

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

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Edited by

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

In memory of Wilhelm Foissner (1948–2020)

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

Centropathidium nov. gen. 127

Key to species 128

Centropathidium verrucosum nov. spec. 128

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

Centropathidium 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 1

General section to “Revision of some spathidiid genera (Alveolata, Ciliophora, Spathidiida)”, including nomenclatural notes¹

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Abstract

In this general section, a brief introduction to the spathidiids, as well as some notes on the material and methods are made. The availability of the names of 20 new species published by Foissner & Xu (2007) is discussed and some nomenclatural problems concerning new species described by Foissner et al. (2002) are treated. In addition, notes on the type/voucher material of *Metacystis mucosa* Foissner, 2016a, *Phialina serranoi* Foissner, 2016a, *Heterometopus meisterfeldi* Foissner, 2016b, and *Heterometopus palaeformis* (Kahl, 1927) Foissner, 2016b are made. A note on the valid ZooBank number of the author Helmut Berger (Salzburg) is provided. A summary of the taxa described and redescribed and of nomenclatural acts made in the present book is presented. In total, four new subspecies, 19 new species, six new genera, and one new family are described, 12 species are transferred to other genera, and 41 known species and two subspecies are reviewed in the book (Chapters 3–13). Further, three “*Spathidium* groups” are briefly discussed (Chapter 3).

Introduction

Spathidiid ciliates have been one of Wilhelm Foissner’s several favourite groups of ciliates, beside the colpodids (e.g., Foissner 1993). But of course, he was fascinated from all ciliate

¹ This chapter should be referenced as follows: Berger H., Xu K. & Foissner W. (2025): General section to “Revision of some spathidiid genera (Alveolata, Ciliophora, Spathidiida)”, including nomenclatural notes. – Ser. Monogr. Cilioph. 6: 1–24.

taxa, as shown by his long lists of publications and taxa treated (Aescht 2018, Aescht & Berger 2008, Berger & Al-Rasheid 2008; <https://www.wfoissner.at>).

In 2001, W. Foissner and co-workers started a detailed revision of spathidiids. For various reasons, they could not finish this monumental work, inter alia, because *Spathidium* Dujardin, 1841 is a very old and speciose genus. A serious monographic treatment of such a large group is extremely time-consuming. In addition, W. Foissner permanently studied new soil samples from all over the world, resulting in the description of many new spathidiid species in international journals (e.g., Foissner 2003, 2003a, 2003b; Foissner et al. 2014).

In 2023, one of us (H. Berger) found a manuscript in Foissner's archive, dealing with some revised spathidiid genera. Since the text of the systematic section and the illustrations were partly ready for publication, we decided to publish this work as we did it with the terrestrial ciliates from Australia (Foissner & Berger 2021). A major part of the present book deals with genera comprising few to several species. As mentioned above, *Spathidium* is a special case because of the high number of described species (about 150 species/subspecies originally assigned; H. Berger, unpublished data). Only a few species of this genus are treated in detail in the present book (see Chapter 3, that is, Foissner et al. 2025a). The Foissner archive comprises material on several other "*Spathidium*"-species, some of them are likely new to science. Perhaps they will be described in a later publication.

Material and methods

For details on sample sites, see individual descriptions. For a general characterisation of spathidiids and for definition of terms, see general section in Foissner & Xu (2007, p. 1–53). This section also deals with the life cycle, parasitism, and methods necessary for studying spathidiids (further works dealing with methods, are, inter alia, Foissner 1991, 2014, Foissner 2021a, b, Foissner et al. 1991, 1999, 2002). Some pages of the systematic section of Foissner & Xu (2007, p. 54) deal with further important details, namely "How to describe a ciliate?", "Species/subspecies concept", "How to use the monograph", and "Key to families".

Permanent slides (protargol preparations) of the new species/subspecies and of species redescribed in the present book are deposited in the collection of microscopic slides in the Biology Centre of the Upper Austrian Museum in Linz (LI; J.-W.-Kleinstrasse 73, 4040 Linz, Austria); for details on this repository, see Aescht (2003, 2008, 2013, 2018). For details on slides (accession numbers = registration numbers = inventory numbers; photographs), see individual species/subspecies.

In the present book, the descriptions of some species contain combined data of two or more populations. Such a practice, which was sometimes applied by Foissner and co-workers, is not recommended because one can never exclude that the populations do not belong to the same species, even when the data are very similar. It is better to describe the type population (in the case of a new species) or the best-studied population (in the case of a redescription) in detail and to mention the deviating features of the other populations in a separate chapter. For the same reason it is recommended to characterise the holotype specimen separately (except when your population is a clone), at least morphometrically (see Weisse et al. 2013; see also ICZN 1999, Recommendation 73C.1). Due to time reasons we (H. Berger, K. Xu) did not write such descriptions new. In some cases, the raw manuscript

did not contain references to some statements, mainly in the Remarks section. An example is the comparison of *Spathidium elongatum* nov. spec. (see Chapter 3, that is, Foissner et al. 2025a) with the type species of *Spathidium*, *Spathidium hyalinum* Dujardin, 1841, a species not yet characterised in detail. Not in all such cases we could add the lacking references.

Foissner & Xu (2007, p. 40, Fig. 28) distinguished nine types of resting cysts (see there for details on this stage of the life cycle). “*Cultellothrix coemeterii*” (now *Neocultellothrix coemeterii* (Kahl, 1943) Foissner & Xu in Berger et al., 2025) has a Type III cyst according to the legend to Figure 28 of Foissner & Xu (2007, p. 38). In the description of this species, Foissner & Xu (2007, p. 279) wrote that this species has a “Type I resting cyst”. A further mistake in Fig. 28 in Foissner & Xu (2007) is the incorrect labelling (VII instead of VIII) of the Type VIII cyst of *Apospathidium atypicum* (now *Apospathidium longicaudatum* (Buitkamp, 1977) Foissner et al., 2025c in present book).

The faunistic records of the known species reviewed in the present work are likely not complete because not each post-2000 work dealing with spathidiids and containing a faunal list was checked in detail. From other groups it is known that such a compilation is extremely time consuming (Berger 1999, 2006, 2008, 2011, 2018a, b, c; Foissner 1993; Foissner & Xu 2007; Foissner et al. 1999; Vdačný & Foissner 2012).

Genus-group names are always written out to improve the search function in the PDF file. In the section “Nomenclature” the German term “Bindevokal” (see Werner 1972, p. 36) is translated as “thematic vowel” according to Terrell et al. (1999, p. 146). Another English translation of “Bindevokal” is “connecting vowel” (<https://en.langenscheidt.com/german-english/bindevokal#sense-1.1.1>; accessed 13 Jul 2024).

The length specifications mentioned in the figure legends refer to the body length (length of cell body), unless otherwise indicated. The difference between cell length and body length in ciliates is explained in Fig. 1.1a, b.²

For photographing the type slides, they have been placed on a white sheet of paper with a 5 mm-grid of black dots. The photos have been taken with a smartphone (Samsung Galaxy S8+) under somewhat suboptimal conditions of illumination and thus they are not perfect. A photographic documentation of the deposited slides has the advantage that the position of marks (usually black ink circles on the cover glass) is known even when they disappear, for example, due to oil immersion or cleaning of the slides. For a more simple and precise method of marking relevant specimens on a microscopic slide, see Berger (2021). With some microscopes it is not possible to go to the “zero point” (= lower left corner of slide) shown in Fig. 2 in Berger (2021). In such a case it is recommended to fix the lower left corner of the cover glass as “zero point”. Anyhow, when you use this method, do not forget to describe which zero point you used. For most slides, a sheet of paper equally sized to the slide is available showing the positions of relevant specimens (e.g., holotype; Fig. 13.2b in Chapter 13, that is, Berger et al. 2025). This sheet of paper was termed “protocol” by Aescht (2008, p.

² Note by H. Berger: As reviewer of international journals and as associate editor of the European Journal of Protistology (Elsevier) I made the experience that some workers prefer the term “cell length” against “body length” in ciliate taxonomy. However, the terms “cell body” or “body” are in general use in protistology, including relevant textbooks on ciliates, for example, in Corliss (1979, p. 12, at term “Cilium”, line 2, “... from the body surface ...”; p. 35, at term “Tentacle”, line 3, “... and localized (often apically) on the body”; p. 38, at legend to Plate I, line 2, “... from apical or anterior pole of body”), in Hausmann et al. (2003, p. 218, at heading “Body bending”, lines 1, 2, “... fold or stretch their cell bodies”), or in Lynn (2008, p. 24, at term “Cortex”, line 2, “... portion or ‘layer’ of the ciliate body”).

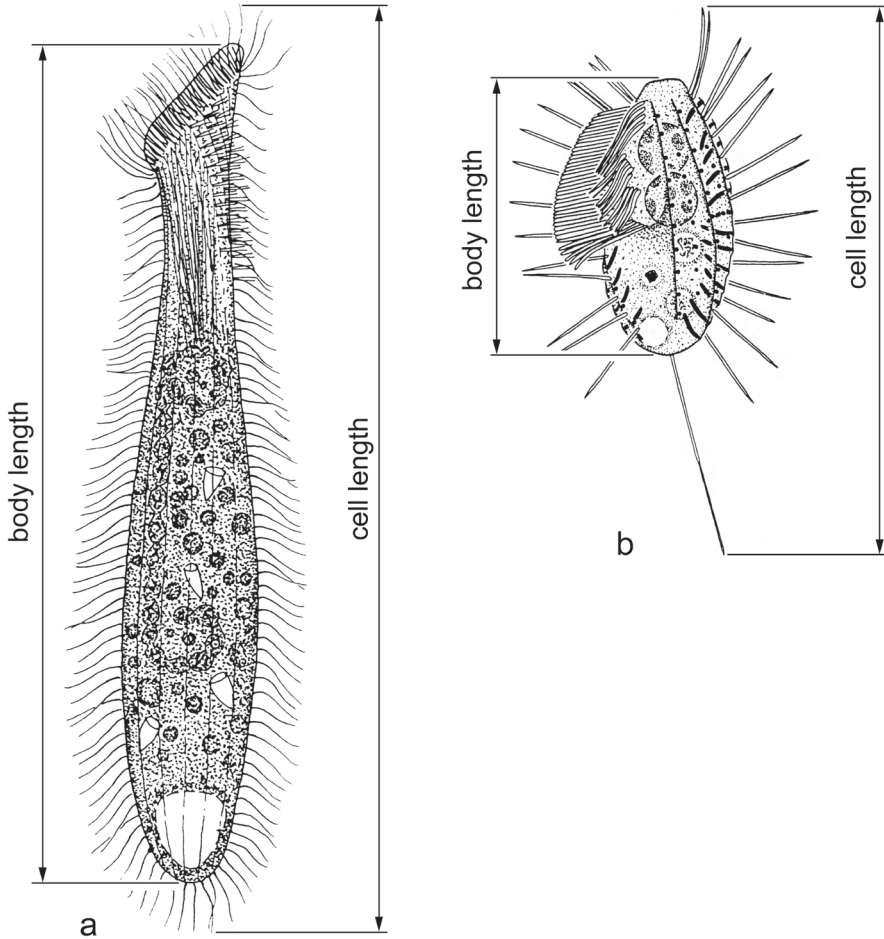


Fig. 1.1a, b Illustrations to demonstrate the difference between cell length and body length in ciliates. *Spathidium rusticanum* in left lateral view (a) and *Apocyclidium obliquum* in ventrolateral view (b) (a, from Foissner 1981; b, from Foissner et al. 2002. From life). Since the cilia (“cylindrical organelles arising from a kinetosomal base projecting from the body surface ...” according to Corliss 1979, p. 12 and Lynn 2008, p. 22) are part of the cell, the cell length comprises the body length plus the length of the cilia which protrude beyond the anterior and posterior end of the cell body. In the present work, the body length is mentioned in the figure legends, unless otherwise indicated.

137, 138). In the plates showing the slides, the protocol is, if available, always shown underneath the corresponding slide. In the print edition, the slides are depicted in original size (76 × 26 mm). For explanation of labelling of slides, see Fig. 8 in Foissner (2021b).

The material studied during the course of the present project was largely collected and analysed before 2000. At that time, a gene sequence analysis was not yet a standard procedure. Thus, for only very few species treated in the present book, phylogenetic analyses based on molecular data are available.

The individual chapters of the present book should be cited as shown in the following example: “Berger H., Xu K. & Foissner W. (2025): General section to “Revision of some

spathidiid genera (Alveolata, Ciliophora, Spathidiida)”, including nomenclatural notes, pp. 1–24. Chapter 1 in: Foissner W., Xu K. & Berger H. (eds): Revision of some spathidiid genera (Alveolata, Ciliophora, Spathidiida). Ser. Monogr. Cilioph. 6: xvi + 465 pp.” or “Berger H., Xu K. & Foissner W. (2025): General section to “Revision of some spathidiid genera (Alveolata, Ciliophora, Spathidiida)”, including nomenclatural notes. – Ser. Monogr. Cilioph. 6: 1–24.”

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

Aescht (2008, p. 219) mentioned that 20 names published by Foissner & Xu (2007) are unavailable “because formal “typification” has been forgotten par lapsus”. At the individual species (e.g., Aescht 2008, p. 143, “*arenicola Protospathidium* Foissner & Xu, 2007”) she wrote under remarks “Nomenclaturally unavailable due to aphory (see Glossary; ICZN 1999, Art 72.3).” Article 72.3 of the ICZN (1999) reads as follows: “Name-bearing types must be fixed originally for nominal species-group taxa established after 1999. A proposal of a new nominal species-group taxon after 1999 (unless denoted by a new replacement name (nomen novum) [Arts. 16.4, 72.7]), must include the fixation of a holotype [Art. 16.4] (see Article 73.1) or syntypes [Art. 73.2]. In the case of syntypes, only those specimens expressly indicated by the author to be those upon which the new taxon was based are fixed as syntypes.” According to Article 16.4 of the ICZN (1999), not only a holotype (or syntypes) must be fixed explicitly (Article 16.4.1), but the original description must also contain a statement that the types are (will be) deposited in a collection and by a statement indicating the name and location of the collection (Article 16.4.2).

Foissner & Xu (2007) did not provide an own chapter “Type material” (as, for example, Foissner 2003b, p. 150) for the individual new species. However, they designated for each new species (for example, *Edaphospathula paradoxa* Foissner & Xu, 2007; p. 67) a single cell as holotype specimen in the legend to the figures (e.g., legend to Fig. 34m–q on page 70 of Foissner & Xu 2007 in present example), that is, the specimen shown in this figure was fixed as holotype. That is, Article 16.4.1 is fulfilled. For Article 16.4.2 the situation is ambiguous. Unfortunately, Foissner & Xu (2007) did not make a comment about the type material in the “General section” (their pages ix, xi, 1–56). Foissner & Xu (2007, p. 60) revised *Edaphospathula fusioplites* (Foissner et al., 2005) Foissner & Xu, 2007. In the sole entry (the original description by Foissner et al. 2005) in the list of synonyms of this species they mentioned that “Type slides with protargol-impregnated specimens from type and voucher localities are deposited in the Oberösterreichische Landesmuseum in Linz, Upper Austria”. The observations from the population from Kenya (a “voucher locality”) are original data in Foissner & Xu (2007, p. 64 and their Table 2). From this statement³ one can conclude that Foissner & Xu (2007) also deposited (or will deposit) the other material (holotypes and paratypes of new species described by Foissner & Xu 2007) in the same collection. For accession numbers

³ The statement is: They deposited original material (= voucher material of a Kenya population of *Edaphospathula fusioplites*) in the Biology Centre of the Upper Austrian Museum in Linz. At *Protospathidium muscicola* Dragesco & Dragesco-Kernéis, 1979, Foissner & Xu (2007, p. 119) also mentioned that type material will be deposited in this depository.

of all these slides, see Aescht (2008).⁴ When this argumentation is accepted, then Article 16.4.2 of the ICZN (1999) is likewise fulfilled and the 20 new names in Foissner & Xu (2007) are available. However, when this explanation is not accepted then the new species of Foissner & Xu (2007) have to be described again, as we did it for *Cultellothrix velhoi* Foissner, 2003a (see Chapter 13, that is, Berger et al. 2025). Whoever makes this correction shall (must?) assign the new species to “Foissner & Xu”.

The following species originally described by Foissner & Xu (2007) are concerned by the problem discussed above (alphabetically arranged according to original combination):

Apertospathula cuneata Foissner & Xu, 2007; p. 346. Remarks: Specimen shown in Fig. 99c, d in Foissner & Xu (2007, p. 347) originally fixed as holotype. Accession numbers of the type slides in the Biology Centre of Upper Austrian Museum in Linz are according to Aescht (2008, p. 151): 2007/36 (holotype); 2007/34, 35, 36 (paratypes).

Apertospathula lajacola Foissner & Xu, 2007; p. 359. Remarks: Specimen shown in Fig. 102k–n in Foissner & Xu (2007, p. 361) originally fixed as holotype. Accession numbers of the type slides in the Biology Centre of Upper Austrian Museum in Linz are according to Aescht (2008, p. 162): 2007/33 (holotype); 2007/29, 30, 31, 32, 33 (paratypes).

Apertospathula longiseta Foissner & Xu, 2007; p. 342. Remarks: Specimen shown in Fig. 98h, i in Foissner & Xu (2007, p. 344) originally fixed as holotype. Accession numbers of the type slides in the Biology Centre of Upper Austrian Museum in Linz are according to Aescht (2008, p. 163): 2007/28 (holotype); 2007/24, 25, 26, 27, 28 (paratypes).

Apertospathula pelobia Foissner & Xu, 2007; p. 362. Remarks: Specimen shown in Fig. 102d, e in Foissner & Xu (2007, p. 363) originally fixed as holotype. Accession numbers of the type slides in the Biology Centre of Upper Austrian Museum in Linz are according to Aescht (2008, p. 172): 2007/45 (holotype); 2007/41, 42, 43, 44 (paratypes).

Apertospathula similis Foissner & Xu, 2007; p. 339. Remarks: Specimen shown in Fig. 97d, e in Foissner & Xu (2007, p. 340) originally fixed as holotype. Accession numbers of the type slides in the Biology Centre of Upper Austrian Museum in Linz are according to Aescht (2008, p. 178): 2007/26 (holotype); 2007/23, 24, 27 (paratypes).

Arcuospathidium deforme Foissner & Xu, 2007; p. 170. Remarks: Specimen shown in Fig. 59e, f in Foissner & Xu (2007, p. 171) originally fixed as holotype. Accession numbers of the type slides in the Biology Centre of Upper Austrian Museum in Linz are according to Aescht (2008, p. 151): 2007/50 (holotype); 2007/42, 43, 45, 46, 47, 48, 49 (paratypes).

Arcuospathidium muscorum rhopaloplites Foissner & Xu, 2007; p. 200. Remarks: Specimen shown in Fig. 66g, h in Foissner & Xu (2007, p. 201) originally fixed as holotype. Accession numbers of the type slides in the Biology Centre of Upper Austrian Museum in Linz are according to Aescht (2008, p. 168): 2007/147 (holotype); 2007/147, 148, 149, 150, 151 (paratypes).

Arcuospathidium pelobium Foissner & Xu, 2007; p. 164. Remarks: Specimen shown in Fig. 58i, j in Foissner & Xu (2007, p. 165) originally fixed as holotype. Accession numbers

⁴ Obviously Foissner & Xu (2007) deposited the type material of all these species already in 2007 according to the accession numbers listed by Aescht (2008). Only for *Arcuospathidium virungense* Foissner & Xu, 2007 no type material has been deposited so far (see below). We will try to find the slide(s) in the private collection of W. Foissner. At least when the whole private slide collection of W. Foissner is deposited in Linz, Article 16.4.2 will be fulfilled. Thus, we preliminarily assume that *Arcuospathidium virungense* is validly described; needs more detailed analysis.

of the type slides in the Biology Centre of Upper Austrian Museum in Linz are according to Aescht (2008, p. 172): 2007/51 (holotype); 2007/52, 53, 54 (paratypes).

Arcuospathidium virungense Foissner & Xu, 2007; p. 213. Remarks: Specimen shown in Fig. 69c, d, f, h in Foissner & Xu (2007, p. 214) originally fixed as holotype. In contrast to the other species listed in this subchapter, so far no type slides have been deposited in the Biology Centre of Upper Austrian Museum in Linz according to Aescht (2008, p. 192; 2018, p. 497). For further details, see footnote 4. “*Arcuospathidium virungense* Foissner & Xu, 2007” in Aescht (2008, p. 192) is an incorrect subsequent spelling.

Armatospathula costaricana Foissner & Xu, 2007; p. 313. Remarks: Specimen shown in Fig. 91j–m in Foissner & Xu (2007, p. 315) originally fixed as holotype. Accession numbers of the type slides in the Biology Centre of Upper Austrian Museum in Linz are according to Aescht (2008, p. 150): 2007/68 (holotype); 2007/65, 66, 67, 68 (paratypes). Aescht (2008, p. 150, 211) incorrectly assumed that this is the type species (= nucleospecies in her terminology) of *Armatospathula* Foissner & Xu, 2007.

Armatospathula periarinata Foissner & Xu, 2007; p. 308. Remarks: Specimen shown in Fig. 90f–h in Foissner & Xu (2007, p. 309) originally fixed as holotype. Accession numbers of the type slides in the Biology Centre of Upper Austrian Museum in Linz are according to Aescht (2008, p. 173): 2007/69 (holotype); 2007/69, 70, 71 (paratypes). Type species of *Armatospathula* Foissner & Xu, 2007. When the argumentation for a valid typification of the species presented above is not accepted, then *Armatospathula* Foissner & Xu, 2007 is, like *Cultellothrix* Foissner, 2003a, not an available genus-group name (see Chapter 13, that is, Berger et al. 2025).

Armatospathula plurinucleata Foissner & Xu, 2007; p. 317. Remarks: Specimen shown in Fig. 92i, j in Foissner & Xu (2007, p. 318) originally fixed as holotype. Accession numbers of the type slides in the Biology Centre of Upper Austrian Museum in Linz are according to Aescht (2008, p. 173): 2007/64 (holotype); 2007/61, 62, 63, 64 (paratypes).

Cultellothrix paucistriata Foissner & Xu, 2007; p. 290. Remarks: Specimen shown in Fig. 86c–e in Foissner & Xu (2007, p. 291) originally fixed as holotype. Accession numbers of the type slides in the Biology Centre of Upper Austrian Museum in Linz are according to Aescht (2008, p. 172): 2007/56 (holotype); 2007/55, 56, 57 (paratypes). For further details on this species, see Chapter 13, that is, Berger et al. (2025).

Cultellothrix tortisticha Foissner & Xu, 2007; p. 294. Remarks: Specimen shown in Fig. 87i, j in Foissner & Xu (2007, p. 296) originally fixed as holotype. Accession numbers of the type slides in the Biology Centre of Upper Austrian Museum in Linz are according to Aescht (2008, p. 183): 2007/59 (holotype); 2007/58, 59, 60 (paratypes).

Edaphospathula brachycaryon Foissner & Xu, 2007; p. 85. Remarks: Specimen shown in Fig. 38j, k in Foissner & Xu (2007, p. 86) originally fixed as holotype. Accession numbers of the type slides in the Biology Centre of Upper Austrian Museum in Linz are according to Aescht (2008, p. 147): 2007/116 (holotype); 2007/116, 117, 118, 119, 120 (paratypes).

Edaphospathula gracilis Foissner & Xu, 2007; p. 88. Remarks: Specimen shown in Fig. 39j, k in Foissner & Xu (2007, p. 90) originally fixed as holotype. Accession numbers of the type slides in the Biology Centre of Upper Austrian Museum in Linz are according to Aescht (2008, p. 157): 2007/113 (holotype); 2007/113, 114, 115 (paratypes).

Edaphospathula inermis Foissner & Xu, 2007; p. 76. Remarks: Specimen shown in Fig. 36e–g in Foissner & Xu (2007, p. 77) originally fixed as holotype. Accession numbers of the type slides in the Biology Centre of Upper Austrian Museum in Linz are according to Aescht (2008, p. 160): 2007/110 (holotype); 2007/110, 111, 112 (paratypes).

Edaphospathula paradoxa Foissner & Xu, 2007; p. 67. Remarks: Specimen shown in Fig. 34m–q in Foissner & Xu (2007, p. 70) originally fixed as holotype. Accession numbers of the type slides in the Biology Centre of Upper Austrian Museum in Linz are according to Aescht (2008, p. 171): 2007/105 (holotype); 2007/101, 102, 103, 104, 105 (paratypes).

Protospathidium arenicola Foissner & Xu, 2007; p. 110. Remarks: Specimen shown in Fig. 43g, h in Foissner & Xu (2007, p. 111) originally fixed as holotype. Accession numbers of the type slides in the Biology Centre of Upper Austrian Museum in Linz are according to Aescht (2008, p. 143): 2007/125 (holotype); 2007/125, 126, 127, 128 (paratypes).

Protospathidium vermiculus (Kahl, 1926) Foissner & Xu, 2007; p. 99. Remarks: Specimen shown in Fig. 41l, m in Foissner & Xu (2007, p. 103) originally fixed as “main neotype specimen”. Accession numbers of the type slides in the Biology Centre of Upper Austrian Museum in Linz are according to Aescht (2008, p. 185): 2007/121, 122, 123, 124 (neotypes).

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

Foissner et al. (2002) described many new species and subspecies (see Foissner et al. 2002, p. 90). According to Articles 16.4 and 72.3 of the ICZN (1999), for species described after 1999 not only a holotype (or syntypes) must be fixed explicitly (Article 16.4.1), but the original description must also contain a statement that the types are (will be) deposited in a collection and by a statement indicating the name and location of the collection (Article 16.4.2). Foissner et al. (2002) fixed a holotype explicitly in many descriptions, especially in the legends to the figures, for example for *Enchelys longitricha* Foissner et al., 2002, on page 102 in the legend to figures 13h, i. For rather many other new species, however, no holotype was explicitly fixed in the descriptions/figure legends, namely for *Paraenchelys pulchra* Foissner et al., 2002 (p. 104), *Enchelyodon megastoma* Foissner et al., 2002 (p. 139), *Trachelophyllum africanum* Foissner et al., 2002 (p. 151), *Trachelophyllum pannonicum* Foissner et al., 2002 (p. 155), *Enchelyotricha jesnerae* Foissner et al., 2002 (p. 186), *Dioplitophrya otti* Foissner et al., 2002 (p. 199), *Clavoplites edaphicus* Foissner et al., 2002 (p. 213), *Supraspathidium etoschense* Foissner et al., 2002 (p. 274), *Supraspathidium armatum* Foissner et al., 2002 (p. 280), *Apobryophyllum vermiforme* Foissner et al., 2002 (p. 357), *Pseudomonilicaryon japonicum* Foissner et al., 2002 (p. 378), *Actinobolina multinucleata* Foissner et al., 2002 (p. 383), *Podophrya tristriata* Foissner et al., 2002 (p. 396), *Metacineta namibiensis* Foissner et al., 2002 (p. 404), *Nassula dragescoi* Foissner et al., 2002 (p. 424), *Nassula granata* Foissner et al., 2002 (p. 427), *Nassula etoschensis* Foissner et al., 2002 (p. 438), *Colpodidium (Colpodidium) horribile* Foissner et al., 2002 (p. 474), *Colpodidium (Colpodidium) trichocystiferum* Foissner et al., 2002 (p. 480), *Colpodidium (Colpodidium) microstoma* Foissner et al., 2002 (p. 485), *Colpodidium (Pseudocolpodidium) bradburyarum* Foissner et al., 2002 (p. 489),

Apocolpodidium (Apocolpodidium) etoschense Foissner et al., 2002 (p. 493), *Apocolpodidium (Phagoon) macrostoma* Foissner et al., 2002 (p. 498), *Frontonia angusta obovate* Foissner et al., 2002 (p. 511), *Plagiocampa pentadactyla* Foissner et al., 2002 (p. 539), *Plagiocampa namibiensis* Foissner et al., 2002 (p. 542), *Plagiocampides halophilus* Foissner et al., 2002 (p. 548), *Parakabliella halophila* Foissner et al., 2002 (p. 598), *Anatoliocirrus capari* Özbek & Foissner in Foissner et al., 2002 (p. 617), *Condylostomides trinucleatus* Foissner et al., 2002 (p. 899), *Colpoda formisanoi* Foissner et al., 2002 (p. 905), *Dragescozoon terricola* Foissner et al., 2002 (p. 912), *Kuehneltiella namibiensis* Foissner et al., 2002 (p. 916), *Parabryophrya etoschensis* Foissner et al., 2002 (p. 957), *Etoschophrya oscillatoriophaga* Foissner et al., 2002 (p. 987), *Rostrophrya namibiensis maldivensis* Foissner et al., 2002 (p. 994), *Rostrophryides africana etoschensis* Foissner et al., 2002 (p. 1000), *Semiplatyophrya acrostoma* Foissner et al., 2002 (p. 1019), *Pseudokreyella etoschensis* Foissner et al., 2002 (p. 1023). However, Foissner et al. (2002) provided a table where the fixation of holotype specimens (marked with a ring of ink on the slide and with the letter “H” on the corresponding sheet of paper; see Foissner et al. 2002, p. 36) on holotype slides is documented. In addition, the accession numbers for the holotype and paratype slides (if available) are given in their Table 1 on pages 37–43. The slides have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI; see Foissner et al. 2002, p. 36). Consequently, Articles 16.4 and 72.3 of the ICZN (1999) are fulfilled for these species which are thus validly published. For details, see also Aescht (2008).

According to Table 1 in Foissner et al. (2002, p. 37), two or three holotype slides have been deposited for several new species/subspecies, namely, *Wolfskasia loeffleri* Foissner et al., 2002 (p. 459, two holotype slides deposited), *Colpoda cavicola amiconucleata* Foissner et al., 2002 (p. 910, three holotype slides deposited), *Maryna namibiensis namibiensis* Foissner et al., 2002 (p. 935, two holotype slides deposited), *Maryna namibiensis costaricensis* Foissner et al., 2002 (p. 942, three holotype slides deposited), *Ilsiella elegans* Foissner et al., 2002 (p. 950, two holotype slides from two different sites deposited), *Plesiocaryon terricola* Foissner et al., 2002 (p. 963, two holotype slides deposited). Since a holotype is usually a single specimen which can be present only on one slide these “holotype” fixations are incorrect; in that cases (very likely) syntypes have been deposited (see ICZN 1999, Article 73.2.1.1; see also, for example, Aescht 2008, p. 149 for *Colpoda cavicola amiconucleata* or Aescht 2008, p. 163 for *Wolfskasia loeffleri*).⁵ In some cases, for example *Maryna namibiensis namibiensis*, Aescht (2008, p. 169) states that Foissner et al. (2002) have deposited only one holotype slide and not two as indicated in their Table 1. All these problems should be discussed and clarified (if necessary) when these species are reviewed.

For *Enchelyodon kenyaensis* Foissner et al., 2002 (p. 128) a holotype was fixed in the original description (Fig. 21f–h in Foissner et al. 2002, p. 129). However, Foissner et al. (2002, p. 39) did not mention a type slide in their Table 1 (see also Aescht 2008, p. 193). On the other hand, Foissner et al. (2002, p. 36) stated that for all new species a holotype slide and at least one paratype slide have been deposited in the Biology Centre of the Upper Austrian Museum in Linz. In the present case, the slides obviously have not yet been deposited in the museum, perhaps because a further new, or an already known species which should be

⁵ Of course, in some cases it would be possible to have two or more holotype slides, for example, when you divide a colony of a peritrich (see ICZN 1999, Articles 72.5.2 and 73.1).

redescribed, is contained. According to Article 16.4.2 of the ICZN (1999), the original description must contain “a statement of intent that they [the slides] will be (or are) deposited in a collection ...”. For that reason, we assume that *Enchelyodon kenyaensis* Foissner et al., 2002 is validly published (see also Aescht 2008, p. 219). We will try to find the slide(s) in the private collection of W. Foissner. At least when the whole private slide collection of W. Foissner is deposited in Linz, Article 16.4.2 will be completely fulfilled.

Foissner et al. (2002, p. 310) established *Protopathidium vermiforme*. Since the original description is invalid, we describe it here as new species:

***Protopathidium vermiforme* Foissner, Agatha & Berger nov. spec.**

(Fig. 1.2a–j)

- 1981 *Protopathidium bonneti* nov. comb. (Buitkamp, 1977) – Foissner, Zool. Jb. Syst. 108: 271, Abb. 4a–j (Fig. 69a–j in Foissner et al. 2002 or Fig. 45a–j in Foissner & Xu 2007; description of Austrian population; misidentification).
- 2002 *Protopathidium vermiforme* nov. spec. – Foissner, Agatha & Berger, Denisia 5: 310, Fig. 69a–j (invalid original description because no holotype, or syntypes, fixed).
- 2007 *Protopathidium vermiforme* Foissner, Agatha & Berger, 2002 – Foissner & Xu, Monogr. biol. 81: 116, Fig. 45a–j (detailed revision of invalid species).
- 2008 *Protopathidium vermiforme* Foissner, Agatha & Berger, 2002 – Aescht, Denisia 23: 219 (note on complex nomenclature).

Nomenclature: The species-group name *vermiform-is, -is, -e* ([m, f, n]; shaped like a worm) is a composite of *vermis* (Latin noun, the worm; Hentschel & Wagner 1996, p. 606) and *-form-is, -is, -e* (Latin adjective [m, f, n]; -shaped; see Hentschel & Wagner 1996, p. 274 at *glómeriformis*) and refers to the vermiform body shape. *Protopathidium* is of neuter gender (Aescht 2001, p. 296), thus, *Protopathidium vermiforme* is the correct name.

Foissner et al. (2002, p. 310) established *Protopathidium vermiforme* basing on *Protopathidium bonneti* (Buitkamp, 1977) sensu Foissner (1981) because this is a misidentification. However, they have forgotten to fix a holotype (or syntypes). In addition, they did not mention a type slide in their Table 1 (see Foissner et al. 2002, p. 42). The explicit fixation of a holotype, or syntypes, is, however, a prerequisite for a valid publication of a new specific or subspecific name erected after 1999 (ICZN 1999, Article 16.4.1). Thus, the original description of *Protopathidium vermiforme* by Foissner et al. (2002) is invalid. To make this species valid, we describe it here as new species. In future this species has to be cited as “*Protopathidium vermiforme* Foissner, Agatha & Berger in Berger, Xu & Foissner, 2025” or as “*Protopathidium vermiforme* Foissner et al. in Berger et al., 2025”.

Foissner & Xu (2007, p. 116) mentioned in the list of synonyms under the entry “2002”, that “Type slides with protargol-impregnated specimens are deposited in the Oberösterreichische Landesmuseum in Linz, Upper Austria, under the name *Protopathidium bonneti*.” This “subsequent type fixation” does not make the original description valid because the fixation of a holotype (or syntypes) must be done in the original description (Foissner et al. 2002) for species described after 1999 (ICZN 1999, Articles 16.4.1, 73.1.3).

Aescht (2008) briefly discussed the lacking typification of *Protopathidium vermiforme* Foissner et al., 2002. She wrote that *Protopathidium vermiforme* is a replacement name for the misidentified *Protopathidium bonneti* sensu Foissner (1981). However, *Protopathidium*

vermiforme Foissner et al., 2002 is not a new replacement name (nomen novum, substitute name; see ICZN 1999, p. 109), but the name of a new species.

Diagnosis: Body size $80-160 \times 5-13 \mu\text{m}$ in vivo. Body vermiform with distinct, oblique oral bulge slightly shorter than widest trunk region. About 15 macronucleus nodules. About 8 ciliary rows, 3 of them anteriorly differentiated to conspicuous dorsal brush with up to $8 \mu\text{m}$ long bristles. Oral kinetofragments composed of each 3 or 4 dikinetids.

Type locality: Grassland soil from the immediate vicinity of the “Wallack-Haus” (47.07039°N 12.83873°E , 2304 m above sea level), an alpine hotel at the Grossglockner Hochalpenstrasse, a famous road connecting Carinthia and Salzburg, Austria.⁶

Type material: Foissner (1981) made no comment on the deposition of type and voucher material. One of us (H. Berger) checked the slide collection in the Biology Centre of the Upper Austrian Museum in Linz for the whereabouts of the voucher slides of *Protospathidium bonneti* sensu Foissner (1981); however, no slide(s) could be found. The huge slide collection in the private archive of Foissner in Salzburg was also checked. However, likewise no slides could be found within reasonable time. Thus, we fix the specimen shown in Fig. 1.2f, g (= Abb. 4f, g in Foissner 1981; = Fig. 69f, g in Foissner et al. 2002) as holotype specimen, in agreement with Article 73.1.4 of the ICZN (1999).⁷

ZooBank registration: urn:lsid:zoobank.org:act:D46B8C4A-AC3F-4E60-951C-F441105D9C38

Remarks (from Foissner et al. 2002 and Foissner & Xu 2007; slightly modified): Foissner (1981) redescribed *Spathidium bonneti* Buitkamp, 1977 from soil of the Austrian Central Alps and transferred it to *Protospathidium* Dragesco & Dragesco-Kernéis, 1979, assuming that Buitkamp (1977) overlooked the protospathidiid oral kinetofragments in his population from the Ivory Coast. However, Dragesco & Dragesco-Kernéis (1986, p. 156) doubted Foissner’s identification and suggested that the Austrian population is a new species and Buitkamp’s species the representative of a new genus. As concerns the species, Foissner et al. (2002), Foissner & Xu (2007), and we fully agree with the French workers because we learned that there are quite a lot of slender spathidiids in soil, some of which have, like Buitkamp’s species, a continuous circumoral kinety, for instance, *Arcuospathidium namibiense* Foissner et al., 2002 (for revision, see Foissner & Xu 2007, p. 177). Comparing the figures of *Protospathidium vermiforme* Foissner et al. nov. spec. (Fig. 1.2a–c) with that of *Spathidium bonneti* (Abb. 4 in Buitkamp 1977; Fig. 62n, o in Foissner & Xu 2007), Foissner’s misidentification appears understandable. Such mistakes are simply caused by the great ignorance of ciliate diversity outside the holarctic region. Whether Buitkamp’s species belongs to *Spathidium* Dujardin, 1841 or *Arcuospathidium* Foissner, 1984 needs further investigation.

⁶ According to Foissner (1981a), “*Protospathidium bonneti*” sensu Foissner (1981) occurred in the Wallack-Haus area only at site 10 (see p. 19 and Abb. 1 in Foissner 1981a). Foissner et al. (2002, p. 310) described the type locality of *Protospathidium vermiforme* as “Grassland soil from the surroundings of the “Wallack-Haus” ...”. According to Foissner (1981a, p. 11), site 10 is a so-called “Schneetälchen”, that is, a snow filled pit which received the drain of a septic tank and was thus strongly fertilised. Anyhow, the population occurred in a soil sample collected in the immediate surroundings of the hotel. The data provided by Foissner (1981a, p. 19) indicate that the present species occurred at four of 16 sites in this alpine area.

⁷ Article 73.1.4 runs as follows: “Designation of an illustration of a single specimen as a holotype is to be treated as designation of the specimen illustrated; the fact that the specimen no longer exists or cannot be traced does not of itself invalidate the designation.”

Cleary, *Protopathidium vermiforme* Foissner et al. nov. spec. needs a redescription from the type locality to obtain detailed information on extrusomes, morphometrics, and molecular phylogeny. In vivo, *Protopathidium vermiforme* is indistinguishable from *Arcuospathidium namibiense* and *Spathidium bonneti*. Thus, protargol preparations are required to reveal the structure of the circumoral kinety: composed of a continuous line of dikinetids in *Spathidium* and *Arcuospathidium* vs. short, dikinetidal fragments attached to the somatic ciliary rows in *Protopathidium* (Fig. 1.2f–j). As concerns the congeners, only *Protopathidium serpens* (Kahl, 1930) and *Protopathidium muscicola* Dragesco & Dragesco-Kernéis, 1979 are similar to *Protopathidium vermiforme* Foissner et al. nov. spec. However, *Protopathidium serpens* is distinctly stouter (<6:1 vs. >10:1) and has a tortuous, irregularly nodule-macronucleus; likewise, *Protopathidium muscicola* is stouter and has the macronucleus nodules scattered.

Description: The following description of the morphology of *Protopathidium vermiforme* Foissner et al. nov. spec. is from Foissner & Xu (2007, p. 117).

Body size 80–160 × 5–13 µm in vivo, usually near 120 × 10 µm. Body slightly to distinctly flattened laterally; vermiform, anterior end obliquely truncate and slightly shorter than broadest trunk region, widest in middle third, posterior portion tail-like narrowed or narrowly rounded; both body ends fragile, that is, often dissolve under coverslip, tail possibly sometimes lacking. Nuclear apparatus in middle body third, composed of about 15 macronucleus nodules, each circa 4.0 × 2.7 µm in size and, likely several micronuclei; macronucleus nodules occasionally incompletely separated, producing more or less moniliform pieces. Contractile vacuole subterminal in base of tail or terminal if tail is lacking or lost, bulges body end when filled completely (Fig. 1.2a–c, e). Extrusomes not studied, possibly rod-shaped. Cortex fragile, bright. Cytoplasm colourless, contains some refractive granules. Moves slowly, worm-like, and thus easily confused with small nematodes at low magnification.

Somatic cilia about 8 µm long in vivo, arranged in about eight bipolar and ordinarily spaced rows more densely ciliated anteriorly than posteriorly, especially first row on right side having about 10 very narrowly spaced cilia anteriorly, similar as in some congeners. Individual ciliary rows composed of about 30 cilia, that is, rather loosely ciliated and attached to circumoral kinetofragments in typical *Protopathidium* pattern (Fig. 1.2a, b, f, i). Dorsal brush three-rowed, not yet studied in detail in vivo, where it is rather conspicuous due to some 8 µm long bristles anteriorly, similar as in *Arcuospathidium namibiense* Foissner et al., 2002; most bristles, however, only 2 µm long; all rows with a short tail of ordinary cilia anteriorly, especially distinct in row 1 composed of only three dikinetids. Row 2 longer than rows 1 and 3, composed of about 15 narrowly spaced dikinetids. Row 3 slightly shorter than row 2, composed of about 10 comparatively widely spaced dikinetids (Fig. 1.2a, b, g, h, j).

Oral bulge distinct in vivo because about 4 µm high and somewhat knobby, slightly twisted along main body axis and likely obovate in frontal view. Individual oral kinetofragments composed of three or four dikinetids. Nematodesmata neither recognisable in vivo nor in protargol preparations (Fig. 1.2a, b, d, f–j).

Occurrence and ecology: *Protopathidium vermiforme* Foissner et al. nov. spec. is very likely confined to terrestrial habitats. The type locality is an alpine grassland in Carinthia, Austria (details, see above).

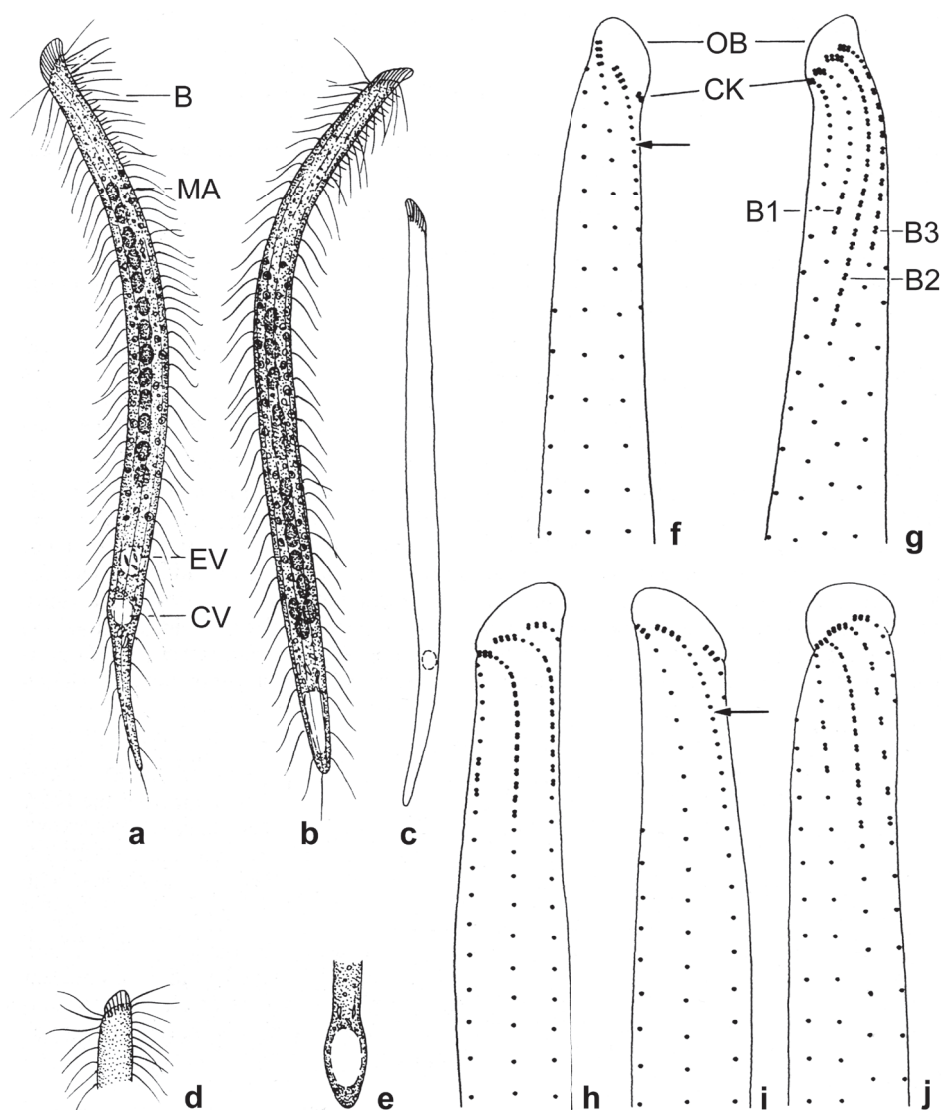


Fig. 1.2a–j *Protospathidium vermiforme* Foissner, Agatha & Berger nov. spec. (from Foissner 1981. a–e, from life; f–j, protargol preparation). **a, b**: Left side views of representative specimens, 125 μ m, 110 μ m. **c**: A very slender individual, 150 μ m. **d**: Dorsolateral view of slightly spiralled anterior body region. **e**: Posterior body end when contractile vacuole is filled. **f–j**: Ciliary pattern in anterior right (f, i), left (g, h), and dorsal (j) body region; figure pairs (f, g; h, i) show both sides of two specimens, length of portions shown 27 μ m (f, g), 46 μ m (h, i), 31 μ m (j). Arrows mark condensation of cilia in anterior portion of a ventrolateral kinety. The protospathidiid oral kinetofragments are very distinct. Brush row 1 consists of three dikinetids far away from the circumoral kinety. The specimen shown in Fig. 1.2f, g is the holotype. B, B1, B2, B3 – dorsal brush (rows), CK – circumoral kinety, CV – contractile vacuole, EV – egestion vacuole, MA – macronucleus, OB – oral bulge.

The Foissner group misidentified this and similar species as *Spathidium bonneti* for a long time (see below and Foissner et al. 2002). Since 2002 it is clear, that there are several

very slender, middle-sized spathidiids belonging to even different genera. Thus, all pre-2002 records are doubtful and not mentioned here. Only the records from sites near to the type locality are reliable, that is, those from the Grossglockner and Gastein region (Austria; Foissner 1981a, Foissner & Peer 1985). These data show that *Protospathidium vermiforme* Foissner et al. nov. spec. is rather common in alpine grassland soils of Austria.

Foissner et al. (2002) described three new species for which illustrations have been designated as type material, namely:

Nassula tuberculata Foissner et al., 2002, p. 433, Fig. 100a–o, 349a–u, 350a, b, Tables 80, 81 (Fig. 349a–u fixed as “type material” according to Foissner et al. 2002, p. 433; according to their Table 1 [p. 40], these “F” (abbreviation for figures) represent the holotype). Remarks: Figures 349a–u show various specimens from the type locality (Saudi Arabia) documented by different methods (in vivo, silver carbonate preparation, scanning electron microscopy, methyl green-pyronin staining). Thus, these figures do not represent a holotype, but a syntype (ICZN 1999, Articles 73.1, 73.2). From a population from Portugal three voucher slides (accession numbers 2002/644–646) have been deposited by Foissner et al. (2002, p. 433, Table 1, p. 40). According to Table 4 in Aescht (2008, p. 194), for *Nassula tuberculata* no type material was designated and deposited. The situation needs a detailed analysis, especially to check if the specimens shown in Fig. 349a–u are indeed syntypes (ICZN 1999, Articles 73.2, 73.2.1.1); if, yes, it has to be checked if one of the specimens shown, can (should) be fixed as lectotype (ICZN 1999, Articles 74.4, 74.7). Needs detailed analysis during redescription or revision.

Rostrophrya namibiensis namibiensis Foissner et al., 2002, p. 992, Fig. 213a–f, 296, 297, 432a–i (not 432a–j as mentioned by Foissner et al. 2002), Table 194 (according to their Table 1 [p. 42], “figures” are fixed as holotype and paratype). Remarks: Foissner et al. (2002) did not fix a single individual shown in the “figures” as holotype. Thus, the type fixation is possibly invalid. If the specimens shown in the “figures” are syntypes or not must be checked during a redescription or a revision. Anyhow, the problem needs detailed analysis.

Rostrophrya fenestrata Foissner et al., 2002, p. 997, Fig. 215a–h, 434b–l, 442j–l, Table 194 (according to their Table 1 [p. 42], “figures” fixed as holotype). Remarks: Foissner et al. (2002) did not fix a single specimen shown in the “figures” as holotype. Thus, the type fixation is possibly invalid. If the specimens shown in the “figures” are syntypes or not must be checked during a redescription or a revision. Anyhow, the problem needs detailed analysis.

Epitholiolus chilensis (Bürger, 1906) Foissner et al., 2002 (p. 165) was neotypified by Foissner et al. (2002; for qualifying conditions according to ICZN 1999, Article 75.3, see Foissner et al. 2002, p. 36). Unfortunately, Foissner et al. (2002) named the specimen shown in their Fig. 31r, s (see Foissner et al. 2002, p. 168) incorrectly as holotype specimen; correct is neotype (for details on terms, see ICZN 1999).

Foissner et al. (2002, p. 608) fixed two holotype specimens for *Parakabliella binucleata* Foissner et al., 2002. For detailed discussion of this nomenclatural mistake, see Berger (2011, p. 449).

Foissner et al. (2002, p. 743, Fig. 162a–d, 396a–c) described “*Gastrostyla* (*Kleinstyla*) *bavariensis* nov. spec.” based on *Gastrostyla minima* Hemberger, 1985 sensu Foissner (1997, p. 225). Unfortunately, they did not fix a holotype, neither in the description section (p.

743, 744) nor in their Table 1 where they listed the type material of the species described in their monograph. Aescht (2008, p. 165) wrote that Foissner et al. (2002) “established” the “new name” *Gastrostyla (Kleinstyla) bavariensis*.⁸ Since the fixation of a holotype (or syntypes) is a prerequisite for a valid description of a new species after 1999, *Gastrostyla (Kleinstyla) bavariensis* Foissner et al., 2002 is invalid (ICZN 1999, Article 16.4.1). In addition, Foissner et al. (2002) did not mention *Gastrostyla bavariensis* in their Table 1 so that Article 16.4.2 is likewise not fulfilled. Since *Gastrostyla (Kleinstyla) bavariensis* is the type species of *Gastrostyla (Kleinstyla)* Foissner et al., 2002 (p. 723) and *Kleinstyla* Foissner et al., 2002 (see Berger 2008, p. 140), the subgenus/genus is likewise invalid (for justification of such a situation, see Chapter 13, that is, Berger et al. 2025). This problem will be correct in Number 7 of the present series.

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

Foissner (2016a) described two new species, namely, *Metacystis mucosa* Foissner, 2016a (on p. 85) and *Phialina serranoi* Foissner, 2016a (on p. 88). In the subchapters “Type material” he wrote that the type slides “have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI).” However, due to unknown reasons the slides have been in the private archive of W. Foissner until recently and thus the slides are not listed by Aescht (2018). In spite of that these two species are valid because he fixed a holotype for each species (*Metacystis mucosa*: his Fig. 5M; *Phialina serranoi*: his Fig. 8G, H) and he mentioned that the type material is deposited in the museum in Linz. Thus, Articles 16.4.1 and 16.4.2 of the ICZN (1999) are fulfilled. The type slides of *Metacystis mucosa* (holotype accession number 2015/832; paratypes 2015/833–842) and *Phialina serranoi* (holotype: 2015/843; paratypes 2015/844–847) have been deposited in the Biology Centre of the Upper Austrian Museum in Linz, together with the slides of the species treated in the present book.

Foissner (2016b, p. 119) described the new species *Heterometopus meisterfeldi*. In the subchapter “Type material” he wrote that the type slides “have been deposited in the Museum of Natural History (Biologiezentrum) in Linz (LI).” However, due to unknown reasons the slides have been in the private archive of W. Foissner until recently. In spite of that *Heterometopus meisterfeldi* Foissner, 2016b is valid because he fixed a holotype (his Fig. 1B, C, 3A) and he mentioned that the type material is deposited in the museum in Linz. Thus, Articles 16.4.1 and 16.4.2 of the ICZN (1999) are fulfilled. The type slides of *Heterometopus meisterfeldi* (holotype accession number 2015/848; paratypes 2015/849–851; these accession numbers are according to the original description, that is, Foissner 2016b, p. 119) have now been deposited in the Biology Centre of the Upper Austrian Museum in Linz, together with the slides of the species treated in the present book. Note that the type slides of *Heterometopus meisterfeldi* are labelled as “*Metopus laminarius*” (in black) and as “Species nova” (in grey; this labelling refers to *Heterometopus meisterfeldi*) (Fig. 1.3a–h). Note further that, according to Aescht (2018, p. 492), the accession numbers changed from 2015/848 to 2015/364 (holotype) and from 2015/849, 2015/850, 2015/851 to “2015/363, 2015/364” (paratypes; one number less, which

⁸ Foissner et al. (2002) did not establish a “new name” as discussed by Aescht (2008), but they described a new species. A new name (nomen novum or replacement name or substitute name) is a name established expressly to replace an already established name, that is, to replace a primary or secondary homonym (ICZN 1999, p. 109, 110).

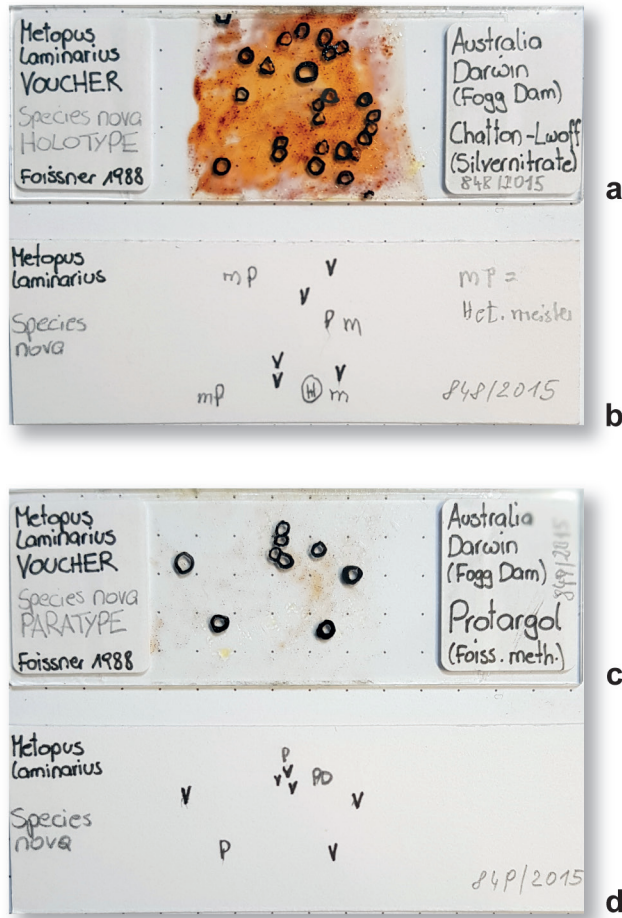


Fig. 1.3a–d *Heterometopus meisterfeldi* Foissner, 2016b (originals. a, Chatton-Lwoff silver nitrate preparation; c, protargol preparation). a, b: Slide (a) and protocol (b) containing holotype (H). Accession number (LI): 2015/848. c, d: Slide (c) and protocol (d) containing paratypes (P) and paratype drawn (PD). Accession number (LI): 2015/849. The terms “Species nova Holotype” and “Species nova Paratype” (written in pencil) refer to *Heterometopus meisterfeldi*. For important note on accession numbers, see text.

is incorrect!). We checked the slide “2015/364” deposited in Linz; it is a paratype slide of *Heterometopus meisterfeldi* and, in addition, contains voucher specimens of *Apometopus* (*Apometopides*) *pyriformis* (Levander, 1894) Foissner, 2016c and *Metopus laminarius* Kahl, 1927a. A correction of this problem will be published in a later paper. In addition, Foissner (2016b, p. 122) redescribed *Heterometopus palaeformis* (Kahl, 1927) Foissner, 2016b. The three voucher slides (accession numbers 2015/852–854) of the population from the Dominican Republic were also in the private archive of W. Foissner until recently. Now they are also finally deposited, together with the slides of the other species treated in the present book, in the Biology Centre of the Upper Austrian Museum in Linz (LI).

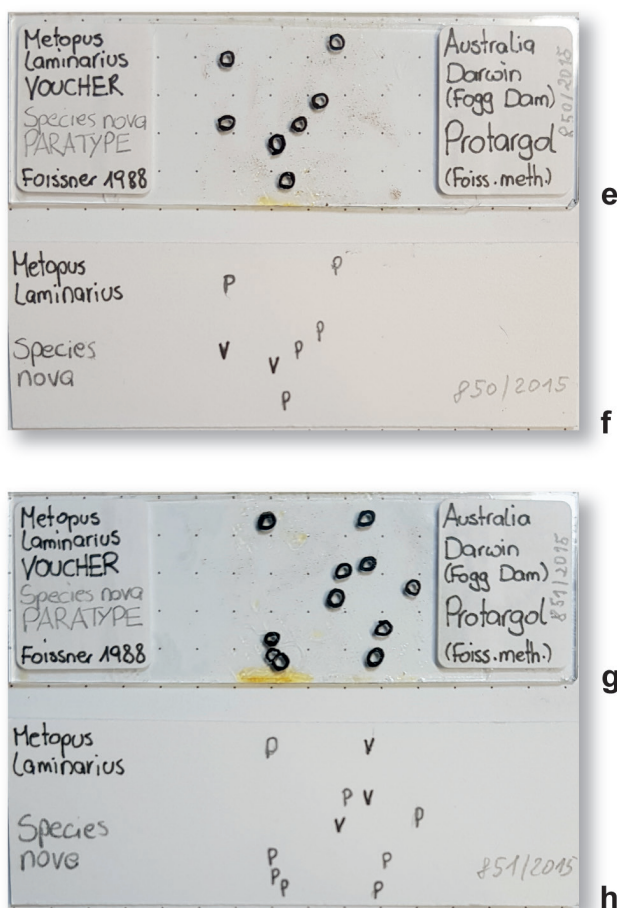


Fig. 1.3e–h *Heterometopus meisterfeldi* Foissner, 2016b (originals. Protargol slide). **e–h:** Slides (e, g) and protocols (f, h) containing paratypes (P). Accession numbers (LI): 2015/850, 2015/851. The term “Species nova Paratype” (written in pencil) refers to *Heterometopus meisterfeldi*. For important note on accession numbers, see text.

Note on ZooBank registration number of author Helmut Berger

Until 31 Oct 2024, Helmut Berger (Consulting Engineering Office for Ecology, Radetzkystrasse 10, 5020 Salzburg, Austria; <https://orcid.org/0000-0002-1726-0082>) was registered in ZooBank (<https://zoobank.org>) under two numbers, namely, (1) urn:lsid:zoobank.org:author:73E0ADD6-EF73-4B10-B3B3-E7EBE8E338CE and (2) urn:lsid:zoobank.org:author:DC477A8E-FC41-494C-A4A1-F23091512449. Since 1 Nov 2024, only the number which was created first is available, that is, the LSID urn:lsid:zoobank.org:author:73E0ADD6-EF73-4B10-B3B3-E7EBE8E338CE is valid and all publications are combined under this record. Berger (2018d) published a taxonomic and nomenclatural summary under the second LSID, which is no longer available.

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

Within the individual paragraphs, the taxa are arranged alphabetically. When you mention one of the new taxa or new combinations listed below you have to replace the corresponding terms (e.g., “nov. spec.”) by the authors of the individual chapter. Examples (from Chapter 13, that is, Berger et al. 2025 and Chapter 12, that is, Foissner et al. 2025b): “*Neocultellothrix velhoi* Foissner nov. spec.” has to be cited in future as “*Neocultellothrix velhoi* Foissner in Berger, Xu & Foissner, 2025”. “*Neocultellothrix atypica* (Wenzel, 1953) Foissner & Xu nov. comb.” has to be cited in future as “*Neocultellothrix atypica* (Wenzel, 1953) Foissner & Xu in Berger, Xu & Foissner, 2025”. “Pharyngospathidiidae nov. fam.” has to be cited in future as “Pharyngospathidiidae Foissner, Xu & Berger, 2025”.

New subspecies (4)

Pharyngospathidium longichilum amphoriforme nov. subspec. (p. 380); *Pharyngospathidium longichilum longichilum* nov. subspec. (p. 378); *Spathidium saprophilum curvioplites* nov. subspec. (p. 71); *Spathidium saprophilum saprophilum* nov. subspec. (p. 68).

New species (19)

Centrospathidium verrucosum nov. spec. (p. 128); *Epispathidium salsum* nov. spec. (p. 166); *Latispathidium arboricola* nov. spec. (p. 229); *Latispathidium brachyoplites* nov. spec. (p. 245); *Latispathidium simile* nov. spec. (p. 238); *Neocultellothrix velhoi* Foissner nov. spec. (p. 436); *Neospathidium africanum* nov. spec. (p. 418); *Neospathidium brachystichos* nov. spec. (p. 424); *Neospathidium longinucleatum* nov. spec. (p. 401); *Pharyngospathidium longichilum* nov. spec. (p. 370); *Pharyngospathidium pseudobavariense* nov. spec. (p. 389); *Protospathidium vermiforme* Foissner, Agatha & Berger nov. spec. (p. 10); *Schmidingerophrya bisticha* nov. spec. (p. 272); *Schmidingerophrya macrothrix* nov. spec. (p. 258); *Semibryophyllum cultellum* nov. spec. (p. 285); *Semibryophyllum palustre* nov. spec. (p. 291); *Spathidium apospathidiiforme* nov. spec. (p. 43); *Spathidium elongatum* nov. spec. (p. 36); *Spathidium saprophilum* nov. spec. (p. 67).

New genera (6)

Centrospathidium nov. gen. (p. 127); *Neocultellothrix* Foissner nov. gen. (p. 434); *Neospathidium* nov. gen. (p. 400); *Pharyngospathidium* nov. gen. (p. 369); *Schmidingerophrya* nov. gen. (p. 257); *Semibryophyllum* nov. gen. (p. 281).

New combinations (13)

Akidodes henleae (Lom, 1959) Lom nov. comb. (p. 435); *Apospathidium longicaudatum* (Buitkamp, 1977) nov. comb. (p. 117); *Centrospathidium faurei* (Kahl, 1930) nov. comb. (p. 136); *Centrospathidium minutum* (Kahl, 1926) nov. comb. (p. 138); *Neocultellothrix atypica* (Wenzel, 1953) Foissner & Xu nov. comb. (p. 439); *Neocultellothrix coemeterii* (Kahl, 1943) Foissner & Xu nov. comb. (p. 443); *Neocultellothrix japonica* (Foissner, 1988) Foissner & Xu nov. comb. (p. 445); *Neocultellothrix lionotiformis* (Kahl, 1930) Foissner & Xu nov. comb. (p. 446); *Neocultellothrix paucistriata* (Foissner & Xu, 2007) nov. comb. (p. 448); *Neocultellothrix tortisticha* (Foissner & Xu, 2007) nov. comb. (p. 449); *Pharyngospathidium*

bavariense (Kahl, 1930) nov. comb. (p. 398); *Pharyngospathidium simplinucleatum* (Kahl, 1930) nov. comb. (p. 399); *Semibryophyllum foliosum* (Foissner, 1983) nov. comb. (p. 303).

New family (1)

Pharyngospathidiidae nov. fam. (p. 367).

Redescriptions, reviews, and others⁹

Apertospathula cuneata Foissner & Xu, 2007 (p. 6); *Apertospathula lajacola* Foissner & Xu, 2007 (p. 6); *Apertospathula longiseta* Foissner & Xu, 2007 (p. 6); *Apertospathula pelobia* Foissner & Xu, 2007 (p. 6); *Apertospathula similis* Foissner & Xu, 2007 (p. 6); *Apospathidium* Foissner et al., 2002 (p. 111); *Apospathidium longicaudatum* (Buitkamp, 1977) nov. comb. (p. 117); *Apospathidium terricola* Foissner et al., 2002 (p. 112); *Arcuospathidium deforme* Foissner & Xu, 2007 (p. 6); *Arcuospathidium muscorum rhopaloplites* Foissner & Xu, 2007 (p. 6); *Arcuospathidium pelobium* Foissner & Xu, 2007 (p. 6); *Arcuospathidium virungense* Foissner & Xu, 2007 (p. 7); *Armatospathula costaricana* Foissner & Xu, 2007 (p. 7); *Armatospathula periarmata* Foissner & Xu, 2007 (p. 7); *Armatospathula plurinucleata* Foissner & Xu, 2007 (p. 7); *Centrospathidium faurei* (Kahl, 1930) nov. comb. (p. 136); *Cephalospatula brasiliensis* Foissner, 2003 (p. 438); *Centrospathidium minutum* (Kahl, 1926) nov. comb. (p. 138); *Cultellothrix paucistriata* Foissner & Xu, 2007 (p. 7); *Cultellothrix tortisticha* Foissner & Xu, 2007 (p. 7); *Edaphospathula brachycaryon* Foissner & Xu, 2007 (p. 7); *Edaphospathula gracilis* Foissner & Xu, 2007 (p. 7); *Edaphospathula inermis* Foissner & Xu, 2007 (p. 8); *Edaphospathula paradoxa* Foissner & Xu, 2007 (p. 8); *Epispathidium* Foissner, 1984 (p. 142); *Epispathidium amphoriforme* (Greeff, 1889) Foissner, 1984 (p. 197); *Epispathidium ascendens* (Wenzel, 1955) Foissner, 1987 (p. 202); *Epispathidium papilliferum* (Kahl, 1930) Foissner, 1984 (p. 174); *Epispathidium regium* Foissner, 1984 (p. 144); *Epispathidium securiforme* (Kahl, 1930) Foissner, 1984 (p. 154); *Epispathidium terricola* Foissner, 1987 (p. 196); *Latispathidium* Foissner et al., 2005 (p. 213); *Latispathidium lanceoplites* (Foissner et al., 2002) Foissner et al., 2005 (p. 215); *Latispathidium truncatum* (Stokes, 1885) Foissner et al., 2005 (p. 218); *Latispathidium truncatum bimacronucleatum* Foissner et al., 2005 (p. 222); *Latispathidium truncatum truncatum* (Stokes, 1885) Foissner et al., 2005 (p. 221); *Neocultellothrix atypica* (Wenzel, 1953) Foissner & Xu nov. comb. (p. 439); *Neocultellothrix cometerii* (Kahl, 1943) Foissner & Xu nov. comb. (p. 443); *Neocultellothrix japonica* (Foissner, 1988) Foissner & Xu nov. comb. (p. 445); *Neocultellothrix lionotiformis* (Kahl, 1930) Foissner nov. comb. (p. 446); *Neocultellothrix paucistriata* (Foissner & Xu, 2007) nov. comb. (p. 448); *Neocultellothrix tortisticha* (Foissner & Xu, 2007) nov. comb. (p. 449); *Pharyngospathidium bavariense* (Kahl, 1930) nov. comb. (p. 398); *Pharyngospathidium simplinucleatum* (Kahl, 1930) nov. comb. (p. 399); *Protospathidium arenicola* Foissner & Xu, 2007 (p. 8); *Protospathidium vermiculus* (Kahl, 1926) Foissner & Xu, 2007 (p. 8); *Semibryophyllum foliosum* (Foissner, 1983) nov. comb. (p. 303); *Semispathidium* Foissner et al., 2002 (p. 312); *Semispathidium armatum* Foissner et al., 2002 (p. 320); *Semispathidium breviarmatum* Foissner & Vdačný in Vdačný & Foissner, 2013 (p. 325); *Semispathidium enchelyodontides* Foissner et al., 2002 (p. 315); *Semispathidium fraterculum* Foissner & Al-Rasheid in Foissner, Hess & Al-Rasheid, 2010 (p. 329); *Semispathidium lagyniforme* (Kahl,

⁹ Note that the species listed in the section “Nomenclatural notes on new species/subspecies described by Foissner et al. (2002)” are not listed in this paragraph.

1930) Foissner et al., 2002 (p. 322); *Semispathidium longiarmatum* Foissner & Vdačný in Vdačný, Slovák & Foissner, 2014 (p. 326); *Semispathidium pulchrum* Foissner, Hess & Al-Rasheid, 2010 (p. 330); Spathidiida Foissner & Foissner, 1988 (p. 26); Spathidiidae Kahl in Doflein & Reichenow, 1929 (p. 27); *Spathidium* Dujardin, 1841 (p. 28); *Spathidium aciculare* Foissner et al., 2002 (p. 65); *Spathidium anguilla* Vuxanovici, 1962 (p. 91); *Spathidium bromelicola* Foissner et al., 2014 (p. 62); *Spathidium dispar* Foissner & Xu in Foissner, 2016 (p. 59); *Spathidium duschli* Foissner, 2016 (p. 59); *Spathidium etoschense* Foissner et al., 2002 (p. 65); *Spathidium faurefremietii* Foissner, 2003 (p. 86); *Spathidium latissimum* Lepsi, 1959 (p. 89); *Spathidium polynucleatum* (Foissner et al., 2002) Jang et al., 2017 (p. 96); *Spathidium polyvacuolatum* Vuxanovici, 1959 (p. 90); *Spathidium rusticanum* Foissner, 1981 (p. 74); *Spathidium wolffi* Foissner et al., 2014 (p. 85); *Supraspathidium* Foissner & Didier, 1981 (p. 335); *Supraspathidium armatum* Foissner et al., 2002 (p. 353); *Supraspathidium elongatum* (Penard, 1922) Foissner & Didier, 1981 (p. 359); *Supraspathidium etoschense* Foissner et al., 2002 (p. 346); *Supraspathidium gigas* (Cunha, 1914) Foissner & Didier, 1981 (p. 361); *Supraspathidium multistriatum* Foissner & Didier, 1981 (p. 339); *Supraspathidium teres* (Stokes, 1886) Foissner & Didier, 1981 (p. 338); *Supraspathidium vermiforme* (Penard, 1922) Foissner & Didier, 1981 (p. 357); The *Spathidium bromelicola* group (p. 61); The *Spathidium elongatum* group (p. 34); The *Spathidium wolffi* group (p. 85).

New name (Replacement name)

Spathidium canadense Wilbert nom. nov. (p. 147) (for *Spathidium macrostomum* Wilbert, 1995, the junior primary homonym of *Spathidium macrostomum* Wang & Nie, 1933).

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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 Phagocon 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, *Isiella* 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*, *Apocyclus* 4
- obovate*, *Frontonia angusta* 9
- oscillatoriphaga*, *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., *Pseudocobnilembus* 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
Wolfskopia 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

