Revision of some spathidiid genera (Alveolata, Ciliophora, Spathidiida)

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Revision of some spathidiid genera (Alveolata, Ciliophora, Spathidiida)

Edited by

Wilhelm **Foissner,** Kuidong **Xu** & Helmut **Berger**

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For nomenclatural purposes, the book should be referenced as follows: Foissner W., Xu K. & Berger H. (Eds) (2025): Revision of some spathidiid genera (Alveolata, Ciliophora, Spathidiida). – Ser. Monogr. Cilioph. **6**: i–xv, 1–465

Cover: *Epispathidium papilliferum* (front; see Fig. 6.11h–j in Chapter 6); *Neospathidium longinucleatum* (back; see Fig. 12.9j–l in Chapter 12)

In memory of Wilhelm Foissner (1948–2020)

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Preface, authorship, acknowledgements, and funding

The spathidiids have been one of several favorite ciliate groups of Wilhelm Foissner. In 2001, W. Foissner started a revision of this large group of haptorids. During processing his huge archive after his sudden death in 2020, I found a well-advanced manuscript dealing with several spathidiid genera. In order to prevent this manuscript from being forgotten, I have decided to publish it in my monographic series on ciliates.

W. Foissner collected most samples, made the in vivo observations, the preparations, many morphometries, and wrote text. K. Xu made morphometries and illustrations, compiled the plates, and wrote text. I updated the text of the raw manuscript, organized the deposition of the slides in the Biology Centre of the Upper Austrian Museum in Linz, wrote the front matter, the general introduction, the material and method section including the summary of taxa (Chapter 1), the brief introduction to the spathidiids (Chapter 2), the chapter on *Neocultellothrix* Foissner nov. gen. (Chapter 13), and the back matter (index). Further, I made the layout and produced the final PDF.

The help of the following persons must be acknowledged: Sabine Agatha, Remigius Geiser, Eva Herzog, Wolf-Dietrich Krautgartner, Brigitte Moser, Birgit Peukert, Fritz Seyrl, and Andreas Zankl. Colleagues who provided samples are acknowledged in the individual species descriptions. I also want to thank Magdalini Christodoulou and Alexandra Aberham at the Biology Centre of the Upper Austrian Museum in Linz for help with the transfer of the Foissner archive from Salzburg to Linz.

Wilhelm Foissner, Kuidong Xu, and co-workers involved in this project got financial support by the Austrian Science Fund FWF (Project P15017-B06, "Monographie der Familie Spathidiidae (Ciliophora)"). I wish to thank Ilse Foissner who generously privately financed my work on this book.

Salzburg
January 2025

Helmut Berger (Publisher)
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Abstract

Foissner W., Xu K. & Berger H. (Eds) (2025): Revision of some spathidiid genera (Alveolata, Ciliophora, Spathidiida). – Ser. Monogr. Cilioph. 6: i–xv, 1–465.

This book deals with some spathidiid taxa. The following genera are treated and established, respectively: *Apospathidium* Foissner et al., 2002; *Centrospathidium* nov. gen.; *Epispathidium* Foissner, 1984; *Latispathidium* Foissner et al., 2005; *Schmidingerophrya* nov. gen.; *Semibryophyllum* nov. gen.; *Semispathidium* Foissner et al., 2002; *Supraspathidium* Foissner & Didier, 1981; *Pharyngospathidium* nov. gen. (type genus of Pharyngospathidiidae nov. fam.); *Neospathidium* nov. gen.; *Neocultellothrix* Foissner nov. gen. The latter genus "replaces" *Cultellothrix* Foissner, 2003, an unavailable genus because no holotype was fixed for the type species in the original description. In addition, 12 *Spathidium* species are reviewed, and three new species assigned to this genus are described. In total, four new subspecies, 19 new species, six new genera, and one new family are described, 13 species are transferred to other genera, and 41 known species and two subspecies are reviewed. Further, three "*Spathidium* groups" are discussed. The type slides of the new species and voucher slides of the redescribed species are documented.

Key words: Alveolata; biogeography; Ciliophora; cyst; diversity; Haptoria; monograph; morphogenesis; nomenclature; Protista; revision; soil biology; systematics; taxonomy

Chapter 9

Semibryophyllum nov. gen. (Ciliophora, Spathidiidae), a new genus characterised by three ordinary dorsal brush rows and several accessory brush rows on the left side[1]

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Abstract

The species classified in *Semibryophyllum* nov. gen. have the three ordinary dorsal brush rows plus several accessory rows on the left side of the body. The ciliature is either in the *Arcuospathidium*- or the *Spathidium*-pattern. Thus, it cannot be excluded that this new genus is non-monophyletic. Two new species (*Semibryophyllum cultellum* nov. spec., type species, type locality in Spain; *Semibryophyllum palustre* nov. spec., type locality Lower Austria) and one known species (*Semibryophyllum foliosum* (Foissner, 1983) nov. comb., type locality in Salzburg, Austria) are assigned. A key to the species is provided.

Semibryophyllum nov. gen.

2005 ***Semibryophyllum* n. g., n. sp.** – Foissner, Berger, Xu & Zechmeister-Boltenstern, Biodiv. Conserv. 14: 634 (unavailable name; see nomenclature).
2007 ***Semibryophyllum*** – Foissner & Xu, Monogr. biol. 81: 15, 155 (unavailable name; see nomenclature).

Nomenclature: Composite of the Latin prefix *semi* (half; Werner 1972, p. 74) and the genus-group name *Bryophyllum*, referring to the similarity with the genus *Bryophyllum* Kahl, 1931 (p. 183). Like *Bryophyllum* of neuter gender (Aescht 2001, p. 275).

[1] This chapter should be referenced as follows: Foissner W., Xu K. & Berger H. (2025): *Semibryophyllum* nov. gen. (Ciliophora, Spathidiidae), a new genus characterised by three ordinary dorsal brush rows and several accessory brush rows on the left side. – Ser. Monogr. Cilioph. 6: 281–310.
For notes on "Material and methods", see Chapter 1 (Berger et al. 2025a).

Table 9.1 Morphometric data on *Semibryophyllum cultellum* nov. spec. (upper line; original data) and *Semibryophyllum palustre* nov. spec. (lower line; original data)[a]

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Body, length	122.1	128.0	21.3	4.9	17.4	80.0	166.0	19
	116.6	111.0	22.8	5.2	19.6	76.0	164.0	19
Body, width	45.3	45.0	7.8	1.8	17.3	31.0	64.0	19
	41.6	43.0	5.7	1.3	13.7	30.0	52.0	19
Body length:width, ratio	2.7	2.8	0.5	0.1	16.7	2.0	3.5	19
	2.8	2.7	0.7	0.2	23.2	1.8	4.4	19
Oral bulge, length of cord	72.6	73.0	16.9	3.9	23.3	41.0	103.0	19
	29.8	29.5	5.5	1.2	18.6	22.0	43.0	20
Body length:oral bulge length, ratio	1.7	1.6	0.2	0.1	12.6	1.4	2.1	19
	3.9	3.9	0.5	0.1	13.8	3.1	5.3	19
Circumoral kinety to end of longest dorsal brush row, distance	21.8	22.0	4.6	1.4	21.3	15.0	32.0	11
	28.6	28.0	4.5	1.0	15.9	17.0	40.0	19
Anterior body end to macronucleus, distance	46.4	45.0	13.5	3.1	29.1	20.0	80.0	19
	37.3	35.0	11.7	2.7	31.3	16.0	58.0	19
Macronuclear figure, length	44.1	44.0	10.5	2.4	23.8	22.0	63.0	19
	35.8	36.0	10.9	2.5	30.5	21.0	70.0	19
Macronucleus, length of largest, straight segment[b]	10.7	11.0	1.0	0.2	9.2	9.0	12.0	19
	77.6	75.0	15.0	3.5	19.4	60.0	100.0	19
Macronucleus, width of largest, straight segment	6.9	7.0	1.0	0.2	15.2	5.0	10.0	19
	7.3	7.0	1.4	0.3	18.8	5.0	10.0	19
Macronuclear segments, number (1 if not segmented)	14.8	15.0	2.3	0.5	15.2	12.0	19.0	19
	2.7	2.0	1.8	0.4	65.8	1.0	6.0	19
Micronuclei, diameter	3.3	3.0	0.3	0.1	10.5	3.0	4.0	19
	3.1	3.0	0.3	0.1	10.0	3.0	4.0	19
Micronuclei, number	14.2	14.0	2.8	0.6	19.6	10.0	19.0	19
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
Somatic kineties, number	21.8	22.0	1.4	0.3	6.4	19.0	24.0	16
	22.2	22.0	1.8	0.4	8.0	19.0	27.0	19
Basal bodies in a right-side kinety, number	109.0	112.0	25.7	9.7	23.6	59.0	136.0	7
	48.5	45.5	12.6	3.2	26.0	32.0	73.0	16
Dorsal brush rows, number	6.1	6.0	0.6	0.2	10.5	5.0	7.0	13
	6.9	7.0	0.5	0.1	7.1	6.0	8.0	17

[a] Data based on mounted, protargol-prepared (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, Mean – arithmetic mean, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean.

[b] Uncoilded length in *Semibryophyllum palustre*.

Foissner et al. (2005) and Foissner & Xu (2007) mentioned this name, but neither provided a definition of the genus (ICZN 1999, Article 13.1.1) nor did they fix a type species (Article 13.3). Thus, *Semibryophyllum* in Foissner et al. (2005) and Foissner & Xu (2007) are nomina nuda (names published after 1930 which fail to conform Article 13). A nomen nudum is not an available name and the name is available for the same or a different concept (for details on the term nomen nudum, see ICZN 1999, p. 111).

Table 9.2 Morphometric data on *Semibryophyllum foliosum* (from Wirnsberger et al. 1984)[a]

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Body, length	73.6	74.5	7.1	2.2	9.6	60.0	83.0	12
Body, width	34.1	32.0	4.8	1.3	14.8	26.0	41.0	13
Macronucleus, width	7.8	7.9	1.0	0.3	12.2	6.5	9.0	8

[a] Data based on mounted, protargol-prepared (Foissner's method) field specimens. Measurements in µm. For abbreviations, see footnote a at Table 9.1.

Diagnosis: Spathidiidae with three ordinary and several accessory dorsal brush rows on left body side; accessory rows become shorter from dorsal to ventral. Ciliature in *Arcuospathidium*- or *Spathidium*-pattern. Oral bulge basically cuneate.

Type species: *Semibryophyllum cultellum* nov. spec.

Species assigned: *Semibryophyllum cultellum* nov. spec. (type species); *Semibryophyllum foliosum* (Foissner, 1983) nov. comb. (original combination *Pseudoprorodon foliosus*); *Semibryophyllum palustre* nov. spec.

ZooBank registration: urn:lsid:zoobank.org:act:19EDB3A9-34F6-497D-92C9-27AF5ADABBE3

Remarks: This new genus comprises *Semibryophyllum cultellum* nov. spec., *Semibryophyllum palustre* nov. spec., and *Semibryophyllum foliosum* (Foissner, 1983) nov. comb. These three species break the rule that spathidiids s. str. have three dorsal brush rows; they have six or more. However, the additional rows are short and inconspicuous; thus, we name them "accessory (dorsal) brush rows (kineties)". The type species has two types of oral bulge extrusomes, which is also unusual for "good" spathidiids, but common in deviating and related genera, such as several *Arcuospathidium* and *Apertospathula* species, and in *Bryophyllum* (for details on these taxa, see Foissner & Xu 2007, p. 146, 331; Foissner & Lei 2004, p. 170). *Semibryophyllum cultellum* has a typical *Arcuospathidium* ciliary pattern, while a *Spathidium* pattern occurs in *Semibryophyllum palustre* and *Semibryophyllum foliosum* (for characterization of patterns, see Foissner & Xu 2007, p. 13). This indicates non-monophyly of the genus. However, we avoid a monotypic genus for *Semibryophyllum cultellum* at the present state of knowledge, though it, indeed, looks rather dissimilar to *Semibryophyllum foliosum* and *Semibryophyllum palustre*. On the other hand, the increased number of brush rows is a very conspicuous feature uniting these species. Further data, including gene sequence analyses, are needed to show whether or not *Semibryophyllum* is monophyletic.

As indicated by the name, *Bryophyllum* Kahl, 1931 highly resembles *Semibryophyllum*, especially the type species *Semibryophyllum cultellum*, which is a characteristic *Bryophyllum*, except of the posteriorly shortened oral bulge (see Kahl 1931, p. 183 and Foissner et al. 2002, p. 340 for descriptions of representative species). Thus, *Semibryophyllum cultellum* might be a true transition species.

Wirnsberger et al. (1984, p. 308) assigned *Semibryophyllum foliosum* to *Cranotheridium* Schewiakoff, 1892[2], mainly due to the dorsally located extrusome bundle. Schewiakoff

[2] Note by H. Berger: Aescht (2001, p. 50) wrote that Schewiakoff (1892, p. 554) did not provide a description or definition of the genus. However, this is incorrect because Schewiakoff (1892) described the type species (fixation by

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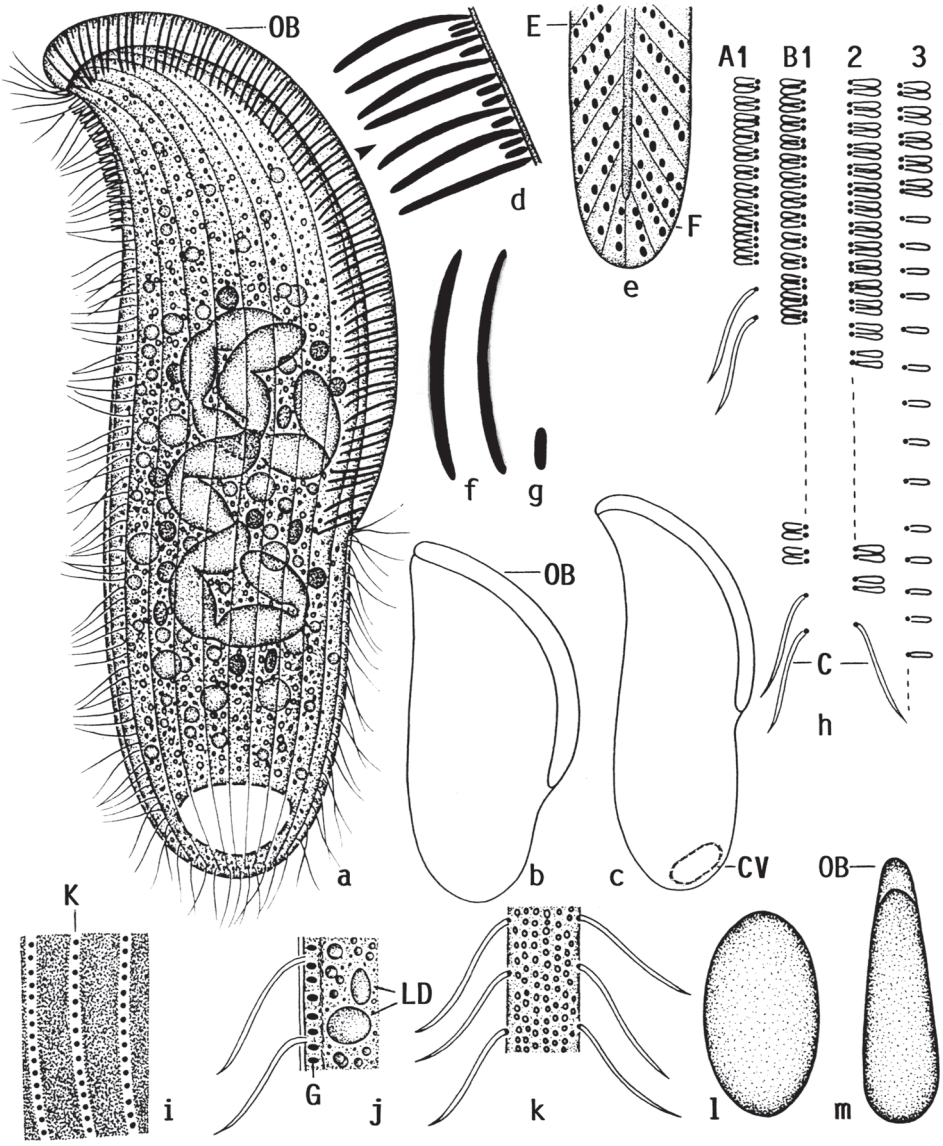


Fig. 9.1a–m *Semibryophyllum cultellum* nov. spec. (originals. a–h, j–m, from life; i, protargol preparation). **a:** Right side view of a representative specimen showing, inter alia, the broadly knife-shaped body and the tortuous macronucleus, 150 µm. **b, c:** Right side view of shape variants. **d, f, g:** *Semibryophyllum cultellum* has long (10 µm) and short (2 µm; arrowhead in d) extrusomes in the oral bulge. **e:** Surface view of posterior (ventral) end of oral bulge containing oblique extrusome rows. **h:** Part of dorsal brush composed of ordinary (B) and accessory (A) rows. Note monokinetidal bristle tail of row 3. **i:** Surface view of cortex distinctly impregnated between kineties. **j, k:** Optical section and surface view of cortex showing cortical granulation. **l, m:** Transverse view of body in postoral (l) and oral region (m). A1 – one of several accessory dorsal brush rows, B1–3 – ordinary dorsal brush rows, C – ordinary somatic cilium, CV – contractile vacuole, E – extrusomes, F – fibre, G – cortical granules, K – somatic kinety (ciliary row), LD – lipid droplets, OB – oral bulge.

(1892, 1893), however, emphasized that the "rod-apparatus" of *Cranotheridium taeniatum* Schewiakoff, 1892 (type species of *Cranotheridium* by monotypy) is highly similar to the oral basket of *Nassula*. This is confirmed by figure (Fig. 9.6e). Accordingly, *Semibryophyllum foliosum* and *Semibryophyllum palustre* should not be allocated to this genus, in spite of distinct similarities in general organization and, especially, body shape. Unfortunately, *Cranotheridium taeniatum* has never been reinvestigated.

Key to species

1 Body broadly knife-shaped with conspicuous, steep oral bulge extending beyond mid-body; macronucleus a nodulate, tortuous strand ..... *Semibryophyllum cultellum* nov. spec. (p. 285)
– Body elongate with inconspicuous, oblique oral bulge extending to second body third; macronucleus reniform or a tortuous strand **2**
2 Body bursiform, about 90 × 40 µm in size; macronucleus reniform; extrusomes fine, about 13 µm long rods ..... *Semibryophyllum foliosum* (p. 303)
– Body bursiform to spatulate, about 130 × 45 µm in size; macronucleus a tortuous strand; extrusomes slightly curved, 7 µm long ..... *Semibryophyllum palustre* nov. spec. (p. 291)

Semibryophyllum cultellum nov. spec.

(Fig. 9.1a–t, 9.2a–l, Table 9.1)

Nomenclature: The species-group name *cultellum* is a Latin noun (small knife; diminutive of *culter*; www.frag-cesar.de, accessed 13 Apr 2023; Hentschel & Wagner 1996, p. 191) and refers to the conspicuously knife-shaped body.

Diagnosis: Body size about 150 × 50 µm in vivo. Body broadly knife-shaped with blade (oral portion) occupying about 60% of body length. Macronucleus moniliform and tortuous. Two types of oral bulge extrusomes: type I elongate fusiform and curved, about 10.0 × 0.6 µm; type II rod-shaped and approximately 2 µm long. On average 22 ciliary rows, about six of them differentiated to inconspicuous dorsal brush occupying up to 18% of body length.

Type locality: Mud from rock-pools at bank of a stream near the old town of Toledo (about 39°55'N 04°W), Spain.[3]

Type material: The slide (Fig. 9.2g, h; accession number 2024/187) containing the holotype (Fig. 9.1n) and two paratype slides (Fig. 9.2i–l; 2024/188, 189) with protargol-prepared specimens have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI).

ZooBank registration: urn:lsid:zoobank.org:act:2A8D9D94-F5DC-42D2-BB0E-12B37537305D

Remarks: *Semibryophyllum cultellum* has a highly characteristic shape which, however, also occurs in several spathidiids, viz., *Spathidium cithara* Penard, 1922 (macronucleus long

monotypy) rather detailed. Thus, Schewiakoff (1892) is the original description of *Cranotheridium* and its type species. Schewiakoff (1893, p. 35, Tafel II, Fig. 35, 36) provided not only a description, but also an illustration.

[3] Note by H. Berger: Foissner did not provide a more detailed description of the location of the sample site.

continued on p. 289

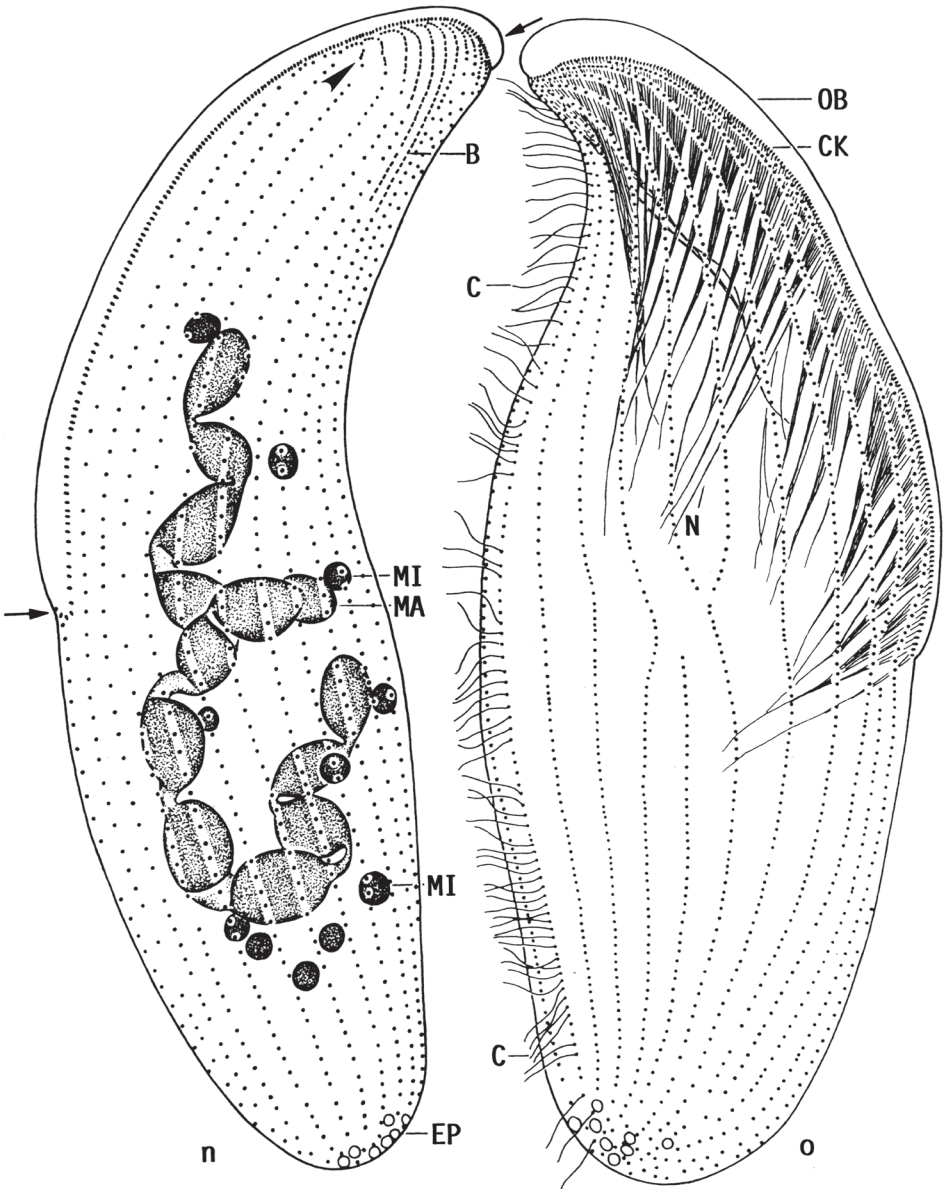


Fig. 9.1n, o *Semibryophyllum cultellum* nov. spec. (originals. Protargol preparation). The ciliary pattern is as in *Arcuospathidium*, that is, the ciliary rows are directed dorsally on both sides, except of the dorsal brush kineties. **n:** Left side view of the holotype showing the long oral bulge (ends marked by arrows) and the minute, ventralmost accessory dorsal brush row (arrowhead), depicted at higher magnification in figure (t); 120 µm. Note the typical, that is, nodular macronucleus. **o:** Right side view of paratype showing the conspicuous oral basket, 140 µm. Note barren basal bodies in kinety at right margin. B – dorsal brush, C – somatic cilia, CK – circumoral kinety, EP – excretory pores, MA – macronucleus, MI – micronucleus, N – nematodesmata, OB – oral bulge.

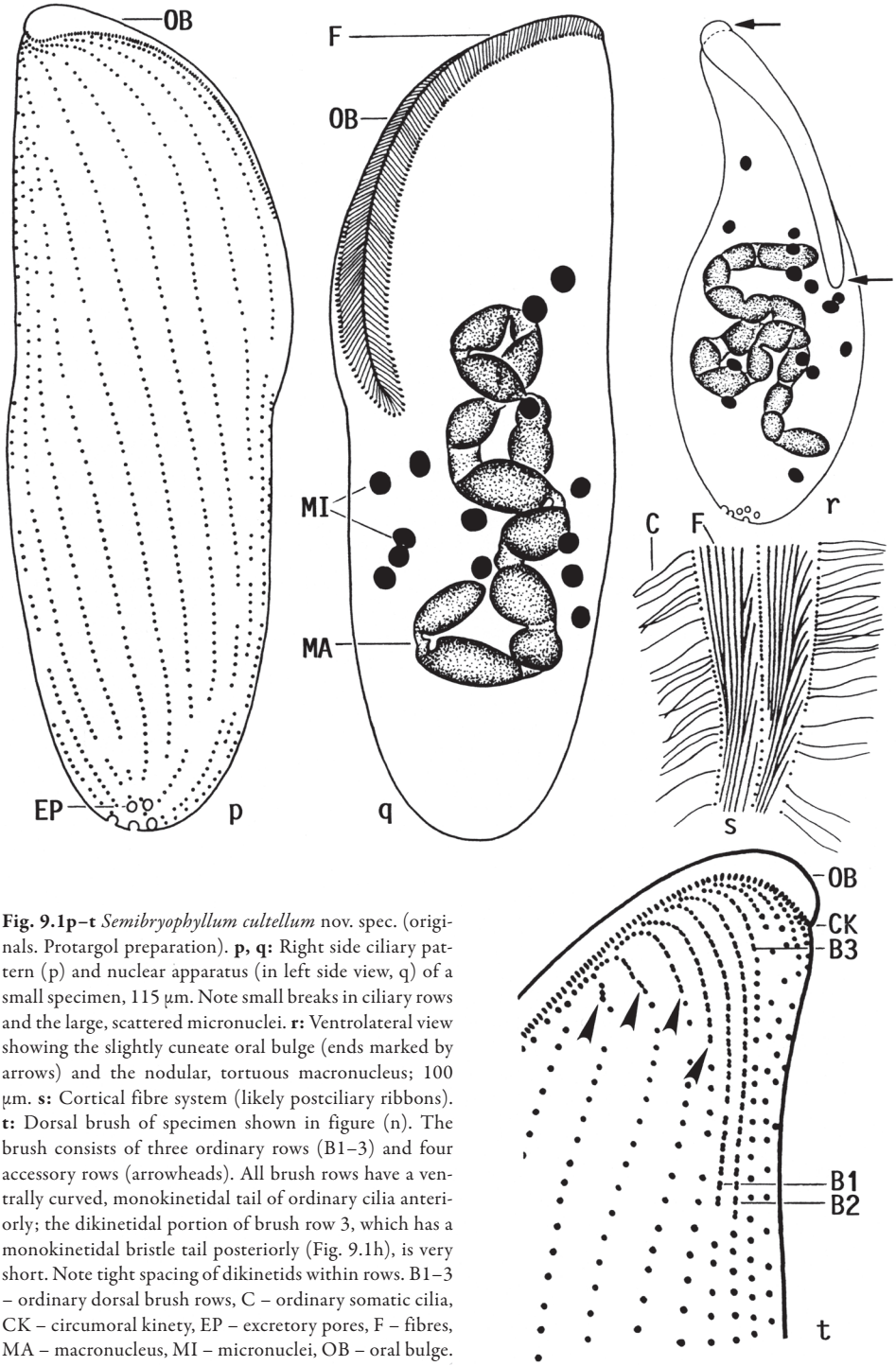


Fig. 9.1p–t *Semibryophyllum cultellum* nov. spec. (originals. Protargol preparation). **p, q:** Right side ciliary pattern (p) and nuclear apparatus (in left side view, q) of a small specimen, 115 µm. Note small breaks in ciliary rows and the large, scattered micronuclei. **r:** Ventrolateral view showing the slightly cuneate oral bulge (ends marked by arrows) and the nodular, tortuous macronucleus; 100 µm. **s:** Cortical fibre system (likely postciliary ribbons). **t:** Dorsal brush of specimen shown in figure (n). The brush consists of three ordinary rows (B1–3) and four accessory rows (arrowheads). All brush rows have a ventrally curved, monokinetidal tail of ordinary cilia anteriorly; the dikinetidal portion of brush row 3, which has a monokinetidal bristle tail posteriorly (Fig. 9.1h), is very short. Note tight spacing of dikinetids within rows. B1–3 – ordinary dorsal brush rows, C – ordinary somatic cilia, CK – circumoral kinety, EP – excretory pores, F – fibres, MA – macronucleus, MI – micronuclei, OB – oral bulge.

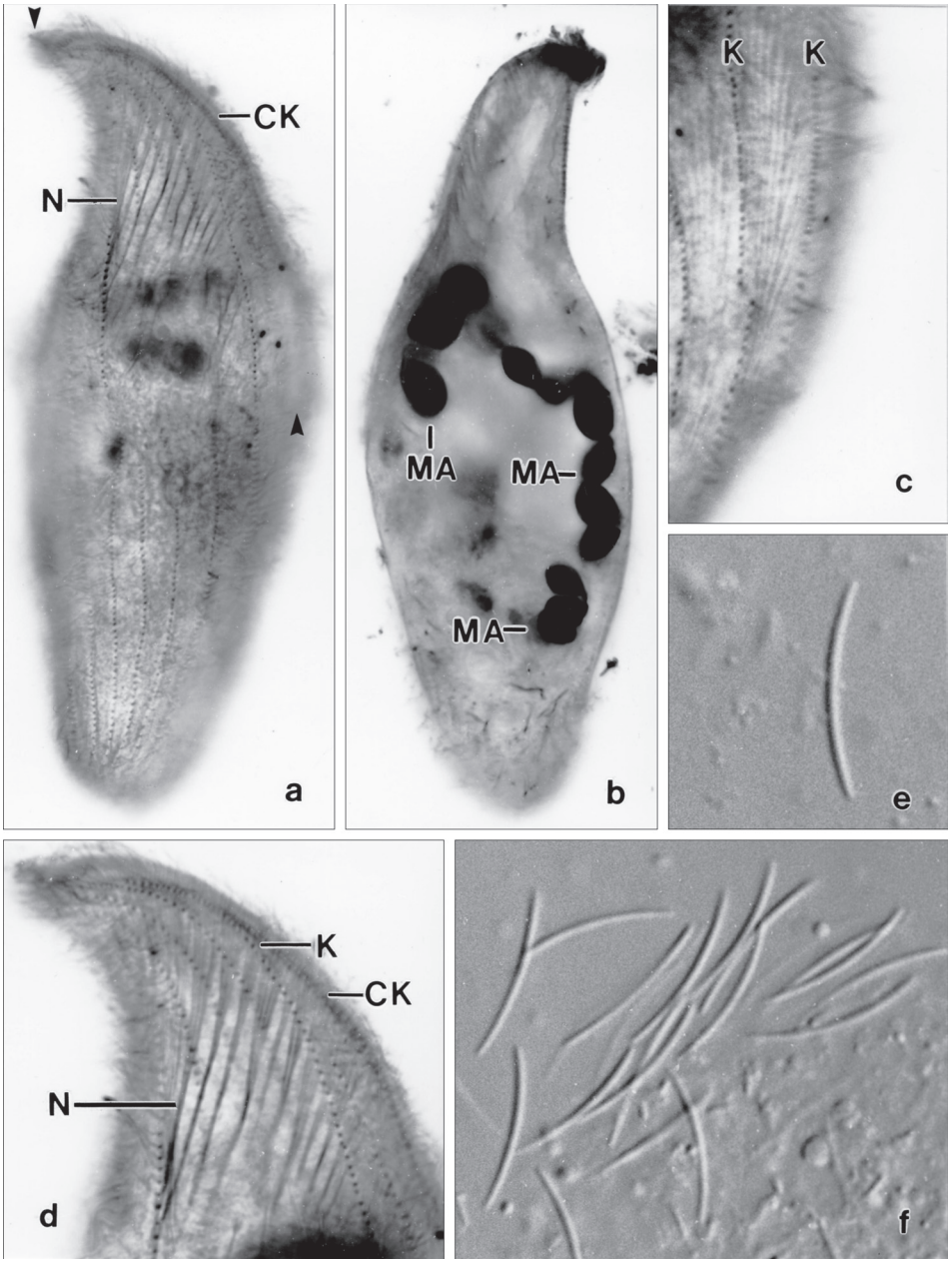
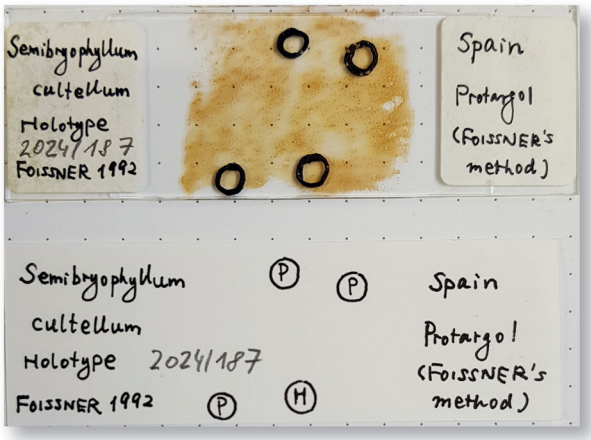


Fig. 9.2a–f *Semibryophyllum cultellum* nov. spec. (originals. a–d, protargol preparation; e, f, from life). **a, b, d:** Overviews showing body shape, the moniliform macronucleus, and the long oral bulge with ends marked by arrowheads. **c:** Cortical fibre system. **e, f:** Extrusomes are about 10 µm long, curved rods. CK – circumoral kinety, K – somatic kineties, MA – macronucleus, N – nematodesmal bundles.

Fig. 9.2g–l *Semibryophyllum cultellum* nov. spec. (originals. Protargol slides). **g, h:** Slide (g) and protocol (h) → containing holotype (H) and paratypes (P). Accession number (LI): 2024/187. **i–l:** Slides (i, k) and protocols (j, l) containing paratypes (P) and paratypes drawn (PD). Accession numbers (LI): 2024/188, 189.



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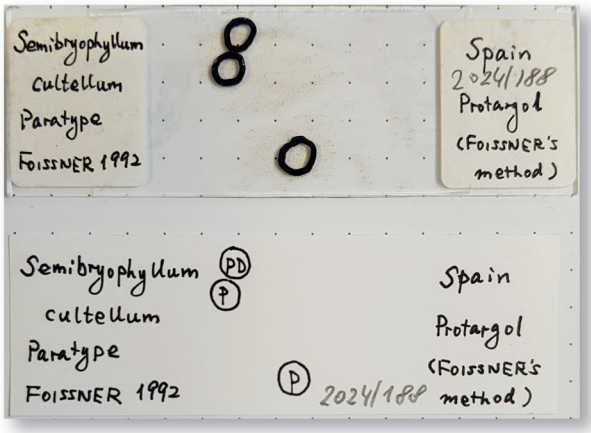

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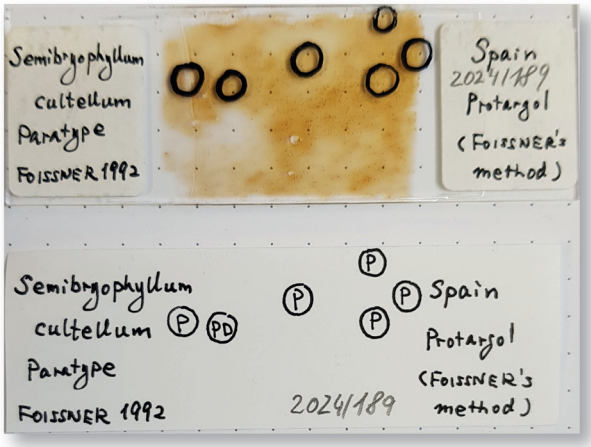

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l

and tortuous vs. ellipsoidal; Penard 1922, p. 27); *Spathidium depressum* Kahl, 1930a (macronucleus long and tortuous vs. reniform; Kahl 1930a, p. 364); *Spathidium inflatum* Vuxanovici, 1962 (macronucleus long and tortuous vs. in 6–8 nodules; about 22 vs. 12 ciliary rows; 150 × 150 µm vs. 60–90 × 30–50 µm; Vuxanovici 1962, p. 331); *Neocultellothrix lionotiformis* (Kahl, 1930b) Foissner in Berger et al., 2025b (6 vs. 3 dorsal brush rows; about 22 vs. 12 ciliary rows; body broad vs. slender, that is, about 3:1 vs. 6–7:1; for details, see Chapter 13, that is, Berger et al. 2025b; Kahl 1930b, p. 165; Foissner 2003, p. 53; Foissner & Xu 2007, p. 269), and *Neocultellothrix velhoi* Foissner in Berger et al., 2025b (6 vs. 3 dorsal brush rows; about 22 vs. 12 ciliary rows; for details, see Chapter 13, that is, Berger et al. 2025b). These are very distinct differences, showing that *Semibryophyllum cultellum* cannot be confused with any described species. In *Bryophyllum*, the oral bulge extends over the posterior body end (vs. 60% of body length; see, for example, Foissner & Lei 2004, p. 170).

Description: Body size highly variable, viz. 100–200 × 35–70 µm in vivo, usually about 150 × 50 µm,

as calculated from some in vivo measurements and the morphometric data (Table 9.1). Body shape very conspicuous and characteristic, viz., like a broad knife with long, strongly convex blade (= oral body portion) occupying up to 70%, on average 60% of body length and short handle (= postoral body portion) moderately broadly rounded posteriorly; length:width ratio considerably variable, that is, 2.0–3.5:1 in protargol preparations, usually near 3:1 both in vivo and prepared cells; handle slightly, blade distinctly flattened laterally and cuneate in transverse view, that is, gradually narrowing from 2:1 on dorsal to 3:1 on ventral side. Dorsal body margin straight to distinctly projecting anteriorly, ventral margin strongly convex in oral portion and distinctly set off from handle by the projecting oral bulge; neck lacking (Fig. 9.1a–c, l–p, r). Macronucleus in middle body third, moniliform and highly tortuous; nodules usually fusiform and occasionally slightly flattened, contain many minute nucleoli. On average 14 micronuclei attached to and far away from macronuclear strand; individual micronuclei of spongious structure and discoidal, that is, about 4 × 4 × 2 µm in vivo (Fig. 9.1a, n, q, r; Table 9.1). Contractile vacuole in posterior end, many excretory pores in pole area. Two types of extrusomes form oblique, short rows in oral bulge (Fig. 9.1a, d, e–g, 9.2e, f): type I slightly fusiform and curved, conspicuous because about 10.0 × 0.6 µm in size; type II rod-shaped and inconspicuous because only 2 µm long. Both types do not impregnate with the protargol method used, but a certain, about 8.0 × 0.3 µm-sized cytoplasmic developmental stage impregnates intensely. Cortex about 1.5 µm thick and highly flexible, contains narrowly spaced rows of minute (≤1 µm), colourless granules; usually impregnated rather distinctly, possibly due to the layer of cortical granules, except along the ciliary rows, which thus appear as white stripes; cortex contains a conspicuous, likely postciliary fibre system (Fig. 9.1i–k, s). Cytoplasm colourless, contains many lipid droplets up to 5 µm across, indicating rapacious mode of life. Glides majestically on microscope slide with oral area occasionally performing slight undulations, quite similar to those known from *Bryophyllum*.

Cilia about 10 µm long in vivo, arranged in an average of 22 rather widely spaced, usually bipolar and equidistant rows abutting on circumoral kinety in typical *Arcuo-spathidium*-pattern, except of dorsal brush kineties, whose anterior tail is curved ventrally, and thus abuts in *Spathidium*- or even *Epispathidium*-pattern. Ciliary rows moderately densely ciliated, composed of ciliated and some bare basal bodies which are inserted irregularly; rows frequently with small irregularities. Dorsal brush inconspicuous, though composed of an average of six rows, because occupying only about 18% of body length and bristles merely up to 4 µm long; consists of very narrowly spaced dikinetids arranged in three ordinary and 2–4 accessory rows. Ordinary brush rows 1 and 2 of similar length, bristles of row 1 approximately 3 µm long, those of row 2 about 4 µm; row 3 distinctly shortened, but with monokinetidal bristle tail extending to at least mid-body, bristles approximately 4 µm long. Accessory brush rows decrease in length from dorsal to ventral, frequently with small irregularities, bristles about 3 µm long. All brush rows have a short, ventrally curved monokinetidal tail with ordinary cilia anteriorly and continue as somatic kineties posteriorly (Fig. 9.1a, h, n–p, t; Table 9.1).

Oral bulge strongly convex, extends 60% of body length on average, distinctly set off from body proper because up to 5 µm high and bright (refractive) due to the many extrusomes contained; slightly cuneate, that is, about 8 µm wide at dorsal and 6 µm at ventral end. Circumoral kinety of same shape as oral bulge, continuous, composed of dikinetids more narrowly spaced in dorsal than ventral half of kinety; circumoral dikinetids each associated

with a cilium, a fine fibre extending into oral bulge, and a long nematodesma. Oral basket conspicuous because composed of distinct nematodesma bundles extending to midline of cell (Fig. 9.1a–c, n–r; Table 9.1).

Occurrence and ecology: As yet found only at the type locality, that is, in a sample of dry mud and moss scrapped off from rock-pools at the bank of a stream in the surroundings of the old town of Toledo, Spain. Thus, it is difficult to know whether *Semibryophyllum cultellum* is a limnetic or terrestrial species. However, the broad shape indicates that freshwater is preferred. On the other hand, the sample, which had pH 7.3 in water, contained over 80 ciliate species, of which were several undescribed and many typical inhabitants of terrestrial habitats.

Semibryophyllum palustre nov. spec.

(Fig. 9.3a–s, 9.4a–w, 9.5a–h, Table 9.1)

2007 ***Semibryophyllum palustre*** – Foissner & Xu, Monogr. biol. 81: 72 (nomen nudum; see nomenclature).

Nomenclature: The species-group name *palust·er*, *-ris*, *-re* (Latin adjective [m, f, n]; marshy, living in marsh; Hentschel & Wagner 1996, p. 453) refers to the floodplain habitat where the species was discovered.

Foissner & Xu (2007) mentioned this name, but they neither provided a definition nor a description or an illustration. Further, the name was not explicitly indicated as new. Thus, the name *Semibryophyllum palustre* in Foissner & Xu (2007) is unavailable and such a name is available for the same or a different concept (ICZN 1999, Articles 13.1.1, 16.1, p. 111).

Diagnosis: Body size about 130 × 45 µm in vivo. Body spatulate to bursiform with about 45° slanted oral bulge indistinctly set off from body proper and approximately two thirds as long as widest trunk region. Macronucleus about 80 µm long, tortuous, more or less distinctly moniliform. Oral bulge extrusomes rod-shaped, about 7 µm long. On average 22 ciliary rows, seven of them differentiated to dorsal brush occupying up to 25% of body length.

Type locality: *Pruno-Fraxinetum* lowland forest soil from the Müllerboden (48°00'N 16°42'E) in Lower Austria, near the city of Vienna, Austria.

Type material: The slide (Fig. 9.5a, b; accession number 2024/190) containing the holotype (Fig. 9.3m–p) and three paratype slides (Fig. 9.5c–h; 2024/191, 192, 193) with protargol-prepared specimens have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI).

ZooBank registration: urn:lsid:zoobank.org:act:779D17F6-A186-453C-87AF-CE0408429624

Remarks: Likely, *Semibryophyllum palustre* is most closely related to *Semibryophyllum foliosum*, as indicated by the similar shape of the body and the oral bulge. They differ significantly in macronucleus shape (a long, tortuous strand vs. elongate reniform) and extrusome length (6–8 µm long, slightly curved rods vs. 10–16 µm long, fine, straight rods). Further, body size (about 130 × 45 µm vs. 90 × 45 µm) and number of ciliary rows (on average 22 vs. 29) differ considerably. *Semibryophyllum palustre* and *Semibryophyllum cultellum* (type species) match in the nuclear pattern and number of ciliary rows, while body shape is markedly

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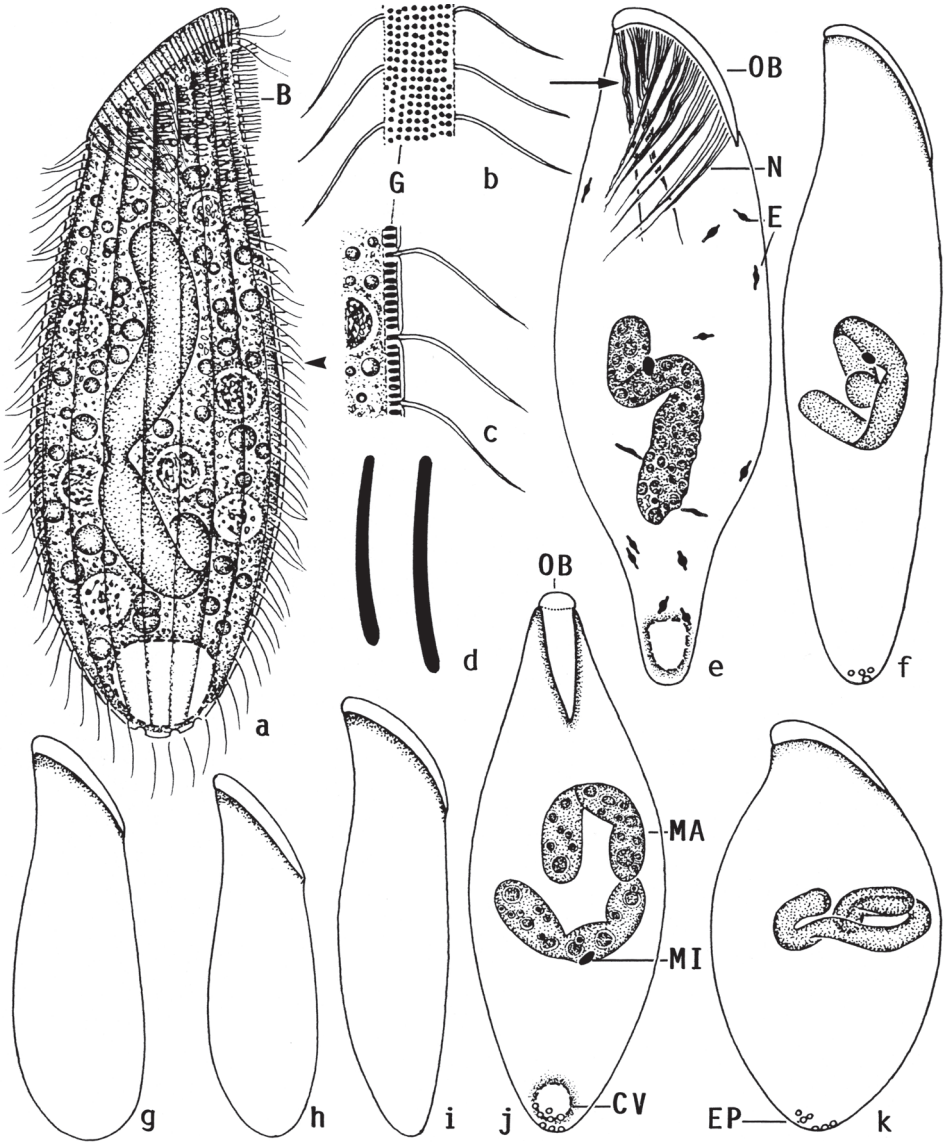
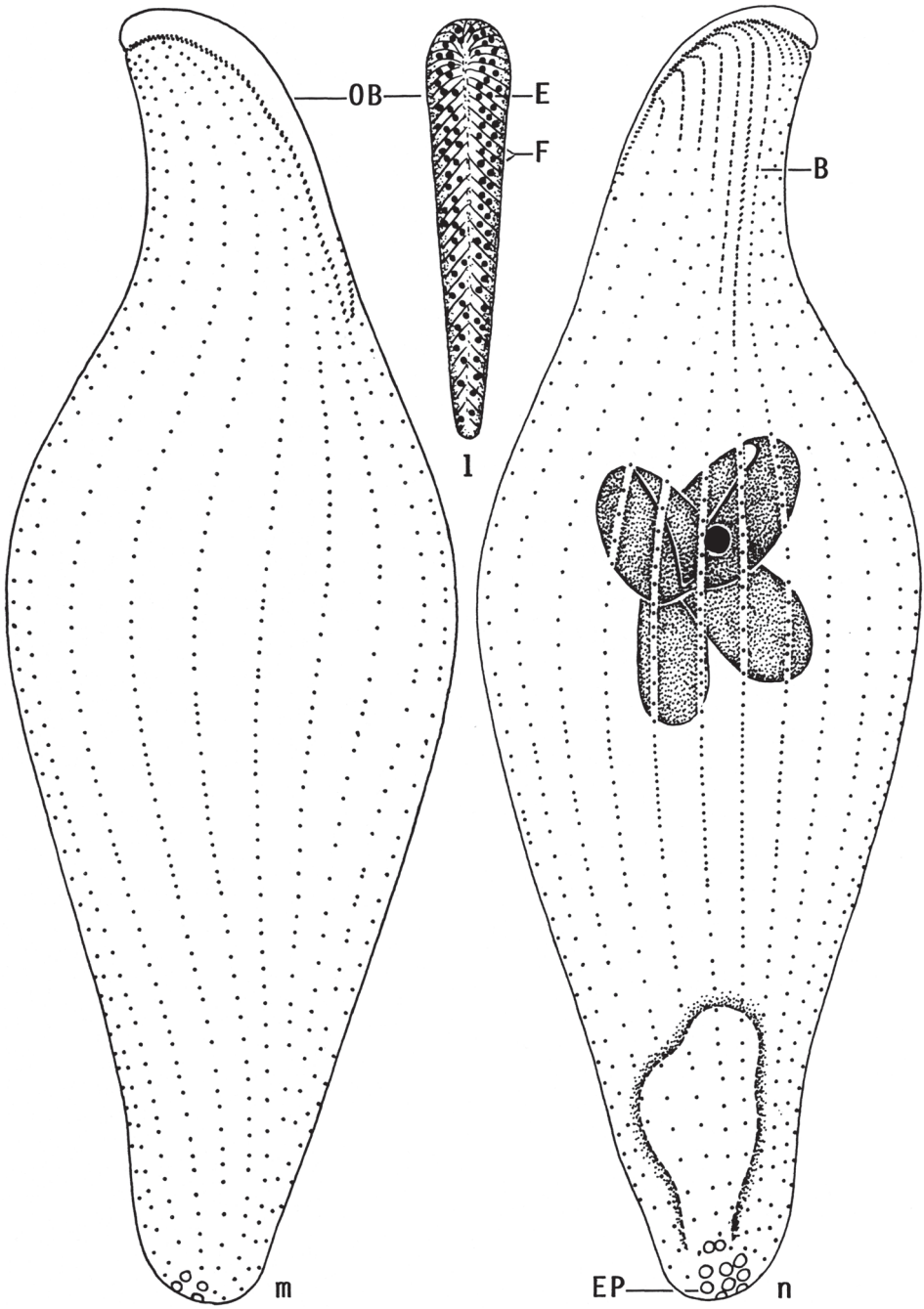


Fig. 9.3a–k *Semibryophyllum palustre* nov. spec. (originals. a–d, g–i, from life; e, f, j, k, protargol preparation). **a:** Left side view of a representative specimen, 130 µm. Arrowhead marks end of monokinetidal bristle tail of dorsal brush row 3. **b, c:** Surface view and optical section showing dense cortical granulation (cp. Fig. 9.4i–l). **d:** Oral bulge extrusomes are indistinctly acicular to rod-shaped and 6–8 µm long. **e, f, j, k:** Variability of body size and shape and macronucleus in protargol preparations (e, f, k, right side views; j, ventral view). Arrow in (e) marks dorsal nematodesmal bundles directed ventrally and thus optically crossing right side bundles. Note the cuneate oral bulge (j). Drawn to scale, 128 µm, 125 µm, 103 µm, 81 µm. **g–i:** Body shape variability in vivo (right side views). B – dorsal brush, CV – contractile vacuoles, E – extrusome, EP – excretory pores, F – fibres, G – cortical granules, MA – macronucleus, MI – micronucleus, N – nematodesmata (oral basket rods), OB – oral bulge.

Fig. 9.3l–n *Semibryophyllum palustre* nov. spec. (originals. l, from life; m, n, protargol preparation). **l:** Frontal view of oral bulge, which is cuneate and studded with extrusomes. **m, n:** Ciliary pattern of right and left side and nuclear apparatus of holotype specimen, 137 µm. For abbreviations, see legend above. For details, see following figures. →

different due to the oral bulge (moderately convex and occupying 26% of body length vs. strongly convex and occupying 60% of body length). Further, *Semibryophyllum cultellum* has two types of extrusomes in the oral bulge, while *Semibryophyllum palustre* has only one type.



Body and macronuclear shape of *Semibryophyllum palustre* highly resemble *Cranotheridium taeniatum* Schewiakoff, 1892 (Fig. 9.6e; type species of *Cranotheridium* by monotypy). However, the populations cannot belong to the same species, even if we assume that Schewiakoff (1892, 1893) misinterpreted the extrusomes as a pharyngeal basket, because then the extrusomes would have a quite different arrangement (scattered vs. localized in dorsal end of oral bulge) and length (6–8 µm vs. about 33 µm, as calculated from Schewiakoff's figure (Fig. 9.6e).

Description: Body size and shape highly variable that it is difficult to select a representative specimen, partially because the population was in an exponential growth phase when observed and preserved for protargol preparation, as shown by a high percentage (about 10%) of very early dividers in the preparations.

Body size 80–190 × 30–55 µm in vivo, usually near 130 × 45 µm, however, up to 250 µm long specimens were occasionally observed; length:width ratio also highly variable, that is,

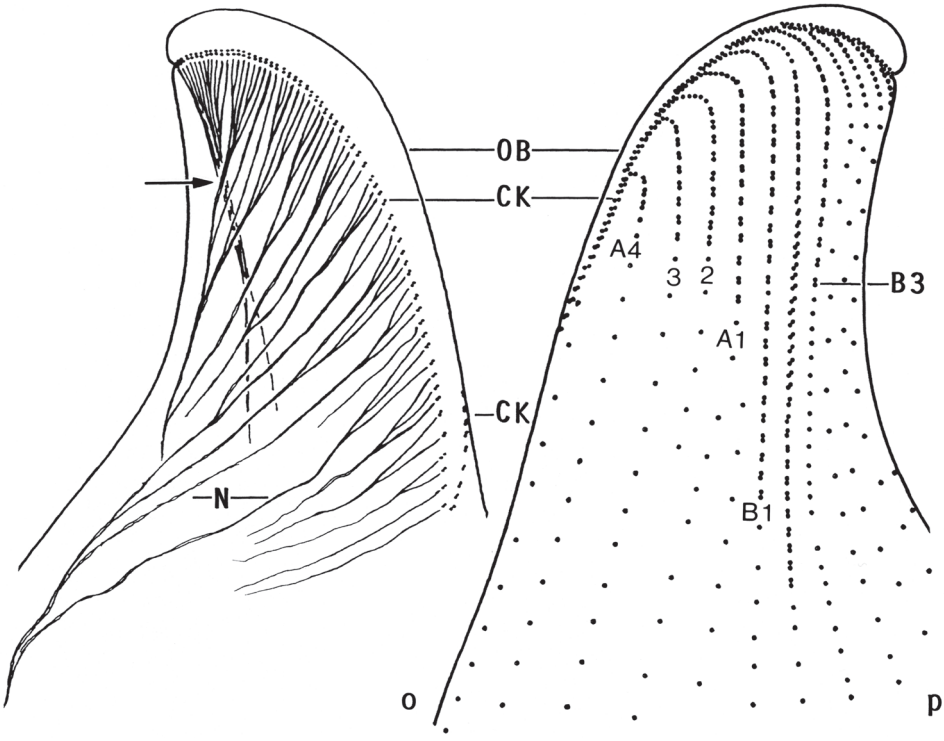


Fig. 9.3o, p *Semibryophyllum palustre* nov. spec. (originals. Protargol preparation). Oral basket in right side view (o) and ciliary pattern of left side (p) of holotype specimen shown in Fig. 9.3m, n; length of oral bulge 40 µm. Arrow in (o) marks dorsal nematodesmal bundles, which extend ventrally and thus optically cross the lateral bundles. Numbers in (p) denote dorsal brush, which consists of three ordinary rows (B1–3) and four accessory rows (A1–4). All brush rows have an anterior tail of ordinary cilia and continue posteriorly as somatic ciliary rows; ordinary brush row 2 has oblique dikinetids in the middle third; and brush row 3 has a monokinetidal tail of rather narrowly spaced, minute bristles (cp. Fig. 9.4a, r, s). Note slightly interrupted circumoral kinetofragments, attached to the ciliary rows. A1–4 – accessory dorsal brush rows, B1–3 – ordinary brush rows, CK – circumoral kinety, N – nematodesmata, OB – oral bulge.

1.8–4.4:1, on average 2.8:1 both in vivo and protargol preparations; highly flexible and up to 30% contractile under moderate cover glass pressure. Body shape distinctly to indistinctly spatulate or bursiform, occasionally fusiform, ellipsoidal, or lanceolate; anterior (oral) body end slightly to rather distinctly convex and slanted by 30–45°, posterior end narrowly to broadly rounded, widest usually in mid-body; ventral and dorsal view usually fusiform because up to 2.5:1 flattened laterally at body ends (Fig. 9.3a, e–k, m, 9.4a, b; Table 9.1). Nuclear apparatus usually in middle body third (Fig. 9.3a, e, f, j, k, n, 9.4g, i, n; Table 9.1). Macronucleus a more or less tortuous strand with an estimated average length of about 80 µm, slightly to distinctly moniliform in two thirds of specimens; studded with small and large nucleoli; becomes distinctly inflated and slightly shorter when division commences, even before distinct changes

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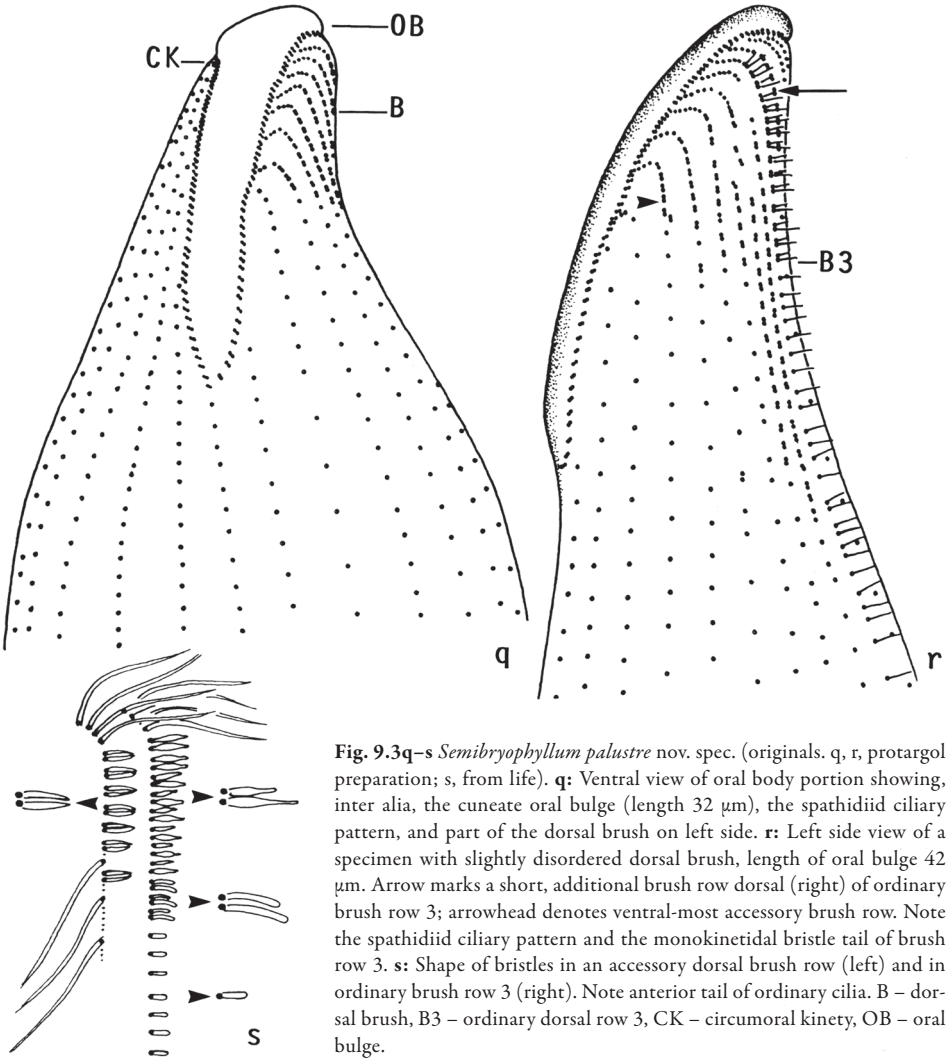


Fig. 9.3q–s *Semibryophyllum palustre* nov. spec. (originals. q, r, protargol preparation; s, from life). **q:** Ventral view of oral body portion showing, inter alia, the cuneate oral bulge (length 32 µm), the spathidiid ciliary pattern, and part of the dorsal brush on left side. **r:** Left side view of a specimen with slightly disordered dorsal brush, length of oral bulge 42 µm. Arrow marks a short, additional brush row dorsal (right) of ordinary brush row 3; arrowhead denotes ventral-most accessory brush row. Note the spathidiid ciliary pattern and the monokinetidal bristle tail of brush row 3. **s:** Shape of bristles in an accessory dorsal brush row (left) and in ordinary brush row 3 (right). Note anterior tail of ordinary cilia. B – dorsal brush, B3 – ordinary dorsal row 3, CK – circumoral kinety, OB – oral bulge.

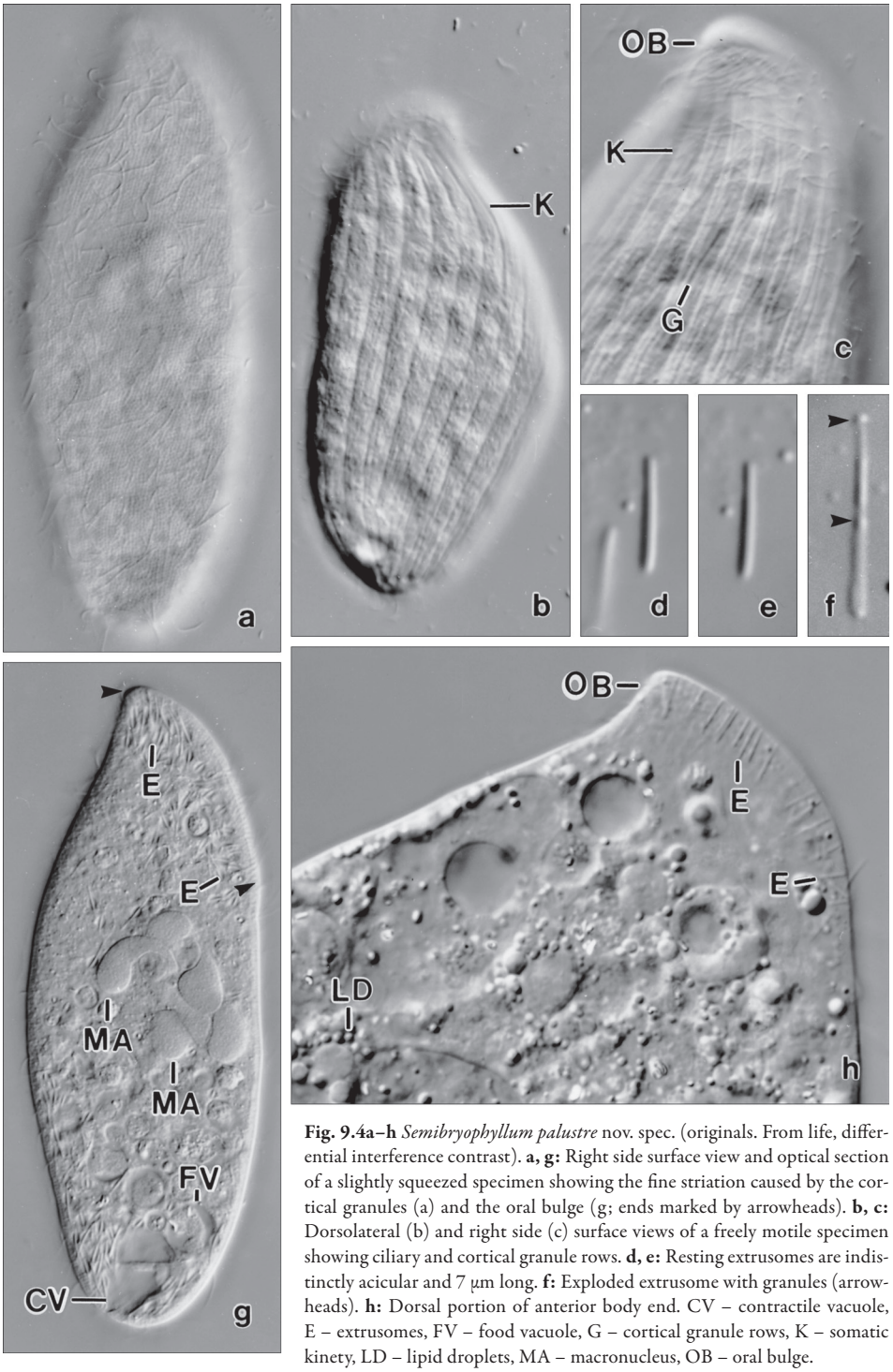


Fig. 9.4a–h *Semibryophyllum palustre* nov. spec. (originals. From life, differential interference contrast). **a, g:** Right side surface view and optical section of a slightly squeezed specimen showing the fine striation caused by the cortical granules (a) and the oral bulge (g; ends marked by arrowheads). **b, c:** Dorsolateral (b) and right side (c) surface views of a freely motile specimen showing ciliary and cortical granule rows. **d, e:** Resting extrusomes are indistinctly acicular and 7 μm long. **f:** Exploded extrusome with granules (arrowheads). **h:** Dorsal portion of anterior body end. CV – contractile vacuole, E – extrusomes, FV – food vacuole, G – cortical granule rows, K – somatic kinety, LD – lipid droplets, MA – macronucleus, OB – oral bulge.

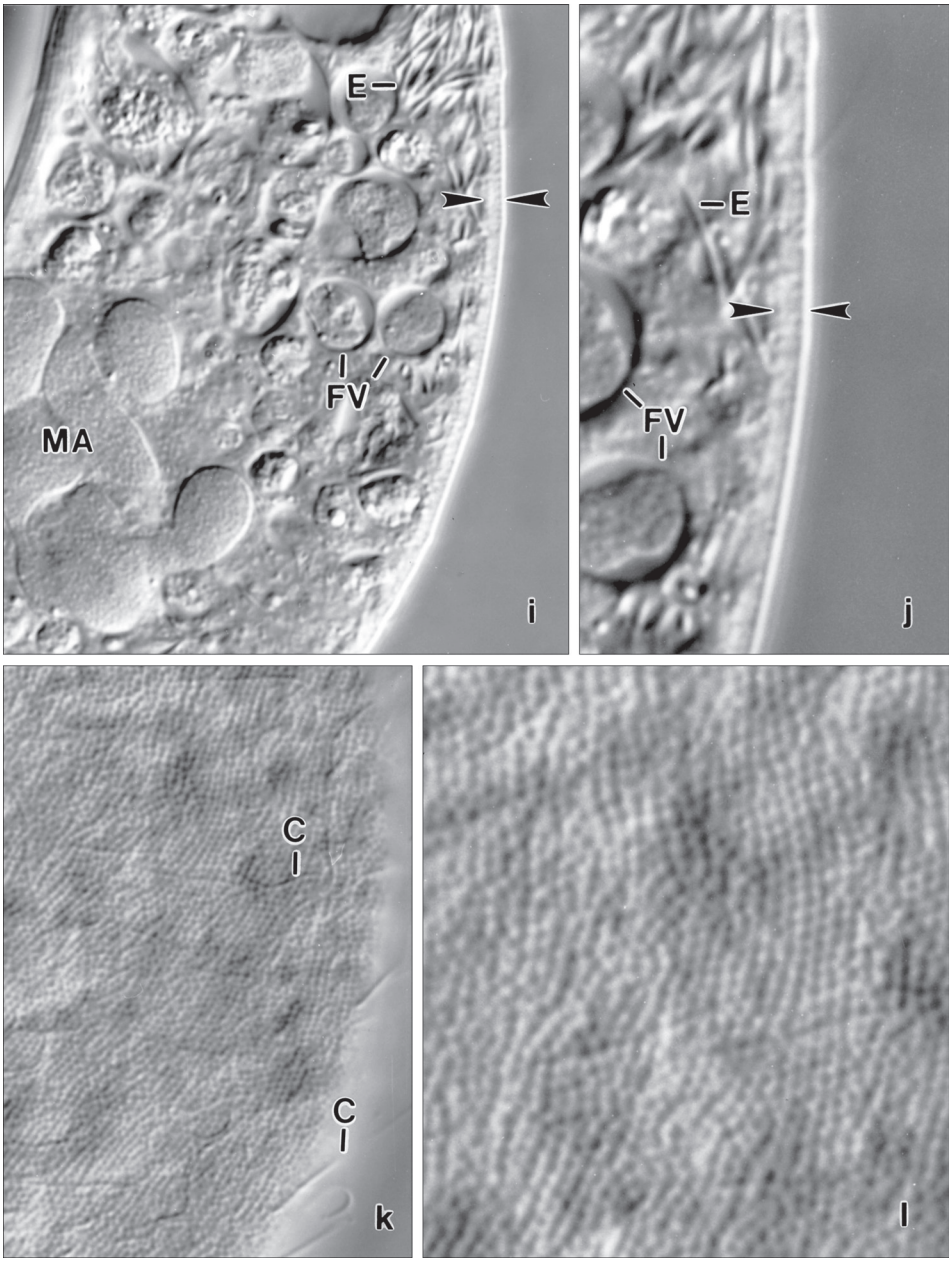


Fig. 9.4i–l *Semibryophyllum palustre* nov. spec. (originals. From life, differential interference contrast). **i, j:** Optical sections showing the thick cortex (marked by opposed arrowheads) produced by the cortical granules and the cortical alveoli. Note the tortuous macronucleus and the many food vacuoles. **k, l:** Surface views showing the reticular pattern produced by the cortical alveoli. C – ordinary somatic cilia, E – extrusomes, FV – food vacuoles, MA – macronucleus.

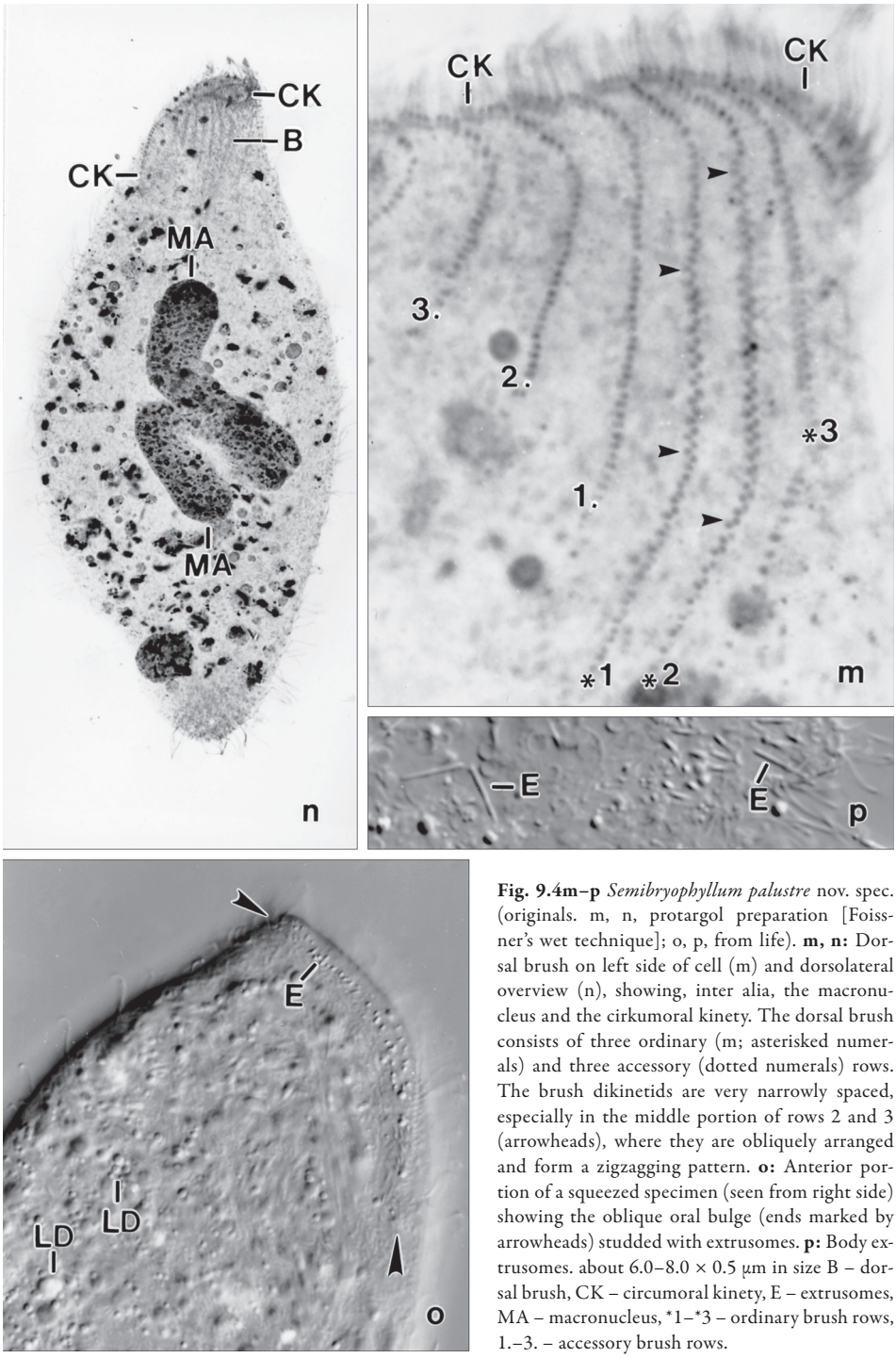


Fig. 9.4m–p *Semibryophyllum palustre* nov. spec. (originals. m, n, protargol preparation [Foissner's wet technique]; o, p, from life). **m, n:** Dorsal brush on left side of cell (m) and dorsolateral overview (n), showing, inter alia, the macronucleus and the cirkumoral kinety. The dorsal brush consists of three ordinary (m; asterisked numerals) and three accessory (dotted numerals) rows. The brush dikinetids are very narrowly spaced, especially in the middle portion of rows 2 and 3 (arrowheads), where they are obliquely arranged and form a zigzagging pattern. **o:** Anterior portion of a squeezed specimen (seen from right side) showing the oblique oral bulge (ends marked by arrowheads) studded with extrusomes. **p:** Body extrusomes. about 6.0–8.0 × 0.5 µm in size B – dorsal brush, CK – circumoral kinety, E – extrusomes, MA – macronucleus, *1–*3 – ordinary brush rows, 1.–3. – accessory brush rows.

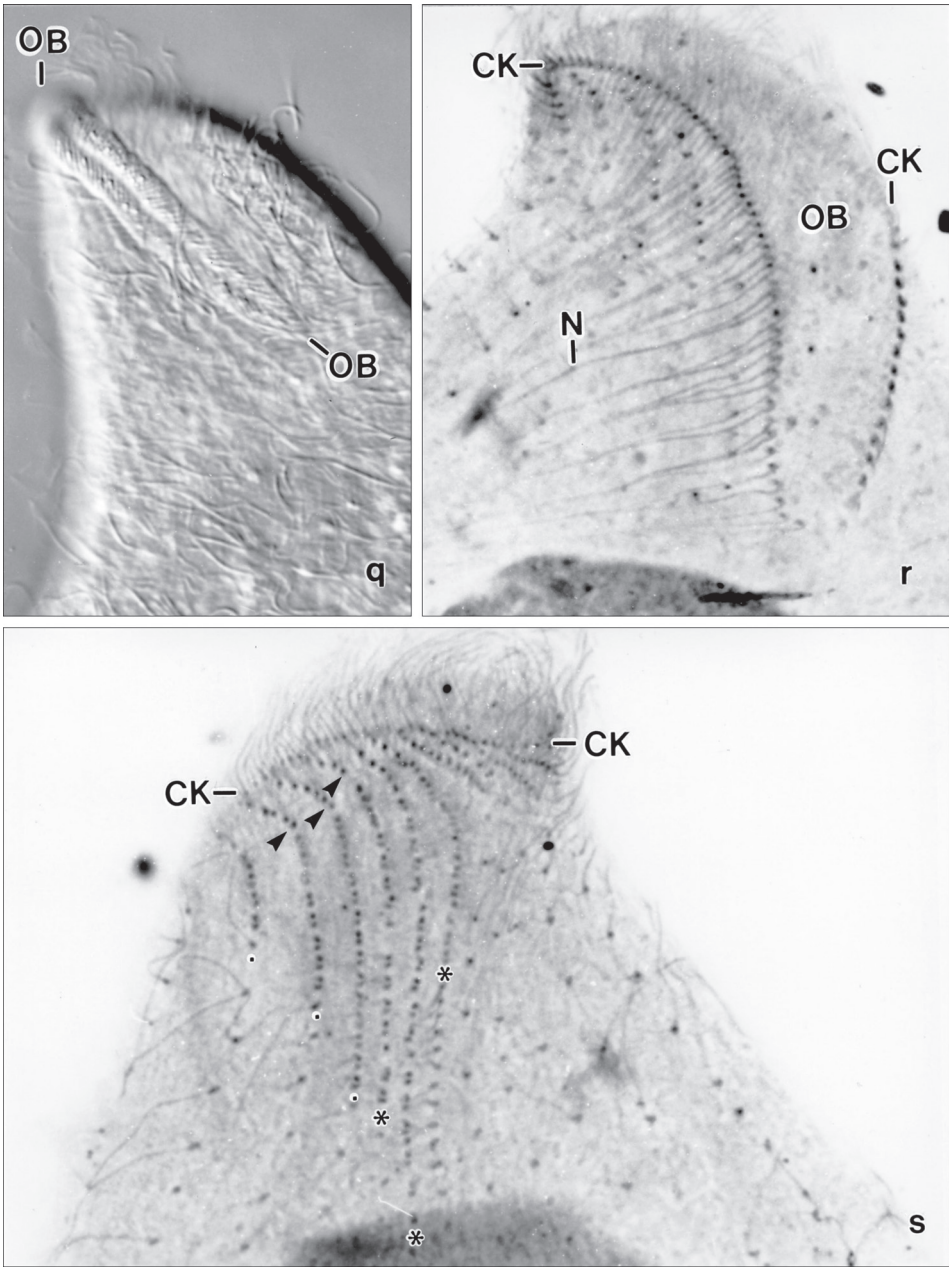


Fig. 9.4q–s *Semibryophyllum palustre* nov. spec. (originals. q, from life; r, s, protargol preparation, Foissner's wet technique). **q, r:** Frontal views of the cuneate oral bulge and circumoral kinety, which consists of rather widely spaced dikinetids associated with long nematodesmata. **s:** The dorsal brush consists of three ordinary (asterisks) and three accessory (dots) rows each with a short tail of ordinary cilia anteriorly (arrowheads). CK – circumoral kinety, N – nematodesmata, OB – oral bulge.

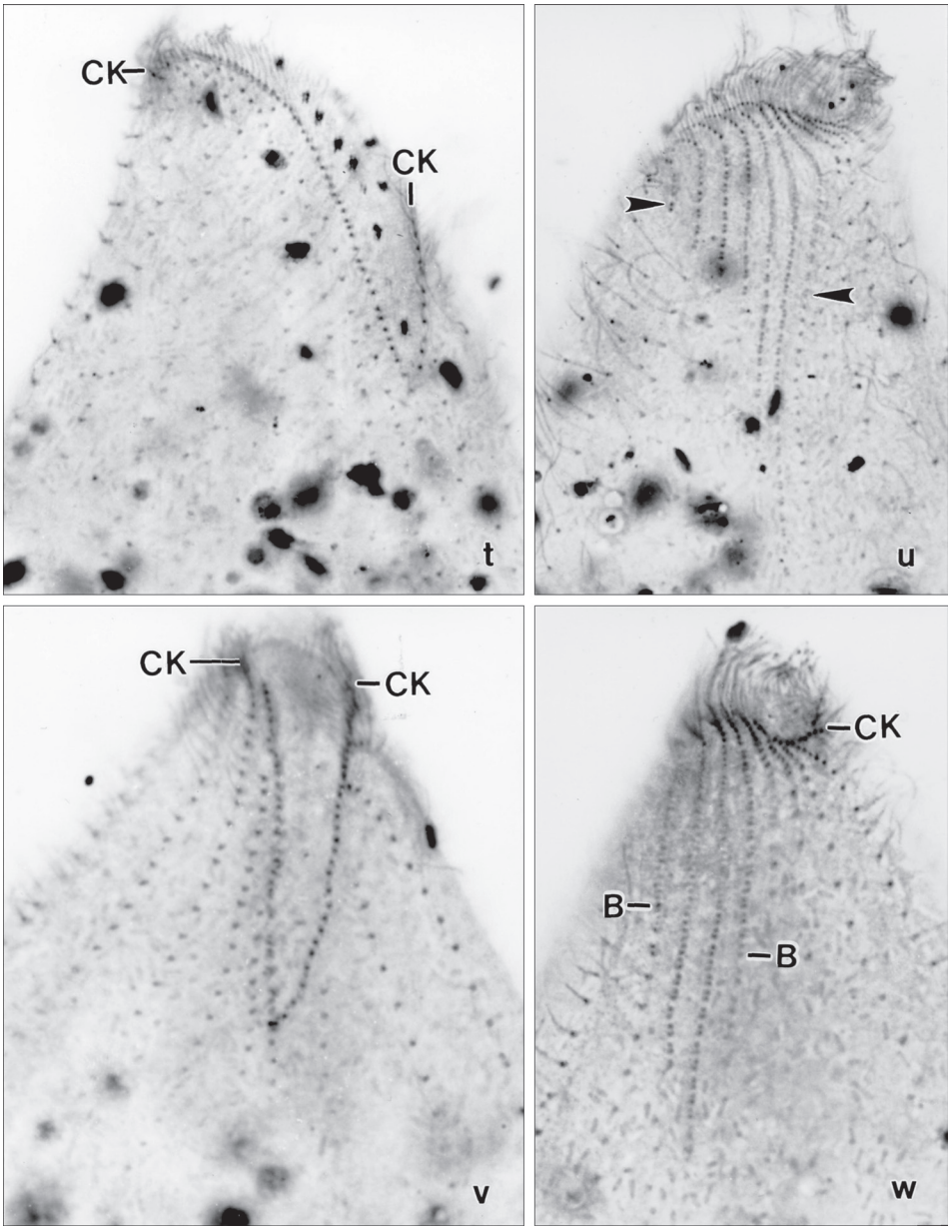


Fig. 9.4t–w *Semibryophyllum palustre* nov. spec. (originals. Protargol preparation, Foissner's wet technique). Ciliary pattern in anterior body portion. **t, u:** Right-ventrolateral and dorso-leftlateral view showing the cuneate circumoral kinety (t) and the dorsal brush (u; arrowheads), which consists of three ordinary (dorsal; right side of micrograph) and four accessory (ventral; left side of micrograph) rows (cp. Fig. 9.4m, s) of narrowly spaced dikinetids. **v, w:** Ventral (v) and dorsal (w) view of same specimen showing the cuneate oral bulge, at which the ciliary rows abut in *Spathidium* pattern, and the slight dorsolateral location of the dorsal brush whose two leftmost rows are not recognizable. B – dorsal brush, CK – circumoral kinety.

Fig. 9.5a–d *Semibryophyllum palustre* nov. spec. (originals. Protargol slides). **a, b:** Slide (a) and protocol (b) containing holotype (H) and paratypes drawn (PD). Accession number (LI): 2024/190. **c, d:** Slide (c) and protocol (d) containing paratypes (P) and paratypes drawn (PD). Accession number (LI): 2024/191.

are recognizable in the ciliary pattern. Micronucleus attached to macronucleus at variable position, inconspicuous because only about 4 × 3 µm in size. Contractile vacuole in posterior body end, no second contractile vacuole anteriorly; about 10 excretory pores in pole area. Definitely, only one type of extrusomes scattered in oral bulge and cytoplasm, where a certain, fusiform developmental stage intensely impregnates with protargol; rarely, the ends of the oral bulge extrusomes also impregnate, as in *Spathidium apospathidiforme* nov. spec. (see Chapter 3, that is, Foissner et al. 2025; Fig. 9.3a, d, e, l, 9.4d–j, o–q). Individual extrusomes rod-shaped to indistinctly acicular and slightly curved, about 6.0–8.0 × 0.5 µm in size. Cortex rather conspicuous because gelatinous, bright due to the granules contained, distinctly furrowed by the ciliary rows, and circa 1 µm thick showing a conspicuous, reticular alveolar pattern; contains narrowly spaced, oblique rows of colourless, minute (≤0.7 × 0.2 µm), but rather strongly refractive granules (Fig. 9.3b, c, 9.4a–c, i–l); distinctness and spacing of granules varies, however, only moderately conspicuous in one of four specimens observed. Cytoplasm colourless, usually with lipid droplets and/or food vacuoles 1–10 µm across. Likely, mainly feeds on ciliates and heterotrophic flagellates obviously digested rapidly because identifiable prey is not recognizable in the 30 specimens observed. Glides and swims rather rapidly on microscope slides and soil particles showing great flexibility, especially under moderate coverslip pressure, as described above.

Cilia about 10 µm long in vivo, arranged in an average of 22 rather widely spaced, usually bipolar and equidistant rows abutting on circumoral kinety in typical *Spathidium* pattern,

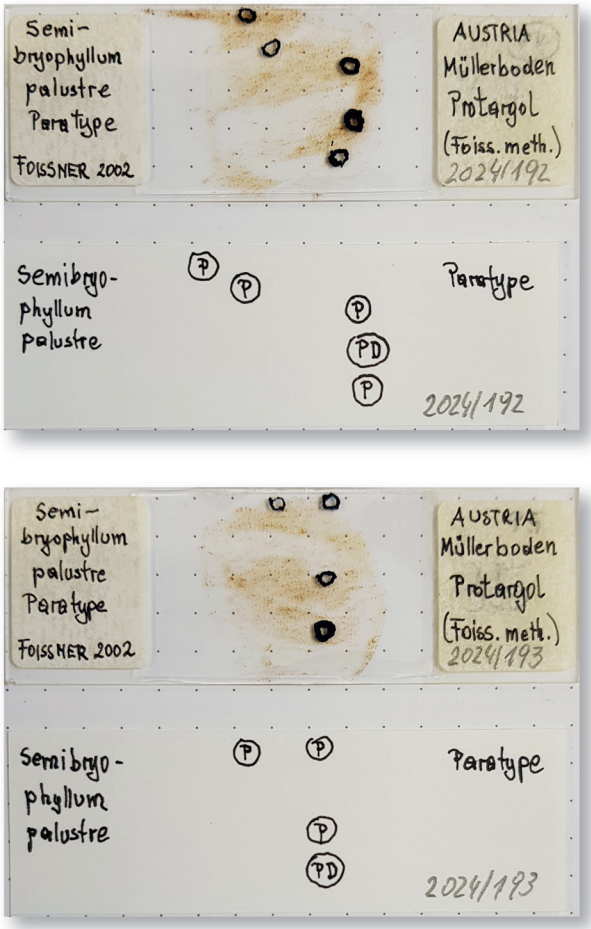


Fig. 9.5e–h *Semibryophyllum palustre* nov. spec. (originals. Protargol slides). **e–h:** Slides (e, g) and protocols (f, h) containing paratypes (P) and paratypes drawn (PD). Accession numbers (LI): 2024/192, 193.

that is, anterior end of right side ciliary rows distinctly curved dorsally and separate from circumoral kinety, while anterior end of left side kineties curved ventrally and attached to circumoral kinety fragments. Ciliary rows moderately densely ciliated, composed of ciliated and some bare basal bodies irregularly interspersed (Fig. 9.3a, m, n, q, r, 9.4a, b, r, t, v; Table 9.1). Dorsal brush rather inconspicuous, though composed of an average of seven rows occupying almost two thirds of left side in oral body portion, because extending only up to 25% of body length and bristles merely up to 4 µm long and hardly thicker than ordinary somatic cilia; consists of narrowly spaced dikinetids arranged in three ordinary and 3–5 accessory rows (Fig. 9.3a, n, p–s, 9.4n, m, s, u, w; Table 9.1)[4]. Individual brush rows extend in rather deep furrows, have a ventrally curved tail of up to 10 ordinary cilia anteriorly, and continue as somatic ciliary rows posteriorly with transition zone sometimes composed of a mixture of bristles and ordinary cilia; frequently small irregularities occur, such as minute breaks and/or dikinetids out of line. Ordinary brush row 1 slightly shorter than row 2, which invariably is the longest of all rows, dikinetids very narrowly spaced and obliquely arranged in middle third of row 2, rarely also of row 1; row 3 distinctly

[4] Ordinary brush row 1 composed of 22.1 dikinetids on average (M = 22, SD = 4.3, SE = 1.0, CV = 19.3, Min = 15, Max = 35, n = 18); row 2 of 27.1 dikinetids on average (M = 25.5, SD = 4.9, SE = 1.2, CV = 18.2, Min = 20, Max = 36, n = 18); row 3 of 11.5 dikinetids on average (M = 12, SD = 2.5, SE = 0.6, CV = 22.0, Min = 6, Max = 15, n = 18). Accessory brush row 1 composed of 12.3 dikinetids on average (M = 12, SD = 3.0, SE = 0.7, CV = 24.2, Min = 8, Max = 18, n = 17); row 2 of 9.1 dikinetids on average (M = 9, SD = 2.3, SE = 0.6, CV = 24.8, Min = 6, Max = 15, n = 17); row 3 of 6.3 dikinetids on average (M = 6, SD = 1.9, SE = 0.5, CV = 29.6, Min = 2, Max = 9, n = 17); row 4 of 3.9 dikinetids on average (M = 4, SD = 1.4, SE = 0.4, CV = 35.2, Min = 2, Max = 6, n = 14). For numbering of brush rows, see Fig. 9.3p.

shorter than rows 1 and 2, but continues to mid-body with rather narrowly spaced, 1–2 µm long, monokinetidal bristles. Accessory dorsal brush rows shorter than ordinary rows 1 and 2, shorten gradually from dorsal to ventral with row closest to ventral side composed of only four dikinetids on average (see footnote). Bristles of ordinary brush rows flask-shaped and about 4 µm long in anterior half of rows, gradually shorten to 2 µm and become rod-shaped in posterior half; anterior bristle of individual dikinetids often slightly shorter than posterior. Bristles of accessory brush rows acicular and close together forming a conical unit (Fig. 9.3a, s).

Oral bulge occupies anterior body end slanted by 30–45°, on average two thirds as long as widest trunk region, usually inconspicuous because hardly set off from body proper and only 4 µm high at dorsal end gradually narrowing to about 2 µm at ventral end; slightly to distinctly convex in laterally oriented specimens and conspicuously cuneate when viewed ventrally with dorsal end circa 10 µm wide in vivo (distance between circumoral kinety 7.2 µm on average in protargol-impregnated specimens; n = 8). Bulge surface arrowhead-like ribbed; oral slit and "second mouth" not recognizable (Fig. 9.3a, e–q, 9.4a–c, g, h, n, o, q, r, v; Table 9.1). Circumoral kinety of same shape as oral bulge, basically continuous, but individual kinetofragments become distinct on left side in obliquely oriented specimens (Fig. 9.3p, 9.4m); composed of dikinetids gradually more narrowly spaced from ventral to dorsal end of kinety; circumoral dikinetids each associated with a cilium, a long nematodesma, and a faintly impregnated fibre extending into oral bulge. Oral basket conspicuous in protargol preparations because composed of distinct nematodesma bundles; number of rods composing individual bundles and length of bundles gradually increase from ventral to dorsal end of circumoral kinety, where bundles extend to mid-body and ventrally, optically intersecting lateral bundles (Fig. 9.3a, e, j, m–r, 9.4m, n, r, t, v).

Occurrence and ecology: As yet found only at the type locality, that is, a loamy floodplain soil in Lower Austria, near the Leitha River, where it occurred at one of two sampling occasions with low abundance six days after wetting the sample (see above). Thus, it is difficult to know whether *Semibryophyllum palustre* is a limnetic or terrestrial species, as in *Semibryophyllum cultellum*. The sample contained over 100, mostly terrestrial ciliate species. See Foissner et al. (2005, p. 619, 620, site M) for details on site and soil.

Semibryophyllum foliosum (Foissner, 1983) nov. comb.

(Fig. 9.6a–d, f–o, Table 9.2)

1979 ***Pseudoprorodon foliosus*** Foissner – Foissner & Adam, Jb. Univ. Salzburg year 1977: 154 (nomen nudum, see nomenclature).

1980 ***Pseudoprorodon foliosus* Foissner** – Foissner, Arch. Protistenk. 123: 109 (nomen ndum, see nomenclature).

1982 ***Pseudoprorodon foliosus*** Foissner – Foissner, Adam & Foissner, Ber. Nat.-Med. Ver. Salzburg 6: 95 (nomen nudum, see nomenclature).

1983 ***Pseudoprorodon foliosus* nov. spec.**[5] – Foissner, Annln naturh. Mus. Wien, 84/B (year 1980): 59, Abb. 6a, b (Fig. 9.6a, b; original description; no type material available).

1984 ***Cranotheridium foliosus* (Foissner, 1983) nov. comb.** – Wirnsberger, Foissner & Adam, Arch. Protistenk. 128: 308, Abb. 8–13, Tabelle 2 (Fig. 9.6c, d, f, h–l, o; redescription, combination with *Cranotheridium*, and neotypification [see nomenclature]; one slide [accession number 1986/16] has been deposited in the Biology Centre of the Upper Austrian Museum in Linz [LI]; see nomenclature).

[5] Foissner (1983) provided the following diagnosis: "Etwa 100 µm großer, blattartig abgeflachter, sapropelophiler *Pseudoprorodon* mit kurzem, gekrümmtem Makronucleus."

1988 ***Cranotheridium foliosum* (Foissner) 1983** – Foissner & Foissner, Catalogus Faunae Austriae Ic: 20 (faunistic overview and silent [not indicated] emendation of name).

2008 ***foliosus Cranotheridium* (Foissner, 1983) Wirnsberger, Foissner & Adam, 1984** and ***Cranotheridium foliosum*** – Aescht, Denisia 23: 156 (note on neotypification by Wirnsberger et al. 1984 and on emendation).

Nomenclature: No etymology has been given in the original description or a later work. The species-group name *folios·us*, *-a*, *-um* (Latin adjective [m, f, n]; leafy, full of leaves; Brown 1954, p. 466; Schubert & Wagner 1979, p. 146; wordsense.eu, accessed 16 Apr 2023) refers to the strongly flattened, leaf-like body ("blattartig abgeflacht" according to the diagnosis by Foissner 1983).

Foissner & Adam (1979), Foissner (1980), and Foissner et al. (1982) mentioned this name, but neither provided a definition, a description, or an illustrations of the species. Thus, *Pseudoprorodon foliosus* in Foissner & Adam (1979), Foissner (1980), and Foissner et al. (1982) is an unavailable name (a nomen nudum) and the name is available for the same or a different concept (ICZN 1999, Article 13.1.1, see p. 111 of ICZN 1999 for definition of the term nomen nudum). *Bryophyllum* (see nomenclature at genus section) and *Cranotheridium* are of neuter gender (Aescht 2001, p. 275, 279). Thus, *foliosum* is correct when used in combination with these genus-group names. Foissner & Foissner (1988; see list above) did not point out the emendation.

Foissner (1983) did not fix a holotype (or syntypes) nor did he make protargol preparations. Thus, no type material (e.g. holotype) is available. Despite that, the species is valid because the explicit fixation of a holotype is necessary only for species described after 1999 (ICZN 1999, Articles 16.4.1, 72.3). Wirnsberger et al. (1984) briefly discussed the problem and fixed their population as neotype. They mentioned that two neotype slides have been deposited in the Upper Austrian Museum in Linz (Wirnsberger et al. 1984, p. 310). However, Aescht (2008, p. 156) wrote that only one slide (accession number 1986/16) is in the museum.[6] In spite of these "problems", we recommend accepting the neotypification by Wirnsberger et al. (1984) because they basically provided all (1–6) qualifying conditions for a valid designation (ICZN 1964, Article 75c).[7] The distance between the sample sites (Großglockner Hochalpenstraße, Salzburg, Foissner 1983 vs. Schloßalm, Bad Hofgastein, Salzburg, Wirnsberger et al. 1984; in both cases samples were taken from small pasture ponds) is only about 20 km (details, see occurrence and ecology).

Diagnosis (based on original data and neotype population): Body size about 90 × 40 µm in vivo. Body shape bursiform with slightly oblique oral bulge indistinctly set off from body proper and almost as long as widest trunk region. Macronucleus reniform. Oral bulge extrusomes rod-shaped, about 13 µm long. Approximately 29 ciliary rows, about eight of them differentiated to dorsal brush occupying up to 35% of body length.

Remarks: The original description is very meager. Thus, most data presented below are from Wirnsberger et al. (1984) and a re-evaluation of their notes. The neotypification by Wirnsberger et al. (1984) should be accepted (see nomenclature), though the redescrip-

[6] Note by H. Berger: Aescht (2008, p. 156) wrote that the neotypification is not mentioned in the paper, which is, however, incorrect because Wirnsberger et al. (1984, p. 310) wrote as subheading "Ausbewahrungsort [sic] des Neotypus" (= storage site of neotype). In addition, Aescht (2008) wrote that "slides" [sic; plural!] were mislabelled as holotype (simultaneously she mentioned that only one slide was deposited in the museum in Linz).

[7] Note by H. Berger: For Wirnsberger et al. (1984), this was the relevant ICZN.

continued on p. 306

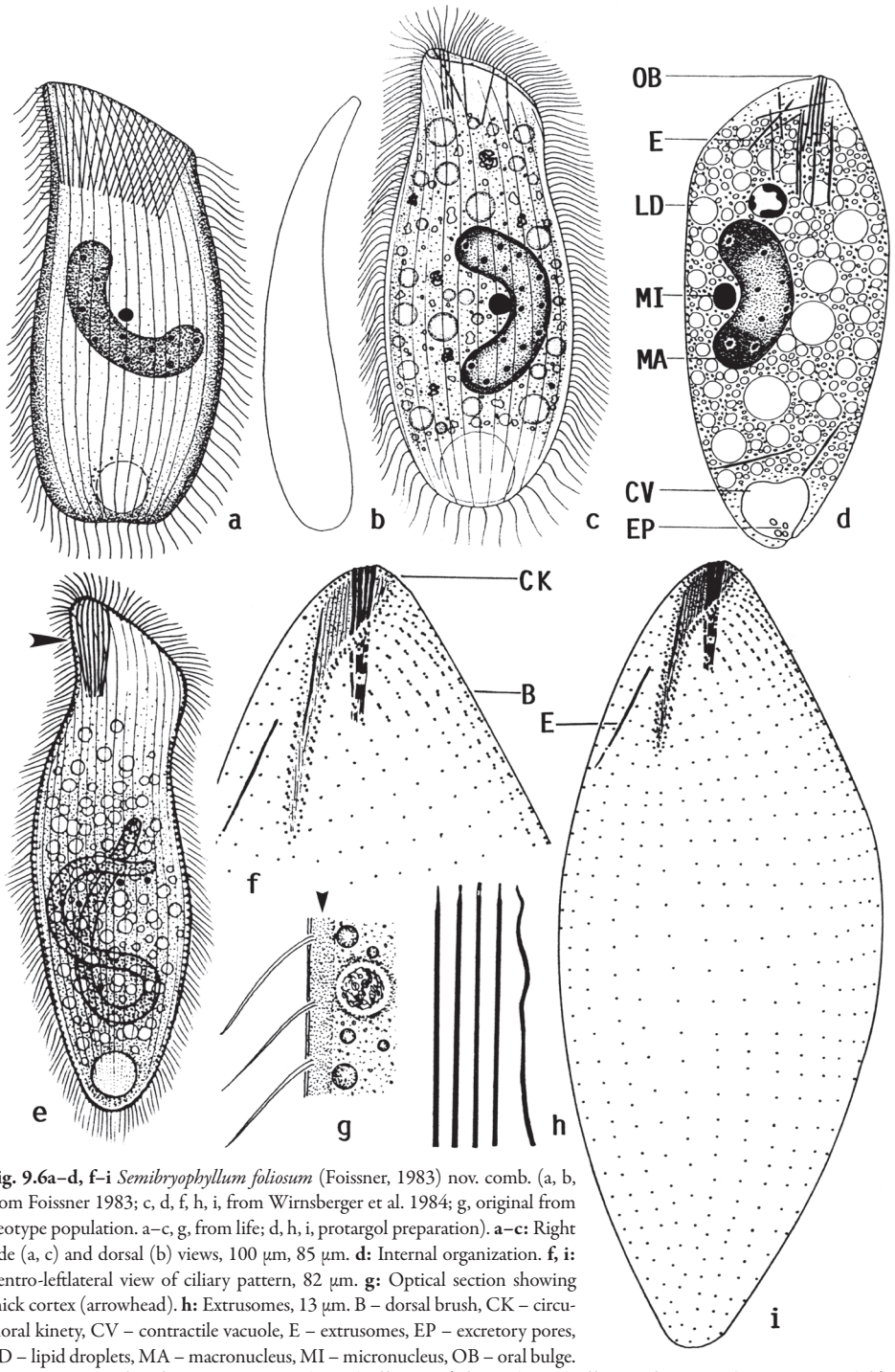


Fig. 9.6a–d, f–i *Semibryophyllum foliosum* (Foissner, 1983) nov. comb. (a, b, from Foissner 1983; c, d, f, h, i, from Wirnsberger et al. 1984; g, original from neotype population. a–c, g, from life; d, h, i, protargol preparation). **a–c:** Right side (a, c) and dorsal (b) views, 100 μm, 85 μm. **d:** Internal organization. **f, i:** Ventro-leftlateral view of ciliary pattern, 82 μm. **g:** Optical section showing thick cortex (arrowhead). **h:** Extrusomes, 13 μm. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuole, E – extrusomes, EP – excretory pores, LD – lipid droplets, MA – macronucleus, MI – micronucleus, OB – oral bulge.

Fig. 9.6e *Cranotheridium taeniatum* Schewiakoff, 1892 (after Schewiakoff 1893 from Curds 1982. From life). Right lateral view, 170 μm. Arrowhead marks oral basket.

tion is also incomplete because the species is difficult to impregnate, likely due to the thick cortex.

Pseudoprorodon foliosus (at present *Cranotheridium foliosum*) is transferred to *Semibryophyllum* (see heading above) because it has a spathidiid organization and many dorsal brush rows, and cannot be assigned to *Cranotheridium*, as explained in the genus discussion above. Further, it is highly similar to *Semibryophyllum palustre*, which doubtlessly is a spathidiid.

Semibryophyllum foliosum differs markedly from *Semibryophyllum cultellum* (shape of body and oral bulge, nuclear pattern, etc.), but is rather similar to *Semibryophyllum palustre*, from which it differs mainly by (i) body size (about 90 × 40 µm vs. 130 × 50 µm), (ii) macronucleus shape (reniform vs. tortuous strand), and (iii) extrusome length (about 13 µm vs. 7 µm) and shape (rod-shaped vs. slightly curved).

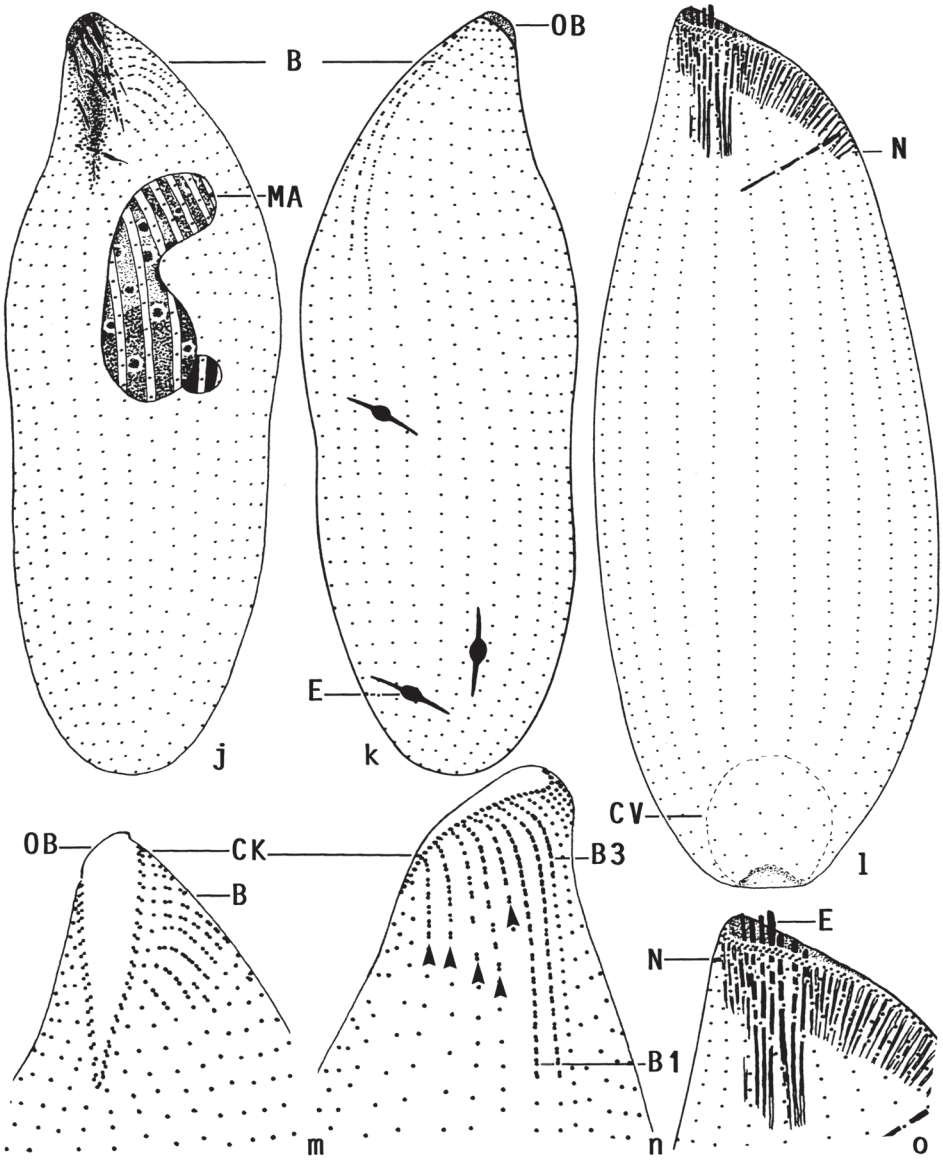
Description (based on populations studied by Foissner 1983 and Wirnsberger et al. 1984; see nomenclature and remarks): Body size 70–100 × 30–50 µm in vivo, usually about 90 × 40 µm. Body bursiform to ellipsoidal with both margins indistinctly sigmoidal, anterior (oral) body end slightly oblique and convex, posterior broadly rounded and wrinkled after systole of contractile vacuole; up to 3:1 flattened laterally, especially in more or less distinctly narrowed anterior body third (Fig. 9.6a–c, j, l; Table 9.2). Macronucleus in middle body third, more or less distinctly reniform with ends often slightly inflated, rarely almost semicircular; nucleoli small and scattered. Micronucleus globular, usually in centre of macronuclear curve. Contractile vacuole in rear end, several excretory pores in pole area. Cytopyge ventral to contractile vacuole. Extrusomes concentrated in dorsal region of oral bulge and scattered throughout bulge and body, rod-shaped, 10–16 µm, usually about 13 µm long in vivo, impregnate with protargol showing needle-like narrowed anterior end (Fig. 9.6a, c, d, f, h, k, l, o). Cortex flexible and conspicuous because bright and almost 2 µm thick, likely due to very narrowly spaced (overlooked) granules, as in *Semibryophyllum palustre*. Cytoplasm colourless, in well-fed specimens packed with colourless, yellowish and orange lipid droplets up to 5 µm across and food vacuoles containing globular green algae, except of strongly flattened and hyaline oral area. Creeps slowly on organic debris.

Cilia about 8 µm long in vivo, arranged in about 29 ordinarily spaced and ciliated rows abutting on circumoral kinety in rather pronounced *Spathidium*-pattern; some rows slightly shortened posteriorly. Dorsal brush moderately conspicuous, composed of 7–9 rows, the longest of which occupy up to 35% of body length; dikinetids bearing about 4 µm long, rather narrowly spaced bristles, arranged in three ordinary and 4–6 accessory rows becoming shorter from dorsal to ventral, as in congeners. All rows have a short, ventrally

Fig. 9.6j–o *Semibryophyllum foliosum* (Foissner, 1983) nov. comb. (from Wirnsberger et al. 1984; n, an unpublished drawing from the neotype population. Protargol preparation). **j, k, m:** Ventral (j, m) and dorsal (k) view of same specimen, which contains many fusiform, developing extrusomes (k); 77 µm. Note the flat, cuneate oral bulge, respectively, circumoral kinety composed of dikinetids. **l, o:** Right side view showing the short nematodesmata (oral basket rods) and the dorsal extrusome bundle, 83 µm. **n:** Left side view of anterior body portion. The ciliary rows are arranged in *Spathidium* pattern, and most are modified to dorsal brush kineties anteriorly. The dorsal brush consists of three ordinary rows (B1–3) and five short, accessory rows (arrowheads). B – dorsal brush, B1, 3 – ordinary dorsal brush rows, CK – circumoral kinety, CV – contractile vacuole, E – extrusomes, MA – macronucleus, N – nematodesmata, OB – oral bulge. →

curved monokinetidal tail with ordinary cilia anteriorly and continue as somatic kineties posteriorly (Fig. 9.6a, c, f, i–k, m, n).

Oral bulge occupies anterior body end, slightly oblique and convex, distinctly cuneate in frontal view, very inconspicuous in lateral view because only 2–3 μm high and hardly set off from body proper. Circumoral kinety of similar shape as oral bulge, widened dorsal portion occasionally rather abruptly narrowed ventrally; composed of ventrally rather widely spaced dikinetids associated with short nematodesmata distinct only in protargol preparations (Fig. 9.6a, c, d, f, i–o).



Occurrence and ecology: So far recorded only from Austria. Foissner (1983) discovered *Semibryophyllum foliosum* in a permanent, acidic (pH 4.8–5.0) brown-water (mainly due to humic substances from soil) pond in the Salzburg part of the Austrian Central Alps, viz., in the "Hexenküche" (witches' kitchen) (47°10'N 12°50'E), an area along the Großglockner Hochalpenstrasse. See Foissner & Adam (1979) for detailed site description, and Foissner et al. (1982) for details on water chemistry. Likely, *Semibryophyllum foliosum* prefers the microaerobic algal mud (up to 0.5 mg/l H_2S), where it occurred with low abundance at eight sampling occasions.

Due to the neotypification by Wirnsberger et al. (1984, see above), the new type locality is the edge of a pasture pool on the Schloßalm (about 47°09'N 13°04'E; about 1950 m above sea-level; details, see Wirnsberger et al. 1984, p. 306 and Aescht 2008, p. 156), an alpine pasture near the village of Bad Hofgastein, Salzburg, Austria. Both sample sites (Foissner 1983, Wirnsberger et al. 1984) are from the same area (distance between only about 20 km) and habitat (alpine pasture pond) so that the qualifying condition (5) of the ICZN (1964, Article 75c; see also ICZN 1999, Article 75.3.6) is fulfilled. Interestingly, *Semibryophyllum palustre* occurs in a similar habitat, viz., floodplain soil, indicating that both species are freshwater inhabitants.

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Index

Systematic index

The index contains all ciliate names mentioned in the book, including vernacular names for example, haptorids. Designations as, for example, "haptorid ciliates" are mentioned under the corresponding vernacular name, that is, "haptorids" in present example. Names in singular (e.g., haptorid) are mentioned under the plural version (e.g., haptorids). The index is two-sided, that is, species appear both with the genus-group name first (for example, *Apospathidium atypicum*) and with the species-group name first (*atypicum*, *Apospathidium*). Valid (mainly in W. Foissner's judgement) species and genera treated in detail are in boldface italics print. Valid taxa not treated in detail in the present book, invalid taxa, junior homonyms, synonyms, outdated combinations, incorrect spellings, and nomina nuda are not in bold. Suprageneric taxa are represented in normal type, valid ones treated in detail in the present work in boldface. A boldface page number indicates the beginning of the description of a valid taxon. "T" indicates the location of the table with the morphometric characterisation; "K" marks a key (e.g., of the genus *Apospathidium*) and the page where a taxon is mentioned in a key. The names on the slide figures and the names of the subchapter "Summary of nomenclatural acts and taxa described in Chapters 1–13" (see Chapter 1, pp. 18–20) are not included.

Table index