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

In memory of Wilhelm Foissner (1948–2020)

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Preface, authorship, acknowledgements, and funding

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

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

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

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

Salzburg
January 2025

Helmut Berger (Publisher)
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Abstract

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

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

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

Chapter 11

Supraspathidium Foissner & Didier, 1981 (Ciliophora, Spathidiidae), a genus whose species have more than one contractile vacuole[1]

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Abstract

Supraspathidium Foissner & Didier, 1981 originally comprised nine species all of them have several contractile vacuoles. Recent studies, however, showed that this feature highly likely evolved several times independently. Thus, in the present revision only seven species are assigned to *Supraspathidium*: *Supraspathidium teres* (Stokes, 1886) Foissner & Didier, 1981 (type species; original combination *Lacrymaria teres*; only known from the original description which is based on in vivo observations only); *Supraspathidium armatum* Foissner, Agatha & Berger, 2002; *Supraspathidium elongatum* (Penard, 1922) Foissner & Didier, 1981; *Supraspathidium etoschense* Foissner, Agatha & Berger, 2002; *Supraspathidium gigas* (Cunha, 1914) Foissner & Didier, 1981; *Supraspathidium multistriatum* Foissner & Didier, 1981; *Supraspathidium vermiforme* (Penard, 1922) Foissner & Didier, 1981. A key to the species is provided.

Supraspathidium Foissner & Didier, 1981

1981 ***Supraspathidium* nov. gen.**[2] – Foissner & Didier, Annls Stn limnol. Besse 15: 255 (original description). Type species (by original designation): *Lacrymaria teres* Stokes, 1886.
2003 ***Supraspathidium*** – Foissner, Acta Protozool. 42: 157 (improved diagnosis and detailed discussion).

[1] This chapter should be referenced as follows: Foissner W., Xu K. & Berger H. (2025): *Supraspathidium* Foissner & Didier, 1981 (Ciliophora, Spathidiidae), a genus whose species have more than one contractile vacuole. – Ser. Monogr. Cilioph. 6: 335–366.
For notes on "Material and methods", see chapter 1 (Berger et al. 2025a).

[2] Foissner & Didier (1981) provided the following diagnosis: "Spathidiidae mit mehreren bis sehr vielen, meist in Längsreihen angeordneten kontraktilen Vakuolen und häufig nur undeutlich vom Körper abgesetztem Mundwulst."

2007 ***Supraspathidium* Foissner et Didier, 1982** – Jankowski, Phylum Ciliophora, p. 564 (generic revision of ciliates; incorrect year).

2008 ***Supraspathidium* Foissner & Didier, 1982** – Lynn, Ciliated protozoa, p. 370 (familial revision of ciliates; incorrect year).

Nomenclature: No etymology has been provided in the original description or a later work. *Supraspathidium* is a composite of *supra-* (Latin; above [in compounds]; Hentschel & Wagner 1996, p. 567) and the genus-group name *Spathidium*. For etymology of *Spathidium* Dujardin, 1841, see Chapter 2, that is, Berger et al. (2025b).[3] Neuter gender according to Aescht (2001, p. 301).

Diagnosis (from Foissner 2003a, p. 157): Massive, densely ciliated Spathidiidae with *Epispathidium*-like ciliary pattern and many (>5) contractile vacuoles, each having several excretory pores, in one or two rows.

Species originally assigned: *Supraspathidium teres* (Stokes, 1886) Foissner & Didier, 1981 (type species; original combination *Lacrymaria teres*); *Supraspathidium canaliculatum* (Lepsi, 1959) Foissner & Didier, 1981 (original combination *Spathidium canaliculatum*); *Supraspathidium elongatum* (Penard, 1922) Foissner & Didier, 1981 (original combination *Cranotheridium elongatum*); *Supraspathidium gigas* (Cunha, 1914) Foissner & Didier, 1981 (original combination *Spathidium gigas*); *Supraspathidium latissimum* (Lepsi, 1959) Foissner & Didier, 1981 (original combination *Spathidium latissimum*; now again in *Spathidium*, see Chapter 3, that is, Foissner et al. 2025a); *Supraspathidium lieberkuehnii* (Bütschli, 1889) Foissner & Didier, 1981 (original combination *Prorodon lieberkuehnii*); *Supraspathidium multistriatum* Foissner & Didier, 1981; *Supraspathidium polyvacuolatum* (Vuxanovici, 1959) Foissner & Didier, 1981 (original combination *Spathidium polyvacuolatum*; now again in *Spathidium*, see Chapter 3, that is, Foissner et al. 2025a); *Supraspathidium vermiforme* (Penard, 1922) Foissner & Didier, 1981 (original combination *Spathidium vermiforme*).

Species now assigned: *Supraspathidium teres* (Stokes, 1886) Foissner & Didier, 1981 (type species); *Supraspathidium armatum* Foissner, Agatha & Berger, 2002; *Supraspathidium elongatum* (Penard, 1922) Foissner & Didier, 1981; *Supraspathidium etoschense* Foissner, Agatha & Berger, 2002; *Supraspathidium gigas* (Cunha, 1914) Foissner & Didier, 1981; *Supraspathidium multistriatum* Foissner & Didier, 1981; *Supraspathidium vermiforme* (Penard, 1922) Foissner & Didier, 1981.

Species misclassified: See Remarks below.

Remarks: This genus poses some problems, mainly due to the unfortunate typification not specified by Foissner & Didier (1981), and the vague original diagnosis (translated from German; German version, see footnote 2): "Spathidiidae with several to many contractile vacuoles in, usually, longitudinal rows and oral bulge frequently only indistinctly set off from body proper". Foissner & Didier (1981) emphasized the increased number of contractile vacuoles as the main feature of *Supraspathidium* and allocated all *Spathidium* species with more than the usual terminal vacuole to this genus (see below). However, recent investigations show that this feature obviously evolved independently in several evolutionary lines, viz., in *Spathidium* Dujardin, 1841, *Arcuospathidium* Foissner, 1984, and *Supraspathidium*. Thus, Foissner (2003a) in his detailed discussion on *Supraspathidium* emended the diagnosis

[3] Note by H. Berger: W. Foissner did not provide an explanation of the name *Supraspathidium* in the present manuscript. We can assume that he wanted to indicate a similarity with *Spathidium* species.

in that it now includes, besides the type species, mainly three species, viz., *Supraspathidium multistriatum*, *Supraspathidium etoschense*, and *Supraspathidium armatum*, which obviously constitute a distinct evolutionary line.

Supraspathidium teres, the type species of the genus, is, unfortunately, insufficiently known, and thus might be different at generic level from the three species mentioned in the previous paragraph. If this is shown by a detailed reinvestigation, the problem can be solved in several ways: (i) If *Lacrymaria teres* matches neither *Supraspathidium* (as defined above) nor any other of the established spathidiid genera, then it should be maintained as *Supraspathidium teres* and the three species listed above are transferred to a new genus; (ii) If the reinvestigation of *Lacrymaria teres* shows that it is basically a "simple" *Spathidium* with two contractile vacuoles, the genus *Supraspathidium* should be abolished and a new genus established for the three *Supraspathidium* species listed above; (iii) Alternatively, species with two contractile vacuoles and a *Spathidium*-like ciliary pattern, for instance, *Spathidium faurefremieti* Foissner, 2003a (for revision, see Chapter 3, that is, Foissner et al. 2025a) and, possibly, the reinvestigated *Supraspathidium teres*, can be classified in *Supraspathidium*, however, with a refined diagnosis as follows: "Spathidiidae with two contractile vacuoles and *Spathidium*-like ciliary pattern". Then, a new genus should be established for the three *Supraspathidium* species listed above.

Of the species originally assigned (see above), *Supraspathidium lieberkuehnii* (Bütschli, 1889) Foissner & Didier, 1981 is now the type species of the genus *Myriokaryon* Jankowski, 1973, which is the nominotypical genus of the Myriokaryonidae Foissner, 2003b (see Foissner 2003b for a detailed review)[4]. The other species are maintained in *Supraspathidium* and reviewed here, except of *Supraspathidium polyvacuolatum*, *Supraspathidium canaliculatum*, and *Supraspathidium latissimum*, which do not match the emended diagnosis and are thus again classified in *Spathidium*. Likely, *Supraspathidium gigas* and *Supraspathidium elongatum*, although reviewed here, belong to the Myriokaryonidae.

Unidentified *Supraspathidium* species were found, inter alia, in Austria (River Krems; AOÖLR 1997, p. 71) and Ukraine (floodplain water bodies of the Dnieper Reservoirs; Kovalchuk 2006, p. 10).

Key to species

1 Body length usually ≥600 µm; many scattered macronuclear nodules; many scattered contractile vacuoles **2**

– Body length usually ≤600 µm; macronucleus usually a long, tortuous strand; contractile vacuoles in a dorsal row or a dorsal and ventral row **3**

2 Oral bulge simple and with single type of about 60 µm long extrusomes .... *Supraspathidium gigas* (p. 361)

[4] Note by H. Berger: Foissner & Didier (1981, p. 255) did not mention the original combination of *Supraspathidium lieberkuehnii*. From the context (e.g., diagnosis of genus in Foissner & Didier 1981; Foissner 2003b) it is clear that they transferred *Prorodon lieberkuehnii* Bütschli, 1889 (legend to Tafel LVII, Fig. 6; original spelling *Prorodon lieberkühnii*) and not *Spathidium lieberkuehnii* Bütschli, 1889 (legend to Tafel LIX, Fig. 1a, b; original spelling *Spathidium lieberkühnii*) to *Supraspathidium*. Interestingly, Foissner (2003b, p. 114) did not mention "*Supraspathidium lieberkuehnii* (Bütschli, 1889) Foissner & Didier, 1981" in the list of synonyms. I suppose that he has forgotten this combination. Berger & Al-Rasheid (2008, p. 81) have likewise overlooked all combinations with *Supraspathidium* made by Foissner & Didier (1981), except that of the type species.

– Oral bulge composed of a short, transverse apical portion with about 80 µm long extrusomes; and a long, strongly oblique ventral portion with short, about 10 µm long extrusomes ..... *Supraspathidium elongatum* (p. 359)

3 (1) Likely many minute macronuclear nodules; a distinct anterior and posterior contractile vacuole connected by a tortuous canal ..... *Supraspathidium teres* (p. 338)

– Macronucleus long and tortuous; five or more contractile vacuoles in a dorsal row or in a dorsal and ventral row **4**

4 Posterior body region tail-like narrowed; contractile vacuoles in a ventral and dorsal row ..... *Supraspathidium armatum* (p. 353)

– Posterior body end bluntly pointed or broadly rounded; contractile vacuoles in a dorsal row **5**

5 Body cylindrical and ribbon-like flattened, posterior end bluntly pointed; likely ≤25 ciliary rows ..... *Supraspathidium vermiforme* (p. 357)

– Body indistinctly spatulate or bursiform, not flattened in posterior half, rear end broadly rounded; >40 ciliary rows **6**

6 Contractile vacuoles in line with dorsal brush; extrusomes slightly to distinctly acicular and curved; about 75 ciliary rows ..... *Supraspathidium multistriatum* (p. 339)

– Contractile vacuoles in dorsolateral row, i.e., left of dorsal brush; extrusomes elongate clavate, not curved.; about 44 ciliary rows ..... *Supraspathidium etoschense* (p. 346)

Supraspathidium teres (Stokes, 1886) Foissner & Didier, 1981

(Fig. 11.7a, b)

1886 ***Lacrymaria teres* sp. nov.** – Stokes, Am. mon. microsc. J. 7: 84, Fig. 14 (Fig. 11.7a; original description; no type material available).

1888 ***Lacrymaria teres*, Stokes** – Stokes, J. Trenton nat. Hist. Soc. 1: 164, Plate IV, fig. 19 (Fig. 11.7a; revision of protists from USA).

1930 ***Spathidium teres* Stokes, 1886** – Kahl, Tierwelt Dtl. 18: 162, Fig. 22$_7$ (Fig. 11.7b; first reviser; combination with *Spathidium*, see nomenclature).

1943 ***Spathidium teres* Stokes** – Kahl, Infusorien, p. 26, Tafel V, Fig. 30 (redrawing of Fig. 11.7b; brief review).

1981 ***Supraspathidium teres* (Stokes, 1886) nov. comb.** – Foissner & Didier, Annls Stn limnol. Besse 15: 255 (combination with *Supraspathidium*, without reinvestigation).

Nomenclature: This is the type species of *Supraspathidium* Foissner & Didier, 1981 by original designation. No derivation of the name has been provided in the original description or a later work. The species-group name *teres* (Latin; rubbed off, rounded, cylindrical in present case; Brown 1954, p. 249; Hentschel & Wagner 1996, p. 576; longish structure with round cross-section, Werner 1972, p. 403) likely refers to the body shape which was described as "elongate-clavata, subcylindrical, ..." by Stokes (1886). The transfer from *Lacrymaria* to *Spathidium* was done by Kahl (1930), but not formally indicated. Likely for that reason, the species was incorrectly mentioned as "*Spathidium teres* Stokes, 1886" by Jankowski (2007, p. 564); the correct spelling, when classified in *Spathidium*, is *Spathidium teres* (Stokes, 1886) Kahl, 1930.

Diagnosis: Not available (see description). Should await reinvestigation.

Remarks: Kahl's (1930) figure (Fig. 11.7b) is a rather inaccurate redrawing of Stokes's (1886) original drawing (Fig. 11.7a). *Supraspathidium teres*, obviously a very rare species

(see below), needs reinvestigation with modern methods. It matches the emended diagnosis of the genus (but see introduction to the genus) because Stokes' (1886) description indicates that further contractile vacuoles may occur between the two main vacuoles, as described by Penard (1922) in *Supraspathidium vermiforme*.

Supraspathidium teres differs from the congeners by the macronucleus (likely many small nodules vs. long strands) and the conspicuous canal connecting the two main contractile vacuoles.

Description: The morphological data are from the original description (Stokes 1886). Body length 170–200 µm in vivo, 6–7 times as long as broad. Body elongate-clavate, subcylindrical, very soft and flexible, narrowest and somewhat attenuate and flattened in anterior portion; anterior (oral) end obliquely and convexly truncate, posterior rounded (Fig. 11.7a). Nuclear apparatus not recognizable, not even after repeated application of reagents and staining fluids (Stokes 1886); thus, we agree with Kahl (1930) that the macronucleus is possibly composed of many, small nodules. Two conspicuous contractile vacuoles, one in rear end, the other in anterior body half near one lateral border, the two connected by a narrow, tortuous, canal-like channel penetrating the cytoplasm, and often laterally developing globular or irregular lacunae. Extrusomes not mentioned. Cytoplasm granular. Cortex finely striate longitudinally, indicating a considerable number of ciliary rows (≥40), considering a body width of about 30 µm. Oral bulge occupies anterior body end, obliquely truncate by about 45°, approximately as long as widest trunk region, hardly set off from body proper, but rather conspicuous because distinctly convex (Fig. 11.7a).

Occurrence and ecology: Yet, *Supraspathidium teres* was found only at the type locality, where it was abundant. Stokes (1886) discovered it in standing water with decaying vegetation from the cypress swamps of South Florida (about 25°N 81°W), USA. *Supraspathidium teres* must be a rare species, or have a very restricted distribution, because we were unable to locate any literature record. Feeds on the ciliate *Dexiotricha plagia* Stokes, 1885a, expands the oral bulge to about 60 µm (Stokes 1886).

Supraspathidium multistriatum Foissner & Didier, 1981

(Fig. 11.1a–n, 11.2a–d, 11.3d, Table 11.1)

1981 ***Supraspathidium multistriata* nov. spec.**[5] – Foissner & Didier, Annls Stn limnol. Besse 15: 255, Abb. 1a–m, 6, 7, Tabelle 1 (Fig. 11.1a–n, 11.2a–d; original description; two protargol slides [syntypes; accession numbers 1981/11, 1981/12; Aescht 2003, p. 391; 2008, p. 167] have been deposited in the Biology Centre of the Upper Austrian Museum in Linz [LI]; for details, see nomenclature).

2002 ***Supraspathidium multistriatum* nom. corr.** – Foissner, Agatha & Berger, Denisia 5: 278, Fig. 60k, l, p (Fig. 11.1a, e, j; comparison with *Supraspathidium etoschense* and emendation [their footnote 7] of species-group name because *Supraspathidium* is of neuter gender; see genus section and ICZN 1999, Article 31.2).

Nomenclature: No derivation of the species-group name has been provided in the original description or a later work. It is a composite of *mult·us*, *-a*, *-um* (Latin adjective, many, numerous; Werner 1972, p. 272), the thematic vowel *·i-*, and the Latin adjective *striat·us*, *-a*,

[5] Foissner & Didier (1981) provided the following diagnosis: "In vivo ungefähr 250–500 × 60–85 µm großes, leicht beutelförmiges, sehr dicht bewimpertes *Supraspathidium* mit durchschnittlich 75 Somakineten. Ungefähr 6 kontraktile Vakuolen in einer Längsreihe zwischen dem unteren Ende der Dorsalbürste und dem hinteren Körperende. Jede Vakuole mit mehreren Exkretionspori. Makronucleus bandartig, verschlungen."

-um (striped, striated, ciliary rows in present case; Hentschel & Wagner 1996, p. 563), referring to the high number of ciliary rows. For note on typification, see Aescht (2008, p. 167). Aescht (2008, p. 167) dated the work by Foissner & Didier (1981) with 1982.

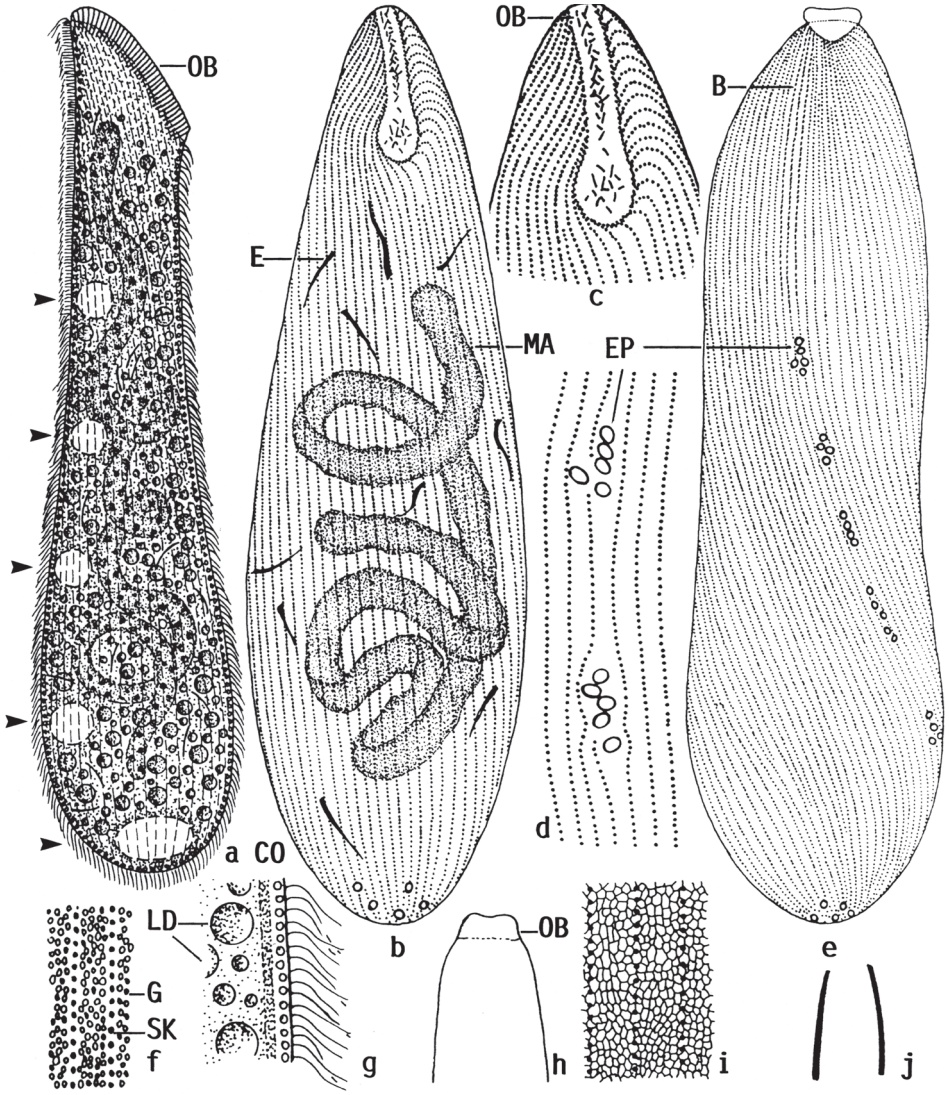

Fig. 11.1a–j *Supraspathidium multistriatum* Foissner & Didier, 1981 (from Foissner & Didier 1981. a, f–h, j, from life; b–e, protargol preparation; i, Klein-Foissner silver nitrate preparation). **a:** Right side view of a 400 µm long specimen. Arrowheads mark contractile vacuoles. **b, c, e:** Ciliary pattern of ventral (b, c) and dorsal (e) side, 212 µm (b), 205 µm (e). The oral bulge is packed with extrusomes, which appear as short rods when seen frontally (actual length up to 20 µm in preparations). **d:** Part of dorsal side showing excretory pores of contractile vacuoles. **f, g:** Surface view and optical section of cortex, which is about 2 µm thick, bright, and contains narrowly spaced rows of yellowish granules. **h:** Dorsal view of anterior body end. **i:** Narrowly meshed silverline pattern in mid-body. **j:** Extrusomes are slightly acicular and about 8 µm long in vivo. B – dorsal brush, CO – cortex, E – extrusomes, EP – excretory pores, G – cortical granules, LD – lipid droplets, MA – macronucleus, OB – oral bulge, SK – somatic kinety.

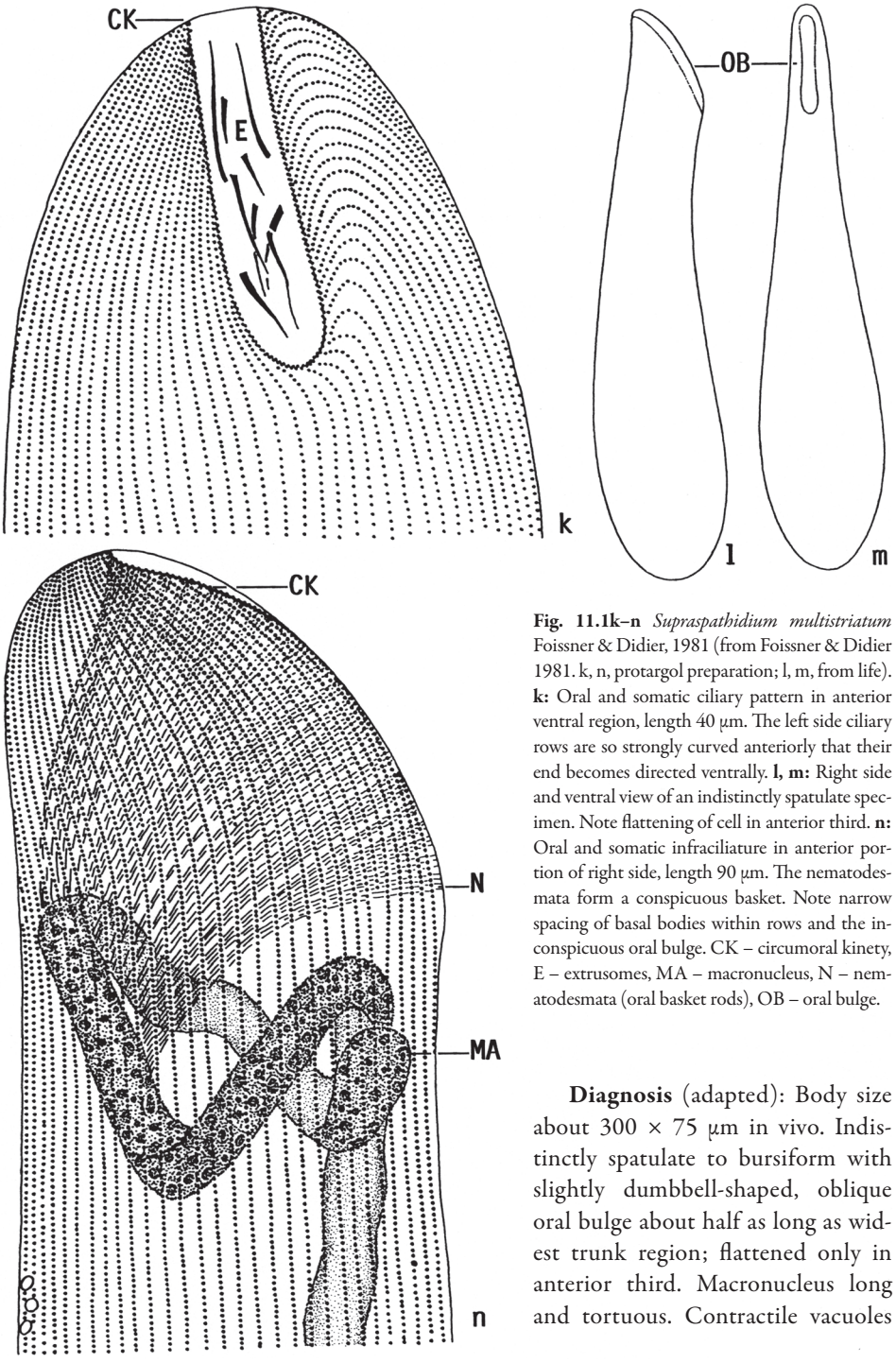

Fig. 11.1k–n *Supraspathidium multistriatum* Foissner & Didier, 1981 (from Foissner & Didier 1981. k, n, protargol preparation; l, m, from life). **k:** Oral and somatic ciliary pattern in anterior ventral region, length 40 µm. The left side ciliary rows are so strongly curved anteriorly that their end becomes directed ventrally. **l, m:** Right side and ventral view of an indistinctly spatulate specimen. Note flattening of cell in anterior third. **n:** Oral and somatic infraciliature in anterior portion of right side, length 90 µm. The nematodesmata form a conspicuous basket. Note narrow spacing of basal bodies within rows and the inconspicuous oral bulge. CK – circumoral kinety, E – extrusomes, MA – macronucleus, N – nematodesmata (oral basket rods), OB – oral bulge.

Diagnosis (adapted): Body size about 300 × 75 µm in vivo. Indistinctly spatulate to bursiform with slightly dumbbell-shaped, oblique oral bulge about half as long as widest trunk region; flattened only in anterior third. Macronucleus long and tortuous. Contractile vacuoles

continued on p. 345

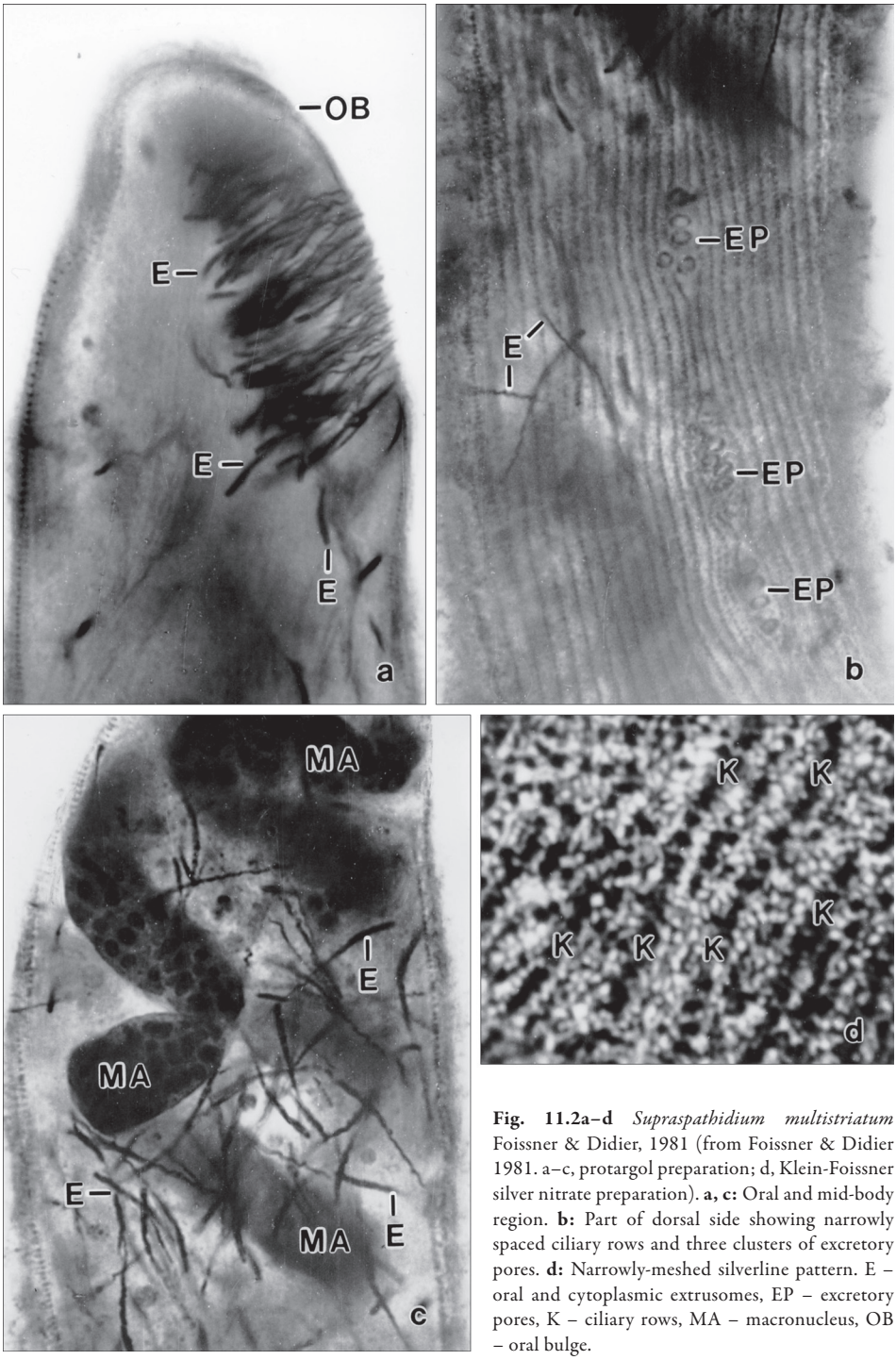

Fig. 11.2a–d *Supraspathidium multistriatum* Foissner & Didier, 1981 (from Foissner & Didier 1981. a–c, protargol preparation; d, Klein-Foissner silver nitrate preparation). **a, c:** Oral and mid-body region. **b:** Part of dorsal side showing narrowly spaced ciliary rows and three clusters of excretory pores. **d:** Narrowly-meshed silverline pattern. E – oral and cytoplasmic extrusomes, EP – excretory pores, K – ciliary rows, MA – macronucleus, OB – oral bulge.

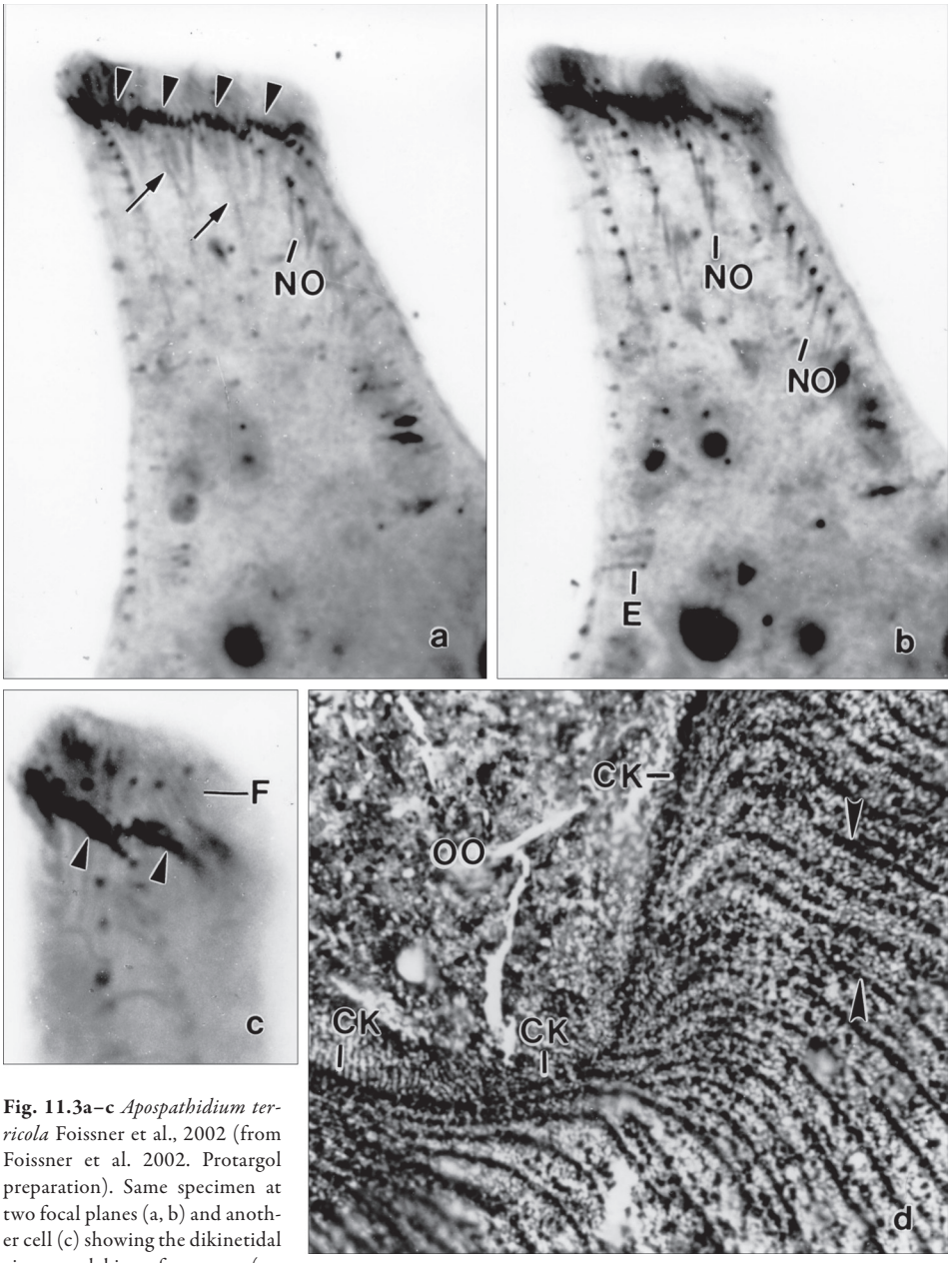

Fig. 11.3a–c *Apospathidium terricola* Foissner et al., 2002 (from Foissner et al. 2002. Protargol preparation). Same specimen at two focal planes (a, b) and another cell (c) showing the dikinetidal circumoral kinetofragments (arrowheads), the oralized somatic monokinetids with nematodesmata, the bulge fibres, and rows of body extrusomes. Arrows denote cuneate nematodesmal bundles originating from the dikinetidal circumoral kinetofragments. For details on this species, see Foissner et al. (2025c). E– extrusome, F – bulge fibres, NO – nematodesmata.

Fig. 11.3d *Supraspathidium multistriatum* Foissner & Didier, 1981 (original. Klein-Foissner silver nitrate preparation). Arrowheads denote regions where the narrowly-meshed silverline pattern is well recognizable. CK – circumoral kinety, OO – ruptured oral opening.

Table 11.1 Morphometric data on *Supraspathidium etoschense* (SE; from Foissner et al. 2002), *Supraspathidium armatum* (SA) from sites (65) and (54) in Namibia (from Foissner et al. 2002), and *Supraspathidium multistriatum* (SM; from Foissner & Didier 1981)[a]

Characteristic	Species	Mean	M	SD	SE	CV	Min	Max	n
Body, length	SE	161.8	155.0	26.2	6.4	16.2	115.0	210.0	17
	SA 65	340.0	335.0	53.5	26.8	15.8	290.0	400.0	4
	SA 54	217.1	210.0	23.5	8.9	10.8	185.0	255.0	7
	SM	251.1	240.0	56.1	17.8	22.4	180.0	350.0	10
Body, width	SE	64.4	66.0	8.6	2.1	13.4	46.0	78.0	17
	SA 65	33.5	34.0	1.7	0.9	5.2	31.0	35.0	4
	SA 54	45.1	48.0	8.1	3.1	18.0	32.0	53.0	7
	SM	71.5	68.0	17.4	5.5	24.3	50.0	110.0	10
Oral bulge, length of chord	SE	27.5	28.0	1.6	0.4	5.9	25.0	30.0	17
	SA 65	47.3	47.0	6.5	3.2	13.7	41.0	55.0	4
	SA 54	38.6	35.0	6.7	2.5	17.4	32.0	52.0	7
	SM	38.8	39.0	8.8	2.8	22.6	25.0	50.0	10
Macronucleus, length (spread; approximations)	SE	267.1	270.0	58.1	14.1	21.7	160.0	390.0	17
	SA 65	335.0	305.0	121.2	60.6	36.2	230.0	500.0	4
	SA 54	245.7	250.0	36.0	13.6	14.7	180.0	300.0	7
Macronucleus, width	SE	8.7	8.0	1.5	0.4	16.8	7.0	11.0	17
	SA 65	9.5	9.0	1.7	0.9	18.2	8.0	12.0	4
	SA 54	8.7	8.0	1.0	0.4	10.9	8.0	10.0	7
	SM	8.9	9.0	1.4	0.4	15.7	7.0	11.0	10
Macronucleus, thickness	SE	about as width							
	SA 65	3.8	4.0	1.0	0.5	25.5	3.0	5.0	4
	SA 54	4.1	4.0	–	–	–	4.0	5.0	7
	SM	about as width							
Brush rows, number	SE	3.0	3.0	0.0	0.0	0.0	3.0	3.0	17
	SA 65	3.0	3.0	0.0	0.0	0.0	3.0	3.0	4
	SA 54	3.0	3.0	0.0	0.0	0.0	3.0	3.0	6
Circumoral kinety to last dikinetid of brush row 1, length	SE	38.0	38.0	9.4	2.3	24.7	25.0	55.0	16
	SA 65	105.0	105.0	–	–	–	95.0	115.0	2
	SA 54	58.7	58.0	10.3	4.2	17.6	47.0	75.0	6
Circumoral kinety to last dikinetid of brush row 2, length	SE	43.6	43.0	7.6	1.9	17.4	30.0	58.0	16
	SA 65	115.0	115.0	–	–	–	105.0	125.0	2
	SA 54	65.8	68.0	11.6	4.7	17.6	50.0	80.0	6
Circumoral kinety to last dikinetid of brush row 3, length	SE	36.3	35.0	6.7	1.7	18.5	20.0	45.0	16
	SA 65	95.0	95.0	–	–	–	80.0	110.0	2
	SA 54	56.0	55.0	9.3	3.8	16.6	45.0	68.0	6
Somatic kineties, number	SE	44.3	44.0	4.4	1.1	10.0	35.0	50.0	17
	SA 65	41.8	43.0	3.4	1.7	8.2	37.0	45.0	4
	SA 54	32.9	34.0	2.8	1.0	8.5	29.0	36.0	7
	SM	74.4	75.0	7.5	2.8	10.1	65.0	86.0	7
Kinetids in 10 µm, number	SE	11.7	12.0	1.7	0.4	14.9	10.0	15.0	17
	SA 65	8.3	9.0	1.7	0.9	20.7	6.0	10.0	4
	SA 54	8.0	8.0	2.2	0.9	28.0	4.0	10.0	7
	SM	16.4	16.0	2.1	0.7	12.6	14.0	22.0	10

Table 11.1 Continued

[a] Data based on mounted, protargol-prepared (Foissner's method) specimens from non-flooded Petri dish cultures (*Supraspathidium etoschense* and *Supraspathidium armatum*) and field material (*Supraspathidium multistriatum*). 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.

in line on dorsal side. Extrusomes in oral bulge curved, rod-shaped to acicular, about 8 µm long. On average 75 ciliary rows.

Remarks: *Supraspathidium multistriatum* resembles only two species, viz., *Supraspathidium vermiforme* (bursiform and not flattened in rear half vs. cylindrical and ribbon-like flattened; about 75 vs. likely ≤25 ciliary rows) and *Supraspathidium etoschense* (contractile vacuoles in line with dorsal brush rows vs. dorsolateral; about 75 vs. 44 ciliary rows).

Description (supplemented by re-evaluation of original data and material): Body size 250–500 × 60–85 µm in vivo, usually about 300 × 75 µm. Indistinctly spatulate to rather distinctly bursiform with strongly varying length:width ratio of 2.5–5.5:1 in protargol preparations, on average near 4:1 both in vivo and prepared cells; neck indistinct; about 2:1 flattened in anterior third. Anterior (oral) end obliquely truncate by about 45°, posterior end broadly rounded (Fig. 11.1a, l, m; Table 11.1). Macronucleus in middle body quarters, long and tortuous, slightly and irregularly nodulated, with many minute nucleoli. One slightly enlarged terminal contractile vacuole and 4–6 smaller contractile vacuoles, each with several elliptical excretory pores between and within ciliary rows; vacuoles (pores) arranged between dorsal brush and posterior body end (Fig. 11.1a, d, e). Extrusomes packed in oral bulge and scattered throughout cytoplasm, curved, and about 8 µm long in vivo; distinctly acicular and up to 20 µm long in protargol-prepared specimens (Fig. 11.1a, c, j, k, 11.2a–c). Cortex very flexible, conspicuous because bright and nearly 2 µm thick, contains narrowly spaced rows of yellowish granules making cells brownish at low magnification (Fig. 11.1f, g). Cytoplasm colourless, packed with lipid droplets up to 10 µm across. Creeps and swims skilfully and moderately rapid.

Cilia about 7 µm long in vivo, very closely spaced (about 0.6 µm, Table 11.1), arranged in an average of 75 narrowly spaced, equidistant rows most of them commencing around circumoral kinety and extending slightly spirally to posterior body end; some rows slightly shortened anteriorly or posteriorly. Right side rows abut on circumoral kinety in very steep angles, while left side rows are conspicuously curved anteriorly abutting on circumoral kinety at right angles, even slightly directed ventrally (Fig. 11.1b, e, k, n; Table 11.1). Three dorsal rows differentiated to brush in anterior quarter to third; brush bristles paired and inconspicuous because only 3 µm long in vivo.

Oral bulge obliquely truncate by about 45°, moderately convex in lateral view, about half as long as widest trunk region, slightly to rather distinctly dumbbell-shaped in frontal view, inconspicuous compared to size of cell because only about 5 µm high and hardly set off from body proper. Circumoral kinety of same shape as oral bulge, composed of narrowly spaced dikinetids associated with fine, about 50 µm long nematodesmata forming conspicuous, conical basket in protargol-prepared specimens (Fig. 11.1a, b, e, h, k–n, 11.2a; Table 11.1).

Silverline pattern narrowly meshed throughout, forming about five or six, indistinctly meridionally oriented mesh rows between each two kineties; individual meshes polygonal, approximately 0.5 µm across; frequently, minute granules occur in mesh corners (Fig. 11.1i, 11.2d, 11.3d).

Occurrence and ecology: Very rare, limnetic species. The type locality of *Supraspathidium multistriatum* is the organic mud of a streamlet in the surroundings of the village of St. Victor-la-Rivière (45°31'N 02°56'E; co-ordinates from Aescht 2008, p. 167), Besse-en-Chandesse region, France. One of us (W. Foissner) found this (or a remarkably similar) species in a streamlet of Bavaria, Germany (no detailed data available). Abundances were low at both locations. Further record (not substantiated by morphological data): benthic during summer in the Tisa River system, Ukraine (Kovalchuk 1999, p. 379).

Supraspathidium etoschense Foissner, Agatha & Berger, 2002

(Fig. 11.4a–l, 11.5a–i, Table 11.1)

2002 ***Supraspathidium etoschense* nov. spec.** – Foissner, Agatha & Berger, Denisia 5: 274, Fig. 60a–j, m, o, 326a–i, Table 52 (Fig. 11.4a–l, 11.5a–i; original description; the slide containing the holotype [accession number 2002/31] and two paratype slides [2002/32, 2002/33] have been deposited in the Biology Centre of the Upper Austrian Museum in Linz; see Foissner et al. 2002, p. 43 and Aescht 2003, p. 385; 2008, p. 154).

Nomenclature: Named after the region where the species was discovered, that is, the Etosha Pan, Namibia (Foissner et al. 2002, p. 275). The holotype is marked on the slide (see Foissner et al. 2002, p. 43), but not indicated in the text of the original description or the legend to the figures, as Foissner et al. (2002) did it for most other new species (e.g., *Spathidium namibicola* Foissner et al., 2002, p. 246, Fig. 53c, d). For a comment on this "problem", see Berger et al. (2025a).

Diagnosis (from Foissner et al. 2002, slightly modified): Body size about 200 × 70 µm in vivo. Body spatulate to bursiform with elliptical, oblique oral bulge about half as wide as broadest postoral region; not flattened. Macronucleus tortuous and up to twice as long as cell. Contractile vacuole row left[6] of dorsal brush. Oral bulge extrusomes elongate clavate, about 7 µm long. On average 44 ciliary rows.

Remarks: The general appearance and the ciliary pattern highly resemble *Supraspathidium multistriatum* (Fig. 1.1a–n, 11.2a–d). There is, however, a conspicuous, unexpected difference, namely the location of the contractile vacuoles: dorsolateral in *Supraspathidium etoschense* (Fig. 11.4l), but in line with the dorsal brush in *Supraspathidium multistriatum* (Fig. 11.1e). Furthermore, the extrusomes are slightly different (straight rods with a subterminal inflation vs. slightly curved rods[7]) and most morphometrics, especially the number of

[6] Note by H. Berger: Foissner et al. (2002, p. 274, 275, 278) wrote that the row of contractile vacuoles and their excretory pores is right of the dorsal brush in *Supraspathidium etoschense*, inter alia, referring to their Fig. 60o (Fig. 11.4l in present work). However, this is incorrect because Fig. 11.4l, a dorsal view, clearly shows that the excretory pores are on the left lateral side of the cell, that is, left of the dorsal brush. Foissner et al. (2002, p. 283) made the same mistake at *Supraspathidium armatum*.

[7] Not studied in detail in *Supraspathidium multistriatum*, according to Foissner's original notes. Thus, the extrusomes of *Supraspathidium etoschense* and *Supraspathidium multistriatum* could be more similar than supposed. Generally, extrusome features are very important. We know of a freshwater species that also looks similar to *Supraspathidium multistriatum*, but has conspicuous, clavate extrusomes.

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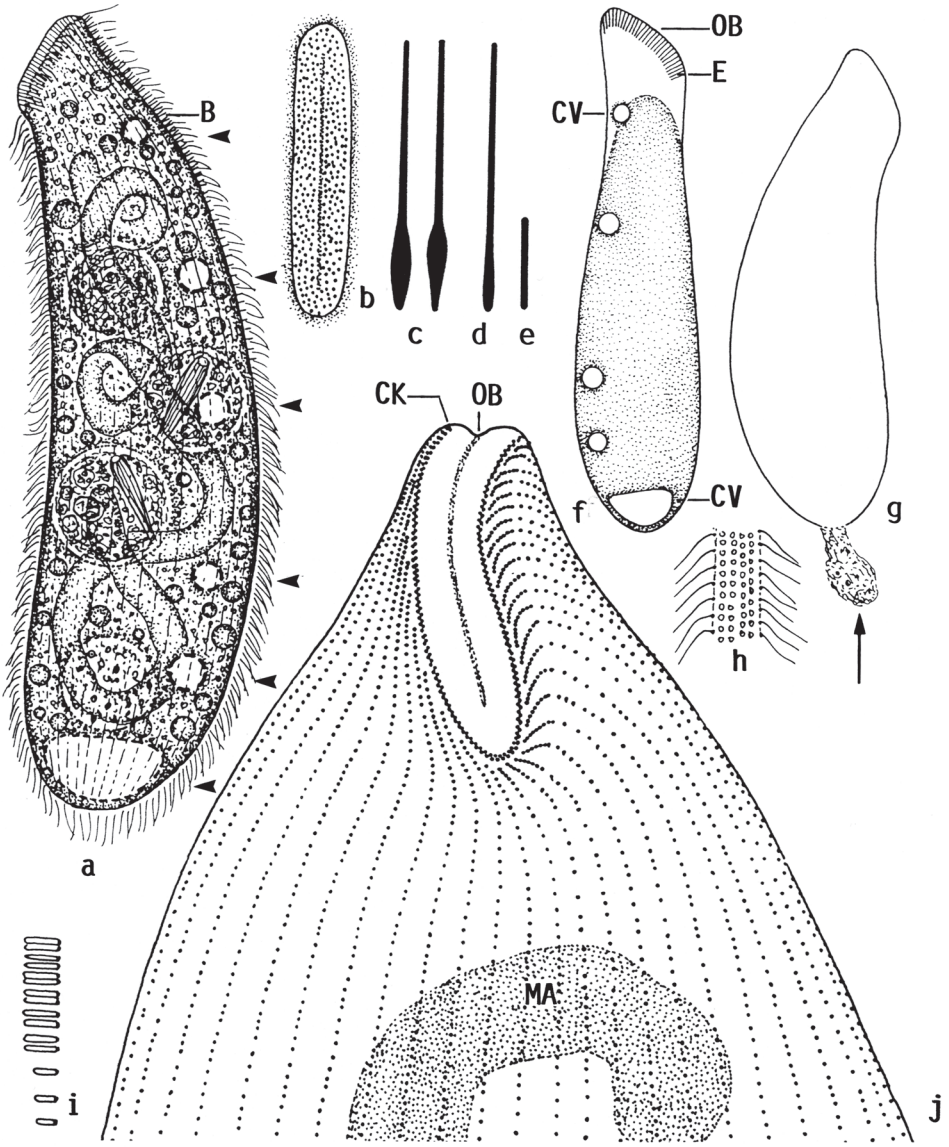


Fig. 11.4a–j *Supraspathidium etoschense* Foissner, Agatha & Berger, 2002 (from Foissner et al. 2002. a–i, from life; j, protargol preparation). **a:** Left side view of a specimen with food vacuoles containing nassulid oral baskets, 220 µm. Arrowheads mark contractile vacuoles whose excretory pores are left of the dorsal brush. Note the massive appearance of the species and the long, tortuous macronucleus. **b:** Oral bulge studded with extrusomes. **c, d:** Shape of extrusomes when attached (c) and detached (d) from oral bulge, length 6–8 µm. **e:** Minute extrusome, 1.5–2.0 µm long. **f:** Ordinarily fed, spatulate specimen. **g:** Bursiform specimen packed with food vacuoles and lipid droplets. Arrow marks excretion of faecal mass. **h:** Surface view showing cortical granulation. **i:** Brush row 3 in the transition zone of dikinetidal and monokinetidal bristles. **j:** Ciliary pattern of ventral anterior region, length 60 µm. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuoles, E – extrusomes, MA – macronucleus, OB – oral bulge.

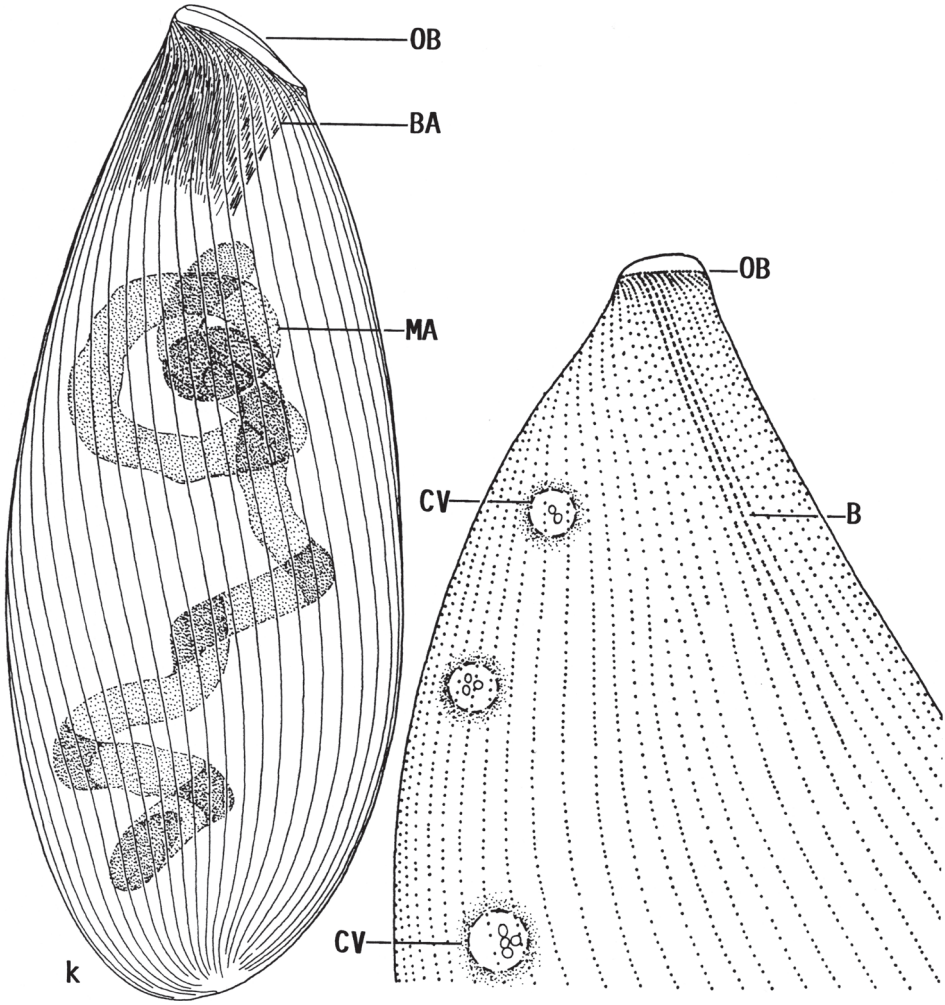


Fig. 11.4k, l *Supraspathidium etoschense* Foissner, Agatha & Berger, 2002 (from Foissner et al. 2002. Protargol preparation). **k:** Right side view of ciliature and macronucleus, 175 µm. Note the flat, inconspicuous oral bulge, a typical feature of *Supraspathidium*. **l:** Dorsal view of anterior body region, length 70 µm. Note the contractile vacuoles, which are left of the dorsal brush, a main difference to *Supraspathidium multistriatum*, where the contractile vacuoles are in and between the kineties bearing the dorsal brush. B – dorsal brush, BA – oral basket, CV – contractile vacuoles, MA – macronucleus, OB – oral bulge.

ciliary rows, do not or only slightly overlap because *Supraspathidium etoschense* is considerably smaller than *Supraspathidium multistriatum* (Table 11.1).

The second species similar to *Supraspathidium etoschense* is *Supraspathidium vermiforme*, which, however, is flattened leaf-like and loosely ciliated, while *Supraspathidium etoschense* is not flattened and comparatively densely ciliated. *Supraspathidium armatum* (see below) differs from *Supraspathidium etoschense* by many features, such as body size and shape and arrangement of the contractile vacuoles.

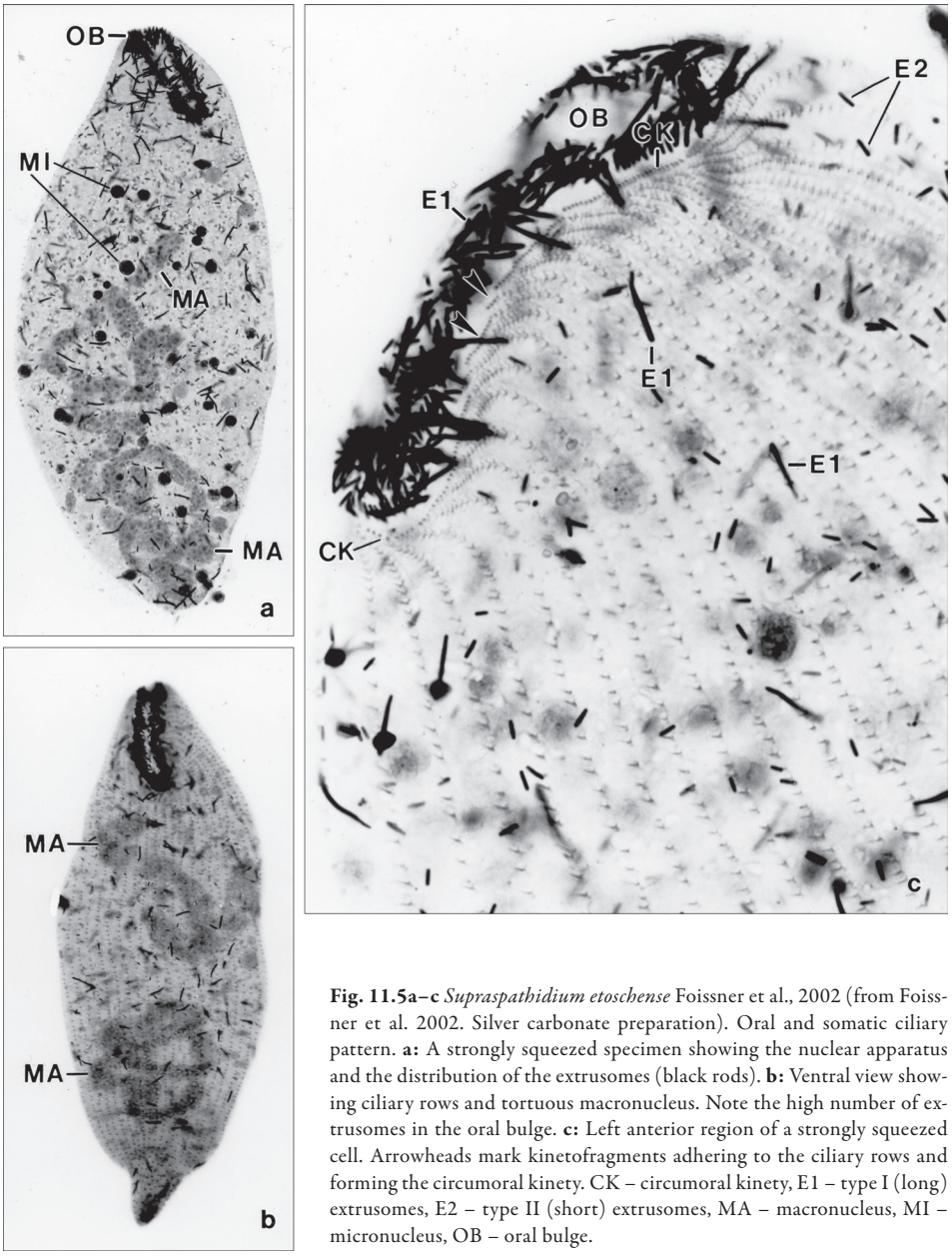
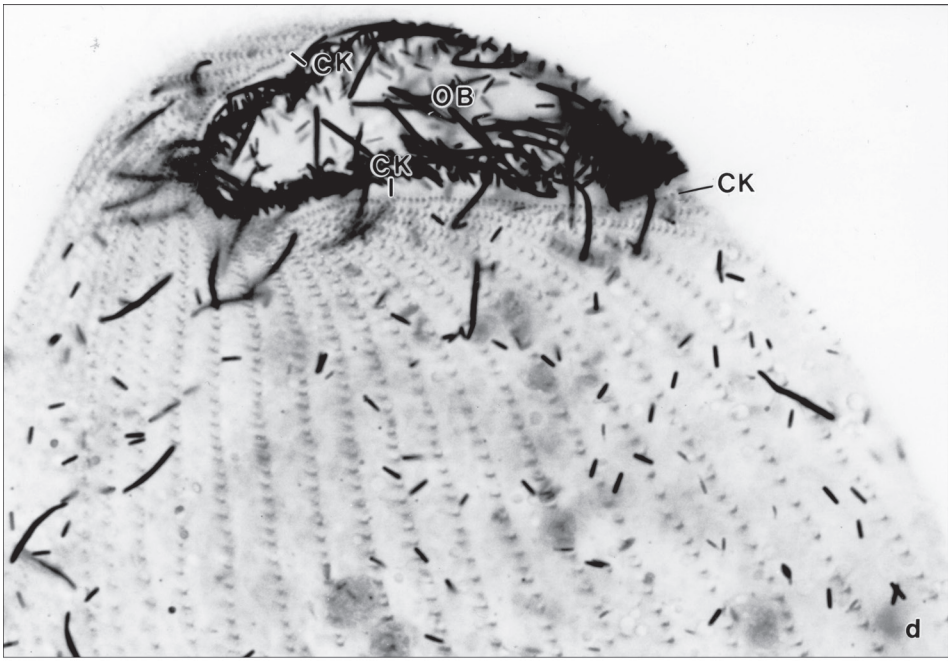
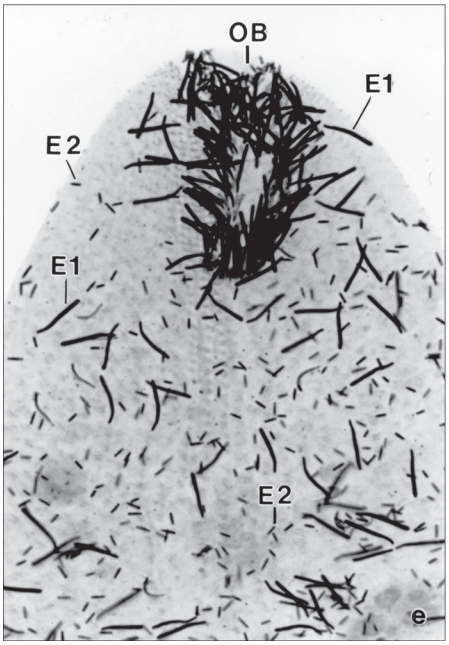


Fig. 11.5a–c *Supraspathidium etoschense* Foissner et al., 2002 (from Foissner et al. 2002. Silver carbonate preparation). Oral and somatic ciliary pattern. **a:** A strongly squeezed specimen showing the nuclear apparatus and the distribution of the extrusomes (black rods). **b:** Ventral view showing ciliary rows and tortuous macronucleus. Note the high number of extrusomes in the oral bulge. **c:** Left anterior region of a strongly squeezed cell. Arrowheads mark kinetofragments adhering to the ciliary rows and forming the circumoral kinety. CK – circumoral kinety, E1 – type I (long) extrusomes, E2 – type II (short) extrusomes, MA – macronucleus, MI – micronucleus, OB – oral bulge.

Description: This species is difficult to impregnate because it is large and usually crammed with food inclusions. Thus, the type slides are of mediocre quality, and especially the excretory pores of the contractile vacuoles are very faintly impregnated. The vacuoles proper, however, are well recognizable under interference contrast illumination. Accordingly, the occurrence of several contractile vacuoles in dorsolateral position is recognizable in the type slides.





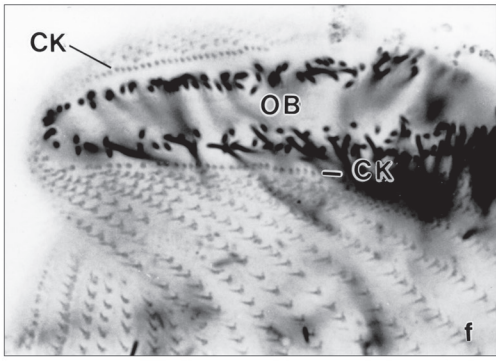


Fig. 11.5d–f *Supraspathidium etoschense* Foissner et al., 2002 (from Foissner et al. 2002. Silver carbonate preparation). Specimens are heavily squashed to show as many details as possible. **d, f:** Frontolateral views showing the circumoral ciliary pattern. Note the short kinetodesmal fibre at the right side of the somatic kinetids. The circumoral kinetids (CK) lack kinetodesmal fibres. **e:** *Supraspathidium etoschense* has many long and short extrusomes (black rods) in the oral bulge and cytoplasm. CK – circumoral kinety, E1, E2 – type I and type II extrusomes, OB – oral bulge.

Body size 140–250 × 50–90 μm in vivo, usually near 200 × 70 μm; length:width ratio about 3:1 in vivo and 2.5:1 in protargol preparations, indicating that specimens became inflated and/or shrunk considerably during preparation (Table 11.1). Body shape also very

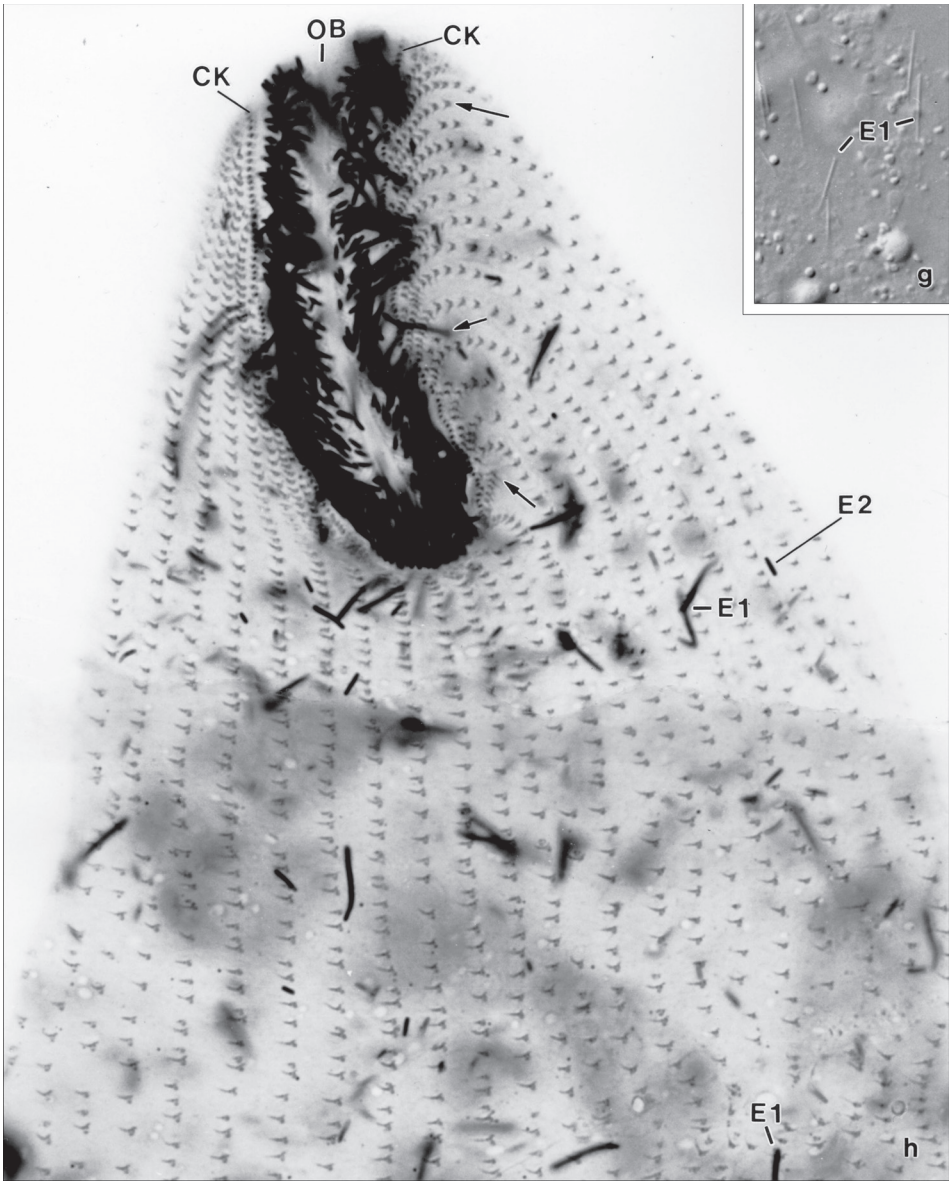


Fig. 11.5g, h *Supraspathidium etoschense* Foissner et al., 2002 (from Foissner et al. 2002. g, from life; h, silver carbonate preparation). Oral and somatic ciliary pattern of anterior ventral region. Note the different course of the ciliary rows right and left of the circumoral kinety. Arrows mark supernumerary kinety fragments. The extrusomes, which are very numerous in the oral bulge, are fine in vivo (g) and thick after silver preparation (h). CK – circumoral kinety, E1, E2 – type I and II extrusomes, OB – oral bulge.

variable, obviously highly dependent on nutrition condition, viz., spatulate, bursiform, elongate bursiform, or cylindrical (Fig. 11.4a, f, g); oral region flattened up to 2:1, postoral portion cylindrical. Macronucleus in main body axis and highly tortuous, at least as long as to

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Fig. 11.5i *Supraspathidium etoschense* Foissner et al., 2002 (from Foissner et al. 2002. Silver carbonate preparation). Ciliary pattern in anterior dorsal portion after silver carbonate preparation. The dorsal brush consists of three rows of closely spaced dikinetids. Occasionally, one or more dorsal brush rows do not extend posteriorly (arrowheads). Note the high number of extrusomes in the oral bulge. B1, 3 – dorsal brush rows, OB – oral bulge on ventral side.

twice as long as body, occasionally slightly nodulated. Several micronuclei, exact number difficult to assess because of many similarly sized and impregnated cell inclusions (Fig. 11.4a, k, 11.5a, b). One large terminal contractile vacuole and 3–6 small contractile vacuoles, each with usually several excretory pores, in dorsolateral position, that is, about 10 kineties left (see footnote at diagnosis above) of dorsal brush (Fig. 11.4a, f, l). Extrusomes packed in oral bulge and scattered in cytoplasm, 6–8 µm long, rod-shaped with fusiform subterminal inflation when attached to oral bulge (Fig. 11.4c, f); inflation almost disappears in preparations (Fig. 11.4c, e, h) and, in vivo, when extrusomes become detached from bulge (Fig. 11.4d, 11.5c–g), a peculiar feature observed in three carefully studied specimens; do not impregnate with protargol, but stain heavily with silver carbonate and become rod-shaped or elongate cuneate. Many minute rods (1.5–2.0 µm), very likely also extrusomes, scattered in oral bulge and cytoplasm, impregnate with silver carbonate (Fig. 11.4e, 11.5c, e, h). Cortex very flexible and rather thick, contains closely spaced rows of colourless granules (mucocysts?) about 1 µm across (Fig. 11.4h). Cytoplasm usually packed with food vacuoles and lipid droplets up to 10 µm across, often colourful due to ingested, cyanobacteria-feeding nassulids and colpodids (e.g., *Nassula granata*, *Kuklikophrya ougandae*). Swims rather rapidly by rotation about main body axis.

Somatic cilia about 10 µm long in vivo, form an average of 44, rather closely spaced, equidistantly arranged rows commencing around circumoral kinety and extending meridionally to posterior body end. Cilia closely spaced within rows (about 1 µm; Table 11.1), especially at anterior end, where short "perioral" fragments are produced. All ciliary rows abut on circumoral kinety, those on right side in very steep angles, those on left side conspicuously curved with anterior portion directed ventrally (Fig. 11.4a, j, k, 11.5c, d, f, h). Three dorsal rows anteriorly differentiated to an about 45 µm long dorsal brush composed of paired, about 3 µm long, rod-shaped bristles; row 3 extends to mid-body with about 2 µm long, monokinetidal bristles and then continues, as the other brush rows usually do, as an ordinary somatic ciliary row (Fig. 11.4a, i, l, 11.5i).

Oral area flattened and usually set off from body proper by a slight constriction. Oral bulge obliquely truncate by about 45°, oblong and bright in frontal view due to the refractive extrusomes contained, inconspicuous compared to size of cell because only about 3 µm high; ciliary rows thus extend almost to anterior body end, producing the pattern characteristic for this kind of spathidiids. Circumoral kinety at base of oral bulge and thus oblong, composed of very closely spaced dikinetids (Fig. 11.4a, b, j, k, 11.5b–d, f, h).

Occurrence and ecology: To date *Supraspathidium etoschense* was only found at the type locality, where it was rather numerous for some days, especially when nassulids were abundant. The type locality is a highly saline soil from the "Etosha Pan Lookout" (18.93065°S 16.48764°E), about 1 km from the margin of the Etosha Pan, Namibia (for further details, see Foissner et al. 2002, p. 29, site 67). Found also in the Etosha Pan sensu stricto (site 58; see Foissner et al. 2002, p. 27, 63b, 278), indicating that it might be a limnetic species.

Supraspathidium armatum Foissner, Agatha & Berger, 2002

(Fig. 11.6a–j, Table 11.1)

2002 ***Supraspathidium armatum* nov. spec.** – Foissner, Agatha & Berger, Denisia 5: 280, Fig. 61a–j, Table 52 (Fig. 11.6a–j; original description; the slide containing the holotype [accession number 2002/29] and one

paratype slide [2002/30] have been deposited in the Biology Centre of the Upper Austrian Museum in Linz [LI]; see Foissner et al. 2002, p. 43 and Aescht 2003, p. 380; 2008, p. 144; see also nomenclature).

Nomenclature: The species-group name *armat·us*, *-a*, *-um* (Latin adjective [m, f, n]; armed, defended; Hentschel & Wagner 1996, p. 103) refers to the conspicuous extrusomes (Foissner et al. 2002).

Foissner et al. (2002) studied two populations from the same area (sites 65 [type locality] and 54; for details, see occurrence and ecology). In total, they deposited four slides, namely two (2002/29; 2002/30) from the population from the type locality and two slides (2002/184, 2002/191) from the site 54 population (see Foissner et al. 2002, p. 43). The description is based on both populations (see Foissner et al. 2002, p. 280 and Table 52). Despite that, the type series consists only of the specimens from the type locality because Foissner et al. (2002, p. 43) designated a holotype (it is marked on the slide, but not indicated as figure in the original description) and paratypes (ICZN 1999, Articles 72.4.1, 72.4.5, 72.4.6). For that reason, the specimens of the site 54 population are voucher specimens, as correctly indicated by Foissner et al. (2002, p. 43). For further comment on type fixation in this species, see Berger et al. (2025a).

Diagnosis (from Foissner et al. 2002, slightly modified): Body size about 350 × 35 µm in vivo. Body elongate lanceolate with distinctly narrowed posterior region; not flattened. Oral bulge elliptical and oblique, longer by one third than broadest postoral region. Macronucleus tortuous, about as long as cell, conspicuously flattened ribbon-like. A row of contractile vacuoles each in ventral and dorsal side. Extrusomes elongate clavate, about 9 µm long. On average 42 ciliary rows.

Remarks: *Supraspathidium armatum* has so many special features (body and extrusome shape, two rows of contractile vacuoles, ribbon-like flattened macronucleus) that it cannot be confused with any other ciliate. However, most morphometrics are highly variable (Table 11.1).

Description: This species was very rare. Foissner et al. (2002) saw only about 10 individuals, of which four could be impregnated with protargol (mediocre quality). Accordingly, the data are not very detailed, especially the morphometry. However, it was carefully observed in vivo and better impregnated in the slides from site 54 (see Foissner et al. 2002, p. 26), where, however, the specimens were considerably smaller and stouter casting doubts on conspecificity (Table 11.1).

Body size 300–400 × 30–40 µm, usually about 350 × 35 µm in vivo; length:width ratio 8.5–12:1, on average near 10:1. Body outline lanceolate, that is, anteriorly obliquely truncate and gradually narrowed posteriorly, where it is usually slightly inflated in protargol preparations; flattened laterally in oral and tail area. Macronucleus in central body portion, highly tortuous and flattened band-like (Fig. 11.6d, e, h; Table 11.1), a rare feature found also in *Protospathidium namibicola* Foissner et al., 2002, albeit less pronounced; contains many minute and rather large nucleoli bulging the nuclear band. Many globular micronuclei which, however, could not be counted because of similarly sized and impregnated cytoplasmic inclusions. Many contractile vacuoles, roughly arranged in two rows: one row in ventral side slightly left of midline, the other somewhat left (see corresponding footnote at *Supraspathidium etoschense* for note on position of dorsal contractile vacuole row) of dorsal brush; most vacuoles with two or more excretory pores (Fig. 11.6a, g, j). Extrusomes packed

continued on p. 356

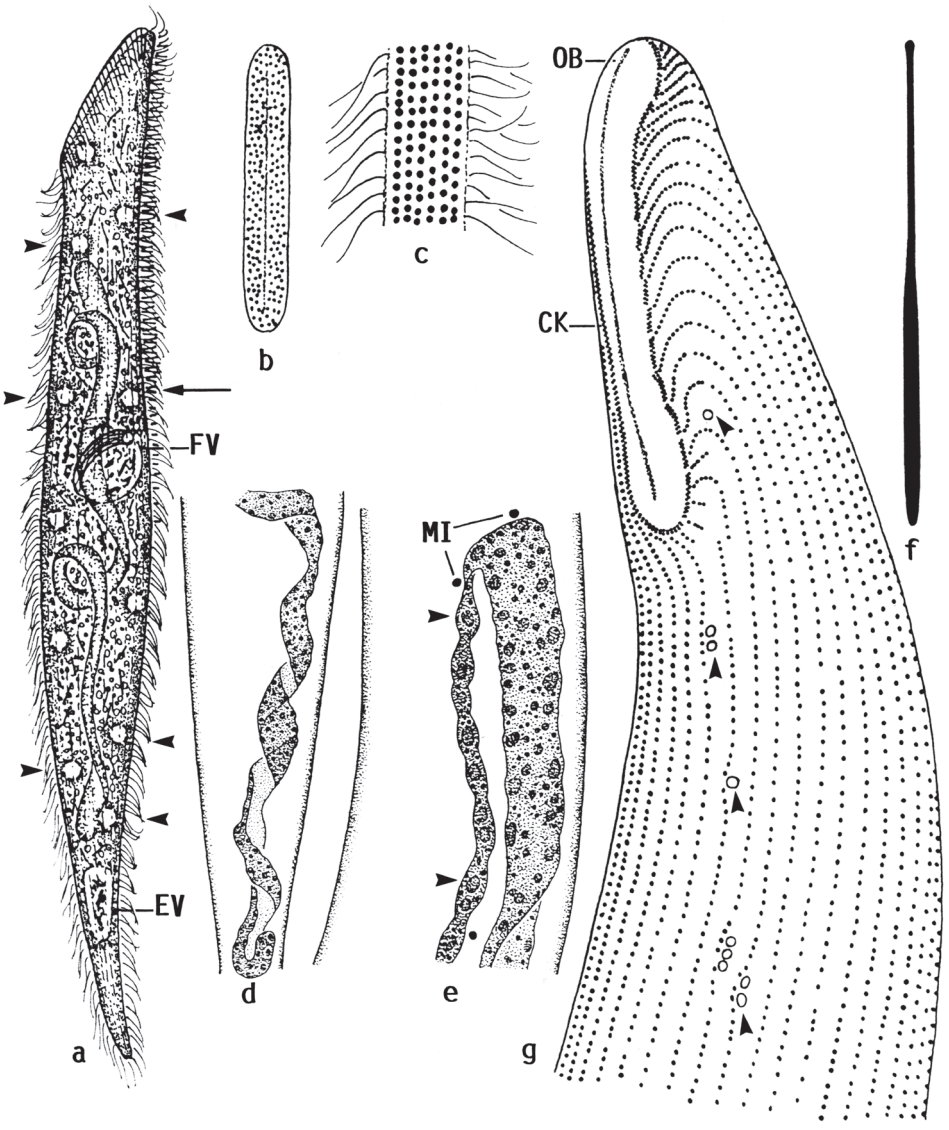

Fig. 11.6a–g *Supraspathidium armatum* Foissner, Agatha & Berger, 2002 (from Foissner et al. 2002. a–c, f, from life; d, e, g, protargol preparation). **a:** Left side view of a representative specimen, 350 µm. Arrow marks end of dikinetidal portion of dorsal brush row 3. Arrowheads denote the two rows of contractile vacuoles. The food vacuole contains a *Nassula*, whose oral basket is still recognizable. **b:** Frontal view of oral bulge, which contains many extrusomes. **c:** Surface view showing rows of yellowish, strongly refractive cortical granules (mucocysts?). **d, e:** The tortuous macronucleus (d, a posterior portion; e, a mid-portion) is flattened ribbon-like, a unique feature of *Supraspathidium armatum*, length 110 µm and 55 µm. The nucleoli bulge the flat nuclear band (arrowheads). **f:** Oral bulge extrusomes are elongate clavate and 8–10 µm long. **g:** Ventroleftlateral view showing ciliary pattern in anterior body region, length 90 µm. Arrowheads mark excretory pores of ventral row of contractile vacuoles. CK – circumoral kinety, EV – egestion (defecation) vacuole, FV – food vacuole (wth *Nassula* sp.), MI – micronuclei, OB – oral bulge.

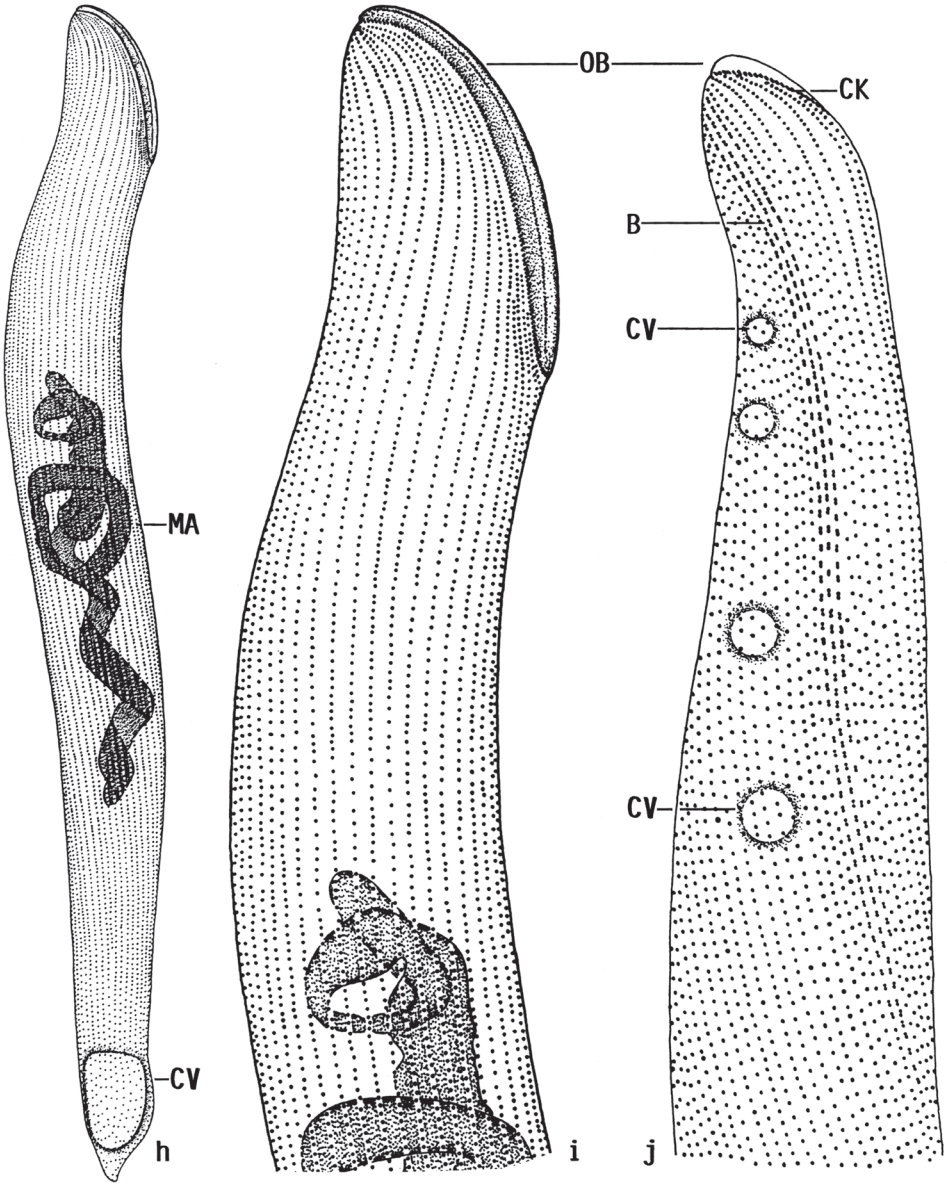

Fig. 11.6h–j *Supraspathidium armatum* Foissner, Agatha & Berger, 2002 (from Foissner et al. 2002. Protargol preparation). Oral and somatic ciliary pattern. **h, i:** Right side overview and detail showing the slender body shape, the narrowly spaced, densely ciliated kineties, and the tortuous macronucleus, 300 µm. **j:** Dorsal view of anterior body portion (length 125 µm), showing that the dorsal contractile vacuole row is somewhat left of the dorsal brush, an important difference to *Supraspathidium multistriatum*, where the vacuoles are within and between the brush kineties. B – dorsal brush, CK – circumoral kinety, CV – contractile vacuole row, MA – macronucleus, OB – oral bulge.

in oral bulge and scattered in cytoplasm, 8–10 µm long, elongate club-shaped, that is, posterior half thicker than anterior which bears minute globule on top (Fig. 11.6a, b, f); do

not impregnate with protargol. Cortex very flexible, contains about six rows of yellowish, highly refractive granules (mucocysts?) between each two ciliary rows (Fig. 11.6c). Cytoplasm colourless, usually packed with lipid droplets 1–3 µm across. Feeds on various ciliates, for instance, *Nassula* species, whose oral basket and extrusomes are recognizable in the food vacuoles. Swims rapidly, in spite of the large size, showing great flexibility when touching obstacles and under the cover glass.

Cilia about 12 µm long, closely spaced, arranged in an average of 42 meridional rows, whose densely ciliated anterior portion forms steep angles with the circumoral kinety on right side, while left side ends are curved ventrally; some rows slightly shortened anteriorly or posteriorly (Fig. 11.6g, i). Three dorsal ciliary rows anteriorly differentiated to an about 120 µm long dorsal brush composed of rod-shaped, 3–4 µm long, comparatively widely spaced bristle pairs; row 3 continues with monokinetidal, 2–3 µm long bristles to at least mid-body (Fig. 11.6a, j; Table 11.1).

Oral area flattened and usually set off from body proper by a slight constriction. Oral bulge obliquely truncate by about 45°, oblong and, although only 3–4 µm high, rather conspicuous due to the many refractive extrusomes contained. Circumoral kinety at base of oral bulge and thus also oblong, its composition of dikinetidal kinetofragments is occasionally well-recognizable (Fig. 11.6a, b, g–i).

Occurrence and ecology: To date *Supraspathidium armatum* was found only at the type locality (Namibian site 65) and a site nearby (Namibian site 54); both are very saline habitats, where it was rare in the non-flooded Petri dish cultures (Foissner et al. 2002; see also Foissner et al. 2008, p. 355). The type locality is a highly saline soil from the margin of the Etosha Pan (according to Foissner et al. 2002, p. 28 at 18°55'S 16°25'E; road to the Halali rest camp, this rest camp is at 19.03519°S 16.470078°E according to Google Maps, accessed 17 Feb 2024), Namibia. For detailed descriptions of both sites, see Foissner et al. (2002, p. 28).

Supraspathidium vermiforme (Penard, 1922) Foissner & Didier, 1981

(Fig. 11.7f–i)

1922 ***Spathidium vermiforme* sp. n.** – Penard, Études infusoires, p. 26, Fig. 21_{1-3} (Fig. 11.7f–h; original description; no type material available).

1930 ***Spathidium vermiforme* Penard, 1922** – Kahl, Tierwelt Dtl. 18: 162, Fig. 22_{13} (Fig. 11.7i; first reviser).

1943 ***Spathidium vermiforme* Penard** – Kahl, Infusorien, p. 26, Tafel V, Fig. 29 (redrawing of Fig. 11.7i; brief review).

1981 ***Supraspathidium vermiforme* (Penard, 1922) nov. comb.** – Foissner & Didier, Annls Stn limnol. Besse 15: 255 (combination with *Supraspathidium*, without reinvestigation).

Nomenclature: No derivation of the name has been provided in the original description or a later work. The species-group name *vermiform·is*, *-is*, *-e* (Latin adjective [m, f, n]; vermiform, vermicular, worm-shaped, resembling a worm; https://en.wiktionary.org/ wiki/ vermiformis; accessed 9 Apr 2023) obviously refers to the slender, worm-like body shape. "*Supraspathidium vermiforme* Penard 1922" in Andrushchyshyn et al. (2006, p. 309) is not correct because the original combination is *Spathidium vermiforme* (see list above).

Diagnosis: Not available. Should await reinvestigation.

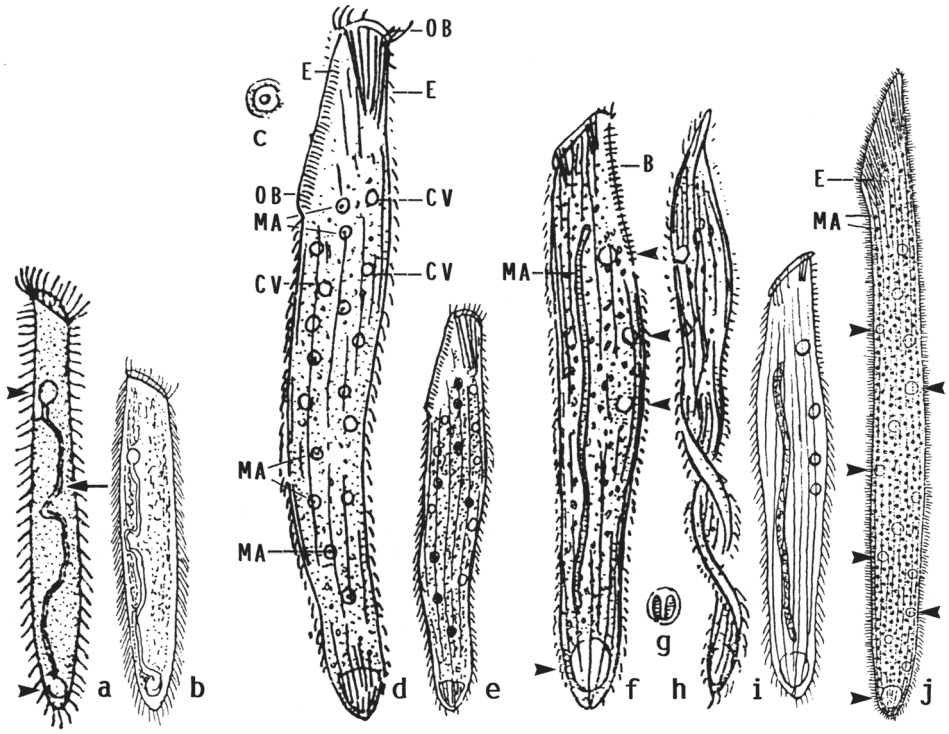

Fig. 11.7a, b *Supraspathidium teres* (Stokes, 1886) Foissner & Didier, 1981 (a, from Stokes 1886; b, after Stokes 1886 from Kahl 1930. From life). Right lateral view, 170–200 μm. Arrowheads denote the contractile vacuoles, the arrow marks the conspicuous canal connecting the anterior and posterior vacuole. Note that Kahl copied Stokes's figure rather inaccurately!

Fig. 11.7c–e *Supraspathidium elongatum* (Penard, 922) Foissner & Didier, 1981 (c, d, from Penard 1922; e, after Penard 1922 from Kahl 1930. From life). **c:** Macronucleus nodule with central nucleolus. **d, e:** Left lateral view, 600 μm. The oral bulge is composed of a short, transverse anterior part with long extrusomes and a long, strongly oblique ventral portion with short extrusomes. Likely, this species belongs to the Myriokaryonidae (see Foissner 2003b). CV – contractile vacuoles, E – extrusomes, MA – macronucleus nodules, OB – oral bulge.

Fig. 11.7f–i *Supraspathidium vermiforme* (Penard, 1922) Foissner & Didier, 1981 (f–h, from Penard 1922; i, after Penard 1922 from Kahl 1930. From life). **f, i:** Left lateral view, 200 μm. Arrowheads mark the contractile vacuoles. Possibly, this species is a senior synonym of *Spathidium faurefremieti* Foissner, 2003a. **g:** The cytoplasm contains many small vesicles with curious inclusions. **h:** Dorsal view showing the ribbon-like flattened body distinctly spiralized in posterior half. B – dorsal brush, MA – macronucleus.

Fig. 11.7j *Supraspathidium gigas* (Cunha, 1914) Foissner & Didier, 1981 (from Cunha 1914. From life). Left lateral view, 600–800 μm. Arrowheads mark contractile vacuoles. Possibly, this species is a junior synonym of *Myriokaryon lieberkuehnii* (see Foissner 2003b). E – extrusomes, MA – macronucleus nodules.

Remarks: The description by Penard (1922) basically matches the emended diagnosis of the genus, but detailed reinvestigation is necessary. See *Spathidium faurefremieti* Foissner, 2003a, which is probably a junior synonym, for detailed discussion (see Foissner 2003a, p. 151 and Chapter 3, that is, Foissner et al. 2025a). Penard (1922) found symbiotic green algae in a second population; perhaps he observed another species (see also occurrence and ecology).

Penard (1922) presumed synonymy with *Litonotus vermicularis* Stokes, 1887 (p. 104), which is, however, now *Homalozoon vermiculare* (Stokes, 1887) Stokes, 1890, the type species of *Homalozoon* Stokes, 1890 (for a review on this species, see Foissner et al. 1995, p. 219).

Supraspathidium vermiforme differs from the congeners mainly by the ribbon-like flattened body and the low number of ciliary rows (likely <25 vs. >40). *Supraspathidium teres* likely has many macronuclear nodules.

Description (based on Penard 1922): Body length usually about 200 μm in vivo, rarely up to 400 μm; width very variable, usually one eighth of length. Body slender, very flexible, and ribbon-like flattened, especially in posterior half, which may be distinctly spiraled; anterior (oral) end obliquely truncate, posterior end narrowly rounded, dorsal side rather distinctly convex (Fig. 11.7f, h). Macronucleus ribbon-like, occasionally nodulate, almost as long as body; one or several micronuclei. A large contractile vacuole in rear body region plus an anterior contractile main vacuole, into which several smaller dorsal vacuoles empty. Extrusomes form bundles in oral bulge, moderately long (12 μm) and rod-shaped, according to Penard's figure. Cytoplasm packed with minute, highly refractive granules making oral body portion dark, and with small vesicles containing curious, horseshoe-shaped inclusions (starch?), possibly food reserves (Fig. 11.7g); green by zoochlorellae in another population (see remarks and occurrence and ecology).

Cilia short and fine, arranged in rather widely spaced rows, likely ≤25 according to Penard's illustrations. Dorsal brush long, that is, extends to second quarter of cell; brush cilia short and inflated proximally (Fig. 11.7f).

Oral bulge occupies anterior body end, obliquely truncated by about 45°, approximately as long as widest trunk region, flat, indistinct because low and hardly set off from body proper (Fig. 11.7f).

Occurrence and ecology: Penard (1922) discovered *Supraspathidium vermiforme* in the sapropelic(?) mud of two ponds in the surroundings (Rouelbeau and Florissant) of Geneva, Switzerland, but at one site the specimens contained zoochlorellae, indicating misidentification. The species was rare at both sites.

There are several records of this species, all from Europe, but they are doubtful because not substantiated by figures and/or morphological data: in March in a draw well near Rome, Italy (Grispini 1938, p. 151; body length 250 μm); *Dicranum scoparium* moss from the God del Fuorn, a 1860 m high mountain in a Swiss National Park (Heinis 1945, p. 530; two specimens with a body length of 200 μm); in two experimental fish ponds at Ochaby, southern Poland (Grabacka 1971, p. 13; Siemińska & Siemińska 1967, p. 59); in the polluted Lielupe River in Latvia during summer (Liepa 1973, p. 32; 1983, p. 136); pond in Vandorf, Ontario, Canada (Andrushchyshyn et al. 2006, p. 309).

Supraspathidium elongatum (Penard, 1922) Foissner & Didier, 1981

(Fig. 11.7c–e)

1922 ***Cranotheridium elongatum* sp. n.** – Penard, Études infusoires, p. 33, Fig. $32_{1, 2}$ (Fig. 11.7c, d; original description, no type material available).

1930 ***Pseudoprorodon (Cranotheridium) elongatus* Penard, 1922** – Kahl, Tierwelt Dtl. 18: 71, Fig. 7_{19} (Fig. 11.7e; combination with *Pseudoprorodon*; first reviser; see nomenclature).

1943 ***Cranotheridium elongatus* Penard** – Kahl, Infusorien, p. 15, Tafel II, Fig. 6 (redrawing of Fig. 11.7e; brief review; incorrect ending of species-group name; ICZN 1999, Article 31.2).

1943 ***Cranotheridium (Ps.?) elongatum* (Pen.)** – Kahl, Infusorien, p. 11, legend to Tafel II, Fig. 6 (see remarks; correct ending of species-group name).

1981 ***Supraspathidium elongatum* (Penard, 1922) nov. comb.** – Foissner & Didier, Annls Stn limnol. Besse 15: 255 (combination with *Supraspathidium*; without reinvestigation).

Nomenclature: No derivation of the name has been provided in the original description or a later work. The species-group name *elongat·us*, *-a*, *-um* (Latin adjective [m, f, n]; elongated, stretched; Hentschel & Wagner 1996, p. 227) obviously refers to the slender, elongated body. The spelling *Pseudoprorodon (Cranotheridium) elongatus* in Kahl (1930) does not mean that Kahl (1930) classified *Cranotheridium* Schewiakoff, 1892 as subgenus of *Pseudoprorodon* Blochmann, 1895, but rather it should indicate that the species was previously classified in *Cranotheridium*.

Diagnosis: Not available. Should await reinvestigation.

Remarks: Penard (1922) classified his species in *Cranotheridium* Schewiakoff, 1892[8] because of the long extrusome bundle in the dorsal end of the oral bulge, reminiscent of the oral basket-like structure found in this genus. However, Kahl (1930; 1943, p. 15) synonymized Penard's species, although with doubt, with *Pseudoprorodon lieberkuehnii* (Bütschli, 1889) Kahl, 1930 (now *Myriokaryon lieberkuehnii* (Bütschli, 1889) Jankowski, 1973, type species of *Myriokaryon* Jankowski, 1973). We basically agree with Kahl, because of the highly characteristic shape of the oral bulge, the main diagnostic feature of the Myriokaryonidae Foissner, 2003b. On the other hand, a classification in *Supraspathidium*, as proposed by Foissner & Didier (1981), seems likewise possible because this genus also contains massive, rather slender species with features similar to those found in *Cranotheridium elongatum*; *Supraspathidium etoschense*, for instance, has two types of extrusomes; *Supraspathidium armatum* has many contractile vacuoles; and *Supraspathidium teres* possibly has numerous macronuclear nodules.

Penard (1922) discussed, as in *Supraspathidium vermiforme* (see above), a synonymy with *Litonotus vermicularis* Stokes, 1887 (p. 104), which is, however, now *Homalozoon vermiculare* (Stokes, 1887) Stokes, 1890, the type species of *Homalozoon* Stokes, 1890 (for a review on this species, see Foissner et al. 1995, p. 219).

Supraspathidium elongatum differs from the congeners by the huge size (length 600 µm vs. ≤500 µm, usually ≤300 µm); the scattered contractile vacuoles (vs. in one or two rows); the scattered macronuclear nodules (vs. a long, tortuous strand, possibly except of *Supraspathidium teres*); the special extrusome apparatus (two distinct size-types in special location vs. mostly one type and scattered, if two types); and the very steep posterior portion of the oral bulge (vs. up to 50°).

Description (based on observations of only two specimens by Penard 1922): Body size about 600 × 70 µm and thus a very conspicuous species. Body vermiform, about 8–10 times as long as broad, moderately flattened, especially in anterior region, broadest in second quarter; apical region slightly attenuate and narrowly rounded, posterior portion bluntly pointed. Numerous small (about 3 µm), globular macronuclear nodules, each with a central nucleolus (Fig. 11.7c), scattered throughout cytoplasm. A large contractile vacuole in

[8] Note by H. Berger: This genus was again described as new genus by Schewiakoff (1893, p. 35). See also footnote 2 in Foissner et al. (2025b).

rear end and many small contractile vacuoles scattered throughout peripheral cytoplasm. Two types of rod-shaped extrusomes: type I in anterior portion of oral bulge, conspicuous because about 80 µm long, as calculated from Penard's illustration, forms some sort of basket, similar to that described by Schewiakoff (1893) in *Cranotheridium*; type II in ventral portion of oral bulge, comparatively short, that is, about 10 µm long. No data available on cortex, cytoplasm, nutrition, and movement.

Cilia fine and short, arranged in an unknown number of equidistant, longitudinal rows which are hardly recognizable.

Oral bulge moderately distinct, in lateral view of same shape as in genus *Cephalospatula* Foissner, 2003b, that is, hook-like with short, transverse anterior portion containing the long extrusomes; and a long, slightly projecting posterior region containing the short extrusomes and extending slightly obliquely to second quarter of ventral side (Fig. 11.7d).

Occurrence and ecology: As yet *Supraspathidium elongatum* was found only by Penard (1922), likely because all workers followed Kahl (1930), who identified such ciliates as *Pseudoprorodon lieberkuehnii* (now in *Myriokaryon*; see remarks), which, however, has a different extrusome apparatus (Foissner 2003b). Nonetheless, *Supraspathidium elongatum*, of which Penard (1922) found only two specimens, should be easily recognizable by the huge size and the special extrusome apparatus.

The type locality of *Supraspathidium elongatum* is (very likely) a limnetic habitat near Geneva, Switzerland. Penard (1922, p. 33, paragraph on "*Litonotus vermicularis*") wrote that he has found two specimens in Rouelbeau. According to the map of Switzerland (https://map.geo.admin.ch/; accessed 17 Feb 2024) we found a limnetic habitat ("Ancien Marais de la Touvière"; "Zone humide de Rouelbeau" according to Google Maps) at 46.24015°N 06.22284°E near the Chateau de Rouelbeau (for details on the renaturation of this lake "Ruisseau de Rouëlbeau", see https://ge.ch/geodata/SIEAU/RENAT /Bilan_10ans_Renaturation_70.pdf; accessed 17 Feb 2024).

Supraspathidium gigas (Cunha, 1914) Foissner & Didier, 1981

(Fig. 11.7j)

1859 "**... sehr grossen und langgestreckten neuen Art, *E. gigas* ...**" – Stein, Organismus der Infusionsthiere I, p. 80 (line 7 from above), 90 ("*E. gigas*" means *Enchelys gigas*; a nomen nudum because too briefly described and no figure provided; likely a senior synonym of *Myriokaryon lieberkuehnii*; see Foissner 2003b, p. 114).

1866 ***Enchelys gigas* Stein spec. indescripta** – Diesing, Sber. Akad. Wiss. Wien, Mathematisch- naturwissenschaftliche Klasse, Abt. I 52 (year 1865): 527 (classification as nomen nudum, that is, as an undescribed species).

1914 ***Spathidium gigas* (Stein 1859)** – Cunha, Mem. Inst. Osw. Cruz 6: 173, Tafel 24, Fig. 7 (Fig. 11.7j; combination of *Enchelys gigas* [see first entry in list] with *Spathidium*; original description because we follow Kahl 1930 in considering Cunha 1914 as founder of *Spathidium gigas*; no type material available).

1930 ***Spathidium gigas***[9] and ***Pseudoprorodon (Spathidium) gigas* Da Cunha** – Kahl, Tierwelt Dtl. 18: 72, Fig. 7_{20} (redrawing of Fig. 11.7j; first reviser; attributes the species to Cunha, with which we agree, see above; combination with *Pseudoprorodon*).

1981 ***Supraspathidium gigas* (Da Cunha, 1914) nov. comb.** – Foissner & Didier, Annls Stn limnol. Besse 15: 255 (combination with *Supraspathidium*).

[9] Kahl (1930, p. 68, legend to figures) wrote "*Spathidium gigas* (Da Cunha)". However, in the present case, "(Da Cunha)" does not mean the author of the species, but the source from which the illustration is.

Nomenclature: As explained in the remarks section, *Enchelys gigas* Stein, 1859 is classified as nomen nudum (Diesing 1866). According to ICZN (1999, p. 111), a nomen nudum is not an available name and therefore the same name may be made available later for the same or a different concept. In the present case it is not clear if Cunha (1914) observed the same species as Stein (1859) or a different one. Anyhow, we agree with Kahl (1930) that it seems reasonable to accept "*Spathidium gigas* Cunha, 1914" as valid name (original combination), although Cunha (1914) did not describe his population as new species. We preliminary accept "*Spathidium gigas* Cunha, 1914" as valid name, especially as the status of this "species" is highly uncertain at the present state of knowledge (see remarks).

The species-group name *gigas* (Greek; huge, giant; Hentschel & Wagner 1996, p. 272) obviously refers to the body size (very large according to Stein 1859, see list of synonyms) of this species. For original description and history, see remarks. The spelling "*Pseudoprorodon (Spathidium) gigas*"in Kahl (1930) does not mean that Kahl (1930) classified *Spathidium* Dujardin, 1841 as subgenus of *Pseudoprorodon* Blochmann, 1895, but rather it should indicate that the species was classified in *Spathidium* by Cunha (1914).

Diagnosis: Not available. Should await reinvestigation.

Remarks:[10] The history of this species is rather complex and thus reviewed in detail. The description in Stein (1859) is very short and lacks an illustration; likely he found the population somewhere in Europe. *Enchelys gigas* Stein, 1859 was classified as "undescribed species" by Diesing (1866). Cunha (1914) provided a more or less detailed description and one illustration of a Brazilian population of the species briefly characterized by Stein (1859). Kahl (1930) obviously considered the description by Cunha (1914) as "authoritative" in that he mentioned Cunha (1914), and not Stein (1859), as author of this species; further, Kahl (1930) transferred it from *Spathidium* to *Pseudoprorodon* Blochmann, 1895.

The generic assignment of the present species is uncertain. Foissner (2003b, p. 114) classified both *Enchelys gigas* Stein, 1859 and "*Spathidium gigas* Cunha, 1914" as synonyms of *Myriokaryon lieberkuehnii* (Bütschli, 1889) Jankowski, 1973. In agreement with Diesing (1866), he classified *Enchelys gigas* Stein, 1859 as nomen nudum (that is, an undescribed species; see Nomenclature above) while he described the synonymy of "*Spathidium gigas* Cunha, 1914" as doubtful ("possibly a "true", large *Spathidium*/*Arcuospathidium*"). However, the shape and size of the oral bulge are rather different in *Myriokaryon lieberkuehnii* (see Foissner 2003b for review) and "*Spathidium gigas* Cunha, 1914", and thus it cannot be excluded that the population described by Cunha (1914) is a *Supraspathidium*, *Arcuospathidium*, or *Spathidium*. Likely, the identity of the organism can be fixed only by a reinvestigation of material from or near from the type locality (Brazil; see below) because the description of Cunha (1914) is incomplete.

Supraspathidium gigas differs from most congeners by the huge size (length 600–800 µm vs. 300 µm) and the scattered macronuclear nodules (vs. a long, tortuous strand) and contractile vacuoles (vs. in one or two rows). It is highly similar to *Supraspathidium elongatum*, except of the oral bulge and extrusome apparatus (cp. Fig. 11.7d, j).

Description (based on Cunha 1914): Body size 600–800 × 40–50 µm in vivo. Cylindrical with flattened and obliquely truncate anterior region. Numerous small macronuclear nodules scattered throughout cytoplasm. A large contractile vacuole in rear end and many

[10] Note by H. Berger: I have re-written this chapter because it was incomplete in the original version by W. Foissner.

small contractile vacuoles scattered in sub-cortical cytoplasm. Oral extrusomes fine, about 60 μm long according to Fig. 11.7j.

Body surface striated by an unknown number of longitudinally extending ciliary rows. Oral bulge occupies obliquely truncated anterior body end, about twice as long as width of trunk, flat, indistinct because hardly set off from body proper; contains many long, fine extrusomes as described above.

Occurrence and ecology: As yet *Supraspathidium gigas* was found only at the type locality where it was very abundant. Cunha (1914, p. 174) found it in freshwater in the surroundings of Manguinhos, Brazil.[11]

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[11] Note by H. Berger: Cunha (1914) did not provide details about the locality. Manguinhos is very likely a district in the city of Rio de Janeiro. In this area is also (very likely) the "Instituto Oswaldo Cruz" (see journal title of Cunha 1914).

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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.

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