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

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

Edited by

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

Series Monographiae Ciliophorae

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

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

In memory of Wilhelm Foissner (1948–2020)

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Preface, authorship, acknowledgements, and funding

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

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

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

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

Salzburg
January 2025

Helmut Berger (Publisher)
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Abstract

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

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

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

Chapter 1

General section to "Revision of some spathidiid genera (Alveolata, Ciliophora, Spathidiida)", including nomenclatural notes[1]

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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 date 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.langen scheidt. 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").

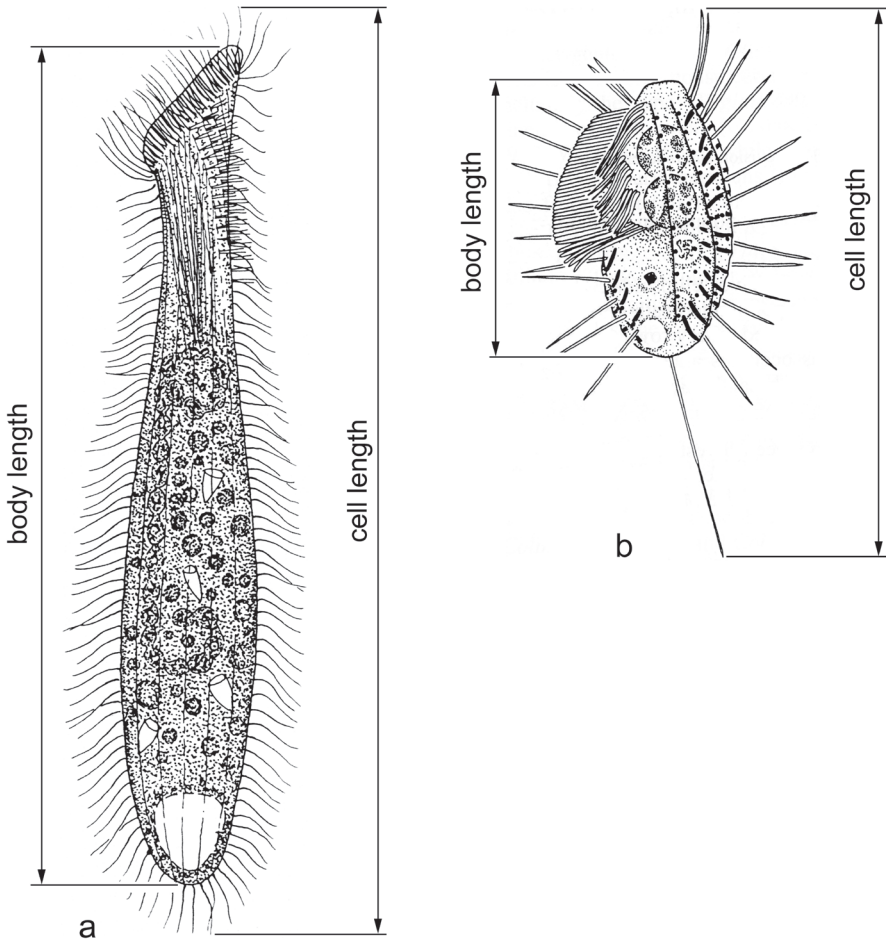

Fig. 1.1a, b Illustrations to demonstrate the difference between cell length and body length in ciliates. *Spathidium rusticanum* in left lateral view (a) and *Apocyclidium obliquum* in ventrolateral view (b) (a, from Foissner 1981; b, from Foissner et al. 2002. From life). Since the cilia ("cylindrical 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 statement[3] 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 preliminary 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 virugense* 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 periarmata 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, 18, 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), *Parakahliella 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, *Wolfkosia loeffleri* Foissner et al., 2002 (p. 459, two holotype slides deposited), *Colpoda cavicola amicronucleata* 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 amicronucleata* or Aescht 2008, p. 163 for *Wolfkosia 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 *Protospathidium vermiforme*. Since the original description is invalid, we describe it here as new species:

Protospathidium vermiforme Foissner, Agatha & Berger nov. spec.

(Fig. 1.2a–j)

1981 ***Protospathidium 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 ***Protospathidium vermiforme* nov. spec.** – Foissner, Agatha & Berger, Denisia 5: 310, Fig. 69a–j (invalid original description because no holotype, or syntypes, fixed).

2007 ***Protospathidium vermiforme* Foissner, Agatha & Berger, 2002** – Foissner & Xu, Monogr. biol. 81: 116, Fig. 45a–j (detailed revision of invalid species).

2008 ***Protospathidium 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. *Protospathidium* is of neuter gender (Aescht 2001, p. 296), thus, *Protospathidium vermiforme* is the correct name.

Foissner et al. (2002, p. 310) established *Protospathidium vermiforme* basing on *Protospathidium 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 *Protospathidium 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 "*Protospathidium vermiforme* Foissner, Agatha & Berger in Berger, Xu & Foissner, 2025" or as "*Protospathidium 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 *Protospathidium 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 *Protospathidium vermiforme* Foissner et al., 2002. She wrote that *Protospathidium vermiforme* is a replacement name for the misidentified *Protospathidium bonneti* sensu Foissner (1981). However, *Protospathidium*

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 × 5–13 µm 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 µm 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 whereabout 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.

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[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, *Protospathidium 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, *Protospathidium 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 *Protospathidium* (Fig. 1.2f–j). As concerns the congeners, only *Protospathidium serpens* (Kahl, 1930) and *Protospathidium muscicola* Dragesco & Dragesco-Kernéis, 1979 are similar to *Protospathidium vermiforme* Foissner et al. nov. spec. However, *Protospathidium serpens* is distinctly stouter (<6:1 vs. >10:1) and has a tortuous, irregularly nodulated macronucleus; likewise, *Protospathidium muscicola* is stouter and has the macronucleus nodules scattered.

Description: The following description of the morphology of *Protospathidium 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 postorally, 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 *Protospathidium* 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: *Protospathidium 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).

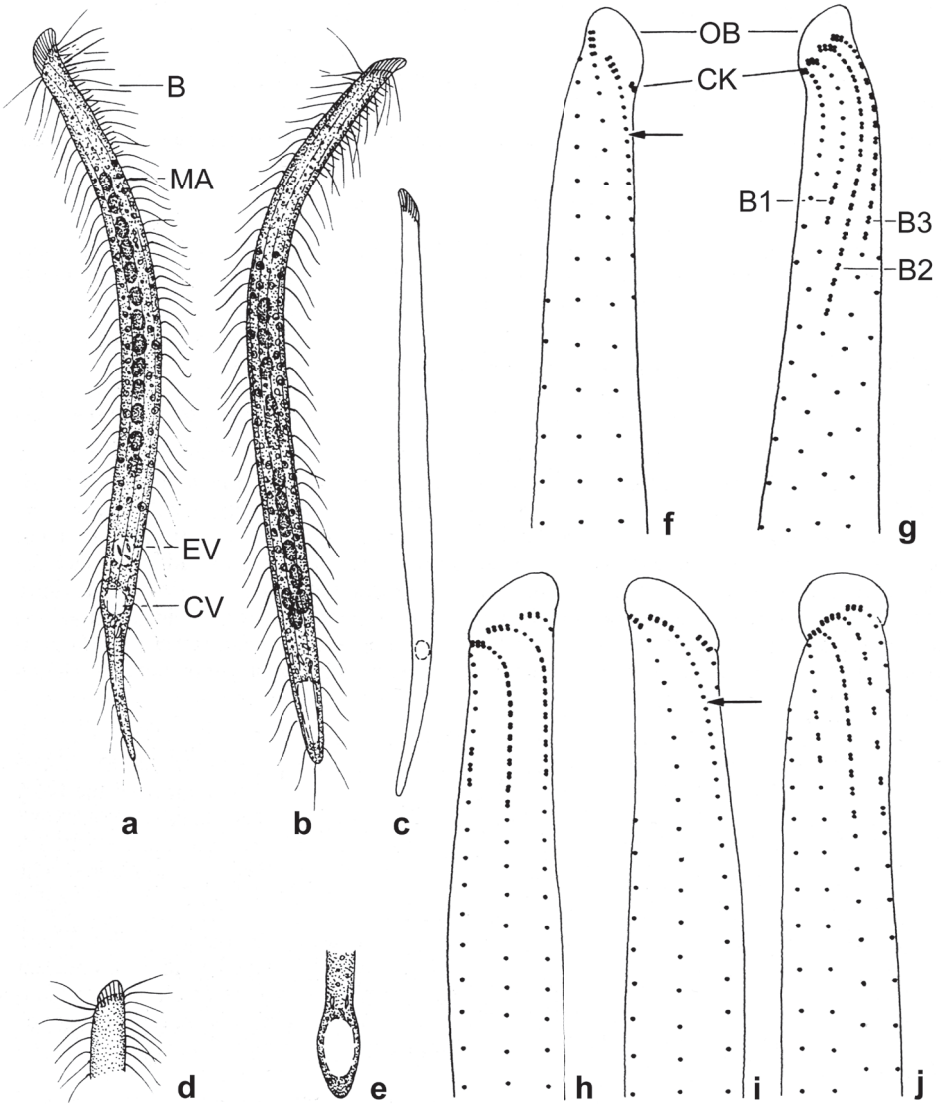

Fig. 1.2a–j *Protospathidium vermiforme* Foissner, Agatha & Berger nov. spec. (from Foissner 1981. a–e, from life; f–j, protargol preparation). **a, b:** Left side views of representative specimens, 125 µm, 110 µm. **c:** A very slender individual, 150 µm. **d:** Dorsolateral view of slightly spiralled 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 µm (f, g), 46 µm (h, i), 31 µm (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 tuberculate* 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 *Parakahliella 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, 2025/851 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).

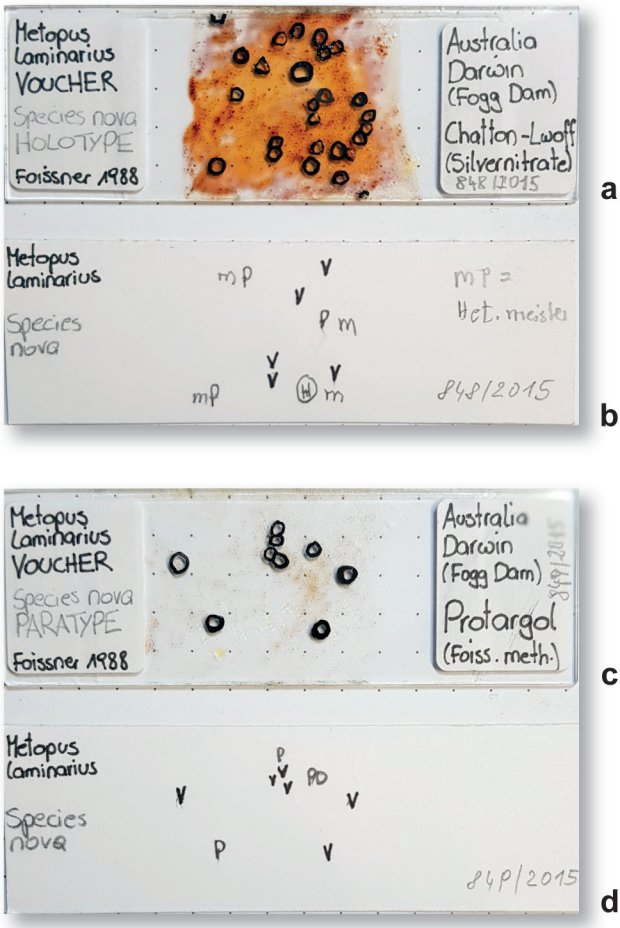

Fig. 1.3a–d *Heterometopus meisterfeldi* Foissner, 2016b (originals. a, Chatton-Lwoff silver nitrate preparation; c, protargol preparation). **a, b:** Slide (a) and protocol (b) containing holotype (H). Accession number (LI): 2015/848. **c, d:** Slide (c) and protocol (d) containing paratypes (P) and 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 Austian Museum in Linz (LI).

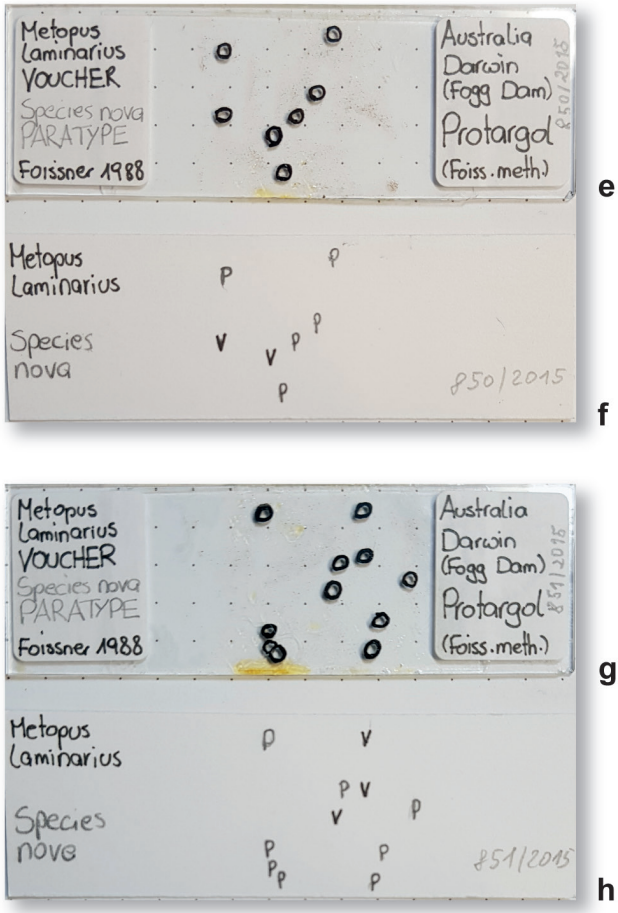

Fig. 1.3e–h *Heterometopus meisterfeldi* Foissner, 2016b (originals. Protargol slide). **e–h:** Slides (e, g) and protocols (f, h) containing paratypes (P). Accession numbers (LI): 2015/850, 2015/851. The term "Species nova Paratype" (written in pencil) refers to *Heterometopus meisterfeldi*. For important 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 summery 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 apospathidiforme* 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 others[9]
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 novv. 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. 3999); *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 faurefremieti* 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 wolfi* 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 wolfi* 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.

Table index