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

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

Edited by

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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

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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 3

Characterisation of 15 species belonging to the genus *Spathidium* Dujardin, 1841 (Ciliophora, Spathidiidae), including three new[1]

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Abstract

The present chapter deals with the description of 15 species assigned to the renowned genus *Spathidium* Dujardin, 1841. Three species are new to science, namely *Spathidium elongatum* nov. spec., *Spathidium apospathidiforme* nov. spec., and *Spathidium saprophilum* nov. spec. Within *Spathidium saprophilum* nov. spec. we distinguish two subspecies: *Spathidium saprophilum saprophilum* nov. subspec. and *Saprophilum saprophilum curvioplites* nov. subspec. Most species reviewed in this chapter can be assigned to three more or less well-defined groups: *Spathidium elongatum* group (*Spathidium elongatum* nov. spec; *Spathidium apospathidiforme* nov. spec., *Spathidium duschli*; *Spathidium dispar*), *Spathidium bromelicola* group (*Spathidium bromelicola*; *Spathidium aciculare*; *Spathidium etoschense*; *Spathidium saprophilum* nov. spec.; *Spathidium rusticanum*), and *Spathidium wolfi* group (*Spathidium wolfi*, *Spathidium faurefremieti*, *Spathidium latissimum*, *Spathidium polyvacuolatum*). Further, *Spathidium anguilla* and *Spathidium polynucleatum* are revised. The type slides (holotype slide and three paratype slides) of *Spathidium wolfi* Foissner et al., 2014 have been finally deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI), as already announced in the original description.

[1] This chapter should be referenced as follows: Foissner W., Xu K. & Berger H. (2025): Characterisation of 15 species belonging to the genus *Spathidium* Dujardin, 1841 (Ciliophora, Spathidiidae), including three new. – Ser. Monogr. Cilioph. 6: 33–109.
For notes on "Material and methods", see Chapter 1 (Berger et al. 2025a).

Characterisation of 15 *Spathidium* species[2]

The present chapter deals with 17 *Spathidium* species (including two subspecies) assigned to three morphological groups. The raw manuscript prepared by W. Foissner contained a fourth group, namely, the *Spathidium procerum* group comprising four species.[3] However, he only finished the text of *Spathidium anquilla* Vuxanovici, 1962. This species is reviewed and redescribed after the third group (p. 91). In addition, *Spathidium polynucleatum* (Foissner et al., 2002) Jang et al., 2017 is reviewed, a species originally assigned to *Epispathidium* (Chapter 6, that is, Foissner et al. 2025a). Note that *Spathidium* is a very large genus, many species of which have to be studied in detail, including a molecular characterization. For a brief comment on *Spathidium* Dujardin, 1841, see Chapter 2 (Berger et al. 2025c).

The *Spathidium elongatum* group

The following four species form a fairly distinct group characterized by the strongly argyrophilic extrusome ends, providing protargol-impregnated specimens with a highly distinct appearance (e.g., Fig. 3.1b, c, u–y, 3.2d, g): *Spathidium elongatum* nov. spec., *Spathidium dispar* Foissner & Xu in Foissner, 2016, *Spathidium apospathidiforme* nov. spec., *Spathidium duschli* Foissner, 2016. Further, all are large and slender (200–300 × 20–35 µm in vivo); have short (as compared to body size), basically rod-shaped extrusomes; possess 15–30 ciliary rows arranged in pronounced *Spathidium* pattern, but with several specific features; have an oblong to cuneate oral bulge; and have an isostichad, relatively short (18–25% of body length) dorsal brush with tail of row 3 not extending to rear body end, except of *Spathidium apospathidiforme*.

Some of the characteristics separating these four species are subtle, but most are conspicuous showing that they are distinct taxa (Table 3.1).

The different macronucleus patterns and extrusome shapes show distinct radiation within the group. Thus, these four species likely represent a separate evolutionary line. However, formal recognition as a distinct genus or subgenus should await further data, especially gene sequence analyses.

The species of the *Spathidium elongatum* group are likely close relatives of *Spathidium procerum* Kahl, 1930a, differing mainly by the extrusomes (with vs. without argyrophilic ends)

[2] Note by H. Berger: The raw manuscript prepared by W. Foissner contained three files dealing with "*Spathidium* groups", namely the *Spathidium elongatum* group (p. 34); the *Spathidium bromelicola* group (p. 61); and the *Spathidium wolfi* group (p. 85). Some new species contained in the raw manuscript (e.g., "*Spathidium dispar* nov. spec."; this name is disclaimed for nomenclatural purposes in the present work, according to ICZN 1999, Article 8.3) have been described in other works by Foissner and co-workers, for example, *Spathidium dispar* Foissner & Xu in Foissner, 2016 (p. 217). In addition, Foissner has scheduled to transfer *Epispathidium polynucleatum* Foissner, Berger & Agatha, 2002 to *Spathidium*, a combination done in the meantime by Jang et al. (2017, p. 956, 971).

[3] W. Foissner provided the following short introduction to this group: "The four species bundled in this group are middle to large-sized (140–250 µm), slender (>8:1), have inconspicuous extrusomes and, especially, scattered macronucleus nodules. The last feature separates it from the *Spathidium elongatum* group, except of *Spathidium duschli* which, however, has more ciliary rows (about 20 vs. 11) and special extrusomes. Certainly, most polynucleate species look rather similar, especially when the considerable variability is taken into account (see *Spathidium turgitorum* Foissner et al., 2002), but at population level they can be reliably distinguished by the shape of the extrusomes and macronucleus, the dorsal brush, and various morphometrics."

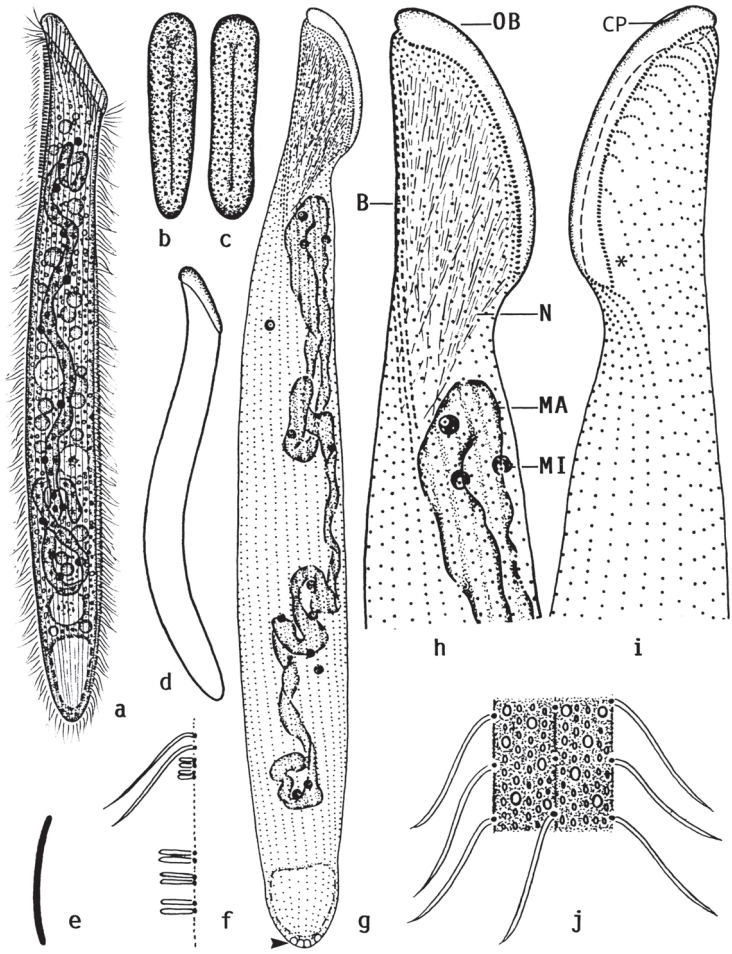

Fig. 3.1a–j *Spathidium elongatum* nov. spec. (originals. a–f, j, from life; g–i, protargol preparation). **a:** Right side view of a representative specimen, 300 μm. **b, c:** Frontal views of oral bulge studded with extrusomes. **d:** Swimming specimen. **e:** Oral bulge extrusome, about 8.0 × 0.5 μm. **f:** Anterior portion of a dorsal brush row. **g–i:** Right (g, h) and left (i) side view of ciliary pattern and nuclear apparatus of holotype specimen, 250 μm. Asterisk in (i) marks bare area between leftmost ventral and ventralmost left side kinety. Arrowhead in (g) marks excretory pores. Dashed line in (i) is the right side outline of the oral bulge. **j:** Surface view showing two size types of cortical granules, an important feature of this species. B – dorsal brush, CP – cytopharyngeal entrance, MA – macronucleus, MI – micronucleus, N – nematodesmata, OB – oral bulge.

and number of ciliary rows (15–30 vs. about 10); as concerns the latter feature, *Spathidium apospathidiforme* is in between *Spathidium procerum* and *Spathidium elongatum*. *Spathidium extensum* Kahl, 1933 (p. 59) and *Spathidium turgitorum* Foissner et al., 2002 (p. 234) are also highly similar to members of the *Spathidium elongatum* group, but lack the argyrophilic extrusome ends and have a *Protospathidium*-like ciliary pattern along the whole right side.

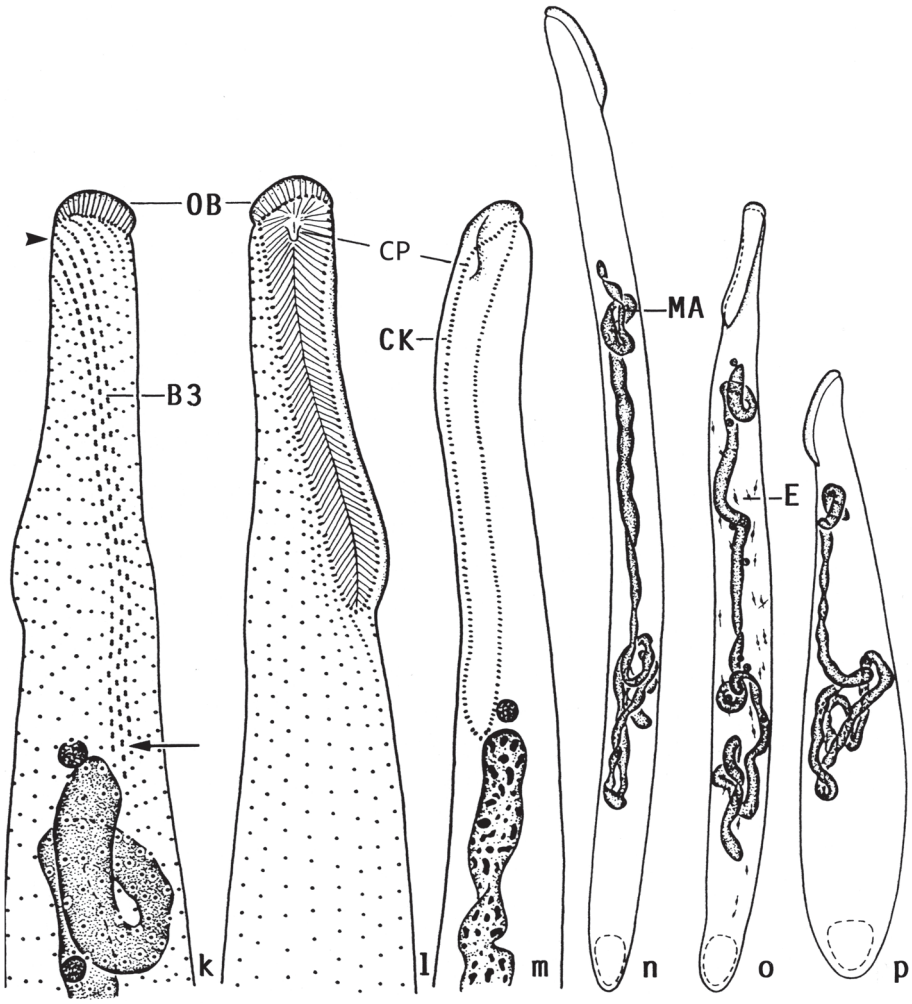

Fig. 3.1k–p *Spathidium elongatum* nov. spec. (originals. Protargol preparation). **k, l:** Dorsal and ventral view of ciliary pattern in anterior body portion, length of oral bulge 45 µm. Arrowhead in (k) marks ordinary cilia at anterior end of dorsal brush rows. Arrow denotes dorsal brush rows ending at almost same level. Fibres originate from the circumoral dikinetids and extend into the oral bulge, where they form an arrow-like pattern. **m:** Ventral view of a specimen with slightly dumbbell-shaped, 56 µm-long circumoral kinety. **n–p:** Size and shape variants of body and macronucleus, drawn to scale: 365 µm, 295 µm, 220 µm. B3 – dorsal brush row 3, CK – circumoral kinety, CP – cytopharyngeal entrance, E – developing extrusomes in cytoplasm, MA – macronucleus, OB – oral bulge.

Spathidium elongatum nov. spec.

(Fig. 3.1a–u, y, 3.2a–p, Tables 3.1, 3.2)

Nomenclature: The species-group name *elongat·us, -a, -um* (Latin adjective; elongate; Hentschel & Wagner 1996, p. 227) refers to the long, slender body shape.

continued on p. 38

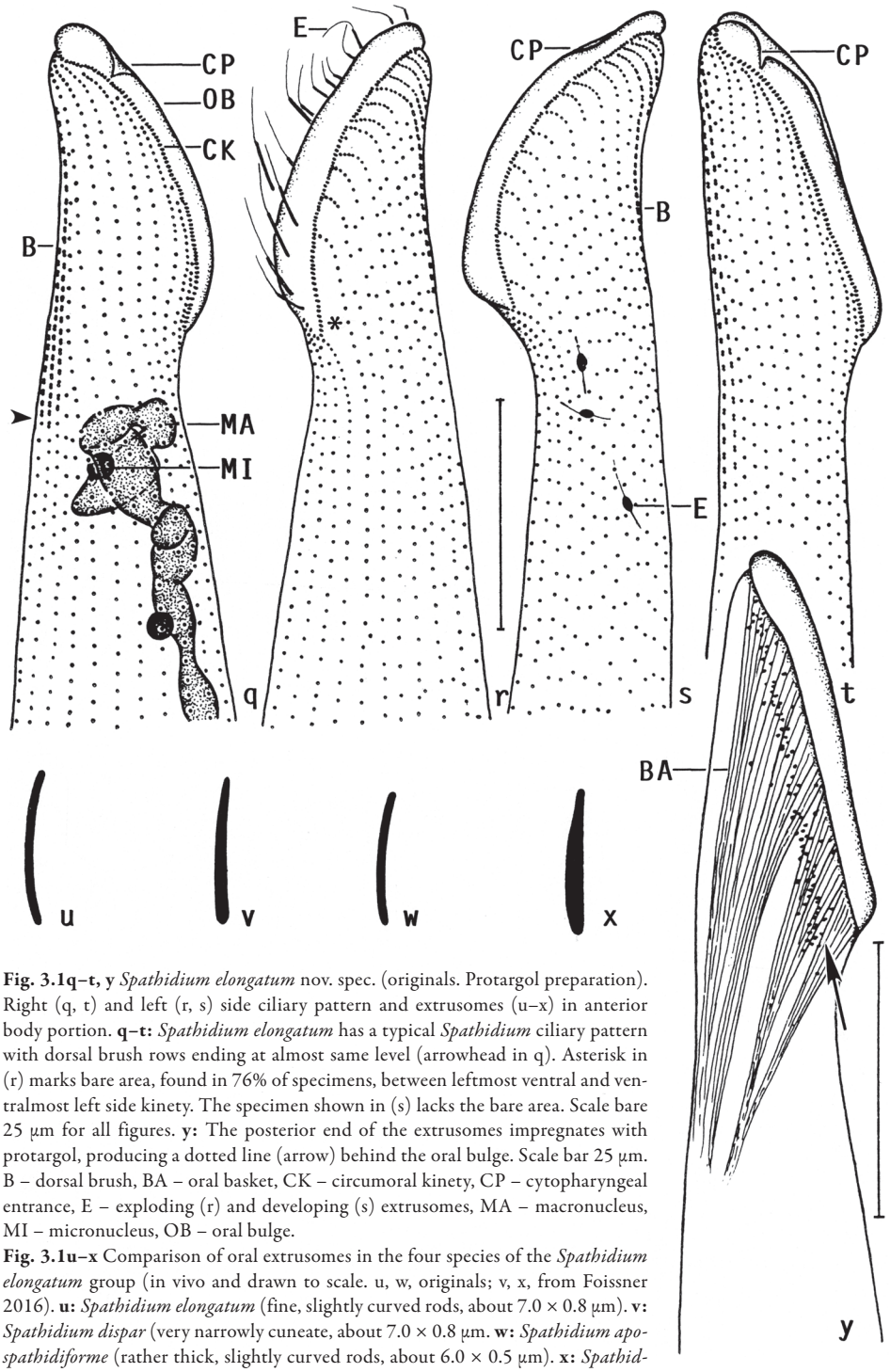

Fig. 3.1q–t, y *Spathidium elongatum* nov. spec. (originals. Protargol preparation). Right (q, t) and left (r, s) side ciliary pattern and extrusomes (u–x) in anterior body portion. **q–t:** *Spathidium elongatum* has a typical *Spathidium* ciliary pattern with dorsal brush rows ending at almost same level (arrowhead in q). Asterisk in (r) marks bare area, found in 76% of specimens, between leftmost ventral and ventralmost left side kinety. The specimen shown in (s) lacks the bare area. Scale bare 25 μm for all figures. **y:** The posterior end of the extrusomes impregnates with protargol, producing a dotted line (arrow) behind the oral bulge. Scale bar 25 μm. B – dorsal brush, BA – oral basket, CK – circumoral kinety, CP – cytopharyngeal entrance, E – exploding (r) and developing (s) extrusomes, MA – macronucleus, MI – micronucleus, OB – oral bulge.

Fig. 3.1u–x Comparison of oral extrusomes in the four species of the *Spathidium elongatum* group (in vivo and drawn to scale. u, w, originals; v, x, from Foissner 2016). **u:** *Spathidium elongatum* (fine, slightly curved rods, about 7.0 × 0.8 μm). **v:** *Spathidium dispar* (very narrowly cuneate, about 7.0 × 0.8 μm. **w:** *Spathidium apospathidiforme* (rather thick, slightly curved rods, about 6.0 × 0.5 μm). **x:** *Spathidium duschli* (asymmetrically obclavate, about 7.0 × 0.8 μm).

Table 3.1 Main morphological and morphometrical features distinguishing the species of the *Spathidium elongatum* group[a]

Species	Characteristic					
	Tail	Nucleus pattern	Extrusome shape	Body size	Bulge length: body width, ratio[b]	Brush dikinetids, total number
Spathidium elongatum	a	tortuous strand	rod-shaped	300 × 30	1.7	116
Spathidium dispar	a	tortuous strand	acicular	300 × 35	1.2	154
Spathidium apospathidiforme	p	tortuous strand	rod-shaped	290 × 23	1.7	82
Spathidium duschli	a	numerous nodules	asymmetrically obclavate	200 × 35	~1.0	93

[a] Measurements in vivo and in µm. Abbreviations: a, absent; p, present. Source of data: Original (*Spathidium elongatum* nov. spec and *Spathidium apospathidiforme* nov. spec.); from Foissner (2016; *Spathidium dispar* and *Spathidium duschli*).

[b] From protargol preparations.

Diagnosis: Body size about 300 × 30 µm in vivo. Very slenderly spatulate to cylindroidal with strongly oblique, slightly cuneate oral bulge about 1.6 times as long as widest trunk region. Macronucleus long and tortuous; multimicronucleate. Oral extrusomes rod-shaped and curved, fine, about 8.0 × 0.5 µm. Two size-types of cortical granules. On average 26 ciliary rows; those of right side distinctly separate from circumoral kinety; leftmost ventral row and first left side kinety anteriorly widely separated, producing an obtriangular[4], bare area in most specimens. Dorsal brush inconspicuous, isostichad and short occupying 20% of body length.

Type locality: Saline grassland soil from the margin of the Zicklacke (about 47°45'N 16°48'E), a flat soda lake near the town of Illmitz, Burgenland, Austria.

Type material: The slide (Fig. 3.2k, l; accession number 2024/122) with the holotype (Fig. 3.1g–i) and two paratype slides (Fig. 3.2m–p; 2024/123, 124) have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI).

ZooBank registration: urn:lsid:zoobank.org:act:A55FA8AB-0140-4091-8217-A7E14FFEFF83

Remarks: Within the group, *Spathidium elongatum* can be confused only with *Spathidium dispar* (Table 3.1). However, they differ by the length of the oral bulge, the number of brush dikinetids, the extrusome shape (Table 3.1); the ciliary pattern (*Spathidium* vs. *Protospathidium*-like on dorsal half of right side; with vs. without bare ventrolateral area); and the two (vs. one) types of cortical granules, a striking feature found only in two other species, viz., *Spathidium hyalinum* Dujardin, 1841 (stouter, viz., 5:1 vs. 10:1 in *Spathidium*

[4] Obtriangular means triangular with the apex downwards (posterior in present case; https://en.wiktionary.org/, accessed 16 Apr 2023).

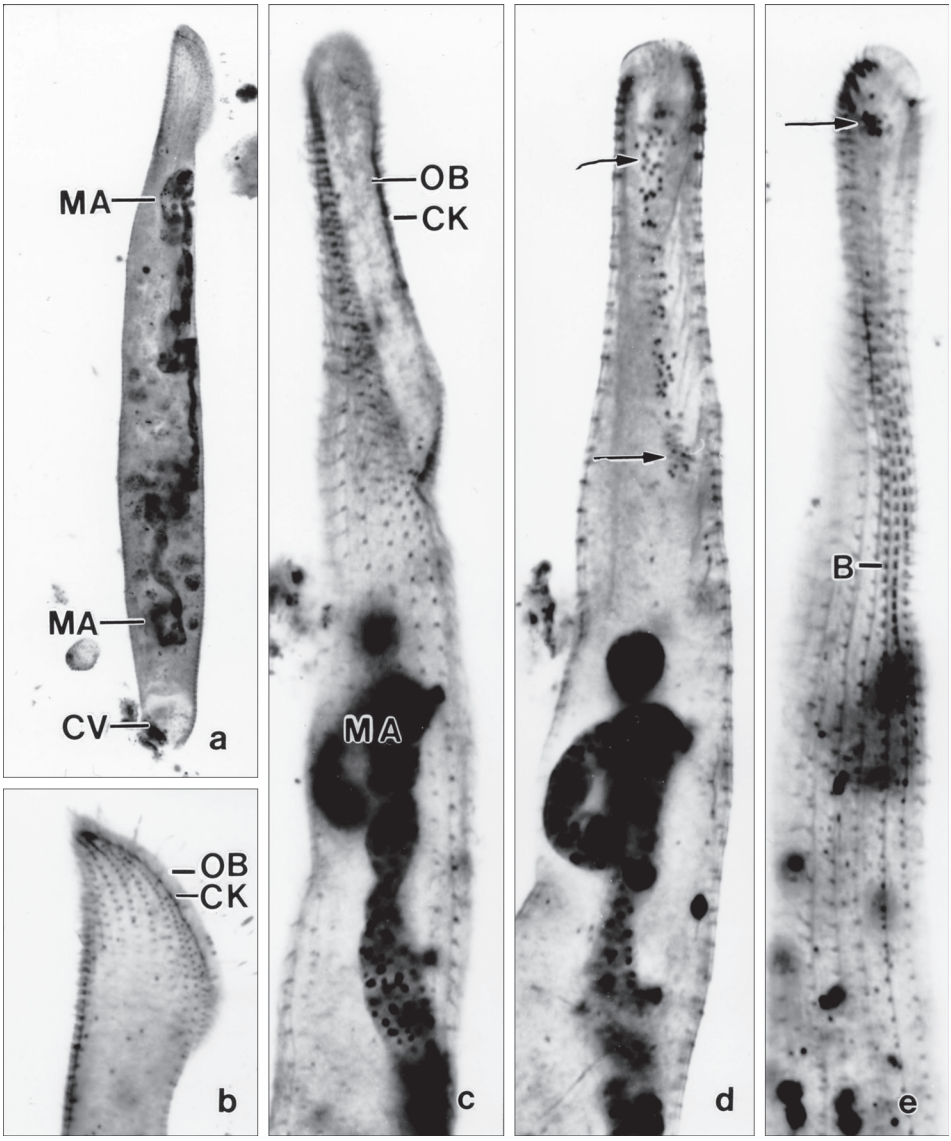

Fig. 3.2a–e *Spathidium elongatum* nov. spec. (originals. Protargol preparation). **a:** Overview (right side) showing the elongate body and the tortuous macronucleus. **b:** Ciliary pattern of right side of anterior body portion, where the rows are curved dorsally and separate from the circumoral kinety, as typical for *Spathidium*. **c, d:** Ventrolateral views of same specimen at two focal planes, showing the elliptical, ventrally bluntly pointed circumoral kinety and a stripe of sharply impregnated granules (arrows) produced by the extrusomes, each containing a granule in the posterior end. **e:** Ciliary pattern in anterior region of dorsal side, where the dorsal brush (B) extends. Arrow marks granule accumulation produced by the extrusomes, each containing a heavily impregnated granule in the proximal end. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuole, MA – macronucleus, OB – oral bulge.

elongatum nov. spec.; extrusomes about 50 µm vs. ≤10 µm) and *Spathidium turgitorum* Foissner et al., 2002 (many macronucleus nodules vs. tortuous strand). Further, *Spathidium*

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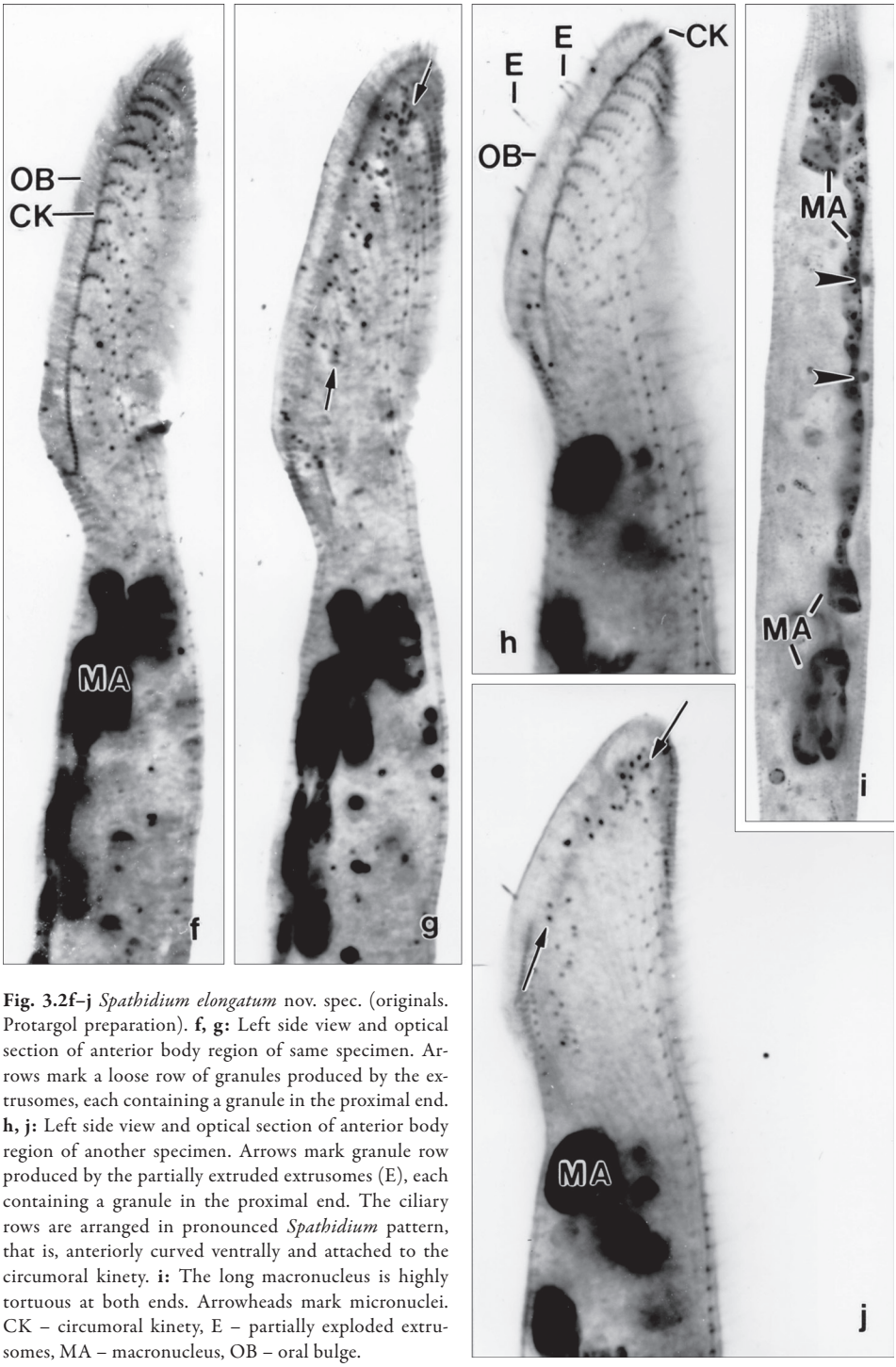

Fig. 3.2f–j *Spathidium elongatum* nov. spec. (originals. Protargol preparation). **f, g:** Left side view and optical section of anterior body region of same specimen. Arrows mark a loose row of granules produced by the extrusomes, each containing a granule in the proximal end. **h, j:** Left side view and optical section of anterior body region of another specimen. Arrows mark granule row produced by the partially extruded extrusomes (E), each containing a granule in the proximal end. The ciliary rows are arranged in pronounced *Spathidium* pattern, that is, anteriorly curved ventrally and attached to the circumoral kinety. **i:** The long macronucleus is highly tortuous at both ends. Arrowheads mark micronuclei. CK – circumoral kinety, E – partially exploded extrusomes, MA – macronucleus, OB – oral bulge.

elongatum is slightly more slender than *Spathidium dispar* (10:1 vs. 8:1) and has a longer, more distinctly coiled macronucleus. As these differences occur in two geographically widely separated populations of *Spathidium dispar*, they are likely stable and sufficient to ascribe the taxa species rank.

The small, stout specimens of *Spathidium elongatum* can be mixed with several other species, especially *Spathidium stammeri* Wenzel, 1959 (oral bulge slightly cuneate vs. dumbbell-shaped, about 25–30 vs. near 20 ciliary rows) and *Spathidium muscicola* Kahl, 1930a (extrusomes ≤10 μm vs. 20–30 μm long). Further, care must be taken not to confuse *Spathidium elongatum* and related species with other large, slender spathidiids, for instance, *Spathidium faurefremieti* Foissner, 2003 and *Arcuospathidium bulli* Foissner, 2000 both having two contractile vacuoles.

Description: Body size highly variable, viz. 220–400 × 20–40 μm in vivo, usually near 300 × 30 μm, as calculated from some in vivo measurements and the morphometric data (Table 3.2). Body shape very narrowly spatulate to cylindroidal with strongly varying length:width ratio of 6–19:1 in protargol preparations, on average near 10:1 both in vivo and in prepared cells; usually, the stouter the smaller and vice versa (Fig. 3.1n–p); neck indistinct, more pronounced ventrally than dorsally, trunk widest in or behind mid-body; flattened only in oral region. Anterior (oral) end fairly (about 60°) slanted, posterior narrowly rounded and frequently bulbous, wrinkled, or bluntly pointed, but never tail-like, due to the contractile vacuole contained (Fig. 3.1a, d, g, n–p). Macronucleus extends in middle quarters of cell, basically a long, tortuous, irregularly nodulated strand with ends frequently conspicuously coiled and twisted; occasionally distinctly nodulated or in two long pieces; nucleoli numerous, 1–2 μm across. Many micronuclei along macronucleus, exact number not recognizable due to many similar-sized and impregnated cytoplasmic inclusions; individual micronuclei of spongious structure and about 3 μm across (Fig. 3.1a, g, k, m–p; Table 3.2). Contractile vacuole in rear body end, four or five excretory pores scattered in pole area; definitely, no second contractile vacuole in anterior body half. Oral bulge extrusomes rod-shaped and slightly curved, 7.0–10.0 × 0.5 μm in vivo and thus fine and inconspicuous, posterior end strongly argyrophilic, forming dotted line underneath oral bulge in protargol preparations, an unusual feature (Fig. 3.1b, c, u, y, 3.2e, g). Released extrusomes of typical toxicyst structure, about 15 μm long, impregnate lightly with the protargol method used (Fig. 3.1r). Many developing, fusiform extrusomes in cytoplasm, often strongly impregnate with protargol, especially the widened mid (Fig. 3.1o, s). Cortex flexible, contains about five rows of yellowish granules between each two kineties; individual granules ellipsoidal and in two distinct size classes, viz., approximately 0.4 × 0.2 μm and 0.8 × 0.4 μm, large granules rare and interspersed among rows of small granules (Fig. 3.1j). Cytoplasm colourless, packed with developing extrusomes (see above), lipid droplets up to 7 μm across, and food vacuoles with remnants of heterotrophic flagellates; subterminal frequently a large vacuole with indigestible debris. Swims and creeps rather rapidly showing worm-like flexibility.

Cilia about 10 μm long in vivo, arranged in an average of 26 equidistant, mostly bipolar, densely ciliated rows abutting on circumoral kinety in typical *Spathidium* pattern (Fig. 3.1a, g–i, q–t; Table 3.2). Right side ciliary rows anteriorly strongly curved dorsally and distinctly separate from circumoral kinety; left side rows, in contrast, attached to circumoral kinety and very densely ciliated anteriorly, frequently with small irregularities, such as minute

breaks and/or supernumerary kinetids outside rows; leftmost ventral and ventralmost left side kinety widely spaced anteriorly, producing large, obtriangular, bare area in 76% (n = 25) of specimens (Fig. 3.1i, r). Dorsal brush inconspicuous because occupying only 20% of body length and bristles merely up to 3 µm long and rod-shaped; all rows have some ordinary cilia anteriorly, commence with some, only 1 µm long bristle pairs, and end posteriorly at nearly same level; row 3 with a monokinetidal tail extending to second third of body; 2 out of 50 specimens have four brush rows (Fig. 3.1a, f, h, k, q, t; Table 3.2).

Oral bulge occupies anterior body end strongly slanted by an angle of about 60°, on average 1.7 times as long as widest trunk region; moderately distinct, that is, slightly set off from body proper and of ordinary height, viz., up to 6 µm dorsally and 4 µm ventrally; surface flat or slightly sigmoidal with convex dorsal

Fig. 3.2k–p *Spathidium elongatum* nov. spec. (originals. Protargol slides). **k, l:** Slide (k) and protocol (l) containing holotype (H) and paratypes (P). Accession number (LI): 2024/122. **m, n:** Slide (m) and protocol (n) containing paratypes drawn (PD) and paratypes (P). Accession number (LI): 2024/123. **o, p:** Slide (o) and protocol (p) containing paratypes drawn (PD) and paratypes (P). Accession number (LI): 2024/124.

portion in 60% (n = 25) of specimens (Fig. 3.1a, d, n, t, y), while distinctly convex, possibly by some shrinkage, in 40% (Fig. 3.1p–s); in frontal view slightly cuneate to oblong with indistinctly narrowed mid-portion; with minute, obconical depression, marking cytopharyngeal entrance, near dorsal end distinct only in well-impregnated and orientated cells (Fig. 3.1i, m, q, s, t). Circumoral kinety of same shape as oral bulge, continuous, composed of narrowly spaced dikinetids each associated with a cilium, an oral basket rod, and a faintly impregnated fibre extending into oral bulge. Nematodesmata fairly distinct and bundled, forming rather conspicuous basket in protargol-prepared specimens (Fig. 3.1a–d, g–t, y; Table 3.2).

Occurrence and ecology: As yet found only at the type locality (see above), where it was moderately abundant in the non-flooded Petri dish culture.

Spathidium apospathidiforme nov. spec.

(Fig. 3.1w, 3.3a–s, 3.4a–s, 3.5a–s, 3.6a–p, Tables 3.1, 3.2)

Nomenclature: The species-group name is a composite of the genus-group name *Apospathidium* Foissner et al., 2002, the thematic vowel *-i-*, and *-form·is*, *-is*, *-e* (Latin adjective [m, f, n]; -shaped; see Hentschel & Wagner 1996, p. 274 at *glómeriformis*), meaning a *Spathidium* shaped like an *Apospathidium*.

Diagnosis: Body size about 290 × 23 µm in vivo. Body shape very slenderly amphoriform with distinct tail and oblique to strongly oblique, elongate elliptical to slightly cuneate oral bulge about 1.7 times as long as widest trunk region. Macronucleus long and tortuous; multimicronucleate. Extrusomes rod-shaped and curved, about 6.0 × 0.5 µm, ends contain an argyrophilic granule. One type of cortical granules. On average 15 ciliary rows arranged in perfect *Spathidium* pattern; dorsal brush inconspicuous, isostichad and short occupying 18% of body length, all rows end at similar level.

Type locality: Highly saline, circumneutral coastal soil from the island Hembadoo (04.481°N 74.393°E), North-Male Atoll, Maldives.

Type material: The slide (Fig. 3.6a, b; accession number 2024/125) with the holotype (Fig. 3.3p–r) and seven paratype slides (Fig. 3.6c–p; 2024/126, 127, 128, 129, 130, 131, 132) have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI).

ZooBank registration: urn:lsid:zoobank.org:act:E5F7C06D-EC3D-41E6-8DC4-CC16458B89DC

Remarks: This species is outstanding in looking like a large *Apospathidium longicaudatum* (Buitkamp, 1977) (for details, see Chapter 4, that is, Foissner et al. 2025b). However, it does not have oralized somatic monokinetids and is thus a true *Spathidium*. As concerns related species, see Table 3.1. Briefly, *Spathidium apospathidiforme* is easily recognized by the amphoriform body shape and the tail-like posterior body portion. Further, it has, on average, only 15 ciliary rows, while *Spathidium elongatum* nov. spec. and *Spathidium dispar* have 22–26 rows (Table 3.1). However, young post-dividers of *Spathidium apospathidiforme* nov. spec. look quite similar to some common spathidiids, especially *Levispatha muscorum* (Dragesco & Dragesco-Kernéis, 1979) Foissner, 2021 (for review, see Foissner and Xu 2007, p. 187) and *Epispathidium ascendens* (for brief review, see Chapter 6, that is, Foissner et al. 2025a).

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Table 3.2 Morphometric data on *Spathidium elongatum* nov. spec. (SE; original data), *Spathidium dispar* from Venezuela (SD1; from Foissner 2016), *Spathidium dispar* from Austria (SD2; from Foissner 2016), and *Spathidium apospathidiforme* nov. spec. (SA; original data)[a]

Characteristic	Species	Mean	M	SD	SE	CV	Min	Max	n
Body, length	SE	269.9	270.0	43.4	9.5	16.1	198.0	365.0	21
	SD1	240.4	240.0	35.0	11.7	14.5	194.0	296.0	9
	SD2	292.3	290.0	60.9	18.4	20.8	185.0	390.0	11
	SA	268.5	270.0	25.0	5.5	9.3	205.0	310.0	21
Body, width	SE	24.9	25.0	4.6	1.0	18.4	19.0	38.0	21
	SD1	29.6	30.0	2.5	0.8	8.3	24.0	32.0	9
	SD2	37.6	38.0	6.7	2.0	17.7	28.0	50.0	11
	SA	21.4	21.0	3.9	0.9	18.3	15.0	29.0	21
Body length:width, ratio	SE	11.2	10.9	2.9	0.6	25.9	5.8	19.2	21
	SD1	8.2	8.1	1.2	0.4	15.2	6.5	10.2	9
	SD2	7.9	7.9	1.5	0.5	19.6	5.1	10.0	11
	SA	13.0	12.9	2.8	0.6	21.2	8.5	17.9	21
Oral bulge (circumoral kinety), maximum length	SE	41.0	40.0	5.9	1.3	14.3	32.0	56.0	21
	SD1	36.0	34.0	5.8	1.9	16.0	30.0	45.0	9
	SD2	39.9	40.0	6.5	2.0	16.2	30.0	52.0	11
	SA	36.7	36.0	4.3	0.9	11.8	29.0	48.0	21
Oral bulge length:body width, ratio	SE	1.7	1.6	0.4	0.1	23.6	0.9	2.7	21
	SD1	1.2	1.2	0.2	0.1	15.2	0.9	1.6	9
	SD2	1.1	1.0	0.2	0.1	17.7	0.8	1.5	11
	SA	1.8	1.7	0.4	0.1	22.3	1.1	2.5	21
Circumoral kinety to last dikinetid of brush row 1, distance	SE	49.3	48.0	7.2	1.6	14.6	40.0	66.0	21
	SD1	49.0	46.0	6.9	2.6	14.1	44.0	63.0	7
	SD2	61.4	60.0	8.2	3.1	13.3	54.0	75.0	7
	SA	41.9	41.0	8.0	1.8	19.2	30.0	56.0	21
Circumoral kinety to last dikinetid of brush row 2, distance	SE	54.0	54.0	8.8	1.9	16.3	42.0	70.0	21
	SD1	57.3	56.0	9.4	3.6	16.5	49.0	76.0	7
	SD2	70.3	70.0	7.4	2.8	10.6	60.0	80.0	7
	SA	48.8	47.0	7.7	1.7	15.8	38.0	63.0	21
Circumoral kinety to last dikinetid of brush row 3, distance	SE	48.6	49.0	6.9	1.5	14.1	37.0	64.0	21
	SD1	57.9	55.0	9.3	3.5	16.0	50.0	76.0	7
	SD2	59.4	60.0	7.3	2.8	12.3	51.0	73.0	7
	SA	44.4	44.0	7.1	1.5	15.9	34.0	60.0	21
Anterior body end to macronucleus, distance	SE	53.4	50.0	14.0	3.1	26.2	38.0	95.0	21
	SD1	84.0	75.0	18.1	6.0	21.5	68.0	120.0	9
	SD2	87.0	90.0	18.6	5.6	21.3	55.0	107.0	11
	SA	54.2	53.0	8.2	1.8	15.1	40.0	70.0	21
Macronucleus figure, length	SE	163.1	165.0	34.5	7.5	21.1	85.0	230.0	21
	SD1	94.0	91.0	29.7	9.9	31.6	58.0	150.0	9
	SD2	147.9	135.0	59.7	18.0	40.4	42.0	260.0	11
	SA	140.3	138.0	21.8	4.8	15.5	97.0	185.0	21
Macronucleus, length (spread)	SE	311.9	320.0	–	–	–	190.0	400.0	21
	SD1	211.7	220.0	–	–	–	120.0	300.0	9
	SD2	256.8	250.0	–	–	–	90.0	410.0	11
	SA	219.0	230.0	–	–	–	115.0	300.0	21

Table 3.2. Continued

Characteristic	Species	Mean	M	SD	SE	CV	Min	Max	n
Macronucleus, width (middle)	SE	4.6	5.0	0.6	0.1	12.8	4 .0	6.0	21
	SD1	5.8	6.0	0.7	0.2	11.5	5.0	7.0	9
	SD2	5.4	5.0	0.8	0.2	15.1	4.0	7.0	11
	SA	4.5	4.0	0.7	0.1	15.0	4.0	6.0	21
Macronucleus, number	SE	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	SD1	1.0	1.0	0.0	0.0	0.0	1.0	1.0	9
	SD2	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11
	SA	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Micronuclei, length	SE	3.0	3.0	0.6	0.1	18.9	2.5	4.5	21
	SD1	6.0	6.0	0.5	0.2	8.3	5.0	7.0	9
	SD2	3.3	3.0	–	–	–	3.0	4.0	7
	SA	2.9	3.0	0.5	0.1	18.6	2.0	4.0	21
Micronuclei, width	SE	3.0	3.0	0.6	0.1	18.9	2.5	4.5	21
	SD1	2.3	2.5	–	–	–	2.0	2.5	9
	SD2	2.4	2.5	–	–	–	2.0	2.5	7
	SA	2.9	3.0	0.5	0.1	18.6	2.0	4.0	21
Somatic kineties, number	SE	25.8	26.0	1.7	0.4	6.7	22.0	29.0	21
	SD1	22.2	22.0	1.5	0.5	6.7	21.0	25.0	9
	SD2	24.2	24.0	2.1	0.6	8.6	20.0	27.0	11
	SA	15.6	15.0	1.4	0.3	8.8	13.0	18.0	21
Ciliated kinetids in a right-side kinety, number	SE	144.3	138.0	28.3	6.2	19.6	105.0	205.0	21
	SD1	178.1	169.0	29.5	9.8	16.6	138.0	221.0	9
	SD2	134.9	128.0	36.8	11.1	27.2	71.0	186.0	11
	SA	110.6	110.0	16.4	3.6	14.8	75.0	140.0	21
Dorsal brush rows, number	SE	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	SD1	3.0	3.0	0.0	0.0	0.0	3.0	3.0	7
	SD2	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
	SA	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Dikinetids in brush row 1, number	SE	36.4	36.0	3.2	0.7	8.9	32.0	43.0	21
	SD1	51.4	54.0	5.5	2.5	10.7	45.0	57.0	5
	SD2	43.0	43.0	4.6	1.9	10.6	37.0	48.0	6
	SA	26.0	27.0	5.1	1.1	19.7	17.0	34.0	21
Dikinetids in brush row 2, number	SE	43.8	43.0	3.9	0.8	8.8	38.0	51.0	21
	SD1	61.0	63.0	8.3	3.7	13.6	50.0	69.0	5
	SD2	61.8	64.5	9.3	3.8	15.0	46.0	70.0	6
	SA	31.2	32.0	4.9	1.1	15.8	20.0	40.0	21
Dikinetids in brush row 3, number	SE	35.4	35.0	3.3	0.7	9.4	32.0	44.0	21
	SD1	51.2	54.0	4.7	2.1	9.1	44.0	55.0	5
	SD2	39.7	39.0	5.9	2.4	14.8	33.0	47.0	6
	SA	24.9	25.0	4.4	1.0	17.5	17.0	37.0	21

[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.

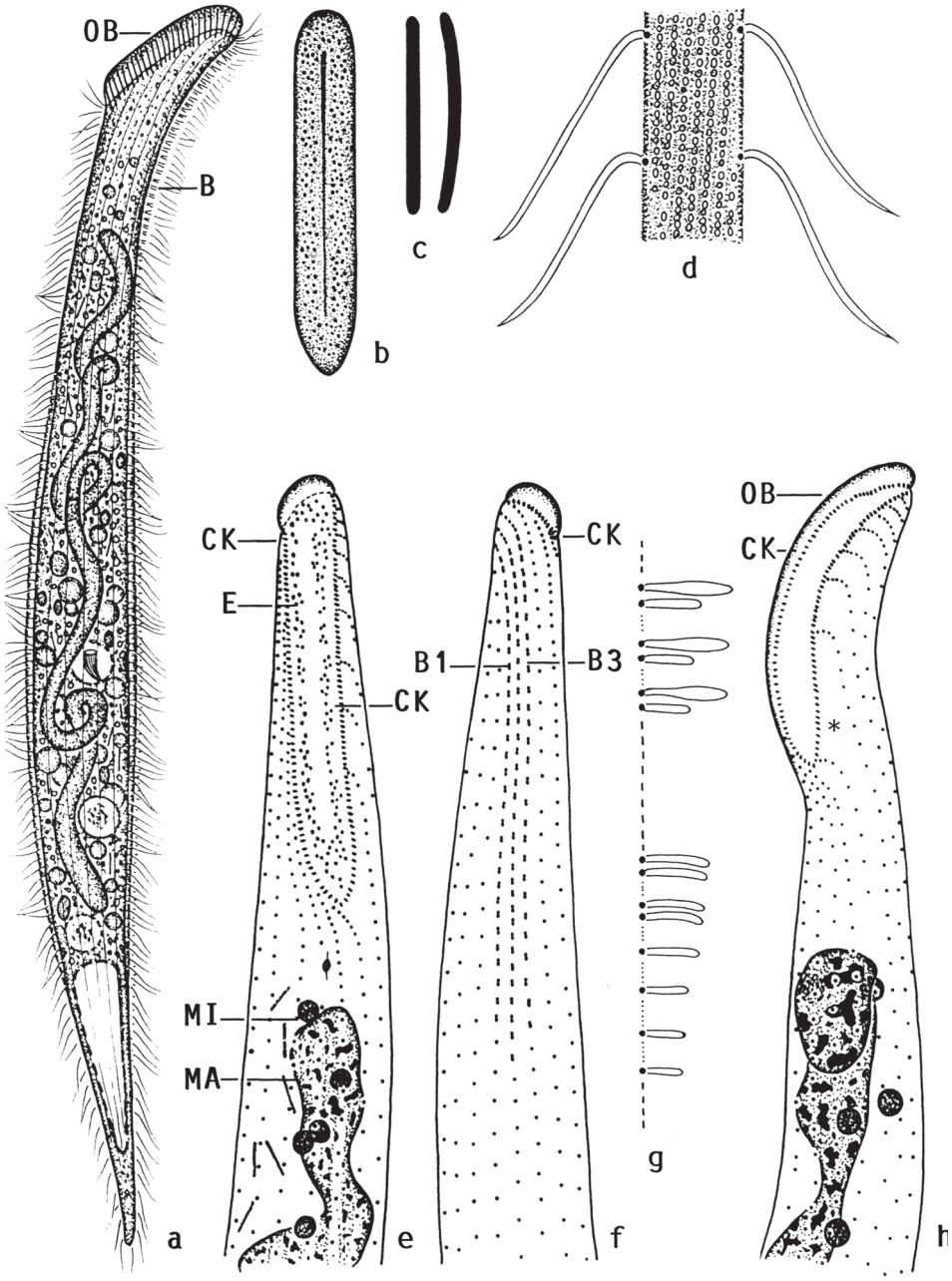

Fig. 3.3a–h *Spathidium apospathidiforme* nov. spec. (originals. a–d, g, from life; e, f, h, protargol preparation). **a:** Left side view of a specimen redrawn from video records, 290 µm. **b:** Frontal view of oral bulge. **c:** Oral bulge extrusome, about 6.0 × 0.5 µm. **d:** Cortical granulation. **e, f:** Ventral and dorsal view of ciliary pattern, length of circumoral kinety 43 µm. **g:** Middle and posterior portion of brush row 3, longest bristles 4 µm. **h:** Left side view of a specimen with a bare area (asterisk), length of oral bulge 31 µm. B – dorsal brush, B1, 3 – dorsal brush rows 1, 3, CK – circumoral kinety, E – extrusomes, MA – macronucleus, MI – micronucleus, OB – oral bulge.

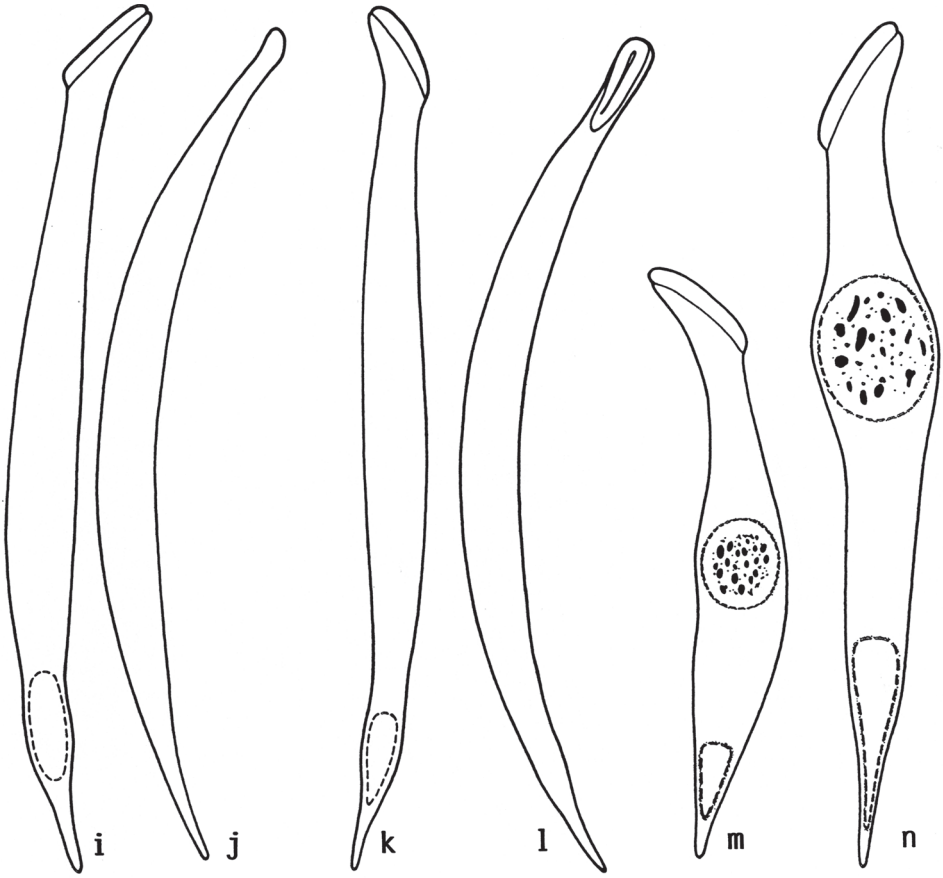

Fig. 3.3i–n *Spathidium apospathidiforme* nov. spec. (originals. From life, redrawn from video records). **i, j:** Left side and dorsal view of same specimen. Note flat oral bulge and body flattening in oral area. **k, l:** Right side and ventral view of a specimen with convex oral bulge and distinct neck. **m, n:** Specimens with a large food vacuole containing remnants of just ingested (hypotrichous?) ciliates.

Ontogenesis of *Spathidium apospathidiforme* is very similar to that of *Spathidium turgitorum* Foissner et al., 2002 (p. 234) and *Levispatha muscorum* (see Berger et al. 1983; Foissner & Xu 2007, p. 187), differing mainly in genus and species-specific features. In *Spathidium turgitorum*, the macronuclear strand disintegrates into many nodules in late post-dividers, while all ciliary rows detach from the circumoral kinetofragments in *Levispatha muscorum*.

Description: Body size moderately variable, viz. 210–340 × 15–35 µm in vivo, usually near 290 × 23 µm, as calculated from some in vivo measurements and the morphometric data (Table 3.2). Body shape highly characteristic and surprisingly similar to that of *Apospathidium longicaudatum* (see Chapter 4, that is, Foissner et al. 2025b), viz., very slenderly amphoriform with anterior (oral) end slanted by about 60° and posterior end tail-like narrowed and bulbous during diastole of contractile vacuole, neck distinct due to the dorsally projecting oral bulge, trunk widest in or behind mid-body, slightly flattened only in oral area;

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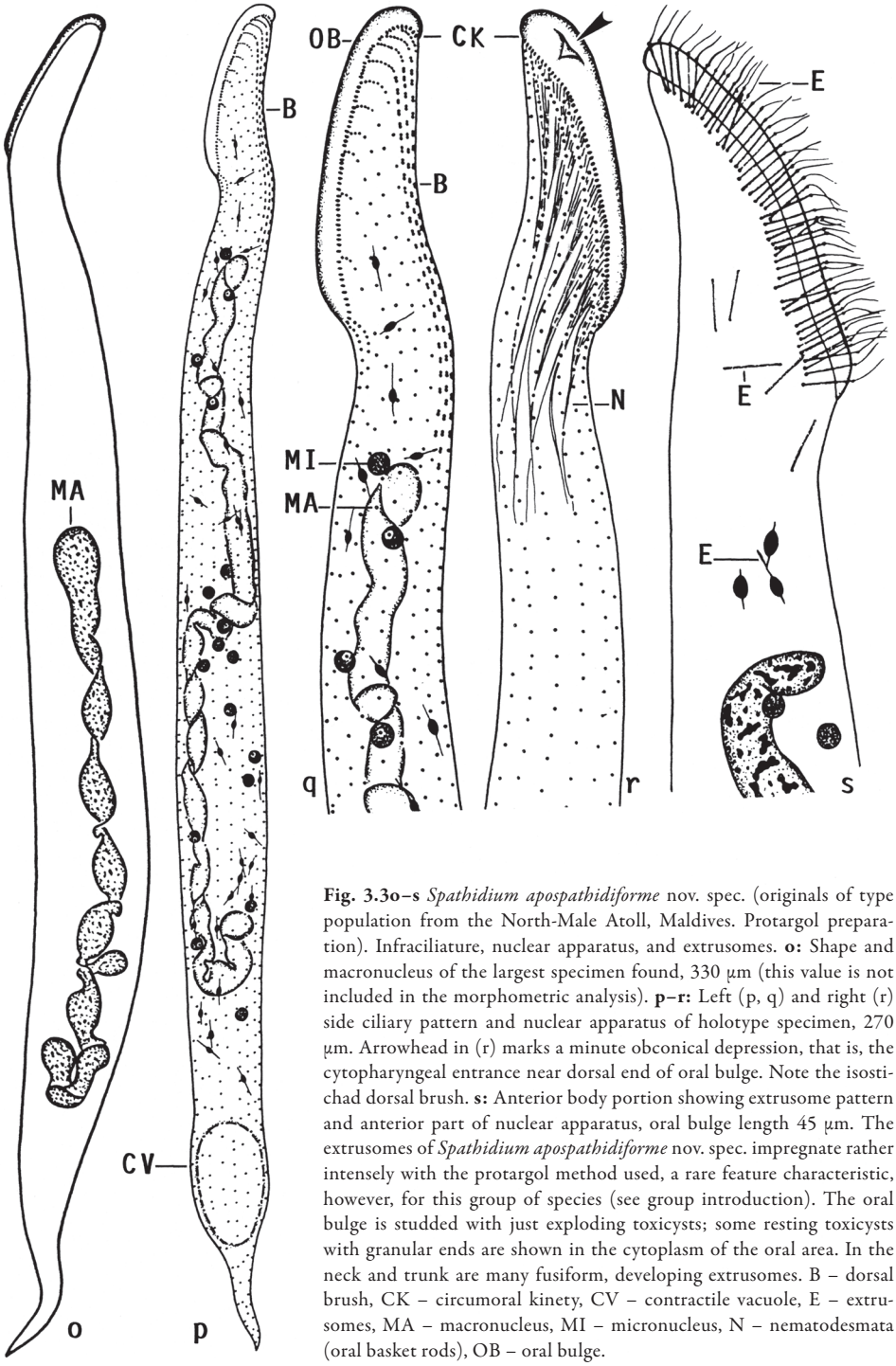


Fig. 3.3o–s *Spathidium apospathidiforme* nov. spec. (originals of type population from the North-Male Atoll, Maldives. Protargol preparation). Infraciliature, nuclear apparatus, and extrusomes. **o:** Shape and macronucleus of the largest specimen found, 330 µm (this value is not included in the morphometric analysis). **p–r:** Left (p, q) and right (r) side ciliary pattern and nuclear apparatus of holotype specimen, 270 µm. Arrowhead in (r) marks a minute obconical depression, that is, the cytopharyngeal entrance near dorsal end of oral bulge. Note the isostichad dorsal brush. **s:** Anterior body portion showing extrusome pattern and anterior part of nuclear apparatus, oral bulge length 45 µm. The extrusomes of *Spathidium apospathidiforme* nov. spec. impregnate rather intensely with the protargol method used, a rare feature characteristic, however, for this group of species (see group introduction). The oral bulge is studded with just exploding toxicysts; some resting toxicysts with granular ends are shown in the cytoplasm of the oral area. In the neck and trunk are many fusiform, developing extrusomes. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuole, E – extrusomes, MA – macronucleus, MI – micronucleus, N – nematodesmata (oral basket rods), OB – oral bulge.

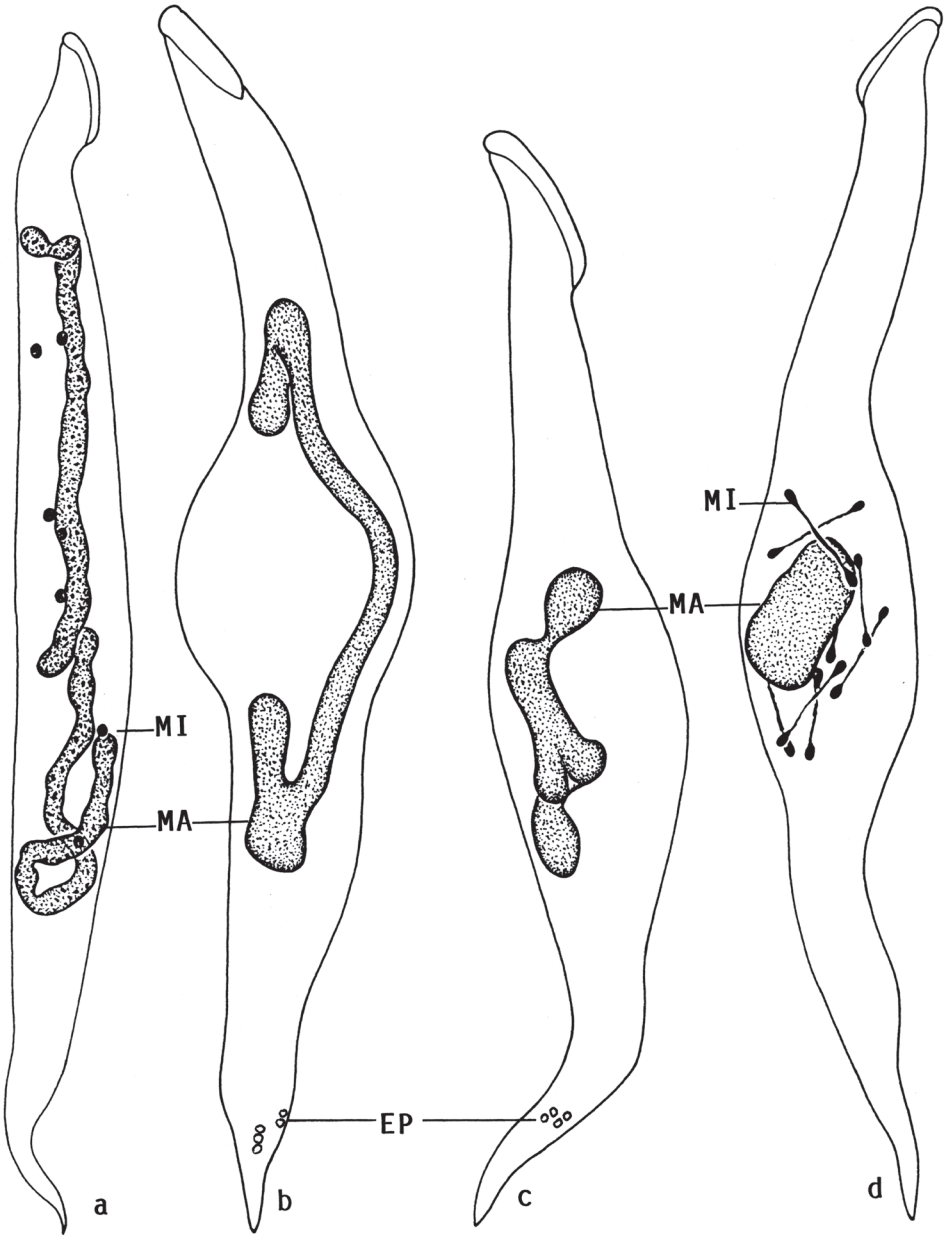


Fig. 3.4a–d *Spathidium apospathidiforme* nov. spec. (originals of type population from the North-Male Atoll, Maldives. Protargol preparation). Body shape and nuclear apparatus of dividers. **a:** Very early divider in right lateral view (cp. Fig. 3.4e) with unchanged body shape and nuclear apparatus, 300 µm. **b:** Early to middle divider (cp. Fig. 3.4f) with strongly inflated mid-body and condensing macronucleus, 270 µm. **c, d:** Middle dividers in right (c) and left (d) lateral view with condensed macronucleus and dividing micronuclei, 250 µm, 285 µm. EP – excretory pores of contractile vacuole, MA – macronucleus, MI – stationary and dividing micronuclei.

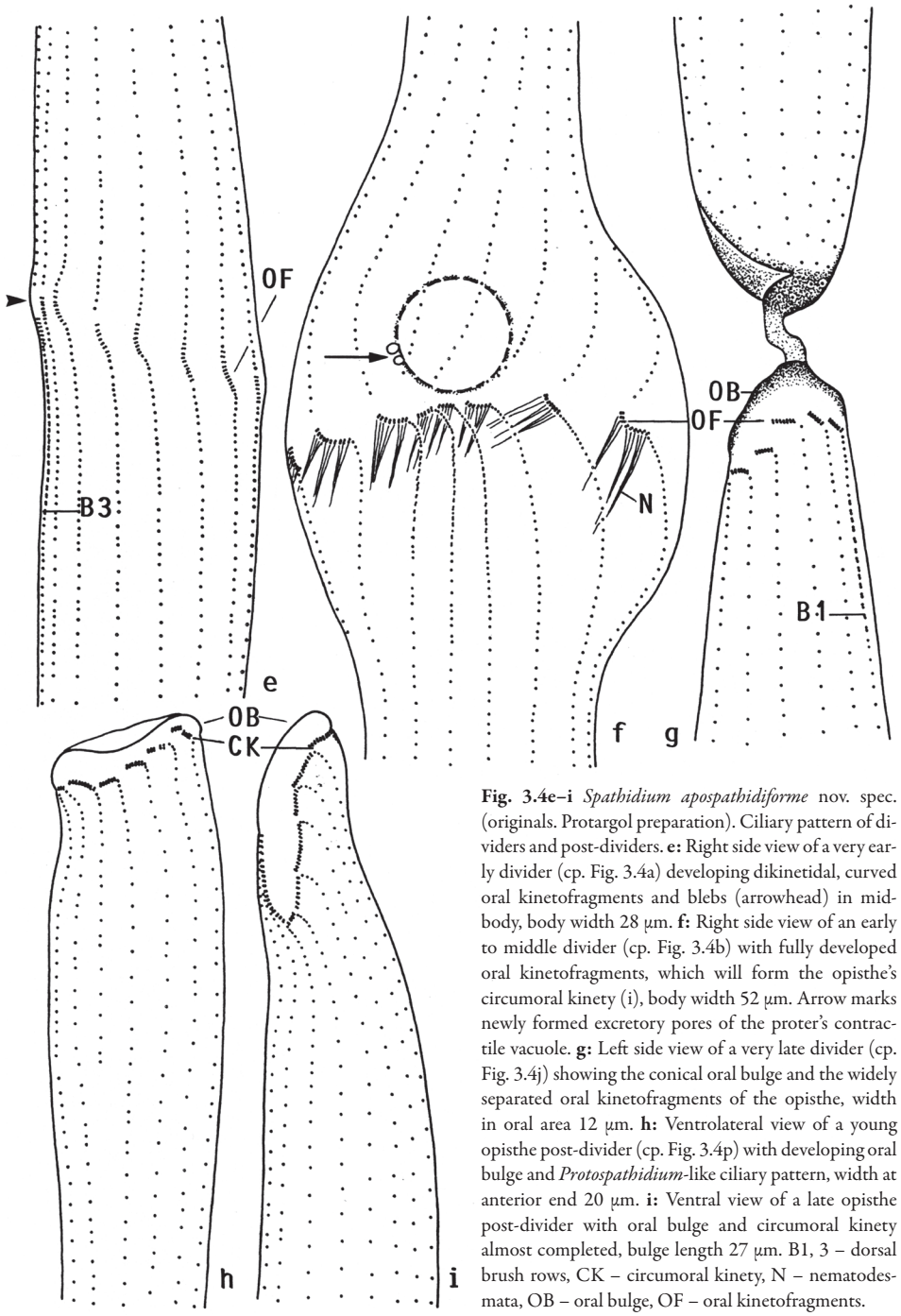


Fig. 3.4e–i *Spathidium apospathidiforme* nov. spec. (originals. Protargol preparation). Ciliary pattern of dividers and post-dividers. **e:** Right side view of a very early divider (cp. Fig. 3.4a) developing dikinetidal, curved oral kinetofragments and blebs (arrowhead) in midbody, body width 28 µm. **f:** Right side view of an early to middle divider (cp. Fig. 3.4b) with fully developed oral kinetofragments, which will form the opisthe's circumoral kinety (i), body width 52 µm. Arrow marks newly formed excretory pores of the proter's contractile vacuole. **g:** Left side view of a very late divider (cp. Fig. 3.4j) showing the conical oral bulge and the widely separated oral kinetofragments of the opisthe, width in oral area 12 µm. **h:** Ventrolateral view of a young opisthe post-divider (cp. Fig. 3.4p) with developing oral bulge and *Protospathidium*-like ciliary pattern, width at anterior end 20 µm. **i:** Ventral view of a late opisthe post-divider with oral bulge and circumoral kinety almost completed, bulge length 27 µm. B1, 3 – dorsal brush rows, CK – circumoral kinety, N – nematodesmata, OB – oral bulge, OF – oral kinetofragments.

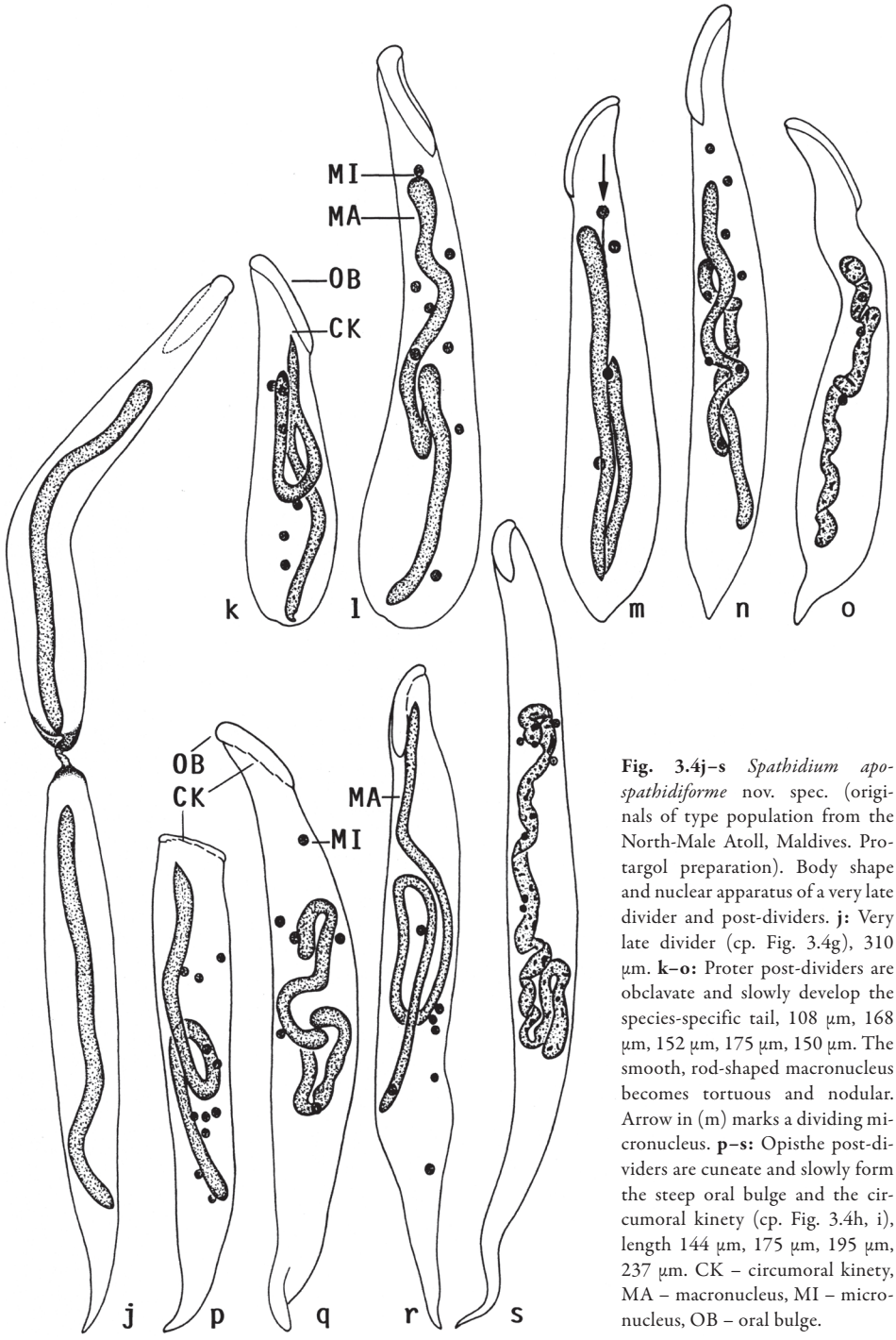


Fig. 3.4j–s *Spathidium apospathidiforme* nov. spec. (originals of type population from the North-Male Atoll, Maldives. Protargol preparation). Body shape and nuclear apparatus of a very late divider and post-dividers. **j:** Very late divider (cp. Fig. 3.4g), 310 µm. **k–o:** Proter post-dividers are obclavate and slowly develop the species-specific tail, 108 µm, 168 µm, 152 µm, 175 µm, 150 µm. The smooth, rod-shaped macronucleus becomes tortuous and nodular. Arrow in (m) marks a dividing micronucleus. **p–s:** Opisthe post-dividers are cuneate and slowly form the steep oral bulge and the circumoral kinety (cp. Fig. 3.4h, i), length 144 µm, 175 µm, 195 µm, 237 µm. CK – circumoral kinety, MA – macronucleus, MI – micronucleus, OB – oral bulge.

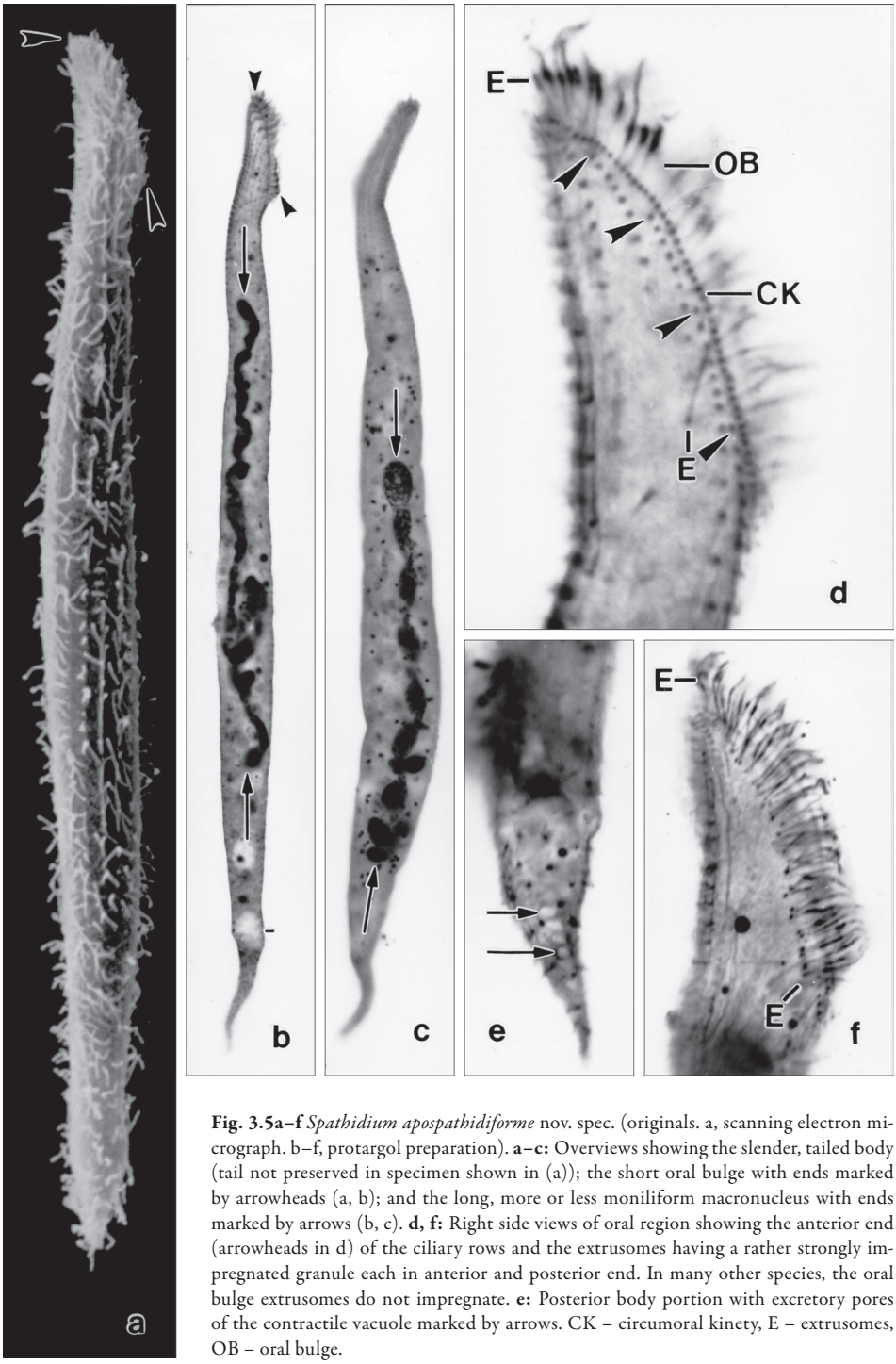


Fig. 3.5a–f *Spathidium apospathidiforme* nov. spec. (originals. a, scanning electron micrograph. b–f, protargol preparation). **a–c:** Overviews showing the slender, tailed body (tail not preserved in specimen shown in (a)); the short oral bulge with ends marked by arrowheads (a, b); and the long, more or less moniliform macronucleus with ends marked by arrows (b, c). **d, f:** Right side views of oral region showing the anterior end (arrowheads in d) of the ciliary rows and the extrusomes having a rather strongly impregnated granule each in anterior and posterior end. In many other species, the oral bulge extrusomes do not impregnate. **e:** Posterior body portion with excretory pores of the contractile vacuole marked by arrows. CK – circumoral kinety, E – extrusomes, OB – oral bulge.

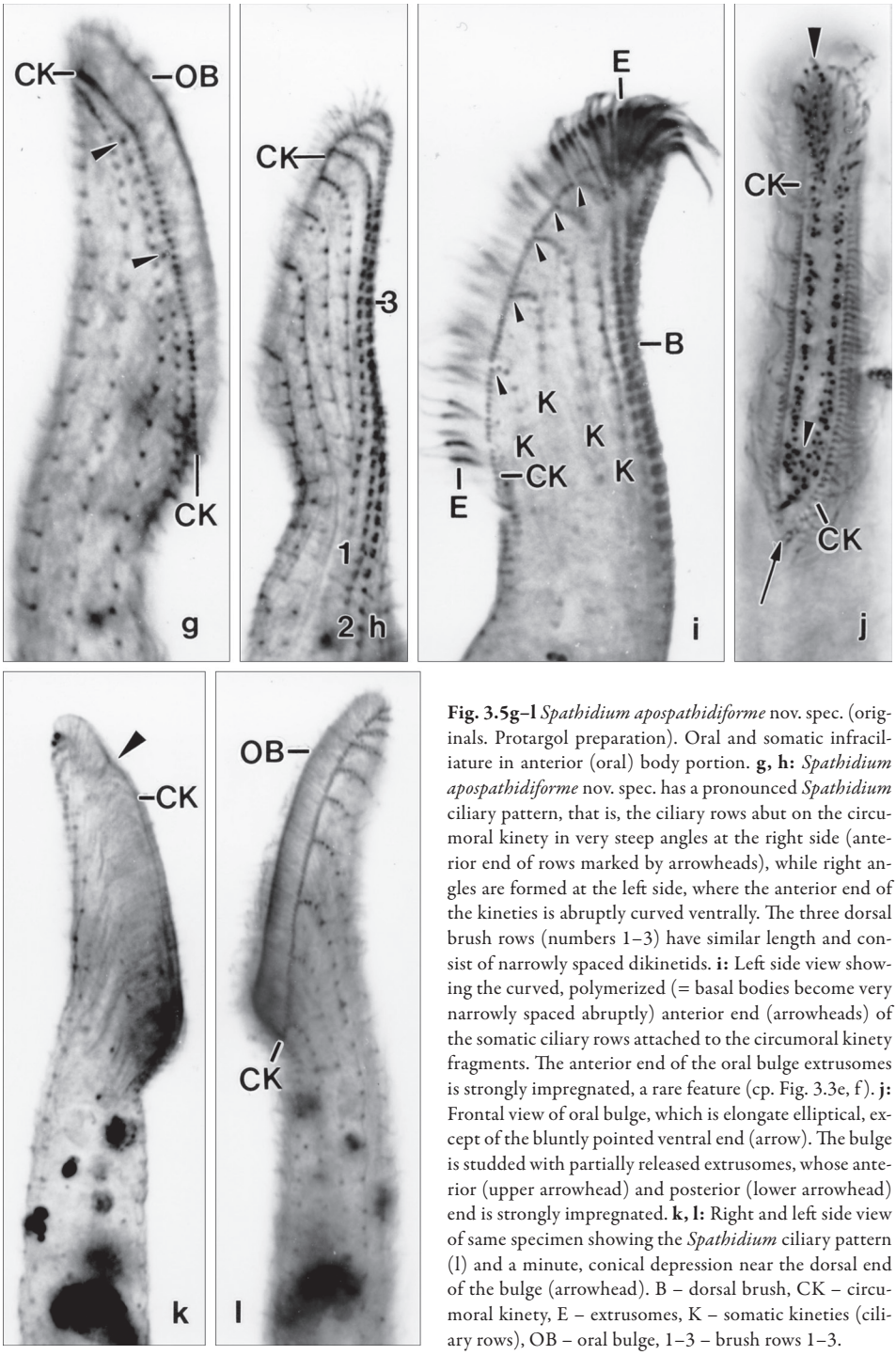


Fig. 3.5g–l *Spathidium apospathidiforme* nov. spec. (originals. Protargol preparation). Oral and somatic infraciliature in anterior (oral) body portion. **g, h:** *Spathidium apospathidiforme* nov. spec. has a pronounced *Spathidium* ciliary pattern, that is, the ciliary rows abut on the circumoral kinety in very steep angles at the right side (anterior end of rows marked by arrowheads), while right angles are formed at the left side, where the anterior end of the kineties is abruptly curved ventrally. The three dorsal brush rows (numbers 1–3) have similar length and consist of narrowly spaced dikinetids. **i:** Left side view showing the curved, polymerized (= basal bodies become very narrowly spaced abruptly) anterior end (arrowheads) of the somatic ciliary rows attached to the circumoral kinety fragments. The anterior end of the oral bulge extrusomes is strongly impregnated, a rare feature (cp. Fig. 3.3e, f). **j:** Frontal view of oral bulge, which is elongate elliptical, except of the bluntly pointed ventral end (arrow). The bulge is studded with partially released extrusomes, whose anterior (upper arrowhead) and posterior (lower arrowhead) end is strongly impregnated. **k, l:** Right and left side view of same specimen showing the *Spathidium* ciliary pattern (l) and a minute, conical depression near the dorsal end of the bulge (arrowhead). B – dorsal brush, CK – circumoral kinety, E – extrusomes, K – somatic kineties (ciliary rows), OB – oral bulge, 1–3 – brush rows 1–3.

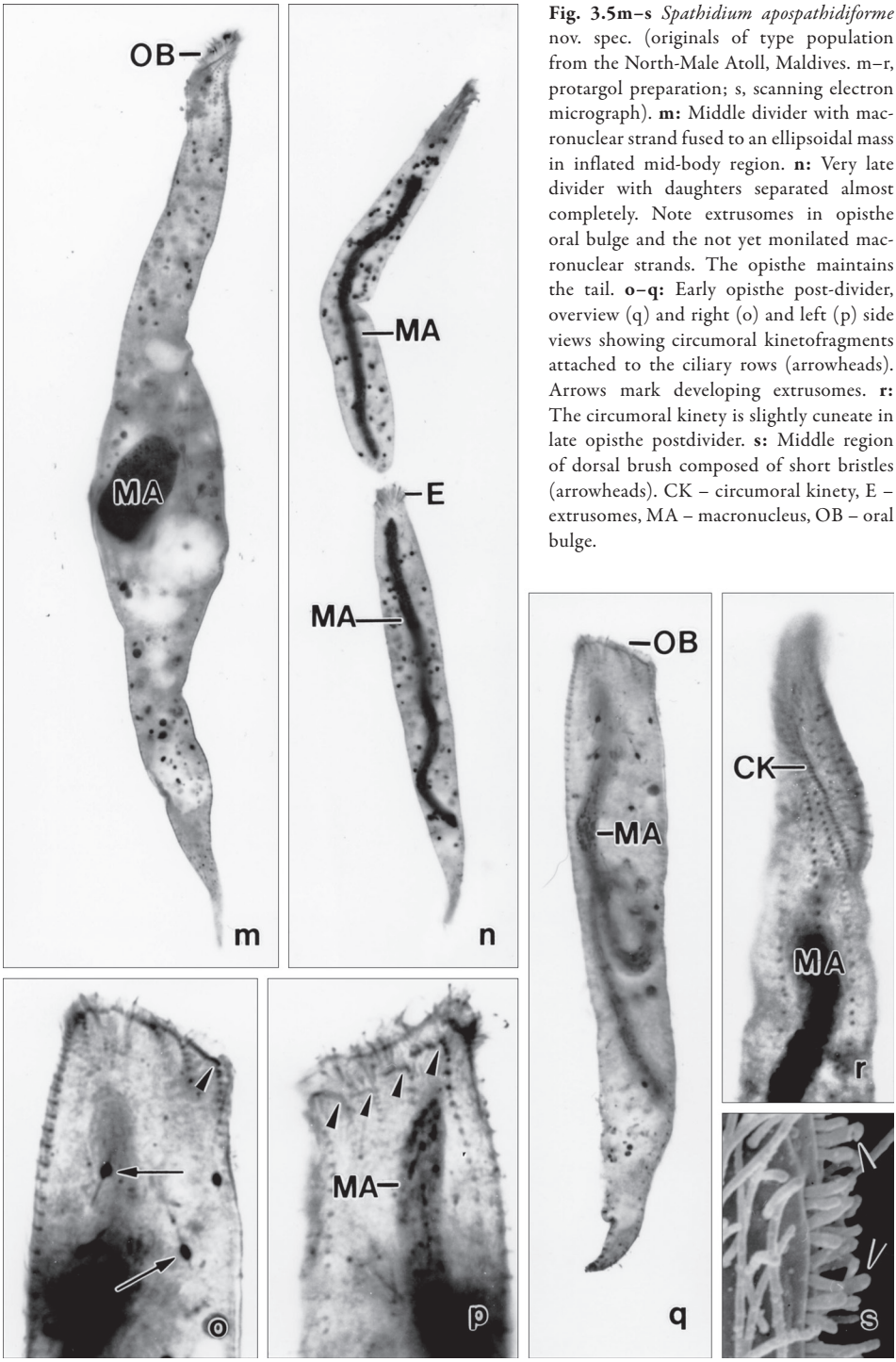
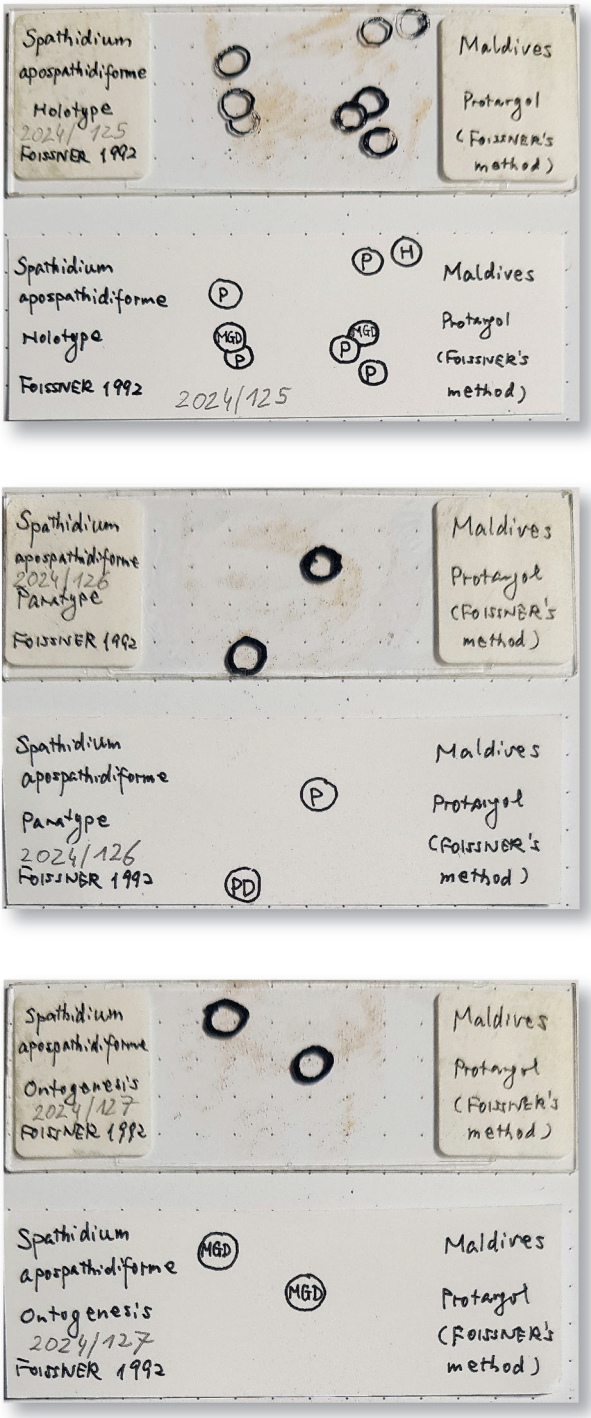
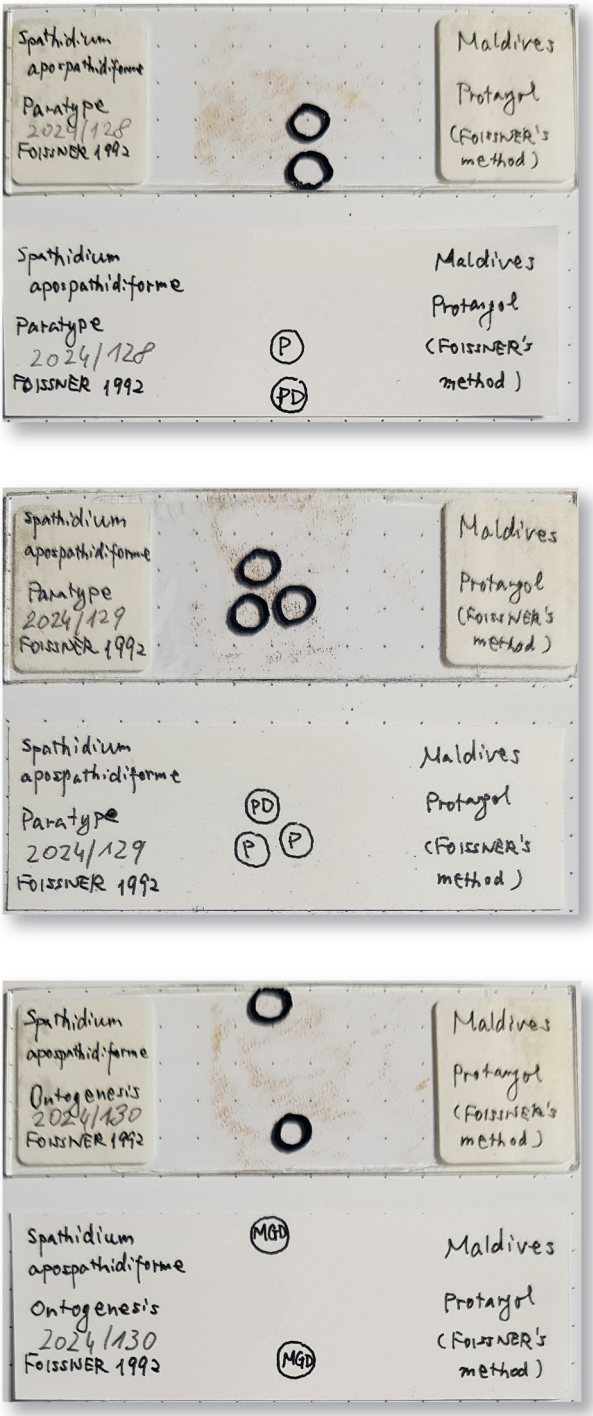


Fig. 3.5m–s *Spathidium apospathidiforme* nov. spec. (originals of type population from the North-Male Atoll, Maldives. m–r, protargol preparation; s, scanning electron micrograph). **m:** Middle divider with macronuclear strand fused to an ellipsoidal mass in inflated mid-body region. **n:** Very late divider with daughters separated almost completely. Note extrusomes in opisthe oral bulge and the not yet monilated macronuclear strands. The opisthe maintains the tail. **o–q:** Early opisthe post-divider, overview (q) and right (o) and left (p) side views showing circumoral kinetofragments attached to the ciliary rows (arrowheads). Arrows mark developing extrusomes. **r:** The circumoral kinety is slightly cuneate in late opisthe postdivider. **s:** Middle region of dorsal brush composed of short bristles (arrowheads). CK – circumoral kinety, E – extrusomes, MA – macronucleus, OB – oral bulge.



length:width ratio rather variable, viz., 8–18:1 in protargol preparations, on average near 13:1 both in vivo and in prepared cells (Fig. 3.3a, i–p, 3.5a–c). Macronucleus extends in middle quarters of cell; basically, a long, tortuous, irregularly nodulated strand; occasionally in two long pieces; nucleoli numerous, lobate to granular. Many micronuclei along macronucleus, exact number not recognizable due to many similar-sized and impregnated cytoplasmic inclusions; individual micronuclei of spongious structure and about 3 µm across (Fig. 3.3a, e, h, o–q, 3.5b, c; Table 3.2). Contractile vacuole in rear body end, several excretory pores slightly subterminally (Fig. 3.3a, i, k, m, n, p, 3.5e); definitely, no second contractile vacuole in anterior body half. Oral bulge extrusomes

Fig. 3.6a–f *Spathidium apospathidiforme* nov. spec. (originals. Protargol slides). **a, b:** Slide (a) and protocol (b) containing holotype (H), paratypes (P), and morphogenetic stages drawn (MGD). Accession number (LI): 2024/125. **c, d:** Slide (c) and protocol (d) containing paratypes drawn (PD) and paratypes (P). Accession number (LI): 2024/126. **e, f:** Slide (e) and protocol (f) containing morphogenetic stages drawn (MGD). Accession number (LI): 2024/127.



rod-shaped and rather distinctly curved, approximately 6.0 × 0.5 µm in vivo and thus moderately distinct, impregnate comparatively strongly with the protargol method used, especially the granular ends, which form a dotted line each on and underneath oral bulge (Fig. 3.3a–e, s, 3.5d, f). Released extrusomes of typical toxicyst structure, about 10 µm long, become stained with protargol (Fig. 3.3s, 3.5i). Many developing, fusiform extrusomes in cytoplasm; they become strongly impregnated with protargol (Fig. 3.3p, q, s). Cortex flexible, contains several distinct rows of minute (about 0.3 µm), colourless granules between each two kineties. Cytoplasm colourless, contains many lipid droplets up to 5 µm across. Feeds on small microthoracid and large hypotrichous(?) ciliates forming big food vacuoles bulging middle portion of body (Fig.

Fig. 3.6g–l *Spathidium apospathidiforme* nov. spec. (originals. Protargol slides). **g, h:** Slide (g) and protocol (h) containing paratype (P) and paratype drawn (PD). Accession number (LI): 2024/128. **i, j:** Slide (i) and protocol (j) containing paratype drawn (PD) and paratypes (P). Accession number (LI): 2024/129. **k, l:** Slide (k) and protocol (l) containing morphogenetic stages drawn (MGD). Accession number (LI): 2024/130.

Fig. 3.6m–p *Spathidium apospathidiforme* nov. spec. (originals. Protargol slides). **m, n:** Slide (m) and protocol (n) containing paratype (P) and morphogenetic stages drawn (MGD). Accession number (LI): 2024/131. **o, p:** Slide (o) and protocol (p) containing paratypes (P), paratypes drawn (PD), and morphogenetic stages drawn (MGD). Accession number (LI): 2024/132.

3.3m, n). Swims and creeps slowly showing great flexibility, especially under mild coverslip pressure.

Cilia about 10 µm long in vivo, arranged in an average of 15 equidistant, bipolar, ordinarily ciliated (average ciliary distance 2.5 µm) rows abutting on circumoral kinety in typical *Spathidium* pattern (Fig. 3.3a, p–s, 3.5d, g–l; Table 3.2). Right side ciliary rows anteriorly strongly curved dorsally and distinctly separate from circumoral kinety; in contrast, left side rows attached to circumoral kinety and very densely ciliated anteriorly, leftmost ventral and first left side kinety widely spaced anteriorly, producing large, obtriangular, bare area in half of specimens, similar as in *Spathidium elongatum* nov. spec. (Fig. 3.3h). Dorsal brush inconspicuous because occupying only 18% of body length and bristles merely up to 4 µm long and slightly clavate; all rows have 5–10 ordinary cilia anteriorly, are composed of a similar number of dikinetids, and end at nearly same level posteriorly; brush rows 1 and 2 continue with ordinary cilia, while row 3 has a monokinetidal bristle tail extending to near rear body end; one out of 100 specimens has a short fourth brush row (Fig. 3.3a, f, g, p, q, 3.5h, i; Table 3.2).

Oral bulge occupies anterior body end strongly slanted by an angle of about 60°, on average 1.7 times as long as widest trunk region; moderately distinct, that is, slightly set off from body proper and of ordinary height; surface flat to slightly convex; in frontal view oblong to slightly cuneate with bluntly pointed ventral end; with minute, obconical depression (cytopharyngeal entrance s. str.) near dorsal end distinct in most protargol-impregnated specimens. Circumoral kinety of same shape as oral bulge, continuous, composed of narrowly

spaced dikinetids each associated with a cilium, an oral basket rod, and a faintly impregnated fibre extending into oral bulge. Nematodesmata fairly distinct and bundled, forming rather conspicuous basket in protargol-impregnated specimens (Fig. 3.3a, b, e, h, i, k, o–s, 3.5a, b, d, f, g–l; Table 3.2).

Ontogenesis (Fig. 3.4a–s, 3.5m–s): The raw material from the non-flooded Petri dish culture contained sufficient dividers to reconstruct the main stages of the ontogenesis and post-divisional growth. Generally, division of *Spathidium apospathidiforme* nov. spec. occurs in freely motile (non-encysted) condition, and fission is homothetogenic and monotomic producing two homopolar, similar-sized daughter cells. Stomatogenesis is holotelokinetal with most main events occurring rather early, that is, in early and early to middle dividers. All basal bodies develop intrakinetally without any special anlagen fields. No changes are recognizable in the parental oral structures and brush rows.

Body shape and contractile vacuole: Early dividers are indistinguishable from interphase trophonts (Fig. 3.4a). Early to middle and middle dividers are considerably stouter than interphase cells because they are inflated in mid-body, where food remnants and the nuclear mass accumulate and the opisthe oral structures are generated (Fig. 3.4b–d, f). Small blebs are recognizable in the prospective fission area of early and middle dividers (Fig. 3.4e); likely, the blebs are related to oral bulge formation and very similar to those shown by Foissner et al. (2002) in scanning electron micrographs of dividing *Spathidium turgitorum*. Further, the proter generates a new contractile vacuole rather early, with excretory pores recognizable in early to middle dividers (Fig. 3.4f). When fission commences, the cell elongates and the daughters separate close in front of the newly formed circumoral kinety (Fig. 3.4g, j).

Early proter post-dividers are obclavate to spatulate and look like common spathi-diids, for instance, *Levispatha muscorum*. The species-specific tail develops gradually in late post-dividers, that is, when the macronucleus becomes nodulated (Fig. 3.4k–o). Early opisthe post-dividers, in contrast, are conspicuously cuneate because they are transverse-truncate anteriorly and inherit the parental tail, which is, however, often stouter than in typical interphase specimens (Fig. 3.4j, p, q). During post-divisional growth, several processes proceed concomitantly in the oral area, viz., the oral bulge develops and steepens, and the circumoral kinety fragments and the anterior end of the ciliary rows arrange to the genus-specific pattern (Fig. 3.4p–s, 3.5o, p, r).

Nuclear apparatus: When the circumoral kinety fragments are recognizable in early dividers, the nuclear apparatus appears unchanged (Fig. 3.4a, e). In early to middle dividers, the macronucleus smoothens and commences to condense towards the center, as indicated by the inflated, shortened ends (Fig. 3.4b); the nucleoli dissolve to minute granules. In middle dividers, the macronucleus has fused to an ellipsoidal mass located in the inflated body center, and is surrounded by the dividing micronuclei, which also migrated to mid-body (Fig. 3.4c, d). In late and very late dividers, the macronuclear mass elongates to a long, smooth rod, which divides in the middle when cytokinesis proceeds (Fig. 3.4j, 3.5n, q). Post-divisional development of the nuclear apparatus is the same in proter and opisthe, viz., the macronucleus gradually elongates and becomes tortuous and nodular, and the nucleoli re-appear (Fig. 3.4j–s). Micronucleus division could not be followed in detail: most divide in middle dividers (Fig. 3.4d), while some divide (a second time?) in post-dividers (Fig. 3.4m).

Infraciliature: The somatic ciliary pattern and the oral ciliature of the opisthe develop as described in *Spathidium turgitorum* (Foissner et al. 2002, p. 241). Thus, we refer to that species and Fig. 3.4e–g in the present work and emphasize post-divisional events. When proter and opisthe separate, the opisthe oral area is a narrow, wrinkled cone, and the short oral kinetofragments are widely separated from each other and arranged transversely to the main body axis (Fig. 3.4g, j). In young post-dividers, the anterior end becomes broader and transverse-truncate, and the kinetofragments arrange step-like and move closer together, producing a perfect *Protospathidium* pattern (Fig. 3.4h, p). Then, the oral bulge becomes longer and distinctly inclined ventrally, while the circumoral kinetofragments gradually align to an uninterrupted circumoral kinety, as typical for *Spathidium* (Fig. 3.4i, r). During this process, the kinetofragments obviously produce additional dikinetids because they are now about twice as long as in very late dividers (cp. Fig. 3.4h, i). The neck is generated by further elongation of the oral bulge.

Occurrence and ecology: As yet found only at the type locality (see above), where it was abundant and reproduced so well in the non-flooded Petri dish culture that ontogenesis could be studied. The highly saline (>20‰) and slightly alkaline (pH 7.5) sample was collected by Wolfgang Petz (Salzburg, Austria) about 15 m inshore in December 1990. It was composed of dark grey, sandy soil mixed with much shrub and coco litter. *Spathidium apospathidiforme* nov. spec. is well adapted to soil life by the slender, highly flexible body.

Spathidium duschli Foissner, 2016

(Tables 3.1, 3.3)

2016 ***Spathidium duschli* nov. spec.** – Foissner, Denisia 35: 207, Fig. 66a–p, 67a–u, Table 25 (Fig. 3.1x; original description. The slide [accession number 2015/132] containing the holotype [Fig. 66k–n in Foissner 2016] and 3 paratype slides [2015/133–135] have been deposited in the Biology Centre of the Upper Austrian Museum in Linz [LI]; see Foissner 2016, p. 208 and Aescht 2018, p. 487. Further, 4 voucher slides have been deposited in the same collection according to Foissner 2016, p. 208).

Remarks: For details (nomenclature, type locality, type material, description, morphometry, illustrations and micrographs, occurrence and ecology, remarks), see Foissner (2016, p. 207).

Diagnosis (from Foissner 2016, slightly modified): Body size in vivo about 200 × 35 µm. Body narrowly to very narrowly spatulate with oblique, cuneate oral bulge approximately as long as widest trunk region. About 100 ellipsoid, scattered macronuclear nodules; multimicronucleate. Oral extrusomes asymmetrically obclavate, about 7.0 × 0.8 µm, proximal end strongly argyrophilic. One size type of cortical granules. About 20 ciliary rows, those in dorsal half of right side attached to circumoral kinetofragments, as in *Protospathidium*; dorsal brush inconspicuous, isostichad and of ordinary length occupying 25% of body length.

Spathidium dispar Foissner & Xu in Foissner, 2016

(Fig. 3.1v, Tables 3.1, 3.2)

2016 ***Spathidium dispar* Foissner & Xu nov. spec.** – Foissner, Denisia 35: 217, Fig. 68a–n, 69a–o, 70a–i, 71a–x, Table 26 (Fig. 3.1v; original description. The slide [accession number 2015/73] containing the holotype

continued on p. 61

Table 3.3 Morphometric data on *Spathidium duschli* from the type locality (upper line; from Foissner 2016) and a site in the surroundings (lower line; from Foissner 2016)[a]

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Body, length	186.6	180.0	26.2	7.9	14.0	140.0	230.0	11
	179.8	184.5	38.5	11.1	21.4	105.0	260.0	12
Body, width	34.0	35.0	6.1	1.8	17.8	24.0	42.0	11
	32.3	32.5	7.1	2.1	21.9	19.0	45.0	12
Body length:width, ratio	5.6	5.8	0.9	0.3	15.5	4.2	6.6	11
	5.6	5.5	1.0	0.3	16.9	4.2	7.6	12
Oral bulge (circumoral kinety),	33.3	34.0	4.5	1.4	13.6	25.0	40.0	11
maximum length	28.8	29.5	5.0	1.5	17.5	20.0	37.0	12
Oral bulge length:body width, ratio	1.0	1.1	0.2	0.1	19.9	0.6	1.2	11
	0.9	1.0	0.1	0.1	15.9	0.7	1.1	12
Oral bulge, height	3.4	3.0	–	–	–	3.0	4.0	9
	3.5	3.0	0.7	0.2	19.9	3.5	5.0	11
Oral bulge, width (distance between	5.4	5.0	–	–	–	4.0	7.0	5
circumoral kinety)	6.9	7.0	0.7	0.3	10.1	6.0	8.0	7
Circumoral kinety to last dikinetid of	44.6	46.0	13.6	4.1	30.4	25.0	70.0	11
brush row 1, distance	34.9	35.0	10.4	3.1	29.8	20.0	48.0	11
Circumoral kinety to last dikinetid of	51.1	52.0	13.1	3.9	25.5	31.0	75.0	11
brush row 2, distance	40.8	39.0	9.7	2.9	23.8	27.0	54.0	11
Circumoral kinety to last dikinetid	46.6	50.0	13.3	4.0	28.5	29.0	70.0	11
of brush row 3, distance	33.8	29.0	11.8	3.6	35.0	20.0	52.0	11
Anterior body end to anteriormost	33.5	33.0	6.2	1.9	18.6	23.0	45.0	11
macronucleus nodule, distance	39.8	38.5	12.4	3.6	31.0	20.0	57.0	12
Macronucleus nodules, length	7.7	7.0	2.9	0.9	37.1	4.0	15.0	11
	9.0	9.0	4.0	1.2	44.8	3.5	17.0	12
Macronucleus nodules, width	3.6	4.0	0.7	0.2	18.5	3.0	5.0	11
	4.0	4.0	0.9	0.3	22.7	3.0	6.0	12
Macronucleus nodules, number	104.5	105.0	–	–	–	60.0	140.0	10
(rough values)	64.1	65.0	–	–	–	30.0	90.0	12
Micronuclei, length	2.9	3.0	0.5	0.2	16.9	2.2	4.0	11
	2.7	2.8	0.6	0.2	23.6	2.0	4.0	11
Micronuclei, width	2.7	2.8	–	–	–	2.2	3.0	11
	2.4	2.5	–	–	–	2.0	3.0	11
Micronuclei, number	30.2	30.0	6.2	2.0	20.6	20.0	41.0	10
	17.9	20.0	5.7	1.7	32.0	8.0	25.0	11
Somatic kineties, number	22.6	23.0	1.8	0.5	7.8	19.0	25.0	11
	17.0	18.0	2.4	0.7	14.0	13.0	20.0	12
Ciliated kinetids in a right-side	86.4	80.0	15.5	4.7	18.0	60.0	120.0	11
kinety, number	98.4	95.5	30.4	9.6	30.9	50.0	146.0	10
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	12
Dikinetids in brush row 1, number	29.6	30.0	7.0	2.1	23.4	20.0	40.0	11
	28.6	30.0	10.5	3.2	36.9	12.0	43.0	11
Dikinetids in brush row 2, number	38.7	40.0	7.3	2.2	18.8	24.0	46.0	11
	36.2	34.0	11.4	3.3	31.4	18.0	52.0	12
Dikinetids in brush row 3, number	26.9	27.0	4.7	1.4	17.5	18.0	35.0	11
	26.5	26.0	7.7	2.2	28.9	14.0	38.0	12

Table 3.3. Continued

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Excretory pores, number	4.9	5.0	1.5	0.9	31.4	3.0	7.0	9
	4.3	4.0	0.7	0.2	16.3	3.0	5.0	9
Oral bulge extrusomes, length	6.7	7.0	0.9	0.3	13.5	5.0	8.0	11
	6.5	6.0	1.4	0.6	21.2	5.0	9.0	6

[a] Data based on mounted, protargol-prepared (Foissner's method), and randomly selected specimens from a non-flooded Petri dish culture (Voucher population) and a "dirty" pure culture with various food ciliates (type population). 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.

[Fig. 68k, m, n in Foissner 2016] and 2 paratype slides [2015/74, 75] have been deposited in the Biology Centre of the Upper Austrian Museum in Linz [LI]; see Foissner 2016, p. 217 and Aescht 2018, p. 487. Further, 3 voucher slides have been deposited in the same collection according to Foissner 2016, p. 217).

Remarks: For details (nomenclature, type locality, description, morphometry, illustrations and micrographs, occurrence and ecology, remarks), see Foissner (2016, p. 217).

Diagnosis (from Foissner 2016; based on Venezuelan type population and an Austrian population, slightly modified): Body size about 300 × 35 μm in vivo. Slenderly spatulate to cylindroid with strongly oblique, slightly cuneate oral bulge about 1.2 times as long as widest trunk region. Macronucleus long and tortuous; multimicronucleate. Oral extrusomes acicular, about 7.0 × 0.8 μm in size, ends deeply argyrophilic. One type of cortical granules. On average 23 ciliary rows, those in dorsal half of right side attached to the circumoral kinetofragments in *Protospathidium* pattern; dorsal brush inconspicuous, isostichad and of ordinary length occupying 24% of body length.

The *Spathidium bromelicola* group

The five species (one split in two subspecies) bundled in this group are medium to large-sized (120–200 μm), rather slender (5–7:1) and, especially, have comparatively short extrusomes (≤10 μm). Generally, most members of the *Spathidium bromelicola* group resemble species of the *Spathidium muscicola* group (not treated in present book; usually stouter, i.e., 3–4:1; extrusomes ≥20 μm long) and the *Spathidium elongatum* group (see above; usually longer, i.e., 200–300 μm; extrusomes with argyrophilic ends).

The species of the *Spathidium bromelicola* group lack prominent features and are thus difficult to distinguish, that is, mostly by morphometrics clearly recognizable only in protargol preparations (Table 3.4). Nonetheless, all are distinct units differing in quite a lot of features, including some main characteristics, such as the number of ciliary rows (10 vs. 20), the shape of the extrusomes (rod-like vs. acicular), and the macronucleus type (cylindroidal vs. long tortuous).

Table 3.4 Features distinguishing five species of the *Spathidium bromelicola* group.[a] For morphometric details, see Tables 3.5–3.8

Characteristic	*Spathidium*					
	bromelicola	*etoschense*	*aciculare*	*rusticanum*	*saprophilum saprophilum*	*saprophilum curvioplites*
Body size in vivo	190 × 30	160 × 25	150 × 30	235 × 27	120 × 20	120 × 20
Body length: width, ratio	6.3	6.4	5.0	5	6	6
Macronucleus, spread length	224	57	130	75	52	?
Extrusomes, length	4	8	8	5	3	4
Extrusomes, shape	narrowly ovate to bluntly fusiform	very narrowly ovate	very narrowly ovate to acicular	rather thick rods	rather thick rods	bluntly fusiform and curved
Ciliary rows, average number	20	10	19	16	11	12
Dorsal brush, % of body length	23	12	26	12	23	22
Dorsal brush, type	isostichad	heterostichad	heterostichad	heterostichad	isostichad	isostichad
Tail of brush row 3	heteromorphic	isomorphic	isomorphic	heteromorphic	isomorphic	?
Brush dikinetids, total number	97	35	84	36	42	64
Oral bulge, shape	narrowly oblong (~7.4:1)	slightly cuneate (~5:1)	oblong (~3.3:1)	oblong	slightly cuneate	slightly cuneate
Oral bulge, length	40	23	18	18	19	19
Oral bulge length:body width, ratio	1.5	1.0	0.6	0.7	1.1	1.1

[a] All measurements in μm.

Spathidium bromelicola Foissner, Wolf, Kumar, Xu & Quintela-Alonso, 2014

(Tables 3.4, 3.5)

2014 ***Spathidium bromelicola* nov. spec.** – Foissner, Wolf, Kumar, Xu & Quintela-Alonso, Acta Protozool. 53: 180, Fig. 16a–k, 17a–i, 18a–j, Table 6 (original description. The slide containing the holotype [Fig. 16g–i in Foissner et al. 2014] and 2 paratype slides have been deposited in the Biology Centre of the Upper Austrian

Museum in Linz [LI] according to Foissner et al. 2014, p. 183. However, the species is not mentioned by Aescht 2018, p. 486).

Remarks: For details (nomenclature, type locality, description, morphometry, illustrations and micrographs, occurrence and ecology, remarks), see Foissner et al. (2014, p. 180).

Diagnosis (from Foissner et al. 2014, slightly modified): Body size about 190 × 30 µm in vivo. Body narrowly to very narrowly spatulate with steep to very steep, narrowly oblong oral bulge pointed ventrally and about 1.5 times as long as widest trunk region. Macronucleus long and tortuous; multimicronucleate. Extrusomes narrowly ovate to bluntly fusiform, about 4.0 × 0.8 µm in size. On average 20 ciliary rows, ventral and first left side row widely spaced anteriorly, producing an obtriangular, bare area in most specimens. Dorsal brush three-rowed, isostichad, occupies about 23% of body length; 25 widely spaced dikinetids in row 3. Type IV resting cysts.

continued on p. 65

Table 3.5 Morphometric data on *Spathidium bromelicola* (from Foissner et al. 2014)[a]

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Body, length	178.1	175.0	19.5	4.3	11.0	150.0	228.0	21
Body, width	27.1	26.0	4.6	1.0	17.1	20.0	36.0	21
Body length:width, ratio	6.7	6.7	1.1	0.2	15.9	5.4	8.8	21
Oral bulge, length	39.8	39.0	4.4	1.0	11.0	33.0	52.0	21
Oral bulge (circumoral kinety), width	5.4	5.0	–	–	–	5.0	6.0	7
Oral bulge, height	3.8	4.0	–	–	–	3.0	4.0	21
Oral bulge length:body width, ratio	1.5	1.4	0.2	0.1	16.0	1.2	1.9	21
Circumoral kinety to last dikinetid of brush row 1, distance	36.3	35.0	4.4	1.0	12.1	30.0	47.0	21
Circumoral kinety to last dikinetid of brush row 2, distance	40.4	40.0	5.4	1.2	13.3	32.0	56.0	21
Circumoral kinety to last dikinetid of brush row 3, distance	35.8	36.0	4.4	1.0	12.4	26.0	47.0	21
Anterior body end to macronucleus, distance	53.3	55.0	11.0	2.4	20.6	34.0	76.0	21
Macronucleus figure, length	91.0	94.0	19.9	4.3	21.9	55.0	132.0	21
Macronucleus, length (spread and thus approximate)	223.8	240.0	–	–	–	150.0	300.0	21
Macronucleus, width in mid	4.8	5.0	0.7	0.2	14.7	4.0	6.0	21
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Micronuclei, diameter	3.3	3.0	0.5	0.1	16.5	3.0	5.0	21
Micronuclei, number	11.6	11.0	2.3	0.5	19.7	9.0	16.0	21
Somatic kineties, number	19.6	20.0	1.3	0.3	6.5	17.0	21.0	21
Kinetids in a right-side kinety, number	94.0	90.0	21.8	4.8	23.2	63.0	155.0	21
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Dikinetids in brush row 1, number	32.3	31.0	4.7	1.0	14.4	25.0	42.0	21
Dikinetids in brush row 2, number	39.0	38.0	5.6	1.2	14.3	33.0	53.0	21
Dikinetids in brush row 3, number	25.4	25.0	3.7	0.8	14.4	21.0	33.0	21

[a] Data based on mounted, protargol-prepared (Foissner's method), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean.

Table 3.6 Morphometric data on *Spathidium aciculare* (upper line; from Foissner et al. 2002) and *Spathidium etoschense* (lower line; from Foissner et al. 2002)[a]

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Body, length	137.3	140.0	25.5	5.9	18.6	85.0	185.0	19
	145.0	145.0	15.9	5.3	10.9	123.0	180.0	9
Body, width	31.5	32.0	3.4	0.8	10.9	26.0	38.0	19
	22.7	22.0	4.9	1.6	21.8	17.0	32.0	9
Body length:width, ratio	4.4	4.3	0.9	0.2	20.2	2.9	6.6	19
	6.7	6.7	1.4	0.5	20.3	4.1	8.2	9
Oral bulge, length	18.4	19.0	2.6	0.6	14.2	12.0	22.0	19
circumoral kinety	22.7	23.0	4.1	1.4	17.9	16.0	29.0	9
Oral bulge, width between	5.5	6.0	0.7	0.2	12.9	4.0	6.0	10
	–	–	–	–	–	–	–	–
Oral bulge, height	3.1	3.0	0.5	0.1	15.6	2.0	4.0	19
	–	–	–	–	–	–	–	–
Circumoral kinety to last dikinetid	26.0	25.0	3.8	0.9	14.6	18.0	33.0	19
of brush row 1, distance	8.0	7.0	3.8	1.4	54.7	4.0	14.0	7
Circumoral kinety to last dikinetid	33.3	35.0	6.8	1.6	20.5	18.0	45.0	19
of brush row 2, distance	18.1	17.0	3.0	1.1	16.4	14.0	23.0	7
Circumoral kinety to last dikinetid	31.2	31.0	7.9	1.8	25.4	9.0	45.0	19
of brush row 3, distance	13.3	13.0	4.0	1.5	30.0	7.0	20.0	7
Anterior body end to macronucleus,	40.3	35.0	12.4	2.9	30.9	23.0	66.0	19
distance	–	–	–	–	–	–	–	–
Macronuclear figure, length	78.5	77.0	23.1	5.3	29.4	45.0	123.0	19
	42.7	39.0	14.5	4.8	33.9	24.0	76.0	9
Macronucleus, length	129.7	140.0	–	–	–	60.0	190.0	19
(spread, data thus approximate)	57.1	55.0	–	–	–	44.0	90.0	9
Macronucleus, width	5.5	5.0	0.8	0.2	15.2	5.0	8.0	19
	6.4	6.0	0.7	0.2	11.3	6.0	8.0	9
Micronucleus, length	2.2	2.0	–	–	–	1.2	3.0	19
	–	–	–	–	–	–	–	–
Micronucleus, width	1.8	1.8	–	–	–	1.2	3.0	19
	–	–	–	–	–	–	–	–
Micronuclei, number				many				
	3.1	3.0	1.1	0.4	34.3	2.0	5.0	7
Somatic kineties, number	18.8	19.0	1.5	0.4	8.2	16.0	23.0	19
	10.4	11.0	1.1	0.4	10.9	9.0	12.0	9
Ciliated kinetids in a right-side	93.1	91.0	13.7	3.1	14.7	65.0	120.0	19
kinety, number	64.0	68.0	9.1	3.7	14.2	46.0	70.0	6
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
	3.1	3.0	–	–	–	3.0	4.0	7
Dikinetids in brush row 1, number	22.8	23.0	4.2	1.0	18.2	17.0	34.0	19
	5.4	6.0	2.1	0.7	39.8	3.0	8.0	7
Dikinetids in brush row 2, number	34.3	36.0	6.1	1.4	17.8	19.0	43.0	19
	17.6	19.0	3.9	1.5	22.0	12.0	21.0	7
Dikinetids in brush row 3, number	26.7	27.0	5.1	1.2	19.2	12.0	38.0	19
	12.3	12.0	2.0	0.7	16.1	9.0	15.0	7

Table 3.6 Continued

[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.

Spathidium aciculare Foissner, Agatha & Berger, 2002

(Tables 3.4, 3.6)

2002 ***Spathidium aciculare* nov. spec.** – Foissner, Agatha & Berger, Denisia 5: 258, Fig. 56a–l, 332e–h, Tables 47, 48 (original description. The slide [accession number 2002/711] containing the holotype [Fig. 56h, i in Foissner et al. 2002] and 4 paratype slides [2002/712–715] have been deposited in the Biology Centre of the Upper Austrian Museum in Linz [LI], see Foissner et al. 2002, p. 42 and Aescht 2008, p. 140).

2007 ***Spathidium aciculare* Foissner, Agatha & Berger, 2002** – Vdačný & Tirjaková, Biologia, Bratislava 62: 726, Fig. 4A–F, 6H (description of population from Slovakia; site where slides deposited not mentioned).

Remarks: For details (nomenclature, type locality, type material, description, morphometry, illustrations and micrographs, occurrence and ecology, remarks) on type population from Australia, see Foissner et al. (2002, p. 258). For comparison with similar species, see Table 3.4. For details on the population from the litter layer of a floodplain from Slovakia, see Vdačný & Tirjaková (2007, p. 726). This European population differs from the Australian type material in the monokinetidal tail of brush row 3 and the length of the extrusomes (Vdačný & Tirjaková 2007).

On superficial observation, easily confused with *Spathidium stammeri* Wenzel, 1959 (extrusomes rod-shaped, oral bulge dumbbell-shaped, dorsal brush isostichad).

Diagnosis (from Foissner et al. 2002, slightly modified): Body size about 150 × 30 μm in vivo. Body shape narrowly spatulate with steep to very steep, oblong oral bulge about two thirds as long as widest trunk region. Macronucleus long and tortuous; multimicronucleate. Extrusomes very narrowly ovate to acicular, about 8 × 1 μm in size. On average 20 ciliary rows, 3 anteriorly differentiated to heterostichad dorsal brush occupying about 26% of body length.

Spathidium etoschense Foissner, Agatha & Berger, 2002

(Tables 3.4, 3.6)

2002 ***Spathidium etoschense* nov. spec.** – Foissner, Agatha & Berger, Denisia 5: 255, Fig. 55a–j, 327j–l, Table 45 (original description. The slide [accession number 2002/17] containing the holotype [Fig. 55e, f in Foissner et al. 2002] and 5 paratype slides [2002/18–22] have been deposited in the Biology Centre of the Upper Austrian Museum in Linz [LI], see Foissner et al. 2002, p. 42 and Aescht 2008, p. 154).

Remarks: For details (nomenclature, type locality, description, morphometry, illustrations and micrographs, occurrence and ecology, remarks) on type population from Namibia, see Foissner et al. (2002, p. 255).

For comparison with similar species, see Table 3.4. Further, size and shape of *Spathidium etoschense* resemble members of the *Spathidium procerum* group (extrusomes rod- shaped; macronucleus distinctly longer; for brief note on this group, see p. 34) and *Apospathidium*

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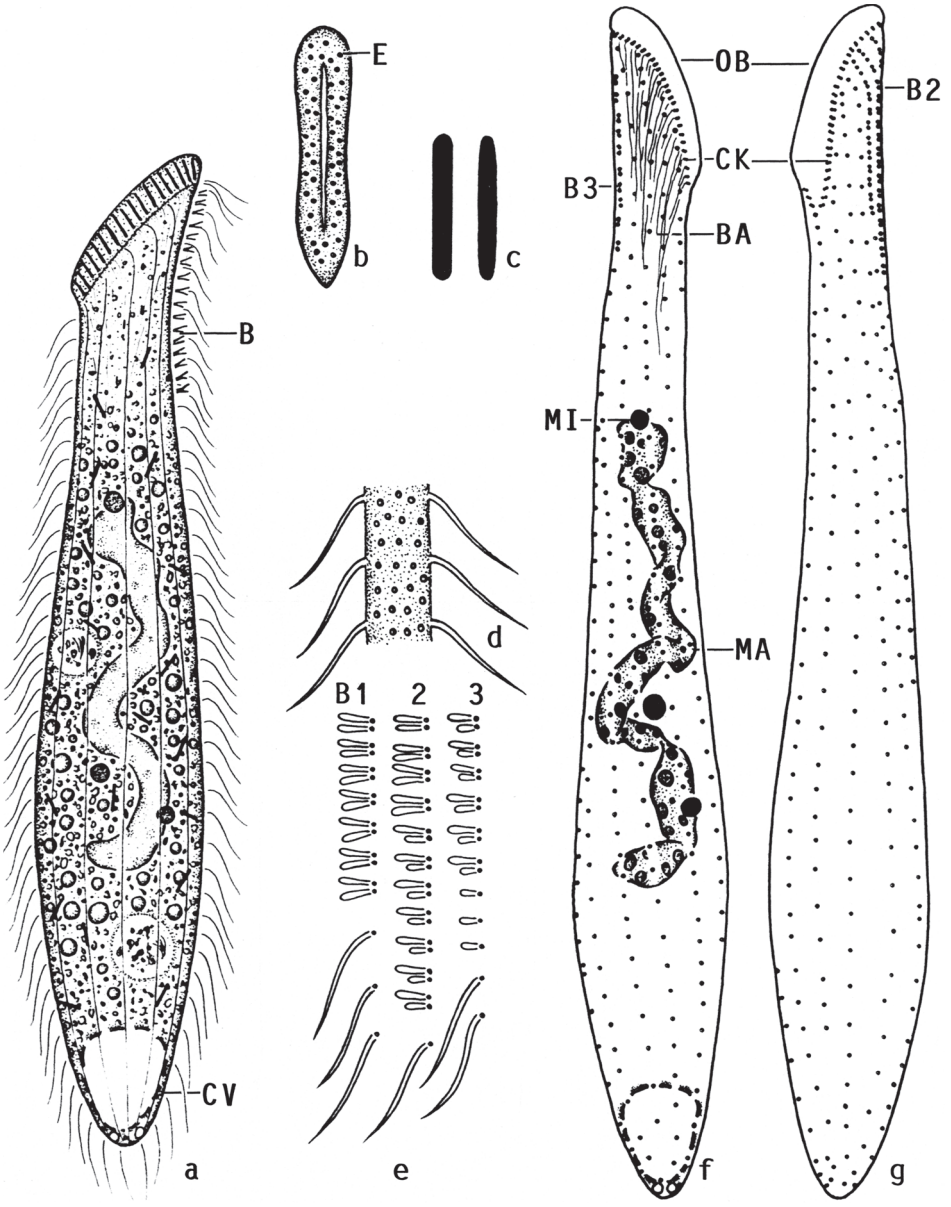

Fig. 3.7a–g *Spathidium saprophilum saprophilum* nov. subspec. (originals. a–e, from life; f, g, protargol preparation). **a:** Left lateral view of a representative specimen showing, inter alia, the dorsal brush, the nuclear apparatus, and the contractile vacuole, 120 μm. **b:** Frontal view of oral bulge packed with extrusomes. **c:** Oral bulge extrusomes, length 3 μm. **d:** Surface view showing cortical granulation somatic cilia of two ciliary rows. **e:** Posterior portion of dorsal brush, largest bristles 4–5 μm long. **f, g:** Ciliary pattern of right (f) and left (g) side and nuclear apparatus of holotype specimen, 128 μm. B – dorsal brush, B1–3 – dorsal brush rows, BA – oral basket, CK – circumoral kinety, CV – contractile vacuole, E – extrusome, MA – macronucleus, MI – micronucleus, OB – oral bulge.

longicaudatum (Buitkamp, 1977) (see Chapter 4, that is, Foissner et al. 2025b) (extrusomes rod-shaped; body tail-like narrowed posteriorly). *Spathidium elmenteitanum* Dietz, 1965 has a similar nucleus as *Spathidium etoschense*, but is only 65–80 × 12–18 µm in size and has very fine, 3 µm long extrusomes (Dietz 1965).

Few specimens were available (Foissner et al. 2002). Thus, more detailed morphometrics should be collected from a more abundant population.

Diagnosis (from Foissner et al. 2002, slightly modified): Body size about 160 × 25 µm in vivo. Narrowly to very narrowly spatulate with steep to very steep, cuneate to narrowly cuneate oral bulge about as long as widest trunk region. Macronucleus curved-cylindroidal, approximately 60 µm long; 3 micronuclei on average. Extrusomes very narrowly ovate, about 8 × 1 µm in size. On average 10 ciliary rows, 3 anteriorly differentiated to heterostichad dorsal brush occupying about 12% of body length.

Spathidium saprophilum nov. spec.

(Fig. 3.7a–s, 3.8a–m, Tables 3.4, 3.7)

Nomenclature: The species-group name *saprophilum* is a composite of the Greek words *sapros* (putrid; Hentschel & Wagner 1996, p. 529) and *philos* (loving; Hentschel & Wagner 1996, p. 471), referring to the saprobic habitats the taxa were discovered.

Diagnosis: Body size 120 × 20 µm in vivo. Body shape narrowly to very narrowly spatulate with oblique, slightly cuneate oral bulge about as long as widest trunk region. Macronucleus a tortuous strand; multimicronucleate. Extrusomes rod-shaped or bluntly fusiform and curved, 3–4 µm long. About 11 or 12 ciliary rows, three anteriorly modified to inconspicuous, isostichad dorsal brush occupying circa 23% of body length; brush rows 1 and 3 of similar length and composed of 13 or 17 and 12 or 20 dikinetids, brush row 2 slightly longer than rows 1 and 3, composed of 17 or 26 dikinetids.

Type locality: Activated sludge tank of sewage treatment plant of a paper mill (about 47°47'N 13°40'E) in the town of Hallein, Salzburg, Austria.

Type material: The slide (Fig. 3.7n, o; accession number 2024/133) with the holotype (Fig. 3.7f, g) and two paratype slides (Fig. 3.7p–s; 2024/134, 135) have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI).

ZooBank registration of *Spathidium saprophilum* nov. spec.: urn:lsid:zoobank.org:act:166F2715-08B0-42D6-A1FA-82CAEB619184

Nominotypical subspecies: *Spathidium saprophilum saprophilum* nov. subspec.

Subspecies assigned: *Spathidium saprophilum saprophilum* nov. subspec. (nominotypical subspecies); *Spathidium saprophilum curvioplites* nov. subspec.

Remarks: We split this species into two subspecies, differing by two subtle features, viz., the shape of the extrusomes (rod-like vs. bluntly fusiform and curved) and the non-overlapping number of dikinetids in all three brush rows (Table 3.7). Generally, such differences are sufficient to separate morphotypes at species level. However, the number of brush dikinetids is often rather variable within and between populations, and the extrusomes are small and details thus difficult to recognize. Further, both morphotypes occur in the same type of habitat, that is, activated sludge. Thus, we prefer to consider them as subspecies at the present state of knowledge.

Within the *Spathidium bromelicola* group, *Spathidium saprophilum* is likely most closely related to *Spathidium rusticanum* Foissner, 1981 (p. 276), although the brush length suggests *Spathidium bromelicola* (p. 62) and *Spathidium aciculare* (p. 65) as closest relatives (for differentiation, see *Spathidium rusticanum* [p. 74] and Table 3.4).

Spathidium saprophilum saprophilum nov. subspec.

(Fig. 3.7a–s, Tables 3.4, 3.7)

Nomenclature: This is the nominotypical subspecies of *Spathidium saprophilum* nov. spec. For etymology, see species.

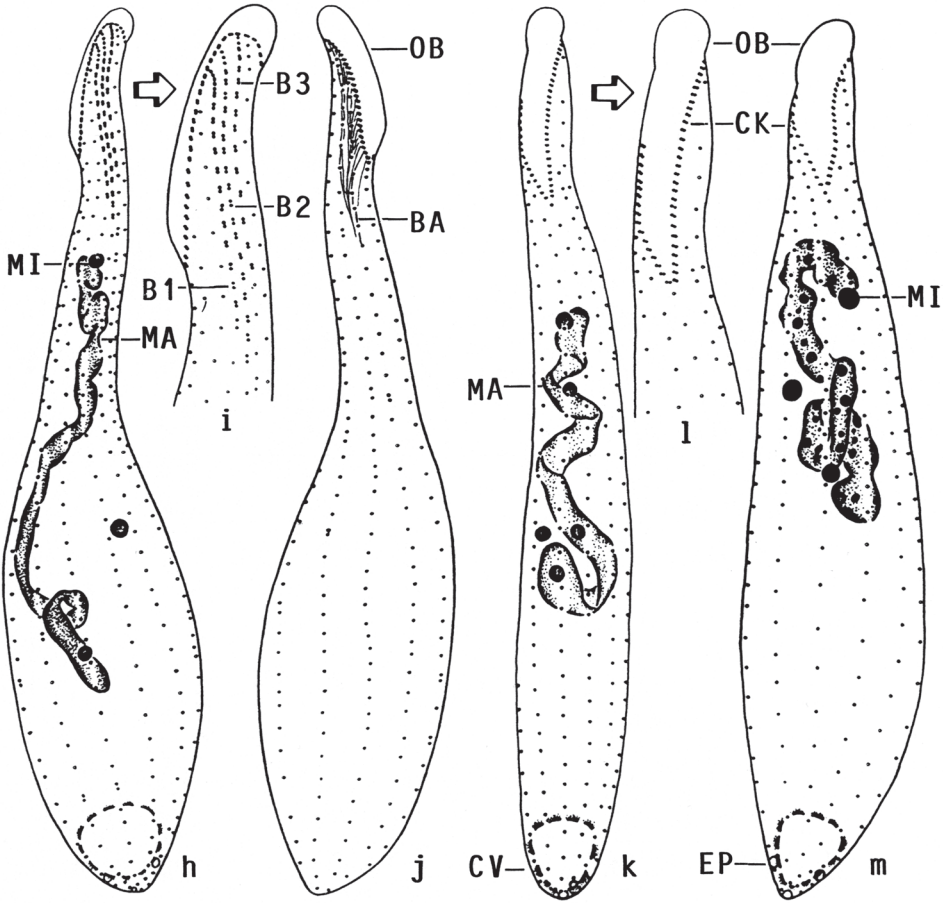

Fig. 3.7h–m *Spathidium saprophilum saprophilum* nov. subspec. (originals. Protargol preparation). Ciliary pattern and nuclear apparatus. **h–j:** Ciliary pattern of left (h) and right (j) side of body and of left anterior body portion (i) of a specimen inflated posteriorly, 125 µm. **k–m:** Ciliary pattern of ventral side and nuclear apparatus of two paratype specimens, 104 µm (k), 98 µm (m). B1–3 – dorsal brush rows, BA – oral basket, CK – circumoral kinety, CV – contractile vacuole, EP – excretory pores of contractile vacuole, MA – macronucleus, MI – micronucleus, OB – oral bulge.

Diagnosis: Extrusomes rod-shaped with narrowed ends. Brush kinetids widely spaced. On average 13 dikinetids in brush row 1, 17 in row 2, and 12 in row 3.

Type locality: Same as for *Spathidium saprophilum* nov. spec., that is, activated sludge tank of sewage treatment plant of a paper mill (about 47°47'N 13°40'E) in the town of Hallein, Salzburg, Austria.

Type material: Same as for *Spathidium saprophilum* nov. spec., that is, the slide (Fig. 3.7n, o; accession number 2024/133) with the holotype (Fig. 3.7f, g) and two paratype slides (Fig. 3.7p–s; 2024/134, 135) have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI).

ZooBank registration of *Spathidium saprophilum saprophilum* nov. subspec.: Same as for species.

Remarks: See discussion under species and Table 3.4.

Description: Body size 80–180 × 10–30 µm in vivo, usually near 120 × 20 µm; length: width ratio 3.4-11.5:1, on average 6:1 both in vivo and protargol preparations (Table 3.7). Body shape fairly constant in vivo, that is, narrowly spatulate to very narrowly spatulate, anterior (oral) body end obliquely truncate, widest in or underneath mid-body, posterior end narrowly rounded; rear half frequently slightly to distinctly inflated in preparations, causing high variability of length:width ratio (Fig. 3.7a, f, h, k; Table 3.7). Macronucleus in middle third of cell, usually a tortuous strand about half as long as body, flattened band-like in circa 10% of specimens; contains many large and small nucleoli. Several micronuclei 2–3 µm across attached or near to macronucleus, one invariably at its anterior end (Fig. 3.7a, f, h, k, m; Table 3.7). Contractile vacuole in rear end, several excretory pores in posterior pole area. Extrusomes accumulated in oral bulge and scattered in cytoplasm, rod-shaped to very narrowly ellipsoidal, about 3 µm long (Fig. 3.7a–c); do not impregnate with the protargol method used. Cortex very flexible, contains several rows of minute (about 0.2 µm), colourless granules between each two kineties. Cytoplasm colourless and often studded with lipid droplets 1–4 µm across. Swims rather rapidly by rotation about main body axis with anterior third performing larger circle than posterior.

Somatic cilia about 8 µm long in vivo, ordinarily spaced, arranged in an average of 11 equidistant, bipolar rows abutting on circumoral kinety in *Spathidium* pattern. Dorsal brush dikinetidal, three-rowed and isostichad, occupies about 22% of body length; all rows have some ordinary cilia anteriorly and continue as somatic kineties posteriorly. Dorsal bristles up to 4–5 µm long in vivo, their pattern highly similar in vivo and in protargol preparations (Fig. 3.7e): bristles of dikinetids of row 1 of same length, posterior bristle shortened in rear half of row 2 and in entire row 3. Brush row 1 composed of an average of 13 dikinetids, longest row 2 of 17 dikinetids, row 3 equal to or slightly shorter than row 1, consists of an average of 12 dikinetids and a few monokinetidal bristles (Fig. 3.7a, f–m; Table 3.7).

Oral bulge of ordinary distinctness, slanted by 45–65°, about as long as widest trunk region, slightly cuneate and dumbbell-shaped in frontal view (Fig. 3.7a, b). Circumoral kinety more distinctly cuneate than oral bulge, composed of ordinarily spaced dikinetids forming continuous row. Oral basket only faintly impregnated with the protargol method used (Fig. 3.7f–m, Table 3.7).

Occurrence and ecology: As yet found only at the type locality (see above), where it was rare.

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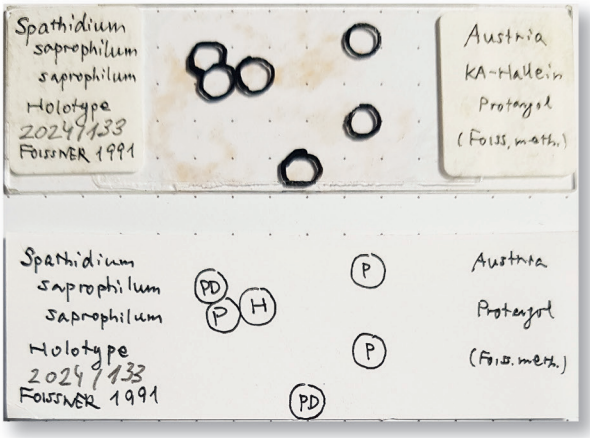
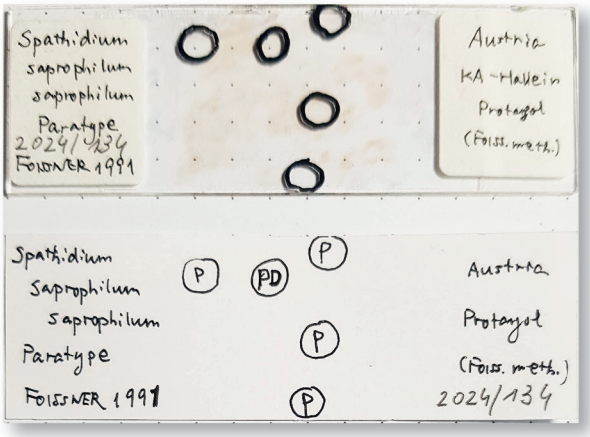


n

o

Fig. 3.7n–s *Spathidium saprophilum* nov. spec. and *Spathidium saprophilum sapophilum* nov. subspec. (originals. Protargol slides). **n, o:** Slide (n) and protocol (o) containing holotype (H), paratypes (P), and paratypes drawn (PD). Accession number (LI): 2024/133. **p, q:** Slide (p) and protocol (q) containing paratypes (P) and paratype drawn (PD). Accession number (LI): 2024/134. **r, s:** Slide (r) and protocol (s) containing paratypes (P). Accession number (LI): 2024/135.



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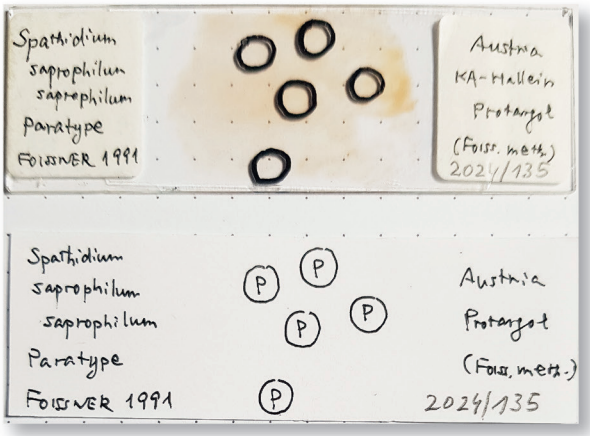

r

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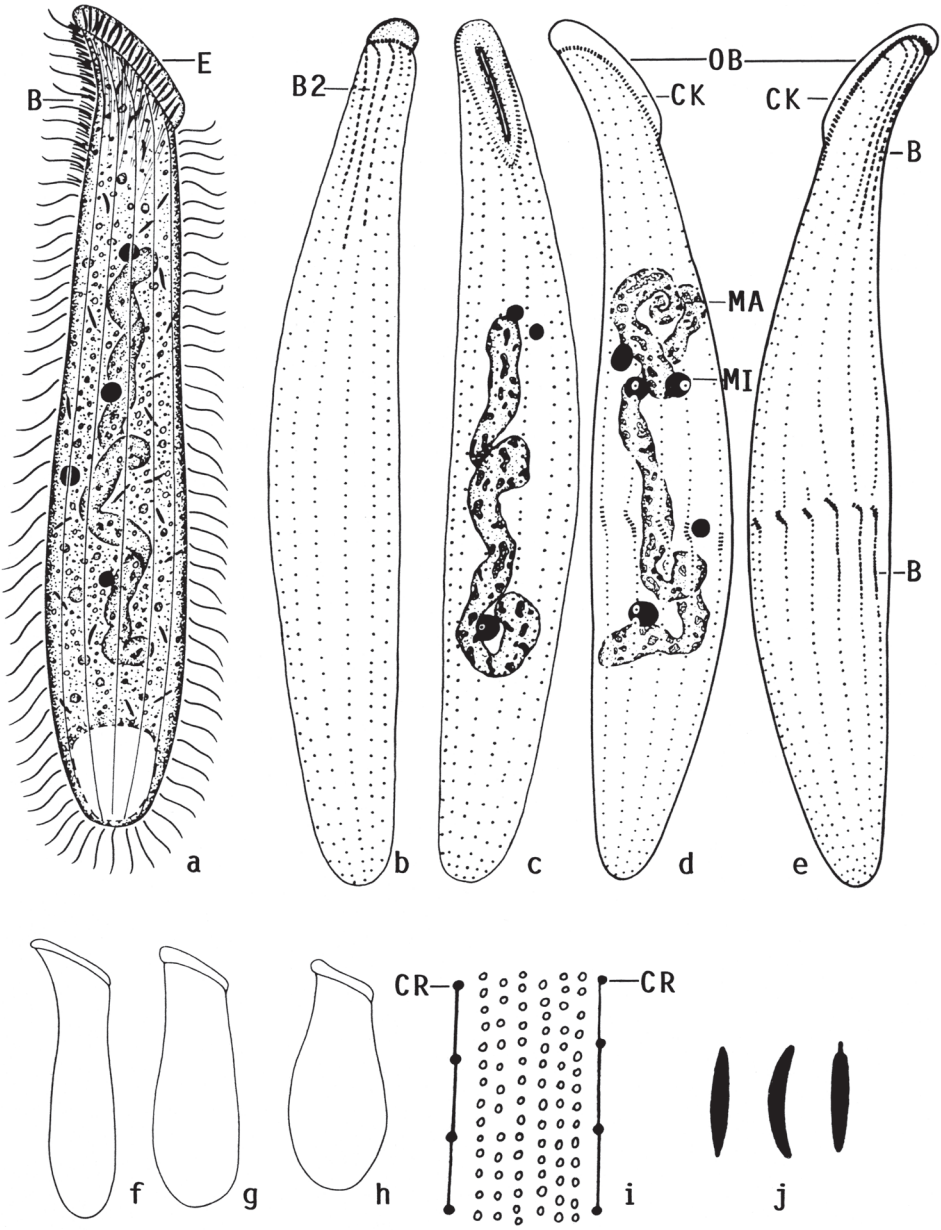
Fig. 3.8a–j *Spathidium saprophilum curvioplites* nov. subspec. (from Augustin & Foissner 1992. a, f–j, from life; b–e, protargol preparation). **a:** Right side view of a representative specimen showinh inter alia, the dorsal brush, the nuclear apparatus, and the contractile vacuole, 120 µm. **b, c:** Ciliary pattern of dorsal (b) and ventral (c) side and nuclear apparatus of holotype specimen, 115 µm. **d, e:** Right and left side view of an early divider, 135 µm. **f–h:** Shape variants. **i:** Cortical granulation. **j:** Extrusomes, length 4 µm. B – dorsal brush, B2 – dorsal brush row 2, CK – circumoral kinety, CR – ciliary rows, E – extrusomes, MA – macronucleus, MI – micronucleus, OB – oral bulge.



Spathidium saprophilum curvioplites **nov. subspec.**

(Fig. 3.8a–o, Tables 3.4, 3.7)

1992 ***Spathidium anguilla*** **Vuxanovici, 1962** – Augustin & Foissner, Arch. Protistenk. 141: 246, Abb. 2a–m, Tabelle 2 (Fig. 3.8a–m, Table 3.7; misidentification; description of Austrian population. Voucher slides with protargol-prepared specimens have been deposited in the Biology Centre of the Upper Austrian Museum

in Linz (LI), see Augustin & Foissner 1992, p. 244; now, these voucher slides become the type slides of *Spathidium saprophilum curvioplites* nov. subspec.).

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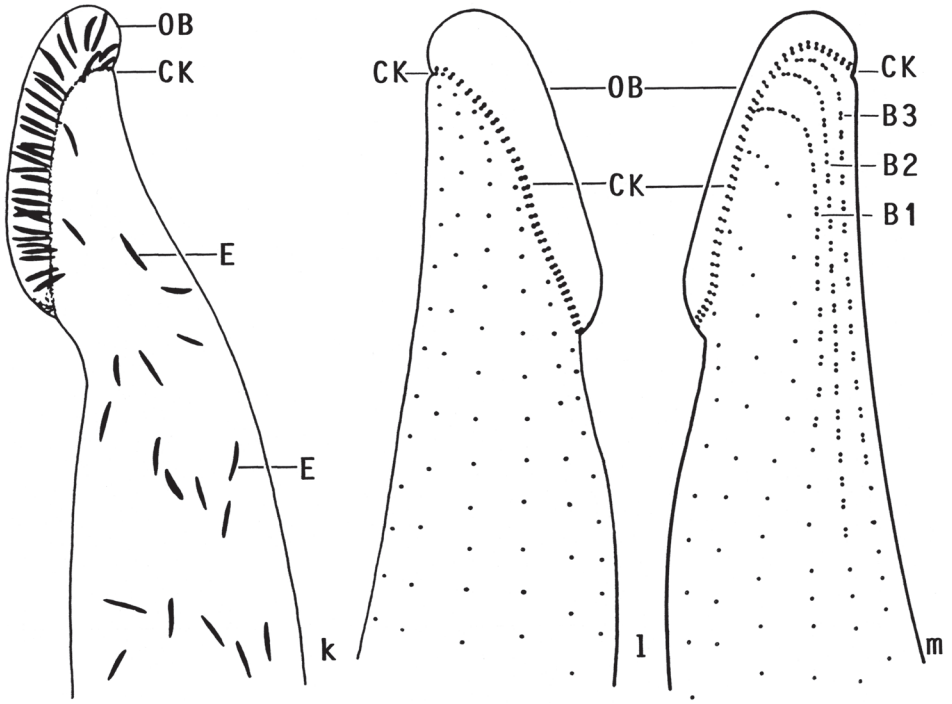


Fig. 3.8k–m *Spathidium saprophilum curvioplites* nov. subspec. (from Augustin & Foissner 1992. Protargol preparation). **k:** Anterior body portion with extrusomes, oral bulge length 28 µm. **l, m:** Ciliary pattern of right and left side in anterior body portion, oral bulge length 24 µm. B1–3 – dorsal brush rows, CK – circumoral kinety, E – extrusomes, OB – oral bulge.

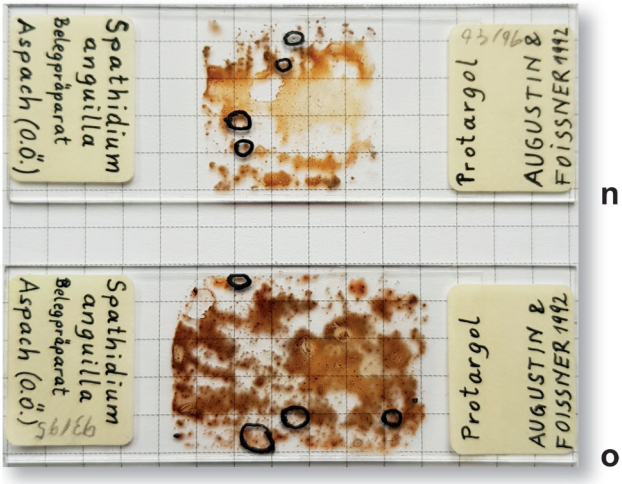


Fig. 3.8n, o *Spathidium saprophilum curvioplites* nov. subspec. (originals. Protargol slides). **n, o:** Slides containing holotype specimens and paratypes. Accession numbers (LI): 1993/95, 1993/96. Photo: Magdalini Christodoulou, Linz.

Table 3.7 Morphometric data on *Spathidium saprophilum saprophilum* nov. subspec. (upper line; original data) and *Spathidium saprophilum curvioplites* nov. subspec. (lower line; from Augustin & Foissner 1992)[a]

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Body, length	106.6	101.2	22.6	4.8	21.2	75.0	160.8	22
	112.8	109.0	20.6	–	18.3	67.0	139.0	27
Body, width	17.9	18.0	4.0	0.9	22.3	8.4	25.2	22
	17.3	16.0	3.6	–	20.8	13.0	29.0	28
Body length:width, ratio	6.2	5.9	1.8	0.4	29.4	3.4	11.5	22
			about 6.5					
Oral bulge, length	19.4	20.4	2.9	0.6	15.1	13.2	24.0	22
	19.1	19.0	3.0	–	15.9	12.0	26.0	28
Oral bulge, width	3.7	3.6	0.6	0.2	17.5	2.5	4.8	9
	–	–	–	–	–	–	–	–
Oral bulge, height	2.3	2.4	0.3	0.1	13.5	1.8	3.0	10
	2.9	3.0	0.5	–	18.7	2.0	4.0	28
Oral bulge length:body width, ratio	1.1	1.1	0.3	0.1	27.6	0.6	2.1	22
			about 1.1					
Circumoral kinety to last	20.3	19.2	3.8	1.0	18.8	13.2	26.4	16
dikinetid of brush row 1, distance	18.8	19.5	1.7	–	9.0	16.0	21.0	10
Circumoral kinety to last dikinetid	23.9	22.2	4.0	1.0	16.6	18.0	30.0	16
of brush row 2, distance	26.0	26.0	1.9	–	7.3	22.0	29.0	10
Circumoral kinety to last dikinetid	19.9	18.6	3.3	0.8	16.6	14.4	25.2	16
of brush row 3, distance	23.5	23.0	2.8	–	11.9	18.0	28.0	10
Anterior body end to	30.8	31.2	7.1	1.5	23.0	13.6	45.1	22
macronucleus, distance	–	–	–	–	–	–	–	–
Macronuclear figure, length	40.0	40.8	9.4	2.0	23.6	24.0	60.0	22
	52.6	52.0	13.1	–	24.9	21.0	77.0	28
Macronucleus, length	52.2	49.2	–	–	–	36.0	72.0	22
(spread, data thus approximate)	–	–	–	–	–	–	–	–
Macronucleus, width	3.5	3.6	0.6	0.1	16.2	2.4	4.8	22
	5.5	5.5	0.9	–	16.4	4.0	8.0	28
Micronucleus, diameter	2.0	2.0	0.3	0.1	15.1	1.5	2.4	22
	2.0	2.0	0.5	–	23.6	1.0	3.0	10
Micronuclei, number	3.6	3.0	0.8	0.2	23.3	3.0	5.0	22
	5.6	6.0	1.5	–	25.4	3.0	8.0	11
Somatic kineties, number	11.1	11.0	0.5	0.1	4.2	10.0	12.0	22
	12.0	12.0	0.7	–	5.5	11.0	13.0	15
Basal bodies in a somatic kinety,	42.9	44.0	7.0	1.5	16.3	28.0	58.0	21
number	47.8	49.5	12.2	–	25.6	31.0	67.0	10
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	17
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	10
Dikinetids in brush row 1, number	13.0	13.0	0.8	0.2	6.3	11.0	14.0	16
	17.4	17.5	1.5	–	8.7	15.0	20.0	10
Dikinetids in brush row 2, number	17.3	17.0	1.4	0.4	8.1	15.0	21.0	16
	26.3	26.0	2.2	–	8.4	23.0	30.0	10
Dikinetids in brush row 3, number	11.8	12.0	1.0	0.3	8.9	10.0	14.0	16
	20.2	20.5	2.4	–	12.1	17.0	24.0	10
Extrusomes, length[b]	2.9	3.0	0.4	–	13.3	2.0	4.0	27

Table 3.7 Continued

[a] Data based on mounted, protargol-prepared (Foissner's method), and randomly selected specimens from sewage treatment plants. 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] *Spathidium saprophilum curvioplites*.

Nomenclature: The species-group name *curvioplites* is a composite of *curv·us*, *-a*, *-um* (Latin adjective [m, f, n]; curved, crooked; Hentschel & Wagner 1996, p. 192), the thematic vowel *·i-*, and the Greek noun *hoplites* (man in armor; soldier, extrusome in present case; Brown 1954, p. 806), referring to the curved extrusomes, a main feature of the subspecies.

Diagnosis: Extrusomes curved and bluntly fusiform. Brush kinetids ordinarily spaced. On average 17 dikinetids in brush row 1, 26 in row 2, and 20 in row 3.

Type locality: Activated sludge tank of sewage treatment plant (48.1904°N 13.3009°E) in the municipality of Aspach, Upper Austria.

Type material: See also list of synonyms. We fix the specimen shown in Fig. 3.8b, c (= Fig. 2b, c in Augustin & Foissner 1992) as holotype. The slides (Fig. 3.8n, o; accession numbers 1993/95, 1993/96) containing the holotype and paratypes are deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI).

ZooBank registration: urn:lsid:zoobank.org:act:61A84712-3BE1-4F55-AC4A-B00325F0EC12

Remarks and description: For details see "Remarks" at *Spathidium anguilla* Vuxanovici, 1962 (p. 91). Briefly, Augustin & Foissner (1992) misidentified their population; it is now considered as a new subspecies of *Spathidium saprophilum*. It is highly similar to *Spathidium saprophilum saprophilum* nov. subspec., except of the features mentioned in the diagnosis (Table 3.4). Thus, we shall not provide an individual description, but refer to the detailed figures and figure explanations, the morphometric data, and to the discussion of the nominotypical subspecies. Further data, especially gene sequence analyses, are needed to check the validity of this taxon.

Occurrence and ecology: As yet found only at the type locality (see above).

Spathidium rusticanum Foissner, 1981

(Fig. 3.9a–x, 3.10a–n, Tables 3.4, 3.8)

1981 ***Spathidium rusticanum* nov. spec.**[5] – Foissner, Zool. Jb. Syst. 108: 276, Fig. 7a–d, 28–30 (Fig. 3.9a–d; original description; no type material deposited, see nomenclature).

1984 ***Spathidium rusticanum* Foissner, 1981** – Foissner, Stapfia, 12: 74, Tabelle 18 (Table 3.8; morphometric characterization of type population).

2002 ***Spathidium rusticanum* Foissner, 1981** - Foissner, Agatha & Berger, Denisia 5: 251, Fig. 54a–m, 327e, Tables 45, 46 (Fig.3.9o–x, Table 3.8; description of Namibian population; three voucher slides [accession

[5] Foissner (1981) provided the following diagnosis: "In vivo etwa 150 × 25µm großes, im vorderen Drittel halsartig verjüngtes und stark abgeflachtes *Spathidium* mit sehr schräg abgestutztem, etwa 20 µm langem Mundwulst und kettenartigem Makronucleus, der aus ungefähr 25, durch breite Brücken verbundenen, etwa 4 × 2,5 µm großen Nodien besteht. 17 dicht bewimperte Somakineten."

numbers 2002/426–428] have been deposited in the Biology Centre of the Upper Austrian Museum in Linz [LI] according to Foissner et al. 2002, p. 43).

Nomenclature: No etymology has been given in the original description or a later work. The species-group name *rustican·us*, *-as*, *-um* (Latin adjective [m, f, n]; rustic, rough, uncouth; frag-cesar.de, accessed 20 May 2023) refers to the rural area (alpine meadow) the species was discovered.

Foissner (1981) made no comment about the whereabout of the type material. According to Aescht (2008, p. 195), type material is neither designated nor deposited. One of use (H. Berger) checked the original notes made by W. Foissner. The specimen shown in Fig. 3.9b, c (= Fig. 7b, c in Foissner 1981) is (very likely) on slide "P34" of the "Seppenbauer 78" slide series. According to a short note on the accompanying document to this slide, W. Foissner noted that this slide is in the Biology Centre of the Upper Austrian Museum in Linz. H. Berger checked the slide collection in the museum in Linz (LI) but could not find the slide. Further, the huge slide collection in the private archive of W. Foissner was checked, but likewise the slide could not be found in reasonable time. At the latest when the complete slide collection of W. Foissner is transferred to Linz, the type material of the present species will be deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI).

Diagnosis (based on three populations, see first paragraph of description below): Body size usually 120–150 × 25–30 μm in vivo. Body narrowly spatulate with oblique, oblong oral bulge in vivo about as long as widest trunk region. Macronucleus usually a tortuous, nodulated strand; multimicronucleate. Oral extrusomes rod-shaped with narrowed ends, 4–6 μm long. On average 13–18 ciliary rows, 3 anteriorly modified to inconspicuous, heterostichad dorsal brush occupying only 10–13% of body length; brush row 1 slightly shorter than row 2, row 3 distinctly shortened and composed of about 6 dikinetids.

Material investigated: Three voucher slides (Fig. 3.10i–n; accession numbers 2024/136, 137, 138) of the Italian population described here (Fig. 3.9e–n) have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI).

Remarks: This is a quite "usually" looking *Spathidium* without any prominent feature. Thus, and because the best characteristics, viz., the nodulated macronucleus and the dorsal brush, are clearly recognizable only in prepared specimens, it is difficult to identify. The species might even consist of two taxa because the Italian population is rather different, that is, has only 13 ciliary rows (vs. 18 [Austria] and 15 [Namibia]; Table 3.8) frequently abutting on circumoral kinety in *Protospathidium*-like pattern.

Spathidium rusticanum highly resembles *Spathidium saprophilum* nov. spec. (p. 67) which also may have a nodulated macronucleus. Thus, the best distinguishing feature is the dorsal brush, whose pattern is highly stable in the three populations of *Spathidium rusticanum* and the two of *Spathidium saprophilum*. The dorsal brush occupies 10–13% of body length in *Spathidium rusticanum*, while 22–23% in *Spathidium saprophilum*. Further, the brush is heterostichad in *Spathidium rusticanum*, while isostichad in *Spathidium saprophilum*, that is, row 3 is distinctly (≥50%) shortened in the former, while only slightly in the latter.

Description: The description includes the two populations cited in the list of synonyms (type population from Austria; population from Namibia) and an Italian population studied in the course of the present work. The Italian population, which developed in a highly saline sample, was selected for well-preserved specimens because rather many cells were inflated or

continued on p. 81

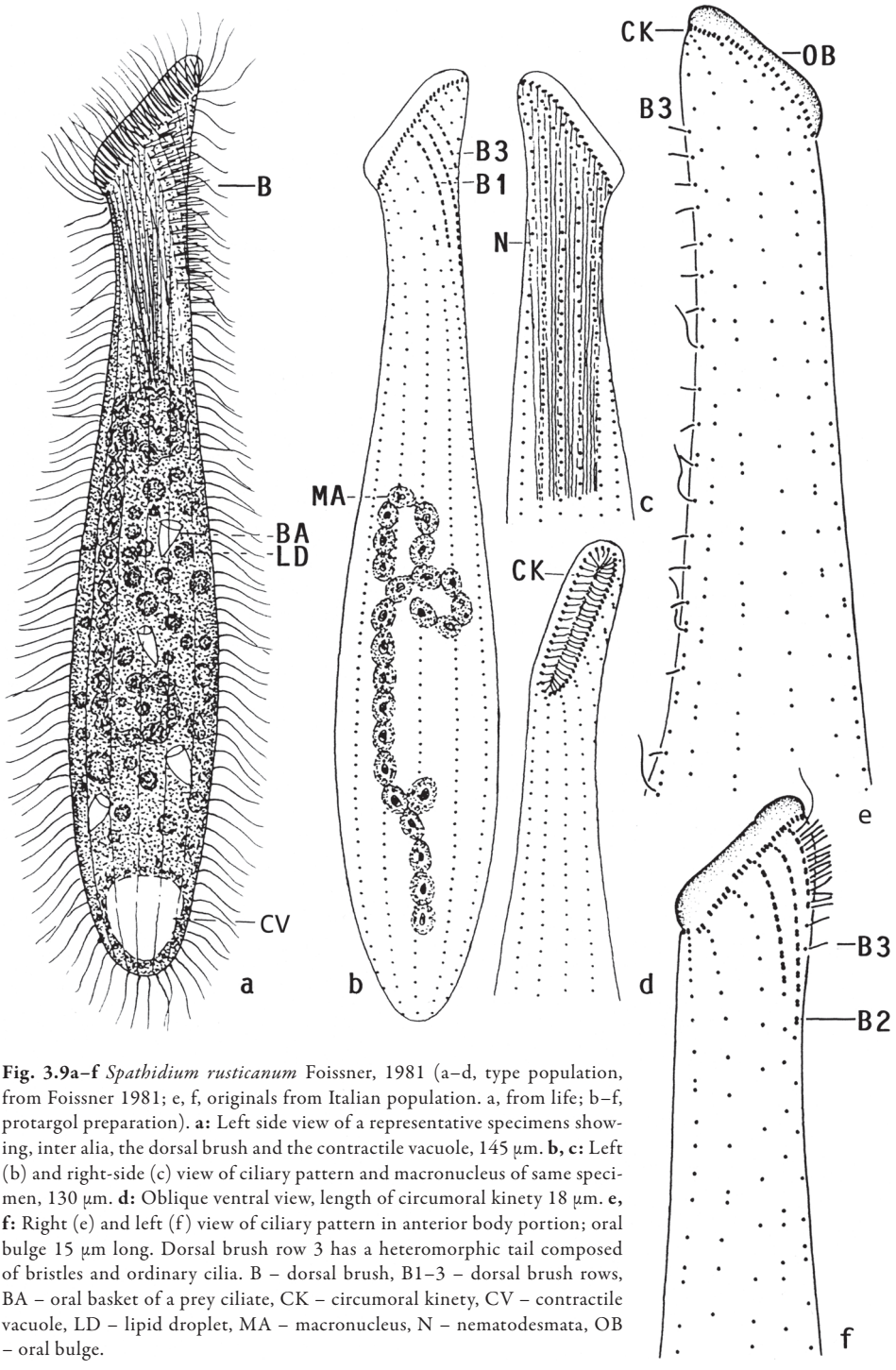


Fig. 3.9a–f *Spathidium rusticanum* Foissner, 1981 (a–d, type population, from Foissner 1981; e, f, originals from Italian population. a, from life; b–f, protargol preparation). **a:** Left side view of a representative specimens showing, inter alia, the dorsal brush and the contractile vacuole, 145 µm. **b, c:** Left (b) and right-side (c) view of ciliary pattern and macronucleus of same specimen, 130 µm. **d:** Oblique ventral view, length of circumoral kinety 18 µm. **e, f:** Right (e) and left (f) view of ciliary pattern in anterior body portion; oral bulge 15 µm long. Dorsal brush row 3 has a heteromorphic tail composed of bristles and ordinary cilia. B – dorsal brush, B1–3 – dorsal brush rows, BA – oral basket of a prey ciliate, CK – circumoral kinety, CV – contractile vacuole, LD – lipid droplet, MA – macronucleus, N – nematodesmata, OB – oral bulge.

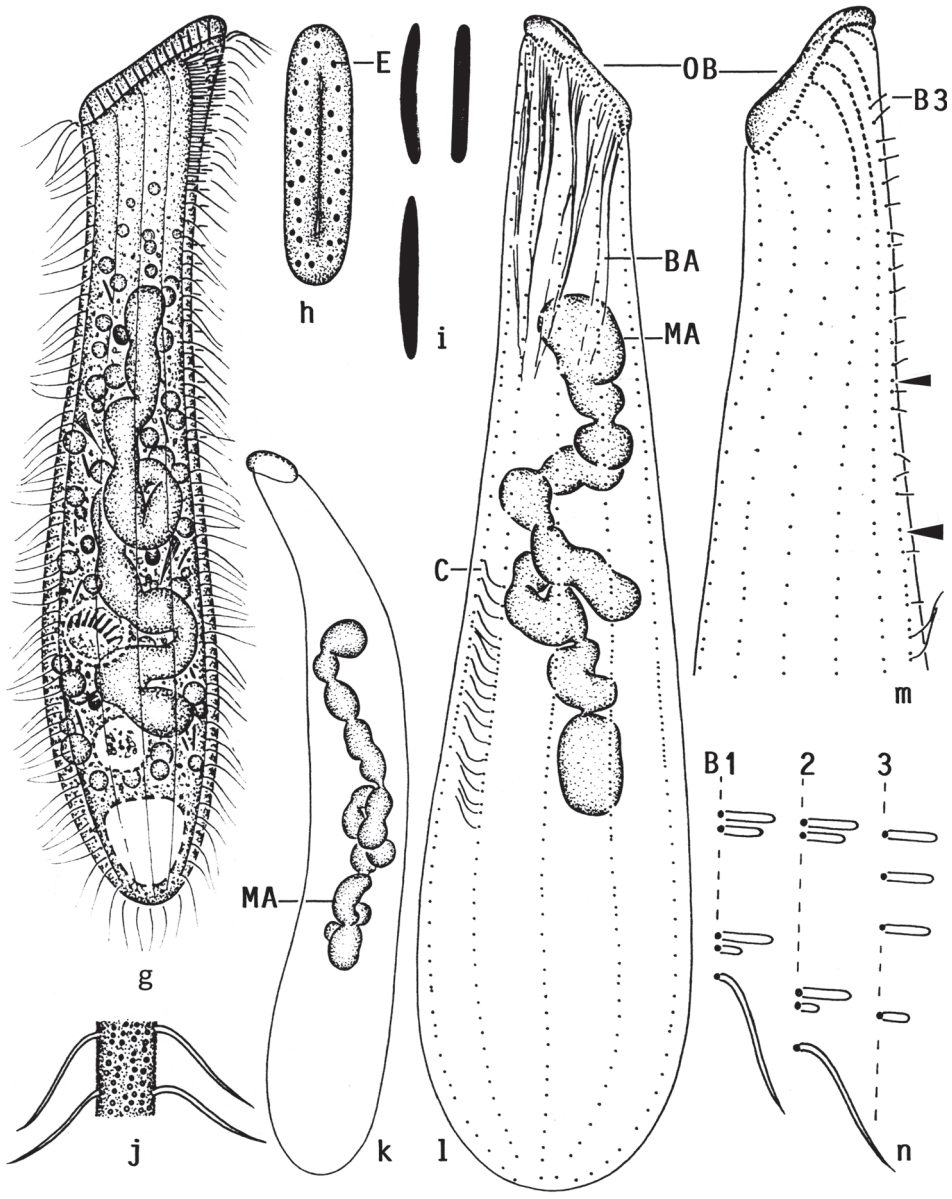


Fig. 3.9g–n *Spathidium rusticanum* Foissner, 1981 (Italian population, originals. g–j, n, from life; k–m, protargol preparation). **g:** Left side view of a representative specimen showinh, inter alia, dorsal brush, nuclear apparatus, and contractile vacuole, 150 µm. **h:** Frontal view of oral bulge showing distribution of extrusomes. **i:** Oral bulge (upper two) and cytoplasmic (lower one) extrusomes, length 4 µm. **j:** Surface view showing cortical granulation. **k:** Macronucleus, 122 µm. **l, m:** Ciliary pattern of right and left side and macronucleus of a very early divider, 138 µm. Arrowheads mark barren basal bodies within the bristle tail of brush row 3. **n:** Posterior half of dorsal brush, bristles up to 4 µm long. B1–3 – dorsal brush rows, BA – oral basket, C – cilia, E – extrusomes, MA – macronucleus, OB – oral bulge.

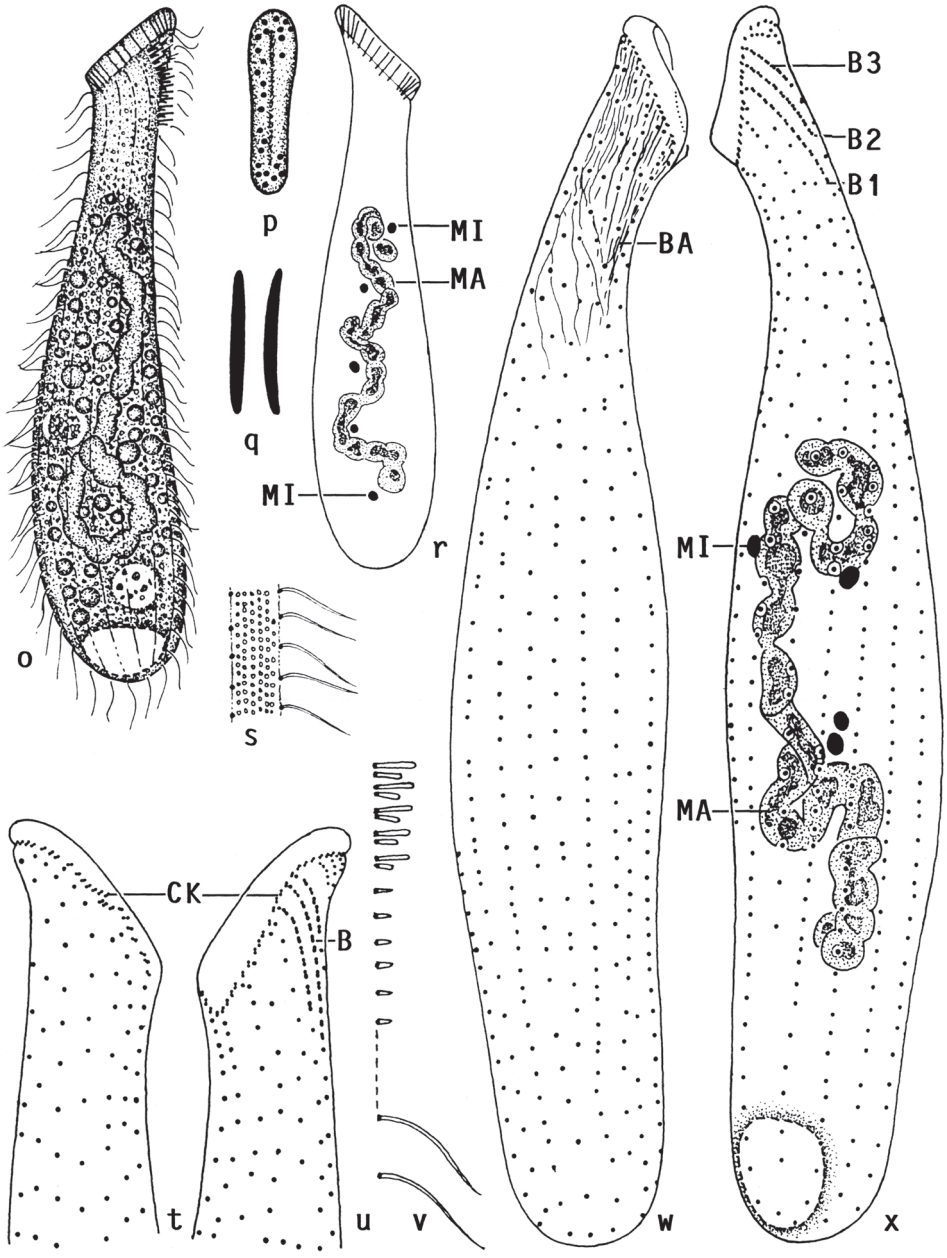


Fig. 3.9o–x *Spathidium rusticanum* Foissner, 1981 (Namibian population, from Foissner et al. 2002. o–s, v, from life; r, t, u, w, x, protargol preparation). **o:** Left side view, 120 µm. **p:** frontal view of oral bulge. **q:** Two views of the same extrusome, length 5 µm. **r:** Right lateral view of shape variant with nuclear apparatus from an impregnated specimen. **s:** Cortical granulation. **t, u:** Ciliary pattern in oral region in right and left side view, oral bulge length 20 µm. **v:** Brush row 3, bristles up to 3 µm long. **w, x:** Right and left side of ciliary pattern of main voucher specimen, 132 µm. B – dorsal brush, B1–3 – dorsal brush rows, BA – oral basket, CK – circumoral kinety, MA – macronucleus, MI – micronucleus.

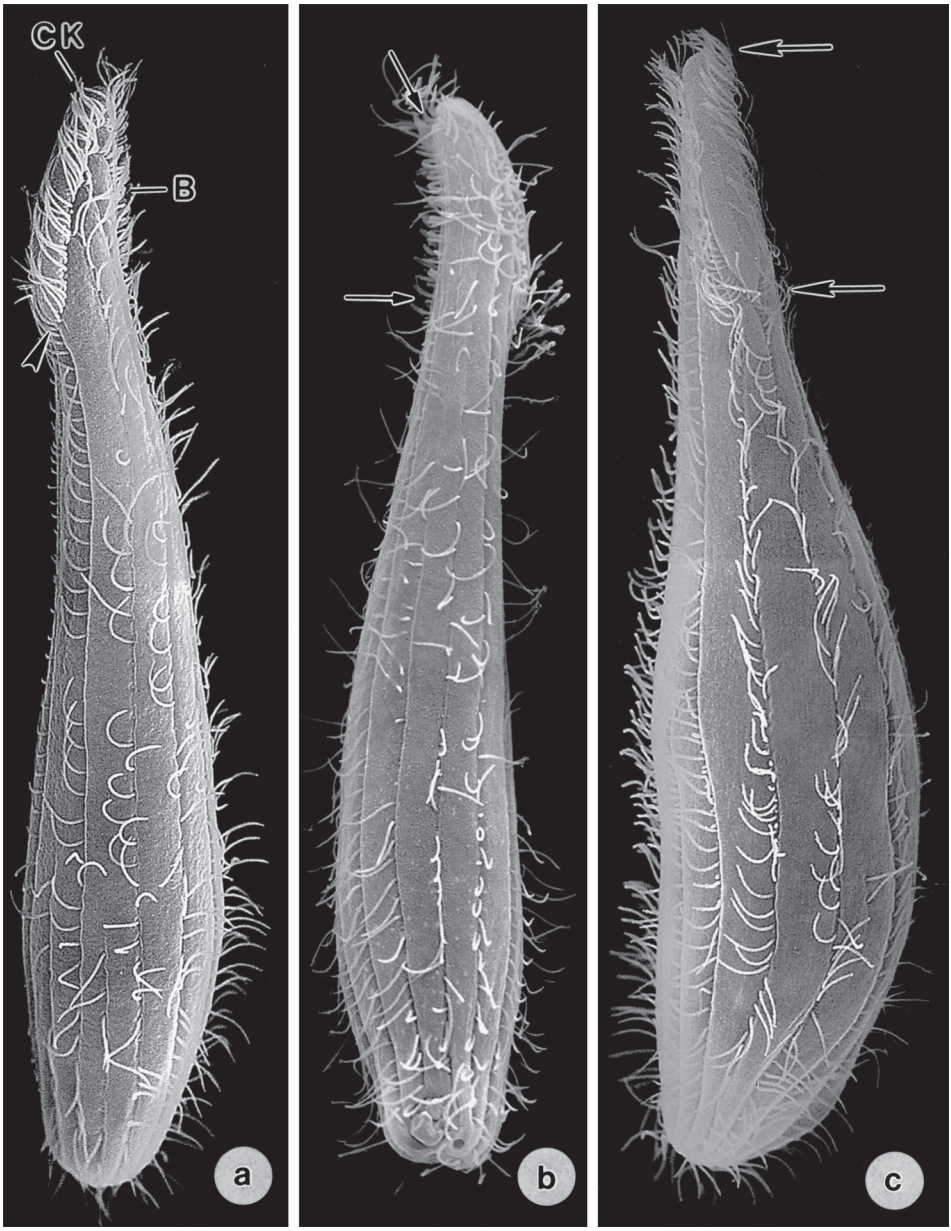


Fig. 3.10a–c *Spathidium rusticanum* Foissner, 1981 (population from Salzburg, originals. Scanning electron micrographs). **a:** Left side view with proximal end of oral bulge marked by arrowhead. **b:** Right side view with short dorsal brush (arrows). **c:** Ventral view showing, inter alia, the flat right side and the vaulted left side as well as the short oral bulge (arrows) shown at higher magnification in Fig. 3.10f. B – dorsal brush, CK – circumoral kinety.

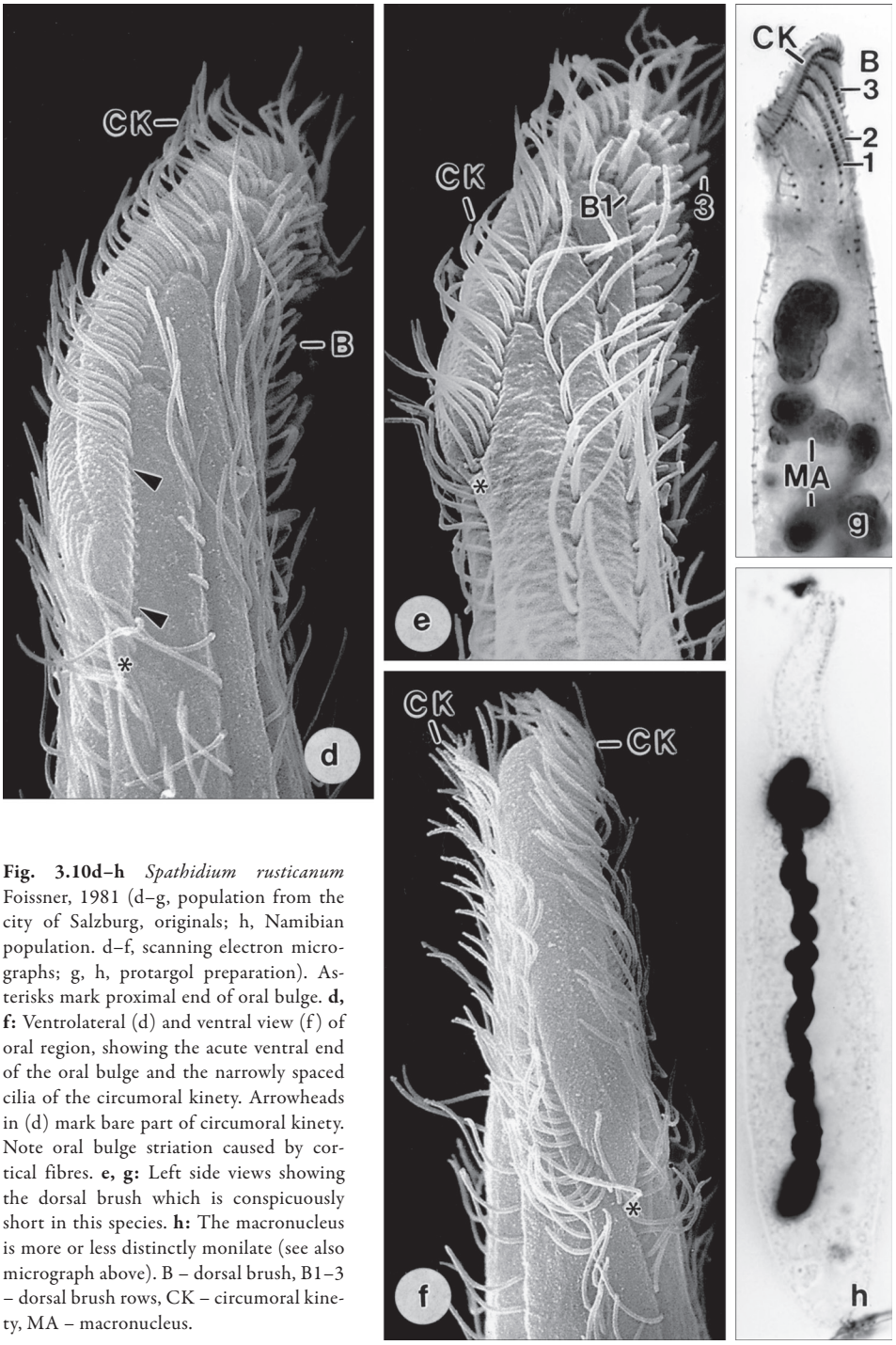
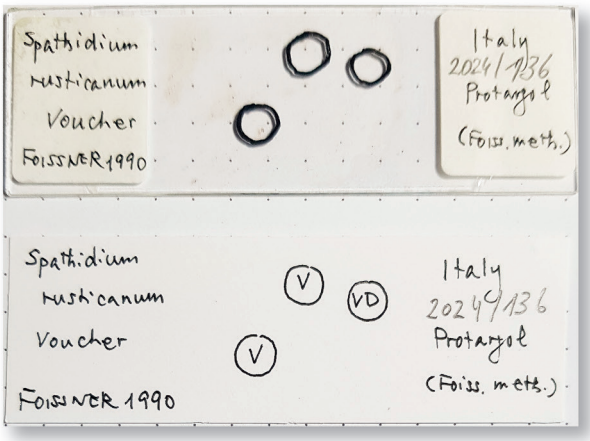


Fig. 3.10d–h *Spathidium rusticanum* Foissner, 1981 (d–g, population from the city of Salzburg, originals; h, Namibian population. d–f, scanning electron micrographs; g, h, protargol preparation). Asterisks mark proximal end of oral bulge. **d, f:** Ventrolateral (d) and ventral view (f) of oral region, showing the acute ventral end of the oral bulge and the narrowly spaced cilia of the circumoral kinety. Arrowheads in (d) mark bare part of circumoral kinety. Note oral bulge striation caused by cortical fibres. **e, g:** Left side views showing the dorsal brush which is conspicuously short in this species. **h:** The macronucleus is more or less distinctly monilate (see also micrograph above). B – dorsal brush, B1–3 – dorsal brush rows, CK – circumoral kinety, MA – macronucleus.



destroyed, as usual in material from highly saline habitats (Fig. 3.9e–n, Table 3.8). For some scanning electron micrographs and figures of the nuclear apparatus of a population from the city of Salzburg (Austria), see Fig. 3.10a–g.

Body size 90–170 × 20–40 µm in vivo, usually near 120–150 × 25–30 µm, as calculated from some in vivo measurements and the morphometric data of the three populations; length:width ratio 3–7:1 in prepared specimens, on average 4–5:1 both in vivo and preparations (Table 3.8). Body narrowly to very narrowly spatulate, anterior (oral) end obliquely truncate occupying about two thirds of widest trunk region usually found behind mid-body, neck laterally flattened about 2:1, conspicuous because often distinctly narrowed and hyaline, posterior end ordinarily rounded; non-contractile but very flexible (Fig. 3.9a, g, o). Nuclear

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Fig. 3.10i–n *Spathidium rusticanum* Foissner, 1981 (originals. Protargol slides). **i–n:** Slides (i, k, m) and protocols (j, l, n) containing voucher specimens (V) and voucher specimens drawn (VD) of Italian population. Accession numbers (LI): 2024/136, 137, 138.

Table 3.8 Morphometric data on three populations of *Spathidium rusticanum*, namely from Italy (upper line; original data from Italian population), Austria (type population, middle line; from Foissner 1984), and Namibia (lower line; from Foissner et al. 2002)[a]

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Body, length	124.3	123.0	14.6	3.3	11.7	102.0	155.0	19
	122.8	124.0	7.1	3.5	5.8	113.0	130.0	4
	114.9	115.0	16.0	4.1	13.9	83.0	140.0	15
Body, width	29.6	30.0	5.6	1.3	18.9	18.0	39.0	19
	24.0	24.0	2.6	1.3	10.8	21.0	27.0	4
	26.0	26.0	4.1	1.1	15.6	17.0	35.0	15
Body length:width, ratio	4.4	4.2	1.0	0.2	23.0	3.0	7.1	19
			about 5.1					
	4.5	4.4	0.9	0.2	19.6	3.4	6.8	15
Oral bulge, length	17.6	18.0	1.9	0.4	10.8	14.0	20.0	19
	18.3	18.0	–	–	–	17.0	20.0	3
	17.5	17.0	2.1	0.5	11.8	15.0	22.0	15
Oral bulge, height[b]	2.5	2.5	0.4	0.1	15.8	2.0	3.0	19
Oral bulge length:body width, ratio	0.6	0.6	0.1	0.0	22.3	0.5	1.0	19
			about 0.8					
			about 0.7					
Circumoral kinety to last dikinetid of brush row 1, distance	12.9	13.0	2.9	0.7	22.1	9.0	17.0	19
	–	–	–	–	–	–	–	–
	10.6	11.0	1.9	0.5	17.8	7.0	14.0	15
Circumoral kinety to last dikinetid of brush row 2, distance	16.6	16.0	2.6	0.6	15.5	13.0	22.0	19
	–	–	–	–	–	–	–	–
	11.5	12.0	2.2	0.6	18.8	7.0	16.0	15
Circumoral kinety to last dikinetid of brush row 3, distance	6.5	6.0	0.8	0.2	11.9	5.0	8.0	19
	–	–	–	–	–	–	–	–
	5.2	5.0	0.9	0.2	18.1	3.0	7.0	15
AE to macronucleus, distance[b]	39.6	40.0	6.8	1.6	17.2	26.0	53.0	19
Macronucleus figure, length	56.5	55.0	11.1	2.5	19.6	40.0	80.0	19
	–	–	–	–	–	–	–	–
	56.5	57.0	13.9	3.6	24.7	33.0	80.0	15
Macronucleus, length (spread, data thus approximate)	85.7	80.0	–	–	–	54.0	140.0	19
	–	–	–	–	–	–	–	–
	79.7	70.0	–	–	–	50.0	110.0	15
Macronucleus, width	5.4	5.0	0.8	0.2	14.2	4.0	7.0	19
	3.8	4.0	0.5	0.3	13.3	3.0	4.0	4
	5.0	5.0	0.7	0.2	13.1	4.0	6.0	15
Macronucleus, number of nodules	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
			invariably 1					
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	15
Micronucleus, diameter[b]	3.3	3.0	0.5	0.2	15.0	3.0	4.0	9
Micronuclei, number	4.0	3.0	1.7	0.6	41.5	3.0	8.0	9
	–	–	–	–	–	–	–	–
			several					
Somatic kineties, number	12.6	12.0	1.4	0.3	11.3	11.0	16.0	19
	17.8	17.0	1.5	0.8	8.5	17.0	20.0	4
	15.2	15.0	0.9	0.2	6.2	14.0	17.0	15

Table 3.8 Continued

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Basal bodies in a right-side somatic kinety, number	64.2	60.0	16.1	3.7	25.1	36.0	97.0	19
	61.3	62.5	4.8	2.4	7.8	55.0	65.0	4
	38.4	38.0	8.9	2.4	23.2	25.0	52.0	15
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	4
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
Dikinetids in brush row 1, number	13.6	13.0	3.5	0.8	25.4	8.0	21.0	19
	about 14 (from original description)							
	9.6	9.0	1.8	0.5	18.4	7.0	14.0	15
Dikinetids in brush row 2, number	17.1	17.0	3.2	0.7	18.9	12.0	25.0	19
	about 19 (from original description)							
	12.3	12.0	2.0	0.5	16.4	7.0	15.0	15
Dikinetids in brush row 3, number	7.2	7.0	1.2	0.3	16.3	6.0	9.0	19
	about 6 (from original description)							
	5.0	5.0	1.3	0.3	25.1	3.0	7.0	15

[a] Data based on mounted, protargol-prepared (Foissner's method), and randomly selected specimens. Measurements in μm. AE – anterior body end, 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] Population from Italy.

apparatus in middle quarters of cell, becomes a globular mass in mid-dividers. Macronucleus usually a tortuous strand composed of 20–30 more or less distinct nodules, occasionally moniliform, rarely very long and highly tortuous; individual nodules frequently with a conspicuous central nucleolus. Several slightly ellipsoidal micronuclei along macronucleus strand, usually difficult to recognize due to many similar-sized and impregnated cytoplasmic inclusions (Fig. 3.9a, b, g, k, l, o, r, x, 3.10g, h; Table 3.8). Contractile vacuole in rear body end, some excretory pores in pole area. Extrusomes scattered in cytoplasm and studded in oral bulge, left bulge half barren in Namibian specimens, rather conspicuous because compact and comparatively thick. Individual oral bulge extrusomes very similar in the populations studied, viz., slightly curved, 4–6 μm long rods with narrowed, rounded ends (Fig. 3.9g–i, o, r, q); cytoplasmic extrusomes very narrowly ellipsoidal, 3–5 μm long, occasionally strongly impregnated with the protargol method used (Fig. 3.9i, lower specimen). Cortex very flexible, contains colourless, minute (0.2 μm), loosely arranged granules in more or less distinct rows between each two kineties. Cytoplasm colourless, usually packed with lipid droplets up to 10 μm across and prey ciliates, such as hypotrichs and microthoracids, whose oral baskets can be recognized. Swims and creeps rather rapidly.

Somatic cilia about 10 μm long in vivo, mostly arranged in bipolar, ordinarily spaced rows, rather loosely ciliated in neck area. Average number of ciliary rows considerably different in the three populations investigated: 18 in Austrian, 15 in Namibian, and only 13 in Italian specimens; usually abut on circumoral kinety in *Spathidium* pattern; in many Italian specimens in more or less distinct *Protospathidium* pattern (Fig. 3.9a–c, e–g, l, m, o, t, u, w,

x; Table 3.8). Dorsal brush very similar in the three populations investigated, that is, three-rowed, heterostichad, and inconspicuous because occupying only 10–13% of body length on average and bristles merely up to 3–4 µm long; all brush rows commence with one or two ordinary cilia anteriorly and continue as somatic kineties posteriorly. Dikinetids ordinarily spaced (about 1 µm) within rows; bristles similar in all rows, that is, anterior bristle of dikinetids decrease in length from 3–4 µm anteriorly to 2–3 µm posteriorly; posterior bristles of dikinetids shortened by about one third. Brush row 1 slightly shorter than row 2, composed of 10–14 dikinetids on average; longest row 2 composed of an average of 12–19 dikinetids, depending on population. Brush row 3 shortened by about 50% and composed of 5–7 dikinetids on average, monokinetidal bristle tail heteromorphic (investigated only in Italian population) and extending to midbody (Italian cells) or to near body end (Namibian specimens); tail bristles decrease in length from 3–4 µm anteriorly to 1–2 µm posteriorly (Fig. 3.9a, b, e–g, m–o, u, v, x; Table 3.8).

Oral bulge slanted by about 35–50°, in vivo about as long as widest trunk region, while shorter by one third in preparations, possibly due to some shrinkage and/or inflation of the trunk; of ordinary distinctness, bright due to the extrusomes contained, 3–4 µm high in vivo and rather distinctly separate from body proper; ∞-shaped in lateral view, oblong to slightly dumbbell-shaped in frontal view; surface flat to slightly concave, with temporary cytostome appearing as a minute concavity near dorsal bulge end. Circumoral kinety oblong with bluntly pointed ventral end, composed of comparatively loosely spaced and often slightly disordered dikinetids each associated with a cilium and a long nematodesma contributing to the rather conspicuous oral basket (Fig. 3.9a–h, l, n–p, r, t, u, w, x; Table 3.8).

Occurrence and ecology: Foissner (1981) discovered *Spathidium rusticanum* in soil from an alpine meadow (1617 m above sea level) from the farm Seppenbauer (47°02'22N 12°51'43"E; estimated from Austrian Map and Google Maps by H. Berger) near the Großglockner-Hochalpenstrassse, an alpine road connecting the states Salzburg and Carinthia, Austria. The Italian population described here, became rather abundant in the non-flooded Petri dish culture of a highly saline soil and litter sample (pH 8) from the bank of a lagoon in Italy.[6] These data already indicated a wide ecological range of *Spathidium rusticanum*. This was substantiated by investigations in Namibia, where *Spathidium rusticanum* occurred in six out of 73 soil samples and a wide variety of habitats: savannahs, road puddles, sand dunes in the escarpment of the Namib Desert, and in a highly saline soil from the margin of the Etosha Pan (Foissner et al. 2002, p. 63a, 63b). The population from Salzburg (Fig. 3.10a–g) is from soil near of the so-called "Krautwächterhäusel" (47.792206°N 13.045734°E), Salzburg, Austria.[7]

Tirjaková (1988, p. 500; 1992, p. 79) reported *Spathidium rusticanum* from field soils and from the riverside of a Danube River arm in Slovakia, respectively. Although reliable records are available only from Europe and Africa, *Spathidium rusticanum* is likely a cosmopolitan. As it is difficult to identify (see remarks) and usually rare, it probably has been sometimes confused with other species or not identified.

[6] Note by H. Berger: According to the slip of paper with the original in vivo notes on the Italian population, the population occurred in "Italien Probe 2, 21.11.90" (= sample 2 from Italy, 21 Nov. 1990). Whether the date is the time of sample collection, or the time of the in vivo investigation is unclear. Further, no details on the sample site are available on the slip of paper.

[7] Note by H. Berger: For details on this very old house (built in 1380), see https://ww.sn.at/wiki/Krautwächter häusel (accessed 02. Feb 2024) and Foissner et al. (2012).

The *Spathidium wolfi* group

Most spathidiids have a single contractile vacuole in rear body end. However, some possess additional vacuoles at various sites. As explained by Foissner & Xu (2007, p. 7), several contractile vacuoles evolved independently in various evolutionary lines of the spathidiids, viz., in *Spathidium*, *Supraspathidium* (see Chapter 11, that is, Foissner et al. 2025), and *Arcuospathidium* (see Foissner & Xu 2007, p. 156). Thus, species cannot be assembled into a single genus.

The *Spathidium wolfi* group comprises species with *Spathidium* ciliary pattern and one or more contractile vacuoles in anterior body half and/or along the dorsal side. Presently, this group contains two well-described and two insufficiently known species; likely, some poorly known *Supraspathidium* species also belong to this group. A species (*Arcuospathidium bulli* Foissner, 2000) with two contractile vacuoles occurs also in the genus *Arcuospathidium* (for revision, see Foissner & Xu 2007, p. 217).

Spathidium wolfi Foissner, Wolf, Kumar, Xu & Quintela-Alonso, 2014

(Fig. 3.11a–e, Table 3.9)

2014 ***Spathidium wolfi* nov. spec.** – Foissner, Wolf, Kumar, Xu & Quintela-Alonso, Acta Protozool. 53: 187, Fig. 19a–l, 20a–f, 21a–c, 22a–k, Table 7 (original description. The slide containing the holotype [Fig. 19k, l, 20a, b in Foissner et al. 2014] and 3 paratype slides have been deposited in the Biology Centre of the Upper Austrian Museum in Linz [LI] according to Foissner et al. 2014, p. 187. However, *Spathidium wolfi* Foissner et al., 2014 is not mentioned by Aescht 2018 in her catalogue on type material; see nomenclature).

Nomenclature: According to Foissner et al. (2014, p. 187), the four type slides have been deposited in the Upper Austrian Museum in Linz. Unfortunately, this is a misinformation because the slides have been in the Foissner Archive in Salzburg until recently. This, however, does not influence the validity of the species because Article 16.4.2 of the ICZN (1999) says that the original publication must contain a statement where the holotype will be (or is) deposited. In addition, the holotype was explicitly fixed by Foissner et al. (2014) as demanded by Article 16.4.1. In the course of the present work, the type material was finally deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI): the slide (accession number 2024/139; Fig. 3.11a) containing the holotype (Fig. 19k ,l, 20a, b in Foissner et al. 2014) and three paratype slides (accession number 2024/140, 141, 142; Fig. 3.11c–e).

Remarks: For details (nomenclature, type locality, description, morphometry, illustrations and micrographs, occurrence and ecology, remarks), see Foissner et al. (2014, p. 187).

Diagnosis (from Foissner et al. 2014, slightly modified): Body size about 135 × 25 µm in vivo. Body very narrowly spatulate to bluntly fusiform with oblique, cuneate oral bulge half as long as widest trunk region. Macronucleus moniliform, composed of an average of 8 ellipsoidal nodules; multimicronucleate. Two contractile vacuoles, one dorsally at margin of anterior and middle body third, the other in rear body end. On average 15 ciliary rows, 3 of them differentiated to isostichad, short dorsal brush occupying 19% of body length; 14 widely spaced dikinetids in row 3.

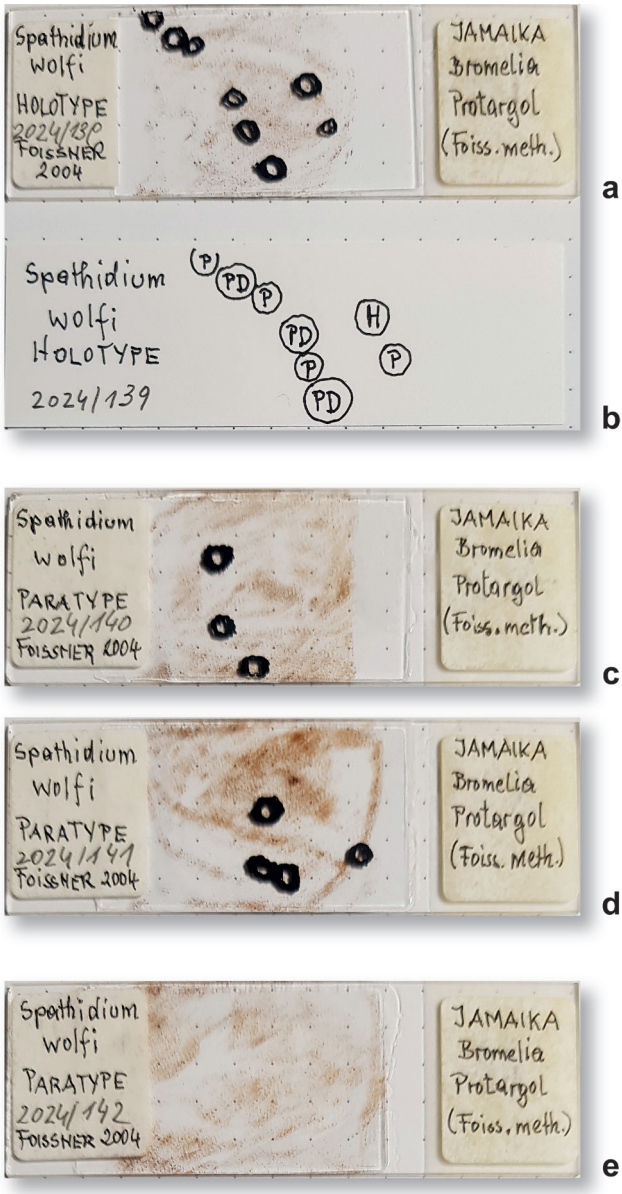

Fig. 3.11a–e *Spathidium wolfi* Foissner et al., 2014 (originals. Protargol slides). For explanation of slide deposition, see Nomenclature at *Spathidium wolfi* above. **a, b:** Slide (a) and protocol (b) containing holotype (H), paratypes (P), and paratypes drawn (PD). Accession number (LI): 2024/139. **c–e:** Three paratype slides containing paratypes. Accession numbers (LI): 2024/140, 141, 142.

Spathidium faurefremieti Foissner, 2003

(Table 3.9)

1962 ***Spathidium faurei* n. sp.** – Tucolesco, Annls Spéléol. 17: 97, fig. 16 (Fig. 59 in Foissner 2003; original description of junior homonym; no type material available).

2003 ***Spathidium faurefremieti* nom. n.** – Foissner, Acta Protozool. 42: 151, 157, Fig. 44–58, 65–70 (rectification of homonymy and redescription based on populations from Kenya, Brazil, and Australia. Five voucher

slides of the population from Kenya have been deposited in the Biology Centre of the Upper Austrian Museum in Linz [LI] according to Foissner 2003, p. 152. According to Foissner 2003, p. 152, the voucher specimens of the Brazilian population are contained in the type slides of *Neocultellothrix velhoi* Foissner in Berger et al., 2025b [accession numbers 2007/72–76; for details on this species, see Berger et al. 2025b] and *Cephalospatula brasiliensis* Foissner, 2003b [accession numbers 2007/72, 2007/73, 2007/75, 2007/76]. For slides, see Fig. 13.2a–i in Chapter 13, that is, Berger et al. 2025b).

Remarks: For details (nomenclature, description of populations from Kenya, Brazil, and Australia, morphometry, illustrations and micrographs, occurrence and ecology, remarks), see Foissner (2003, p. 151, 157), but also the original description (Tucolesco 1962). No improved diagnosis has been provided by Foissner (2003). It should await neotypification. In populations recorded in the meantime, it should be stated whether the specimens resemble Tucolesco's (1962) or Foissner's (2003) descriptions. It cannot be excluded that *Spathidium faurefremieti* is synonymous with *Spathidium vermiforme* Penard, 1922 (see *Supraspathidium vermiforme*; for details, see Chapter 11, that is, Foissner et al. 2025 and Foissner 2003, p. 158).

continued on p. 89

Table 3.9 Morphometric data on *Spathidium wolfi* (upper line; from Foissner et al. 2014) and *Spathidium faurefremieti* from Kenya (middle line; from Foissner 2003) and Brazil (lower line; from Foissner 2003)[a]

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Body, length	118.9	117.0	10.8	2.4	9.1	100.0	145.0	21
	213.8	202.5	41.6	12.0	19.4	160.0	305.0	12
	255.9	240.5	43.4	14.5	16.9	186.0	330.0	9
Body, width	29.9	30.0	4.9	1.1	16.4	21.0	44.0	21
	15.6	15.0	2.2	0.7	14.3	13.0	20.0	12
	28.3	27.0	8.6	2.9	30.2	21.0	47.0	9
Body length:width, ratio	4.1	3.9	0.9	0.2	22.3	2.5	6.0	21
	13.9	12.9	2.9	0.8	20.6	10.4	20.3	12
	9.6	10.9	2.8	0.9	28.9	4.9	12.3	9
Oral bulge, length	14.6	14.0	1.4	0.3	9.8	12.0	17.0	21
	22.7	22.0	2.0	0.6	9.2	19.0	25.0	12
	25.6	26.0	3.0	1.0	11.6	20.0	30.0	9
Body width:oral bulge length, ratio	2.1	2.1	0.3	0.1	15.3	1.4	2.9	21
Oral bulge, height[b]	3.2	3.0	–	–	–	2.0	4.0	21
Oral bulge, width[b]	5.7	6.0	0.7	0.2	12.6	5.0	7.0	21
Anterior body end to macronucleus, distance[b]	39.7	39.0	7.7	1.7	19.5	29.0	58.0	21
Anterior body end to anteriormost	41.3	41.0	3.0	0.7	7.3	36.0	47.0	21
excretory pore, distance	91.7	90.0	16.5	4.8	18.0	66.0	122.0	12
	91.3	90.0	14.2	4.7	15.6	60.0	110.0	9
Circumoral kinety to end of brush	20.3	21.0	2.3	0.5	11.4	16.0	24.0	21
row 1, distance	38.4	36.5	5.8	1.7	15.0	30.0	48.0	12
	39.2	40.0	8.9	3.0	22.7	22.0	52.0	9
Circumoral kinety to end of brush	22.5	23.0	2.6	0.6	11.7	17.0	27.0	21
row 2, distance	43.3	40.0	8.5	2.5	19.6	30.0	58.0	12
	47.8	50.0	9.7	3.2	20.3	30.0	62.0	9

Table 3.9 Continued

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Circumoral kinety to end of brush row 3, distance	19.4	19.0	2.8	0.6	14.4	15.0	26.0	21
	37.7	37.5	7.2	2.1	19.1	30.0	50.0	12
	35.6	36.0	9.2	3.1	25.8	20.0	47.0	9
Macronucleus figure, length	38.4	35.0	10.1	2.2	26.2	27.0	68.0	21
	105.6	96.5	28.8	8.3	27.3	66.0	165.0	12
	115.0	105.0	26.0	8.7	22.6	82.0	150.0	9
Macronucleus, length (spread)[b]	65.7	60.0	–	–	–	45.0	105.0	21
Macronucleus, width in middle	5.1	5.0	0.4	0.1	7.6	4.0	6.0	21
	3.6	4.0	–	–	–	3.0	4.0	12
	6.0	6.0	1.0	0.3	16.7	5.0	8.0	9
Macronucleus nodules, number[b]	8.1	8.0	1.4	0.3	17.1	5.0	11.0	21
Micronuclei, largest diameter	2.3	2.2	–	–	–	2.0	3.0	21
	3.1	3.0	–	–	–	3.0	3.5	12
	4.9	5.0	–	–	–	4.0	6.0	7
Micronuclei, number	8.6	8.0	2.8	0.6	31.9	6.0	17.0	21
	8.5	8.5	1.0	0.3	11.8	7.0	10.0	12
	9.5	9.5	1.5	0.6	15.8	8.0	12.0	6
Somatic kineties, number (including brush rows)	15.0	15.0	1.1	0.2	7.5	13.0	17.0	21
	11.7	11.0	0.9	0.3	7.6	11.0	13.0	12
	17.1	17.0	1.3	0.4	7.4	15.0	19.0	9
Ciliated kinetids in a right-side kinety, number	41.2	40.0	8.8	1.9	21.3	23.0	65.0	21
	90.4	82.5	24.6	7.1	27.2	64.0	152.0	12
	62.1	63.0	7.2	2.7	11.6	50.0	70.0	9
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	12
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	9
Dikinetids in brush row 1, number	15.5	16.0	2.3	0.5	15.1	12.0	22.0	21
	23.3	23.0	5.5	1.6	23.6	15.0	32.0	12
	24.0	25.0	3.6	1.2	15.0	15.0	27.0	9
Dikinetids in brush row 2, number	18.1	19.0	2.7	0.6	14.8	12.0	22.0	21
	29.5	29.5	6.6	1.9	22.4	20.0	40.0	12
	34.8	34.0	4.7	1.6	13.6	25.0	42.0	9
Dikinetids in brush row 3, number	14.1	14.0	1.9	0.4	13.3	11.0	19.0	21
	19.2	18.5	3.1	0.9	16.0	14.0	23.0	12
	23.1	23.0	3.8	1.3	16.4	17.0	27.0	9
Excretory pores of anterior vacuole, number	2.6	3.0	–	–	-	2.0	3.0	21
	3.3	3.0	1.5	0.4	45.7	2.0	7.0	12
	similar as above, but difficult to count							
Excretory pores of posterior contractile vacuole, number[b]	2.9	3.0	–	–	–	2.0	4.0	21

[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] Values refer to *Spathidium wolfi*.

Spathidium latissimum Lepsi, 1959

(Fig. 3.12a)

1959 ***Spathidium latissimum* n. sp.** – Lepsi, Arch. Protistenk. 104: 259, Abb. 7 (Fig. 3.12a; original description; no type material available).
1965 ***Spathidium latissimum*** – Lepsi, Protozoologie, p. 811, Fig. 247h (Fig. 3.12a; brief note).
1981 ***Supraspathidium latissimum* (Lepsi, 1959) nov. comb.** – Foissner & Didier, Annls Stn limnol. Besse 15: 255 (combination with *Supraspathidium*).

Nomenclature: No etymology has been provided in the original description or a later work. The species-group name *latissim·us, -a, -um* (Latin adjective [m, f, n], superlative of *lat·us, -a, -um*; wide, broad, expanded, flat; Hentschel & Wagner 1996, p. 359) obviously refers to the broad body (length:width ratio about 1.5:1).

Remarks: This is a very characteristic species which we diagnosed according to the original description; none the less, it should be reinvestigated with modern methods. The huge oral bulge indicates that it could belong to the genus *Epispathidium* (see Chapter 6, that is, Foissner et al. 2025a). For brief note on misclassification in the genus *Supraspathidium*, see Chapter 11, that is, Foissner et al. (2025).

Diagnosis: Body size about 90 × 60 µm in vivo. Body broadly spatulate with axe-shaped, slightly oblique oral bulge about as long as widest trunk region. Macronucleus possibly globular. Two contractile vacuoles, one behind proximal end of oral bulge, the other in rear body portion. Extrusomes granular, but conspicuous because highly refractive.

Description (literal translation of German text from Lepsi 1959): Body broad, 90 µm long, trunk unusually strongly inflated, posterior end broadly rounded. Oral bulge shaped like an axe, extends to mid-body, ventral end marked by minute concavity; widely projects dorsally, producing distinct neck. Central region of body studded with dark grains of various size, covering the (likely globular) macronucleus. Contractile vacuole in rear body end, a second contractile vacuole near proximal end of oral bulge underlaid by conspicuous granules, likely trichocysts.

Occurrence and ecology: The type locality of *Spathidium latissimum* is a ditch near the Colentina River in the surroundings of Bucharest (about 44°28'N 26°09'E), Romania. It was rare in the clear water which contained floating filamentous green algae. Lepsi (1959) discovered this species in February and classified it as mesosaprobic; trials to culture the species failed. No further records found.

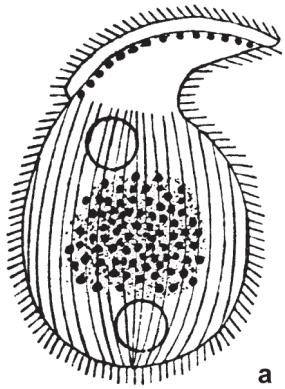

Fig. 3.12a *Spathidium latissimum* Lepsi, 1959 (from Lepsi 1959. From life, nuclear apparatus after methyl-green staining). Left-lateral view showing, inter alia, darkish granules covering the macronucleus which is likely globular and an anterior and a posterior contractile vacuole, 90 µm.

Spathidium polyvacuolatum Vuxanvici, 1959

(Fig. 3.13a)

1959 ***Spathidium polyvacuolatum* n. sp.** – Vuxanovici, Studii Cerc. Biol. 11: 322, Plansa VI, fig. 40 (Fig. 3.13a; original description; no type material available).

1981 ***Supraspathidium polyvacuolatum* (Vuxanovici, 1959) nov. comb.** – Foissner & Didier, Annls Stn limnol. Besse 15: 255 (combination with *Supraspathidium*).

Nomenclature: No etymology has been given in the original description or a later work. The species-group name *polyvacuolat·us*, *-a*, *-um* (having many vacuoles) is a composite of the Greek quantifier *polys* (many; Hentschel & Wagner 1996, p. 485) and the Latin adjective *vacuolat·us*, *-a*, *-um* (vacuolated [m, f, n]; en.wiktionary.org/wiki/vacuolatus; accessed 27.05.2023). The name obviously refers to the vacuoles in the anterior body half.

Diagnosis: A redescription should be awaited.

Remarks: This poorly described species, which is based on observations of a single specimen, needs detailed reinvestigation. Vuxanovici (1959) did not mention whether the anterior vacuoles are contractile. Despite these problems, we do not reject *Spathidium polyvacuolatum* because it has a definite combination of features most found also in other species of the genus: large body size (length 220 µm); many scattered macronu-cleus nodules; 20 µm long, rod-shaped extrusomes; four vacuoles in anterior body half. This combination of features resembles *Spathidum polynucleatum* (p. 96; extrusomes 10 µm vs. 20 µm; oral bulge thick and twisted vs. ordinary; no specific vacuoles in anterior body half) and *Spathidium duschli* (p. 59; extrusomes 7 µm long and comparatively thick vs. 20 µm and rod-shaped; no specific vacuoles in anterior body half). For note on classification in *Supraspathidium* by Foissner & Didier (1981), see *Supraspathidium* (Chapter 11, that is, Foissner et al. 2025).

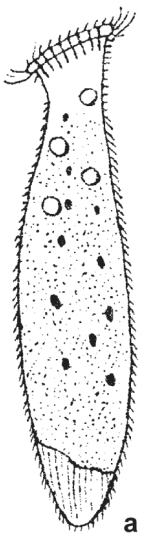

Fig. 3.13a *Spathidium polyvacuolatum* (from Vuxanovici 1959. From life?). Left-lateral view showing, inter alia, four vacuoles in the anterior body portion and the nuclear nodules (black), 220 µm.

Description (literal translation of Rumanian text of Vuxanovici 1959): Length 220 µm. Similar to *Spathidium plurinucleatum* André, 1916[8], as concerns body shape and the many small nuclei; differs by the 20 µm long oral bulge trichocysts, the more distinctly convex and longer oral bulge producing a distinct neck, and the four vacuoles in anterior body half. Cytoplasm clear, yellowish granulated.

Occurrence and ecology: As yet found only at the type locality, that is, Lake Herăstrău, Rumania. Vuxanovici (1959) observed a single specimen in a water sample with rotting aquatic plants in March 1958.

Two further *Spathidium* species

In the raw manuscript, W. Foissner had the intention to describe a fourth *Spathidium* group, namely the *Spathidium procerum* group comprising four species. He proposed the following text for this group:

[8] Original combination: *Spathidium spathula plurinucleata* André, 1916 (p. 626). For revision, see Kahl (1930b, p. 157).

"The four species bundled in this group are middle- to large-sized (140–250 µm), slender (>8:1), have inconspicuous extrusomes and, especially, scattered macronucleus nodules. The last feature separates it from the *Spathidium elongatum* group (p. 34), except of *Spathidium duschli* which, however, has more ciliary rows (about 20 vs. 11) and special extrusomes. Certainly, most polynucleate species look rather similar, especially when the considerable variability is taken into account (see *Spathidium turgitorum* Foissner et al., 2002), but at population level they can be reliably distinguished by the shape of the extrusomes and macronucleus, the dorsal brush, and various morphometrics."

The only species reviewed by W. Foissner in this group was *Spathidium anguilla* (see below). Because of time constraints we do not review the lacking species (*Spathidium procerum* Kahl, 1930a, p. 380; for redescription, see, inter alia, Foissner 1984, p. 71; for some original micrographs of resting cysts, see Fig. 3.15e–i. *Spathidium turgitorum* Foissner et al., 2002; p. 234. The fourth species was not mentioned by W. Foissner). Perhaps, *Spathidium polynucleatum* (Foissner et al., 2002) Jang et al., 2017 (original combination *Epispathidium polynucleatum*) is the fourth species belonging to the *Spathidium procerum* group, because it also has a fragmented macronucleus and is rather slender. In the raw manuscript W. Foissner had the intention to transfer this species from *Epispathidium* to *Spathidium*, an act now already done by Jang et al. (2017).

Spathidium anguilla Vuxanovici, 1962[9]

(Fig. 3.14a–i, 3.15a–d, Table 3.10)

1962 ***Spathidium anguilla* n. sp.** – Vuxanovici, Studii Cerc. Biol. 14: 208, Plansa IV, fig. 27 (Fig. 3.14a; original description; no type material available).

1984 ***Spathidium anguilla* Vuxanovici, 1962** – Foissner, Stapfia 12: 71, Abb. 36a–h, Tabelle 18 (Fig. 3.14b–i; detailed redescription; one voucher slide [accession number 1984/52] has been deposited in the Biology Centre of the Upper Austrian Museum in Linz [LI]; for details, see nomenclature).

Nomenclature: No etymology has been provided in the original description or a later work. The species-group name *anguilla* (Latin noun; eel; Brown 1954, p. 295) obviously refers to the slender body shape.

The "neotypification" mentioned by Aescht (2008, p. 142) is invalid because Foissner (1984, p. 8) only briefly mentioned that he has deposited at least one slide of the species redescribed in the Biology Centre of the Upper Austrian Museum in Linz (see also bold note in Aescht 2008, p. 138). According to Aescht (2008, p. 142), Foissner mislabeled the voucher slide as paratype (for definition of paratype, see ICZN 1999, Article 72.4.5). For the qualifying conditions of a valid neotypification, see ICZN (1999, Article 75.3).

Diagnosis: Should await neotypification.

Remarks: The original description is based on in vivo observations of a single specimen from the sapropelic mud of a lake. Thus, the data situation is fairly incomplete so that a neo-

[9] Note by H. Berger: In the raw manuscript, W. Foissner planned to classify the terrestrial population from Austria (Foissner 1984) as neotype of *Spathidium anguilla* which was originally found in the sapropelic mud of a lake near Bucharest, Romania. We refrain from such a step, because of the different habitats (mesoxerophytic grassland, limestone grassland [Mesobrometum] in population from Austria vs. sapropelic mud in a lake) and the fact that the present work is not reviewed.

Table 3.10 Morphometric data on *Spathidium anguilla* (from Foissner 1984)[a]

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Body, length	119.9	122.0	15.4	4.0	14.5	112.0	196.0	15
Body, width	14.5	15.0	2.3	0.6	16.0	10.0	18.0	15
Oral bulge, length	22.1	20.0	4.8	1.3	21.8	17.0	34.0	15
Circumoral kinety to last dikinetid of brush row 2, distance	20.1	21.0	2.8	0.7	14.2	15.0	27.0	15
Macronucleus figure, length	66.3	66.0	14.3	3.7	21.6	40.0	96.0	15
Macronucleus nodules, length	6.4	6.0	1.4	0.4	21.6	4.2	8.4	15
Macronucleus nodules, width	3.6	3.5	0.8	0.2	21.1	2.5	4.5	15
Macronucleus nodules, number	25.6	26.0	5.8	1.5	22.6	16.0	35.0	15
Micronucleus, diameter	1.9	1.6	0.5	0.1	25.5	1.4	2.8	15
Micronuclei, number	7.8	8.0	2.0	0.5	25.7	4.0	11.0	15
Somatic kineties, number	10.9	11.0	1.1	0.3	10.1	9.0	13.0	15
Basal bodies in a somatic kinety left of brush, number	62.3	57.0	11.3	2.9	18.2	45.0	85.0	15
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
Dikinetids in brush row 1, number	about 14–19 (from figures; n = 2)							
Dikinetids in brush row 2, number	about 14–20 (from figures; n = 2)							
Dikinetids in brush row 3, number	about 11 (from figure; n = 1)							

[a] Data based on mounted, protargol-prepared (Foissner's method) and randomly selected specimens. 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.

typification is indicated. Specifically, the lack of reliable data on the macronucleus pattern makes *Spathidium anguilla* indeterminable. The terrestrial population described by Foissner (1984) seems to be remarkably similar. The populations match in the slender shape which varies from 5.8–13.3:1 (about 11:1 according to Vuxanovici's figure 3.14a), the oblique oral bulge, and the short extrusomes. Despite these agreements, we recommend a neotypification via a population from a true limnetic (sapropelic) habitat in Europe, preferable from near the type locality (Bucharest, Romania). The habitats of the type population and the Austrian population described by Foissner (1984) are not entirely different, because the lowland forest in Austria is flooded from time to time.

Most congeners differ from *Spathidium anguilla* by the rod-shaped (vs. very narrowly ellipsoidal) extrusomes, except for *Spathidium metabolicum* Pomp & Wilbert, 1988 (p. 482) which, however, has a moniliform macronucleus, ovate extrusomes, and a distinctly shortened brush row 1. *Spathidium anguilla* also resembles members of the *Spathidium bromelicola* group (p. 61), which have the same type of extrusomes but are shorter (5–6:1 vs. ≥8:1) and possess a single macronucleus strand.

Augustin & Foissner (1992) likewise redescribed *Spathidium anguilla*. They based their identification on Foissner's observation of some specimens with a nodulated or moniliform macronucleus strand. With today's knowledge, these few specimens are post-dividers, as evident from *Spathidium turgitorum* Foissner et al., 2002, a similar species with rod-shaped (vs. very narrowly ellipsoidal) extrusomes. Thus, the population described by Foissner (1984)

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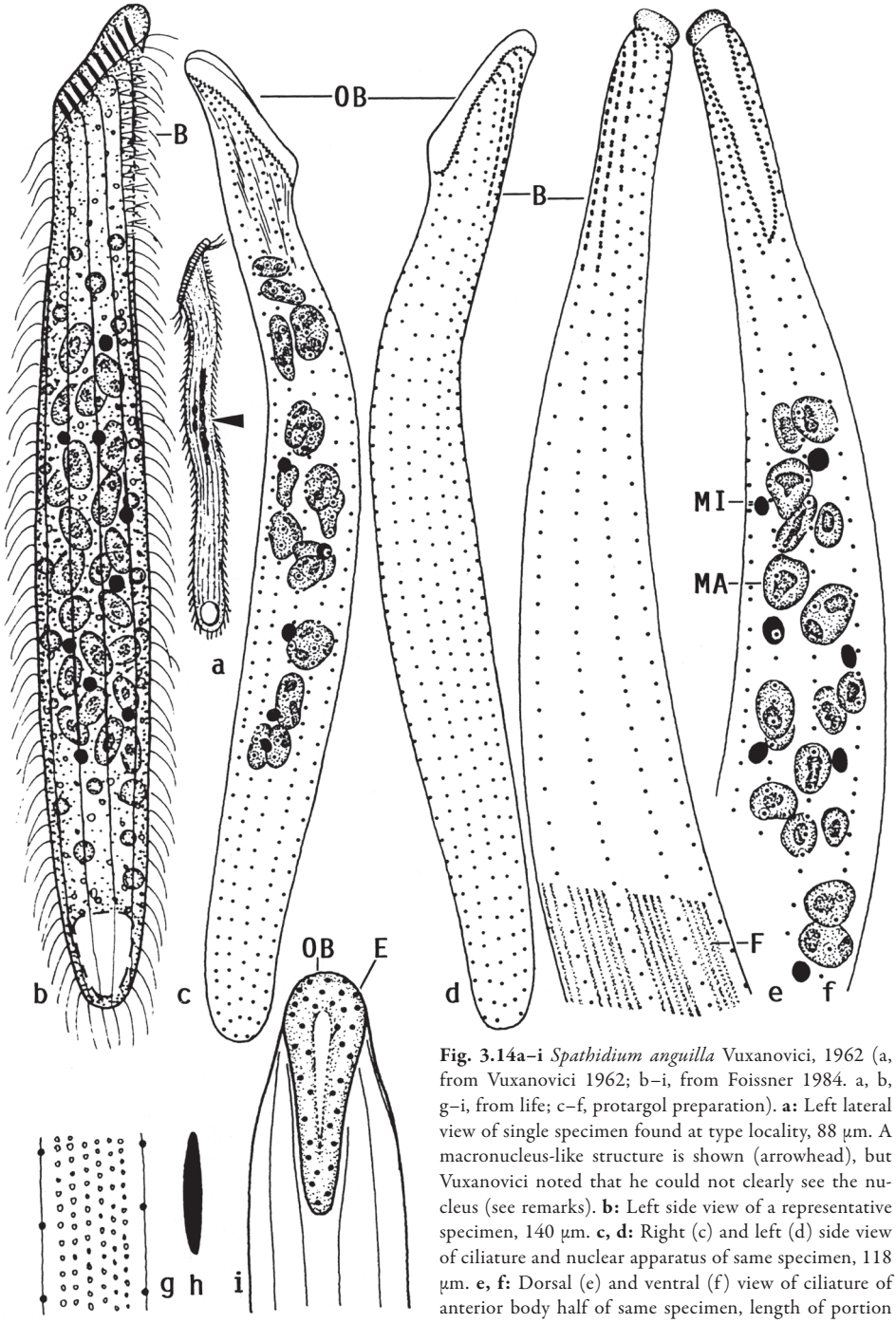

Fig. 3.14a–i *Spathidium anguilla* Vuxanovici, 1962 (a, from Vuxanovici 1962; b–i, from Foissner 1984. a, b, g–i, from life; c–f, protargol preparation). **a:** Left lateral view of single specimen found at type locality, 88 µm. A macronucleus-like structure is shown (arrowhead), but Vuxanovici noted that he could not clearly see the nucleus (see remarks). **b:** Left side view of a representative specimen, 140 µm. **c, d:** Right (c) and left (d) side view of ciliature and nuclear apparatus of same specimen, 118 µm. **e, f:** Dorsal (e) and ventral (f) view of ciliature of anterior body half of same specimen, length of portion 72 µm. The nuclear apparatus is composed of many (26 on average) macronucleus nodules and some micronuclei. **g:** Cortical granulation. **h:** Extrusome, 4 µm. **i:** Ventral view of oral region. B – dorsal brush, E – extrusome, F – fibres, MA – macronucleus nodule, MI – micronucleus, OB – oral bulge.

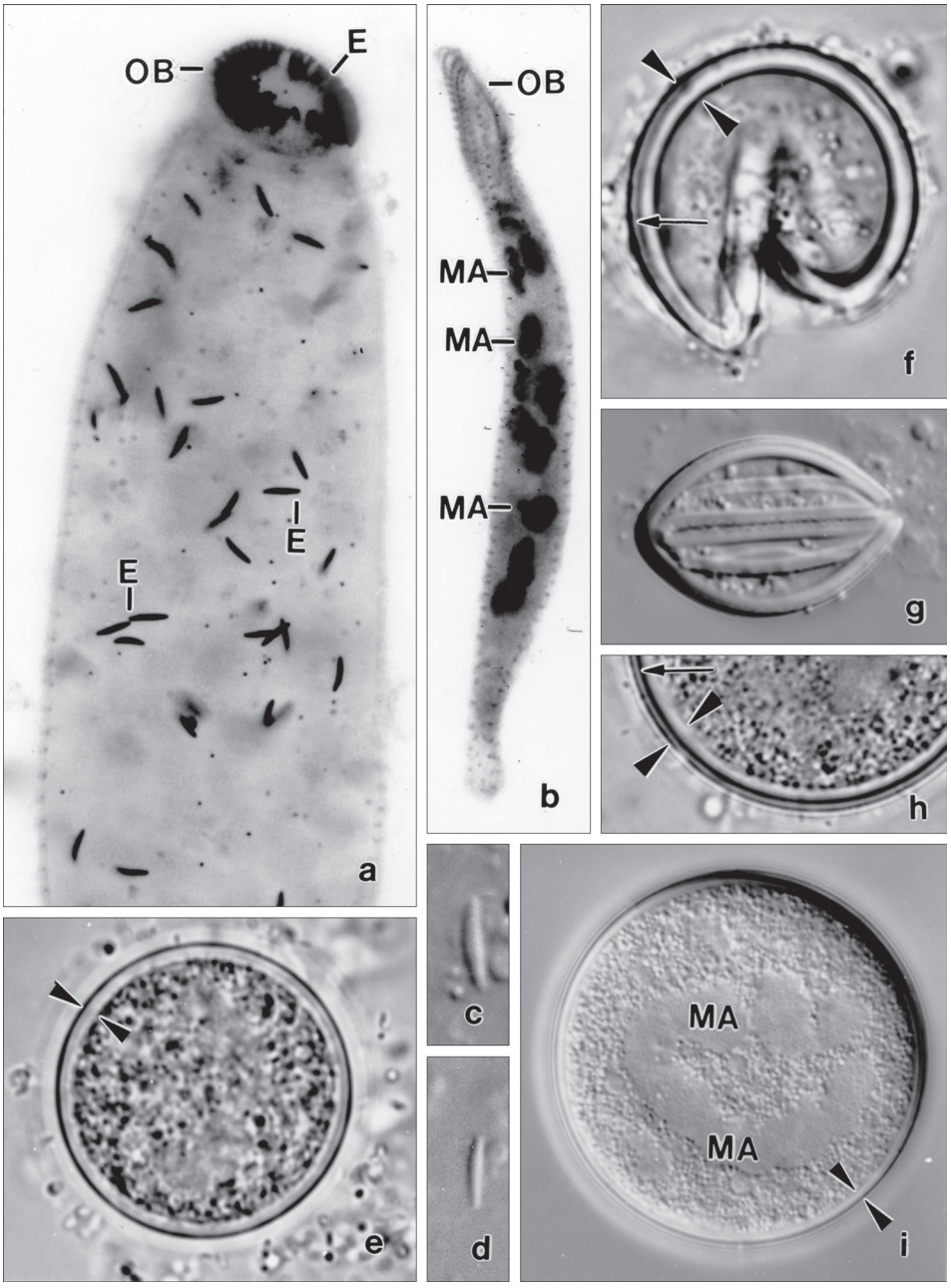

Fig. 3.15a–d *Spathidium anguilla* Vuxanovici, 1962 (a, b, originals of population studied by Foissner 1984; c, d, from Namibian specimen. a, silver carbonate preparation; b, protargol preparation; c, d, from life). **a:** The extrusomes are clearly recognizable when the silver carbonate method is applied. **b:** Nuclear apparatus. **c, d:** Oral bulge extrusomes. E – extrusomes, MA – macronucleus nodules, OB – oral bulge.
Fig. 3.15e–i *Spathidium procerum* Kahl, 1930a (originals. From life). **e, f, h, i:** Resting cysts. Opposed arrowheads mark total wall, arrows denote thin outer membrane. **g:** If appropriately squashed, the cyst wall assumes the curious shape shown.

has scattered macronucleus nodules distinctly different from the long macronucleus strand of the activated sludge specimens studied by Augustin & Foissner (1992). Their population is now classified as *Spathidium saprophilum curvioplites* nov. subspec. (p. 71).

Description: Since it is not quite certain that the populations described by Vuxanovici (1962) and Foissner (1984) are conspecific, we describe the populations separately (see remarks).

Type population (from Vuxanovici 1962)[10]: Body size 88.5 µm. Habitus closely resembles *Spathidium procerum* Kahl, 1930b, but it is four times smaller and differs also in the habitat (sapropel from a lake vs. *Sphagnum* near Hamburg and terrestrial(?) mosses from Tyrol, Austria). They also differ in the oral bulge which is proportionally longer and more slanted in *Spathidium anguilla*. Oral bulge extrusomes 2.0–2.5 µm long. Dorsal brush not clearly seen. Shape of macronucleus not clearly seen (moniliform?). Few ciliary rows. Cytoplasm transparent, fine-grained. Movement like a worm, slow, without pauses. A single individual in sapropel. Lake Fundeni, Bucharest, June 1960.

Population described by Foissner (1984; supplemented with data from original notes by W. Foissner): Body size in vivo 110–200 × 10–20 µm, usually near 140 × 15 µm, as calculated from some in vivo measurements and the morphometric data; length:width ratio 5.8–13.3:1, on average about 9:1 both in vivo and in protargol preparations (Table 3.10). Body shape fairly stable, viz., very narrowly spatulate to cylindrical and occasionally serpentine; anterior (oral) end obliquely slanted, neck indistinct, slightly widened in mid-body, posterior end narrowly rounded (Fig. 3.14b, c, 3.15b); laterally flattened up to 2:1 in anterior quarter; very flexible and slightly contractile under mild coverslip pressure. Most macronuclear nodules scattered in central quarters of cell; individual nodules globular to ellipsoidal, often with a distinct, central nucleolus; rarely specimens, very likely early postdividers, with a nodulated or moniliform macronucleus strand. On average eight globular micronuclei scattered among macronucleus nodules (Fig. 3.14b, c, f, 3.15b: Table 3.10). Contractile vacuole in rear body end. Extrusomes studded in oral bulge and scattered in cytoplasm, bluntly fusiform to very narrowly ellipsoidal and slightly asymmetrical, in vivo about 4.0 × 0.8 µm in size; do not impregnate with the protargol method used, but stain heavily with silver carbonate (Fig. 3.14a, h, i, 3.15a, d, e). Cortex very flexible, contains 6–10 rows of colourless granules and 4–6 (postciliary?) fibre bundles between two kineties each. Cytoplasm colourless, studded with lipid droplets 1–3 µm across. Glides and swims moderately fast by rotation about main body axis, describing a wide circle with anterior body portion.

Somatic cilia about 8 µm long in vivo, arranged in an average of 11 ordinarily spaced, usually bipolar, densely ciliated rows abutting on circumoral kinety in typical *Spathidium* pattern (Fig. 3.14a, c, d; Table 3.10). Dorsal brush in usual location, heterostichad, inconspicuous because occupying only 17% of body length and bristles merely up to 3 µm long.

[10] The original description reads as follows: "Mărimea: 88.5 µ. Ca habitus se aseamănă foarte mult cu *Sp. procerum* Kahl, 1930; este însă de patru ori mai mică; diferă de biotop, specia studiată de noi fiind dulcicolă. Mai diferă prin buza orală proportional mai lungă şi mai înclinată spre dreapta. 'Trihociştii faringiali lungi de 2–2.5 µ; peria dorsală neobservată bine; forma nucleului, neconcludentă (moniliform?). Striata rară; plasma transparentă, cu granulaţii fine; mişcările infuzoului lente, vermiforme, fără pause. Un singur exemplar în sapropel. Lacul Fundeni, Bucureşti, iunie 1960." This text has been translated into English by DeepL and by PONS (https://de.pons.com/ accessed 4 June 2023) and subsequently adapted by H. Berger.

Brush rows 1 and 2 of similar length, each composed of about 14–19 dikinetids. Brush row 3 distinctly shortened comprising only about 11 dikinetids (Fig. 3.14a, d, e; Table 3.10).

Oral bulge occupies anterior body end slanted by 45–60°, on average 1.5times longer than widest trunk region; of ordinary distinctness, that is, about 5 µm high dorsally and 3 µm ventrally; slightly sigmoidal in lateral view, cuneate to narrowly cuneate in ventral view. Circumoral kinety continuous and of similar shape as oral bulge, that is, distinctly cuneate (Fig. 3.14a, c, f, i, 3.15b; Table 3.10).

Occurrence and ecology: Type locality of *Spathidium anguilla* is the sapropelic mud from Lake Fundeni (about 44°25'N 26°10'E), Bucharest, Romania. Foissner (1984) found it in soil under a *Mesobrometum* in a lowland forest (48.36247°N 15.92934°E) along the Danube River near the village of Bierbaum am Kleebühel (183 m above sea-level), Lower Austria (for details on soil and vegetation, see "Profil 1" in Foissner et al. 1985, p. 85).

The following records are mainly (exclusively?) based on the redescription by Foissner (1984): coastal sand dunes of northern Germany (Goralczyk & Verhoeven 1999); "technosoil" near Oldenburg, Germany (Niebuhr 1989, p. 82; Niebuhr in Foissner 2000a, p. 259); in five out of 73 samples from Namibia, namely soil from savannahs and waterholes as well as from a highly saline (2%) site in the surroundings of the Etosha Pan (Foissner et al. 2002, p. 56, 63a, 67, 70); benthal of Ukrainian part of Dniester river and marshes of Danube Delta (Kovalchuk 2017, p. 79).

These data and that in Foissner (1998, p. 209) indicate that *Spathidium anguilla* (as described by Foissner 1984) is an euryoecious cosmopolitan, occurring in both limnetic and terrestrial habitats. Biomass of 10^6 specimens about 25 mg (population described by Foissner 1984; Foissner 1998, p. 209).

Spathidium polynucleatum (Foissner, Agatha & Berger, 2002) Jang, Vd'ačný, Shazib & Shin, 2017

(Fig. 3.16a–n, 3.17a–v, Table 3.11)

2002 ***Epispathidium polynucleatum* nov. spec.** – Foissner, Agatha & Berger, Denisia 5: 312, Fig. 70a–m, 329a–u, Table 58 (Fig. 3.14a–m, 3.17a–u; original description; the slide [accession number 2002/281] containing the holotype [Fig. 70c–e in Foissner et al. 2002] and three paratype slides [2002/282–284] have been deposited in the Biology Centre of the Upper Austrian Museum in Linz [LI]; see also Aescht 2008, p. 174).

2017 ***Spathidium polynucleatum* (Foissner et al., 2002) comb. nov.** – Jang, Vd'ačný, Shazib & Shin, J. nat. Hist. 51: 956, Fig. 8a–g, 9a–l, Table 2 (detailed description of population from Korea; combination with *Spathidium*; whereabout of voucher slides not mentioned).

Nomenclature: The species-group name *polynucleat*·us, -a, -um (having many macronucleus nodules) is a composite of the Greek *polys* (many; Hentschel & Wagner 1996, p. 483) and the Latin adjective *nucleat*·us, -a, -um ([m, f, n]; nut kernel-like; Hentschel & Wagner 1996, p. 429) and refers to the many macronucleus nodules (Foissner et al. 2002, p. 312).

Diagnosis (from Foissner et al. 2002, slightly modified): Body size about 190 × 30 µm in vivo. Body narrowly spatulate. Oral bulge massive, oblique, oblong, and screwed like a propeller blade, approximately as long as widest trunk region. On average 30 ellipsoidal, scattered macronucleus nodules; multimicronucleate. Extrusomes rod-shaped and distinctly curved, about 10.0 × 0.5 µm. An average of 22 ciliary rows, 3 of them anteriorly differentiated to

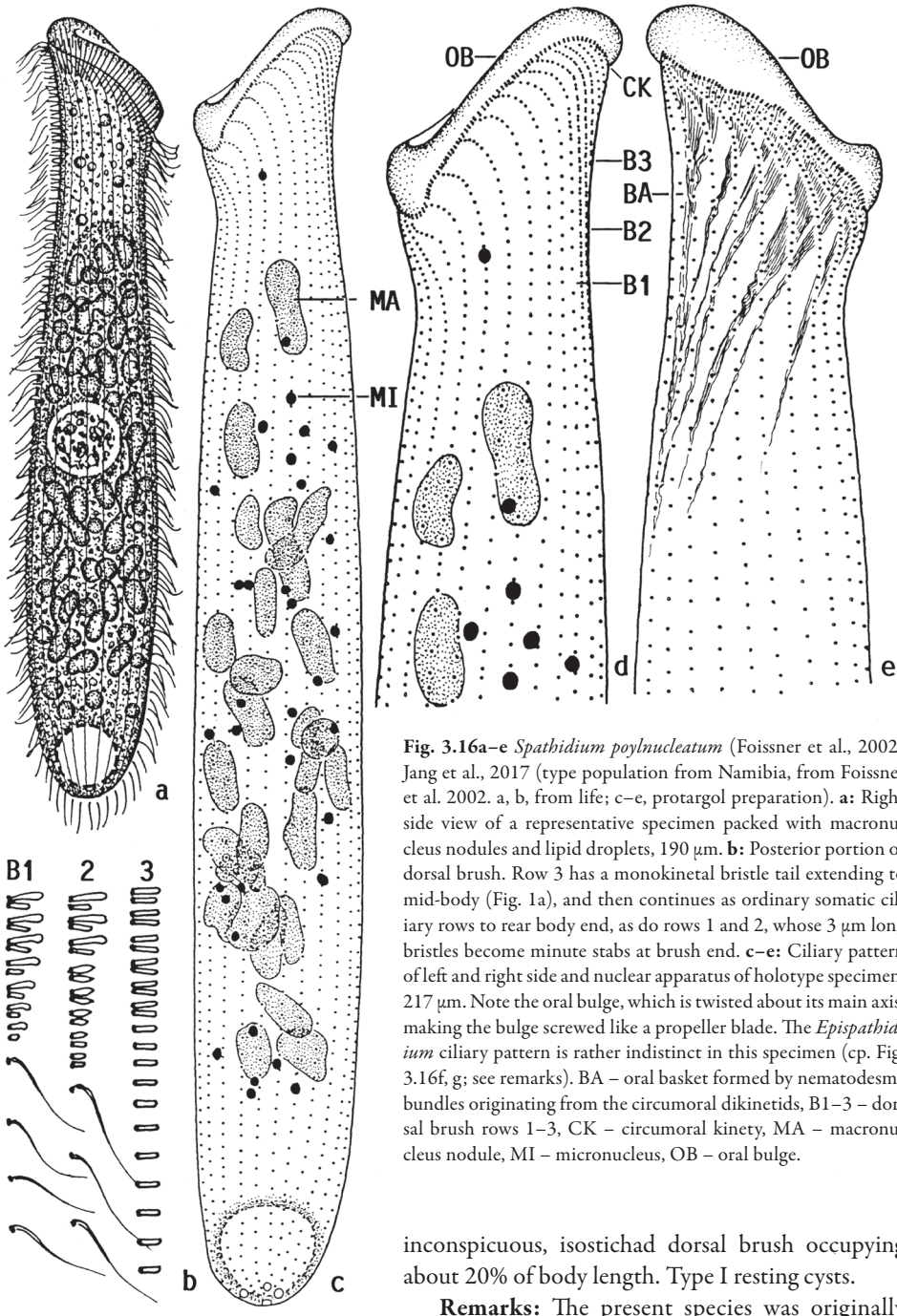

Fig. 3.16a–e *Spathidium poylnucleatum* (Foissner et al., 2002) Jang et al., 2017 (type population from Namibia, from Foissner et al. 2002. a, b, from life; c–e, protargol preparation). **a:** Right side view of a representative specimen packed with macronucleus nodules and lipid droplets, 190 μm. **b:** Posterior portion of dorsal brush. Row 3 has a monokinetal bristle tail extending to mid-body (Fig. 1a), and then continues as ordinary somatic ciliary rows to rear body end, as do rows 1 and 2, whose 3 μm long bristles become minute stabs at brush end. **c–e:** Ciliary pattern of left and right side and nuclear apparatus of holotype specimen, 217 μm. Note the oral bulge, which is twisted about its main axis, making the bulge screwed like a propeller blade. The *Epispathidium* ciliary pattern is rather indistinct in this specimen (cp. Fig. 3.16f, g; see remarks). BA – oral basket formed by nematodesma bundles originating from the circumoral dikinetids, B1–3 – dorsal brush rows 1–3, CK – circumoral kinety, MA – macronucleus nodule, MI – micronucleus, OB – oral bulge.

inconspicuous, isostichad dorsal brush occupying about 20% of body length. Type I resting cysts.

Remarks: The present species was originally classified in *Epispathidium* (for review, see Chapter 6, that is, Foissner et al. 2025a), but the ciliature is reminiscent of both *Spathidium* and *Epispathidium*, because the left side kineties are usually only slightly curved ventrally; however, some specimens show a typical

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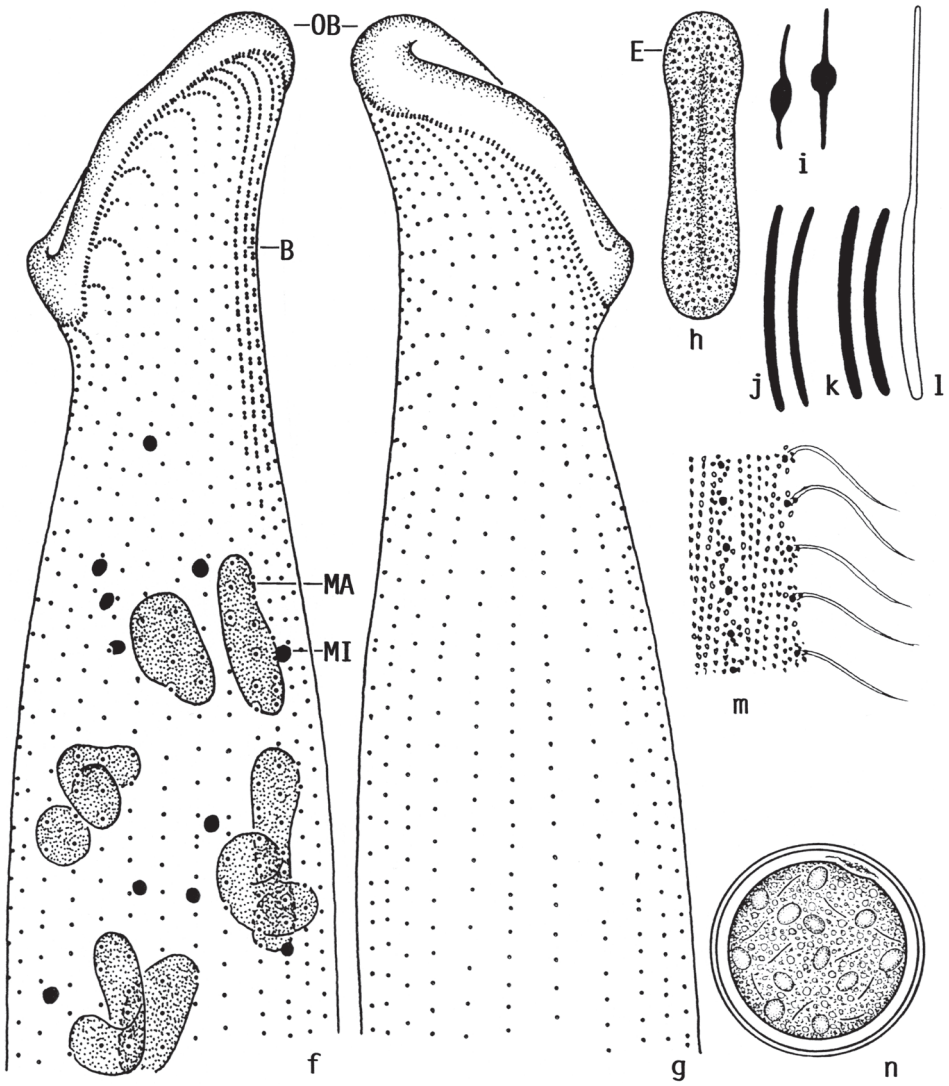


Fig. 3.16f–n *Spathidium poylnucleatum* (Foissner et al., 2002) Jang et al., 2017 (f–m, from Foissner et al. 2002; f, g, k (left figure), l, population from Australia; h–j, m, type population from Namibia; k (right figure), population from Venezuela; n, original, population from Dominican Republic. f, g, i, protargol preparation; h, j–n, from life). **f, g:** Left (f) and right (g) side view of anterior body region of Australian specimen showing the typical *Epispathidium* pattern: the densely ciliated anterior portion of the left side ciliary rows is curved ventrally to run in parallel with the circumoral kinety, which is thus seemingly doubled. However, this pattern is pronounced in only few specimens, both in the Australian and Namibian population. Note the ∞-shaped oral bulge (cp. Fig. 3.16d, e), a curious pattern produced by a rather distinct twist of its main axis making the bulge screwed like a propeller blade. **h:** Frontal view of oral bulge studded with extrusomes. **i:** Developing extrusomes in the cytoplasm. **j:** oral bulge extrusomes. **k:** Oral bulge extrusomes of Australian (left) and Venezuelan (right) specimens, length 10 µm. **l:** Exploded extrusome. **m:** Surface view showing cortical granulation. **n:** Resting cyst, diameter 45 µm. The cysts are globular, colourless, smooth, and have two distinct walls. B – dorsal brush, E – extrusomes, MA – macronucleus nodule, MI – micronucleus, OB – oral bulge.

Fig. 3.17a–c *Spathidium polynucleatum* (Foissner et al., 2002) Jang et al., 2017 (from Foissner et al. 2002. Namibian specimens in the scanning electron microscope). The figures show the slender shape and the inconspicuous oral bulge, which is about as long as the maximum trunk width. The ciliature is condensed underneath the oral bulge due to the densely ciliated and distinctly curved anterior end of the ciliary rows (see also following figures!). Arrowheads delimit the monokinetidal bristle tail of brush row 3, which continues posteriorly as an ordinary somatic kinety, like brush rows 1 and 2. The tail of brush row 3 is comparatively short in *Spathidium polynucleatum*, that is, extends only to about mid-body while to posterior body end in many other species; possibly, this is an additional feature of this species. E – partially released extrusomes (toxicysts), OB – oral bulge.

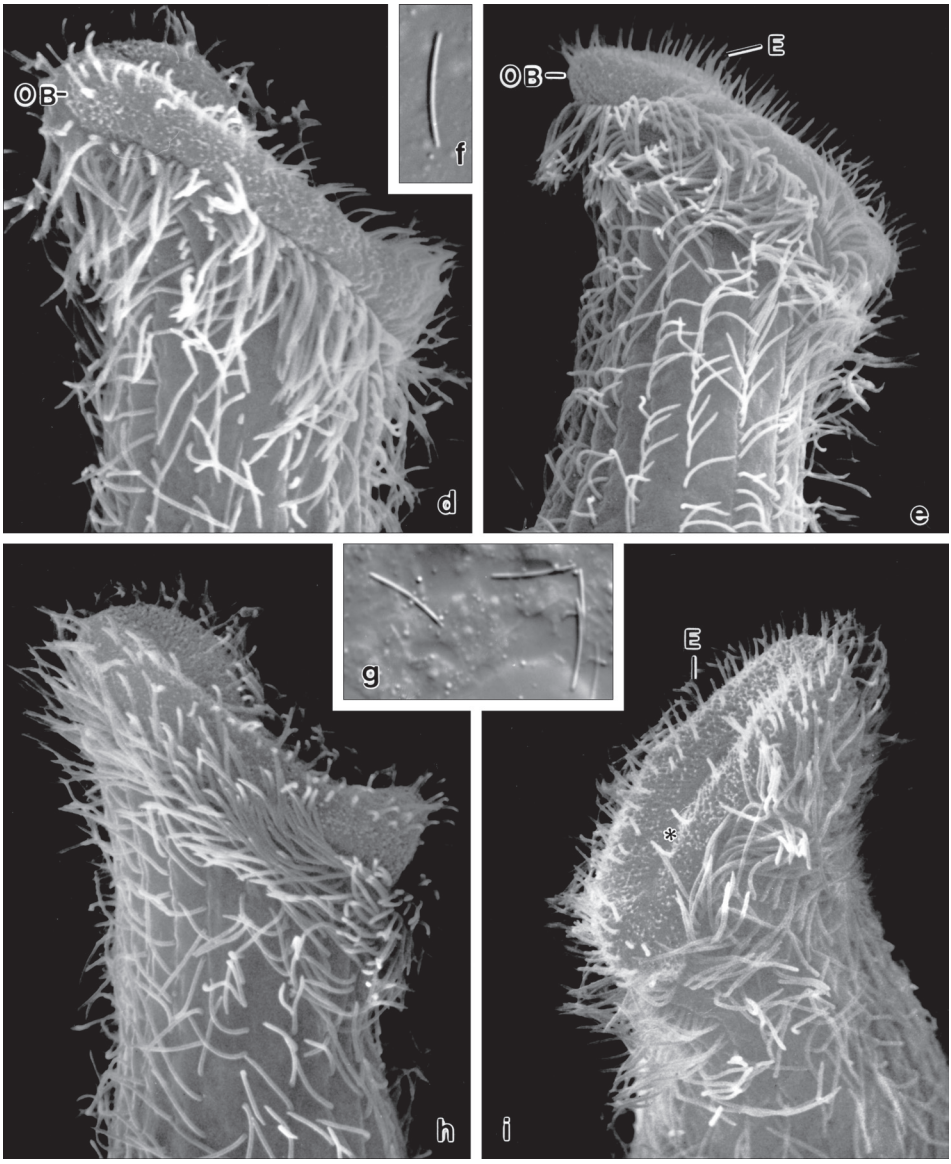


Fig. 3.17d–i *Spathidium polynucleatum* (Foissner et al., 2002) Jang et al., 2017 (from Foissner et al. 2002, Namibian specimens. d, e, h, i, scanning electron micrographs; f, g, from life). **d, e, h:** Right side views of anterior body portion showing extrusomes leaving the thick oral bulge, which is not flat but slightly screwed about its main axis. **f, g:** The extrusomes are slightly curved, about 10 µm long, fine rods, highly similar to those from the Australian specimens (Fig. 3.17o, p). **i:** Oblique ventrolateral view of oral area showing the elliptical oral bulge with a flat furrow (asterisk) in the centre. E – extrusomes, OB – oral bulge.

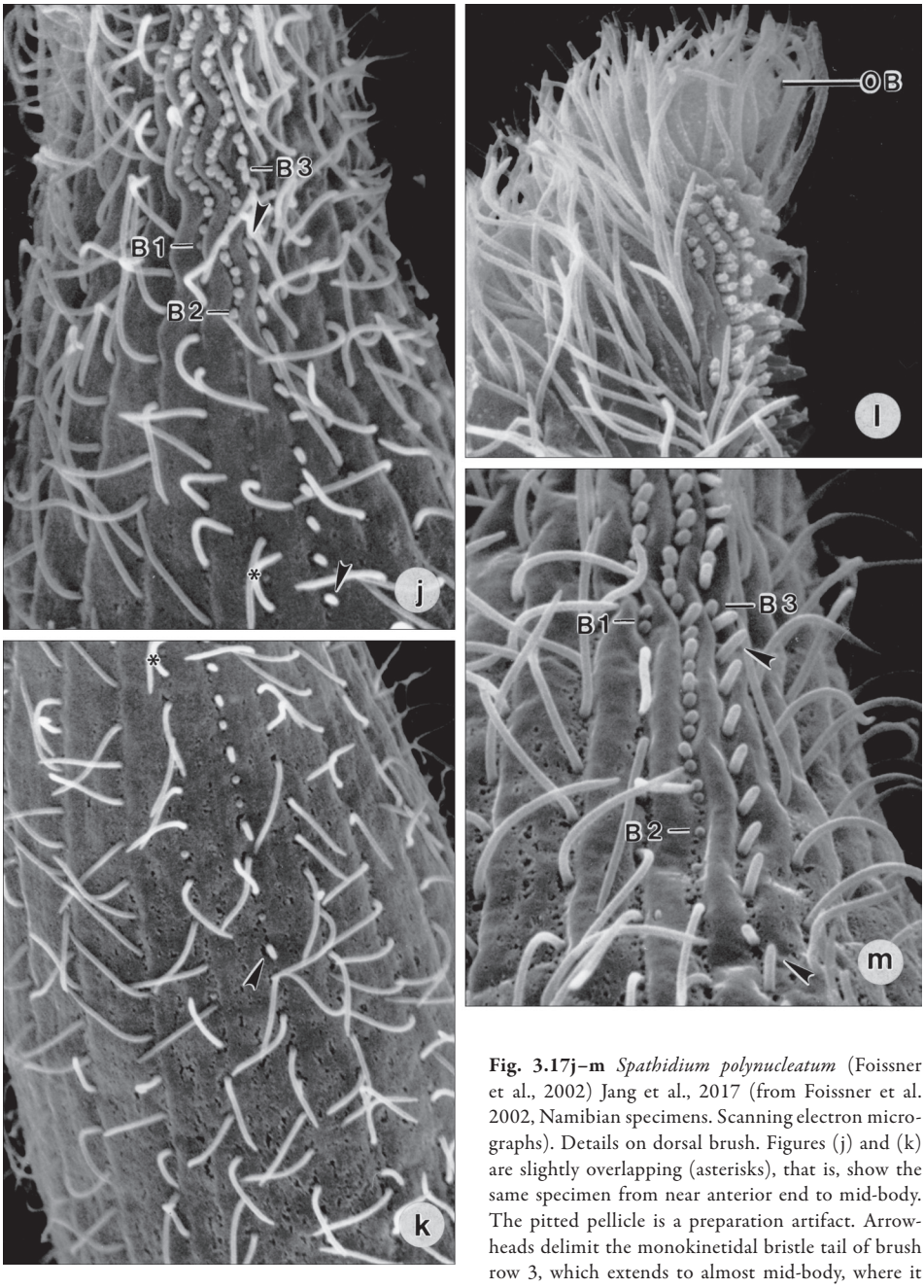
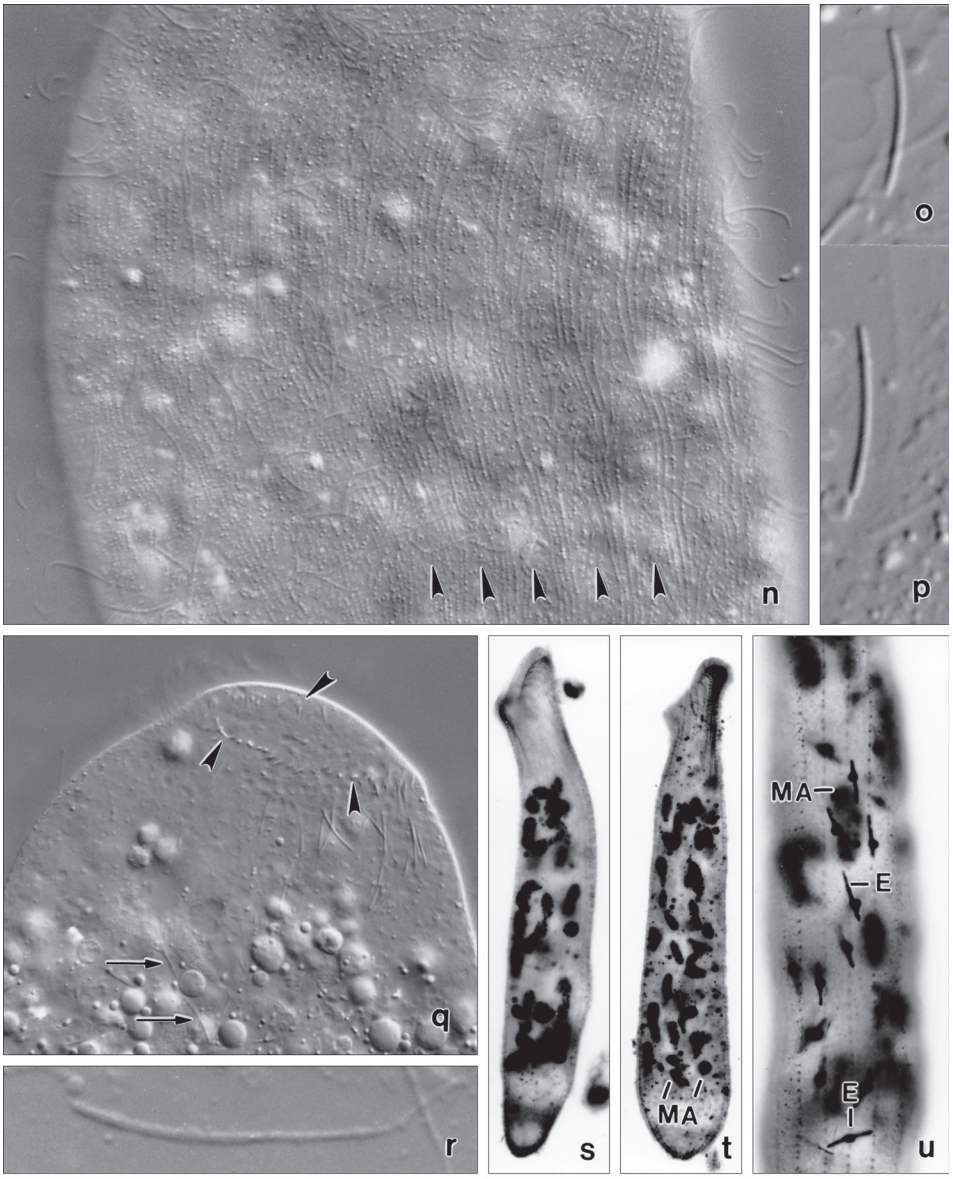


Fig. 3.17j–m *Spathidium polynucleatum* (Foissner et al., 2002) Jang et al., 2017 (from Foissner et al. 2002, Namibian specimens. Scanning electron micrographs). Details on dorsal brush. Figures (j) and (k) are slightly overlapping (asterisks), that is, show the same specimen from near anterior end to mid-body. The pitted pellicle is a preparation artifact. Arrowheads delimit the monokinetidal bristle tail of brush row 3, which extends to almost mid-body, where it changes to an ordinary somatic kinety; brush rows 1 and 2 lack a bristle tail and also continue posteriorly as ordinary ciliary rows (m). The dikinetidal brush bristles are slightly inflated distally and gradually decrease in length from about 3 µm anteriorly to minute stubs posteriorly (j, m). Generally, *Spathidium polynucleatum* has an inconspicuous dorsal brush because it occupies only about 20% of body length and the bristles are merely 3 µm long in vivo. B1–3 – dorsal brush rows, OB – oral bulge.



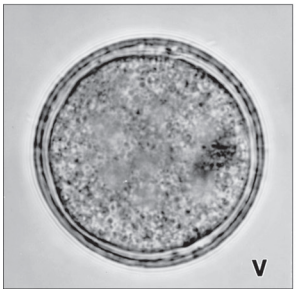


Fig. 3.17n–v *Spathidium polynucleatum* (Foissner et al., 2002) Jang et al., 2017 (from Foissner et al. 2002, n–r, Australian specimens; s–u, Namibian specimens; v, original, Dominican Republic. n–r, v, from life; s–u, protargol preparation). **n:** Surface view showing rows of cortical granules between the kineties (arrowheads). **o, p:** Resting extrusomes, length 10 µm. **q:** Heavily squeezed anterior body portion showing extrusomes anchored to oral bulge (arrowheads) and scattered in the cytoplasm (arrows). **r:** Exploded extrusome. **s, t:** Nuclear pattern and body shape. **u:** Mid-region showing developing extrusomes. **v:** Resting cyst. The wall is smooth, composed of two distinct layers, and colourless. E – developing extrusomes, MA – macronucleus nodules.

Epispathidium pattern (Fig. 3.16f, g). Because of this intermediate ciliature as well as the fact that it clusters with other *Spathidium* species in molecular phylogenies, Jang et al. (2017) transferred it to *Spathidium* (see list of synonyms). For detailed comparison with similar species, see Foissner et al. (2002, p. 315).

Description: Two populations were studied in detail by Foissner et al. (2002), namely, one from Namibia (type population) and one from Australia. They are indistinguishable, as also evident from the very similar morphometrics (Table 3.11). The description, however, is mainly based on the Namibian population, which was cultivated (in Eau de Volvic enriched with some crushed wheat grains to stimulate growth of small food ciliates) and investigated with the scanning electron microscope.

Body size 130–230 × 25–40 µm, usually near 190 × 30 µm in vivo; length:width ratio 5.0–9.4:1, frequently 6–7:1 both in vivo and protargol preparations (Table 3.11). Body shape constant and conspicuous, that is, cylindrical because oral bulge about as wide as broadest postoral body region and flattened only in oral area (Fig. 3.16a, c, 3.17a–c). Macronucleus pattern highly variable because nodules develop from a tortuous strand in post-dividers; thus, about 5% of specimens have a single or few long macronucleus pieces (see discussion). Ripe cells possess an average of 30 scattered, globular to elongate ellipsoidal, rather large (12 × 5 µm) nodules, each with a branched nucleolus or a few globular nucleoli. Many scattered micronuclei 1.5–2.5 µm across (Fig. 3.16a, c, 3.17s, t). Contractile vacuole in rear end, several excretory pores in posterior pole area. Extrusomes virtually identical in Namibian, Australian, and Venezuelan population (Fig. 3.16a, i–k, 3.17e–g, i, o–r): ripe organelles fine, distinctly curved rods with slightly narrowed ends, 8.0–10.0 (on average 9.3, n = 11) × 0.4–0.6 µm in size, studded in oral bulge, except for midline, do not impregnate with the protargol method used; many developing extrusomes scattered in cytoplasm, 6–8 µm long and with a conspicuous centric or acentric inflation about 2 µm across, impregnate heavily with protargol. Cortex highly flexible, indistinctly furrowed by ciliary rows, contains innumerable, colourless granules about 4.0 µm across; granules around basal bodies of cilia and between kineties, form slightly oblique rows along or upon postciliary microtubule ribbons (Fig. 3.16g, 3.17n). Cytoplasm colourless and hyaline in oral area, while usually packed with macronucleus nodules and lipid droplets 1–8 µm across in postoral region. Feeds on small and medium-sized ciliates (*Protocyclidium terricola*, *Vorticella astyliformis*, *Colpoda maupasi*) ingested whole and thus recognizable in the cytoplasm of the predator. Swims rather rapidly by rotation about main body axis and shows great flexibility when creeping on soil particles or organic debris.

Somatic cilia about 10 µm long and rather closely spaced (2 µm on average; Table 3.11), especially in anterior portion of rows, where a conspicuous ciliary corona is produced; arranged in an average of 22 straight, bipolar kineties with anterior end of left side rows slightly to distinctly curved ventrally. Dorsal brush of ordinary structure, inconspicuous because occupying merely 20% of body length and composed of bristles only up to 3 µm long in vivo; middle brush row slightly longer than right and left; row 3 has a monokinetidal trail extending to mid-body; frequently some dikinetids in first ordinary ciliary row right of brush kinety 1; further details, see Fig. 3.16a–g, l, m, 3.17c, j–m, Table 3.10.

Oral bulge slanted by about 45°, conspicuous, although not longer than trunk width, because (i) thick and up to 5 µm high, (ii) ∞-shaped in lateral and dumbbell-shaped in frontal

continued on p. 105

Table 3.11 Morphometric data on *Spathidium polynucleatum* from Namibia (upper line, type population; from Foissner et al. 2002) and Australia (middle line; from Foissner et al. 2002). In the lower line the values of both populations are combined[a]

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Body, length	173.7	169.0	19.8	5.7	11.4	140.0	217.0	12
	182.2	187.0	25.9	7.8	14.2	143.0	216.0	11
	176.0	174.0	21.6	4.6	12.3	140.0	217.0	23
Body, width	29.3	28.0	3.8	1.1	12.9	26.0	40.0	12
	27.5	27.0	2.3	0.7	8.5	23.0	32.0	11
	28.6	28.0	3.3	0.7	11.5	23.0	40.0	23
Body length:width, ratio	6.0	6.0	0.9	0.3	15.1	5.0	8.0	12
	6.7	7.0	1.3	0.4	19.7	5.0	9.4	11
	6.3	6.0	1.2	0.2	18.4	5.0	9.4	23
Oral bulge, length	27.3	28.0	2.4	0.7	8.9	22.0	31.0	12
	26.1	26.0	2.8	0.9	10.9	23.0	32.0	11
	26.6	27.0	2.5	0.5	9.6	22.0	32.0	23
Oral bulge, height	4.0	4.0	0.7	0.2	18.5	3.0	5.0	12
	2.8	3.0	–	–	–	2.0	3.0	11
	3.4	3.0	0.9	0.2	26.6	2.0	5.0	23
Circumoral kinety to last dikinetid of brush row 1, distance	28.2	28.0	3.9	1.1	13.5	22.0	34.0	12
	28.9	30.0	5.6	1.7	19.4	15.0	36.0	11
	28.3	29.0	4.5	1.0	5.8	15.0	36.0	23
Circumoral kinety to last dikinetid of brush row 2, distance	33.6	35.0	3.1	0.9	4.4	28.0	38.0	12
	34.7	35.0	4.2	1.3	12.2	25.0	40.0	11
	34.3	35.0	3.7	0.8	10.8	25.0	40.0	23
Circumoral kinety to last dikinetid of brush row 3, distance	28.8	30.0	2.3	0.7	8.1	24.0	32.0	12
	32.1	33.0	5.6	1.7	17.4	21.0	40.0	11
	30.5	30.0	4.5	1.0	14.9	21.0	40.0	23
Anterior body end to anteriormost macronucleus nodule, distance	33.5	34.0	4.1	1.2	12.2	29.0	43.0	12
	32.9	34.0	7.0	2.1	21.4	19.0	46.0	11
	32.8	34.0	5.3	1.1	16.1	19.0	46.0	23
Macronucleus nodules, length	13.3	14.0	2.9	0.8	21.6	8.0	18.0	12
	9.7	10.0	3.6	1.1	37.5	5.0	16.0	11
	11.4	12.0	3.6	0.8	31.9	5.0	18.0	23
Macronucleus nodules, width	4.8	5.0	0.8	0.2	15.9	4.0	6.0	12
	5.3	5.0	1.1	0.3	20.8	4.0	7.0	11
	5.0	5.0	1.0	0.2	19.2	4.0	7.0	23
Macronucleus nodules, number[b]	28.8	32.0	7.8	1.8	27.2	12.0	40.0	19
	32.6	35.0	10.3	2.4	31.7	10.0	50.0	19
	30.8	33.0	9.2	2.2	30.0	10.0	50.0	38
Micronuclei, number	28.7	28.0	5.6	1.6	19.5	20.0	40.0	12
	29.5	30.0	.9	2.1	23.3	15.0	40.0	11
	28.9	30.0	6.2	1.3	21.3	15.0	40.0	23
Somatic kineties, number	21.9	22.0	1.2	0.4	5.7	20.0	25.0	12
	24.6	25.0	2.3	0.7	8.8	21.0	28.0	11
	23.3	22.0	2.2	0.5	9.6	20.0	28.0	23
Ciliated kinetids in a right-lateral somatic kinety, number	92.4	87.0	13.7	4.0	14.8	80.0	120.0	12
	90.1	80.0	18.0	5.4	19.9	70.0	130.0	11
	90.8	84.0	15.7	3.4	17.3	70.0	130.0	23

Table 3.11 Continued

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	12
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	23
Dikinetids in brush row 1, number	22.4	23.0	1.9	0.6	8.6	20.0	27.0	12
	22.8	22.0	2.6	0.8	11.6	19.0	28.0	11
	22.6	23.0	2.3	0.5	10.2	19.0	28.0	23
Dikinetids in brush row 2, number	28.3	28.0	2.5	0.7	8.9	22.0	32.0	12
	28.8	30.0	3.3	1.0	11.6	23.0	32.0	11
	28.4	28.0	2.9	0.6	10.1	22.0	32.0	23
Dikinetids in brush row 3, number	20.8	21.0	1.5	0.4	7.4	18.0	23.0	12
	23.1	23.0	2.8	0.5	12.3	19.0	28.0	11
	21.8	22.0	2.6	0.6	11.7	18.0	28.0	23

[a] Data based on mounted, protargol-prepared (Foissner's method), and randomly selected specimens from a pure culture (Namibia) and a non-flooded Petri dish culture (Australia). 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] Specimens (likely post-dividers) with ≤5 macronucleus nodules were excluded, that is, four cells in Namibia and three in Australia.

view, and (iii) bright due to the many extrusomes contained. The curious shape of the basically elongate elliptical bulge (Fig. 3.17i) is produced by a rather distinct twist of its main axis, making the bulge screwed like a propeller blade (Fig. 3.17d, e, h). Circumoral kinety continuous and (sometimes indistinctly) separate from ciliary rows, composed of dikinetids each associated with a cilium and a rather long nematodesma; nematodesmata of neighbouring kinetids form more or less distinct bundles producing a rather conspicuous oral basket (Fig. 3.16a, d, e, l–g, 3.17a–e, h, i, Table 3.11).

Conjugation: Specimens are connected in the oral area during conjugation. Postconjugates have 4–6 globular, rather large macronucleus nodules.

Resting cyst (original observations): Resting cysts have been studied in a population from the Dominican Republic, viz., from a bark sample from a tree at top of a hill behind the Hotel Riu Merengue (Fig. 3.16n, 3.17v). Type III structure (see Foissner & Xu 2007, p. 38; for brief note, see also Chapter 1, that is, Berger et al. 2025a); 46.4 µm across (M = 44.0 µm, SD = 6.3 µm, CV = 13.5%, Min = 42 µm, Max = 60 µm, n = 7); wall = 1.5–2.0 µm thick, composed of two thin, narrowly spaced membranes very flexible under mild coverglass pressure where they distinctly extend; colourless, except of wall, which has a distinct, blueish shimmer under bright field illumination; cell occasionally some micrometers apart from wall and packed with moderately refractive globules 0.5–3.0 µm across; extrusomes and macronucleus nodules maintained; some irregularly-shaped material between wall and cell; wall more or less densely covered with sessile bacteria (Type I cysts have, according to Foissner & Xu 2007, p. 38, a much more pronounced mucous envelope).

Occurrence and ecology: The type locality of *Spathidium polynucleatum* is soil and litter under a *Euphorbia* cushion at east margin (26°40'S 16°50'E) of the Namib desert,

Namibia (Foissner et al. 2002). However, *Spathidium polynucleatum* occurs not only in Namibia (type locality), but also in the Republic of South Africa (Cape Peninsula; mosses and soil from stones and Fynbos plants; pH 6.1), Australia (soil from rain forest near Cairns; pH 3.9; Fig. 3.16f, g, l), and South America (Venezuela; highly saline soil from a small pan in the Morrocoy National Park; pH 7.3; Fig. 3.16k). For record from Dominican Republic, see paragraph on resting cyst. *Spathidium polynucleatum* has been found also in Laurasia, namely in soil from deciduous forests of Austria (Foissner et al. 2005, p. 627). Jang et al. (2017, p. 941) isolated the Korean population from soil from the surroundings of a maple tree in Yeungnam University, Daehak-ro, Gyeongsan-si, Gyeongsangbuk-do (35.826°N 128.758°E). Obviously, this species has a wide ecological range and global distribution.

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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