

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

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

In memory of Wilhelm Foissner (1948–2020)

Contents

Preface, authorship, acknowledgements, and funding xiii

Abstract xv

Chapter 1

H. Berger, K. Xu & W. Foissner

General section to “Revision of some spathidiid genera (Alveolata, Ciliophora, Spathidiida)”, including nomenclatural notes 1

Abstract 1

Introduction 1

Material and methods 2

Notes on so-called, nomenclaturally unavailable names of species due to aphory 5

Nomenclatural notes on new species/subspecies described by Foissner et al. (2002) 8

Protospathidium vermiforme Foissner, Agatha & Berger nov. spec. 10

Notes on type slides of species described by Foissner (2016a, b) 15

Note on ZooBank registration number of author Helmut Berger 17

Summary of nomenclatural acts and of taxa described in Chapters 1–13 18

New subspecies 18

New species 18

New genera 18

New combinations 18

New family 19

Redescriptions, reviews, and others 19

New name (Replacement name) 20

Funding 20

References 20

Chapter 2

H. Berger, K. Xu & W. Foissner

Spathidiida Foissner & Foissner, 1988 (Ciliophora, Litostomatea, Haptoria): a brief introduction 25

Abstract 25

Spathidiida Foissner & Foissner, 1988 26

Key to subtaxa (families) of the Spathidiida Foissner & Foissner, 1988 27

Spathidiidae Kahl in Doflein & Reichenow, 1929 27

Spathidium Dujardin, 1841 28

Funding 29

References 29

Chapter 3

W. Foissner, K. Xu & H. Berger

Characterisation of 15 species belonging to the genus *Spathidium* Dujardin, 1841 (Ciliophora, Spathidiidae), including three new 33

Abstract	33
Characterisation of 15 <i>Spathidium</i> species	34
The <i>Spathidium elongatum</i> group	34
<i>Spathidium elongatum</i> nov. spec.	36
<i>Spathidium apospathidiforme</i> nov. spec.	43
<i>Spathidium duschli</i> Foissner, 2016	59
<i>Spathidium dispar</i> Foissner & Xu in Foissner, 2016	59
The <i>Spathidium bromelicola</i> group	61
<i>Spathidium bromelicola</i> Foissner, Wolf, Kumar, Xu & Quintela-Alonso, 2014	62
<i>Spathidium aciculare</i> Foissner, Agatha & Berger, 2002	65
<i>Spathidium etoschense</i> Foissner, Agatha & Berger, 2002	65
<i>Spathidium saprophilum</i> nov. spec.	67
<i>Spathidium saprophilum saprophilum</i> nov. subspec.	68
<i>Spathidium saprophilum curvioplites</i> nov. subspec.	71
<i>Spathidium rusticanum</i> Foissner, 1981	74
The <i>Spathidium wolffi</i> group	85
<i>Spathidium wolffi</i> Foissner, Wolf, Kumar, Xu & Quintela-Alonso, 2014	85
<i>Spathidium faurefremietii</i> Foissner, 2003	86
<i>Spathidium latissimum</i> Lepsi, 1959	89
<i>Spathidium polyvacuolatum</i> Vuxanovici, 1959	90
Two further <i>Spathidium</i> species	90
<i>Spathidium anguilla</i> Vuxanovici, 1962	91
<i>Spathidium polynucleatum</i> (Foissner, Agatha & Berger, 2002) Jang, Vd'ačný, Shazib & Shin, 2017	96
Funding	106
Acknowledgements	106
References	106

Chapter 4

W. Foissner, K. Xu & H. Berger

***Apospathidium* Foissner et al., 2002 (Ciliophora, Spathidiidae), a genus whose species have oralized somatic kineties 111**

Abstract 111

Apospathidium Foissner, Agatha & Berger, 2002 111

Key to species 112

Apospathidium terricola Foissner, Agatha & Berger, 2002 112

Apospathidium longicaudatum (Buitkamp, 1977) nov. comb. 117

Funding 124

Acknowledgements 124

References 125

Chapter 5

W. Foissner, K. Xu & H. Berger

***Centrospathidium* nov. gen. (Ciliophora, Spathidiidae), a new genus whose type**

species was discovered in an Australian floodplain 127

Abstract 127

Centrospathidium nov. gen. 127

Key to species 128

Centrospathidium verrucosum nov. spec. 128

Centrospathidium faurei (Kahl, 1930) nov. comb. 136

Centrospathidium minutum (Kahl, 1926) nov. comb. 138

Funding 138

Acknowledgements 139

References 139

Chapter 6

W. Foissner, K. Xu & H. Berger

***Epispathidium* Foissner, 1984 (Ciliophora, Spathidiidae), a genus where the circumoral kinety is completely separated from the somatic kineties 141**

Abstract 141

Epispathidium Foissner, 1984 142

Key to species 143

Epispathidium regium Foissner, 1984 144

Epispathidium securiforme (Kahl, 1930) Foissner, 1984 154

Epispathidium salsum nov. spec. 166

Epispathidium papilliferum (Kahl, 1930) Foissner, 1984 174

Brief review of other species assigned to *Epispathidium* Foissner, 1984 196

Epispathidium terricola Foissner, 1987 196

Epispathidium amphoriforme (Greeff, 1889) Foissner, 1984 197

Epispathidium ascendens (Wenzel, 1955) Foissner, 1987 202

Funding 207

Acknowledgements 207

References 207

Chapter 7

W. Foissner, K. Xu & H. Berger

***Latispathidium* Foissner et al., 2005 (Ciliophora, Spathidiidae), a genus whose species have the dorsal brush on the left body side 213**

Abstract 213

Latispathidium Foissner, Berger, Xu & Zechmeister-Boltenstern, 2005 213

Key to species 215

Latispathidium lanceoplites (Foissner, Agatha & Berger, 2002) Foissner, Berger, Xu & Zechmeister-Boltenstern, 2005 215

Latispathidium truncatum (Stokes, 1885) Foissner, Berger, Xu & Zechmeister-Boltenstern, 2005 218

Key to subspecies 220

Latispathidium truncatum truncatum (Stokes, 1885) Foissner, Berger, Xu & Zechmeister-Boltenstern, 2005 221

Latispathidium truncatum bimacronucleatum Foissner, Berger, Xu & Zechmeister-Boltenstern, 2005 222
Latispathidium arboricola nov. spec. 229
Latispathidium simile nov. spec. 238
Latispathidium brachyoplites nov. spec. 245
Funding 252
Acknowledgements 252
References 253

Chapter 8

W. Foissner, K. Xu & H. Berger

***Schmidingerophrya* nov. gen. (Ciliophora, Spathidiidae), a new genus whose species have only two dorsal brush rows 257**

Abstract 257
Schmidingerophrya nov. gen. 257
Key to species 258
Schmidingerophrya macrothrix nov. spec. 258
Schmidingerophrya bisticha nov. spec. 272
Funding 279
Acknowledgements 279
References 279

Chapter 9

W. Foissner, K. Xu & H. Berger

***Semibryophyllum* nov. gen. (Ciliophora, Spathidiidae), a new genus characterised by three ordinary dorsal brush rows and several accessory brush rows on the left side 281**

Abstract 281
Semibryophyllum nov. gen. 281
Key to species 285
Semibryophyllum cultellum nov. spec. 285
Semibryophyllum palustre nov. spec. 291
Semibryophyllum foliosum (Foissner, 1983) nov. comb. 303
Funding 308
Acknowledgements 308
References 308

Chapter 10

W. Foissner, K. Xu & H. Berger

***Semispathidium* Foissner et al., 2002 (Ciliophora, Spathidiidae), a genus whose species have a discoidal oral bulge and *Spathidium*-like oral and somatic ciliature 311**

Abstract 311
Semispathidium Foissner, Agatha & Berger, 2002 312
Key to species 315
Semispathidium enchelyodontides Foissner, Agatha & Berger, 2002 315

<i>Semispathidium armatum</i> Foissner, Agatha & Berger, 2002	320
<i>Semispathidium lagyniforme</i> (Kahl, 1930) Foissner, Agatha & Berger, 2002	322
<i>Semispathidium breviararmatum</i> Foissner & Vdačný in Vdačný & Foissner, 2013	325
<i>Semispathidium longiararmatum</i> Foissner & Vdačný in Vdačný, Slovák & Foissner, 2014	326
<i>Semispathidium fraterculum</i> Foissner & Al-Rasheid in Foissner, Hess & Al-Rasheid, 2010	329
<i>Semispathidium pulchrum</i> Foissner, Hess & Al-Rasheid, 2010	330
Funding	330
Acknowledgements	331
References	331

Chapter 11

W. Foissner, K. Xu & H. Berger

***Supraspathidium* Foissner & Didier, 1981 (Ciliophora, Spathidiidae), a genus whose species have more than one contractile vacuole** 335

Abstract 335

Supraspathidium Foissner & Didier, 1981 335

Key to species 337

Supraspathidium teres (Stokes, 1886) Foissner & Didier, 1981 338

Supraspathidium multistriatum Foissner & Didier, 1981 339

Supraspathidium etoschense Foissner, Agatha & Berger, 2002 346

Supraspathidium armatum Foissner, Agatha & Berger, 2002 353

Supraspathidium vermiforme (Penard, 1922) Foissner & Didier, 1981 357

Supraspathidium elongatum (Penard, 1922) Foissner & Didier, 1981 359

Supraspathidium gigas (Cunha, 1914) Foissner & Didier, 1981 361

Funding 363

Acknowledgements 363

References 363

Chapter 12

W. Foissner, K. Xu & H. Berger

Pharyngospathidiidae nov. fam. (Ciliophora, Spathidiida), a group of spathidiids with a permanent cytopharynx 367

Abstract 367

Pharyngospathidiidae nov. fam. 367

Key to genera 369

Pharyngospathidium nov. gen. 369

Key to species and subspecies 369

Pharyngospathidium longichilum nov. spec. 370

Pharyngospathidium longichilum longichilum nov. subspec. 378

Pharyngospathidium longichilum amphoriforme nov. subspec. 380

Pharyngospathidium pseudobavariense nov. spec. 389

Pharyngospathidium bavariense (Kahl, 1930) nov. comb. 398

Pharyngospathidium simplinucleatum (Kahl, 1930) nov. comb. 399
Neospathidium nov. gen. 400
 Key to species 400
Neospathidium longinucleatum nov. spec. 401
Neospathidium africanum nov. spec. 418
Neospathidium brachystichos nov. spec. 424
 Funding 428
 Acknowledgements 428
 References 429

Chapter 13

H. Berger, K. Xu & W. Foissner

Supplement to the Arcuospathidiidae Foissner & Xu, 2007: *Neocultellothrix* Foissner nov. gen. (Ciliophora, Haptoria, Arcuospathidiidae) with *Neocultellothrix velhoi* Foissner nov. spec. as type species, and transfer of six species from the unavailable genus *Cultellothrix* Foissner, 2003 to *Neocultellothrix* Foissner nov. gen., a step to fix a serious nomenclatural problem 433
 Abstract 433
Neocultellothrix Foissner nov. gen. 434
 Key to species 436
Neocultellothrix velhoi Foissner nov. spec. 436
 Note on type material of *Cephalospathula brasiliensis* Foissner, 2003b 438
Neocultellothrix atypica (Wenzel, 1953) Foissner & Xu nov. comb. 439
Neocultellothrix coemeterii (Kahl, 1943) Foissner & Xu nov. comb. 443
Neocultellothrix japonica (Foissner, 1988) Foissner & Xu nov. comb. 445
Neocultellothrix lionotiformis (Kahl, 1930) Foissner nov. comb. 446
Neocultellothrix paucistriata (Foissner & Xu, 2007) nov. comb. 448
Neocultellothrix tortisticha (Foissner & Xu, 2007) nov. comb. 449
 Funding 450
 Acknowledgements 450
 References 450

Index

Systematic index 453

Table index 465

Preface, authorship, acknowledgements, and funding

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

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

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

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

Salzburg
January 2025

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Abstract

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

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

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

Chapter 4

Apospathidium Foissner et al., 2002 (Ciliophora, Spathidiidae), a genus whose species have oralized somatic kineties¹

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Abstract

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

Apospathidium Foissner, Agatha & Berger, 2002

2002 *Apospathidium* nov. gen. – Foissner, Agatha & Berger, Denisia 5: 334 (original description). Type species (by original designation): *Apospathidium terricola* Foissner, Agatha & Berger, 2002.

2007 *Apospathidium* Foissner, Agatha et Berger, 2002 – Jankowski, Phylum Ciliophora, p. 564 (generic revision of ciliates).

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

¹ This chapter should be referenced as follows: Foissner W., Xu K. & Berger H. (2025): *Apospathidium* Foissner et al., 2002 (Ciliophora, Spathidiidae), a genus whose species have oralized somatic kineties. – Ser. Monogr. Cilioph. 6: 111–126.

For notes on “Material and methods”, see Chapter 1 (Berger et al. 2025a).

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

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

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

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

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

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

Key to species

- 1 Body narrowly amphoriform (length:width ratio in vivo 4:1) with an average of 11 ciliary rows, of which 4 are differentiated to a dorsal brush *Apospathidium terricola* (p. 112)
- Body very narrowly amphoriform (length:width ratio in vivo 9:1) with an average of 9 ciliary rows, of which 3 are differentiated to a dorsal brush *Apospathidium longicaudatum* (p. 117)

Apospathidium terricola Foissner, Agatha & Berger, 2002

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

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

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

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

continued on p.114

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

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

Table 4.1 Continued

Characteristic	Mean	M	SD	SE	CV	Min	Max	n
Ciliated kinetids in a lateral kinety, number	64.3	55.0	17.2	6.5	26.8	48.0	95.0	7
	38.9	38.0	6.8	2.3	17.4	30.0	49.0	9
	45.1	45.0	6.5	1.5	14.5	35.0	60.0	19
Dorsal brush rows, number ^c	3.9	4.0	–	–	–	3.0	4.0	8
	3.9	4.0	0.3	0.1	8.6	3.0	4.0	9
	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19
Dikinetids in brush row 1, number	7.4	8.0	3.3	1.5	44.4	4.0	11.0	5
	–	–	–	–	–	–	–	–
	6.4	6.0	1.5	0.3	22.9	4.0	9.0	19
Dikinetids in brush row 2, number	11.3	9.0	7.1	3.5	62.7	6.0	21.0	4
	–	–	–	–	–	–	–	–
	12.1	12.0	2.2	0.5	17.8	8.0	16.0	19
Dikinetids in brush row 3, number	11.8	13.0	2.9	1.3	25.0	7.0	14.0	5
	–	–	–	–	–	–	–	–
	4.5	4.0	0.7	0.2	15.6	3.0	6.0	19
Dikinetids in brush row 4, number	4.8	4.5	2.5	1.3	52.1	2.0	8.0	4
	–	–	–	–	–	–	–	–
	–	–	–	–	–	–	–	–

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

^b For the Slovakian population of *Apospathidium terricola*, the diameter is given.

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

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

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

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

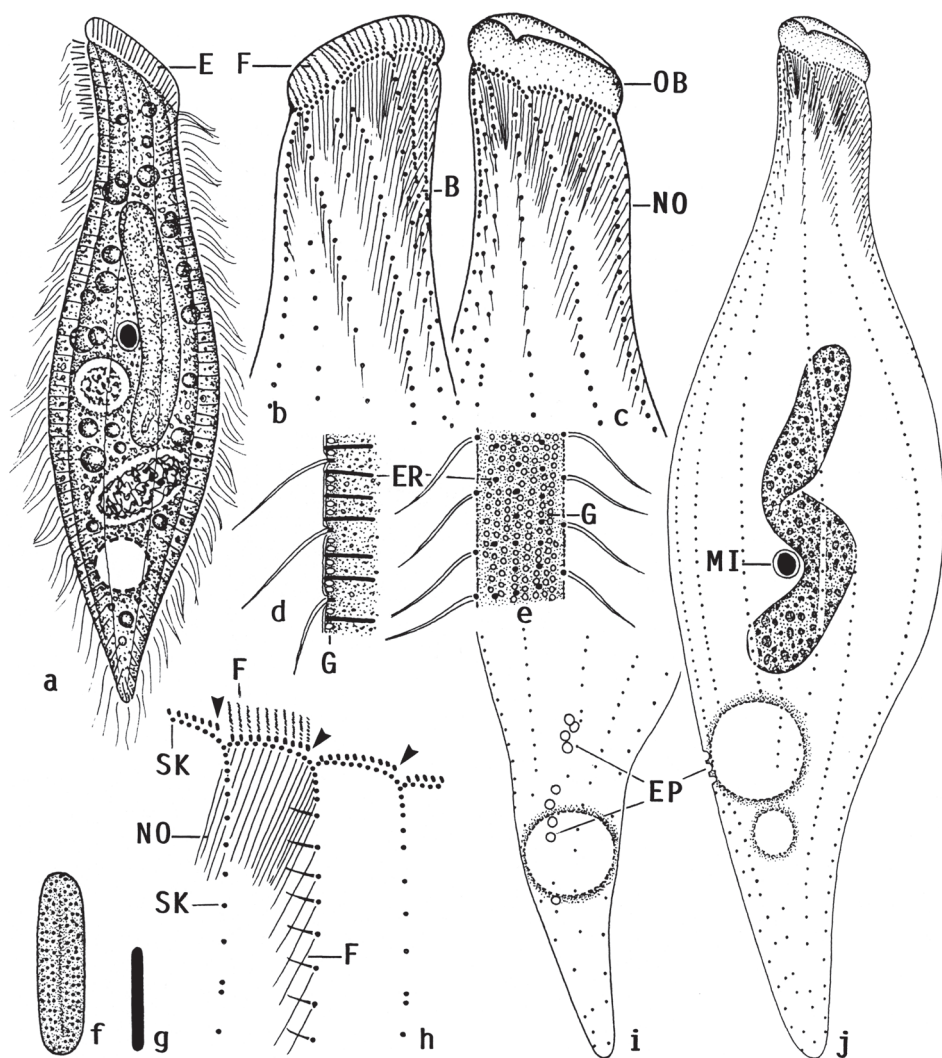


Fig. 4.1a–j *Apospathidium terricola* Foissner et al., 2002 (from Foissner et al. 2002. a, d–g, from life; b, c, h–j, protargol preparation). **a**: Right side view of representative specimen, 145 μ m. Note the subterminal contractile vacuole and the fine body extrusomes anchored to the pellicle. **b,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

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

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

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

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

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

Notes on population described by Vďačný & Tirjaková (2007): The specimens of the population from Slovakia basically correspond with the Namibian individuals. However, the European specimens are considerably smaller in vivo ($70\text{--}130 \times 20\text{--}40\ \mu\text{m}$ vs. $130\text{--}170 \times$

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

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

Apospathidium longicaudatum (Buitkamp, 1977) nov. comb.

(Fig. 4.2a–r, 4.3a–h, Table 4.1)

- 1974 *Spathidium atypicum* n. sp. – Buitkamp & Wilbert, Acta Protozool. 13: 202, Abb. 2 (Fig. 4.2a; original description; for type material from Canada and primary homonymy, see nomenclature).
- 1977 *Spathidium longicaudatum* n. nom. – Buitkamp, Decheniana 130: 117 (replacement name because of preoccupation, see nomenclature).
- 1981 *Spathidium longicaudatum* Buitkamp und Wilbert, 1974; Buitkamp 1977 – Foissner, Zool. Jb. Syst. 108: 275, Abb. 6a–f (Fig. 4.2b–f; description of Austrian population; site where voucher material is deposited not mentioned, see nomenclature; authorship incorrect).
- 2002 *Apospathidium atypicum* (Buitkamp & Wilbert, 1974) nov. comb. – Foissner, Agatha & Berger, Denisia 5: 338, Fig. 77a–j, Table 62 (Fig. 4.2h–r; description of population from Kenya; five voucher slides [accession numbers 2002/518, 2002/519, 2002/520, 2002/521, 2002/522; see Foissner et al. 2002, p. 37] with protargol-prepared specimens have been deposited in the Biology Centre of the Upper Austrian Museum in Linz [LI]).

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

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

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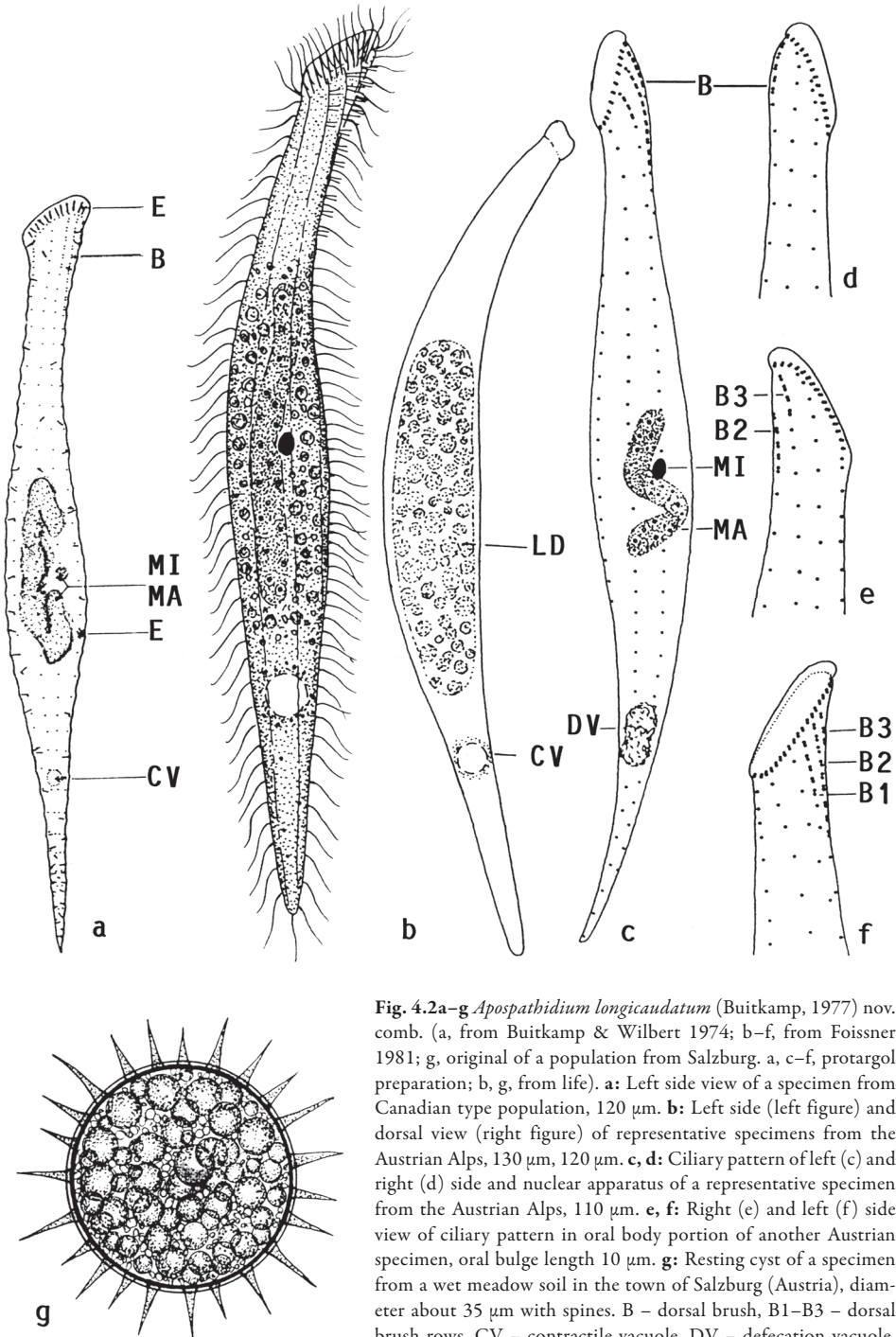


Fig. 4.2a–g *Apaspathidium longicaudatum* (Buitkamp, 1977) nov. comb. (a, from Buitkamp & Wilbert 1974; b–f, from Foissner 1981; g, original of a population from Salzburg. a, c–f, protargol preparation; b, g, from life). **a**: Left side view of a specimen from Canadian type population, 120 µm. **b**: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

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

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

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

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

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

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

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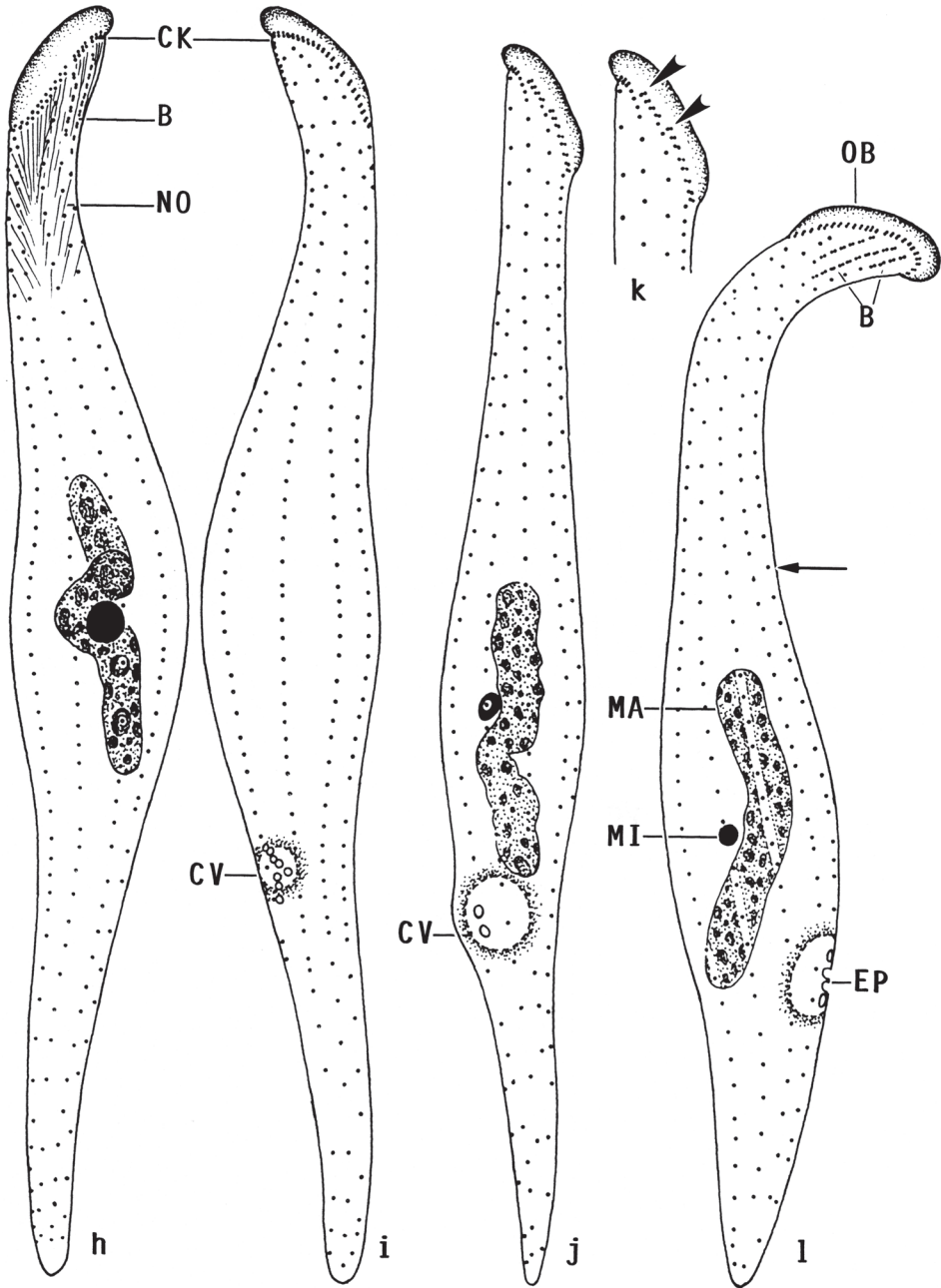


Fig. 4.2h-l *Apospathidium longicaudatum* (Buitkamp, 1977) nov. comb. (from Foissner et al. 2002. Protargol preparation). Ciliary pattern of Kenyan specimens after protargol preparation. **h, i**: Left and right side view of a representative specimen, 120 μ m. **j, k**: Right side view of a specimen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

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

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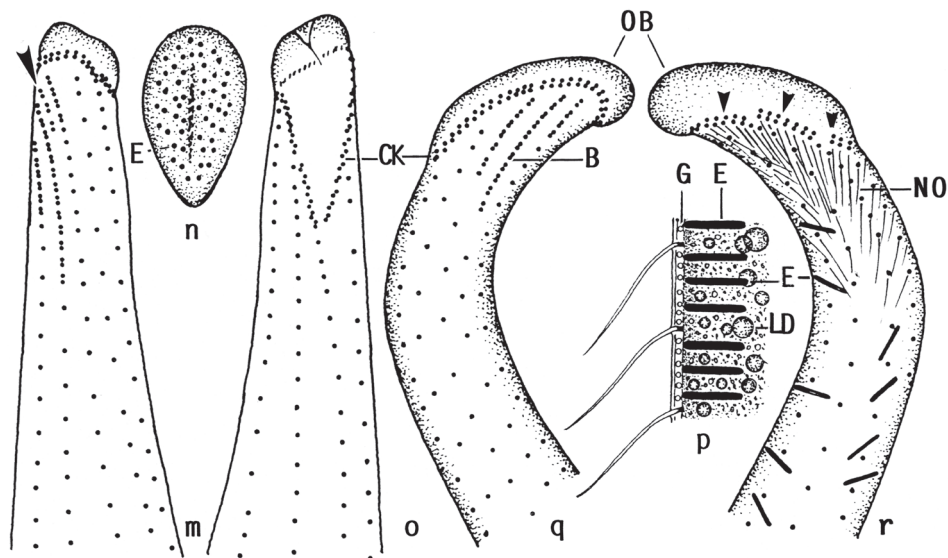


Fig. 4.2m–r *Apospathidium longicaudatum* (Buitkamp, 1977) nov. comb. (from Foissner et al. 2002, Kenyan specimens. m, o, q, r, protargol preparation; n, p, from life). **m, o:** Ciliary pattern of anterior dorsal and ventral side of same specimen showing the cuneate circumoral kinety and a short brush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

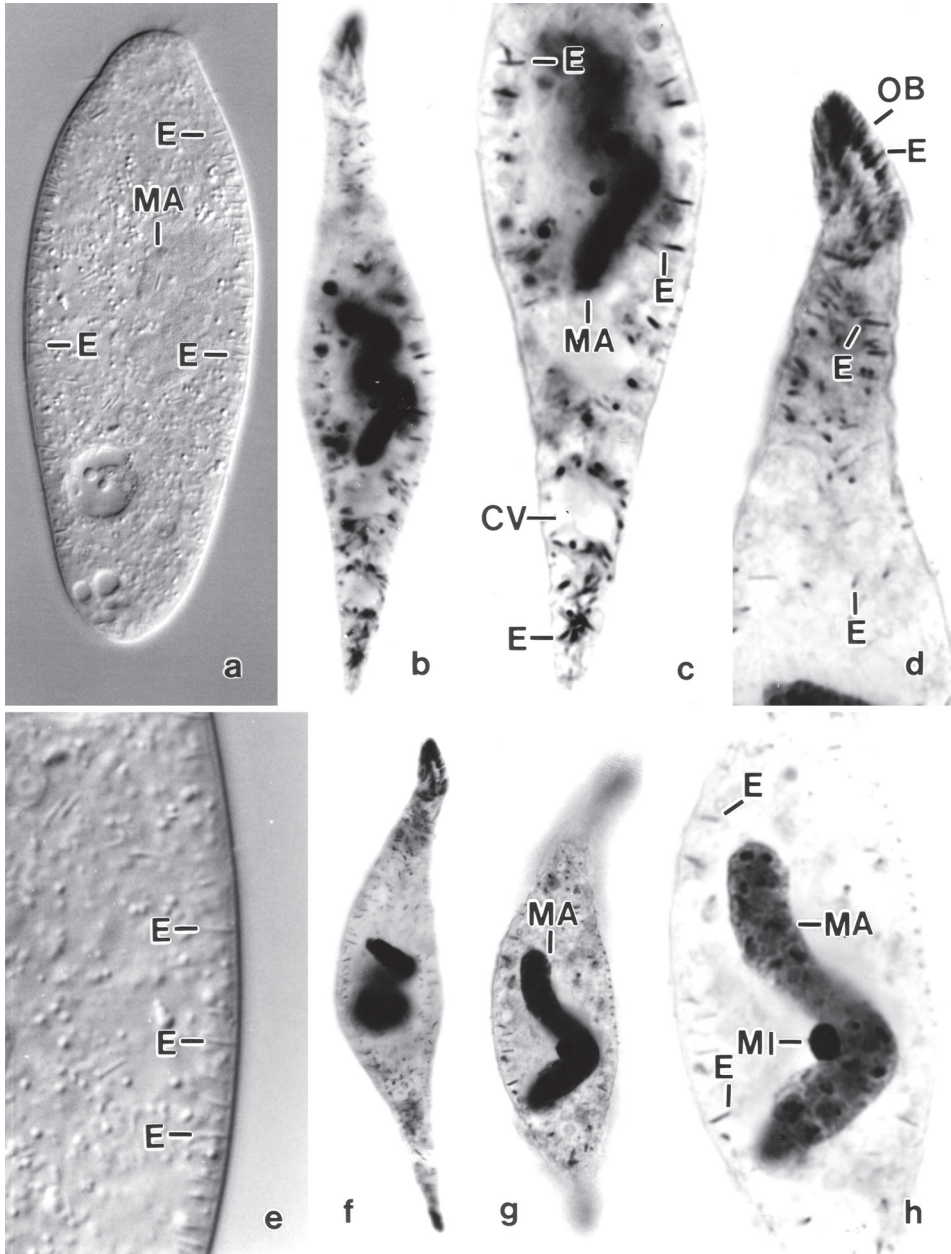


Fig. 4.3a–h *Apospathidium longicaudatum* (Buitkamp, 1977) nov. comb. (originals; a, e, specimens from Hawaii; b–d, f–h, Namibian site 16 specimens, see Foissner et al. 2002. a, e, from life; b–d, f–h, protargol preparation). **a, e:** A heavily squashed specimen showing the rod-shaped, about 3 µm long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

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

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

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

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

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

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

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

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

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

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

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² Note by H. Berger: For details on this very old house (built in 1380), see “<https://www.sn.at/wiki/Krautwächterhäusel>” and Foissner et al. (2012).

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

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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.

- Acaryophrya* 143, 207
aciculare*, *Spathidium 33, 62T, 64T, **65**, 68, 220T, 227
acrostoma, *Semiplatyophrya* 9
 Actinobolidae 28
Actinobolina multinucleata 8
 Actinobolinidae 28
affine, *Gonostomum* 381, 382
africana etoschensis, *Rostrophryides* 9
africanum*, *Neospathidium 367, 395, 400, 400K, 401, **418**, 427T
africanum, *Trachelophyllum* 8
Afrothrix 434
Akidodes 435
Akidodes henleae 435
Akidodes symmetricus 435
 Alveolata xv, 1
amicronucleata, *Colpoda cavicola* 9
amphoriforme amphoriforme, *Epispathidium* 162
amphoriforme amphoriforme, *Spathidium* 157, 158, 200T, 201
amphoriforme rectitoratum, *Epispathidium* 198
amphoriforme rectitoratum, *Spathidium* 155, 158, 160, 197, 198, 200T, 201
amphoriforme securiforme, *Epispathidium* 154, 160
amphoriforme securiforme, *Spathidium* 142, 154, 155, 157, 158, 160, 62, 200T, 201, 380
amphoriforme*, *Epispathidium 141, 142, 143K, 145, 158, 160, 164, **197**, 200T, 211, 368, 372, 385
amphoriforme, *Epispathidium amphoriforme* 162
amphoriforme*, *Pharyngospathidium longicbilum 155, 160, 162, 367, 369, 369K, 370, 370T, 371T, 378, **380**, 401
amphoriforme, *Spathidium* 142, 155, 157, 158, 197, 198, 200T, 201
amphoriforme, *Spathidium amphoriforme* 157, 158, 200T, 201
Anatoliocirrus capari 9
anguilla*, *Spathidium 33, 34, 71, 74, **91**, 92T, 276

- angusta obovate*, *Frontonia* 9
Apertospathula 239, 241, 283
Apertospathula cuneata 6
Apertospathula lajacola 6
Apertospathula longiseta 6
Apertospathula pelobia 6
Apertospathula similis 6
Apertospathulidae 25, 27
Apobryophyllum 143, 206
Apobryophyllum schmidingeri 445
Apobryophyllum vermiforme 8
Apocolpodidium Apocolpodidium etoschense 9
Apocolpodidium etoschense, *Apocolpodidium* 9
Apocolpodidium Phagoon macrostoma 9
Apocyclidium obliquum 4
Apometopus Apometopus pyriformis 16
Apometopus pyriformis, *Apometopus* 16
apospathidiforme, *Spathidium* 33, 34, 35, 37, 38, 38T, 43, 44T, 112, 114, 119, 301
Apospathidium xv, 28, 43, 111, 112K, 312
Apospathidium atypicum 3, 112, 117
Apospathidium longicaudatum 3, 43, 47, 65, 67, 111, 112, 112K 113T, 114, 117
Apospathidium terricola 111, 112K, 112, 113T, 119, 343
arboricola, *Latispathidium* 213, 214, 215K, 229, 236T, 266
arcuospathidiid 241
Arcuospathidiidae 25, 27, 433
Arcuospathidium 11, 12, 26, 85, 143, 149, 206, 214, 281, 283, 286, 336, 362, 445, 447
Arcuospathidium atypicum 440
Arcuospathidium australe 439, 440, 441, 442, 443
Arcuospathidium bulli 41, 85
Arcuospathidium coemeterii 443
Arcuospathidium cultriforme 446
Arcuospathidium cultriforme cultriforme 196
Arcuospathidium cultriforme lionotiforme 446
Arcuospathidium cultriforme scalpriforme 447
Arcuospathidium deforme 6
Arcuospathidium japonicum 435, 445
Arcuospathidium lionotiforme 446, 447
Arcuospathidium multinucleatum 149
Arcuospathidium muscorum rhopaloplites 6
Arcuospathidium namibiense 11, 12, 214, 233, 235, 258, 266
Arcuospathidium pelobium 6
Arcuospathidium vermiforme 270
Arcuospathidium virugense 7
Arcuospathidium virungense 7
Arcuospathidium vlassaki 214
arenicola, *Protospathidium* 5, 8
Armatospathula 7
Armatospathula costaricana 7
Armatospathula periarmata 7
Armatospathula plurinucleate 7
armatum, *Semispithidium* 311, 312, 313T, 315K, 315, 320, 328
armatum, *Supraspathidium* 8, 335, 336, 337, 338K, 344T, 345T, 348, 353, 360
ascendens, *Epispithidium* 43, 141, 142, 144K, 202
ascendens, *Spathidium* 142, 202, 207
astyliformis, *Vorticella* 103
atypica, *Cultellothrix* 440
atypica, *Neocultellothrix* 18, 117, 241, 242, 243, 433, 435, 436K, 439
atypicum, *Apospathidium* 3, 112, 117
atypicum, *Arcuospathidium* 440
atypicum, *Spathidium* 117, 435, 439, 441, 442, 443
australe, *Arcuospathidium* 439, 440, 441, 442, 443
australiensis, *Bilamellophrya* 134
australiensis, *Levispatha* 418
Australothrix 434
Balantidion 143, 206
bavariense bavariense, *Spathidium* 398
bavariense simplinucleatum, *Spathidium* 398, 399
bavariense, *Pharyngospathidium* 367, 369, 369K, 390, 392, 395, 398, 399, 400
bavariense, *Spathidium* 142, 369, 389, 398, 400
bavariense, *Spathidium bavariense* 398
bavariense, *Spathidium Epispithidium?* 142

- bavariensis*, *Gastrostyla* 15
bavariensis, *Gastrostyla Kleinstyla* 14, 15
 Belonophryina 26
Bilamellophrya australiensis 134
bimacronucleatum, *Latispathidium truncatum* 215, 217T, 219, 220T, 220K, 222
binucleate, *Parakabliella* 14
bisticha, *Schmidingerophrya* 257, 258, 258K, 266, 267, 268T, 270, 271, 272
blattereri, *Enchelydium* 129, 134, 414, 415
bonneti, *Protospathidium* 10
bonneti, *Spathidium* 11, 12, 13, 266, 275
brachycaryon, *Edaphospathula* 7, 238, 242
brachyoplites, *Latispathidium* 213, 214, 215K, 245, 251T
brachystichos, *Neospathidium* 265, 266, 267, 400, 401K, 401, 422, 424, 427T
brachystichos, *Spathidium* 265
bradburyarum, *Colpodidium Pseudocolpodidium* 8
brasiliensis, *Cephalospatula* 87, 434, 437, 438, 439, 441, 442
breviarmatum, *Semispathidium* 311, 312, 315K, 325, 328
bromelicola group, *Spathidium* 33, 34, 61, 62T, 68
bromelicola, *Spathidium* 33, 61, 62T, 62, 63T, 68, 92
Bryophyllum 281, 283, 289, 304
bulli, *Arcuospathidium* 41, 85
Bursaria fluviatilis 418

campylum, *Dexiostoma* 207
canadense, *Spathidium* 141, 147, 170, 172, 367, 372
canaliculatum, *Spathidium* 336
canaliculatum, *Supraspathidium* 336, 337
capari, *Anatoliocirrus* 9
cavicola amiconucleata, *Colpoda* 9
Centrospathidium xv, 28, 127, 136, 138
Centrospathidium faurei 127, 128, 128K, 134, 136
Centrospathidium minutum 127, 128, 128K, 137, 138

Centrospathidium verrucosum 127, 128K, 128, 129T, 138
Centrospathidium verruculosum 129, 134, 135
Cephalospatula brasiliensis 87, 434, 437, 438, 439, 441, 442
chilensis, *Epitholiolus* 14
Ciliophora xv, 25, 33, 111, 127, 141, 213, 257, 281, 335, 367
cithara, *Spathidium* 285
claviforme group, *Spathidium* 233
claviforme, *Spathidium* 215, 233
Clavoplites edaphicus 8
coemeterii, *Arcuospathidium* 443
coemeterii, *Cultellothrix* 3, 444
coemeterii, *Neocultellothrix* 3, 433, 435, 436K, 443
coemeterii, *Spathidium* 435, 443
Colpoda 152
Colpoda cavicola amiconucleata 9
Colpoda fastigata 207
Colpoda formisanoi 9
Colpoda inflata 149
Colpoda maupasi 103
colpodid(s) 1
Colpodidium Colpodidium horribile 8
Colpodidium Colpodidium microstoma 8
Colpodidium Colpodidium trichocystiferum 8
Colpodidium horribile, *Colpodidium* 8
Colpodidium microstoma, *Colpodidium* 8
Colpodidium Pseudocolpodidium bradburyarum 8
Colpodidium trichocystiferum, *Colpodidium* 8
Condyllostomides trinucleatus 9
costaricana, *Armatospathula* 7
costaricensis, *Maryna namibiensis* 9
Cranotheridium 283, 285, 294, 303, 304, 360, 361
Cranotheridium elongatum 336, 359, 360
Cranotheridium elongatus 360
Cranotheridium elongatus, *Pseudoprorodon* 359, 360
Cranotheridium foliosum 304, 306
Cranotheridium foliosus 303, 304
Cranotheridium Ps.? *elongatum* 360

- Cranotheridium taeniatum* 285, 294, 305
Cultellothrix xv, 7, 143, 206, 233, 433, 434, 435, 440, 444, 446, 447, 448, 449
Cultellothrix atypica 440
Cultellothrix coemeterii 3, 444
Cultellothrix japonica 445
Cultellothrix lionotiforme 447
Cultellothrix lionotiformis 446
Cultellothrix paucistriata 7, 435, 448
Cultellothrix tortisticha 7, 435, 449
Cultellothrix velhoi 6, 433, 434, 435, 436, 437, 438
cultellum, *Semibryophyllum* 281, 282T, 283, 285K, **285**, 291, 293, 303, 306
cultriforme cultriforme, *Arcuospathidium* 196
cultriforme lionotiforme, *Arcuospathidium* 446
cultriforme scalpriforme, *Arcuospathidium* 447
cultriforme, *Arcuospathidium* 446
cultriforme, *Arcuospathidium cultriforme* 196
cuneata, *Apertospathula* 6
curvioplites, *Spathidium saprophilum* 33, 62T, 67, 70, **71**, 73T
cylindricum, *Spathidium* 314

deforme, *Arcuospathidium* 6
depressa, *Frontonia* 191
depressum, *Spathidium* 289
Dexiostoma campylum 207
Dexiotricha plagia 339
Didiniina 25, 26
Dioplitophrya otti 8
dispar, *Spathidium* 33, 34, 37, 38, 38T, 41, 44T, **59**
dragescoi, *Nassula* 8
Dragescozoon terricola 9
Drepanomonas revoluta 373, 379
dschli, *Spathidium* 33, 34, 37, 38, 38T, **59**, 60T, 90, 91

edaphicus, *Clavoplites* 8
Edaphospathula brachycaryon 7, 238, 242
Edaphospathula fusioplites 5, 224, 227, 228, 276
Edaphospathula gracilis 7, 238, 242
Edaphospathula inermis 8

Edaphospathula paradoxa 5, 8, 250
elegans, *Ilsiella* 9
elementitanum, *Spathidium* 67
elongatum group, *Spathidium* 33, **34**, 44T, 61, 91
elongatum, *Cranotheridium* 336, 359, 360
elongatum, *Cranotheridium* Ps.? 360
elongatum, *Supraspathidium* 335, 337, 338K, 339, 358, **359**, 362
elongatus, *Cranotheridium* 360
elongatus, *Pseudoprorodon* *Cranotheridium* 359, 360
Enchelydium 368, 414
Enchelydium blattereri 129, 134, 414, 415
Enchelydium thecatum 414, 415
Enchelyina 111, 112
Enchelyodon 143, 207, 311, 312, 314, 315, 318, 320, 322, 368
Enchelyodon kenyaensis 9, 10
Enchelyodon megastoma 8
Enchelyodon terrenus 315, 316, 320
Enchelyodon vermiformis 314, 320
Enchelyodontidae 368
enchelyodontides, *Semispithidium* 311, 312, 313T, 315K, **315**, 320, 322, 328
Enchelyotricha jesnerae 8
Enchelys 143, 206, 315, 320
Enchelys gigas 361, 362
Enchelys longitricha 8
Enchelys polynucleata 326
Enchelys spathula 162
Enchelys terricola 315
Epispithidium xv, 26, 27, 28, 34, 89, 91, 97, 141, **142**, 224, 290, 336, 367, 368, 369, 372, 374, 385, 395, 401, 423
Epispithidium amphoriforme 141, 142, 143K, 145, 158, 160, 164, **197**, 200T, 211, 368, 372, 385
Epispithidium amphoriforme amphoriforme 162
Epispithidium amphoriforme rectitoratum 198
Epispithidium amphoriforme securiforme 154, 160
Epispithidium ascendens 43, 141, 142, 144K, **202**

- Epispathidium papilliferum* 141, 142, 143K, 147, 174, 192T, 194T, 211
Epispathidium polynucleatum 34, 91, 96, 141, 142
Epispathidium regium 141, 142, 143, 143K, 144, 150T, 160, 164, 170, 172, 395, 423
Epispathidium salsum 141, 142, 143K, 147, 166, 167T
Epispathidium securiforme 141, 142, 143, 143K, 154, 154T, 200T, 201, 372
Epispathidium sp. 211
Epispathidium terricola 141, 142, 143K, 196, 224, 228, 372
Epispathidium? *bavariense*, *Spathidium* 142
Epitholiolus chilensis 14
etoschense, *Apocolpodidium* *Apocolpodidium* 9
etoschense, *Spathidium* 33, 62T, 64T, 65, 214, 220T, 225, 227, 276
etoschense, *Spathidium seppelti* 149, 423
etoschense, *Supraspathidium* 8, 335, 336, 338K, 344T, 345T, 345, 346, 354, 360
etoschensis, *Nassula* 8
etoschensis, *Parabryophrya* 9
etoschensis, *Pseudokreyella* 9
etoschensis, *Rostrophryides africana* 9
Etoschophrya oscillatoriophaga 9
extensum, *Spathidium* 35
falciforme, *Spathidium* 230, 233
fastigata, *Colpoda* 207
faurefremietii, *Spathidium* 33, 41, 86, 87T, 337, 358
faurei, *Centrospathidium* 127, 128, 128K, 134, 136
faurei, *Spathidium* 86, 136
fenestrata, *Rostrophrya* 14
fluviatilis, *Bursaria* 418
foliosum, *Cranotheridium* 304, 306
foliosum, *Semibryophyllum* 281, 283T, 283, 285, 285K, 291, 303
foliosus, *Cranotheridium* 303, 304
foliosus, *Pseudoprorodon* 283, 303, 304, 306
formisanoi, *Colpoda* 9
fraterculum, *Semispathidium* 311, 312, 315K, 328, 329, 330
Frontonia angusta obovate 9
Frontonia depressa 191
fusioplites, *Edaphospathula* 5, 224, 227, 228, 276
fusioplites, *Protospathidium* 224
Gastrostyla bavariensis 15
Gastrostyla Kleinstyla 15
Gastrostyla Kleinstyla bavariensis 14, 15
Gastrostyla minima 14
Gigantothrix 434
gigas, *Enchelys* 361, 362
gigas, *Pseudoprorodon Spathidium* 361, 362
gigas, *Spathidium* 336, 361, 362
gigas, *Supraspathidium* 335, 336, 337K, 358, 361
Gonostomum affine 381, 382
Gonostomum strenuum 319
gracilis, *Edaphospathula* 7, 238, 242
granata, *Nassula* 8, 353
group, *Spathidium bromelicola* 33, 34, 61, 62T, 68
group, *Spathidium claviforme* 233
group, *Spathidium elongatum* 33, 34, 44T, 61, 91
group, *Spathidium procerum* 34, 65, 90, 91
group, *Spathidium wolffi* 33, 34, 85
gymnostomatid 368
gymnostomes 324
halophila, *Parakabliella* 9
halophilus, *Plagiocampides* 9
Haptoria xv, 25, 26, 433
haptorids 25
henleae, *Akidodes* 435
Heterometopus meisterfeldi 1, 15, 16, 17
Heterometopus palaeformis 1, 16
histriomuscorum, *Sterkiella* 416
Holophrya 257
Holophryidae 27
holsatae, *Spathidium* 414
Homalozoon 359, 360
Homalozoon vermiculare 359, 360

- horribile*, *Colpodidium* *Colpodidium* 8
hyalinum, *Spathidium* 3, 28, 38, 160
hypotrachs 83
- Ilisiella elegans* 9
inermis, *Edaphospathula* 8
inflata, *Colpoda* 149
inflatum, *Spathidium* 289
- japonica*, *Cultellothrix* 445
japonica, *Neocultellothrix* 433, 435, 436K, 445
japonicum, *Arcuospathidium* 435, 445
japonicum, *Pseudomonilicaryon* 8
japonicum, *Spathidium* 446
jesnerae, *Enchelyotricha* 8
- kenyaensis*, *Enchelyodon* 9, 10
Kleinstyla 15
Kleinstyla bavariensis, *Gastrostyla* 14, 15
Kleinstyla, *Gastrostyla* 15
Kreutzophrya 312, 314
Kreutzophrya sphagnicola 312, 314
Kuehneltiella namibiensis 9
Kuklikophrya ougandae 353
- Lacrymaria* 219, 338
Lacrymaria teres 335, 336, 337, 338
Lacrymaria truncata 218, 221
Lacrymaria truncatum, *Spathidium* 219, 221
Lacrymaria, *Spathidium* 219
lagyniforme, *Semispathidium* 311, 312, 313T, 315K, 315, 320, 322, 328
lagyniforme, *Spathidium* 312
Lagynophrya 143, 206
lajacola, *Apertospathula* 6
laminarius, *Metopus* 15, 16
Lamtostyla 277
lanceoplites, *Latispathidium* 213, 214, 215K, 215, 217T, 225
lanceoplites, *Spathidium* 213, 215
Latispathidium xv, 28, 213
Latispathidium arboricola 213, 214, 215K, 229, 236T, 266
Latispathidium brachyoplites 213, 214, 215K, 245, 251T
Latispathidium lanceoplites 213, 214, 215K, 215, 217T, 225
Latispathidium simile 213, 214, 215K, 232, 238, 244T, 443
Latispathidium truncatum 213, 214, 215K, 218, 221, 249
Latispathidium truncatum bimacronucleatum 215, 217T, 219, 220T, 220K, 222
Latispathidium truncatum truncatum 215, 219, 220K, 221, 223, 224, 226, 227
latissimum, *Spathidium* 33, 89, 336
latissimum, *Supraspathidium* 89, 336, 337
Legendrea 28, 211
Legendrea loyzeae 211
Levispatha australiensis 418
Levispatha muscorum 43, 47, 58
lieberkuehnii, *Myriokaryon* 358, 360, 362
lieberkuehnii, *Prorodon* 336, 337
lieberkuehnii, *Pseudoprorodon* 360, 361
lieberkuehnii, *Spathidium* 337
lieberkuehnii, *Supraspathidium* 336, 337
lieberkühni, *Spathidium* 136, 337
lieberkühni, *Prorodon* 337
lionoliforme, *Spathidium* 447
lionotiforme, *Arcuospathidium* 446, 447
lionotiforme, *Arcuospathidium cultriforme* 446
lionotiforme, *Cultellothrix* 447
lionotiforme, *Spathidium* 435, 446, 447
lionotiformis, *Cultellothrix* 446
lionotiformis, *Neocultellothrix* 289, 433, 435, 436K, 445, 446
Lionotus 447
Litonotus 447
Litonotus vermicularis 359, 360, 361
Litostomatea 25
loeffleri, *Wolffkossia* 9
longiarmatum, *Semispathidium* 311, 312, 315K, 326, 329, 330
longicaudatum, *Apospathidium* 3, 43, 47, 65, 67, 111, 112, 112K 113T, 114, 117
longicaudatum, *Spathidium* 117, 119
longichilum amphoriforme, *Pharyngospathid-*

- ium* 155, 160, 162, 367, 369, 369K, 370, 370T, 371T, 378, **380**, 401
- longichilum longichilum*, *Pharyngospathidium* 367, 369K, 370, 371T, 372, 373, 374, 375, 376, 377, **378**, 386, 387, 401
- longichilum*, *Pharyngospathidium* 367, 369, 369K, **370**, 378
- longichilum*, *Pharyngospathidium longichilum* 367, 369K, 370, 371T, 372, 373, 374, 375, 376, 377, **378**, 386, 387, 401
- longicolum*, *Spathidium* 314
- longinucleatum*, *Neospathidium* 129, 134, 367, 400, 400K, **401**, 413T, 422
- longiseta*, *Apertospathula* 6
- longitricha*, *Enchelys* 8
- loyezae*, *Legendrea* 211
- lucidum*, *Spathidium* 414
- macrostoma*, *Apocolpodidium* *Phagoon* 9
- macrostoma*, *Spathidium* 149
- macrostomum*, *Spathidium* 141, 149, 367, 372, 374
- macrothrix*, *Schmidingerophrya* 257, 258, 258K, **258**, 268T, 272, 275, 425
- magna*, *Pseudofuscheria* 418
- maldivensis*, *Rostrophrya namibiensis* 9
- Maryna namibiensis costaricensis* 9
- Maryna namibiensis namibiensis* 9
- maupasi*, *Colpoda* 103
- megastoma*, *Enchelyodon* 8
- meisterfeldi*, *Heterometopus* 1, 15, 16, 17
- metabolicum*, *Spathidium* 92
- Metacineta namibiensis* 8
- Metacystis mucosa* 1, 15
- Metopus laminarius* 15, 16
- microstoma*, *Colpodidium Colpodidium* 8
- microthoracids* 83
- minima*, *Gastrostyla* 14
- minutum*, *Centrospathidium* 127, 128, 128K, 137, **138**
- minutum*, *Spathidium* 339
- mucosa*, *Metacystis* 1, 15
- multinucleata*, *Actinobolina* 8
- multinucleatum*, *Arcuospathidium* 149
- multistriata*, *Supraspathidium* 339
- multistriatum*, *Supraspathidium* 335, 336, 337, 338K, **339**, 344T, 345T, 345, 346, 348, 356
- musciola*, *Protospathidium* 5, 12, 326
- musciola*, *Spathidium* 41, 61, 196, 197, 443
- muscorum rhopaloplites*, *Arcuospathidium* 6
- muscorum*, *Levispatha* 43, 47, 58
- Myriokaryon* 337, 360, 361
- Myriokaryon lieberkuehnii* 358, 360, 362
- Myriokaryonidae* 337, 368
- namibicola*, *Protospathidium* 354
- namibicola*, *Spathidium* 346
- namibiense*, *Arcuospathidium* 11, 12, 214, 233, 235, 258, 266
- namibiensis costaricensis*, *Maryna* 9
- namibiensis maldivensis*, *Rostrophrya* 9
- namibiensis namibiensis*, *Maryna* 9
- namibiensis namibiensis*, *Rostrophrya* 14
- namibiensis*, *Kuehneltiella* 9
- namibiensis*, *Maryna namibiensis* 9
- namibiensis*, *Metacineta* 8
- namibiensis*, *Plagiocampa* 9
- namibiensis*, *Rostrophrya namibiensis* 14
- Nassula* 357
- Nassula dragescoi* 8
- Nassula etoschensis* 8
- Nassula granata* 8, 353
- Nassula tuberculata* 14
- Neocultellothrix* xiii, xv, 213, 214, 241, 433, **434**, 436K
- Neocultellothrix atypica* 18, 117, 241, 242, 243, 433, 435, 436K, **439**
- Neocultellothrix coemeterii* 3, 433, 435, 436K, **443**
- Neocultellothrix japonica* 433, 435, 436K, **445**
- Neocultellothrix lionotiformis* 289, 433, 435, 436K, 445, **446**
- Neocultellothrix paucistriata* 433, 435, 436K, **448**
- Neocultellothrix tortisticha* 245, 433, 435, 436K, **449**

- Neocultellothrix velhoi* 18, 87, 289, 433, 435, 436K, **436**
- Neospathidium* xv, 149, 367, 368, 369K, **400**, 400K
- Neospathidium africanum* 367, 395, 400, 400K, 401, **418**, 427T
- Neospathidium brachystichos* 265, 266, 267, 400, 401K, 401, 422, **424**, 427T
- Neospathidium longinucleatum* 129, 134, 367, 400, 400K, **401**, 413T, 422
- obliquum*, *Apocyclidium* 4
- obovate*, *Frontonia angusta* 9
- oscillatorioiphaga*, *Etoschophrya* 9
- otti*, *Dioplitophrya* 8
- ougandae*, *Kuklikophrya* 353
- palaeformis*, *Heterometopus* 1, 16
- palustre*, *Semibryophyllum* 281, 282T, 283, 285, 285K, **291**, 306, 308
- pannonicum*, *Trachelophyllum* 8
- papillatum*, *Spathidium* 189
- papilliferum*, *Epispathidium* 141, 142, 143K, 147, **174**, 192T, 194T, 211
- papilliferum*, *Spathidium* 142, 14, 180, 189, 190
- papilliferum*, *Vartospathidium* 174
- Parabryophrya etoschensis* 9
- paradoxa*, *Edaphospathula* 5, 8, 250
- Paraenchelys pulchra* 8
- Parakabliella binucleate* 14
- Parakabliella halophila* 9
- paucistriata*, *Cultellothrix* 7, 435, 448
- paucistriata*, *Neocultellothrix* 433, 435, 436K, **448**
- pelobia*, *Apertospathula* 6
- pelobium*, *Arcuospathidium* 6
- pentadactyla*, *Plagiocampa* 9
- periar mata*, *Armatospathula* 7
- peritrich* 9
- Phagoon macrostoma*, *Apocolpodidium* 9
- Pharyngospathidiidae** xv, 18, 25, 27, **367**, 369K
- pharyngospathidiids 368
- Pharyngospathidium* xv, 149, 318, 367, 368, 369K, **369**, 369K, 401
- Pharyngospathidium bavariense* 367, 369, 369K, 390, 392, 395, **398**, 399, 400
- Pharyngospathidium longichilum* 367, 369, 369K, **370**, 378
- Pharyngospathidium longichilum amphoriforme* 155, 160, 162, 367, 369, 369K, 370, 370T, 371T, 378, **380**, 401
- Pharyngospathidium longichilum longichilum* 367, 369K, 370, 371T, 372, 373, 374, 375, 376, 377, **378**, 386, 387, 401
- Pharyngospathidium pseudobavariense* 367, 369, 369K, 370T, 371, **389**, 398, 422
- Pharyngospathidium simplinucleatum* 367, 369, 369K, 391, **399**, 401, 403, 425
- Phialina serranoi* 1, 15
- plagia*, *Dexiotricha* 339
- Plagiocampa namibiensis* 9
- Plagiocampa pentadactyla* 9
- Plagiocampides halophilus* 9
- Plesiocaryon terricola* 9
- plurinucleate*, *Armatospathula* 7
- plurinucleate*, *Spathidium spathula* 90
- plurinucleatum*, *Spathidium* 90
- Podophrya* 164
- Podophrya tristriata* 8
- polymorphum*, *Spathidium* 202, 205, 206
- polynucleate*, *Enchelys* 326
- polynucleatum*, *Epispathidium* 34, 91, 96, 141, 142
- polynucleatum*, *Spathidium* 33, 34, 91, **96**, 104T, 141, 142, 147, 205
- polyvacuolatum*, *Spathidium* 33, **90**, 336
- polyvacuolatum*, *Supraspathidium* 90, 336, 337
- procerum* group, *Spathidium* 34, 65, 90, 91
- procerum*, *Spathidium* 34, 35, 91, 94, 95, 250
- Prorodon lieberkuehnii* 336, 337
- Prorodon lieberkuehnii* 337
- Protista xv
- Protocyclidium terricola* 103
- protospathidiids 245
- Protospathidium* 11, 12, 27, 35, 38, 50, 59, 61, 75, 83, 143, 216, 239, 261, 266, 276, 312

- Protospathidium arenicola* 5, 8
Protospathidium bonneti 10
Protospathidium fusioplites 224
Protospathidium muscicola 5, 12, 326
Protospathidium namibicola 354
Protospathidium serpens 12, 250
Protospathidium terricola 215
Protospathidium vermiculus 8, 215
***Protospathidium vermiforme* 10, 266, 276**
 Protospathidiidae 25, 27
Ps. ? elongatum, *Cranotheridium* 360
***pseudobavariense*, *Pharyngospathidium* 367, 369, 369K, 370T, 371, 389, 398, 422**
Pseudocohnilembus sp. 270
Pseudocolpodidium, *bradburyarum*, *Colpodidium* 8
Pseudofuscheria magna 418
Pseudoholophrya 143, 207
Pseudokreyella etoschensis 9
Pseudomonilicaryon japonicum 8
Pseudoprorodon 303, 359, 360, 361, 362
Pseudoprorodon Cranotheridium elongatus 359, 360
Pseudoprorodon foliosus 283, 303, 304, 306
Pseudoprorodon lieberkuehnii 360, 361
Pseudoprorodon Spathidium gigas 361, 362
pulchra, *Paraenchelys* 8
***pulchrum*, *Semispathidium* 311, 312, 315K, 328, 329, 330**
pyriformis, *Apometopus Apometopus* 16
pyriformis, *Tetrachymena* 416

rectitoratum, *Epispathidium amphoriforme* 198
rectitoratum, *Spathidium* 160
rectitoratum, *Spathidium amphoriforme* 155, 158, 160, 197, 198, 200T, 201
***regium*, *Epispathidium* 141, 142, 143, 143K, 144, 150T, 160, 164, 170, 172, 395, 423**
revoluta, *Drepanomonas* 373, 379
rhopaloplites, *Arcuospathidium muscorum* 6
Rostrophrya fenestrata 14
Rostrophrya namibiensis maldivensis 9
Rostrophrya namibiensis namibiensis 14
Rostrophryides africana etoschensis 9

***rusticanum*, *Spathidium* 4, 33, 62T, 68, 74, 82T, 425**

***salsum*, *Epispathidium* 141, 142, 143K, 147, 166, 167T**
saprophilum curvioplites, *Spathidium* 33, 62T, 67, 70, 71, 73T
saprophilum saprophilum, *Spathidium* 33, 62T, 66, 67, 68, 73T, 74
saprophilum, *Spathidium* 33, 67, 68, 69, 74, 75, 95
saprophilum, *Spathidium saprophilum* 33, 62T, 66, 67, 68, 73T, 74
scalpriforme, *Arcuospathidium cultriforme* 447
schmidingeri, *Apobryophyllum* 445
***Schmidingerophrya* xv, 28, 257, 258K**
***Schmidingerophrya bisticha* 257, 258, 258K, 266, 267, 268T, 270, 271, 272**
Schmidingerophrya macrobrix 257, 258, 258K, 258, 268T, 272, 275, 425
securiforme, *Epispathidium* 141, 142, 143, 143K, 154, 154T, 200T, 201, 372
securiforme, *Epispathidium amphoriforme* 154, 160
securiforme, *Spathidium* 155, 158
securiforme, *Spathidium amphoriforme* 142, 154, 155, 157, 158, 160, 62, 200T, 201, 380
***Semibryophyllum* xv, 28, 258, 281, 285K**
***Semibryophyllum cultellum* 281, 282T, 283, 285K, 285, 291, 293, 303, 306**
***Semibryophyllum foliosum* 281, 283T, 283, 285, 285K, 291, 303**
***Semibryophyllum palustre* 281, 282T, 283, 285, 285K, 291, 306, 308**
Semiplatyophrya acrostoma 9
***Semispathidium* xv, 28, 143, 207, 311, 312, 315K**
***Semispathidium armatum* 311, 312, 313T, 315K, 315, 320, 328**
***Semispathidium breviarmatum* 311, 312, 315K, 325, 328**
***Semispathidium enchelyodontides* 311, 312, 313T, 315K, 315, 320, 322, 328**
***Semispathidium fraterculum* 311, 312, 315K,**

- 328, **329**, 330
Semispathidium lagyniforme 311, 312, 313T, 315K, 315, 320, **322**, 328
Semispathidium longiarmatum 311, 312, 315K, **326**, 329, 330
Semispathidium pulchrum 311, 312, 315K, 328, 329, **330**
Semispathidium sp. 326
seppelti etoschense, *Spathidium* 149, 423
seppelti seppelti, *Spathidium* 423
seppelti, *Spathidium* 395, 423
seppelti, *Spathidium seppelti* 423
serpens, *Protospathidium* 12, 250
serpens, *Spinispatha* 250
serranoi, *Phialina* 1, 15
simile, *Latispathidium* 213, 214, 215K, 232, **238**, 244T, 443
similis, *Apertospathula* 6
simplinucleatum, *Pharyngospathidium* 367, 369, 369K, 391, **399**, 401, 403, 425
simplinucleatum, *Spathidium* 369, 399
simplinucleatum, *Spathidium bavariense* 398, 399
sp., *Epispathidium* 211
sp., *Pseudocohnilembus* 270
sp., *Semispathidium* 326
sp., *Spathidium* 221, 423
Spathidia 29
spathiidiid(s) xiii, 1, 3, 25, 26, 143, 368
Spathidiida 25, **26**, 27K
Spathidiidae 25, 26, **27**, 33, 111, 112, 127, 141, 142, 213, 214, 257, 281, 283, 312, 335, 336, 337, 367, 368
Spathidiina 26, 368, 434
Spathidium xv, 1, 2, 3, 11, 12, 25, 26, 27, **28**, 29, 33, 34, 38, 39, 43, 53, 59, 75, 83, 85, 91, 97, 103, 111, 127, 136, 141, 142, 143, 160, 170, 190, 197, 204, 213, 214, 224, 228, 258, 260, 276, 283, 290, 306, 311, 312, 314, 319, 320, 335, 336, 337, 338, 361, 362, 367, 369, 374, 395, 400, 401, 403, 423
Spathidium aciculare 33, 62T, 64T, **65**, 68, 220T, 227
Spathidium amphoriforme 142, 155, 157, 158, 197, 198, 200T, 201
Spathidium amphoriforme amphoriforme 157, 158, 200T, 201
Spathidium amphoriforme rectitoratum 155, 158, 160, 197, 198, 200T, 201
Spathidium amphoriforme securiforme 142, 154, 155, 157, 158, 160, 62, 200T, 201, 380
Spathidium anguilla 33, 34, 71, 74, **91**, 92T, 276
Spathidium apospathidiforme 33, 34, 35, 37, 38, 38T, **43**, 44T, 112, 114, 119, 301
Spathidium ascendens 142, 202, 207
Spathidium atypicum 117, 435, 439, 441, 442, 443
Spathidium bavariense 142, 369, 389, 398, 400
Spathidium bavariense bavariense 398
Spathidium bavariense simplinucleatum 398, 399
Spathidium bonneti 11, 12, 13, 266, 275
Spathidium brachystichos 265
Spathidium bromelicola 33, 61, 62T, **62**, 63T, 68, 92
***Spathidium bromelicola* group** 33, 34, **61**, 62T, 68
Spathidium canadense 141, **147**, 170, 172, 367, 372
Spathidium canaliculatum 336
Spathidium cithara 285
Spathidium claviforme 215, 233
Spathidium claviforme group 233
Spathidium coemeterii 435, 443
Spathidium cylindricum 314
Spathidium depressum 289
Spathidium dispar 33, 34, 37, 38, 38T, 41, 44T, **59**
Spathidium duschli 33, 34, 37, 38, 38T, **59**, 60T, 90, 91
Spathidium elmenteitanum 67
Spathidium elongatum 3, 33, 34, 35, **36**, 38T, 57
Spathidium elongatum 3, 33, 34, 35, **36**, 38T, 57
***Spathidium elongatum* group** 33, **34**, 44T, 61, 91

- Spathidium Epispathidium? bavariense* 142
Spathidium etoschense 33, 62T, 64T, **65**, 214, 220T, 225, 227, 276
Spathidium extensum 35
Spathidium falciforme 230, 233
Spathidium faurefremietii 33, 41, **86**, 87T, 337, 358
Spathidium faurei 86, 136
Spathidium gigas 336, 361, 362
Spathidium gigas, *Pseudoprorodon* 361, 362
Spathidium holsatae 414
Spathidium hyalinum 3, 28, 38, 160
Spathidium inflatum 289
Spathidium japonicum 446
Spathidium Lacrymaria 219
Spathidium Lacrymaria truncatum 219, 221
Spathidium lagyniforme 312
Spathidium lanceoplites 213, 215
Spathidium latissimum 33, **89**, 336
Spathidium lieberkuehnii 337
Spathidium lieberkühni 136, 337
Spathidium lionoliforme 447
Spathidium lionotiforme 435, 446, 447
Spathidium longicaudatum 117, 119
Spathidium longicolum 314
Spathidium lucidum 414
Spathidium macrostoma 149
Spathidium macrostomum 141, 149, 367, 372, 374
Spathidium metabolicum 92
Spathidium minutum 128, 138
Spathidium muscicola 41, 61, 196, 197, 443
Spathidium namibicola 346
Spathidium papillatum 189
Spathidium papilliferum 142, 14, 180, 189, 190
Spathidium plurinucleatum 90
Spathidium polymorphum 202, 205, 206
Spathidium polynucleatum 33, 34, 91, **96**, 104T, 141, 142, 147, 205
Spathidium polyvacuolatum 33, **90**, 336
Spathidium procerum 34, 35, 91, 94, 95, 250
Spathidium procerum group 34, 65, 90, 91
Spathidium rectitoratum 160
Spathidium rusticanum 4, 33, 62T, 68, 74, 82T, 425
Spathidium saprophilum 33, 67, 68, 69, 74, 75, 95
Spathidium saprophilum curvioplites 33, 62T, 67, 70, **71**, 73T
Spathidium saprophilum saprophilum 33, 62T, 66, 67, **68**, 73T, 74
Spathidium securiforme 155, 158
Spathidium seppelti 395, 423
Spathidium seppelti etoschense 149, 423
Spathidium seppelti seppelti 423
Spathidium simplinucleatum 369, 399
Spathidium sp. 221, 423
Spathidium spathula 162, 219, 368, 414
Spathidium spathula plurinucleate 90
Spathidium stammeri 41, 65, 204
Spathidium teres 338
Spathidium terricola 196, 228
Spathidium truncatum 219, 221
Spathidium turgitorum 34, 35, 39, 47, 58, 59, 91, 92, 214
Spathidium vermiculus 138
Spathidium vermiforme 87, 336, 357
Spathidium wolffi 33, **85**, 87T
Spathidium wolffi group 33, 34, **85**
spathula plurinucleate, *Spathidium* 90
spathula, *Enchelys* 162
spathula, *Spathidium* 162, 219, 368, 414
sphagnicola, *Kreutzophrya* 312, 314
Spinispatha serpens 250
stammeri, *Spathidium* 41, 65, 204
Sterkiella histriomuscorum 416
strenuum, *Gonostomum* 319
Supraspathidium xv, 28, 85, 89, 90, 335, **335**, 337K
Supraspathidium armatum 8, 335, 336, 337, 338K, 344T, 345T, 348, **353**, 360
Supraspathidium canaliculatum 336, 337
Supraspathidium elongatum 335, 337, 338K, 339, 358, **359**, 362
Supraspathidium etoschense 8, 335, 336, 338K, 344T, 345T, 345, **346**, 354, 360
Supraspathidium gigas 335, 336, 337K, 358, **361**

- Supraspathidium latissimum* 89, 336, 337
Supraspathidium lieberkuehnii 336, 337
Supraspathidium multistriata 339
Supraspathidium multistriatum 335, 336, 337, 338K, **339**, 344T, 345T, 345, 346, 348, 356
Supraspathidium polyvacuolatum 90, 336, 337
Supraspathidium teres 335, 336, 338K, **338**, 358, 359, 360
Supraspathidium vermiforme 87, 335, 336, 338K, 339, 345, 348, **357**, 360
symmetricus, *Akidodes* 435

taeniatum, *Cranotheridium* 285, 294, 305
teres, *Lacrymaria* 335, 336, 337, 338
teres, *Spathidium* 338
teres, *Supraspathidium* 335, 336, 338K, **338**, 358, 359, 360
terrenus, *Enchelyodon* 315, 316, 320
terricola, *Apospathidium* 111, 112K, **112**, 113T, 119, 343
terricola, *Dragescozoon* 9
terricola, *Enchelys* 315
terricola, *Epispathidium* 141, 142, 143K, **196**, 224, 228, 372
terricola, *Plesiocaryon* 9
terricola, *Protocyclidium* 103
terricola, *Protospathidium* 215
terricola, *Spathidium* 196, 228
Tetrahymena pyriformis 416
Teuthophrys 206
thecatium, *Enchelydium* 414, 415
tortisticha, *Cultellothrix* 7, 435, 449
tortisticha, *Neocultellothrix* 245, 433, 435, 436K, **449**
Trachelophyllum 143
Trachelophyllum africanum 8
Trachelophyllum pannonicum 8
trichocystiferum, *Colpodidium Colpodidium* 8
trinucleatus, *Condyllostomides* 9
tristriata, *Podophrya* 8
truncata, *Lacrymaria* 218, 221

truncatum bimacronucleatum, *Latispathidium* 215, 217T, 219, 220T, 220K, **222**
truncatum truncatum, *Latispathidium* 215, 219, 220K, **221**, 223, 224, 226, 227
truncatum, *Latispathidium* 213, 214, 215K, **218**, 221, 249
truncatum, *Latispathidium truncatum* 215, 219, 220K, **221**, 223, 224, 226, 227
truncatum, *Spathidium* 219, 221
truncatum, *Spathidium Lacrymaria* 219, 221
tuberculata, *Nassula* 14
turgitorum, *Spathidium* 34, 35, 39, 47, 58, 59, 91, 92, 214

Vartospathidium 174, 180, 190
Vartospathidium papilliferum 174
velhoi, *Cultellothrix* 6, 433, 434, 435, 436, 437, 438
velhoi, *Neocultellothrix* 18, 87, 289, 433, 435, 436K, **436**
vermiculare, *Homalozoon* 359, 360
vermicularis, *Litonotus* 359, 360, 361
vermiculus, *Protospathidium* 8, 215
vermiculus, *Spathidium* 138
vermiforme, *Apobryophyllum* 8
vermiforme, *Arcuospathidium* 270
vermiforme, *Protospathidium* **10**, 266, 276
vermiforme, *Spathidium* 87, 336, 357
vermiforme, *Supraspathidium* 87, 335, 336, 338K, 339, 345, 348, **357**, 360
vermiformis, *Enchelyodon* 314, 320
verrucosum, *Centrospathidium* 127, 128K, **128**, 129T, 138
verruculosum, *Centrospathidium* 129, 134, 135
virugense, *Arcuospathidium* 7
virugense, *Arcuospathidium* 7
vlassaki, *Arcuospathidium* 214
Vorticella astyliformis 103

wolffi group, *Spathidium* 33, 34, **85**
wolffi, *Spathidium* 33, **85**, 87T
Wolfskasia loeffleri 9

Table index

Table 3.1	<i>Spathidium elongatum</i> group 38
Table 3.2	<i>Spathidium elongatum</i> , <i>Spathidium dispar</i> , <i>Spathidium apospathidiforme</i> 44
Table 3.3	<i>Spathidium duschli</i> 60
Table 3.4	<i>Spathidium bromelicola</i> 62
Table 3.5	<i>Spathidium bromelicola</i> 63
Table 3.6	<i>Spathidium aciculare</i> , <i>Spathidium etoschense</i> 64
Table 3.7	<i>Spathidium sapophilum</i> , <i>Spathidium sapophilum curvioplites</i> 73
Table 3.8	<i>Spathidium rusticanum</i> 82
Table 3.9	<i>Spathidium wolffi</i> , <i>Spathidium faurefremietii</i> 87
Table 3.10	<i>Spathidium anguilla</i> 92
Table 3.11	<i>Spathidium polynucleatum</i> 104
Table 4.1	<i>Apospathidium terricola</i> , <i>Apospathidium longicaudatum</i> 113
Table 5.1	<i>Centrospathidium verrucosum</i> 129
Table 6.1	<i>Epispathidium regium</i> 150
Table 6.2	<i>Epispathidium securiforme</i> 154
Table 6.3	<i>Epispathidium salsum</i> 167
Table 6.4	<i>Epispathidium papilliferum</i> 192
Table 6.5	<i>Epispathidium papilliferum</i> 194
Table 6.6	<i>Spathidium amphoriforme</i> 200
Table 7.1	<i>Latispathidium lanceoplites</i> , <i>Latispathidium truncatum bimicronucleatum</i> 217
Table 7.2	<i>Latispathidium truncatum bimicronucleatum</i> , <i>Spathidium aciculare</i> , <i>Spathidium etoschense</i> 220
Table 7.3	<i>Latispathidium arboricola</i> 236
Table 7.4	<i>Latispathidium simile</i> 244
Table 7.5	<i>Latispathidium brachyoplites</i> 251
Table 8.1	<i>Schmidingerophrya macrothrix</i> , <i>Schmidingerophrya bisticha</i> 268
Table 8.2	<i>Schmidingerophrya macrothrix</i> 272
Table 9.1	<i>Semibryophyllum cultellum</i> , <i>Semibryophyllum palustre</i> 282
Table 9.2	<i>Semibryophyllum foliosum</i> 283
Table 10.1	<i>Semispathidium enchelyodontides</i> , <i>Semispathidium armatum</i> , <i>Semispathidium lagyniforme</i> 313
Table 11.1	<i>Supraspathidium etoschense</i> , <i>Supraspathidium armatum</i> , <i>Supraspathidium multistriatum</i> 344
Table 12.1	<i>Pharyngospathidium longichilum amphoriforme</i> 370
Table 12.2	<i>Pharyngospathidium longichilum longichilum</i> , <i>Pharyngospathidium longichilum amphoriforme</i> , <i>Pharyngospathidium pseudobavariense</i> 371
Table 12.3	<i>Neospathidium longinucleatum</i> 413
Table 12.4	<i>Neospathidium africanum</i> , <i>Neospathidium brachystichos</i> 427

