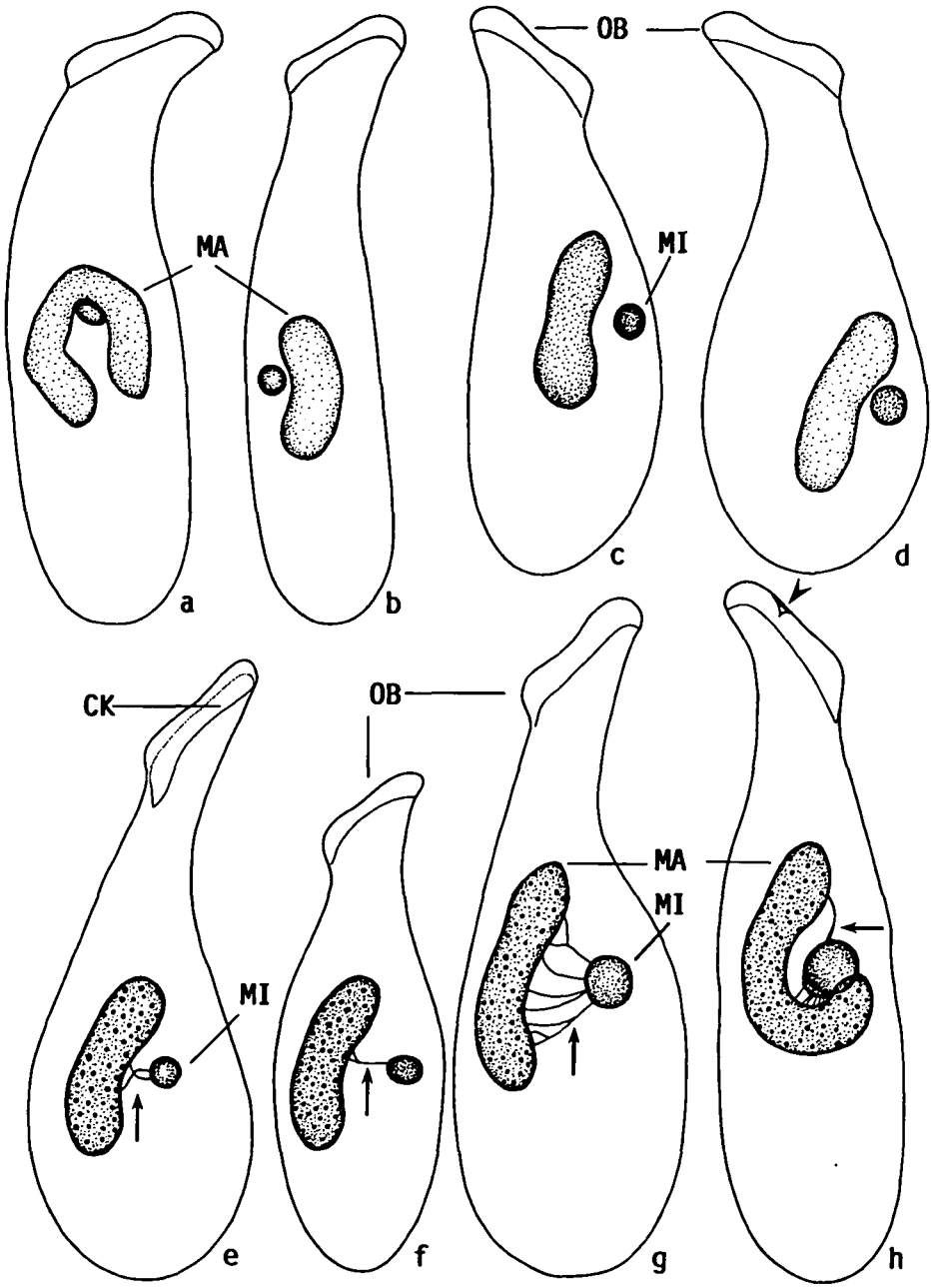


Fig. 32a-h: *Arcuospathidium coemeterii*, morphostatic specimens (a-f) and early (g, h) dividers after protargol impregnation. **a-d:** Variability, length 62-70 µm. **e-h:** Macro- and micronucleus are connected by fibres (arrows), length 65(f)-95(g) µm. Arrowhead denotes temporary cytostome. CK – circumoral kinety, MA – macronucleus, MI – micronucleus, OB – oral bulge.

close to) the macronucleus; (iii) 14 vs. 12 ciliary rows; (iv) oral bulge shorter than widest trunk region by 20% (vs. as long as) and invariably slightly depressed in centre (vs. slightly concave, convex, or sigmoidal); (v) temporary cytostome occasionally (Fig. 32h) recognizable in protargol preparations (vs. seen only in SEM micrographs).

Table 7: Morphometric data on *Arcuospathidium coemeterii* in morphostatic and dividing specimens from the Klausen-Leopoldsdorf population.

Characteristics[1]	Stages	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Body, length	Morphostatic	64.2	64.0	4.0	1.0	6.3	58.0	72.0	15
	Very Early	71.4	71.0	5.2	1.3	7.3	61.0	82.0	15
	Early	79.0	80.0	7.3	2.2	9.3	66.0	89.0	11
	Early middle	77.2	80.0	10.6	4.3	13.8	63.0	87.0	6
	Middle	70.3	69.0	-	-	-	68.0	74.0	3
	Late	72.0	75.0	-	-	-	65.0	76.0	3
	Very late	67.5	-	-	-	-	60.0	75.0	2
Body, width	Morphostatic	20.1	21.0	2.9	0.8	14.5	16.0	24.0	15
	Very Early	21.6	22.0	3.2	0.8	15.0	17.0	28.0	15
	Early	20.0	19.0	2.8	0.9	14.1	17.0	26.0	11
	Early middle	25.3	24.0	2.4	1.0	9.6	24.0	30.0	6
	Middle	25.3	25.0	-	-	-	25.0	26.0	3
	Late	24.0	23.0	-	-	-	23.0	26.0	3
	Very late	22.5	-	-	-	-	22.0	23.0	2
Body length:width, ratio	Morphostatic	3.2	3.0	0.5	0.1	14.6	2.7	4.2	15
	Very Early	3.3	3.2	0.6	0.2	18.1	2.6	4.5	15
	Early	4.0	4.3	0.8	0.2	18.9	2.8	4.9	11
	Early middle	3.1	3.2	0.6	0.2	19.4	2.2	3.6	6
	Middle	2.8	2.8	-	-	-	2.7	2.8	3
Oral bulge, length	Morphostatic	16.3	17.0	2.0	0.5	12.4	12.0	19.0	15
Circumoral kinety to last dikinetid of brush row 1, distance	Morphostatic	12.1	12.0	1.2	0.3	9.8	10.0	14.0	13
Circumoral kinety to last dikinetid of brush row 2, distance	Morphostatic	13.3	13.0	1.5	0.4	11.2	12.0	17.0	13
Circumoral kinety to last dikinetid of brush row 3, distance	Morphostatic	6.4	6.0	1.2	0.3	18.7	5.0	8.0	13
Macronucleus figure, length	Morphostatic	19.7	18.0	4.0	1.0	20.0	16.0	30.0	15
	Very Early	29.1	27.5	5.3	1.4	18.3	21.0	40.0	15
	Early	31.3	31.0	4.8	1.4	15.3	24.0	42.0	11
	Early middle	25.8	29.0	6.2	2.5	23.9	17.0	31.0	6
	Middle	15.0	15.0	-	-	-	13.0	17.0	3
Macronucleus, width	Morphostatic	5.5	5.0	0.6	0.2	11.7	5.0	7.0	15
Macronucleus, number	Morphostatic	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Micronucleus, largest diameter	Morphostatic	3.7	3.5	0.6	0.2	15.9	3.0	5.0	15
	Very Early	6.9	6.8	1.1	0.3	15.4	5.5	9.5	15
	Early	9.9	10.0	1.7	0.5	17.1	7.5	13.0	11
	Early middle	10.4	10.5	1.6	0.7	15.6	8.5	13.0	6

continued

Table 7: Continued

Characteristics[1]	Stages	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Micronucleus, number	Morphostatic	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Somatic kineties, number	Morphostatic	14.4	14.0	0.9	0.2	6.0	13.0	16.0	13
Basal bodies in a right side kinety, number	Morphostatic	19.8	19.0	3.6	1.2	18.0	15.0	26.0	9
Dorsal brush rows, number	Morphostatic	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
Dikinetids in brush row 1, number	Morphostatic	10.9	11.0	2.3	0.7	21.5	7.0	15.0	11
Dikinetids in opisthe's brush	Early	6.5	7.0	1.0	0.5	15.4	5.0	7.0	4
row 1, number	Middle	7.3	8.0	-	-	-	6.0	8.0	3
	Late and very late	8.5	8.5	1.3	0.6	15.2	7.0	10.0	4
	Post-divider	8.6	8.0	2.6	1.2	30.3	5.0	12.0	5
Dikinetids in brush row 2, number	Morphostatic	12.1	12.0	1.4	0.4	12.0	10.0	15.0	11
Dikinetids in opisthe's brush	Early	7.5	8.0	1.9	1.0	25.5	5.0	9.0	4
row 2, number	Middle	11.0	11.0	-	-	-	10.0	12.0	3
	Late and very late	10.3	10.0	0.5	0.3	4.9	10.0	11.0	4
	Post-divider	8.8	9.0	2.0	0.9	23.3	7.0	12.0	5
Dikinetids in brush row 3, number	Morphostatic	5.7	5.0	1.3	0.4	23.5	4.0	9.0	11
Dikinetids in opisthe's brush	Early	4.3	4.0	0.5	0.3	11.8	4.0	5.0	4
row 3, number	Middle	4.7	4.0	-	-	-	4.0	6.0	3
	Late and very late	5.5	6.0	1.0	0.5	18.2	4.0	6.0	4
	Post-divider	5.4	5.0	1.5	0.7	28.1	4.0	7.0	5
Dikinetids in circumoral kinety, number	Morphostatic	67.4	65.0	10.6	3.5	15.8	52.0	80.0	9
Dikinetids in opisthe's oral	Early	49.0	48.0	-	-	-	44.0	55.0	3
kinetofragments, number	Middle	51.0	50.0	-	-	-	49.0	54.0	3
	Late and very late	48.5	48.0	8.9	4.4	18.2	40.0	58.0	4
	Post-divider	49.3	48.5	5.4	2.7	10.9	44.0	56.0	4

[1] Data based on mounted and protargol-impregnated (FOISSNER's method) specimens from a non-flooded Petri dish culture. 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, $\bar{x}$ – arithmetic mean.

An outstanding feature of the Klausen-Leopoldsdorf population of *A. coemeterii* are very fine, radiate and/or ramose, fibrous connections between the micronucleus and macronucleus, recognizable in five out of forty-four specimens analysed (Fig. 32e-h). The frequency of these structures, which likely originate from the micronucleus, increases in early dividers, where they are recognizable in eight out of 21 appropriately oriented specimens, suggesting some function in nuclear division. Unfortunately, we could not follow the origin of these structures during division. In the neotype population, which we checked for such connections, the micronucleus is too close to the macronucleus.

Ontogenesis: Very early dividers are slightly larger than morphostatic specimens (Fig. 32g, 33b-d; Table 7). Division commences with the production of basal bodies in or slightly underneath mid-body in those kineties which bear the dorsal brush in proter and opisthe. Usually, even an oblique dikinetid, obviously belonging to the prospective oral kinetofragments, is recognizable at the anterior end of each developing brush kinety (Fig. 33c). Soon after, basal body proliferation occurs in all ciliary rows, dikinetids assemble in the opisthe brush kineties, and minute oral kinetofragments, each usually composed of one to five dikinetids, develop at the anterior end of the broken ciliary rows (Fig. 33d). The macronucleus elongates from about 20 µm to 29 µm, but the nucleoli appear unchanged. The micronucleus almost doubles its size from an average of 3.7 µm to 6.9 µm (Fig. 32g, 33b-d, 34; Table 7).

Early dividers are the largest and slenderest cells within the population because they are significantly longer, but not wider than morphostatic cells. Interestingly, they have a slight indentation in the prospective fission area (Fig. 32h, 33e-g; Table 7). The new oral kinetofragments now consist of three to six dikinetids, that is, are basically completed, but the final, total number of kinetids is possibly obtained only in late post-dividers, as indicated by counts of the circumoral dikinetids (Table 7). The newly formed kinetofragments detach from the somatic kineties and commence to curve rightwards, those on the left side slightly earlier than those on the right (Fig. 33e, f). The opisthe's dorsal brush is almost completed, except of one or two dikinetids, which are added in mid-dividers; no monokinetids remain between circumoral kinety and the individual brush rows. An early divider with a fourth brush row right of row 1 in the proter lacks this row in the opisthe (Fig. 33f). The macronucleus now elongates to its maximum length of about 31 µm and assumes an oblong, slightly curved shape; the nucleoli still appear unchanged. The micronucleus, which is now close to the macronucleus in nine out of 11 appropriate stages, increases to about 10 µm in size and becomes somewhat spongious (Fig. 32h, 33g, 35, 37; Table 7).

Early mid-dividers have the same length as early dividers, but are inflated in mid-body, where the indentation in the prospective fission area is still recognizable (Fig. 33h, i; Table 7). While the ciliary pattern is very similar to that of early dividers, the nuclear apparatus shows distinct changes: the macronucleus commences to shorten towards the centre, as indicated by the inflated ends; the nucleoli disappear; and the micronucleus, whose spongious content detaches from the nuclear membrane, approaches its maximum size of 10.5 µm on average, that is, shows a really conspicuous, three-fold increase compared to the interphase size. A new proter contractile vacuole and excretory pores are generated dorsolaterally above the prospective fission area (Fig. 33h, i).

Middle dividers keep the maximum body width of about 25 µm, but shorten to a length of 70 µm becoming fusiform (Fig. 33j-m, 36; Table 7). The new oral kinetofragments are horizontally arranged on the left side, while still slanted on the right. The dorsal brush is now complete, that is, no further increase occurs in the number of dikinetids (Table 7). The macronucleus condenses to a globular, homogenously impregnated mass. The micronucleus begins to divide, soon becoming distinctly dumb-bell shaped because the hemispherical halves are connected by a conspicuous, centrally constricted fibre bundle.

Late dividers are slightly larger than morphostatic cells and re-form the division furrow in mid-body (Fig. 33n-q; Table 7). The newly produced somatic basal bodies have fully developed cilia and become evenly distributed in the rows. The opisthe's oral kineto

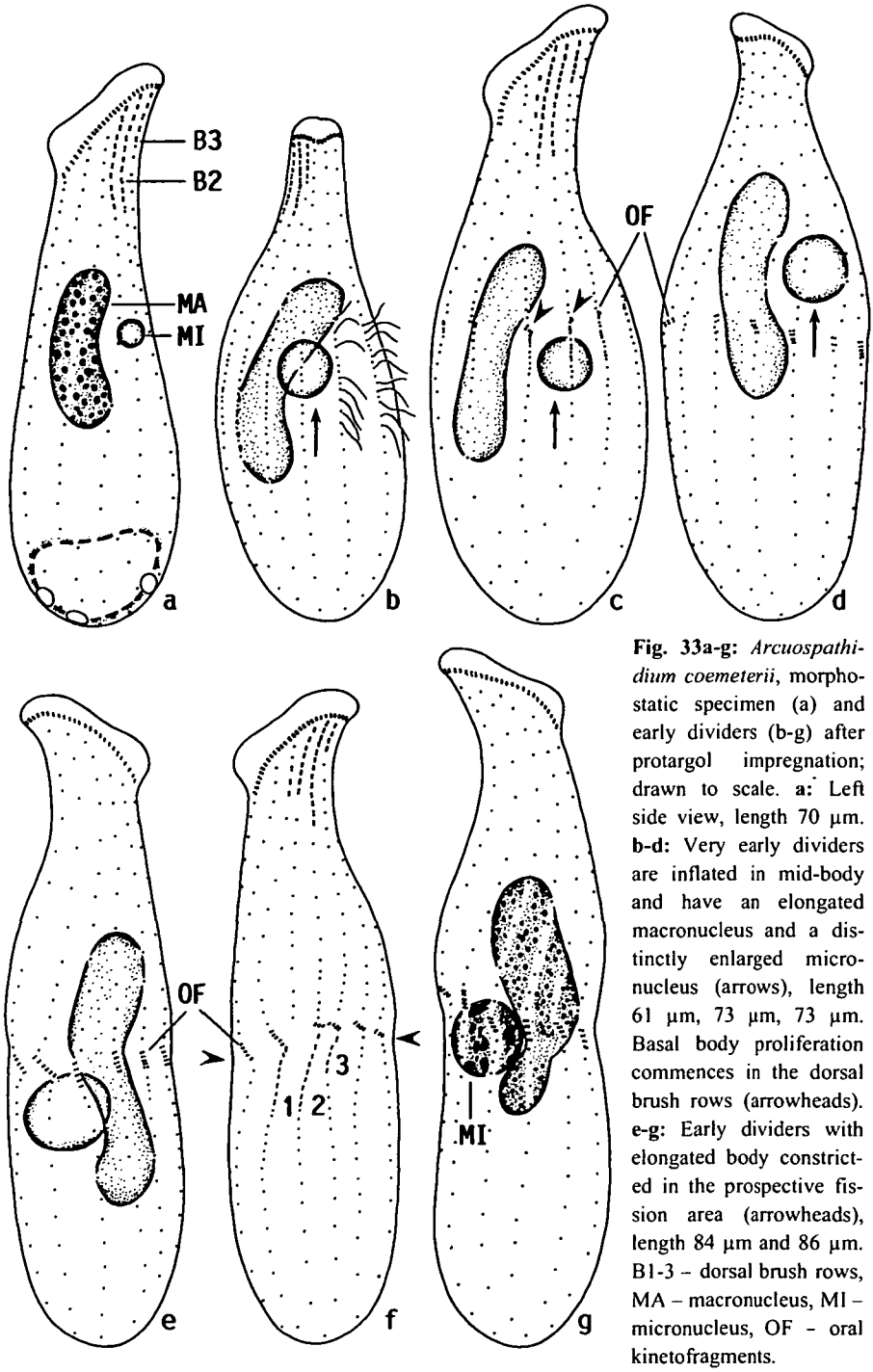


Fig. 33a-g: *Arcuospathidium coemeterii*, morphostatic specimen (a) and early dividers (b-g) after protargol impregnation; drawn to scale. **a:** Left side view, length 70 µm. **b-d:** Very early dividers are inflated in mid-body and have an elongated macronucleus and a distinctly enlarged micronucleus (arrows), length 61 µm, 73 µm, 73 µm. Basal body proliferation commences in the dorsal brush rows (arrowheads). **e-g:** Early dividers with elongated body constricted in the prospective fission area (arrowheads), length 84 µm and 86 µm. B1-3 – dorsal brush rows, MA – macronucleus, MI – micronucleus, OF – oral kinetofragments.

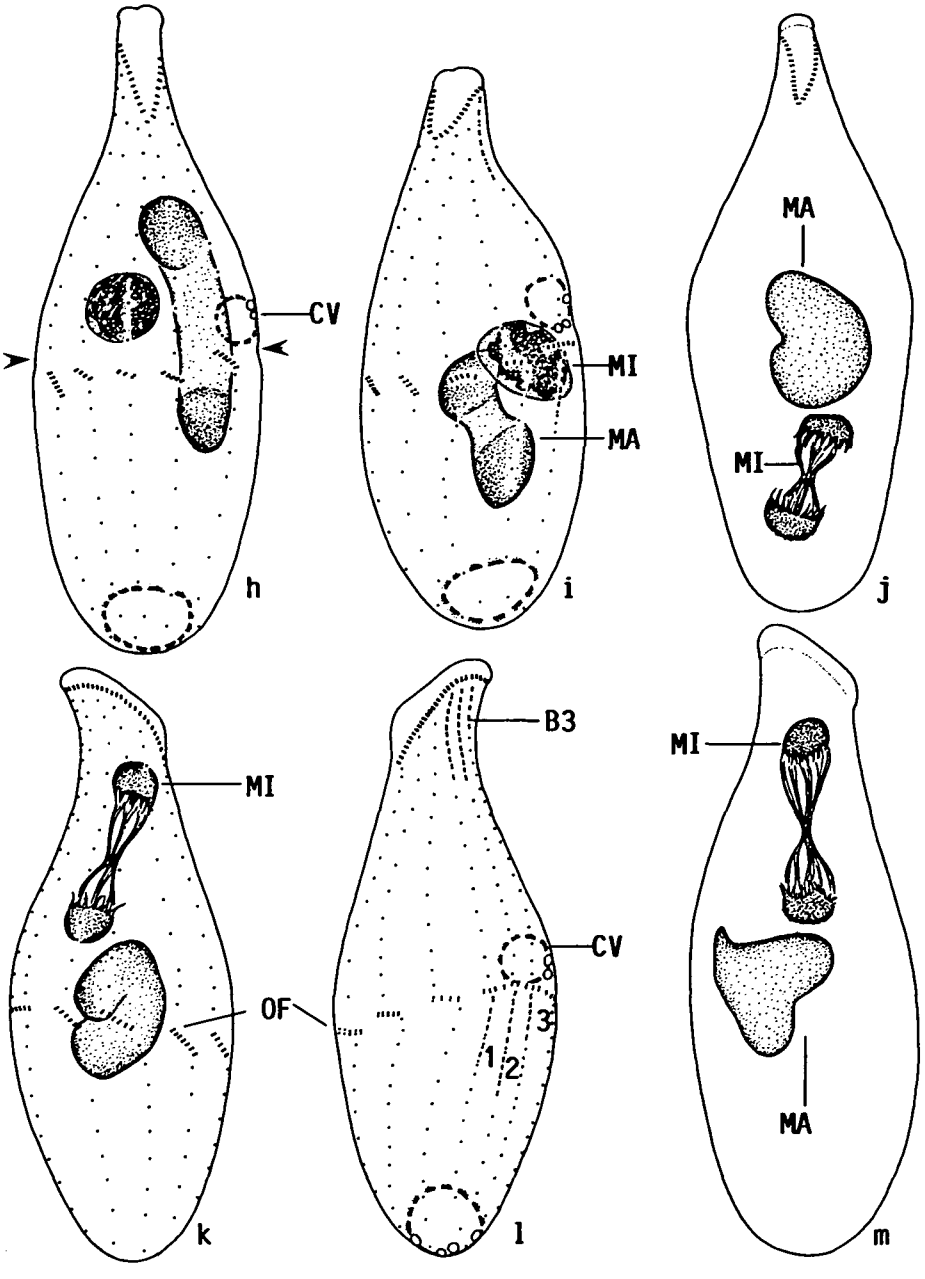
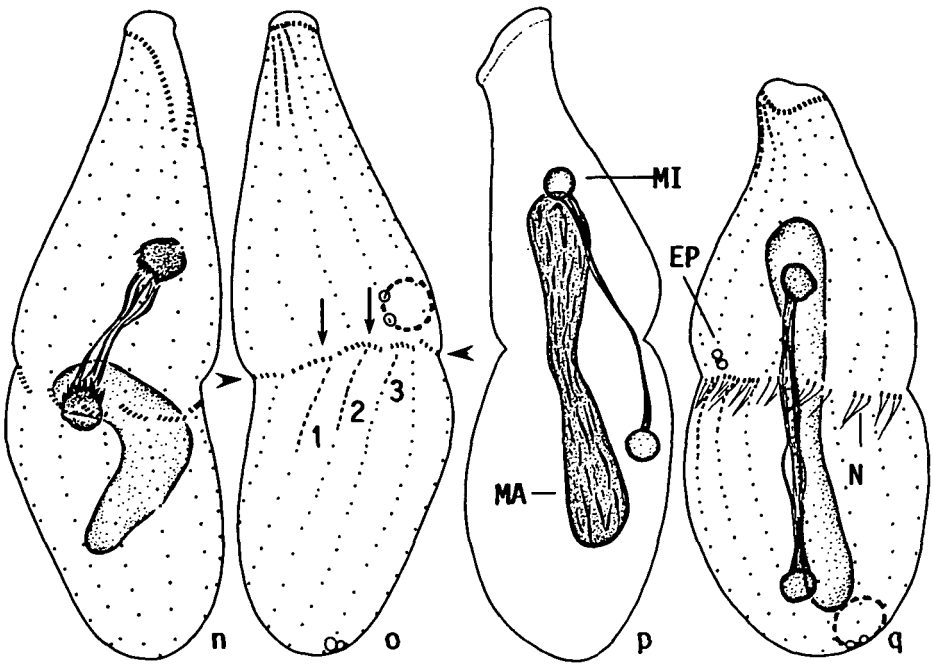


Fig. 33h-m: *Arcuospathidium coemeterii*, middle dividers; drawn to scale. **h:** Early mid-divider, length 74 µm. Arrowheads mark disappearing central constriction. **i:** Early mid-divider with condensing macronucleus and elongating micronucleus, length 63 µm. **j-m:** Middle dividers with condensed macronucleus and dividing micronucleus, length 68 µm, 69 µm, 74 µm. B1-3 – dorsal brush, CV – contractile vacuole, MA – macronucleus, MI – micronucleus, OF – oral kinetofragments.



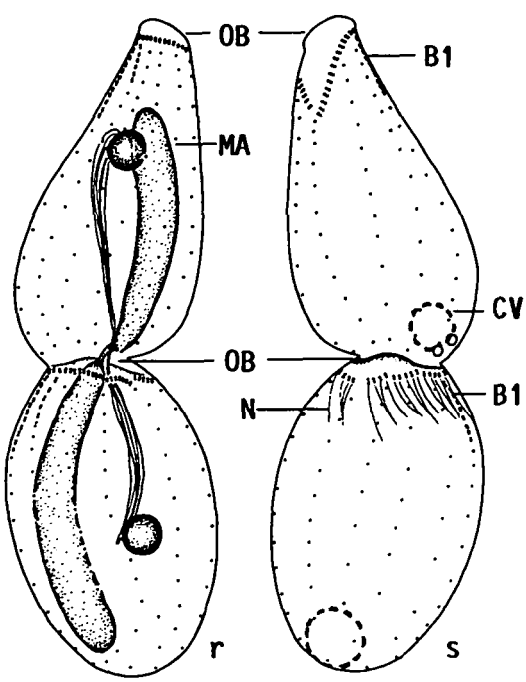


Fig. 33n-s: *Arcuospathidium coemeterii*, body shape, ciliary pattern and nuclear apparatus of late dividers after protargol impregnation; drawn to scale. **n, o:** Ventral and dorsal view of an early late divider showing the developing division furrow (arrowheads), the elongating macronucleus mass and the dividing micronucleus, length 75 µm. Arrows mark the opisthe's oral kinetofragments. **p, q:** Late dividers, length 76 µm and 65 µm. The dividing macronucleus becomes dumb-bell shaped and the divided micronuclei become globular. The opisthe's nematodesmata develop from the oral kinetofragments. **r, s:** Dorsal and ventral view of a very late divider, length 75 µm. The opisthe has an incomplete, convex oral bulge. The rod-shaped daughter's macronuclei and the globular micronuclei are still connected by fibres. B1-3 – dorsal brush rows, CV – new contractile vacuole, EP – new excretory pores, MA – macronucleus, MI – micronucleus, N – nematodesmata, OB – oral bulge.

fragments, which are slightly concave ventrally and convex dorsally, loosely align horizontally in the prospective fission area and develop oral basket rods (nematodesmata). The macronuclear mass, which now contains fibrous structures, becomes C-shaped and, somewhat later, extends to a long rod constricting in the mid, that is, in the prospective fission area. The daughter's micronuclei, which are still connected by long, parallel fibres, move apart; gradually smoothen their outline; and condense to compact, spherical masses.

Very late dividers have a similar length as morphostatic specimens and are distinctly furrowed in the prospective fission area (Fig. 33r, s; Table 7). A bare protuberance, that is, the precursor of the oral bulge, develops at the anterior end of the opisthe. The ciliary rows are distinctly separate from the opisthe's kinetofragments and still meridionally arranged, viz., do not show the *Arcuospathidium* pattern typical for the species. The opisthe's oral kinetofragments now move together, obviously due to the body's constriction in the fission area, forming a slightly irregular, continuous circumoral kinety. The macronucleus has divided into two rod-shaped pieces, each almost as long as the daughter's body and pointed in the fission area. The micronuclei, which are still connected by a long, distinct fibre bundle, are smoothly globular and increase in size.

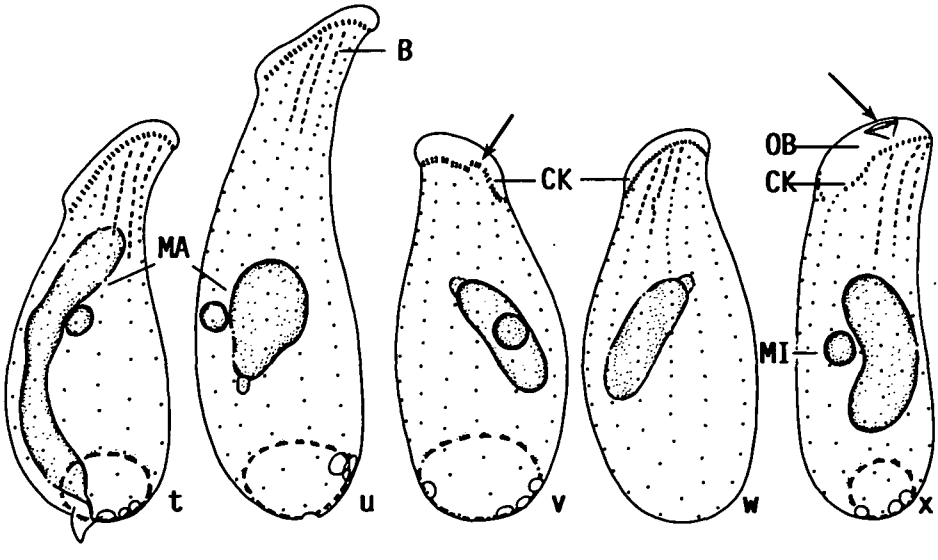


Fig. 33t-x: *Arcuospathidium coemeterii*, body shape, ciliary pattern and nuclear apparatus of post-dividers after protargol impregnation; drawn to scale. **t:** Left side view of a just separated proter post-divider with irregular posterior body end and long, posteriorly tapered macronucleus, length 45 µm. **u:** A late proter post-divider recognizable by the posteriorly tapered macronucleus, length 58 µm. **v, w:** Right and left side view of same opisthe post-divider with small, slightly oblique oral bulge and anteriorly tapered macronucleus, length 44 µm. Arrow denotes slightly disordered right side circumoral kinety. **x:** Left side view of another opisthe post-divider (length 45 µm) with well developed macronucleus, but not yet finished oral bulge with a conical indentation, likely the temporary mouth and/or the site where the daughters separated. B – dorsal brush, CK – circumoral kinety, MA – macronucleus, MI – micronucleus, OB – oral bulge.

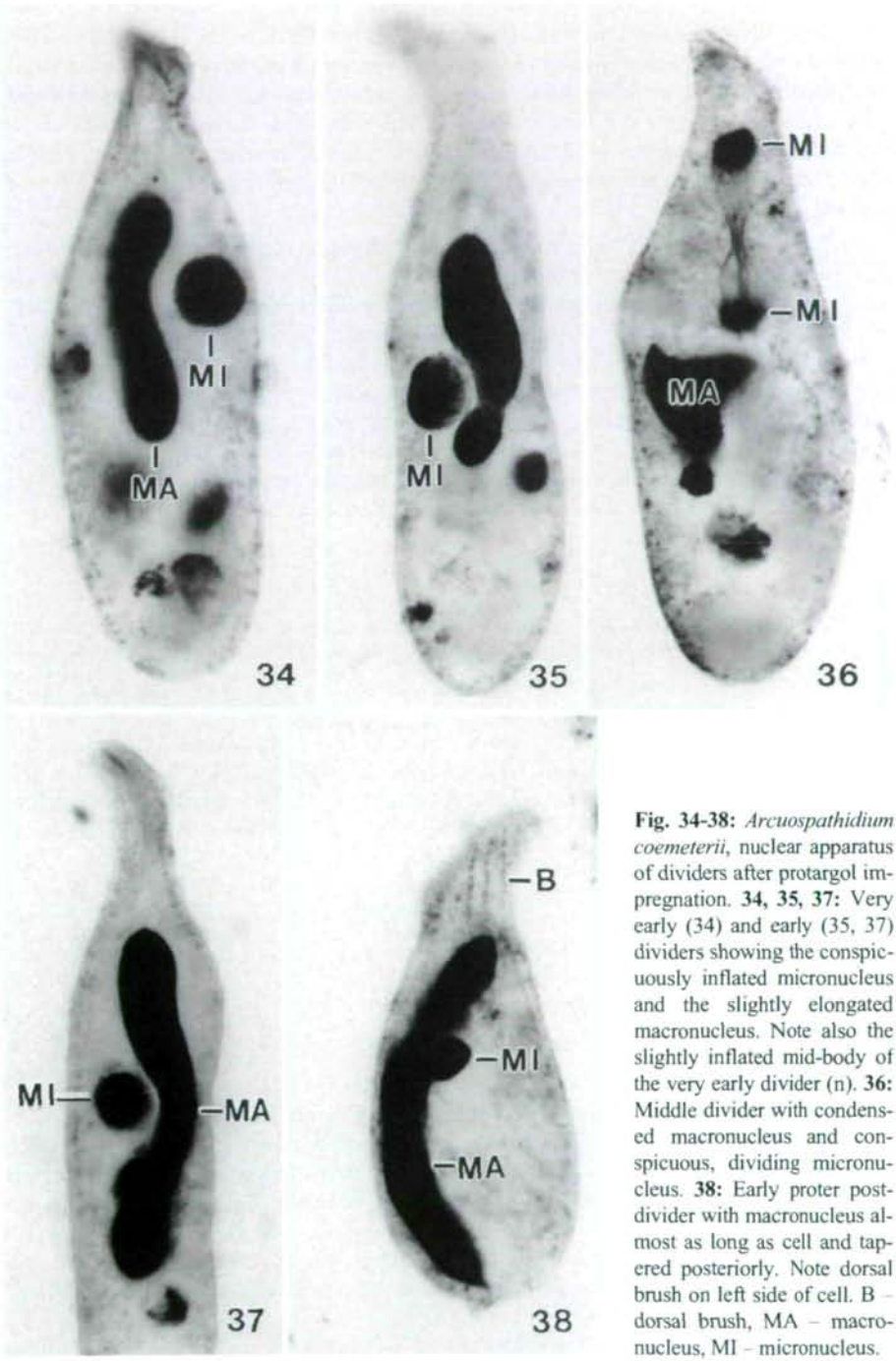


Fig. 34-38: *Arcuospathidium coemeterii*, nuclear apparatus of dividers after protargol impregnation. **34, 35, 37:** Very early (34) and early (35, 37) dividers showing the conspicuously inflated micronucleus and the slightly elongated macronucleus. Note also the slightly inflated mid-body of the very early divider (n). **36:** Middle divider with condensed macronucleus and conspicuous, dividing micronucleus. **38:** Early proter post-divider with macronucleus almost as long as cell and tapered posteriorly. Note dorsal brush on left side of cell. B – dorsal brush, MA – macronucleus, MI – micronucleus.

Very late dividers are only slightly larger than morphostatic cells (Table 7). Thus, early post-dividers are recognizable by the small size and tapered macronucleus; opisthe post-dividers, additionally, have a small, somewhat irregular and transverse-truncate oral bulge (Fig. 33t-x, 38). Unfortunately, only two late opisthe post-dividers were found. Both not yet have an *Arcuospathidium* ciliary pattern, which is thus obviously obtained only in fully grown cells, possibly in that the dorsal bulge half grows faster and pulls up the ciliary rows. Further, some circumoral dikinetids are possibly produced post-divisionally, as explained above. Post-divisional development of the nuclear apparatus is the same in proter and opisthe, viz., the macronucleus gradually shortens to obtain the species-specific shape, and the micronucleus moves to mid-macronucleus.

The parental oral apparatus and dorsal brush do not show any changes during division, as in the few other members of the family investigated so far. No bulbs are recognizable in the division area, at least with the light microscope.

Ontogenetic comparison: Ontogenesis of *A. coemeterii* is similar to that of *A. muscorum* (BERGER et al. 1983), *Spathidium turgitorum* (FOISSNER et al. 2002) and *Protospathidium serpens* (FOISSNER & XU 2005), but shows the following peculiarities, some of which, however, might have been overlooked in previous studies: (i) early dividers show a transient indentation in the prospective fission area (Fig. 33e-h), a curious feature as yet found only in *Protospathidium serpens*; (ii) the macronucleus distinctly elongates in early dividers (Table 7), while it remains unchanged in all other species investigated so far; (iii) the micronucleus shows a three-fold size increase and thus becomes very conspicuous in early middle dividers (Fig. 33g-i; Table 7), while it merely doubles size in other species; (iv) the left side oral kinetofragments curve rightwards earlier than the right side ones (Fig. 33e, f, k, l), a curious feature not described in other species; (v) the oral kinetofragments detach from the somatic kineties and curve rightwards earlier in *Arcuospathidium coemeterii* (in early dividers; Fig. 33k, l) than in *A. muscorum* (in middle dividers); (vi) likely, there is some post-divisional growth of the circumoral kinety (Table 7); (vii) *A. coemeterii* forms the circumoral kinety in a simple way, viz., by alignment of the newly produced kinetofragments one after the other (Fig. 33n-s), while complicated shaping and fusion processes occur in *A. muscorum* (BERGER et al. 1983); (viii) shaping of the oral bulge and circumoral ciliature occurs distinctly later in *Arcuospathidium* (Fig. 33r-x) and *Spathidium* than in *Protospathidium*, viz., in late post-dividers, respectively, very late dividers; (ix) the *Arcuospathidium* ciliary pattern develops via a *Protospathidium* pattern in very late post-dividers, likely by asymmetrical growth of the oral bulge, suggesting that it is an apomorphic feature.

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Zusammenfassung

Wir beschreiben zwei neue Bryophylliden, nämlich *Bryophyllum longisetum* nov. spec. und *Apobryophyllum sulcatum* nov. spec. Ergänzende Beobachtungen werden mitgeteilt für *Neobryo-*

phyllum penardi und *N. paucistriatum*. Auf diesen Beobachtungen und Literaturdaten basiert die neue Familie Bryophyllidae FOISSNER nov. fam., die die Genera *Bryophyllum* KAHL 1931, *Apobryophyllum* FOISSNER 1998 und *Neobryophyllum* FOISSNER nov. gen. enthält. Die Bryophyllidae sind durch den langen, sich bis zum Körperende erstreckenden Mundwulst charakterisiert und haben sich aus den Spathidiidae entwickelt. Die Dorsalbürste ist isomorph (*Bryophyllum*, *Neobryophyllum*) oder heteromorph (*Apobryophyllum*) und aus drei (*Bryophyllum*) oder mehr als drei (*Apobryophyllum*, *Neobryophyllum*) Reihen aufgebaut. Die Ontogenese von *Arcuospathidium coemeterii* (KAHL 1943) zeigt einige spezielle Merkmale, was darauf hinweist, dass die Teilungsmuster der Spathidiiden vielfältiger sind als bisher angenommen.

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