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**

Series Monographiae Ciliophorae

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Editors/authors
Wilhelm Foissner†, University of Salzburg, Hellbrunnerstrasse 34, 5020 Salzburg, Austria; https:// www.wfoissner.at, https://orcid.org/0000-0003-4528-0176
Kuidong Xu, Laboratory of Marine Organism Taxonomy and Phylogeny, Qingdao Key Laboratory of Marine Biodiversity and Conservation, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China; https://orcid.org/0000-0002-5186-519X, kxu@qdio.ac.cn
Helmut Berger, Consulting Engineering Office for Ecology, Radetzkystrasse 10, 5020 Salzburg, Austria; https://www.protozoology.com, https://orcid.org/0000-0002-1726-0082, berger.helmut@protozoology.com

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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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Chapter 13

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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

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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 4

Apospathidium Foissner et al., 2002 (Ciliophora, Spathidiidae), a genus whose species have oralized somatic kineties[1]

W. Foissner[a], K. Xu[b] & H. Berger[c]

[a] Wilhelm Foissner†, University of Salzburg, Hellbrunnerstrasse 34, 5020 Salzburg, Austria
[b] Kuidong Xu, Laboratory of Marine Organism Taxonomy and Phylogeny, Qingdao Key Laboratory of Marine Biodiversity and Conservation, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071 and University of Chinese Academy of Sciences, Beijing 100049, China
[c] Helmut Berger, Consulting Engineering Office for Ecology, Radetzkystrasse 10, 5020 Salzburg, Austria

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Abstract

Species assigned to *Apospathidium* Foissner, Agatha & Berger, 2002 look like *Spathidium* species. However, they differ from other spathidiids by so-called oralized somatic kineties, a characteristic so far known mainly from the Enchelyina. At present, *Apospathidium terricola* Foissner, Agatha & Berger, 2002 (type species) and *Apospathidium longicaudatum* (Buitkamp, 1977) nov. comb. are assigned to this genus. They differ in body shape and the number of somatic kineties and dorsal brush rows.

Apospathidium Foissner, Agatha & Berger, 2002

2002 ***Apospathidium* nov. gen.** – Foissner, Agatha & Berger, Denisia 5: 334 (original description). Type species (by original designation): *Apospathidium terricola* Foissner, Agatha & Berger, 2002.
2007 ***Apospathidium* Foissner, Agatha et Berger, 2002** – Jankowski, Phylum Ciliophora, p. 564 (generic revision of ciliates).

Nomenclature: According to Foissner et al. (2002), the genus-group name *Apospathidium* is a composite of the Greek prefix *apo-* (derived from; according to Brown 1954, p. 96, the prefix *apo-* means: from, off, away, after, without, separate) and the Greek genus-group name *Spathidium* (spatulate animal; see also nomenclature at genus *Spathidium*, Chapter 2, that

[1] This chapter should be referenced as follows: Foissner W., Xu K. & Berger H. (2025): *Apospathidium* Foissner et al., 2002 (Ciliophora, Spathidiidae), a genus whose species have oralized somatic kineties. – Ser. Monogr. Cilioph. 6: 111–126.
For notes on "Material and methods", see Chapter 1 (Berger et al. 2025a).

is, Berger et al. 2025c), referring to the presumed nearest relative. Neuter gender (see Aescht 2001, p. 300).

Diagnosis (from Foissner et al 2002, slightly modified): Amphoriform Spathidiidae (?) with oblique oral bulge. Oral basket rods (nematodesmata) originate from circumoral kinety and oralized somatic monokinetids in anterior region of ciliary rows.

Species originally assigned: *Apospathidium terricola* Foissner, Agatha & Berger, 2002 (type species); *Apospathidium atypicum* (Buitkamp & Wilbert, 1974) Foissner, Agatha & Berger, 2002 (now *Apospathidium longicaudatum* (Buitkamp, 1977) nov. comb.).

Species now assigned: *Apospathidium terricola* Foissner, Agatha & Berger, 2002 (type species); *Apospathidium longicaudatum* (Buitkamp, 1977) nov. comb.

Remarks: These ciliates look like ordinary *Spathidium* species. However, protargol impregnation reveals a unique feature as yet known mainly from the Enchelyina Foissner & Foissner, 1988, viz., oralized somatic monokinetids (Fig. 4.1h, 4.2r). Thus, we cannot exclude that the spathidiid features evolved convergently and *Apospathidium* belongs to the Enchelyina. However, the general appearance and some specific features, such as the location and structure of the oral kinetofragments, are so near to *Spathidium* that an enchelyine relationship of *Apospathidium terricola* and *Apospathidium longicaudatum* is unlikely.

At present, two *Apospathidium* species are known. Likely, only few species are undiscovered because we do not have any in our material. One species, which looks quite similar to *Apospathidium longicaudatum*, is an ordinary, new *Spathidium*, viz., *Spathidium apospathidiforme* nov. spec. (see Chapter 3, that is, Foissner et al. 2025a).

Key to species

1 Body narrowly amphoriform (length:width ratio in vivo 4:1) with an average of 11 ciliary rows, of which 4 are differentiated to a dorsal brush ..... *Apospathidium terricola* (p. 112)

– Body very narrowly amphoriform (length:width ratio in vivo 9:1) with an average of 9 ciliary rows, of which 3 are differentiated to a dorsal brush ..... *Apospathidium longicaudatum* (p. 117)

Apospathidium terricola Foissner, Agatha & Berger, 2002

(Fig. 4.1a–j, Table 4.1; Fig. 11.3a–c in Foissner et al. 2025b)

2002 ***Apospathidium terricola* nov. spec.** – Foissner, Agatha & Berger, Denisia 5: 334, Fig. 76a–j, 330a–c, Table 62 (Fig. 4.1a–j and Fig. 11.3a–c in Foissner et al. 2025b; original description. The slide containing the holotype [Fig. 4.1b, c, i, j; accession number 2002/478, see Aescht 2008, p. 180] and two paratype slides [2002/481, 2002/482] have been deposited in the Biology Centre of the Upper Austrian Museum in Linz [LI]. Two voucher slides [2002/479, 480] of the second population from Namibia [from site 5, see occurrence and ecology] have been deposited in the same collection, see Foissner et al. 2002, p. 37).

2007 ***Apospathidium terricola* Foissner, Agatha et Berger, 2002** – Vdačný & Tirjaková, Biologia, Bratislava 62: 728, Fig. 5A–M, Table 3 (detailed description of a population from Slovakia; see nomenclature).

Nomenclature: The species-group name *terricola* (Latin; living in soil) refers to the habitat the species was discovered (Foissner et al. 2002). Vdačný & Tirjaková (2007) did not

continued on p.114

Table 4.1 Morphometric data on *Apospathidium terricola* (upper line, type population, from Foissner et al. 2002; middle line, population from Slovakia, from Vdačný & Tirjaková 2007), and *Apospathidium longicaudatum* (lower line, from Foissner et al. 2002)[a]

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Body, length	131.6	132.5	11.4	4.0	8.6	115.0	150.0	8
	84.3	79.7	19.6	6.5	23.2	53.1	117.7	9
	113.3	110.0	15.5	3.6	13.9	82.0	152.0	19
Body, width	33.3	32.0	8.1	3.1	24.7	24.0	47.0	8
	19.2	18.8	4.1	1.4	21.4	12.5	23.4	9
	18.0	17.0	3.5	0.8	19.3	13.0	28.0	19
Body length:width, ratio	4.2	3.8	1.0	0.7	24.4	2.8	5.6	7
	4.6	4.3	1.6	0.5	34.5	2.3	8.2	9
	6.3	6.3	1.1	0.3	16.9	4.3	8.4	19
Oral bulge, length	17.6	17.0	2.8	1.1	16.0	15.0	22.0	7
	8.8	9.4	2.1	0.7	24.3	5.5	11.3	9
	13.5	14.0	1.9	0.4	14.0	9.0	16.0	19
Oral bulge, height	3.6	4.0	–	–	–	3.0	4.0	7
	2.5	2.3	1.0	0.3	39.9	1.3	4.7	9
	2.4	2.0	–	–	–	2.0	3.0	19
Anterior body end to macronucleus,	39.8	47.0	15.0	5.3	37.6	19.0	53.0	8
distance	33.7	37.5	8.6	2.9	25.5	18.0	43.4	9
	46.1	45.0	6.0	1.4	13.0	34.0	56.0	19
Macronucleus, length (extended	47.1	45.0	–	–	–	35.0	85.0	8
when curved; values thus approximate)	23.9	21.4	8.0	33.3	2.7	15.3	39.1	9
	30.9	30.0	–	–	–	18.0	40.0	19
Macronucleus, width	6.8	7.0	0.7	0.3	10.4	6.0	8.0	8
	5.6	5.2	0.9	0.3	16.1	4.5	7.2	9
	4.8	5.0	0.5	0.1	10.4	4.0	6.0	19
Micronucleus, length[b]	5.1	5.0	–	–	–	5.0	6.0	8
	3.3	3.3	0.6	0.2	18.7	2.7	4.7	9
	2.9	3.0	–	–	–	2.0	4.5	19
Micronucleus, width	4.6	5.0	–	–	–	3.5	5.0	8
	–	–	–	–	–	–	–	–
	2.7	3.0	–	–	–	2.0	4.0	19
Circumoral kinety to end of	7.4	7.0	2.5	1.1	33.9	5.0	10.0	5
brush row 1, distance	4.7	4.7	1.6	0.7	33.4	3.1	6.3	5
	6.0	6.0	1.4	0.3	22.8	4.0	9.0	19
Circumoral kinety to end of	10.8	9.0	5.2	2.6	48.0	7.0	18.0	4
brush row 2, distance	6.6	4.7	3.4	1.5	51.6	3.1	10.9	5
	11.1	11.0	1.5	0.3	13.3	8.0	13.0	19
Circumoral kinety to end of	11.4	11.0	3.0	1.3	26.0	7.0	15.0	5
brush row 3, distance	4.2	3.1	2.9	1.3	69.5	2.3	9.4	5
	4.2	4.0	0.6	0.1	14.5	3.0	5.0	19
Circumoral kinety to end of	5.5	5.0	1.7	0.9	31.5	4.0	8.0	4
brush row 4, distance	3.7	3.6	0.8	0.4	21.5	3.0	4.7	4
	–	–	–	–	–	–	–	–
Somatic kineties, number	11.3	11.0	1.3	0.5	11.1	10.0	13.0	7
	10.4	10.0	1.0	0.3	9.7	9.0	12.0	9
	9.4	9.0	1.2	0.3	12.9	8.0	13.0	19

Table 4.1 Continued

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Ciliated kinetids in a lateral kinety, number	64.3	55.0	17.2	6.5	26.8	48.0	95.0	7
	38.9	38.0	6.8	2.3	17.4	30.0	49.0	9
	45.1	45.0	6.5	1.5	14.5	35.0	60.0	19
Dorsal brush rows, number[c]	3.9	4.0	–	–	–	3.0	4.0	8
	3.9	4.0	0.3	0.1	8.6	3.0	4.0	9
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
Dikinetids in brush row 1, number	7.4	8.0	3.3	1.5	44.4	4.0	11.0	5
	–	–	–	–	–	–	–	–
	6.4	6.0	1.5	0.3	22.9	4.0	9.0	19
Dikinetids in brush row 2, number	11.3	9.0	7.1	3.5	62.7	6.0	21.0	4
	–	–	–	–	–	–	–	–
	12.1	12.0	2.2	0.5	17.8	8.0	16.0	19
Dikinetids in brush row 3, number	11.8	13.0	2.9	1.3	25,0	7.0	14.0	5
	–	–	–	–	–	–	–	–
	4.5	4.0	0.7	0.2	15.6	3.0	6.0	19
Dikinetids in brush row 4, number	4.8	4.5	2.5	1.3	52.1	2.0	8.0	4
	–	–	–	–	–	–	–	–
	–	–	–	–	–	–	–	–

[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] For the Slovakian population of *Apospathidium terricola*, the diameter is given.

[c] Three-rowed in 1 out of 8 specimens in type population of *Apospathidium terricola*.

mention the repository where the voucher slides are deposited. Probably they are, like the type slides of the new subspecies described in this work, deposited in the Department of Zoology, Faculty of Natural Sciences, Comenius University in Bratislava, Slovak Republic (Vdačný & Tirjaková 2007, p. 720).

Diagnosis (from Foissner et al. 2002, slightly modified): Body size about 150 × 35 µm in vivo. Body narrowly amphoriform with short tail and oblique oral bulge about two thirds as long as widest trunk region. Macronucleus cylindroidal. Single micronucleus about 5 µm across. Contractile vacuole distinctly subterminal. Oral bulge and body extrusomes rod-shaped, about 5 µm long, the latter in 2 or 3 rows between each two kineties. On average 11 ciliary rows, four of them anteriorly differentiated to an inconspicuous heterostichad dorsal brush occupying about 10% of body length.

Remarks: *Apospathidium terricola* has, like the single congener, *Apospathidium longicaudatum*, a highly characteristic amphoriform body and thus cannot be confused with any other member of the family, except of *Spathidium apospathidiforme* nov. spec. (see Chapter 3, that is, Foissner et al. 2025a), which is much larger (150 µm vs. 290 µm) and lacks body extrusomes. Both *Apospathidium* species are easily distinguished in vivo and protargol preparations by the length:width ratio (in vivo near 4:1 vs. 9:1), the number of extrusome rows

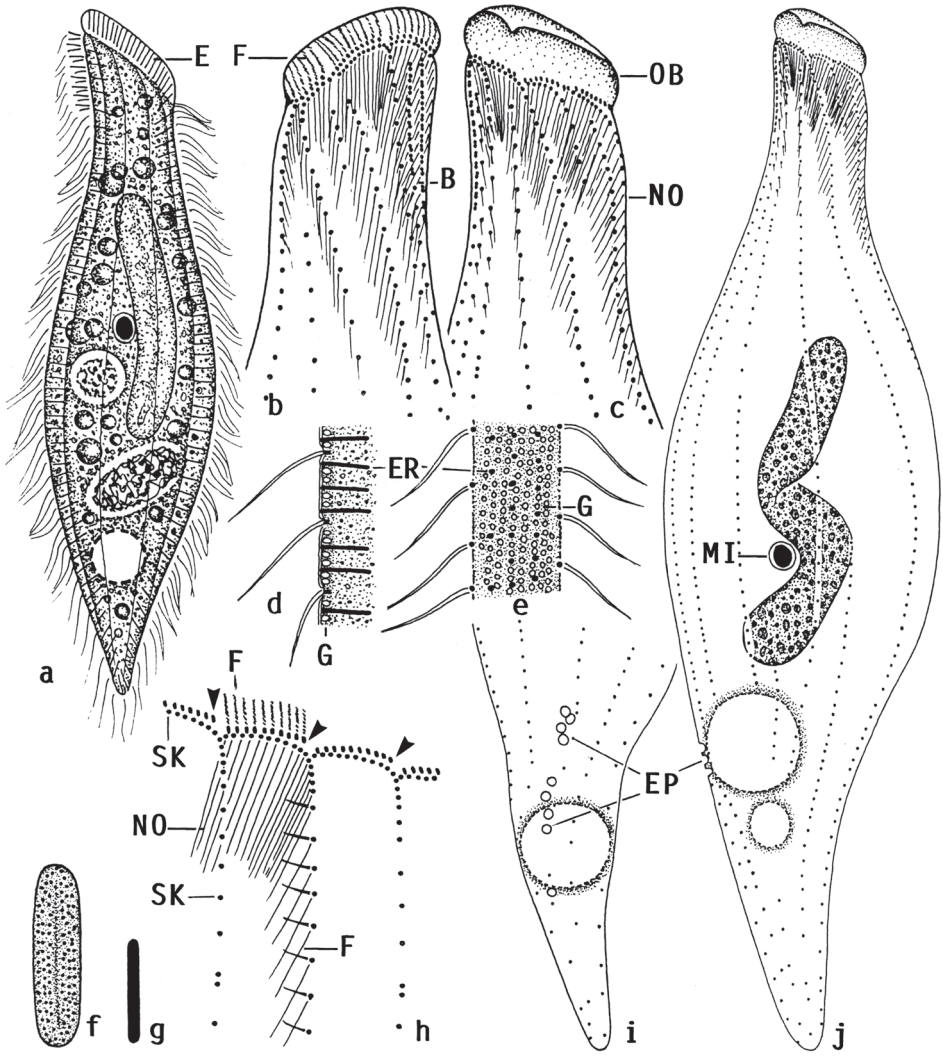

Fig. 4.1a–j *Apospathidium terricola* Foissner et al., 2002 (from Foissner et al. 2002. a, d–g, from life; b, c, h–j, protargol preparation). **a:** Right side view of representative specimen, 145 µm. Note the subterminal contractile vacuole and the fine body extrusomes anchored to the pellicle. **b, c, h–j:** Infraciliature of left (b) and right (c, h, j) side and nuclear apparatus of holotype specimen (b, c, j), and posterior dorsolateral portion (i) of an individual from another site. Details of the oral infraciliature are shown in figure (h): arrowheads mark stepped dikinetidal oral kinetofragments attached to the somatic kineties, which have oralized (with nematodesmata) monokinetids in the anterior region. **d, e:** Optical section and surface view showing rows of body extrusomes and cortical granules. **f:** Frontal view of oral bulge packed with extrusomes. **g:** Oral bulge and body extrusome, about 5.0 × 0.5 µm. B – dorsal brush, E – oral extrusomes, EP – excretory pores, ER – rows of body extrusomes, F – fibres, G – cortical granules, MI – micronucleus, NO – nematodesmata originating from somatic monokinetids, OB – oral bulge, SK – somatic kinety (ciliary row).

between the kineties (several vs. one), the number of ciliary rows (11 vs. 9), and the number of dorsal brush rows (4 vs. 3).

Description of Namibian specimens (type population; from Foissner et al. 2002): The species was rare at two sites, and only one specimen from type locality was observed in vivo, but two of the five specimens contained in the protargol slides were excellently impregnated. Morphometry was supplemented with three specimens from the second site. Altogether, data were sufficient for a reliable description, but should be refined from a more abundant population.

Body size 130–170 × 25–50 μm in vivo, usually near 150 × 35 μm, length:width ratio 2.8–5.6:1, on average near 4:1 both in vivo and in protargol preparations, where specimens are slightly inflated in mid-body. Body narrowly amphoriform with oblique oral bulge about two thirds as long as widest trunk region, and with narrowed neck and bluntly pointed posterior end (Fig. 4.1a, j; Table 4.1); flattened laterally, acontractile. Macronucleus in middle third of cell, cylindrical and more or less distinctly tortuous, circa 50 × 7 μm; nucleoli globular or lobate. Micronucleus attached to mid-region of macronucleus, about 5 μm across and surrounded by a distinct membrane. Contractile vacuole and circa 10 dorsolateral excretory pores in rather long row far subterminal (Fig. 4.1a, i, j). Extrusomes of oral bulge and body rod-shaped, circa 5 μm long, form several indistinct rows in oral bulge and between each two somatic kineties; posterior half usually impregnates with protargol (Fig. 4.1a, d, e–g). Cortex flexible, contains closely spaced rows of about 1 μm-sized granules, between which the strongly refractive extrusomes appear as bright dots (Fig. 4.1d, e). Cytoplasm colourless, contains many lipid droplets up to 10 μm across and large food vacuoles with remnants of protozoa. Glides rather rapidly on microscope slide.

Cilia arranged in an average of 11 widely spaced, bipolar, ordinarily ciliated rows distinctly curved at base of oral bulge, where conspicuous dikinetidal kinetofragments form a stepped circumoral kinety. Dorsal brush four-rowed (three-rowed in one out of eight specimens) and heterostichad, inconspicuous because occupying only 10% of body length and bristles merely up to 4 μm long; all rows continue as somatic kineties posteriorly; row 1 composed of an average of eight dikinetids, row 2 of nine, row 3 of 13, and row 4 of four (Fig. 4.1a–c, j; Fig. 11.3a–c in Chapter 11, that is, Foissner et al. 2025b; Table 4.1).

Oral bulge about two thirds as long as widest trunk region and about 5 μm high in vivo, obliquely truncate and slightly convex, elliptical in frontal view; contains faintly impregnated fibres originating from anterior basal bodies of circumoral kinety and extend obliquely to the slightly acentric pharyngeal entrance. Circumoral kinety elliptical, composed of conspicuous, dikinetidal kinetofragments attached to the somatic kineties; individual fragments composed of 7–14 dikinetids, showing the different (angular) orientation of the basal bodies very clearly (Fig. 4.1h); fragments stepped because slightly curved and distance between basal bodies of individual dikinetids becomes gradually wider from distal to proximal, a curious feature shown in Fig. 4.1h. Oral basket inconspicuous because not sharply defined and basket rods (nematodesmata) do not form bundles. Nematodesmata originate from circumoral kinetofragments (possibly even from both bodies of a pair) and up to 20 oralized somatic monokinetids in anterior region of ciliary rows (Fig. 4.1a–c, h, j; Fig. 11.3a–c in Chapter 11, that is, Foissner et al. 2025b; Table 4.1).

Notes on population described by Vdačný & Tirjaková (2007): The specimens of the population from Slovakia basically correspond with the Namibian individuals. However, the European specimens are considerably smaller in vivo (70–130 × 20–40 μm vs. 130–170 ×

25–50 µm) and in protargol preparations (on average 84.3 × 19.2 µm vs. 131.6 × 33.3 µm) (Vdačný & Tirjaková 2007, p. 728). For that reason, the macronucleus and the dorsal brush rows are shorter and composed of fewer dikinetids. For detailed description and illustrations, see Vdačný & Tirjaková (2007). For morphometric characterization, see Table 4.1. The Slovakian population has, like the type population, invariably one macronucleus (n = 9) and one micronucleus (n = 9).

Occurrence and ecology: *Apospathidium terricola* is a terrestrial species so far only recorded from Namibia and Slovakia. The type locality is mud and soil from granitic, dry rock-pools on the Spitzkoppe (21°45'S 15°08'E), an Inselberg in the Namib Escarpment, Namibia (for details on this locality, see sample site 41 in Foissner et al. 2002, p. 23). Foissner et al. (2002, p. 336) recorded it also in circumneutral soil from an *Aloe dichotoma* forest in the dwarf shrub savannah at the Gariganus Guest Farm, about 30 km northeast of the town of Keetmanshoop, Namibia (Foissner et al. 2002, p. 16, site 5). The rock-pool habitat indicates that this species might occur also in limnetic biotopes. Vdačný & Tirjaková (2007) found it in sandy soil mixed with roots and small twigs with pH 6.0 in Borievka (48°10'N 19°54'E), Cerová vrchovina highlands, Slovakia.

Apospathidium longicaudatum (Buitkamp, 1977) nov. comb.

(Fig. 4.2a–r, 4.3a–h, Table 4.1)

1974 ***Spathidium atypicum* n. sp.** – Buitkamp & Wilbert, Acta Protozool. 13: 202, Abb. 2 (Fig. 4.2a; original description; for type material from Canada and primary homonymy, see nomenclature).

1977 ***Spathidium longicaudatum* n. nom.** – Buitkamp, Decheniana 130: 117 (replacement name because of preoccupation, see nomenclature).

1981 ***Spathidium longicaudatum* Buitkamp und Wilbert, 1974; Buitkamp 1977** – Foissner, Zool. Jb. Syst. 108: 275, Abb. 6a–f (Fig. 4.2b–f; description of Austrian population; site where voucher material is deposited not mentioned, see nomenclature; authorship incorrect).

2002 ***Apospathidium atypicum* (Buitkamp & Wilbert, 1974) nov. comb.** – Foissner, Agatha & Berger, Denisia 5: 338, Fig. 77a–j, Table 62 (Fig. 4.2h–r; description of population from Kenya; five voucher slides [accession numbers 2002/518, 2002/519, 2002/520, 2002/521, 2002/522; see Foissner et al. 2002, p. 37] with protargol-prepared specimens have been deposited in the Biology Centre of the Upper Austrian Museum in Linz [LI]).

Nomenclature: No derivation of the names has been provided in the original description or later works. The species-group name *atypic·us*, *-a*, *-um* (Greek adjective [m, f, n]) is a composite of the Greek prefix *a-* (general meaning: negation; Werner 1972, p. 58) and the Greek adjective *typic·us*, *-a*, *-um* (typical, archetypical, normal, genuine; Hentschel & Wagner 1996, p. 597), referring to the atypical (slender amphoriforme, slender spindle-shaped) body shape. Note that the shape is not "atypical" for an *Apospathidium*, but only for *Spathidium*, the genus to which the species was originally allocated. The species-group name *longicaudat·us*, *-a*, *-um* is a composite of *longus* (Latin; long; Hentschel & Wagner 1996, p. 370) and *caudat·us*, *-a*, *-um* (Latin adjective [m, f, n]; tailed, having a tail; Hentschel & Wagner 1996, p. 157), obviously referring to the long, tailed posterior body portion of this species.

Spathidium atypicum Buitkamp & Wilbert, 1974 is a primary junior homonym (ICZN 1999, Article 53.3; but not a junior synonym!) of *Spathidium atypicum* Wenzel, 1953 (p. 81; now *Neocultellothrix atypica* (Wenzel, 1953) Foissner & Xu in Berger et al., 2025b; for

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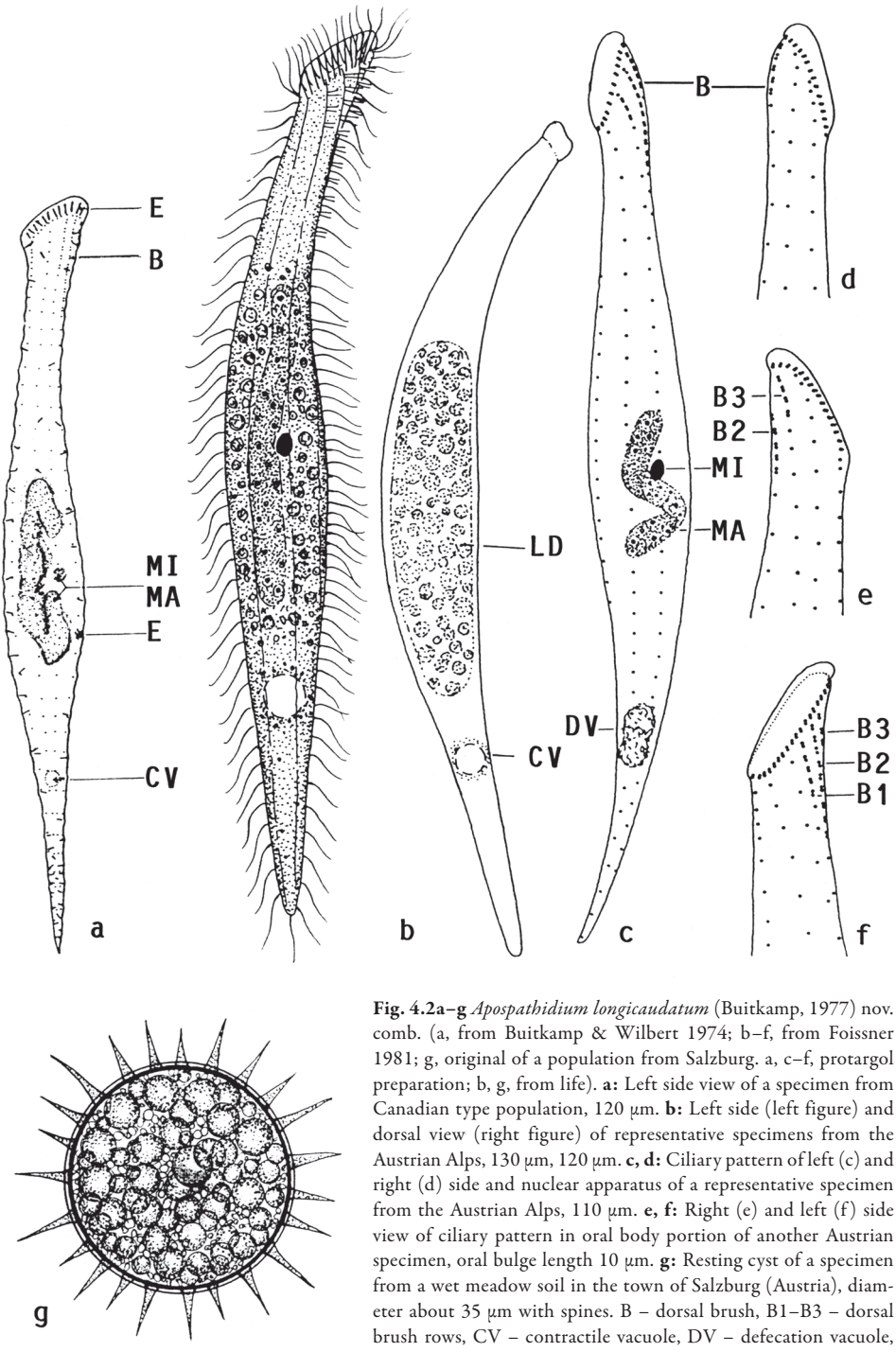

Fig. 4.2a–g *Apospathidium longicaudatum* (Buitkamp, 1977) nov. comb. (a, from Buitkamp & Wilbert 1974; b–f, from Foissner 1981; g, original of a population from Salzburg. a, c–f, protargol preparation; b, g, from life). **a:** Left side view of a specimen from Canadian type population, 120 µm. **b:** Left side (left figure) and dorsal view (right figure) of representative specimens from the Austrian Alps, 130 µm, 120 µm. **c, d:** Ciliary pattern of left (c) and right (d) side and nuclear apparatus of a representative specimen from the Austrian Alps, 110 µm. **e, f:** Right (e) and left (f) side view of ciliary pattern in oral body portion of another Austrian specimen, oral bulge length 10 µm. **g:** Resting cyst of a specimen from a wet meadow soil in the town of Salzburg (Austria), diameter about 35 µm with spines. B – dorsal brush, B1–B3 – dorsal brush rows, CV – contractile vacuole, DV – defecation vacuole, E – oral bulge and body extrusomes, LD – lipid droplets, MA – macronucleus, MI – micronucleus.

details, see Berger et al. 2025b). According to ICZN (1999, Article 57.2), junior primary homonyms are permanently invalid. For that reason, Buitkamp (1977a) introduced the replacement name (substitute name, new name) "*Spathidium longicaudatum* n. nom." (see ICZN 1999, Article 60.3). Article 23.9.5 of the ICZN (1999) does not apply, because it obviously refers to taxa described before 1899. In addition, the taxa have been considered congeneric after 1899. Foissner et al. (2002, p. 338) referred to ICZN (1999, Article 59) which is, however, only valid for secondary homonyms. Thus, the correct names of the present species are, at present, *Spathidium longicaudatum* Buitkamp, 1977 (original combination) and *Apospathidium longicaudatum* (Buitkamp, 1977) nov. comb. The new combination in *Apospathidium* is necessary because *Spathidium longicaudatum* Buitkamp, 1977 was never transferred to this genus. In the name "*Spathidium longicaudatum* Buitkamp & Wilbert" (including variants) mentioned by Foissner et al. (1985, p. 109), Blatterer & Foissner (1988, p. 9), and Tirjaková (1988, p. 500), the authorship is incorrect (see heading above).

According to Foissner et al. (2002, p. 338), the type slides (= protargol preparations made by Buitkamp & Wilbert 1974) are completely bleached. They refrained from a neotypification because their material is from a different biogeographic region (Kenya vs. Canada) and the validity of the species not threatened at present. Thus, neotypification can await redescription of a Canadian or, at least, North American population. Voucher slides of the Kenyan specimens have been deposited by Foissner et al. (2002; see list of synonyms).

Improved diagnosis (from Foissner et al. 2002 [including data from Buitkamp & Wilbert 1974], slightly modified): Body size about 125 × 15 μm in vivo. Body very narrowly amphoriform with fairly distinct tail and oblique oral bulge about two thirds as long as widest trunk region. Macronucleus cylindrical. Single micronucleus approximately 4 μm across. Contractile vacuole subterminal (about 22% in front of rear body end). Oral and body extrusomes rod-shaped, 3–4 μm long, the latter likely in one row between each two kineties. On average nine ciliary rows, three of them anteriorly differentiated to inconspicuous, distinctly heterostichad dorsal brush occupying about 10% of body length.

Remarks: The observations of Foissner et al. (2002) basically match the description by Buitkamp & Wilbert (1974) and the redescription by Foissner (1981), except of the oral basket, whose special structure was not recognized by Buitkamp & Wilbert (1974) and Foissner (1981). The Austrian specimens supposedly lack body extrusomes and have an elliptical circumoral kinety. However, the data by Foissner (1981) are not very detailed, and thus the differences might have been caused by incomplete observations. This is supported by recent observations on specimens from Salzburg (Austria): they have body extrusomes like all other populations.

Apospathidium longicaudatum differs from *Apospathidium terricola* by the cuneate (vs. elliptical) oral bulge, the number of ciliary (8 or 9 vs. 11) and dorsal brush rows (3 vs. 4), and most morphometrics (Table 4.1). Basically, *Apospathidium terricola* is more massive than *Apospathidium longicaudatum*, which makes them easily distinguishable even in vivo. *Spathidium apospathidiforme* nov. spec. (see Chapter 3, that is, Foissner et al. 2025a) differs from *Apospathidium longicaudatum*, inter alia, by body size (290 × 23 μm vs. 125 × 15 μm), number of ciliary rows (15 vs. 9), and the lack of body extrusomes.

Description: The text below is a compilation of all descriptions available (Buitkamp & Wilbert 1974, Foissner 1981, Foissner et al. 2002) and some original data.

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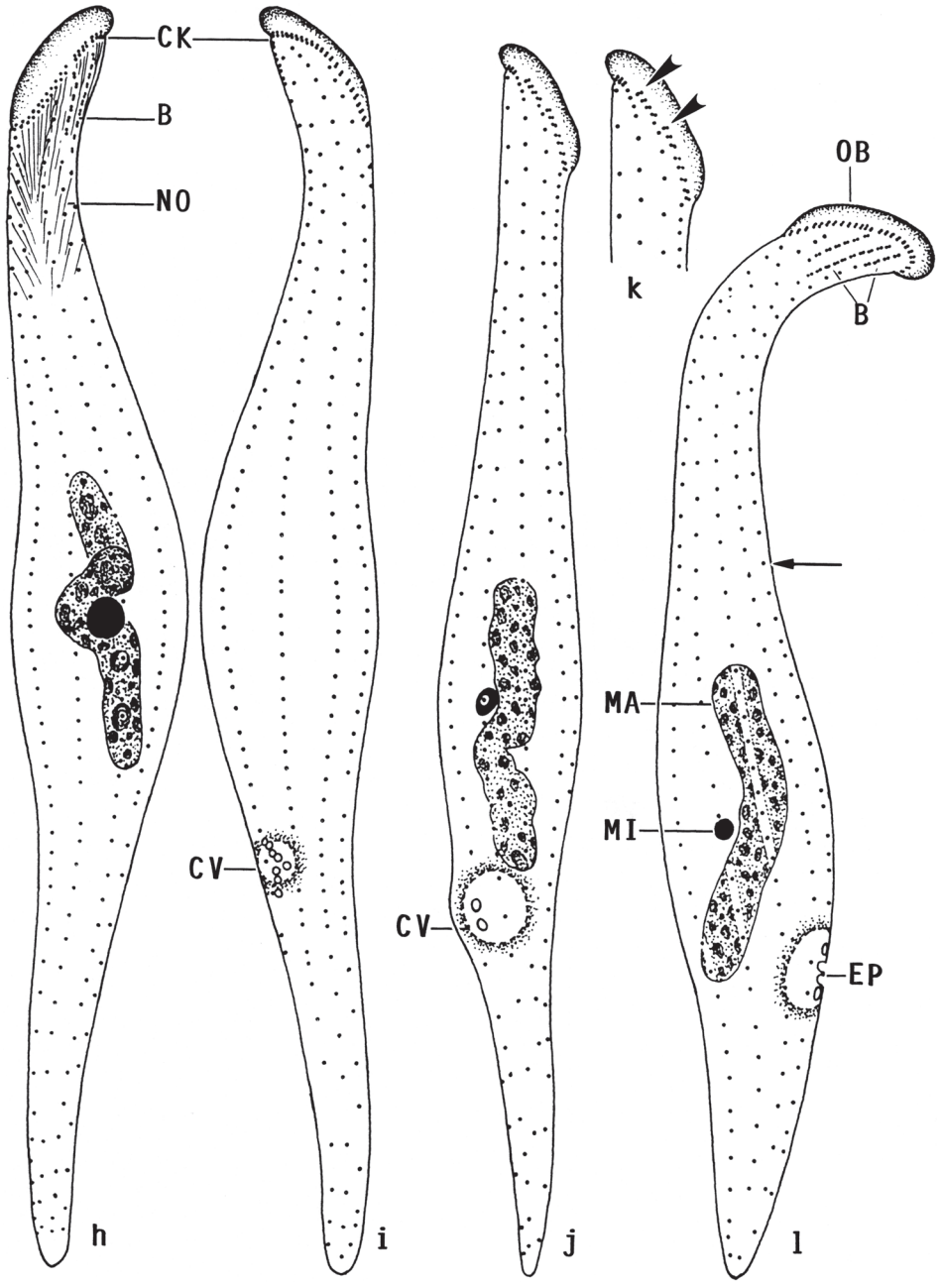

Fig. 4.2h–l *Apospathidium longicaudatum* (Buitkamp, 1977) nov. comb. (from Foissner et al. 2002. Protargol preparation). Ciliary pattern of Kenyan specimens after protargol preparation. **h, i:** Left and right side view of a representative specimen, 120 µm. **j, k:** Right side view of a specimen with separated oral kinetofragments (arrowheads), 120 µm. **l:** Dorsolateral view of another specimen, shown at higher magnification in Fig. 4.2q, r, 105 µm. Arrow denotes end of bristle tail of brush row 3. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuole, EP – excretory pores, MA – macronucleus, MI – micronucleus, NO – oralized somatic nematodesmata, OB – oral bulge.

Body size 80–170 × 10–30 µm in vivo, usually near 120 × 15 µm, length:width ratio often about 9:1 in vivo, while near 6:1 in protargol preparations, where specimens tend to be inflated in mid-body (Table 4.1). Body very slenderly amphoriform with oblique anterior end/oral bulge about two thirds as long as widest trunk region, narrowed neck, and tail-like posterior third, in some specimens almost as long as body proper; flattened only in oral region, acontractile (Fig. 4.2a–d, h, j, l; Table 4.1). Nuclear apparatus in widened middle third of body. Macronucleus cylindroidal (up to 50 × 6 µm in vivo) and more or less tortuous; nucleoli numerous, small. Micronucleus near or attached to middle third of macronucleus, conspicuous because compact and circa 5 × 3 µm in size (Fig. 4.2a, b, d, h, j, l, 4.3c, g, h; Table 4.1). Contractile vacuole with up to 10 dorsolateral, scattered excretory pores, about 22% in front of rear body end in Kenyan population (mean = 24.4 µm, SD = 7.5 µm, CV = 30.8%, Min = 13 µm, Max = 40 µm, n = 19), that is, behind base of tail (Fig. 4.2a–d, i, j, l). Oral bulge and somatic extrusomes likely somewhat different because only the latter lightly impregnate with protargol (Fig. 4.2a, b, p, r). The following shapes and sizes were observed: rod-shaped, about 2 µm long in protargol preparations (Canadian type

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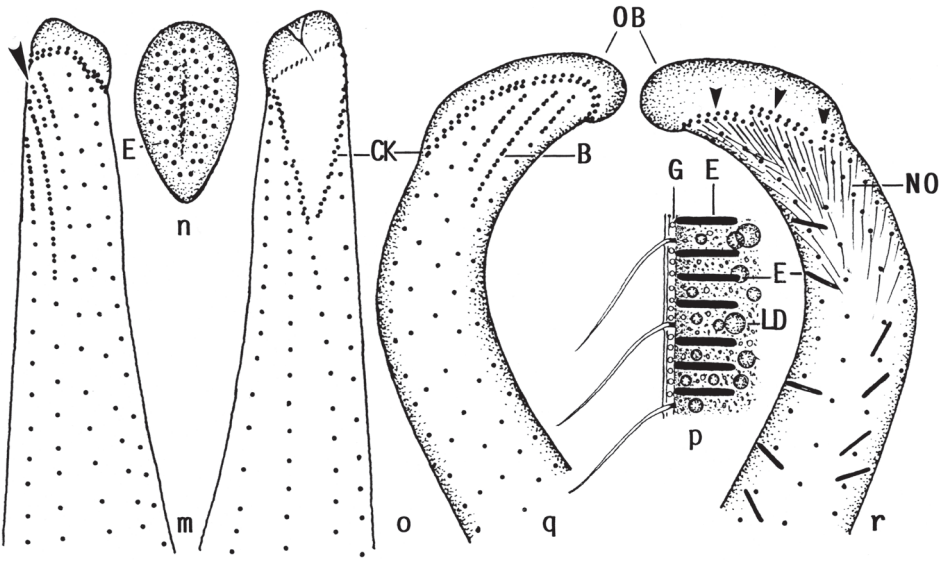

Fig. 4.2m–r *Apospathidium longicaudatum* (Buitkamp, 1977) nov. comb. (from Foissner et al. 2002, Kenyan specimens. m, o, q, r, protargol preparation; n, p, from life). **m, o:** Ciliary pattern of anterior dorsal and ventral side of same specimen showing the cuneate circumoral kinety and a short brush fragment (arrowhead in (o)) between rows 2 and 3; width at oral bulge 6 µm. **n:** The oral bulge is obovate, while the circumoral kinety is cuneate (o). **p:** Optical section of somatic cortex studded with 3.5 µm long extrusomes, a main feature of the species and genus. **q, r:** Details of the oral and somatic ciliary pattern of left (q) and right (r) side of the specimen shown in Fig. 4.2l, length of oral bulge 15 µm. Arrowheads mark incompletely aligned circumoral kinetofragments producing a protospathidiid pattern. The oral basket (r) is inconspicuous and fundamentally different from that of *Spathidium* because it is made of fine nematodesmata originating from the circumoral dikinetids **and** from the basal bodies in the anterior portion of the somatic ciliary rows (oralized somatic monokinetids). Note the short, inconspicuous dorsal brush and the extrusomes in the somatic cortex. B – dorsal brush, CK – circumoral kinety, E – extrusomes, G – cortical granules, LD – lipid droplets, NO – nematodesmata originating from oralized somatic monokinetids, OB – oral bulge.

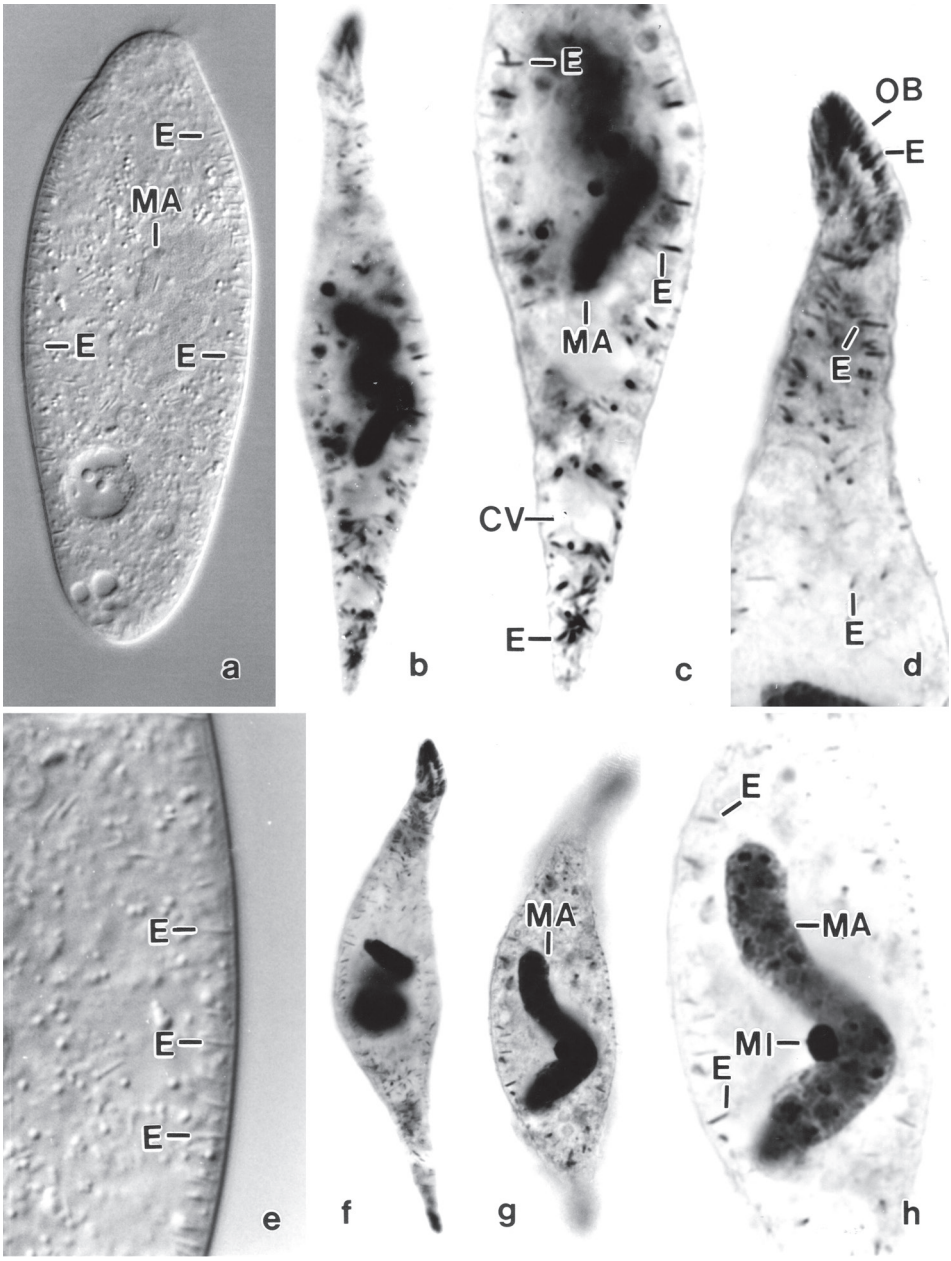

Fig. 4.3a–h *Apospathidium longicaudatum* (Buitkamp, 1977) nov. comb. (originals; a, e, specimens from Hawaii; b–d, f–h, Namibian site 16 specimens, see Foissner et al. 2002. a, e, from life; b–d, f–h, protargol preparation). **a, e:** A heavily squashed specimen showing the rod-shaped, about 3 µm long body extrusomes, which are difficult to recognize. **b–d, f–h:** Representative specimens showing the typical body shape, the short, tortuous macronucleus, the subterminal contractile vacuole, and the extrusomes. CV – contractile vacuole, E – extrusomes, MA – macronucleus, MI – micronucleus, OB – oral bulge.

population); rod-shaped, 2.8–3.5 × ~0.4 µm in vivo (Namibian site 1 specimens, Foissner et al. 2002); rod-shaped, oral extrusomes 4 µm long, body extrusomes about 2.5 × 0.2 µm in vivo (Namibian site 2; Fig. 4.3c, d, h); slightly fusiform and 3 µm long in vivo (Namibian sites 16, 17); rod-shaped and fine, about 4.0 × 0.2 µm in vivo (Venezuelan population; Foissner 2016; original observation); rod-shaped and about 3 µm long (specimens from Hawaii, Fig. 4.3a, e; original observation). Cortex very flexible, occasionally slightly ribbed by the extrusomes in preserved specimens, contains inconspicuous rows of minute, colourless granules. Cytoplasm colourless, contains many lipid droplets up to 5 µm across mainly in middle body portion. Feeds on ciliates and naked amoebae (Buitkamp & Wilbert 1974). Glides on and between soil particles showing great flexibility; swims rather rapidly, performing wide rotations with anterior body half.

Cilia about 8 µm long in vivo, arranged in an average of 8 or 9 ordinarily spaced, bipolar rows more densely ciliated anteriorly than posteriorly. Ciliary rows arranged in indistinct *Spathidium* pattern, that is, anteriorly curved dorsally on right side, while abutting on circumoral kinety in more or less steep angles on left side; right side rows, rarely also those of left side, usually attached to the individual circumoral kinetofragments. Dorsal brush three-rowed, inconspicuous because occupying only 10% of body length, and bristles merely 3–4 µm long anteriorly and 2 µm posteriorly; heterostichad, with row 3 distinctly shorter than rows 1 and 2, but with short monokinetidal tail of 1.5 µm long bristles (Fig. 4.2a, b, d–q; Table 4.1).

Oral bulge in vivo 10–20 µm long, that is, about two thirds as long as widest trunk region, 2–3 µm high, obliquely arranged and slightly convex, obovate in frontal view; circumoral kinety, in contrast, distinctly cuneate, a remarkable difference observed in several specimens (Fig. 4.2n, o). Kinetofragments of right half of circumoral kinety often incompletely aligned, producing the stepped (protospathidiid) pattern typical of the genus (Fig. 4.2j, k, q, r). Oral basket inconspicuous and thus neither recognized by Buitkamp & Wilbert (1974) nor by Foissner (1981), composed of fine nematodesmata originating from (i) circumoral kinety and (ii) up to 10 oralized somatic monokinetids in anterior region of ciliary rows (Fig. 4.2h, r).

Resting cyst: Of five specimens isolated from a soil sample collected in the town of Salzburg (Austria), three produced colourless resting cysts. Cysts of Type VIII according to Foissner & Xu (2007, p. 38), that is, conspicuous because studded with compact, flexible, 3–7 µm long, straight, rarely slightly curved spines; cysts 35–40 µm across including spines, diameter without spines about 27 µm (Fig. 4.2g). Cyst wall about 1 µm thick, composed of a thin outer membrane and a thick, compact inner layer associated with the spines. Cytoplasm studded with lipid droplets about 0.5–5.0 µm in diameter.

Occurrence and ecology: *Apospathidium longicaudatum* has been reported from all main biogeographic regions, except of Antarctica (Foissner 1998, p. 209; Foissner et al. 2002, p. 50). Interestingly, the species is sometimes rather frequent (20–36% of samples; Foissner et al. 1985, p. 109; Tirjaková 1988, p. 500), but never develops high abundances in the non-flooded Petri dish cultures. With its slender, flexible body, *Apospathidium longicaudatum* is perfectly adapted to terrestrial habitats and to exploit even narrow soil pores. There is also a limnetic record from a bog-pond in Slovakia which is, however, not substantiated by morphological data (Tirjaková 1992, p. 294).

The type locality of *Apospathidium longicaudatum* is a dry, very hard, loamy Prairie soil (natural grassland, Chernozemic brown soils; "Matador Project") collected in Southern Saskatchewan (50.70°N 107.72°W), Canada (Buitkamp & Wilbert 1974, p. 201). For details on the Matador project, see Ripley (1972). Further records from the Holarctic region: common in European soils, viz., in lowland and alpine pastures (Berthold 1994; Buitkamp 1977a, p. 116; Foissner 1981, p. 265); agricultural fields (Foissner et al. 1985, p. 109; Tirjaková 1988, p. 500); and lowland and ordinary forests with circumneutral pH (Foissner et al. 1985, p. 109).

The data from the resting cysts (Fig. 4.2g) are from a population from soil near of the so-called "Krautwächterhäusel" (47.792206N° 13.045734°E), a very old house in the city of Salzburg, Austria (collected likely by W. Foissner in 2004).[2]

Paleotropic records: soils from Kenya (Fig. 4.2h–r) and Namibia, where Foissner et al. (2002, p. 58a, b, 338) found *Apospathidium longicaudatum* in 6 out of 73 samples, mainly in dunes of the Namib Escarpment (pH 5.4–7.2).

Neotropic record: slightly saline soil and litter sample (pH 6.7) from the surroundings of the village of Choroni, Henry Pittier National Park, north coast of Venezuela (Foissner 2016, p. 25).

Australian records: pasture soil (pH 6.2) in the surroundings of Bushy Park, Tasmania, and *Eucalyptus* forest soil (pH 4.7) in the Belair National Park, Adelaide, southern Australia (Blatterer & Foissner 1988, p. 3, 9, sites 7 and 11). In addition, we found it in Hawaii (Fig. 4.3a, e).[3]

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[2] Note by H. Berger: For details on this very old house (built in 1380), see "https://ww.sn.at/wiki/Krautwächter häusel" and Foissner et al. (2012).

[3] Note by H. Berger: In the text of the raw manuscript the record from Hawaii shown in Fig. 4.3a, e was not mentioned. I did not find notes on the sample site. Perhaps the population was isolated from a Hawaii-sample studied by Xu & Foissner (2005, p. 6).

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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