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

Series Monographiae Ciliophorae
Series Editor: Helmut Berger, Consulting Engineering Office for Ecology, Salzburg
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Berger H. (2018): urn:lsid:zoobank.org:author:DC477A8E-FC41-494C-A4A1-F230915 12449: taxonomic and nomenclatural summary. – Series Monographiae Ciliophorae, Number 4: 1–52

Foissner W. & Berger H. (Eds) (2021): Terrestrial ciliates (Protista, Ciliophora) from Australia and some other parts of the world. – Series Monographiae Ciliophorae, Number 5: i–xii, 1–380

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

PDFs are Open Access

Number **6,** Year **2025**

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

Edited by

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

Series Monographiae Ciliophorae

Berger, Consulting Engineering Office for Ecology, Salzburg, Austria

Imprint

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Publisher: Helmut Berger, Consulting Engineering Office for Ecology, Radetzkystrasse 10, 5020 Salzburg, Austria

Layout: Helmut Berger with Adobe InDesign; Adobe Garamond Pro

Print: Printed in Austria by druck.at

Print edition: 40 copies

Sale of print edition: Helmut Berger, Consulting Engineering Office for Ecology, Radetzkystrasse 10, 5020 Salzburg, Austria

Publication date: 31 January 2025

Series title: Series Monographiae Ciliophorae. **Number:** 6. **Year:** 2025

Abbreviation of series title: Ser. Monogr. Cilioph.

Internet address of series: https://www.protozoology.com/smc

ZooBank registration of book: urn:lsid:zoobank.org:pub:EC8FAA43-A15B-4EDE-985C-A4132D3467E1

ISBN 978-3-902147-08-0

Information: This work has been published without peer-review process.

Archives: Print copies have been deposited at the following Austrian libraries: Österreichische Nationalbibliothek, Josefsplatz 1, Postfach 25, 1015 Wien; Universitätsbibliothek Salzburg, Kapitelgasse 4–6, 5020 Salzburg; Salzburger Landesarchiv, Michael-Pacher-Strasse 40, 5020 Salzburg. The PDF (Open Access) is available, inter alia, at https://www.protozoology.com/smc, https://www.wfoissner.at, and https://www.researchgate.net

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

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

In memory of Wilhelm Foissner (1948–2020)

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Preface, authorship, acknowledgements, and funding

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

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

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

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

Salzburg
January 2025

Helmut Berger (Publisher)
www.protozoology.com

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 7

Latispathidium Foissner et al., 2005 (Ciliophora, Spathidiidae), a genus whose species have the dorsal brush on the left body side[1]

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ZooBank registration of present chapter
urn:lsid:zoobank.org:pub:D87A5078-9CB7-4E66-9B24-058A6639001C

Abstract

Latispathidium Foissner et al., 2005 has, like *Neocultellothrix* Foissner & Xu in Berger et al., 2025b, the dorsal brush on the left body side, while in the other spathidiids the brush rows are usually arranged on the dorsal side or slightly dorsolaterally. At present, *Latispathidium* comprises five species with *Latispathidium lanceoplites* (Foissner et al., 2002) Foissner et al., 2005 as type species. *Latispathidium truncatum* (Stokes, 1885) Foissner et al., 2005 is the second species originally assigned. In the present work, three new species are described, namely, *Latispathidium arboricola* nov. spec. (from Costa Rica), *Latispathidium brachyoplites* nov. spec. (from South Africa), and *Latispathidium simile* nov. spec. (from Australia). A key to the species is provided.

Latispathidium Foissner, Berger, Xu & Zechmeister-Boltenstern, 2005

2005 ***Latispathidium* nov. gen.**[2] – Foissner, Berger, Xu & Zechmeister-Boltenstern, Biodiv. Conserv. 14: 644 (original description). Type species (by original designation): *Spathidium lanceoplites* Foissner, Agatha & Berger, 2002.

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[1] This chapter should be referenced as follows: Foissner W., Xu K. & Berger H. (2025): *Latispathidium* Foissner et al., 2005 (Ciliophora, Spathidiidae), a genus whose species have the dorsal brush on the left body side. – Ser. Monogr. Cilioph. 6: 213–255.
For notes on "Material and methods", see Chapter 1 (Berger et al. 2025a).

[2] Foissner et al. (2005) provided the following diagnosis: "Spathidiidae with dorsal brush on left side of cell and ciliature in *Spathidium* pattern."

Nomenclature: *Latispathidium* is a composite of the Latin noun *latus* (lateral side) and the genus-group name *Spathidium* (small spatula; for etymology of this genus-group name, see Chapter 2, that is, Berger et al. 2025c), referring to both, the laterally located dorsal brush and the *Spathidium*-like general appearance (Foissner et al. 2005). Like *Spathidium* of neuter gender (Aescht 2001, p. 300).

Improved diagnosis: Spathidiidae with dorsal brush on left side. Ciliature basically in *Spathidium* pattern, but right-side rows usually separate from circumoral kinety.

Species originally assigned: *Latispathidium lanceoplites* (Foissner et al., 2002) Foissner et al., 2005 (type species); *Latispathidium truncatum* (Stokes, 1885) Foissner et al., 2005 (with two subspecies).

Species now assigned: *Latispathidium lanceoplites* (Foissner et al., 2002) Foissner et al., 2005 (type species); *Latispathidium arboricola* nov. spec.; *Latispathidium brachyoplites* nov. spec.; *Latispathidium simile* nov. spec.; *Latispathidium truncatum* (Stokes, 1885) Foissner et al., 2005 (with two subspecies).

Remarks: The diagnosis was slightly improved because three right-side ciliary patterns occur in *Spathidium*: (i) Ciliary rows separate from circumoral kinety; (ii) ciliary rows attached to continuous or almost continuous circumoral kinety; (iii) ciliary rows attached to more or less distinctly protospathidiid circumoral kinetofragments, that is, discontinuous circumoral kinety.

Both, *Latispathidium* and *Neocultellothrix* Foissner & Xu in Berger et al., 2025b have the dorsal brush on the left side of the cell, while the basic ciliary pattern is as in *Spathidium* Dujardin, 1841 and *Arcuospathidium* Foissner, 1984, which have the brush located dorsally or dorsolaterally. A slightly dorsolateral location of the dorsal brush is also recognizable in some specimens of the various *Latispathidium* species (Fig. 7.3l, m, 7.9n). Thus, the distinction from *Spathidium* is not very sharp, but helpful for recognizing evolutionary trends and species in this large and highly diverse group.

At first glance, the lateral location of the dorsal brush appears to be caused by spatial constraints, viz., the narrowness of the anterior body half and/or the low number of ciliary rows, especially in *Latispathidium lanceoplites*. However, an evolutionary interpretation is more likely because there are quite a number of similarly sized and shaped *Spathidium* and *Arcuospathidium* species, which have the brush exactly on the dorsal side, for instance, *Spathidium turgitorum* Foissner et al., 2002, *Spathidium etoschense* Foissner et al., 2002 (Fig. 55g in Foissner et al. 2002), *Arcuospathidium vlassaki* Foissner, 2002 and *Arcuospathidium namibiense* Foissner et al., 2002 (Foissner & Xu 2007; Foissner et al. 2002).

Spathidium and *Latispathidium* form a special group within the spathidiids: they have a *Spathidium*-type ciliary pattern, that is, the ciliary rows adhere to the individual circumoral kinetofragments, especially on the left side. This is an indication of a common ancestor and might be used for a (sub)-familial split if further (molecular?) evidence support such relationship.

Latispathidium was established with two species by Foissner et al. (2005). We add three new species, suggesting that further taxa wait to be discovered. One of the new species, *Latispathidium simile*, was found only in rain forest soils of Australia, Malaysia, and South America, suggesting a preference for such biotopes and a restricted distribution in Gondwana.

Key to species

1 Macronucleus ellipsoidal ..... *Latispathidium lanceoplites* (p. 215)
– Macronucleus not as above **2**
2 Many macronucleus nodules in more or less distinct rows ..... *Latispathidium arboricola* nov. spec. (p. 229)
– Macronucleus not as above **3**
3 Macronucleus composed of two nodules with micronucleus in between; extrusomes ≤1 µm long ..... *Latispathidium simile* nov. spec. (p. 238)
– Macronucleus a spiralized and/or tortuous strand; extrusomes basically rod-shaped and ≥6 µm long or ovate and <2 µm long **4**
4 Extrusomes basically rod-shaped and ≥6 µm long ..... *Latispathidium truncatum* (p. 218)
– Extrusomes ovate and ≤2 µm long ..... *Latispathidium brachyoplites* nov. spec. (p. 245)

Latispathidium lanceoplites (Foissner, Agatha & Berger, 2002) Foissner, Berger, Xu & Zechmeister-Boltenstern, 2005

(Fig. 7.1a–l, 7.3n, Table 7.1)

2002 ***Spathidium lanceoplites* nov. spec.** – Foissner, Agatha & Berger, Denisia 5: 267, Fig. 58a–l, Table 50 (Fig. 7.1a–l; original description. Thre type slides with protargol-prepared specimens have been deposited in the Biology Centre of the Upper Austrian Museum in Linz [LI], accession numbers according to Aescht 2008, p. 162: 2002/351 [containing holotype, Fig. 58e, f in Foissner et al. 2002 and Fig. 7.1e, f in present work], 2002/342, 2002/358).

2005 ***Latispathidium lanceoplites* (Foissner, Agatha and Berger 2002) nov. comb.** – Foissner, Berger, Xu & Zechmeister-Boltenstern, Biodiv. Conserv. 14: 644 (fixation as type species of genus and combination with *Latispathidium*).

Nomenclature: The species-group name *lanceoplites* is a composite of the Latin noun *lancea* (lance; Hentschel & Wagner 1996, p. 356) and the Greek noun *(h)oplites* (soldier, extrusome in present case; Brown 1954, p. 806): The name refers to the lanceolate extrusomes (Foissner et al. 2002, p. 269).

Diagnosis (from Foissner et al. 2002, slightly modified): Body size about 80 × 15 µm in vivo. Body narrowly to very narrowly spatulate with oblique, obovate, minute oral bulge about one third as long as widest trunk region. Macronucleus elongate ellipsoidal. Extrusomes cuneate to ovate, about 2.0 × 0.8 µm in size. On average 7 ciliary rows, three of them anteriorly differentiated into inconspicuous, heterostichad (row 3 shortened by about 45%) dorsal brush occupying 16% of body length.

Remarks: For distinction from *Latispathidium truncatum*, see *Latispathidium truncatum bimicronucleatum*. *Latispathidium lanceoplites* has the same body size, body shape, and nuclear apparatus as *Spathidium claviforme* Kahl, 1930a (Foissner 1987, p. 228) and *Protospathidium terricola* Foissner, 1998 (Foissner & Xu 2007, p. 93). Despite this, in vivo it is easily separated from these species by the minute extrusomes (obovate and 1.5–2.0 µm vs. 4.0–6.0 µm long, fine rods) and the low number of ciliary rows (on average 7 vs. 12, respectively, 21). *Latispathidium lanceoplites* is also rather similar to *Protospathidium vermiculus*

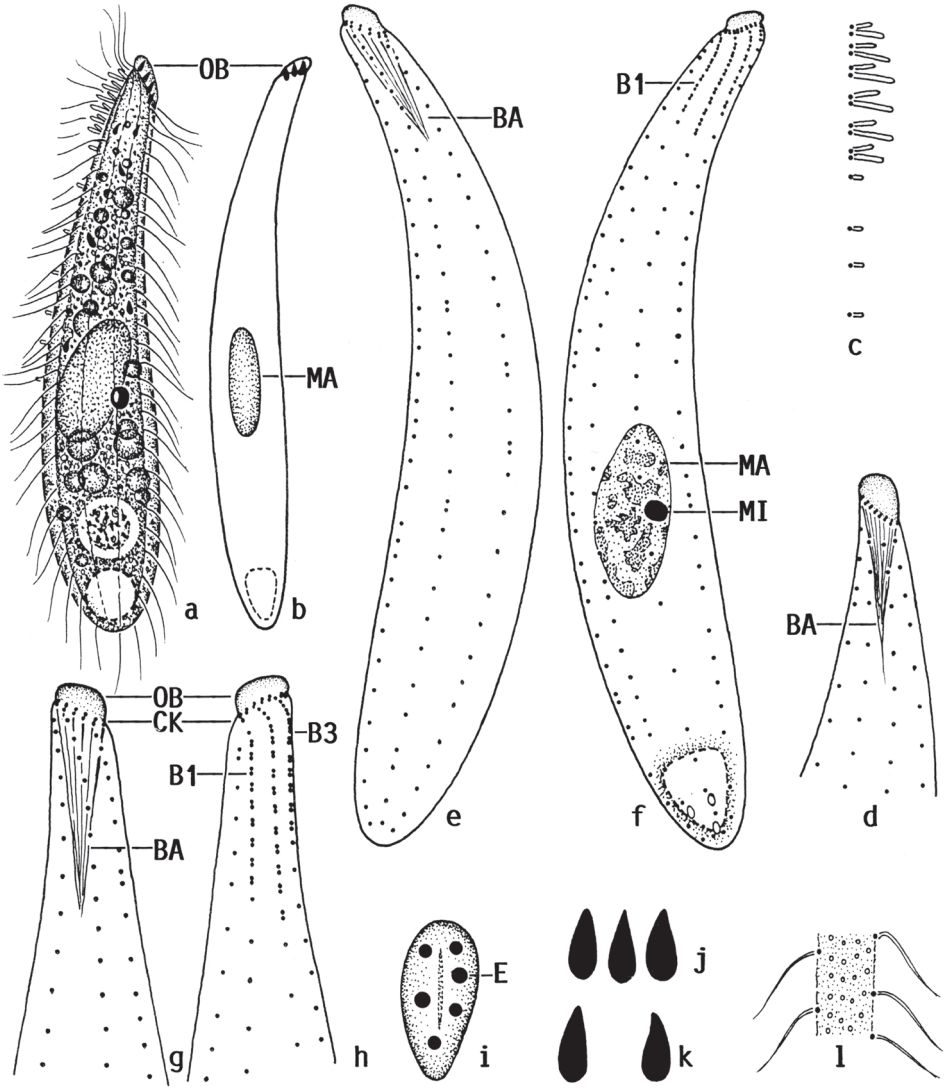

Fig. 7.1a–l *Latispathidium lanceoplites* (Foissner et al., 2002) Foissner et al., 2005 (from Foissner et al. 2002. a–c, i–l, from life; d–h, protargol preparation). **a:** Right side view of a representative specimen, 80 μm. **b:** A slender specimen. **c:** Posterior portion of brush row 3, which has a tail of about eight 1-μm-long, monokinetidal bristles. **d:** Ventrolateral view of anterior body region, oral bulge length 4.5 μm. **e, f:** Ciliary pattern of right and left side and nuclear apparatus of holotype specimen, 88 μm. **h:** Ciliary pattern in right and left anterior region, oral bulge length 5 μm. Note the laterally located dorsal brush and the widely spaced circumoral dikinetids. See also Fig. 7.3n at *Latispathidium truncatum bimacronucleatum*. **i:** Frontal view of oral bulge containing some thick extrusomes. **j, k:** Oral bulge extrusomes of specimens from Namibian sites 49 (j) and 33 (k), 1.5–2.0 × 0.8 μm. **l:** Loose cortical granulation. B1–3 – dorsal brush rows, BA – oral basket, CK – circumoral kinety, E – extrusomes, MA – macronucleus, MI – micronucleus, OB – oral bulge.

(Kahl, 1926) Foissner & Xu, 2007 (p. 99) which, however, is smaller (50–75 μm) and has oblong, 3–4 μm long extrusomes and a distinct *Protospathidium* ciliary pattern.

continued on p. 218

Table 7.1 Morphometric data on *Latispathidium lanceoplites* (upper line; from Foissner et al. 2002) and *Latispathidium truncatum bimicronucleatum* (lower line; from Foissner et al. 2005)[a]

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Body, length	74.2	72.0	16.9	3.9	22.8	42.0	120.0	19
	82.9	83.0	10.4	2.3	12.6	66.0	101.0	21
Body, width	14.4	14.0	2.9	0.7	20.5	10.0	23.0	19
	13.7	14.0	1.7	0.4	12.4	11.0	17.0	21
Body length:width, ratio	5.2	4.8	1.0	0.2	19.0	3.5	6.5	19
	6.1	6.2	0.9	0.2	14.9	4.2	7.6	21
Oral bulge, length (cord of circumoral kinety)	4.1	4.0	0.8	0.2	19.0	3.0	6.0	19
	9.3	9.0	0.6	0.1	6.7	8.0	10.0	21
Oral bulge, height	1.9	2.0	–	–	–	1.5	2.5	19
	3.1	3.0	–	–	–	3.0	3.5	8
Circumoral kinety to last dikinetid of brush row 1, distance	9.1	9.0	2.0	0.5	22.1	6.0	14.0	19
	15.7	16.0	2.1	0.5	13.6	12.0	20.0	19
Circumoral kinety to last dikinetid of brush row 2, distance	11.6	11.0	2.2	0.5	18.8	8.0	18.0	19
	15.2	15.0	1.5	0.3	9.9	12.0	18.0	19
Circumoral kinety to last dikinetid of brush row 3, distance	7.5	7.0	2.6	0.6	34.2	4.0	15.0	19
	7.5	7.0	1.0	0.2	12.9	6.0	10.0	19
Anterior body end to macronucleus, distance	34.7	35.0	8.8	2.0	25.3	20.0	57.0	19
	33.7	34.0	9.3	2.0	27.5	17.0	52.0	21
Macronucleus (figure), length	16.1	16.0	2.0	0.4	12.4	13.0	20.0	19
	31.8	32.0	7.9	1.7	24.9	20.0	48.0	21
Macronucleus, width	6.4	6.0	1.0	0.2	15.9	5.0	8.0	19
	5.1	5.0	0.6	0.1	12.3	4.0	6.0	21
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	19
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Micronucleus, length	2.9	3.0	–	–	–	2.0	4.0	8
	3.0	3.0	0.6	0.1	18.5	2.5	4.5	21
Micronucleus, width	2.3	2.5	–	–	–	1.7	3.0	8
	–	–	–	–	–	–	–	–
Micronuclei, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	8
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Somatic kineties, number	7.3	7.0	0.7	0.2	10.2	7.0	10.0	19
	14.5	14.0	1.0	0.2	6.8	13.0	16.0	21
Ciliated kinetids in a right-side kinety, number	31.6	32.0	3.6	0.8	11.5	22.0	37.0	19
	30.4	32.0	7.9	1.7	26.0	18.0	43.0	21
Dorsal brush rows, number[b]	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	21
Dikinetids in brush row 1, number	7.7	8.0	1.1	0.3	14.3	6.0	9.0	19
	14.8	15.0	2.8	0.6	18.6	10.0	19.0	19
Dikinetids in brush row 2, number	10.1	10.0	1.4	0.3	13.6	6.0	12.0	19
	14.4	15.0	1.7	0.4	11.9	12.0	18.0	19
Dikinetids in brush row 3, number	6.1	6.0	1.6	0.4	25.6	4.0	11.0	19
	6.4	6.0	0.7	0.2	10.7	5.0	8.0	19

[a] Data based on mounted, protargol-prepared (Foissner's method), and randomly selected specimens from non-flooded Petri dish cultures. Measurements in µm. For abbreviations, see same footnote at Table 7.2.

[b] Only two rows in one out of 30 specimens of *Latispathidium lanceoplites*.

Description: Body size 45–130 × 10–20 µm in vivo, usually near 80 × 15 µm; length:width ratio also highly variable, viz., 3.5–6.5:1, on average 5.2:1 in protargol preparations, up to 8:1 in vivo (Fig. 7.1b; Table 7.1). Body shape inconspicuous, that is, oblong to indistinctly spatulate, rarely almost cylindroidal, slightly flattened only in oral area (Fig. 7.1a, e). Nuclear apparatus on average slightly behind mid-body, consists of an ellipsoidal (2:1) to elongate ellipsoidal (3:1) macronucleus with lobate nucleoli and a broadly ellipsoidal micronucleus attached to macronucleus. Contractile vacuole in rear end, several excretory pores subterminal on left side. Extrusomes scattered in oral bulge and cytoplasm; bulge extrusomes slightly asymmetrical, cuneate to ovate, although minute, that is, only about 1.5–2.0 × 0.8 µm in size, rather distinct because strongly refractive in vivo; posterior half occasionally impregnates with the protargol method used (Fig. 7.1a, b, i–k). Cortex flexible, contains comparatively widely spaced rows of loosely arranged, minute granules about 0.3 µm across. Cytoplasm colourless, in well-fed specimens filled with lipid droplets up to 6 µm across, leaving blank oral area, which is thus hyaline. Likely feeds on protists, as indicated by the fatty inclusions. Movement without peculiarities.

Somatic cilia about 7 µm long in vivo and ordinarily spaced, arranged in an average of only seven equidistant, bipolar kineties forming anteriorly a *Spathidium*-pattern which, however, is rather indistinct due to the low number of rows. Dorsal brush occupies anterior left side of cell, of usual structure, inconspicuous because occupying only 16% of body length and bristles merely up to 4 µm long. Brush row 1 composed of an average of eight bristles; middle row 2 slightly longer than row 1 and distinctly longer than dikinetidal portion of row 3 composed of an average of 10 dikinetids; anterior portion of row 3 composed of an average of six dikinetids, followed by about eight 1 µm long bristles forming a tail extending to mid-body (Fig. 7.1a, c–h, 7.3n; Table 7.1).

Oral bulge minute because less than half as long as widest trunk region, but rather conspicuous due to the refractive and thus bright extrusomes contained; moderately convex in lateral view and distinctly obovate when viewed ventrally. Circumoral kinety also obovate, composed of few, comparatively loosely spaced dikinetids associated with fine nematodesmata forming a conspicuously conical oral basket (Fig. 7.1a, b, d–i, 7.3n; Table 7.1).

Occurrence and ecology: To date found at the type locality, that is, mud and soil from road puddles in the Bambatsi Guest Farm (site 49 in Foissner et al. 2002, p. 25; 20°10'S 15°25'E), Namibia, a semiterrestrial biotope. In addition, Foissner et al. (2002, p. 270) recorded it from a sand dune in the Namib Escarpment (site 33 in their work), indicating that it prefers terrestrial habitats. *Latispathidium lanceoplites* is well adapted to soil life by the small, slender body (Foissner et al. 2002).

Latispathidium truncatum (Stokes, 1885) Foissner, Berger, Xu & Zechmeister-Boltenstern, 2005

(Fig. 7.2a–c, 7.3a–m, p, q, 7.4a–o, Tables 7.1, 7.2)

1885 ***Lacrymaria truncata*, sp. nov.** – Stokes, Ann. Mag. nat. Hist., 15: 442, Plate XV, fig. 10 (Fig. 7.2a; original description; no type material available).

1888 ***Lacrymaria truncata*, Stokes** – Stokes, J. Trenton nat. Hist. Soc. 1: 165, Plate IV, fig. 23 (redrawing of Fig. 7.2a; review of ciliates from the USA).

1930 ***Spathidium (Lacrymaria) truncatum* Stokes, 1885** – Kahl, Tierwelt Dtl. 18: 159, Fig. 22_{12} (Fig. 7.2b, redrawing of Fig. 7.2a; combination with *Spathidium*; revision of ciliates).

1943 ***Spathidium truncatum* Stokes** – Kahl, Infusorien, p. 26, Tafel V, Fig. 27 (redrawing of Fig. 7.2b; brief review).

1962 ***Spathidium* sp.** – Vuxanovici, Studii Cerc. Biol. (Biol. Anim.) 14: 210, Plansa IV, Fig. 28 (Fig. 7.2c; for details, see occurrence and ecology).

2005 ***Latispathidium truncatum* (Stokes 1885) nov. comb.**[3] – Foissner, Berger, Xu & Zechmeister-Boltenstern, Biodiv. Conserv. 14: 645, Fig. 5a–h, i–m, p, q, 6a–g, Table 7 (Fig. 7.3a–m, p, q; characterisation of species).

2005 ***Latispathidium truncatum truncatum* (Stokes 1885) nov. comb., nov. stat.** – Foissner, Berger, Xu & Zechmeister-Boltenstern, Biodiv. Conserv. 14: 645, Fig. 5h (Fig. 7.2a; classification as subspecies; see nomenclature).

2005 ***Latispathidium truncatum bimicronucleatum* nov. sspec.** – Foissner, Berger, Xu & Zechmeister-Boltenstern, Biodiv. Conserv. 14: 645, Fig. 5a–g, i–m, p, q, 6a–g, Table 7 (Fig. 7.3a–m, p, q, 7.4a–g; original description of new subspecies; for type material, see nomenclature at subspecies).

Nomenclature: No explicit etymology has been provided in the original description (Stokes 1885). The species-group name *truncat·us*, *-a*, *-um* (Latin verb in participle? [m, f, n]; truncate, mutilated; www.frag-cesar.de; accessed 28 April 2023) obviously refers to "the frontal border of which is somewhat dilated and obliquely truncate" (Stokes 1885). "*Spathidium (Lacrymaria)*" in Kahl (1930b) does not mean that he classified *Lacrymaria* as subgenus of *Spathidium*, but rather it should indicate that this species was originally classified in *Lacrymaria*.

The term "nov. stat." (new status) was not correctly used by Foissner et al. (2005) at the nominotypical subspecies because they did not apply the name of an infrasubspecific entity to a subspecies or species.[4] For correct use of the term "stat. nov.", see ICZN (1999, Recommendation 16A and Article 45.5.1).

Improved diagnosis: Body length 70–125 µm. Body narrowly spatulate to obclavate with oblique, short oral bulge distinctly narrower than widest trunk region. Macronucleus tortuous and extending almost whole body length or spiralized in middle third of body. Several micronuclei distributed along macronucleus strand or one each near ends of macronucleus.

Remarks: Foissner et al. (2005) split this species into two subspecies, differing mainly in the micronucleus pattern. The diagnosis is incomplete because the nominotypical subspecies is not yet redescribed. The classification in *Latispathidium* is based on the detailed investigation of a very similar population differing from the population studied by Stokes (1885) mainly in the micronucleus pattern (see *Latispathidium truncatum bimicronucleatum*). Only a detailed reinvestigation of the nominotypical subspecies can support or disprove this classification. Classified as junior synonym of *Spathidium spathula* (Müller, 1773) Bütschli, 1889 by Schewiakoff (1896, p. 132); for redescription of this species, see Foissner (1984, p. 70).

[3] Foissner et al. (2005) provided the following extended diagnosis for *Latispathidium truncatum* (to include the subspecies *Latispathidium truncatum bimicronucleatum*): "Length 70–125 µm. Obclavate to slenderly bursiform with slanted, short oral bulge distinctly narrower than widest trunk region. Macronucleus tortuous and almost extending whole body length or spiralized in middle third of body. Several micronuclei distributed along macronuclear strand or one each near to ends of macronucleus."

[4] Note by H. Berger: The term "nov. stat." was also not correctly used by Berger (2006, p. 70, see "new ranks"; 2008, p. 68, see "new ranks"; 2011, p. 43, see "new ranks") and Foissner (2021, p. 56, see "new status").

Table 7.2 Comparison of main morphometrics in *Latispathidium truncatum bimicronucleatum* (upper line; from Foissner et al. 2005), *Spathidium aciculare* (middle line; from Foissner et al. 2002), and *Spathidium etoschense* (lower line; from Foissner et al. 2002)[a, b]

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Body, length	82.9	83.0	10.4	2.3	12.6	66.0	101.0	21
	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	13.7	14.0	1.7	0.4	12.4	11.0	17.0	21
	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
Oral bulge, length	9.3	9.0	0.6	0.1	6.7	8.0	10.0	21
	18.4	19.0	2.6	0.6	14.2	12.0	22.0	19
	22.7	23.0	4.1	1.4	17.9	16.0	29.0	9
Somatic kineties, number	14.5	14.0	1.0	0.2	6.8	13.0	16.0	21
	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
Dikinetids in brush row 1, number	14.8	15.0	2.8	0.6	18.6	10.0	19.0	19
	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	14.4	15.0	1.7	0.4	11.9	12.0	18.0	19
	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	6.4	6.0	0.7	0.2	10.7	5.0	8.0	19
	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

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

[b] For brief review of *Spathidium aciculare* and *Spathidium etoschense*, see Chapter 3, that is, Foissner et al. (2025b, p. 65).

Key to subspecies

1 One micronucleus each near ends of macronucleus strand; extrusomes finely acicular, about 7.0 × 0.5 μm ..... *Latispathidium truncatum bimicronucleatum* (p. 222)

– Several micronuclei distributed along macronucleus strand; extrusomes possibly rod-shaped and >10 μm long ..... *Latispathidium truncatum truncatum* (p. 221)

Latispathidium truncatum truncatum (Stokes, 1885) Foissner, Berger, Xu & Zechmeister-Boltenstern, 2005

(Fig. 7.2a–c)

1885 ***Lacrymaria truncata*, sp. nov.** – Stokes, Ann. Mag. nat. Hist. 15: 442, Plate XV, fig. 10 (Fig. 7.2a; original description; no type material available).

1888 ***Lacrymaria truncata*, Stokes** – Stokes, J. Trenton nat. Hist. Soc. 1: 165, Plate IV, fig. 23 (redrawing of Fig. 7.2a; review of ciliates from the USA).

1930 ***Spathidium (Lacrymaria) truncatum* Stokes, 1885** – Kahl, Tierwelt Dtl. 18: 159, Fig. 22_{12} (Fig. 7.2b, redrawing of Fig. 7.2a; combination with *Spathidium*; revision of ciliates).

1943 ***Spathidium truncatum* Stokes** – Kahl, Infusorien, p. 26, Tafel V, Fig. 27 (redrawing of Fig. 7.2b; brief review).

1962 ***Spathidium* sp.** – Vuxanovici, Studii Cerc. Biol. (Biol. Anim.) 14: 210, Plansa IV, Fig. 28 (Fig. 7.2c; for details, see occurrence and ecology).

2005 ***Latispathidium truncatum truncatum* (Stokes 1885) nov. comb., nov. stat.** – Foissner, Berger, Xu & Zechmeister-Boltenstern, Biodiv. Conserv. 14: 645, Fig. 5h (Fig. 7.2a; classification as subspecies; see nomenclature).

Nomenclature: For nomenclature, see same chapter at *Latispathidium truncatum*. The present subspecies is the nominotypical subspecies.

Diagnosis (from Foissner et al. 2005, slightly modified): Body length about 125 µm. Several micronuclei along macronucleus strand.

Remarks: See same chapter at *Latispathidium truncatum bimicronucleatum*.

Description: We provide a verbatim quote of the rather detailed text of Stokes (1885, p. 442). "Body flask-shaped or clavate, flattened, very soft and flexible, four and one half to five times as long as broad, narrowed into a neck-like region anteriorly, the frontal border of which is somewhat dilated and obliquely truncate, the apical groove conspicuous; the posterior extremity rounded; entire surface strongly and longitudinally striate; cuticular

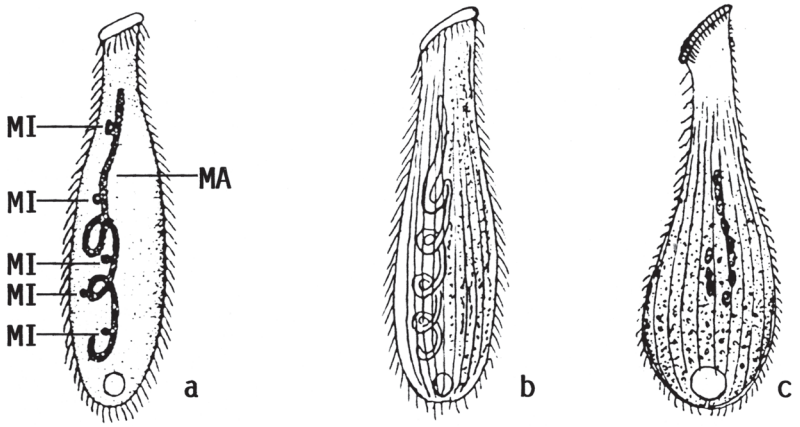

Fig. 7.2a–c *Latispathidium truncatum truncatum* (Stokes, 19985) Foissner et al., 2005. (a, from Stokes 1885; b, from Kahl 1930a after Stokes 1885; c, from Vuxanovici 1962a. From life). **a:** Left lateral view, about 127 µm. **b:** Although redrawn from Stokes (1885), differing considerably from the original (a). **c:** *Spathidium* sp., 130 µm; perhaps identical with *Latispathidium truncatum truncatum*.

cilia long and fine; oral aperture terminal, followed by a long conical membranous pharynx, visible only after death; apical groove bearing a single row of cilia; contractile vesicle single, spherical, postero-terminal; nucleus long, band-shaped, variously curved and twisted, having several laterally-attached nuclei; anal aperture postero-terminal. Length of body 1/200 inch (= 127 μm)." About the locomotion, Stokes (1885, p. 443) wrote: "The movements of the infusorian are rapid and usually by rotation on the long axis".

Stokes (1885) provides the following remarks to this species: "It is remarkable for the very long and band-like nucleus, and especially for the capacious conical pharyngeal passage. [...] It is here visible only after the animalcule's death, which in this instance was accomplished by the glycerole of tannin, when it becomes conspicuous, and is seen to occupy almost the entire width of the frontal border, thence tapering to an acute termination and extending through about one third of the entire body. In most of the species the apical extremity is conical; here, however, it is conspicuously flattened, oblique, and truncate".

Occurrence and ecology: The type locality of *Latispathidium truncatum truncatum* is a standing water (shallow pond with dead leaves) in central New Jersey, USA (Stokes 1885, p. 437, 442). Few records are available in the literature, and all are unsubstantiated, that is, do not contain morphological data: periphyton of a lake in Hungary (Tamás & Gellért 1959, p. 239); rather frequent in the Donghu Lake, Wuhan, China (Shen & Gu 1965, p. 172); Dragitchevo village pond in the surroundings of Sofia, Bulgaria (Detcheva 1976, p. 306); and, possibly, in the Fundeni Lake near Bucharest, Rumania, where Vuxanovici (1962) found some specimens of this or a similar species. He provided a figure (Fig. 7.2c) and a brief description: body length 130 μm; reniform in transverse optical section; macronucleus a long, moniliform strand; contractile vacuole in rear end, with single excretory pore; oral bulge extrusomes 4 μm long; cilia 4–5 μm long, arranged in about 10 rows per side. If all these records are correct, then *Latispathidium truncatum truncatum* is a limnetic (sub)species occurring in ponds and lakes.

Latispathidium truncatum bimicronucleatum Foissner, Berger, Xu & Zechmeister-Boltenstern, 2005

(Fig. 7.3a–g, i–m, p, q, 7.4a–o, Tables 7.1, 7.2)

2005 ***Latispathidium truncatum bimicronucleatum* nov. sspec.** – Foissner, Berger, Xu & Zechmeister-Boltenstern, Biodiv. Conserv. 14: 645, Fig. 5a–g, i–m, p, q, 6a–g, Table 7 (Fig. 7.3a–m, p, q, 7.4a–g; original description of new subspecies; for type material, see nomenclature).

Nomenclature: The (sub)species-group name *bimicronucleat·us, -a, -um* (Latin adjective [m, f, n]; having two micronuclei; Foissner et al. 2005) is a composite of the Latin quantifier *bi-* (two; Werner 1972, p. 110), the Greek adjective *micr-* (small; Werner 1972, p. 265), the thematic vowel ·o-, and the Latin adjective *nucleat·us, -a, -um* (like the kernel of a nut; Hentschel & Wagner 1996, p. 429); it refers to the two micronuclei.

Foissner et al. (2005, p. 646) wrote that the type material (one holotype slide and two paratype slides) have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI). However, this statement was incorrect, that is, the slides have not been deposited in the Museum (see Aescht 2008, p. 192). According to ICZN (1999, Article 16.4), the

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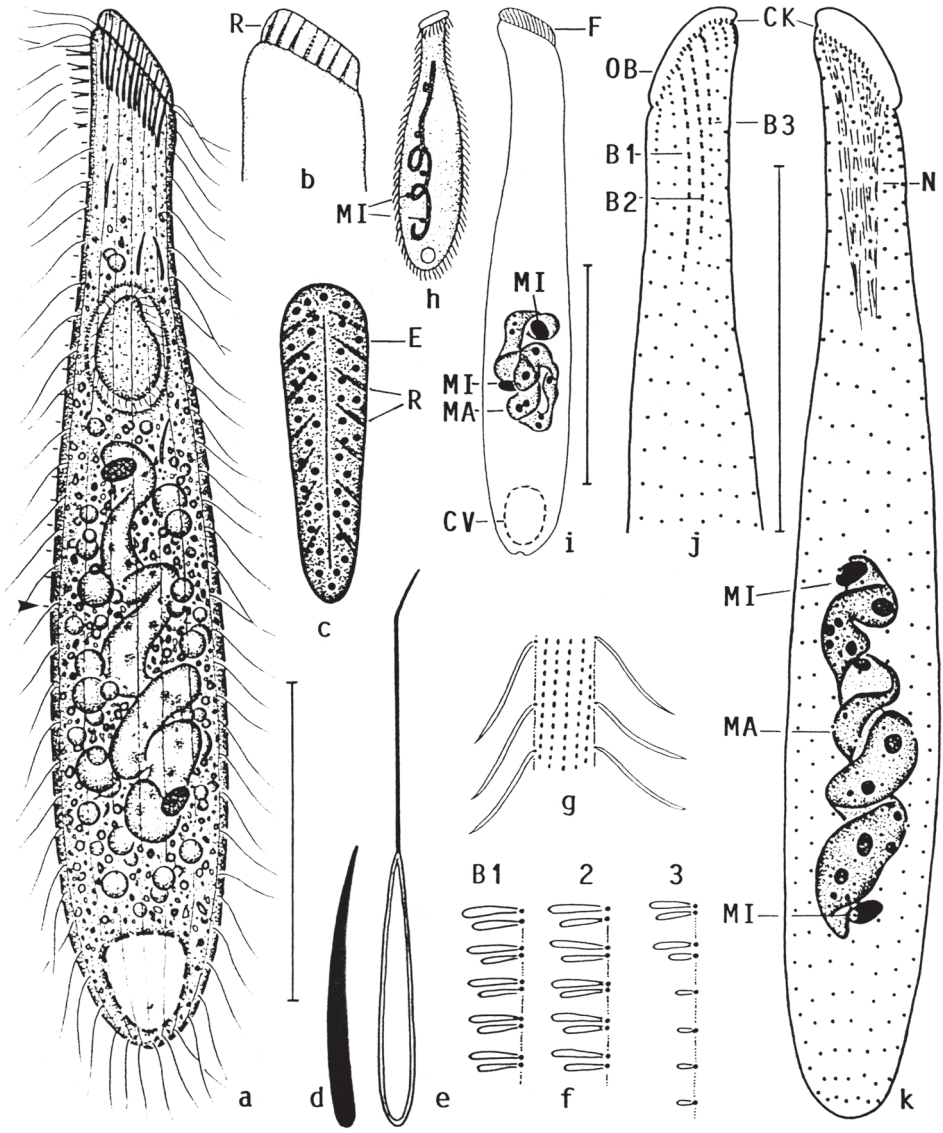

Fig. 7.3a–g, i–k *Latispathidium truncatum bimicronucleatum* Foissner et al., 2005 (from Foissner et al. 2005. a–g, from life; i–k, protargol preparation). **a:** Right lateral view of a representative specimen, 100 µm. Arrowhead marks last bristle of tail of brush row 3. **b, c:** Lateral and frontal view of oral bulge showing ridge-like granule accumulations and extrusomes. **d:** Oral bulge extrusome, length 7 µm. **e:** Exploded toxicyst, length 15 µm. **f:** Middle portion of dorsal brush. **g:** Surface view showing cortical granulation. **i:** Specimen with tortuous macronucleus, 78 µm. **j, k:** Ciliary pattern of left (j) and right (k) side of holotype specimen, 94 µm. B1–3 – dorsal brush rows, CK – circumoral kinety, CV – contractile vacuole, E – extrusome, F – fibres, MA – macronucleus, MI – micronucleus, N – nematodesmata, OB – oral bulge, R – granule ridge.

Fig. 7.3h *Latispathidium truncatum truncatum* (Stokes, 19985) Foissner et al., 2005 (from Stokes 1885. From life). Left lateral view, about 127 µm; differs from the European population by the micronucleus pattern.

name bearing types of species and subspecies described after 1999 have to be fixed explicitly. In addition, the work must contain a statement where the type material, will be (or is) deposited (ICZN 1999, Article 16.4.2). Since Foissner et al. (2005, p. 646, 647, their Fig. 5j, k) fixed a specimen as holotype and since they mentioned the collection (Biology Centre of the Upper Austrian Museum in Linz), the description is valid. The type slides (Fig. 7.4h, i, holotype slide, accession number 2024/165; Fig. 7.4k–n, two paratype slides, accession numbers 2024/166, 167) have finally been deposited in the Biology Centre of the Upper Austrian Museum in Linz together with the slides of the other taxa treated in the present book. The slide containing the holotype of *Latispathidium truncatum bimacronucleatum* also contains the holotype of *Edaphospathula fusioplites* (Foissner et al., 2005) Foissner & Xu, 2007[5] (Fig. 74.h, j; accession number 2024/165) and one paratype slide of *Latispathidium truncatum bimacronucleatum* is simultaneously a paratype slide of *Edaphospathula fusioplites* (Fig. 7.4m, o; 2024/ 167; see also Foissner & Xu 2007, p. 60).

Diagnosis (from Foissner et al. 2005, slightly modified): Body size about 100 × 15 µm in vivo. Obclavate with oblique oral bulge about two thirds as long as widest trunk region. Macronucleus in middle third of body, spiralized. Invariably two micronuclei, one each near or attached to ends of macronucleus. Extrusomes finely acicular, about 7.0 × 0.5 µm. On average 14 ciliary rows, three of them anteriorly differentiated to dorsal brush occupying 19% of body length; brush row 3 distinctly shortened.

Remarks: This population is fairly similar to *Latispathidium truncatum truncatum* (Stokes, 1885), the poorly known, not yet redescribed nominotypical subspecies from North America. The main difference concerns the micronucleus pattern, viz., several micronuclei distributed along the macronucleus strand, as definitely stated, and shown (Fig. 7.3h) by Stokes (1885) vs. one each at ends of macronucleus (Fig. 7.3k, l, p, q). Certainly, this is a rather sophisticated feature, but sufficient to separate our population at subspecies level, considering that the pattern is highly constant and unusual. Possibly, there is a second main difference, viz., the extrusomes, which Stokes (1885), unfortunately, did not mention, but likely misinterpreted as a long (about one third of body length), conical pharyngeal basket. This interpretation, which we apply in the following species comparison, is reasonable because the oral basket of small and middle-sized spathidiids is very fine and thus hardly recognizable in the light microscope, even with interference contrast optics, while long, rod-shaped extrusomes, for instance, those of *Epispathidium terricola* Foissner, 1987 (p. 234; see Chapter 6, that is, Foissner et al. 2025a) are easily recognized with an ordinary bright field microscope. Indeed, *Latispathidium truncatum bimicronucleatum* looks, at first glance, like a small *Epispathidium terricola* which, however, differs markedly by the location of the dorsal brush (dorsally vs. laterally), the number of ciliary rows (39 vs. 14 on average), the extrusomes (40 µm vs. 7 µm long), and the arrangement of the ciliary rows (*Epispathidium* vs. *Spathidium* pattern).

Latispathidium truncatum bimicronucleatum is easily distinguished from the congeners by the acicular extrusomes. It differs distinctly from similar *Spathidium* species, especially

[5] Note by H. Berger: The original combination of this species is *Protospathidium fusioplites* Foissner et al., 2005 (p. 660; specimens shown in their Fig. 9m–o originally fixed as holotype; in addition, the collection [LI] was mentioned; thus, this species is likewise valid). Foissner et al. (2005, p. 660) mentioned two paratype slides, indicating that the slide 2024/166 shown in Fig. 7.4k contains also paratype specimens of *Protospathidium fusioplites*, although W. Foissner did not made a "protocol".

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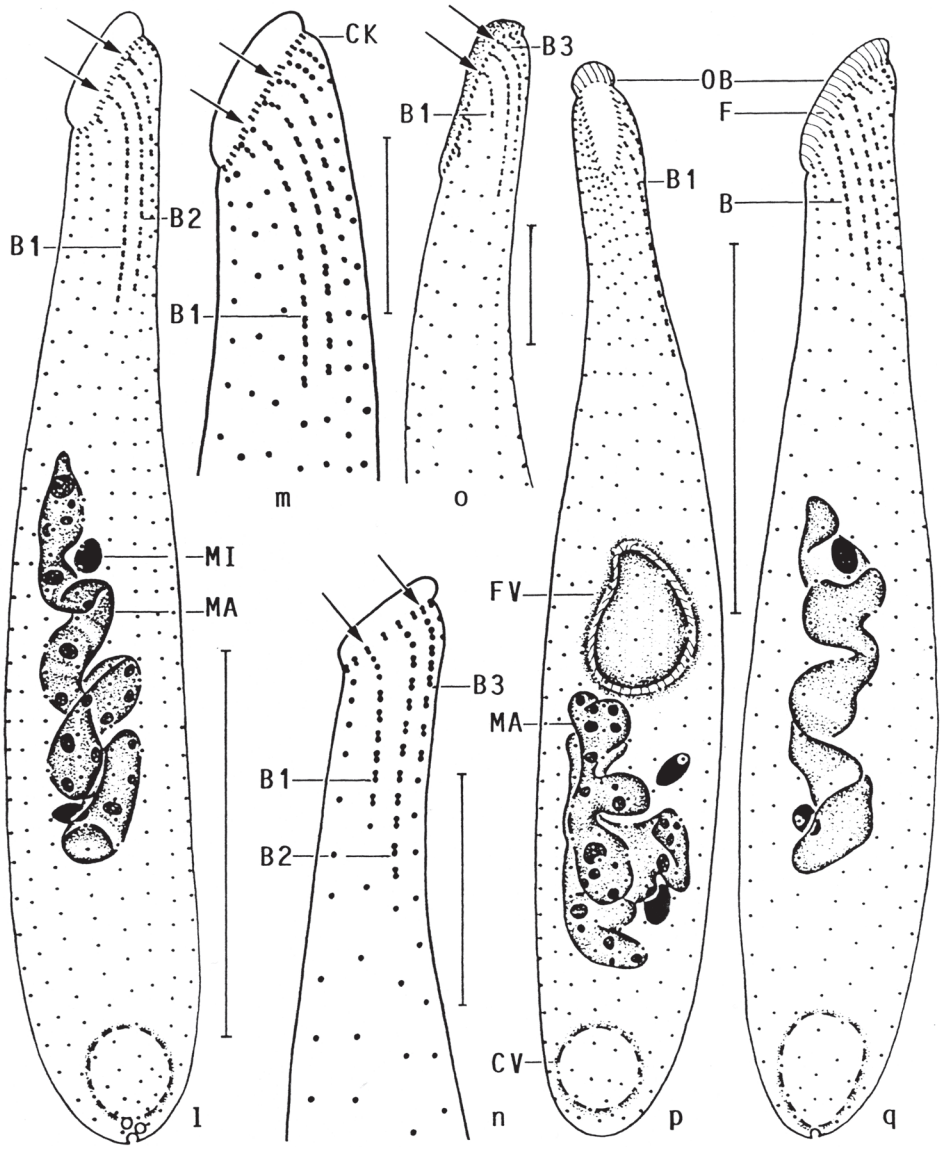

Fig. 7.3l, m, p, q *Latispathidium truncatum bimicronucleatum* Foissner et al., 2005 (from Foissner et al. 2005. Protargol preparation). **l, m:** Ciliary pattern of left side and nuclear apparatus, 89 μm. Arrows mark dorsal brush in centre of left side**. p:** Ventral view of a specimen with lobate macronucleus, 86 μm. **q:** A specimen with four brush rows and strongly flattened macronucleus, 86 μm. B – dorsal brush, B1–3 – dorsal brush rows, CK – circumoral kinety, CV – contractile vacuole, F – fibres, FV – food vacuole, MA – macronucleus, MI – micronucleus, OB – oral bulge.

Fig. 7.3n *Latispathidium lanceoplites* (Foissner et al., 2002) Foissner et al., 2005 (original, that is, new figure from type population. Protargol preparation). Left anterior region (for details, see remarks). Arrows mark dorsal brush in centre of left side. B – dorsal brush, B1–3 – dorsal brush rows.

Fig. 7.3o *Spathidium etoschense* Foissner et al., 2002 (from Foissner et al. 2002. Protargol preparation). Dorsolateral view (for details, see remarks). Arrows mark dorsal brush which is located dorsolaterally in this species. B – dorsal brush, B1–3 – dorsal brush rows.

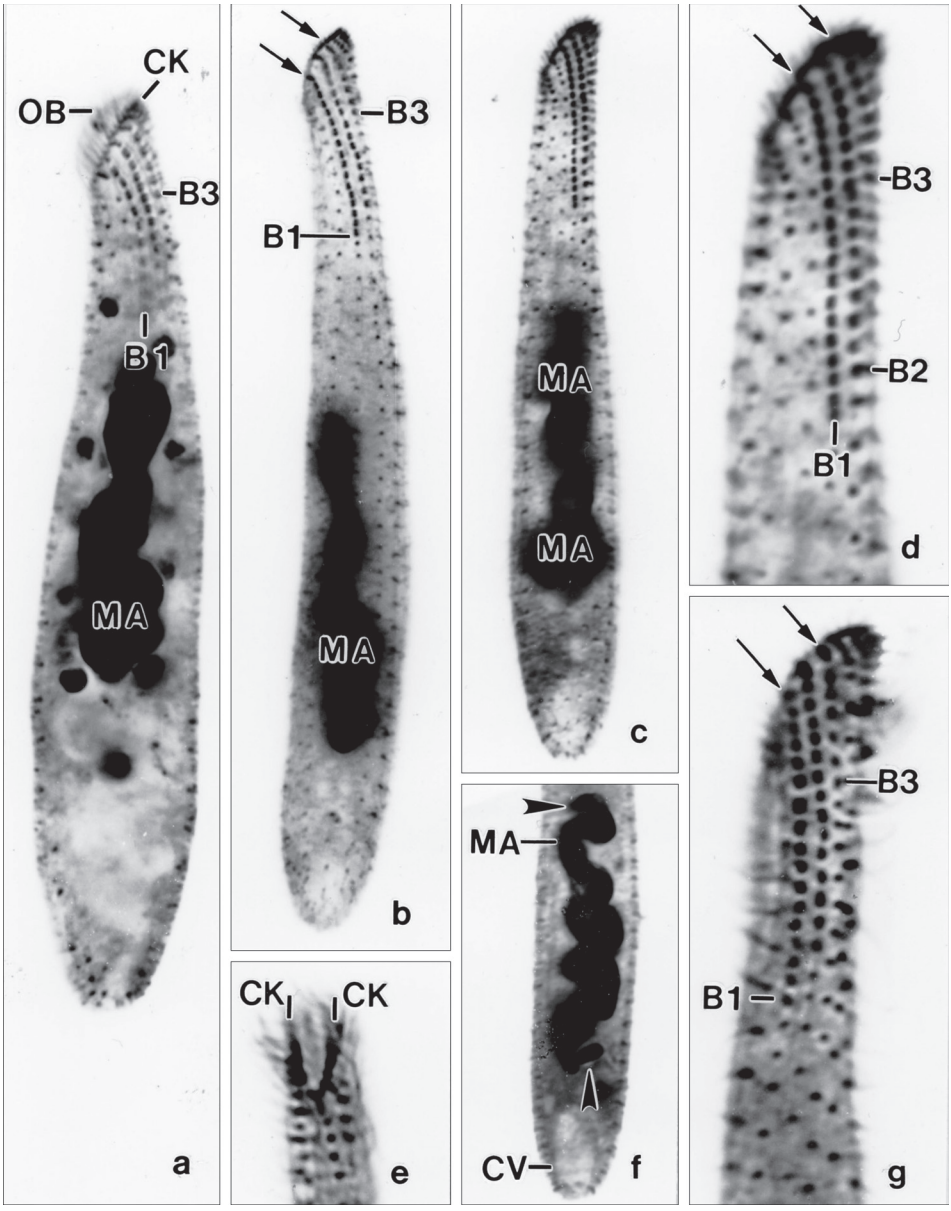

Fig. 7.4a–g *Latispathidium truncatum bimicronucleatum* Foissner et al., 2005 (from Foissner et al. 2005. Protargol preparation). Ciliary and nuclear pattern. Note cylindrical to obclavate body shape and macronucleus in middle body third. Arrows denote the genus-specific dorsal brush location in centre of left side, while the arrowheads in (f) mark the main subspecies-specific feature, viz., a micronucleus each at the ends of the macronucleus (several micronuclei distributed along macronucleus strand in *Latispathidium truncatum truncatum*; Fig. 7.3h). The dorsal brush consists of three rows of paired bristles (dikinetids) at the anterior end of three left lateral ciliary rows; row 3 is strongly shortened. B1–B3 – dorsal brush rows, CK – circumoral kinety, CV – contractile vacuole, MA – macronucleus, OB – oral bulge.

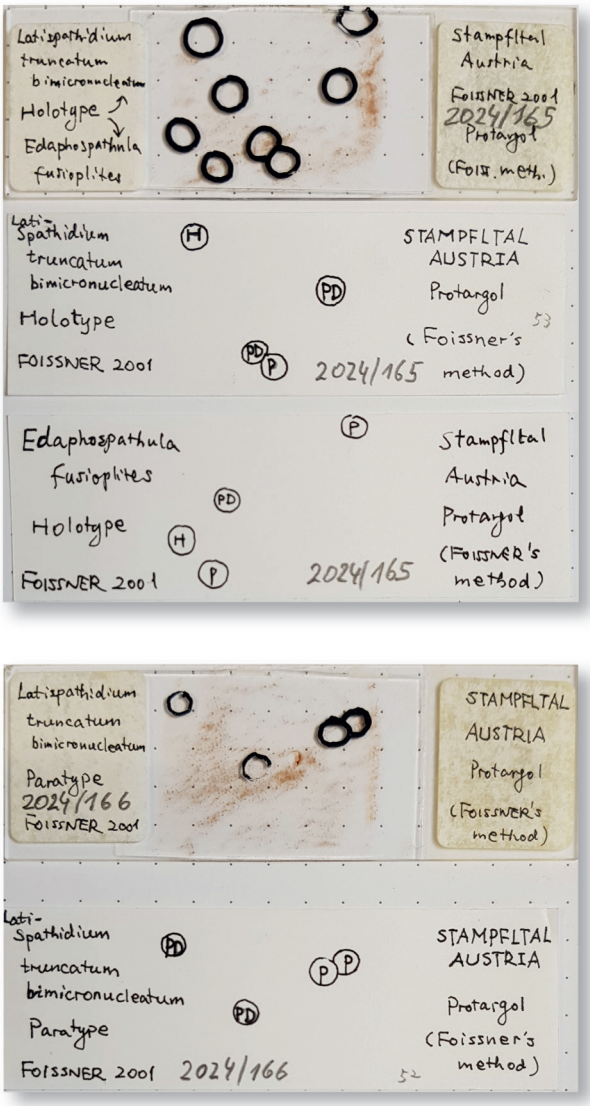

Fig. 7.4h–l *Latispathidium truncatum bimicronucleatum* Foissner et al., 2005 (originals. Protargol slides). **h, i:** Slide (h) and protocol (i) containing holotype (H), paratypes (P), and paratypes drawn (PD). Accession number (LI): 2024/165. **j:** Protocol of slide 2024/165 (h), which simultaneously contains the holotype specimen of *Edaphospathula fusioplites* (Foissner et al., 2005) Foissner & Xu, 2007. **k, l:** Slide (k) and protocol (l) containing paratypes drawn (PD) and paratypes (P) of *Latispathidium truncatum bimicronucleatum*. Accession number (LI): 2024/166.

from *Spathidium aciculare* Foissner et al., 2002 (p. 258; see Chapter 3, that is, Foissner et al. 2025b) and *Spathidium etoschense* Foissner et al., 2002 (Fig. 55g in Foissner et al. 2002), by the special location of the dorsal brush. Furthermore, these species differ also in several main morphometrics, especially the length of the oral bulge and of dorsal brush rows 1 and 2, and the number of circumoral dikinetids between each two somatic kineties (on average 2.4 vs. 5.0). Nonetheless, several main features of *Spathidium aciculare*, for instance, body shape, size, and nuclear pattern match those of *Latispathidium truncatum truncatum* (Stokes, 1885) suggesting that *Spathidium aciculare* might be a junior synonym, especially, if further investigations disprove our hypothesis that the species of Stokes (1885) has long, rod-shaped extrusomes, as explained above (Table 7.2); unfortunately, Foissner et al. (2002) did not include *Latispathidium truncatum truncatum* in the species comparison.

Description: Body size 70–110 × 10–20 μm in vivo, usually near 100 × 15 μm, as calculated from some in vivo measurements and the morphometric data (Table 7.1); length:width ratio 4.2–7.6:1, on average near 6:1 both in vivo and in protargol preparations. Body size

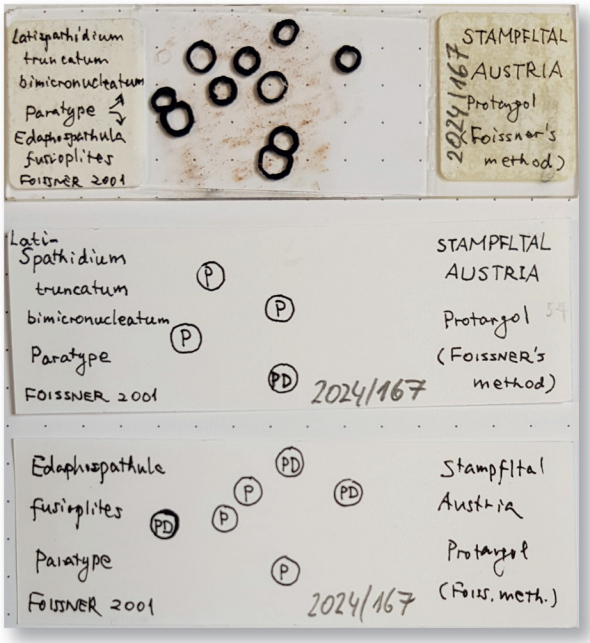

Fig. 7.4m–o *Latispathidium truncatum bimicronucleatum* Foissner et al., 2005 (originals. Protargol slides). **m, n:** Slide (m) and protocol (n) containing paratypes (P) and paratypes drawn (PD). Accession number (LI): 2024/165. **o:** Protocol of slide 2024/167 (m), which simultaneously contains the paratypes and paratypes drawn (PD) of *Edaphospathula fusioplites* (Foissner et al., 2005) Foissner & Xu, 2007.

and shape similar to *Epispathidium terricola* Foissner, 1987 (see chapter 6, Foissner et al. 2025a; now *Spathidium terricola* (Foissner, 1987) Jang et al., 2017), but smaller and more slender, frequently almost cylindrical or obclavate because oral bulge hardly widened and on average shorter than widest trunk region by one third; neck in vivo typically more pronounced ventrally than dorsally; anterior body end obliquely truncate, posterior one narrowly rounded; flattened only in oral region (Fig. 7.3a, i, k, l, q, 7.4a–c); very flexible but acontractile. Macronucleus in middle third of body, in most specimens rather distinctly spiralized and, interestingly, distinctly flattened, in some specimens even ribbon-like (>3:1); rarely highly tortuous or lobate, about 50 µm long when despiralized; contains several large and small nucleoli. Invariably two ellipsoidal to broadly ellipsoidal micronuclei (on average 3 × 2 µm in protargol preparations), one each near or attached to ends of macronucleus, an unusual feature in spathidiids (Fig. 7.3a, i, k, l, p, q, 7.4a–c, f). Contractile vacuole in rear body end, several excretory pores in pole area. Extrusomes accumulated in oral bulge and scattered in cytoplasm, inconspicuous in vivo because acicular and about 7.0 × 0.5 µm in size (Fig. 7.3a, d); those attached to oral bulge never impregnate with the protargol method used, while a certain, acicular, 4.0–4.5 × 0.7–0.8 µm-sized cytoplasmic developmental stage impregnates faintly. Released extrusomes of typical toxicyst structure, about 15 µm long (Fig. 7.3e). Cortex very flexible, contains about five granule rows between each two kineties; granules minute, that is, approximately 0.4 × 0.2 µm, but rather refractive and thus distinct in vivo. Cytoplasm colourless, usually contains many lipid droplets 1–5 µm across; rarely occur specimens with a large food vacuole containing ciliate prey. Swims rapidly by rotation about main body axis.

Cilia 8–9 µm long in vivo, arranged in an average of 14 equidistant, bipolar, ordinarily spaced, but rather loosely ciliated rows abutting on circumoral kinety in acute (on right side) or almost right angles (on left side), as typical for *Spathidium*. Dorsal brush perfectly

on left side of cell, rarely, it is located slightly dorsolaterally (Fig. 7.3j, l, m, p, q, 7.4a–d, g); dikinetidal and three-rowed, occupying 19% of body length on average, a fourth row occurs in one out of more than 50 specimens analyzed (Fig. 7.3q); all rows with one or few ordinary cilia anteriorly, continue as somatic kineties posteriorly; bristles up to 4–5 µm long in vivo, length gradually decreases posteriorly, anterior bristle of dikinetids longer than posterior. Brush rows 1 and 2 of similar length, each composed of 15 dikinetids on average; row 3 invariably distinctly shorter than rows 1 and 2, comprises an average of only six dikinetids, but has a monokinetidal tail of 1 µm long bristles extending to mid-body, occasionally to near body end (Fig. 7.3a, f, j, l, m, 7.4a–d, g; Table 7.1).

Oral bulge obliquely slanted by about 45°, conspicuously short, that is, only about two thirds as long as widest trunk region; slightly cuneate in frontal view; about 3 µm high and 3 µm wide in vivo, dorsally slightly higher than ventrally; contains rows of very densely spaced cortical granules, forming conspicuous, ridge-like accumulations (Fig. 7.3b, c). Circumoral kinety at base of oral bulge and also slightly cuneate, composed of ordinarily spaced dikinetids (two or three, on average 2.4 between two kineties each) forming continuous row; each dikinetid associated with a cilium, a fibre extending into the oral bulge, and a basket rod. Oral basket hardly recognizable in vivo and also inconspicuous in protargol preparations (Fig. 7.3i–m, p, q).

Occurrence and ecology: The type locality of *Latispathidium truncatum bimacronucleatum* is a *Pinus nigra* forest soil in the Stampfltal (47°53'N 16°02'E) near Vienna, Austria, where it was moderately abundant (Foissner et al. 2005). This species is well adapted to the soil habitat by its slender body. No further records substantiated by morphological data published.

Latispathidium arboricola nov. spec.

(Fig. 7.5a–f, j–p, 7.6a–v, Table 7.3)

Nomenclature: The species-group name *arboricola* (Latin; *arboricole*, tree-dwelling; details, see Hentschel & Wagner 1996, p. 99) refers to the habitat (see below) where the species was discovered.

Diagnosis (based on two populations from Costa Rica): Body size about 90 × 12 µm in vivo. Very narrowly spatulate and more or less distinctly obclavate with oblique oral bulge about two thirds as long as widest trunk region. On average 17 macronucleus nodules and two micronuclei. Extrusomes ovate, circa 1.5 × 0.7 µm. On average seven somatic ciliary rows, three anteriorly differentiated to conspicuous, heterostichad (rows 1 and 3 shortened by about 40%), short (only ~11% of body length) dorsal brush with up to 25 µm long bristles in anterior part of row 3.

Type locality: Moss and lichens from coco palms at the seacoast near the hotel Punta Cocles (09°40'N 82°40'W), that is, about 48 km south of the town of Puerto Viejo, Limon, Caribbean southeast coast of Costa Rica.

Type material: The protargol slide (Fig. 7.6i, j; accession number 2024/168) containing the holotype specimen (Fig. 7.5f, j, k) and three paratype slides (Fig. 7.6k–p; 2024/169, 170, 171) of the population from the type locality have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI). Three voucher slides (Fig. 7.6q–v; 2024/172,

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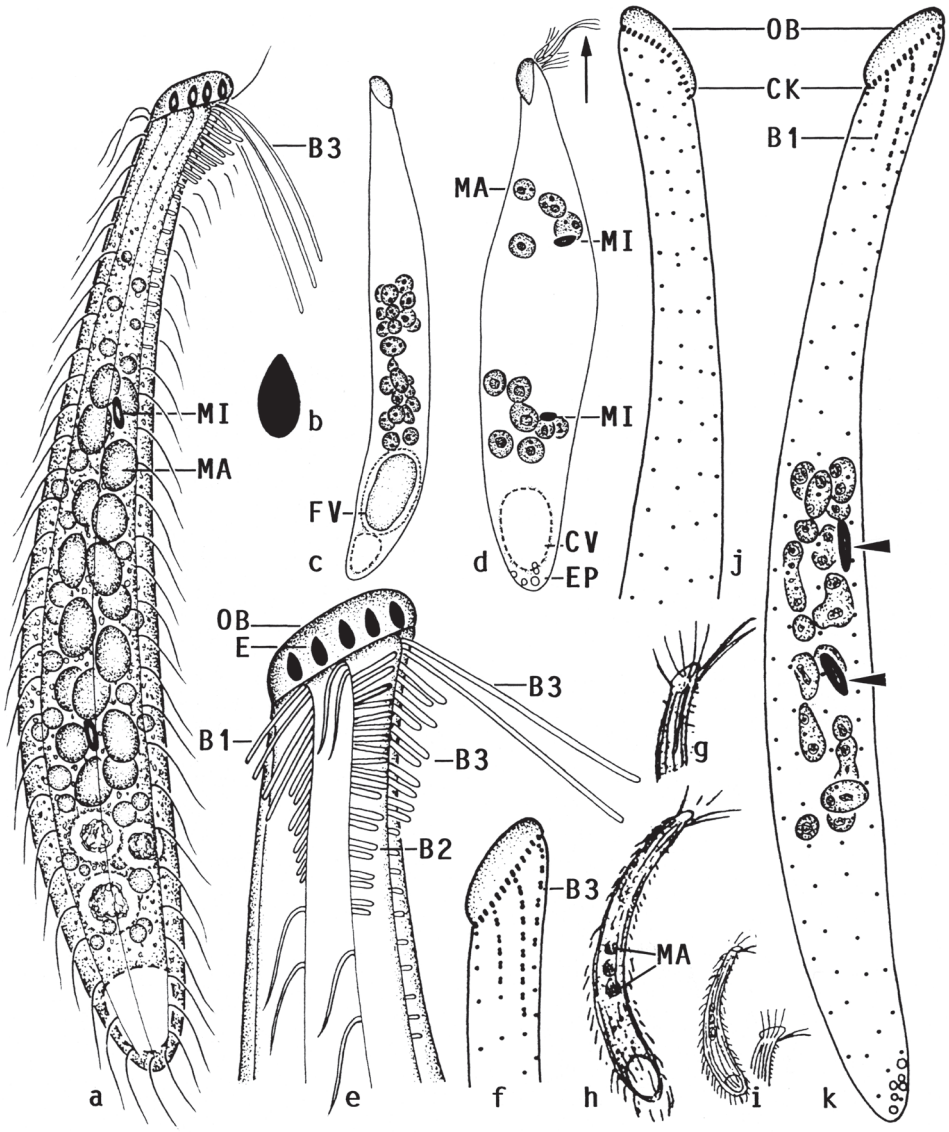

Fig. 7.5a–f, j, k *Latispathidium arboricola* nov. spec., type population (originals. a, b, e, from life; c, d, f, j, k, protargol preparation). **a, e:** Left side views of representative specimens, 90 µm. Note the complex dorsal brush with up to 25 µm long bristles. **b:** Extrusome, length 1.5 µm. **c, d:** Nuclear patterns, 76 µm (c), 80 µm (d). Arrow marks long bristles of brush row 3, well recognizable in this preparation. **f, j, k:** Right and left side ciliary pattern and nuclear apparatus of holotype specimen, 85 µm. Arrowheads mark micronuclei. B1–B3 – dorsal brush (rows), CV – contractile vacuole, E – extrusomes, EP – excretory pores, FV – food vacuole, MA – macronucleus nodules, MI – micronuclei, OB – oral bulge.

Fig. 7.5g–i *Spathidium falciforme* (Penard, 1922) Kahl, 1930 (g, h, from Penard 1922; i, after Penard 1922 from Kahl 1930b). This species resembles *Latispathidium arboricola* but has only two to three macronucleus nodules. MA – macronucleus nodules.

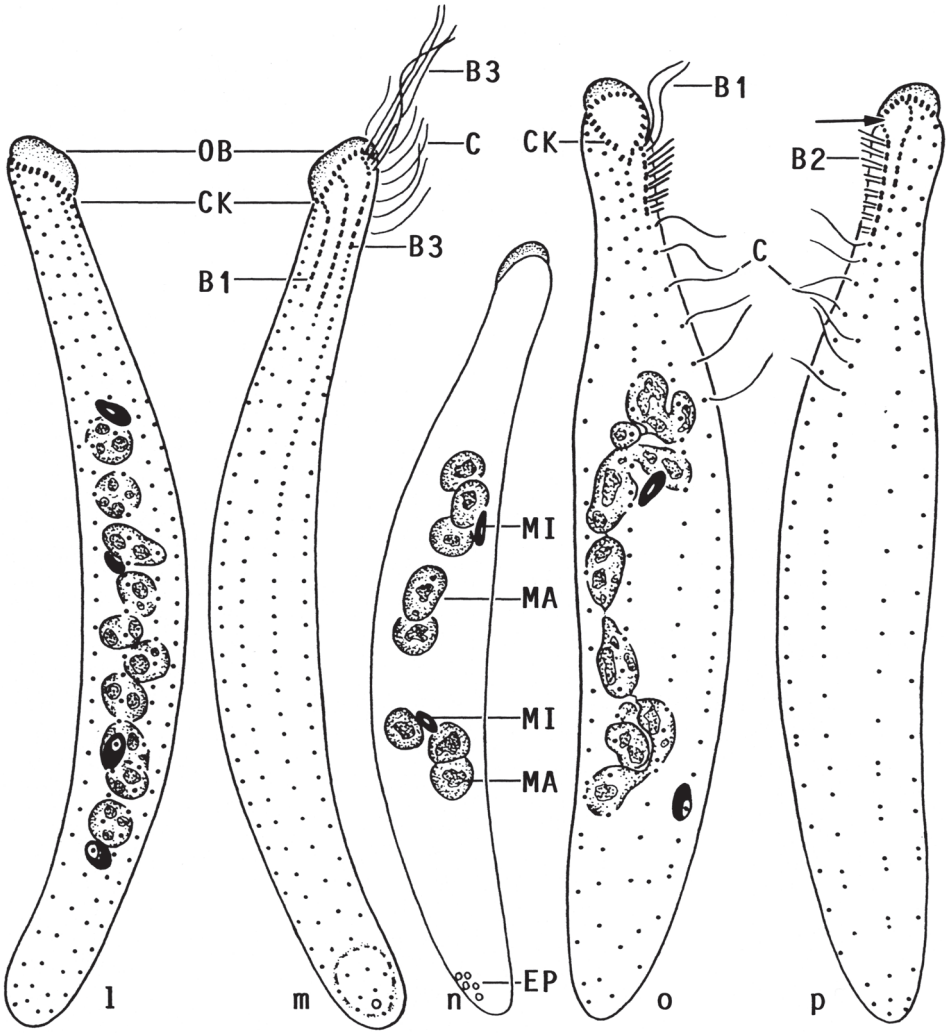

Fig. 7.5l–p *Latispathidium arboricola* nov. spec., population from Monte Verde, Costa Rica (originals. Protargol preparation). **l, m:** Right and left side ciliary pattern and nuclear apparatus of a representative specimen, 61 μm. The dorsal brush is on the left side of the cell, and the long bristles of brush row 3 are recognizable even in the preparations (although strongly shrunken, like the somatic cilia, as usual with this preparation procedure). **n:** Nuclear pattern of another specimen, 66 μm. **o, p:** Ventral and dorsal view of another well-impregnated specimen, 64 μm. Note ordinary cilia or bristles at anterior end of brush row 1. Brush rows 2 and 3 form a spatulate pattern (arrow) because they are V-like spread anteriorly (cp. Fig. 7.5m). B – dorsal brush, B1–3 – dorsal brush rows, C – ordinary somatic cilia, CK – circumoral kinety, EP – excretory pores, MA – macronucleus nodules, MI – micronuclei, OB – oral bulge.

173, 174) of the population from a horse pasture (see occurrence and ecology) have been deposited at the same museum.[6]

[6] Note by H. Berger: W. Foissner designated the specimens from the type locality as holotype and paratypes. Thus, the slides designated as "voucher" (population from the horse pasture) do not belong to the type series (for details, see

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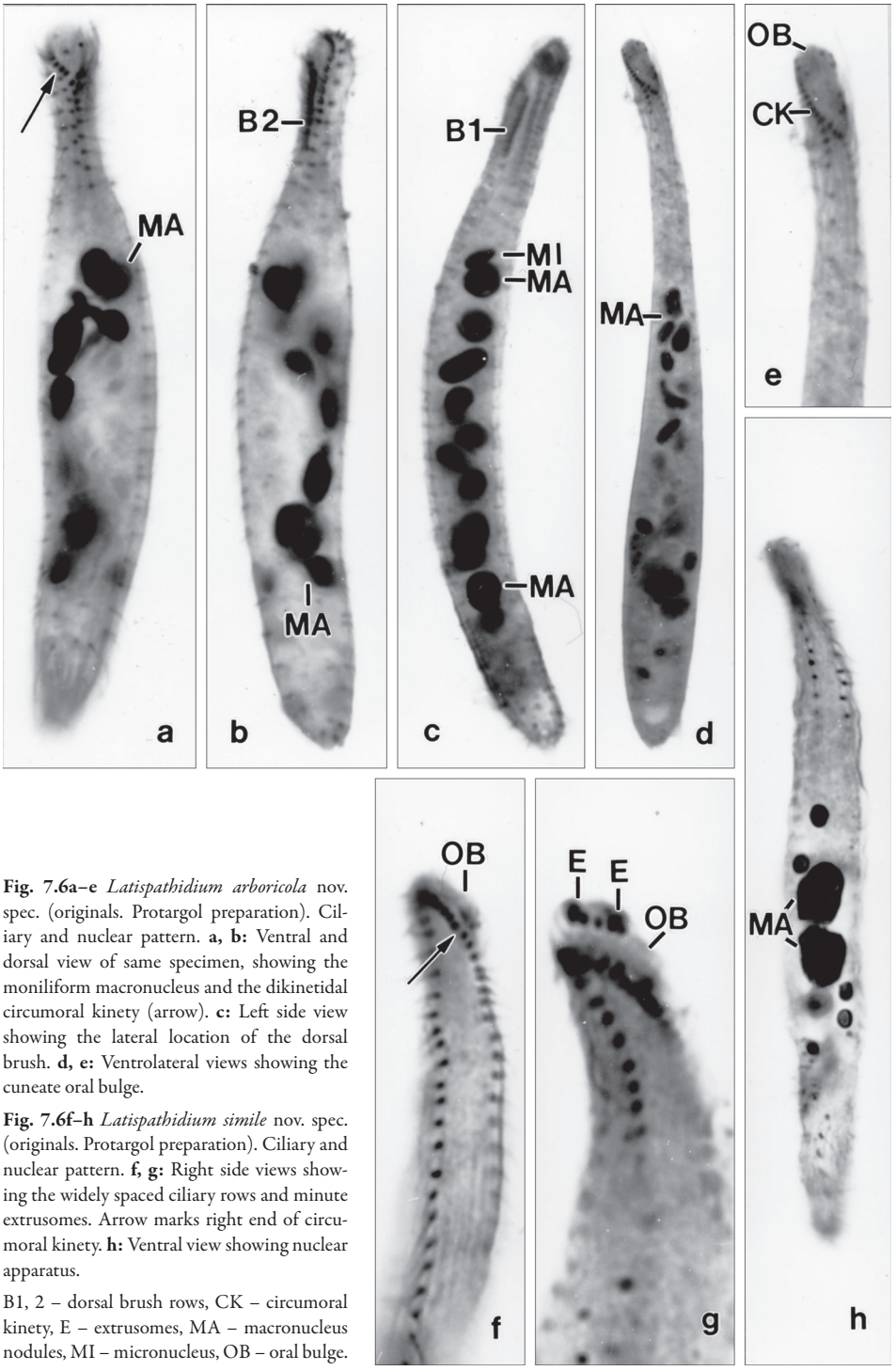

Fig. 7.6a–e *Latispathidium arboricola* nov. spec. (originals. Protargol preparation). Ciliary and nuclear pattern. **a, b:** Ventral and dorsal view of same specimen, showing the moniliform macronucleus and the dikinetidal circumoral kinety (arrow). **c:** Left side view showing the lateral location of the dorsal brush. **d, e:** Ventrolateral views showing the cuneate oral bulge.

Fig. 7.6f–h *Latispathidium simile* nov. spec. (originals. Protargol preparation). Ciliary and nuclear pattern. **f, g:** Right side views showing the widely spaced ciliary rows and minute extrusomes. Arrow marks right end of circumoral kinety. **h:** Ventral view showing nuclear apparatus.

B1, 2 – dorsal brush rows, CK – circumoral kinety, E – extrusomes, MA – macronucleus nodules, MI – micronucleus, OB – oral bulge.

ZooBank registration: urn:lsid:zoobank.org:act:999D32E1-3B7F-425C-BFEE-E5AAB26F4D7D

Remarks: *Latispathidium arboricola* highly resembles *Arcuospathidium namibiense* Foissner et al., 2002, except for body size (about 90 × 12 μm vs. 160 × 10 μm) and the length:width ratio (about 7.5:1 vs. 16:1); actually, the former appears as a small, stout variant of the latter (for revision of *Arcuospathidium namibiense* see Foissner & Xu 2007, p. 177). There are, however, also morphological differences, especially in details of the dorsal brush and the right side ciliary rows, which are more widely separated from the circumoral kinety in *Arcuospathidium namibiense*. Thus, both are distinct species. Size and shape of *Latispathidium arboricola* highly resemble species of the *Spathidium claviforme* group[7] which, however, have a different nuclear pattern (macronucleus reniform or a long, tortuous strand) and longer, rod-shaped or acicular extrusomes (for redescription of *Spathidium claviforme* Kahl, 1930a, p. 389, see Foissner 1987, p. 228).

Latispathidium arboricola also highly resembles *Spathidium falciforme* (Penard, 1922) Kahl, 1930 (p. 163) except for the nuclear pattern, which Penard (1922, p. 52) describes as follows: "Deux, ou trois, masses nucléaires arrondies, chacune avec un micronoyau très petit (Fig. 7.5g, h)". We cannot assume misobservation because Penard (1922) was a careful worker and his species was later recorded by several authors, though these reports are not substantiated by appropriate data. Likely, *Spathidium falciforme* belongs to the spathidiids with two macronucleus nodules and a micronucleus in between, as found in several *Cultellothrix* (see Foissner & Xu 2007, p. 267 and Chapter 13, that is, Berger et al. 2025b) and *Latispathidium* species. Thus, we classify our multinucleate populations as a new species.

Description: Two populations of *Latispathidium arboricola* were investigated from distinctly different habitats in Costa Rica; however, in vivo observations are available only from specimens of the type locality. Both populations had low abundance in the non-flooded Petri dish cultures, that is, only 14 specimens, including two dividing cells, were found in the eight slides from the type locality, and seven cells occurred in the slides from the second site. Nevertheless, the two populations match well both in morphology and morphometry (Fig. 7.5j–m; Table 7.3). Thus, the data are combined in the diagnosis and description, but not in Table 7.3.

Body size 60–120 × 8–25 μm in vivo, usually near 90 × 12 μm, specimens from type locality slightly larger than those from second site; length:width ratio 3.5–10.6:1 in preserved specimens, on average about 7.5:1 both in vivo and protargol preparations (Table 7.3). Body very narrowly spatulate or obclavate and curved dorsally with convex ventral side; anterior end (oral bulge) slanted, posterior narrowly rounded, rarely bluntly pointed or inflated by the contractile vacuole; widest in or behind mid-body, rarely distinctly flattened laterally (Fig. 7.5a, c, k, l, n, o, 7.6d). Nuclear apparatus in middle quarters of cell, with a tendency of nodules to form a cluster each anteriorly and posteriorly in type locality specimens, where two early dividers have perfectly scattered macronucleus nodules, likely representing the ordinary pattern (Fig. 7.5a, c, d, k, l, n, o, 7.6a–d; Table 7.3); on average 17 macronucleus nodules, usually scattered in specimens from type locality, while frequently in line and some even connected by a fine strand in specimens from second site; individual nodules globular

ICZN 1999, Articles 72.4.1, 72.4.6).

[7] This group was not characterised in the raw manuscript by W. Foissner.

Fig. 7.6i–n *Latispathidium arboricola* nov. spec. (originals. Protargol slides). **i, j:** Slide (i) and protocol (j) containing holotype (H), paratypes (P), and paratypes drawn (PD). Accession number (LI): 2024/168. **k–n:** Slides (k, m) and protocols (l, n) containing paratypes (P) and paratypes drawn (PD). Accession numbers (LI): 2024/169, 170.

to ellipsoidal, about 5 × 3 µm in size, contain few nucleoli up to 2 µm across. Two ellipsoid to lanceolate micronuclei near macronucleus nodules; four micronuclei occur in a specimen from the second site (Fig. 7.5l). Contractile vacuole in rear body end, some terminally to slightly subterminally located excretory pores. Oral bulge extrusomes ovate and about 1.5 × 0.6–0.8 µm in size, although minute rather conspicuous because compact and thus highly refractive (Fig. 7.5a, b, e); rarely faintly impregnate with the protargol method used. Cortex flexible, cortical granulation not studied. Cytoplasm colourless, contains some lipid droplets 1–3 µm across and up to 12 µm-sized vacuoles with prey remnants. Movement without peculiarities.

Somatic cilia about 8 µm long in vivo, shrunken to 4 µm in preparations, as usual; arranged in an average of seven equidistant, bipolar,

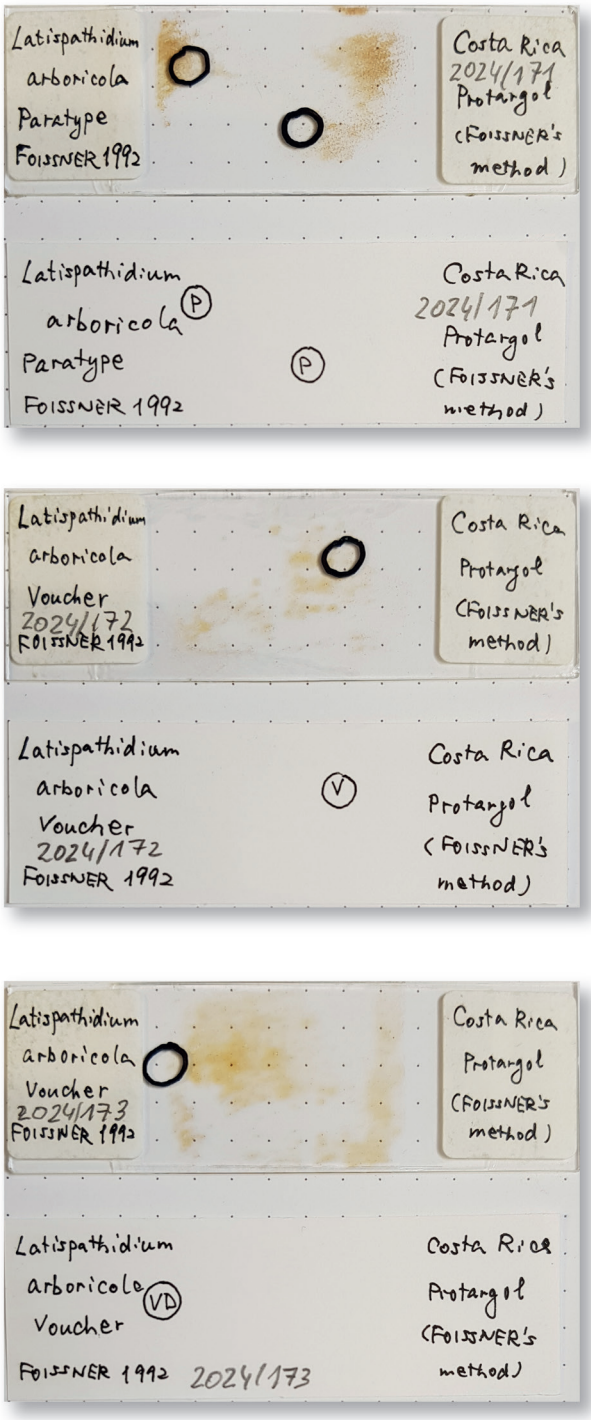

Fig. 7.6o–t *Latispathidium arboricola* nov. spec. (originals. Protargol slides). **o, p:** Slides (o) and protocol (p) containing paratypes (P). Accession numbers (LI): 2024/171. **q–t:** Voucher slides (q, s) and protocols (r, t) of population from a horse pasture in Costa Rica (V, voucher specimen; VD, voucher specimen drawn). Accession numbers (LI): 2024/172, 173.

loosely ciliated rows abutting on circumoral kinety, except for the right side rows. No ciliary rows between ventral kinety and brush row 1 because brush occupies left side of cell (Fig. 7.5a, e, j–p, 7.6a, b; Table 7.3). Dorsal brush three-rowed and conspicuous, though occupying only 11% of body length, because having 2–4, on average three 20–25 µm long bristles at anterior end of row 3, an outstanding feature also occurring in *Arcuospathidium namibiense* Foissner et al., 2002 (Fig. 7.5a, e, 7.6b, c). Bristles well recognizable also in the protargol preparations, but shrunken to about 10 µm, like the somatic cilia described above (Fig. 7.5d, m). Brush rows slightly V-like spread and more or less distinctly curved ventrally at anterior end; all rows commence with one or a few monokinetids and continue as somatic kineties posteriorly (Fig. 7.5a, e, f, k, m, o, p, 7.6b, c; Table 7.3). Dorsal brush row 1 right of

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Table 7.3 Morphometric data on *Latispathidium arboricola* nov. spec. from Costa Rican type locality (upper line; original data) and another Costa Rican site (middle line; original data). The lower line combines the two populations[a]

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Body, length	81.4	77.0	10.8	3.1	13.3	66.0	102.0	12
	68.4	66.0	11.3	4.3	16.5	55.0	88.0	7
	76.6	76.0	12.5	2.9	16.3	55.0	102.0	19
Body, width	11.7	10.0	4.1	1.2	35.3	8.0	22.0	12
	9.0	9.0	1.4	0.5	15.7	7.0	11.0	7
	10.7	10.0	3.6	0.8	33.5	7.0	22.0	19
Body length:width, ratio	7.6	8.0	2.4	0.7	30.9	3.5	10.6	12
	7.7	7.9	1.4	0.5	17.7	5.8	9.8	7
	7.7	7.9	2.0	0.5	26.2	3.5	10.6	19
Oral bulge, length	6.8	7.0	1.1	0.3	16.3	5.0	8.0	12
	6.4	6.0	1.3	0.5	20.7	5.0	8.0	7
	6.7	7.0	1.2	0.3	17.7	5.0	8.0	19
Oral bulge length:body width, ratio	0.6	0.7	0.2	0.1	30.0	0.3	0.9	12
	0.7	0.7	0.1	0.1	20.4	0.5	0.9	7
	0.7	0.7	0.2	-	26.4	0.3	0.9	19
Oral bulge, width	3.4	3.5	–	–	–	3.0	4.0	7
	3.3	–	–	–	–	3.0	3.5	2
	3.3	3.5	–	–	–	3.0	4.0	9
Oral bulge, height	2.2	2.0	–	–	–	2.0	3.0	12
	1.7	1.5	–	–	–	1.5	2.0	7
	2.0	2.0	0.4	0.1	20.9	1.5	3.0	19
Circumoral kinety to last dikinetid of brush row 1, distance	4.9	5.0	0.7	0.2	15.1	4.0	6.0	10
	4.6	5.0	1.3	0.5	27.8	2.0	6.0	7
	4.8	5.0	1.0	0.2	20.4	2.0	6.0	17
Circumoral kinety to last dikinetid of brush row 2, distance	8.5	9.0	1.3	0.4	14.9	6.0	10.0	10
	8.9	8.0	1.2	0.5	13.7	8.0	11.0	7
	8.6	9.0	1.2	0.3	14.1	6.0	11.0	17
Circumoral kinety to last dikinetid of brush row 3, distance	5.7	6.0	0.9	0.3	16.6	4.0	7.0	10
	5.6	6.0	–	–	–	5.0	6.0	7
	5.6	6.0	0.8	0.2	13.9	4.0	7.0	17
Anterior body end to anteriormost macronucleus nodule, distance	23.0	24.0	6.8	2.0	29.8	14.0	35.0	12
	20.4	20.0	4.6	1.8	22.8	15.0	30.0	7
	22.1	20.0	6.1	1.4	27.8	14.0	35.0	19
Macronucleus figure, length	35.3	30.5	9.0	2.6	25.4	27.0	54.0	12
	33.4	30.0	5.3	2.0	15.7	30.0	42.0	7
	34.6	30.0	7.7	1.8	22.2	27.0	54.0	19
Macronucleus nodules, length	4.5	4.5	1.6	0.5	36.1	2.0	7.0	12
	3.9	4.0	0.6	0.2	15.5	3.0	5.0	7
	4.3	4.0	1.3	0.3	31.4	2.0	7.0	19
Macronucleus nodules, width	2.9	3.0	1.0	0.3	34.2	2.0	5.0	12
	2.4	2.0	–	–	–	2.0	3.0	7
	2.7	3.0	0.9	0.2	31.9	2.0	5.0	19
Macronucleus nodules, number	17.0	18.0	4.7	1.3	27.5	8.0	25.0	12
	13.4	11.0	5.5	2.1	40.8	9.0	23.0	7
	15.7	17.0	5.1	1.2	32.8	8.0	25.0	19

Table 7.3 Continued

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Micronuclei, length	3.2	3.0	–	–	–	2.5	4.0	8
	2.4	2.0	–	–	–	2.0	3.0	7
	2.8	3.0	0.6	0.2	23.2	2.0	4.0	15
Micronuclei, width	1.3	1.4	–	–	–	1.0	1.5	8
	1.3	1.5	–	–	–	1.0	1.5	7
	1.3	1.5	–	–	–	1.0	1.5	15
Micronuclei, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	8
	2.3	2.0	0.8	0.3	33.1	2.0	4.0	7
	2.1	2.0	0.5	0.1	24.2	2.0	4.0	15
Circumoral dikinetids, number	24.8	25.0	–	–	–	24.0	25.0	4
	22.5	22.5	2.4	1.2	10.6	20.0	25.0	4
	23.6	24.5	2.0	0.7	8.4	20.0	25.0	8
Somatic kineties, number	7.2	7.0	0.9	0.3	12.2	6.0	8.0	11
	7.4	8.0	1.0	0.4	13.1	6.0	8.0	7
	7.3	8.0	0.9	0.2	12.3	6.0	8.0	18
Basal bodies in a right-side somatic kinety, number	32.0	33.5	3.7	1.5	11.5	25.0	35.0	6
	33.9	33.0	5.8	2.2	17.2	26.0	43.0	7
	33.0	33.0	4.8	1.3	14.7	25.0	43.0	13
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	7
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	18
Dikinetids in brush row 1, number	4.7	5.0	–	–	–	4.0	5.0	9
	4.9	5.0	2.0	0.7	40.2	1.0	7.0	7
	4.8	5.0	1.3	0.3	27.2	1.0	7.0	16
Dikinetids in brush row 2, number	8.7	9.0	0.9	0.3	10.0	7.0	10.0	9
	9.9	8.0	2.8	1.1	28.4	7.0	14.0	7
	9.2	9.0	2.0	0.5	21.5	7.0	14.0	16
Dikinetids in brush row 3, number	5.0	5.0	0.7	0.2	14.1	4.0	6.0	9
	5.9	6.0	0.9	0.3	15.4	5.0	7.0	7
	5.4	5.0	0.9	0.2	16.5	4.0	7.0	16

[a] Data based on mounted and protargol-prepared (Foissner's method) specimens from non-flooded Petri dish cultures. All well preserved cells available were used. 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.

midline of left cell side, composed of an average of five dikinetids with some up to 10 μm long cilia or bristles anteriorly; longest row 2 in midline of left cell side, composed of about nine dikinetids with bristles decreasing in length from about 5 μm anteriorly to 2 μm posteriorly; row 3 left of midline of left cell side, composed of an average of six dikinetids with bristles as described for row 2, anterior tail composed of up to 25 μm long bristles, as described above, posterior tail extends to second third of body with 1 μm long bristles.

Oral bulge slanted by 25–45°, inconspicuous because shorter by 30% than widest trunk region, less than 3 μm high, and indistinctly separate from body proper; surface flat to slightly

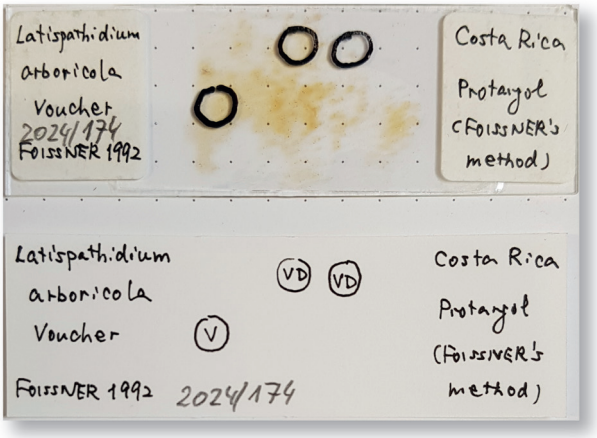

Fig. 7.6u, v *Latispathidium arboricola* nov. spec. (originals. Protargol slides). **u, v:** Voucher slide (u) and protocol (v) of a population from a horse pasture in Costa Rica (V, voucher specimen; VD, voucher specimen drawn). Accession number: 2024/174.

convex, rarely concave. Circumoral kinety obovate, composed of ordinarily spaced dikinetids (on average three kinetids between two kineties each) forming a continuous row; oral basket not recognizable (Fig. 7.5a, e, j–p, 7.6e; Table 7.3).

Occurrence and ecology: *Latispathidium arboricola* nov. spec. was found at two contrasting sites in Costa Rica, viz., (i) at the type locality (mosses and lichens on trunk of coco palms near the seacoast, moderately saline, pH 5; see description of type locality above); and (ii) in soil from a horse pasture (formerly rain forest) on the Monte Verde in the central area of the country. Possibly, the last-mentioned habitat is usually preferred, as indicated by the rather small, slender body. In the non-flooded Petri dish cultures, *Latispathidium arboricola* was very rare at both sites.

Latispathidium simile nov. spec.

(Fig. 7.6f–h, 7.7a–s, 7.8a–l, Table 7.4)

Nomenclature: The species-group name *simil·is, -is, -e* (Latin adjective [m, f, n]; similar; Hentschel & Wagner 1996, p. 546) refers to the similarity with *Edaphospathula brachycaryon* Foissner & Xu, 2007 and *Edaphospathula gracilis* Foissner & Xu, 2007 (for revision of these two species, see Foissner & Xu 2007).

Diagnosis (based on several populations): Body size about 80 × 8 µm in vivo. Body very narrowly spatulate with oblique oral bulge about two thirds as long as widest trunk region. Two macronucleus nodules with a micronucleus in between. Extrusomes ovate and about 0.8 × 0.5 µm in size. Five or six ciliary rows, three anteriorly differentiated to moderately conspicuous, strongly heterostichad (row 1 consisting of only 1 or 2 dikinetids), short (~15% of body length) dorsal brush with up to 5 µm long bristles.

Type locality: Humic soil of a fern epiphyte in the rainforest near the town of Cairns (17°S 145°E), Australia.

Type material: The protargol slide (Fig. 7.8a, b; accession number 2024/175) containing the holotype specimen (Fig. 7.7k, l) and two paratype slides (Fig. 7.8c–e; 2024/176, 177) of the population from the type locality in Australia as well as four voucher slides (Fig.

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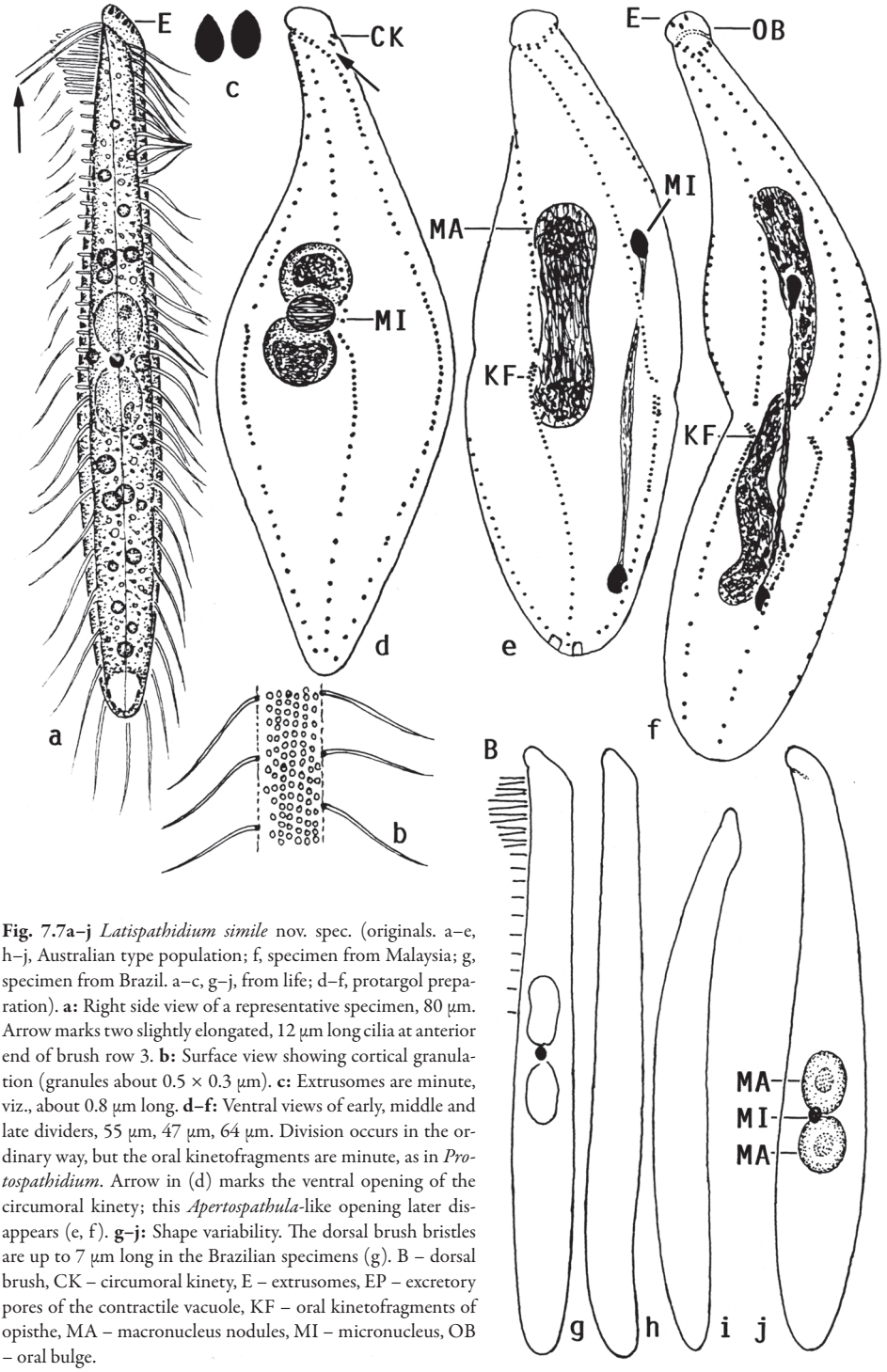

Fig. 7.7a–j *Latispathidium simile* nov. spec. (originals. a–e, h–j, Australian type population; f, specimen from Malaysia; g, specimen from Brazil. a–c, g–j, from life; d–f, protargol preparation). **a:** Right side view of a representative specimen, 80 µm. Arrow marks two slightly elongated, 12 µm long cilia at anterior end of brush row 3. **b:** Surface view showing cortical granulation (granules about 0.5 × 0.3 µm). **c:** Extrusomes are minute, viz., about 0.8 µm long. **d–f:** Ventral views of early, middle and late dividers, 55 µm, 47 µm, 64 µm. Division occurs in the ordinary way, but the oral kinetofragments are minute, as in *Protospathidium*. Arrow in (d) marks the ventral opening of the circumoral kinety; this *Apertospathula*-like opening later disappears (e, f). **g–j:** Shape variability. The dorsal brush bristles are up to 7 µm long in the Brazilian specimens (g). B – dorsal brush, CK – circumoral kinety, E – extrusomes, EP – excretory pores of the contractile vacuole, KF – oral kinetofragments of opisthe, MA – macronucleus nodules, MI – micronucleus, OB – oral bulge.

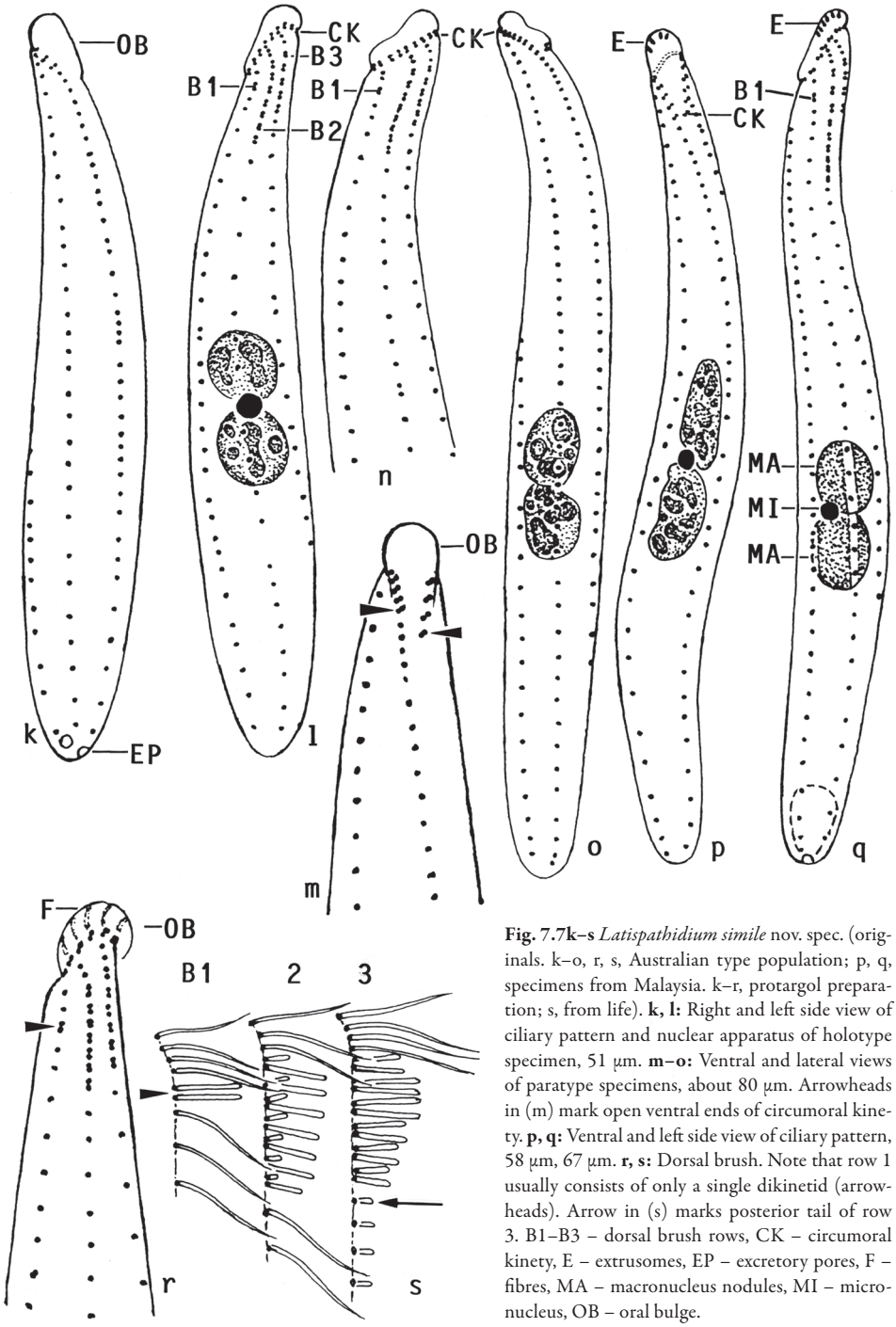

Fig. 7.7k–s *Latispathidium simile* nov. spec. (originals. k–o, r, s, Australian type population; p, q, specimens from Malaysia. k–r, protargol preparation; s, from life). **k, l:** Right and left side view of ciliary pattern and nuclear apparatus of holotype specimen, 51 µm. **m–o:** Ventral and lateral views of paratype specimens, about 80 µm. Arrowheads in (m) mark open ventral ends of circumoral kinety. **p, q:** Ventral and left side view of ciliary pattern, 58 µm, 67 µm. **r, s:** Dorsal brush. Note that row 1 usually consists of only a single dikinetid (arrowheads). Arrow in (s) marks posterior tail of row 3. B1–B3 – dorsal brush rows, CK – circumoral kinety, E – extrusomes, EP – excretory pores, F – fibres, MA – macronucleus nodules, MI – micronucleus, OB – oral bulge.

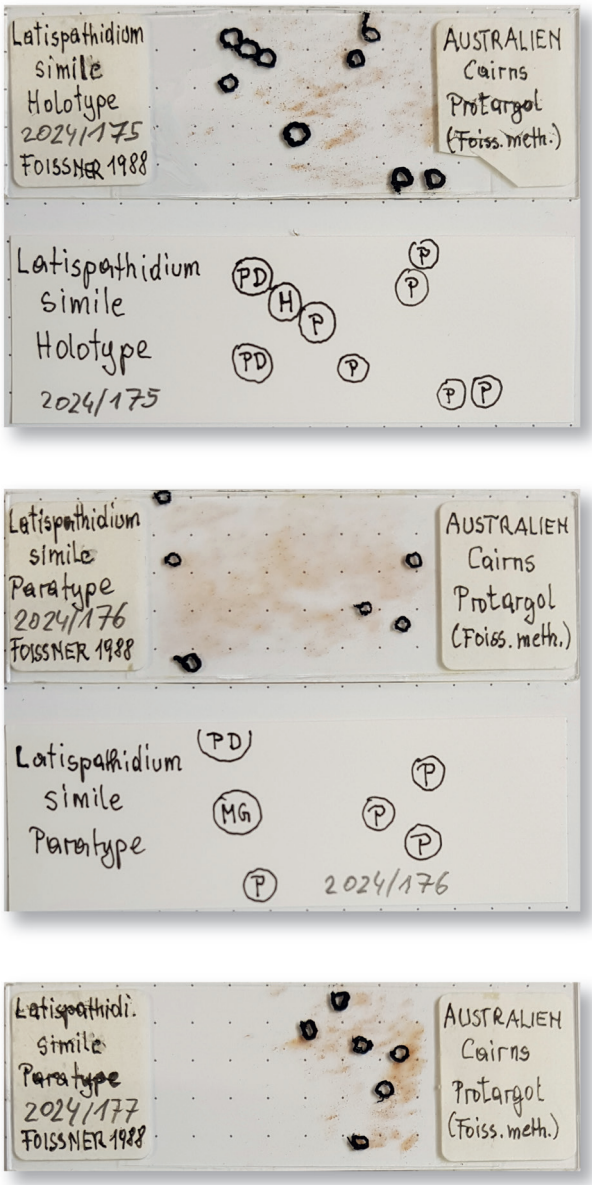

Fig. 7.8a–e *Latispathidium simile* nov. spec. (originals. Protargol slides). **a, b:** Slide (a) and protocol (b) containing holotype (H), paratypes (P), paratypes drawn (PD), and morphogenetic stage (MG). Accession number (LI): 2024/175. **c–e:** Slides (c, e) and protocol (d) containing paratypes (P) and paratypes drawn (PD). Accession numbers (LI): 2024/176, 177.

7.8f–l; 2024/178, 179, 180, 181; population from Malaysia) have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI).[8]

ZooBank registration: urn:lsid:zoobank.org:act:DA62BCF2-77CF-4FCB-9B33-6DE9 8FF9E495

Remarks: The laterally located dorsal brush classify these populations in *Latispathidium*, while the ventrally opened circumoral kinety indicates a relationship with *Apertospathula* Foissner et al., 2002 (for revision, see Foissner & Xu 2007, p. 331). As the ciliature is more spathidiid than arcuospathidiid, we classify them in *Latispathidium*. If further such species are found, they should be separated from *Latispathidium* at genus or subgenus rank.

The distinctive nuclear apparatus distinguishes *Latispathidium simile* nov. spec. from all congeners and most other spathidiids, except of some species of the genus *Neocultellothrix*

[8] Note by H. Berger: Foissner designated the specimens from Cairns, Australia (type locality) as holotype and paratypes. Thus, the slides containing specimens from Malaysia and designated as "voucher" do not belong to the type series (ICZN 1999, Articles 72.4.1, 72.4.6). The voucher slides with material from Malaysia also contain specimens of *Neocultellothrix atypica* (Wenzel, 1953) Foissner & Xu in Berger et al, 2025b (for details, see Chapter 13, that is, Berger et al. 2025b).

Fig. 7.8f–j *Latispathidium simile* nov. spec. (originals. Protargol slides). **f–j:** Voucher slides (f, h, j) and protocols (g, i) of population from Malaysia (V, voucher specimen; VD, voucher specimen drawn; MGD, morphogenetic stage drawn). Accession numbers (LI): 2024/178, 179, 180. W. Foissner designated the preparations as voucher slides and thus the "P" (for paratype specimen) and "PD" (for paratype drawn) are incorrect labels. The labelling for *Latispathidium simile* nov. spec. on the protocols was made in ink (black). These slides (f, h, j) also contain voucher material of *Neocultellothrix atypica* (Wenzel, 1953) Foissner & Xu in Berger et al., 2025b (labelling on protocols [g, i] made with pencil and thus grey).

Foissner in Berger et al., 2025b, which are distinctly stouter (Berger et al. 2025b; Foissner 2003, p. 48; Foissner & Xu 2007, p. 267). Thus, it is easily identified by two features recognizable also in vivo, namely, the nuclear apparatus and the minute extrusomes. However, the overall appearance highly resembles *Edaphospathula brachycaryon* Foissner & Xu, 2007 and *Edaphospathula gracilis* Foissner & Xu, 2007.

Description: Four populations of *Latispathidium simile* nov. spec., discovered in habitats ranging from Australia to South America, have been investigated. However, detailed studies were done only on the Australian and Malaysian specimens (Table 7.4). All populations match well, and thus the data are combined in the diagnosis and the description, but not in Table 7.4 (for a critical note on this practice, see Chapter 1, that is, Berger et al. 2025a).

Body size 50–110 × 6–12 μm in vivo, usually near 80–90 × 8–10 μm; very fragile and thus shrunken by up to 30% in protargol preparations, also changing the length:width ratio

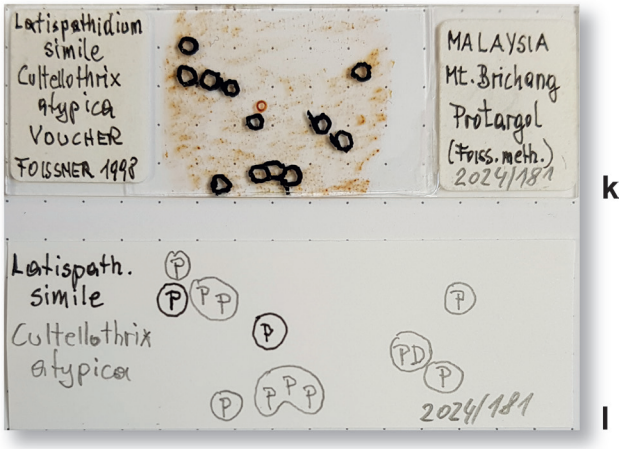

Fig. 7.8k, l *Latispathidium simile* nov. spec. (originals. Protargol slide). **k, l:** Voucher slide (k) and protocol (l) containing specimens of population from Malaysia (labelling in black). Accession number (LI): 2024/181. This slide (k) also contains voucher material of *Neocultellothrix atypica* (Wenzel, 1953) Foissner & Xu in Berger et al., 2025b (labelling in grey). Note that W. Foissner incorrectly designated the voucher specimens as paratypes (P); correct would be "V" (for voucher) (for details, see text).

from about 9:1 to near 6:1 because most specimens are more or less distinctly inflated in mid-body, that is, in the nuclear area (Table 7.4). Body very narrowly spatulate to rod-shaped, often slightly curved; anterior end (oral bulge) oblique, posterior end narrowly rounded, widest usually in or behind mid-body; hardly flattened laterally (Fig. 7.6h, 7.7a, g–j, k, o–q; Table 7.4). Nuclear apparatus in or behind mid-body, conspicuous, although hyaline, because usually composed of two globular to broadly ellipsoidal macronucleus nodules and a globular micronucleus in between or beside; other macronuclear patterns (reniform, dumbbell shaped, or two more or less distinctly connected nodules) occur in about 30% of specimens. Nucleoli scattered, globular; in vivo, a specimen with central nucleoli was observed (Fig. 7.6h, 7.7a, g, j, l, o–q; Table 7.4). Contractile vacuole in rear body end, about three excretory pores in pole area. Five to ten extrusomes attached to dorsal half of oral bulge, impregnate intensely in Malaysian specimens; very minute, that is, approximately 0.6–0.8 × 0.4–0.6 µm in vivo and about 0.5 × 0.3 µm in protargol preparations, shape thus not exactly recognizable, likely ovate or very bluntly fusiform (Fig. 7.6g, 7.7a, c, p, q,). Cortex thin and very flexible, contains about seven granule rows between each two kineties; individual granules colourless and circa 0.5 × 0.3 µm in size, more refractive in Malaysian than in Australian specimens. Cytoplasm colourless and rather hyaline, contains some lipid droplets 1–3 µm across. Swims and crawls moderately fast, performing serpentine movements.

Somatic cilia about 8 µm long in vivo, arranged in five or six equidistant, bipolar, rather loosely ciliated rows abutting on circumoral kinety; ventral row anteriorly more densely ciliated and connected with circumoral kinety. No ciliary rows between ventral row and brush row 1 because brush occupies left side of cell (Fig. 7.6f, g, 7.7a, k–q; Table 7.4). Dorsal brush three-rowed and fairly conspicuous because bristles up to 5 µm long in vivo, occupies only 12–15% of body length; conspicuous in preparations because row 1 usually consists of only one, rarely of two bristle pairs. Brush row 2 slightly longer than row 3, composed of up to 5 µm long, rod-shaped bristles gradually decreasing in length anteriorly and posteriorly; anterior bristle of dikinetids distinctly shorter than posterior. Row 3 similar to row 2, but bristles of dikinetids of same length and cilia of anterior tail elongated to 12 µm; posterior tail extends to mid-body with 2 µm long bristles (Fig. 7.7a, g, l, n, q–s; Table 7.4).

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Table 7.4 Morphometric data on *Latispathidium simile* nov. spec. from Australian type locality (upper line; original data) and Malaysia (lower line; original data)[a]

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Body, length	55.9	53.0	10.3	2.3	18.5	43.0	81.0	21
	59.6	63.0	10.7	3.6	18.0	43.0	77.0	9
Body, width	9.4	9.0	1.8	0.4	18.9	7.0	14.0	21
	10.2	10.0	3.2	1.1	30.9	6.0	15.0	9
Body length:width, ratio	6.1	5.8	1.3	0.3	21.4	3.9	9.3	21
	6.4	6.3	2.4	0.8	37.6	3.3	10.5	9
Oral bulge, length	6.4	6.0	1.1	0.2	16.7	5.0	8.0	21
	6.8	7.0	0.8	0.3	12.3	6.0	8.0	9
Oral bulge, height	2.1	2.0	0.7	0.2	35.1	1.5	4.5	21
	2.1	2.0	0.4	0.1	19.7	1.5	3.0	9
Oral bulge length:body width, ratio	0.7	0.7	0.2	0.1	23.2	0.4	1.0	21
	0.7	0.6	0.3	0.1	46.2	0.5	1.2	9
Circumoral kinety to last dikinetid	2.5	2.0	0.6	0.1	23.8	2.0	4.0	21
of brush row 1, distance	1.9	2.0	–	–	–	1.0	2.0	9
Circumoral kinety to last dikinetid	7.2	7.0	0.8	0.2	10.6	6.0	9.0	21
of brush row 2, distance	9.1	9.0	2.5	0.8	27.1	5.0	12.0	9
Circumoral kinety to last dikinetid	6.0	6.0	0.7	0.2	12.4	5.0	7.0	21
of brush row 3, distance	7.0	7.0	0.9	0.3	12.4	6.0	8.0	9
Anterior body end to anteriormost	24.6	23.0	5.5	1.2	22.2	16.0	38.0	21
macronucleus nodule, distance	27.7	27.0	5.5	1.8	19.7	18.0	34.0	9
Macronucleus figure, length	6.1	6.0	0.9	0.2	15.5	5.8	8.0	21
	5.9	6.0	0.8	0.3	13.3	5.0	7.0	9
Macronucleus nodules, width	5.1	5.0	0.6	0.1	12.3	4.0	7.0	21
	4.0	4.0	0.9	0.3	21.7	3.0	5.0	9
Macronucleus nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
	2.0	2.0	0.0	0.0	0.0	2.0	2.0	9
Micronuclei, length	1.8	2.0	–	–	–	1.5	2.5	21
	1.8	1.5	–	–	–	1.5	2.5	9
Micronuclei, width	1.7	1.5	–	–	–	1.5	2.0	21
	1.6	1.5	–	–	–	1.5	2.0	9
Micronuclei, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
	1.0	1.0	0.0	0.0	0.0	1.0	1.0	9
Circumoral dikinetids, number	11.1	11.0	1.3	0.3	11.7	9.0	13.0	21
	9.8	10.0	1.0	0.3	9.9	9.0	12.0	9
Somatic kineties, number	5.1	5.0	–	–	–	5.0	6.0	21
	5.0	5.0	0.0	0.0	0.0	5.0	5.0	9
Basal bodies in a right-side somatic	37.9	38.0	6.7	1.5	17.8	30.0	50.0	21
kinety, number	33.8	32.0	8.3	2.8	24.6	26.0	52.0	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	9
Dikinetids in brush row 1, number	1.1	1.0	–	–	–	1.0	2.0	21
	1.1	1.0	–	–	–	1.0	2.0	9
Dikinetids in brush row 2, number	7.0	7.0	1.0	0.2	13.9	5.0	9.0	21
	7.4	7.0	2.0	0.7	27.0	5.0	11.0	9
Dikinetids in brush row 3, number	5.6	5.0	0.8	0.2	14.6	4.0	7.0	21
	4.9	5.0	0.5	0.2	16.7	4.0	6.0	9

Table 7.4 Continued

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Monokinetids between circumoral kinety and brush row 3	3.0	3.0	0.8	0.2	27.9	2.0	5.0	21
	3.0	3.0	0.5	0.2	16.7	2.0	4.0	9

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

Oral bulge slanted by 25–55°, usually about 40°, inconspicuous because shorter by about 30% than widest trunk region, less than 3 μm high, and gradually merging into body proper ventrally; surface flat to slightly concave. Circumoral kinety obovate, open ventrally with right end slightly shortened or commencing at same level as left; forms continuous row composed of comparatively widely spaced dikinetids, occasionally producing an *Edaphospathula*-pattern on left side. Faintly impregnated fibres originate from circumoral dikinetids and extend into the temporary cytostome; nematodesmata not recognizable (Fig. 7.6f–h, 7.7a, g–r; Table 7.4).

Notes on cell division: Some dividers (Fig. 7.7d–f) show that (i) ontogenesis basically matches that of other spathidiids; (ii) the body becomes strongly inflated in the early stages; (iii) the macronucleus nodules fuse; (iv) the kinetofragments consist of three or four dikinetids, as in protospathidiids; and (v) the circumoral kinety of the proter becomes circular, that is, the ventral cleft disappears in middle to late dividers.

Occurrence and ecology: We found *Latispathidium simile* nov. spec. at the type locality (epiphytic fern humus, pH 3.4; found in moderate number 12 d after wetting the air-dried sample; details, see type locality above); in Malaysia (moderately abundant in soil mosses from the fog rainforest on top of Mount G. Brinchang, Cameron Highlands); the Reunion Islands (brown soil mixed with some moss and grass litter from the highlands, pH 6.1; sample kindly provided by Ing. Klee, Munich, Germany); and in Brazil (Terra firma secondary rain forest soil from bank of Rio Negro in the surroundings of Hotel Tropical at Manaus, 03°S 60°W; this is also the type locality of *Neocultellothrix tortisticha* (Foissner & Xu, 2007) Berger et al., 2025b). All these habitats are Gondwanan rainforest sites, indicating that *Latispathidium simile* prefers this environment. As it is a highly characteristic species, it is either absent or very rare in Laurasia. With the slender, highly flexible body, *Latispathidium simile* is very well adapted to live in narrow soil pores.

Latispathidium brachyoplites nov. spec.

(Fig. 7.9a–o, 7.10a–r, Table 7.5)

Nomenclature: Apposite noun composed of the Greek words *brachy* (short; Hentschel & Wagner 1996, p. 136) and *(h)oplites* (soldier, extrusome in present case; Brown 1954, p. 806); the species-group name refers to the minute, ovate extrusomes, a main feature of the species.

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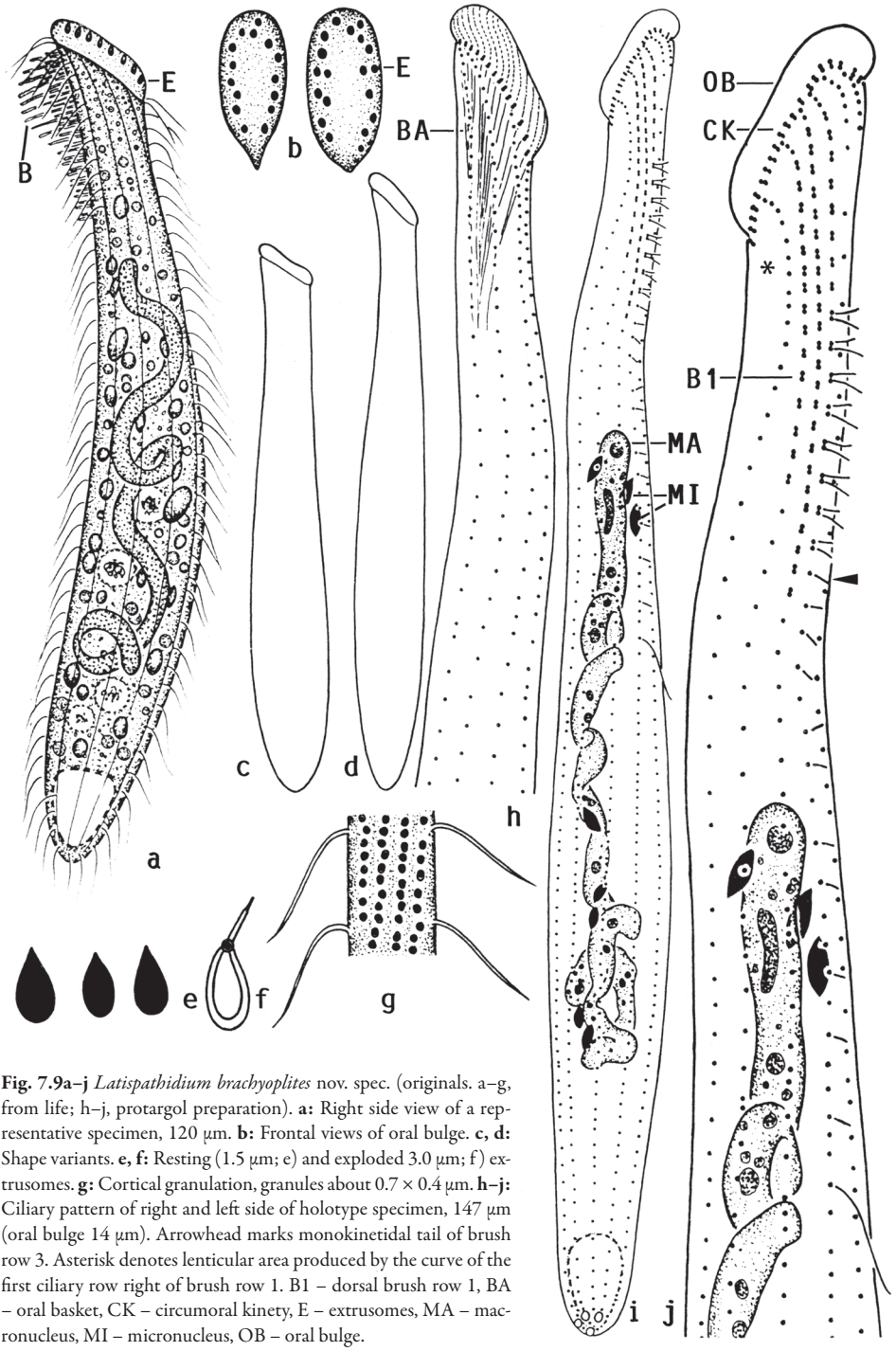

Fig. 7.9a–j *Latispathidium brachyoplites* nov. spec. (originals. a–g, from life; h–j, protargol preparation). **a:** Right side view of a representative specimen, 120 µm. **b:** Frontal views of oral bulge. **c, d:** Shape variants. **e, f:** Resting (1.5 µm; e) and exploded 3.0 µm; f) extrusomes. **g:** Cortical granulation, granules about 0.7 × 0.4 µm. **h–j:** Ciliary pattern of right and left side of holotype specimen, 147 µm (oral bulge 14 µm). Arrowhead marks monokinetidal tail of brush row 3. Asterisk denotes lenticular area produced by the curve of the first ciliary row right of brush row 1. B1 – dorsal brush row 1, BA – oral basket, CK – circumoral kinety, E – extrusomes, MA – macronucleus, MI – micronucleus, OB – oral bulge.

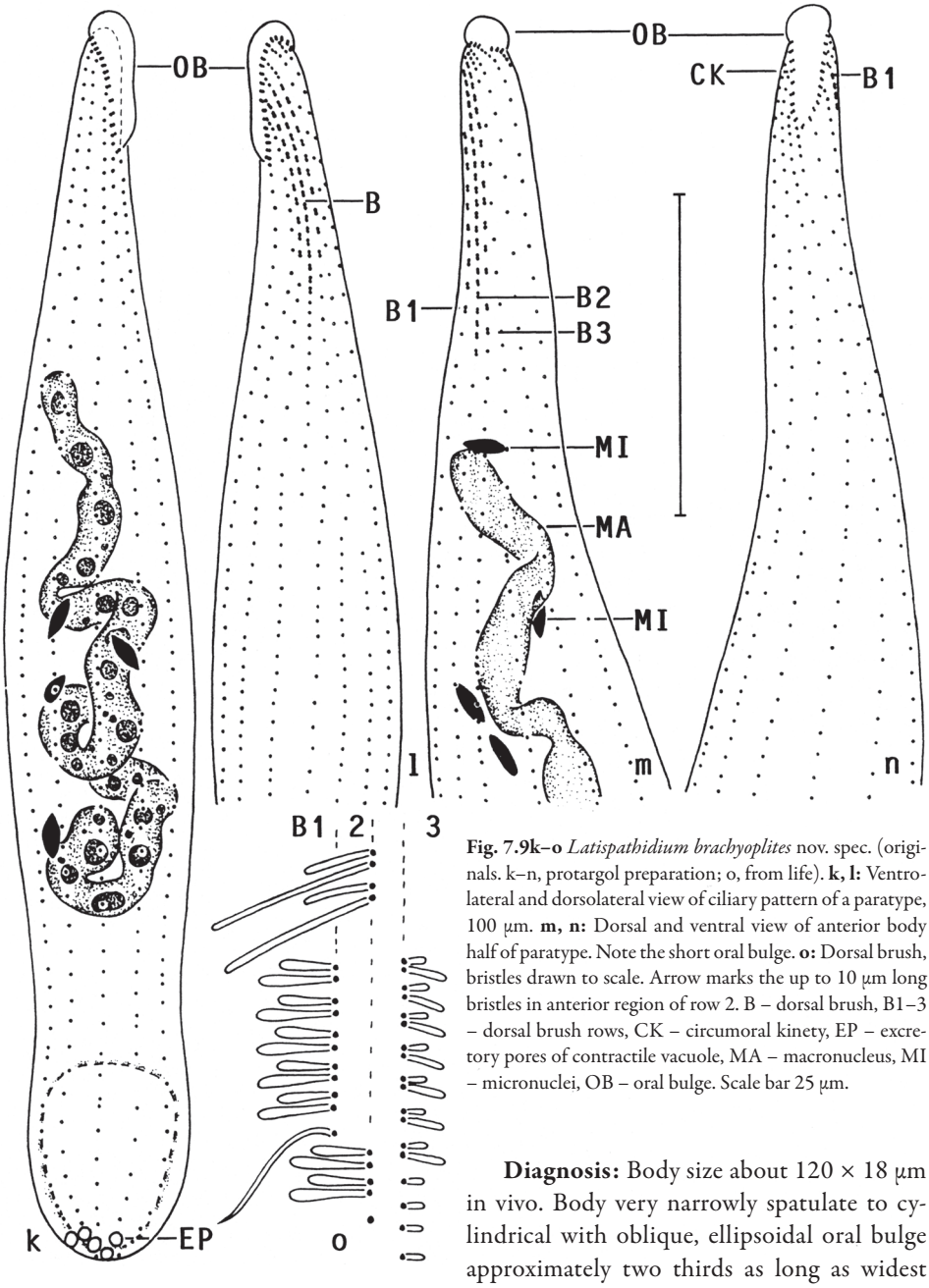

Fig. 7.9k–o *Latispathidium brachyoplites* nov. spec. (originals. k–n, protargol preparation; o, from life). **k, l:** Ventrolateral and dorsolateral view of ciliary pattern of a paratype, 100 µm. **m, n:** Dorsal and ventral view of anterior body half of paratype. Note the short oral bulge. **o:** Dorsal brush, bristles drawn to scale. Arrow marks the up to 10 µm long bristles in anterior region of row 2. B – dorsal brush, B1–3 – dorsal brush rows, CK – circumoral kinety, EP – excretory pores of contractile vacuole, MA – macronucleus, MI – micronuclei, OB – oral bulge. Scale bar 25 µm.

Diagnosis: Body size about 120 × 18 µm in vivo. Body very narrowly spatulate to cylindrical with oblique, ellipsoidal oral bulge approximately two thirds as long as widest trunk region. Macronucleus long and tortuous; multimicronucleate. Extrusomes ovate, 1.0–1.5 × 0.7–1.0 µm. On average 12 ciliary rows, three of them differentiated anteriorly to conspicuous, heterostichad (row 1 shortened by about 25%), moderately long (~20% of body length) dorsal brush with up to 10 µm long bristles in anterior region of row 2.

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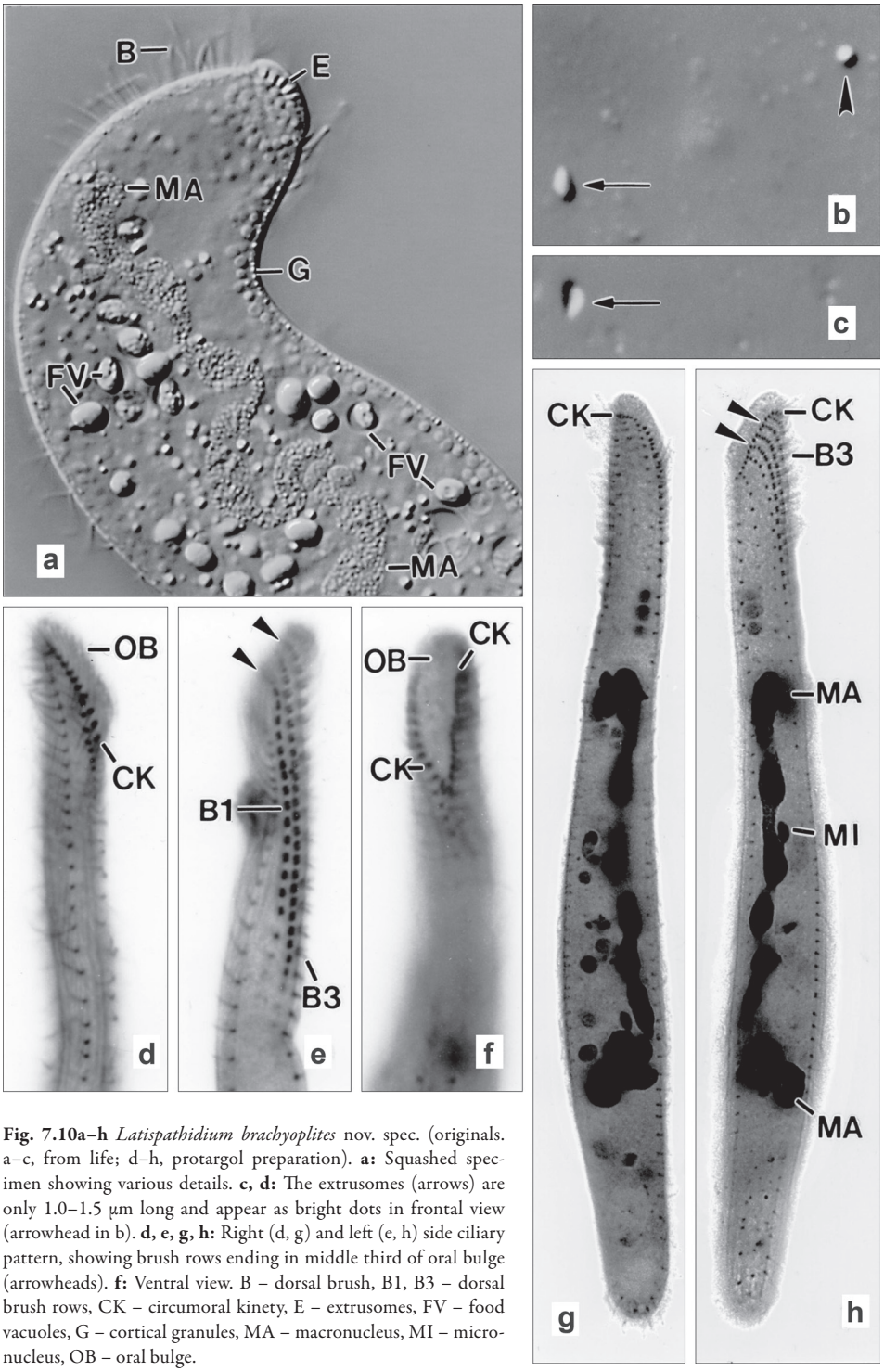

Fig. 7.10a–h *Latispathidium brachyoplites* nov. spec. (originals. a–c, from life; d–h, protargol preparation). **a:** Squashed specimen showing various details. **c, d:** The extrusomes (arrows) are only 1.0–1.5 µm long and appear as bright dots in frontal view (arrowhead in b). **d, e, g, h:** Right (d, g) and left (e, h) side ciliary pattern, showing brush rows ending in middle third of oral bulge (arrowheads). **f:** Ventral view. B – dorsal brush, B1, B3 – dorsal brush rows, CK – circumoral kinety, E – extrusomes, FV – food vacuoles, G – cortical granules, MA – macronucleus, MI – micronucleus, OB – oral bulge.

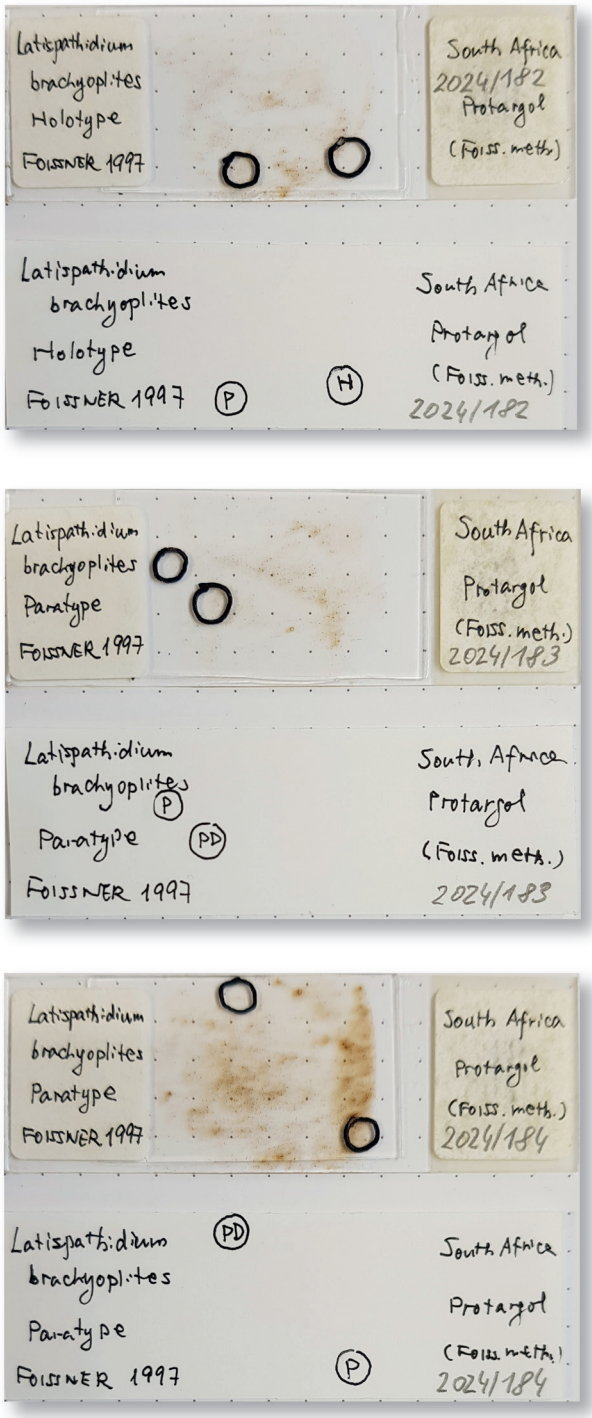

Fig. 7.10i–n *Latispathidium brachyoplites* nov. spec. (originals. Protargol slides). **i, j:** Slide (i) and protocol (j) containing holotype (H) and paratypes (P). Accession number (LI): 2024/182. **k–n:** Slides (k, m) and protocols (l, n) containing paratypes (P) and paratypes drawn (PD). Accession numbers (LI): 2024/183, 184.

Type locality: Sandy soil from a secondary deciduous forest around the picnic site "Crocodile Pool" in the Hluhluwe Game Reserve (28°S 32°E), Republic of South Africa.

Type material: The protargol slide (Fig. 7.10i, j; accession number 2024/182) containing the holotype (Fig. 7.9h–j) and four paratype slides (Fig. 7.10k–r; 2024/183, 184, 185, 186) have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI).

ZooBank registration: urn:lsid:zoobank.org:act:B6CCEF8E-2482-4232-ACE2-6D87 E096913B

Remarks: Within *Latispathidium*, only *Latispathidium truncatum* and *Latispathidium brachyoplites* have a long, tortuous macronucleus. However, both are easily distinguished by, inter alia, the extrusomes (about 7 µm and acicular vs. <2 µm and ovate) and the dorsal brush (without vs. with long bristles). These features separate *Latispathidium brachyoplites*

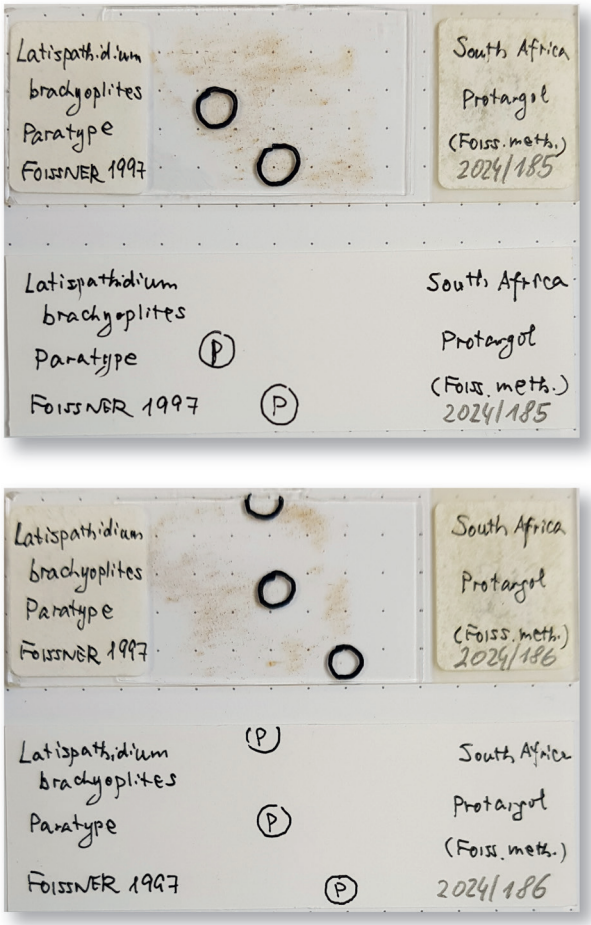

Fig. 7.10o–r *Latispathidium brachyoplites* nov. spec. (originals. Protargol slides). **o–r:** Slides (o, q) and protocols (p, r) containing paratypes (P). Accession numbers (LI): 2024/185, 186.

also from some similar species of other genera, especially *Spinispatha serpens* (Kahl, 1930b) Foissner, 2021 (previously *Protospathidium serpens* (Kahl, 1930b) Foissner, 1981), *Edaphospathula paradoxa* Foissner & Xu, 2007, and *Spathidium procerum* Kahl, 1930a.

Description: This new species was very rare 3 d after wetting the sample and disappeared after sampling the percolate for preparations; in eight protargol slides, only 13 specimens were found, including two malformed cells. Nonetheless, the species can be properly described because detailed in vivo observations and 11 well-impregnated specimens are available; variability coefficients are fairly high, as usual for weak, growing or decreasing populations.

Body size 80–160 × 15–22 µm in vivo, usually about 120 × 18 µm, as calculated from some in vivo measurements and the morphometric data; length:width ratio highly variable, viz., 4.4–11.3:1 in impregnated specimens, on average near 6.6:1 both in vivo and in protargol preparations (Table 7.5). Body usually very narrowly spatulate and slightly curved dorsally, rarely cylindroidal or somewhat obclavate, widest frequently behind mid-body, neck indistinct; anterior (oral) end oblique, posterior ordinarily rounded, rarely bluntly pointed or inflated due to the contractile vacuole contained (Fig. 7.9a, c, d, i, k, 7.10d–h). Macronucleus in middle body quarters, long and tortuous; nucleoli globular to elongate, up to 6 µm long. On average seven, usually lenticular, rarely ellipsoidal micronuclei near or attached to macronucleus strand (Fig. 7.9a, j, k, 7.10a, h). Contractile vacuole in rear body end, some excretory pores in pole area. Extrusomes accumulated in margin of oral bulge, ovate and minute, that is, 1.0–1.5 × 0.7–1.0 µm in size; do not impregnate with the protargol method used. Discharged extrusomes ovate with an about 1.5 µm long process associated with a bright granule proximally (Fig. 7.9a, b, e, f, 7.10b, c). Cortex flexible, contains about four

Table 7.5 Morphometric data on *Latispathidium brachyoplites* nov. spec. (original data)[a]

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Body, length	107.9	107.0	22.4	6.8	20.8	75.0	147.0	11
Body, width	16.9	17.0	2.8	0.8	16.6	13.0	22.0	11
Body length:width, ratio	6.6	5.8	2.1	0.6	31.6	4.4	11.3	11
Oral bulge, length	10.9	11.0	1.9	0.6	17.6	8.0	14.0	11
Oral bulge, height	2.5	2.5	–	–	–	2.0	3.0	11
Oral bulge length:body width, ratio	0.7	0.6	0.2	0.1	31.0	0.4	1.1	11
Circumoral kinety to last dikinetid of brush row 1, distance	16.1	15.0	3.2	1.0	19.7	13.0	22.0	11
Circumoral kinety to last dikinetid of brush row 2, distance	21.4	20.0	4.6	1.4	21.5	15.0	30.0	11
Circumoral kinety to last dikinetid of brush row 3, distance	20.4	20.0	4.7	1.4	23.0	14.0	28.0	11
Anterior body end to macronucleus, distance	30.7	29.0	7.2	2.2	23.5	22.0	47.0	11
Macronucleus figure, length	51.8	45.0	18.2	5.5	35.1	30.0	90.0	11
Macronucleus, length (spread and thus approximate)	91.4	80.0	–	–	–	55.0	200.0	11
Macronucleus, width (middle)	3.3	3.0	0.6	0.2	19.8	3.0	5.0	11
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	11
Micronuclei, length	3.3	3.0	0.7	0.2	21.6	2.0	4.0	11
Micronuclei, width	1.6	1.5	–	–	–	1.0	2.0	11
Micronuclei, number	7.2	7.0	1.8	0.5	24.8	5.0	10.0	11
Somatic kineties, number	11.3	12.0	1.3	0.4	12.0	9.0	13.0	11
Basal bodies in a right-side kinety, number	57.0	55.0	13.6	4.1	23.9	35.0	88.0	11
Dorsal brush rows, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	11
Dikinetids in brush row 1, number	12.0	13.0	2.3	0.7	19.4	8.0	15.0	11
Dikinetids in brush row 2, number	18.6	18.0	3.0	0.9	16.1	15.0	24.0	11
Dikinetids in brush row 3, number	14.3	14.0	2.8	0.8	19.6	10.0	18.0	11
Circumoral dikinetids, number	33.5	33.0	6.3	1.9	18.8	26.0	47.0	11
Circumoral dikinetids between two somatic ciliary rows on left side of body, number	2.3	2.0	–	–	–	2.0	3.0	11
Circumoral dikinetids between two somatic ciliary rows on right side of body, number	4.7	5.0	0.9	0.3	19.1	4.0	7.0	11

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

rows of conspicuous granules between each two kineties; granules about 0.7 × 0.4 µm in size, colourless, compact and thus strongly refractive and distinct in vivo; cortical fibre system well impregnated and structured as in other spathidiids. Cytoplasm colourless, contains moderately many globular and irregularly shaped lipid droplets up to 3 µm across and some small food vacuoles with unidentifiable contents. Movement without peculiarities.

Somatic cilia about 8 µm long in vivo, arranged in an average of 12 equidistant, bipolar, ordinarily spaced and ciliated rows abutting on circumoral kinety in typical *Spathidium*

pattern, an unusual mode in *Latispathidium* usually having the right-side rows separated from the circumoral kinety. Somatic kinety right (ventral) of brush row 1 usually rather distinctly convex anteriorly, producing lenticularly widened ventrolateral area subapically (Fig. 7.9a, h–k, 7.10h; Table 7.5). Dorsal brush dikinetidal, three-rowed and heterostichad, conspicuous because bristles up to 10 µm long in anterior portion of row 2; all rows commence with some ordinary cilia anteriorly and continue as somatic kineties posteriorly. Brush row 1 distinctly shorter than rows 2 and 3, composed of an average of 12 dikinetids associated with clavate bristles 3 µm (anterior bristle of dikinetids) to 4 µm (posterior bristle) long. Brush row 2 longest, composed of an average of 18 dikinetids slightly more narrowly spaced than those of rows 1 and 3; bristle length similar as in row 1, except for anterior region having posterior basal body of dikinetids associated with an up to 10 µm long, rod-shaped bristle. Row 3 slightly shorter than row 2, composed of an average of 14 rather widely spaced dikinetids associated with very short bristles 1 µm (anterior bristle of dikinetids) to 2 µm (posterior bristle) long; followed by a monokinetidal tail extending to second third of body with 1 µm long bristles (Fig. 7.9a, i, j, l, m, o, 7.10c, h; Table 7.5).

Oral bulge of ordinary distinctness, oblique, about two thirds as long as widest trunk region, in vivo 3–4 µm high and rather distinctly separate from body proper; ellipsoidal to oblong with pointed ventral end in frontal view, surface flat to slightly concave; cytopharyngeal opening not recognizable. Circumoral kinety cuneate to narrowly obovate, slightly ∞-shaped in lateral view; continuous, composed of an average of 33 dikinetids each associated with a cilium, a nematodesma, and a fibre extending to bulge centre. Nematodesmata rather distinct because bundled and intensely impregnated (Fig. 7.9a–c, h–l, n, 7.10d, f–h; Table 7.5).

Occurrence and ecology: *Latispathidium brachyoplites* nov. spec. was found only at the type locality, where it was very rare in the non-flooded Petri dish culture. However, this might have been caused by too early fixation of the culture, which was only 3 d old. The very sandy, acidic soil (pH 5.2 in water) contained many humus particles and grass roots, and the 1–2 cm thick litter layer was spotted with whitish accumulations of fungal hyphae.

Funding

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)"). Helmut Berger thanks Ilse Foissner who generously privately financed his work on this project.

Acknowledgements

According to an already published work dealing with this project, the help of the following persons has to be acknowledged: Sabine Agatha, Remigius Geiser, Eva Herzog, Wolf-Dietrich Krautgartner, Brigitte Moser, Birgit Peukert, Fritz Seyrl, and Andreas Zankl. We also want to thank Magdalini Christodoulou and Alexandra Aberham at the Biology Centre of the Upper Austrian Museum in Linz.

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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