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

**Series Monographiae Ciliophorae**
**Series Editor:** Helmut Berger, Consulting Engineering Office for Ecology, Salzburg
For details, see website at https://www.protozoology.com/smc

---

**Berger H. (2018):** *Cyrtohymena citrina* (Berger & Foissner, 1987) Foissner, 1989 (original combination: *Steinia citrina* Berger & Foissner, 1987) (Ciliophora, Hypotricha): update 1.0 on monographic treatment. – Series Monographiae Ciliophorae, Number 1: 1–16

**Berger H. (2018):** Six mainly little-known *Cyrtohymena* species (Ciliophora, Hypotricha): update 1.0 on monographic treatment. – Series Monographiae Ciliophorae, Number 2: 1–24

**Berger H. (2018):** *Cyrtohymena* Foissner, 1989 and *Cyrtohymena muscorum* (Kahl, 1932) Foissner, 1989 (original combination *Oxytricha (Steinia) muscorum* Kahl, 1932) (Ciliophora, Hypotricha): update 1.0 on monographic treatment. – Series Monographiae Ciliophorae, Number 3: 1–28

**Berger H. (2018):** urn:lsid:zoobank.org:author:DC477A8E-FC41-494C-A4A1-F230915 12449: taxonomic and nomenclatural summary. – Series Monographiae Ciliophorae, Number 4: 1–52

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

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

---

PDFs are Open Access

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

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

Edited by

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

Series Monographiae Ciliophorae

Berger, Consulting Engineering Office for Ecology, Salzburg, Austria

## Imprint

**Editors/authors**
*Wilhelm Foissner*†, University of Salzburg, Hellbrunnerstrasse 34, 5020 Salzburg, Austria; https:// www.wfoissner.at, https://orcid.org/0000-0003-4528-0176
*Kuidong Xu*, Laboratory of Marine Organism Taxonomy and Phylogeny, Qingdao Key Laboratory of Marine Biodiversity and Conservation, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China; https://orcid.org/0000-0002-5186-519X, kxu@qdio.ac.cn
*Helmut Berger*, Consulting Engineering Office for Ecology, Radetzkystrasse 10, 5020 Salzburg, Austria; https://www.protozoology.com, https://orcid.org/0000-0002-1726-0082, berger.helmut@protozoology.com

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

**Layout:** Helmut Berger with Adobe InDesign; Adobe Garamond Pro

**Print:** Printed in Austria by druck.at

**Print edition:** 40 copies

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

**Publication date:** 31 January 2025

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

**Abbreviation of series title:** Ser. Monogr. Cilioph.

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

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

**ISBN 978-3-902147-08-0**



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

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

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

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

In memory of Wilhelm Foissner (1948–2020)

# 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 *Spathidium* species **34**
The *Spathidium elongatum* group **34**
*Spathidium elongatum* nov. spec. **36**
*Spathidium apospathidiforme* nov. spec. **43**
*Spathidium duschli* Foissner, 2016 **59**
*Spathidium dispar* Foissner & Xu in Foissner, 2016 **59**
The *Spathidium bromelicola* group **61**
*Spathidium bromelicola* Foissner, Wolf, Kumar, Xu & Quintela-Alonso, 2014 **62**
*Spathidium aciculare* Foissner, Agatha & Berger, 2002 **65**
*Spathidium etoschense* Foissner, Agatha & Berger, 2002 **65**
*Spathidium saprophilum* nov. spec. **67**
*Spathidium saprophilum saprophilum* nov. subspec. **68**
*Spathidium saprophilum curvioplites* nov. subspec. **71**
*Spathidium rusticanum* Foissner, 1981 **74**
The *Spathidium wolfi* group **85**
*Spathidium wolfi* Foissner, Wolf, Kumar, Xu & Quintela-Alonso, 2014 **85**
*Spathidium faurefremieti* Foissner, 2003 **86**
*Spathidium latissimum* Lepsi, 1959 **89**
*Spathidium polyvacuolatum* Vuxanovici, 1959 **90**
Two further *Spathidium* species **90**
*Spathidium anguilla* Vuxanovici, 1962 **91**
*Spathidium polynucleatum* (Foissner, Agatha & Berger, 2002) Jang, Vďačný, Shazib & Shin, 2017 **96**
Funding **106**
Acknowledgements **106**
References **106**

**Chapter 4**

W. Foissner, K. Xu & H. Berger
***Apospathidium* Foissner et al., 2002 (Ciliophora, Spathidiidae), a genus whose species have oralized somatic kineties 111**
Abstract **111**
*Apospathidium* Foissner, Agatha & Berger, 2002 **111**
Key to species **112**
*Apospathidium terricola* Foissner, Agatha & Berger, 2002 **112**
*Apospathidium longicaudatum* (Buitkamp, 1977) nov. comb. **117**
Funding **124**
Acknowledgements **124**
References **125**

**Chapter 5**

W. Foissner, K. Xu & H. Berger
***Centrospathidium* nov. gen. (Ciliophora, Spathidiidae), a new genus whose type**

**species was discovered in an Australian floodplain 127**
Abstract **127**
*Centrospathidium* nov. gen. **127**
Key to species **128**
*Centrospathidium verrucosum* nov. spec. **128**
*Centrospathidium faurei* (Kahl, 1930) nov. comb. **136**
*Centrospathidium minutum* (Kahl, 1926) nov. comb. **138**
Funding **138**
Acknowledgements **139**
References **139**

**Chapter 6**

W. Foissner, K. Xu & H. Berger
***Epispathidium* Foissner, 1984 (Ciliophora, Spathidiidae), a genus where the circumoral kinety is completely separated from the somatic kineties 141**
Abstract **141**
*Epispathidium* Foissner, 1984 **142**
Key to species **143**
*Epispathidium regium* Foissner, 1984 **144**
*Epispathidium securiforme* (Kahl, 1930) Foissner, 1984 **154**
*Epispathidium salsum* nov. spec. **166**
*Epispathidium papilliferum* (Kahl, 1930) Foissner, 1984 **174**
Brief review of other species assigned to *Epispathidium* Foissner, 1984 **196**
*Epispathidium terricola* Foissner, 1987 **196**
*Epispathidium amphoriforme* (Greeff, 1889) Foissner, 1984 **197**
*Epispathidium ascendens* (Wenzel, 1955) Foissner, 1987 **202**
Funding **207**
Acknowledgements **207**
References **207**

**Chapter 7**

W. Foissner, K. Xu & H. Berger
***Latispathidium* Foissner et al., 2005 (Ciliophora, Spathidiidae), a genus whose species have the dorsal brush on the left body side 213**
Abstract **213**
*Latispathidium* Foissner, Berger, Xu & Zechmeister-Boltenstern, 2005 **213**
Key to species **215**
*Latispathidium lanceoplites* (Foissner, Agatha & Berger, 2002) Foissner, Berger, Xu & Zechmeister-Boltenstern, 2005 **215**
*Latispathidium truncatum* (Stokes, 1885) Foissner, Berger, Xu & Zechmeister-Boltenstern, 2005 **218**
Key to subspecies **220**
*Latispathidium truncatum truncatum* (Stokes, 1885) Foissner, Berger, Xu & Zechmeister-Boltenstern, 2005 **221**

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

**Chapter 8**

W. Foissner, K. Xu & H. Berger
***Schmidingerophrya* nov. gen. (Ciliophora, Spathidiidae), a new genus whose species have only two dorsal brush rows 257**
Abstract **257**
*Schmidingerophrya* nov. gen. **257**
Key to species **258**
*Schmidingerophrya macrothrix* nov. spec. **258**
*Schmidingerophrya bisticha* nov. spec. **272**
Funding **279**
Acknowledgements **279**
References **279**

**Chapter 9**

W. Foissner, K. Xu & H. Berger
***Semibryophyllum* nov. gen. (Ciliophora, Spathidiidae), a new genus characterised by three ordinary dorsal brush rows and several accessory brush rows on the left side 281**
Abstract **281**
*Semibryophyllum* nov. gen. **281**
Key to species **285**
*Semibryophyllum cultellum* nov. spec. **285**
*Semibryophyllum palustre* nov. spec. **291**
*Semibryophyllum foliosum* (Foissner, 1983) nov. comb. **303**
Funding **308**
Acknowledgements **308**
References **308**

**Chapter 10**

W. Foissner, K. Xu & H. Berger
***Semispathidium* Foissner et al., 2002 (Ciliophora, Spathidiidae), a genus whose species have a discoidal oral bulge and *Spathidium*-like oral and somatic ciliature 311**
Abstract **311**
*Semispathidium* Foissner, Agatha & Berger, 2002 **312**
Key to species **315**
*Semispathidium enchelyodontides* Foissner, Agatha & Berger, 2002 **315**

*Semispathidium armatum* Foissner, Agatha & Berger, 2002 **320**
*Semispathidium lagyniforme* (Kahl, 1930) Foissner, Agatha & Berger, 2002 **322**
*Semispathidium breviarmatum* Foissner & Vdačný in Vdačný & Foissner, 2013 **325**
*Semispathidium longiarmatum* Foissner & Vdačný in Vdačný, Slovák & Foissner, 2014 **326**
*Semispathidium fraterculum* Foissner & Al-Rasheid in Foissner, Hess & Al-Rasheid, 2010 **329**
*Semispathidium pulchrum* 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

Helmut Berger (Publisher)
www.protozoology.com

# Abstract

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

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

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

# Chapter 12

# Pharyngospathidiidae nov. fam. (Ciliophora, Spathidiida), a group of spathidiids with a permanent cytopharynx[1]

**W. Foissner[a], K. Xu[b] & H. Berger[c]**

[a] Wilhelm Foissner†, University of Salzburg, Hellbrunnerstrasse 34, 5020 Salzburg, Austria
[b] Kuidong Xu, Laboratory of Marine Organism Taxonomy and Phylogeny, Qingdao Key Laboratory of Marine Biodiversity and Conservation, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071 and University of Chinese Academy of Sciences, Beijing 100049, China
[c] Helmut Berger, Consulting Engineering Office for Ecology, Radetzkystrasse 10, 5020 Salzburg, Austria

**ZooBank registration of present chapter**
urn:lsid:zoobank.org:pub:176530A7-956A-4BD3-A589-F9358ABAF6C4

## Abstract

The members of the Pharyngospathidiidae nov. fam. are characterized by a permanent cytopharynx supported by distinct microtubule ribbons forming an inner oral basket. *Pharyngospathidium* nov. gen. and *Neospathidium* nov. gen. are assigned to the new family. The nominotypical genus comprises four species, including the type species *Pharyngospathidium longichilum* nov. spec. (with two subspecies *Pharyngospathidium longichilum longichilum* nov. subspec., *Pharyngospathidium longichilum amphoriforme* nov. subspec.), *Pharyngospathidium pseudobavariense* nov. spec., *Pharyngospathidium bavariense* (Kahl, 1930) nov. comb., *Pharyngospathidium simplinucleatum* (Kahl, 1930) nov. comb. *Pharyngospathidium* nov. gen. differs from *Neospathidium* nov. gen. by the somatic ciliature, which is arranged in the *Epispathidium*-pattern in the former and in the *Spathidium*-pattern in the latter. *Neospathidium* comprises *Neospathidium longinucleatum* nov. spec. (type species), *Neospathidium africanum* nov. spec., and *Neospathidium brachystichos* nov. spec. A key to the species is provided. *Spathidium macrostomum* Wilbert, 1995 is a junior primary homonym of *Spathidium macrostomum* Wang & Nie, 1933. For the junior homonym we introduce the replacement name *Spathidium canadense* Wilbert nom. nov.

## Pharyngospathidiidae nov. fam.

2007 **Pharyngospathidiidae** – Foissner & Xu, Monogr biol. 81: 15, 17, 56, 330 (nomen nudum).

[1] This chapter should be referenced as follows: Foissner W., Xu K. & Berger H. (2025): Pharyngospathidiidae nov. fam. (Ciliophora, Spathidiida), a group of spathidiids with a permanent cytopharynx. – Ser. Monogr. Cilioph. 6: 367–431. For notes on "Material and methods", see Chapter 1 (Berger et al. 2025a).

**Diagnosis:** Spathidiina with permanent cytopharynx supported by conspicuous transverse microtubule ribbons forming a distinct inner oral basket. Oral bulge usually conspicuous, elliptical to dumbbell-shaped, often slightly twisted about main axis making it screwed like a propeller blade.

**Nominotypical genus:** *Pharyngospathidium* nov. gen.

**Genera assigned:** *Pharyngospathidium* nov. gen. (type genus); *Neospathidium* nov. gen.

**ZooBank registration:** urn:lsid:zoobank.org:act:F303EEA7-F581-4E13-84BE-8A5AB5E6C1D9

**Remarks:** Most spathidiid and gymnostomatid ciliates have a temporary oral bulge cytostome usually recognizable only in the scanning electron microscope and in protargol preparations as a minute, obconical depression in which the transverse microtubule bundles of the circumoral dikinetids converge (Fig. 12.1c, n, o, 12.9n). However, there are exceptions, for instance, in the family Enchelyodontidae Foissner et al., 2002, where the genus *Enchelydium* Kahl, 1930a has an "open mouth", that is, a cytopharyngeal opening, while *Enchelyodon* Claparède & Lachmann, 1859 has a hemispherical or plate-like "closed" oral bulge (Foissner et al. 2002, p. 121). The same patterns occur in the Spathidiidae s. l., where we rank this difference as a family character because the species with open mouth have the somatic ciliature arranged either in *Spathidium* (*Neospathidium* nov. gen.) or *Epispathidium* pattern (*Pharyngospathidium* nov. gen.), as in the Spathidiidae. This and the Myriokaryonidae Foissner, 2003 show that the various spathidiid ciliary patterns evolved independently several times within the spathidiids (Xu & Foissner 2005).

The permanent cytopharynx causes that the Pharyngospathidiidae developed two distinct oral baskets, viz., an outer basket formed, as usual, by the nematodesmata (ciliary roots of the circumoral dikinetids), and an inner basket formed by the transverse microtubule ribbons originating from the circumoral dikinetids and extending into the oral bulge, where they support the pharyngeal wall. Basically, this pattern is found in all haptorids (Foissner & Foissner 1988; Lynn & Small 2002), but the transverse microtubule ribbons are more strongly developed in the Pharyngospathidiidae than in ordinary spathidiids and gymnostomatids. This interpretation of the oral structures of the Pharyngospathidiidae still needs to be confirmed by transmission electron microscopy, but is very likely correct because of the great conformity of the gross oral pattern in haptorids (Foissner & Foissner 1988; Lynn & Small 2002).

Further distinguishing features between the Spathidiidae and Pharyngospathidiidae are the oral bulge, which is usually more conspicuous in the Pharyngospathidiidae, and the dorsal brush, which is usually longer in the Spathidiidae. In most pharyngospathidiids, the oral bulge is slightly inflated at the ends and rather distinctly twisted about the main axis making it screwed like a propeller blade or, in lateral view, like a screwed, recumbent number 8.

Most Pharyngospathidiidae described here are new species, and some of them likely have been mixed previously with several "classical" spathidiids, especially members of the *Spathidium spathula* group and the *Epispathidium amphoriforme* cluster. These species have a very similar general appearance as several pharyngospathidiids, but definitely lack a permanent cytopharynx.

Most Pharyngospathidiidae are rare, at least, hardly grow to reasonable numbers in the non-flooded Petri dish cultures. Thus, most of the existing species are likely still undiscovered.

## Key to genera

**1** Somatic ciliature in *Epispathidium* pattern ..... *Pharyngospathidium* nov. gen. (p. 369)
– Somatic ciliature in *Spathidium* pattern ..... *Neospathidium* nov. gen. (p. 400)

## *Pharyngospathidium* nov. gen.

**Nomenclature:** *Pharyngospathidium* is a composite of the Greek noun *pharynx* (pharynx, gullet; Hentschel & Wagner 1996, p. 471) and the genus-group name *Spathidium* Dujardin, 1841 (for etymology, see Chapter 3, that is, Foissner et al. 2025a), referring to the permanent cytopharynx and the similarity to the genera *Spathidium*/*Epispathidium* Foissner, 1984. Like *Spathidium*, of neuter gender (Aescht 2001, p. 300). *Pharyngospathidium* in *Pharyngospathidium longichilum amphoriforme* in Durán-Ramírez et al. (2015, p. 18) is a nomen nudum (ICZN 1999, p. 111).

**Diagnosis:** Somatic ciliature in *Epispathidium* pattern, that is, ciliary rows separate from continuous circumoral kinety and anteriorly so strongly curved that they run almost in parallel with the circumoral kinety. Three dorsal brush kineties.

**Type species:** *Pharyngospathidium longichilum* nov. spec.

**Species assigned:** *Pharyngospathidium longichilum* nov. spec. (type species; with two subspecies); *Pharyngospathidium bavariense* (Kahl, 1930) nov. comb. (original combination *Spathidium bavariense*); *Pharyngospathidium pseudobavariense* nov. spec.; *Pharyngospathidium simplinucleatum* (Kahl, 1930) nov. comb. (original combination *Spathidium simplinucleatum*).

**ZooBank registration:** urn:lsid:zoobank.org:act:5E3FA1D9-20D8-4946-A04E-1A3E9DB0EB67

**Remarks:** See same chapter at the Pharyngospathidiidae (p. 368).

## Key to species and subspecies

**1** Macronucleus in many nodules ..... **2**
– Macronucleus long, tortuous strand, or short and horseshoe-shaped ..... **3**
**2** Body length ≤140 µm; about 30 equidistant ciliary rows; oral bulge halves of similar width ..... *Pharyngospathidium pseudobavariense* nov. spec. (p. 389)
– Body length ≥140 µm; about 20 ciliary rows, approximately 8 on left side and 12 on right; right bulge half twice as wide than left ... *Pharyngospathidium bavariense* (p. 398)
**3** Macronucleus a long, tortuous strand ..... *Pharyngospathidium longichilum* nov. spec. (p. 370) **4**
– Macronucleus short, horseshoe-shaped .. *Pharyngospathidium simplinucleatum* (p. 399)
**4** Body massive, mushroom-shaped, oral bulge distinctly longer than trunk width. 45 ciliary rows on average ..... *Pharyngospathidium longichilum longichilum* nov. subspec. (p. 378)
– Body spatulate to elongate amphoriform, oral bulge only slightly longer than trunk width. 39 ciliary rows on average ..... *Pharyngospathidium longichilum amphoriforme* nov. subspec. (p. 380)

## *Pharyngospathidium longichilum* nov. spec.

(Fig. 12.1a–o, 12.2a–f, 12.3a–t, 12.4a–i, 12.5a–t, Tables 12.1, 12.2)

**Nomenclature:** The species-group name is a composite of the Latin adjective *long*·us, -a, -um ([m, f, n]; long; Hentschel & Wagner 1996, p. 370) and *-chilos* (Greek adjective; having a lip, in German "-lippig"; Schubert & Wagner 1979, p. 103), referring to the very long oral bulge, a main feature of the subspecies.

**Diagnosis** (includes two subspecies): Body size about 135 × 55 µm or 160 × 65 µm in vivo. Mushroom-shaped or amphoriform with oblique, elongate elliptical oral bulge about 1.5 or 1.2 times as long as widest trunk region. Macronucleus long and more or less tortuous. Two types of extrusomes: type I rod-shaped with narrowed ends and curved, 10–15 *µm long*; type II rod-shaped and 2–3 *µm long*. On average 45 or 39 ciliary rows, three anteriorly modified to strongly heterostichad dorsal brush occupying about 29% or 26% of body length; row 3 only about half as long as rows 1 and 2, which are of similar length.

**Type locality:** Sandy, saline coastal soil near Punta Pirikiki (about 09°39'29"N 82°45'16"W), circa 54 km south of the town of Limon, Caribbean coast of Costa Rica.

**Type material:** The slide (Fig. 12.5i, j; accession number 2024/198) containing the holotype (Fig. 12.1j, k) and two paratype slides (Fig. 12.5k–n; 2024/199, 200) have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI). This is also the type material of *Pharyngospathidium longichilum longichilum* nov. subspec.

**Subspecies included:** *Pharyngospathidium longichilum longichilum* nov. subspec. (nominotypical subspecies); *Pharyngospathidium longichilum amphoriforme* nov. subspec.

**ZooBank registration:** urn:lsid:zoobank.org:act:D4AB1D16-CF30-476D-BE6F-5F1E6DE1C169

**Remarks:** We split this species into two subspecies, differing mainly in the size and shape of body (135 × 55 µm and mushroom-shaped vs. 160 × 65 µm and amphoriform or spatulate) and oral bulge (in protargol preparations 80 µm long and inconspicuously dumb-

continued on p. 372

**Table 12.1** Ratios in *Pharyngospathidium longichilum amphoriforme* nov. subspec. from life (upper line; original data) and after protargol preparation (lower line; original data)[a]

| Characteristic | Mean | M | SD | SE | CV | Min | Max | n |
|---|---|---|---|---|---|---|---|---|
| Oral bulge:neck width | 1.4 | 1.4 | 0.1 | 0.0 | 3.8 | 1.4 | 1.5 | 7 |
| | 1.9 | 1.8 | 0.3 | 0.1 | 15.8 | 1.4 | 2.5 | 21 |
| Body width:neck width | 1.2 | 1.3 | 0.1 | 0.0 | 5.0 | 1.1 | 1.3 | 7 |
| | 1.6 | 1.5 | 0.3 | 0.1 | 18.7 | 1.3 | 2.6 | 21 |
| Oral bulge length:body width | 1.1 | 1.1 | 0.1 | 0.0 | 5.2 | 1.1 | 1.2 | 7 |
| | 1.2 | 1.1 | 0.2 | 0.0 | 15.0 | 0.9 | 1.5 | 21 |
| Body length:trunk width | 2.4 | 2.5 | 0.2 | 0.1 | 8.5 | 2.2 | 2.7 | 7 |
| | 3.1 | 3.0 | 0.4 | 0.1 | 14.2 | 2.2 | 4.1 | 21 |

[a] In vivo data based on video records of specimens from the non-flooded Petri dish culture used for protargol preparation. Data of prepared cells, see Table 12.2. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Mean – arithmetic mean, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean.

**Table 12.2** Morphometric data on *Pharyngospathidium longichilum longichilum* nov. subspec. (upper line; original data), *Pharyngospathidium longichilum amphoriforme* nov. subspec. (middle line; original data), and *Pharyngospathidium pseudobavariense* nov. spec. (lower line; original data from type population)[a]

| Characteristic | Mean | M | SD | SE | CV | Min | Max | n |
|---|---|---|---|---|---|---|---|---|
| Body, length | 121.9 | 120.0 | 12.5 | 2.7 | 10.3 | 95.0 | 153.0 | 21 |
| | 145.0 | 148.0 | 15.5 | 3.4 | 10.7 | 112.0 | 168.0 | 21 |
| | 100.4 | 100.0 | 9.9 | 2.1 | 9.8 | 84.0 | 120.0 | 21 |
| Body, widest trunk region | 52.8 | 50.0 | 7.7 | 1.7 | 14.6 | 42.0 | 69.0 | 21 |
| | 47.4 | 46.0 | 7.2 | 1.6 | 15.2 | 33.0 | 62.0 | 21 |
| | 47.0 | 46.0 | 6.3 | 1.4 | 13.3 | 34.0 | 61.0 | 21 |
| Body length:trunk width, ratio | 2.3 | 2.4 | 0.3 | 0.1 | 13.4 | 1.5 | 2.8 | 21 |
| | 3.1 | 3.0 | 0.4 | 0.1 | 14.2 | 2.2 | 4.1 | 21 |
| | 2.2 | 2.2 | 0.3 | 0.1 | 11.9 | 1.6 | 2.6 | 21 |
| Oral bulge, length (cord) | 80.8 | 79.0 | 9.8 | 2.1 | 12.1 | 63.0 | 100.0 | 21 |
| | 56.3 | 56.0 | 6.0 | 1.3 | 10.7 | 47.0 | 71.0 | 21 |
| | 39.5 | 40.0 | 4.9 | 1.1 | 12.4 | 30.0 | 51.0 | 21 |
| Oral bulge length:trunk width, ratio | 1.5 | 1.5 | 0.2 | – | 11.3 | 1.2 | 1.9 | 21 |
| | 1.2 | 1.2 | 0.2 | – | 14.8 | 0.9 | 1.5 | 21 |
| | 0.8 | 0.9 | 0.1 | – | 11.4 | 0.6 | 1.0 | 21 |
| Oral bulge, height | 3.9 | 4.0 | 0.5 | 0.1 | 12.6 | 3.0 | 5.0 | 21 |
| | 4.8 | 5.0 | 0.6 | 0.1 | 13.1 | 4.0 | 6.0 | 21 |
| | 5.6 | 6.0 | 0.9 | 0.2 | 16.6 | 4.0 | 8.0 | 21 |
| Circumoral kinety to last dikinetid of brush row 1, distance | 33.7 | 33.0 | 3.8 | 0.8 | 11.4 | 26.0 | 40.0 | 21 |
| | 37.2 | 38.0 | 4.3 | 1.2 | 11.5 | 31.0 | 43.0 | 13 |
| | 23.6 | 24.0 | 3.1 | 0.7 | 13.1 | 18.0 | 31.0 | 21 |
| Circumoral kinety to last dikinetid of brush row 2, distance | 35.6 | 35.0 | 3.7 | 0.8 | 10.4 | 30.0 | 43.0 | 21 |
| | 37.2 | 38.0 | 3.7 | 1.0 | 9.9 | 32.0 | 42.0 | 13 |
| | 25.0 | 25.0 | 3.0 | 0.7 | 12.2 | 19.0 | 31.0 | 21 |
| Circumoral kinety to last dikinetid of brush row 3, distance | 17.5 | 17.0 | 1.8 | 0.4 | 10.3 | 15.0 | 21.0 | 21 |
| | 17.2 | 17.0 | 1.9 | 0.5 | 10.9 | 15.0 | 21.0 | 13 |
| | 11.4 | 12.0 | 1.3 | 0.3 | 11.3 | 9.0 | 13.0 | 21 |
| Anterior body end to macronucleus/ anteriormost macronucleus nodule, distance | 49.2 | 47.0 | 11.7 | 2.6 | 23.8 | 23.0 | 70.0 | 21 |
| | 43.0 | 43.0 | 8.4 | 1.8 | 19.5 | 20.0 | 58.0 | 21 |
| | 30.4 | 30.0 | 6.6 | 1.4 | 21.8 | 10.0 | 40.0 | 21 |
| Macronucleus figure, length | 44.1 | 40.0 | 9.2 | 2.0 | 20.7 | 30.0 | 65.0 | 21 |
| | 73.1 | 73.0 | 13.2 | 2.9 | 18.1 | 47.0 | 98.0 | 21 |
| | 56.8 | 60.0 | 9.1 | 2.0 | 16.1 | 32.0 | 71.0 | 21 |
| Macronucleus (spread, thus approximate) or macronucleus nodules, length | 148.8 | 150.0 | – | – | – | 100.0 | 200.0 | 21 |
| | 124.3 | 125.0 | – | – | – | 60.0 | 165.0 | 21 |
| | 10.0 | 10.0 | 3.9 | 0.9 | 39.1 | 5.0 | 21.0 | 21 |
| Macronucleus (width in middle third) or macronucleus nodules, width | 6.2 | 6.0 | 0.6 | 0.1 | 9.4 | 5.0 | 7.0 | 21 |
| | 7.6 | 8.0 | 0.9 | 0.2 | 11.5 | 6.0 | 9.0 | 21 |
| | 4.8 | 5.0 | 0.9 | 0.2 | 18.7 | 3.0 | 6.0 | 21 |
| Macronucleus nodules, number | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 | 1.0 | 1.0 | 21 |
| | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 | 1.0 | 1.0 | 21 |
| | 29.2 | 30.0 | 6.7 | 1.5 | 22.8 | 16.0 | 41.0 | 21 |
| Micronuclei, across[b] | 2.8 | 3.0 | 0.4 | 0.1 | 13.4 | 2.0 | 3.5 | 21 |
| Micronuclei, number[b] | 16.0 | 16.0 | 5.0 | 1.1 | 31.4 | 8.0 | 24.0 | 21 |
| Somatic kineties, number[b] | 44.8 | 45.0 | 2.3 | 0.5 | 5.1 | 41.0 | 49.0 | 21 |

**Table 12.2** Continued

| Characteristic | Mean | M | SD | SE | CV | Min | Max | n |
|---|---|---|---|---|---|---|---|---|
| Somatic kineties, number | 39.8 | 39.0 | 1.9 | 0.4 | 4.7 | 36.0 | 44.0 | 21 |
| | 29.9 | 30.0 | 1.2 | 0.3 | 4.0 | 28.0 | 33.0 | 21 |
| Basal bodies in a right-side kinety, number | 58.0 | 58.0 | 8.8 | 1.9 | 15.1 | 48.0 | 78.0 | 21 |
| | – | – | – | – | – | – | – | – |
| | 51.1 | 51.0 | 9.9 | 2.2 | 19.3 | 36.0 | 75.0 | 21 |
| Dorsal brush rows, number | 3.0 | 3.0 | 0.0 | 0.0 | 0.0 | 3.0 | 3.0 | 21 |
| | 3.0 | 3.0 | 0.0 | 0.0 | 0.0 | 3.0 | 3.0 | 21 |
| | 3.0 | 3.0 | 0.0 | 0.0 | 0.0 | 3.0 | 3.0 | 21 |
| Dikinetids in brush row 1, number | 29.8 | 29.0 | 3.9 | 0.9 | 13.3 | 24.0 | 37.0 | 21 |
| | 37.5 | 37.0 | 3.7 | 1.0 | 9.9 | 33.0 | 44.0 | 13 |
| | 26.4 | 26.0 | 3.8 | 0.8 | 14.4 | 21.0 | 36.0 | 21 |
| Dikinetids in brush row 2, number | 35.7 | 36.0 | 4.1 | 0.9 | 11.5 | 29.0 | 43.0 | 21 |
| | 37.0 | 37.0 | 3.8 | 1.0 | 10.2 | 30.0 | 44.0 | 13 |
| | 28.0 | 27.0 | 3.4 | 0.7 | 12.1 | 23.0 | 36.0 | 21 |
| Dikinetids in brush row 3, number | 17.5 | 18.0 | 2.5 | 0.6 | 14.5 | 13.0 | 22.0 | 21 |
| | 15.8 | 16.0 | 1.8 | 0.5 | 11.3 | 13.0 | 20.0 | 13 |
| | 11.4 | 12.0 | 1.5 | 0.3 | 13.1 | 8.0 | 14.0 | 21 |

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

[b] This line refers to *Pharyngospathidium longichilum longichilum*.

bell-shaped vs. 56 μm long and elongate elliptical), the macronucleus pattern (usually highly tortuous vs. frequently C-shaped to sigmoidal), and the number of somatic ciliary rows (45 vs. 39). Both subspecies differ distinctly from *Pharyngospathidium pseudobavariense* nov. spec. not only by the macronucleus pattern (strand vs. scattered nodules), but also by the considerably higher number of ciliary rows (about 39–45 vs. 30).

*Pharyngospathidium longichilum* nov. spec. has an *Epispathidium*-like overall appearance, and thus it looks rather similar to some *Epispathidium* species, especially, *Epispathidium amphoriforme* and *Epispathidium securiforme* (for revision of *Epispathidium*, see Chapter 6, that is, Foissner et al. 2025b). However, both have a temporary cytostome (vs. permanent cytopharynx in *Pharyngospathidium*) and a different number of ciliary rows (on average 28 in *Epispathidium amphoriforme* and 54 in *Epispathidium securiforme* vs. 39–45). Certain specimens of *Epispathidium terricola* (see Chapter 6, that is, Foissner et al. 2025b) also resemble *Pharyngospathidium longichilum amphoriforme*, differing, however, distinctly in the length of the extrusomes (about 40 μm vs. 10–15 μm).

*Pharyngospathidium longichilum longichilum* resembles *Spathidium macrostomum* Wang & Nie, 1933 and *Spathidium canadense* Wilbert in Foissner, Xu & Berger, 2025b[2] as well,

[2] *Spathidium macrostomum* Wilbert, 1995 (p. 274) is a junior primary homonym of *Spathidium macrostomum* Wang & Nie, 1933 (p. 25; original spelling *Spathidium macrostoma*), and the junior name is permanently invalid (ICZN 1999, Article 57.2). Thus, Foissner et al. (2025b, p. 147) introduced the new name *Spathidium canadense* Wilbert

continued on p. 378

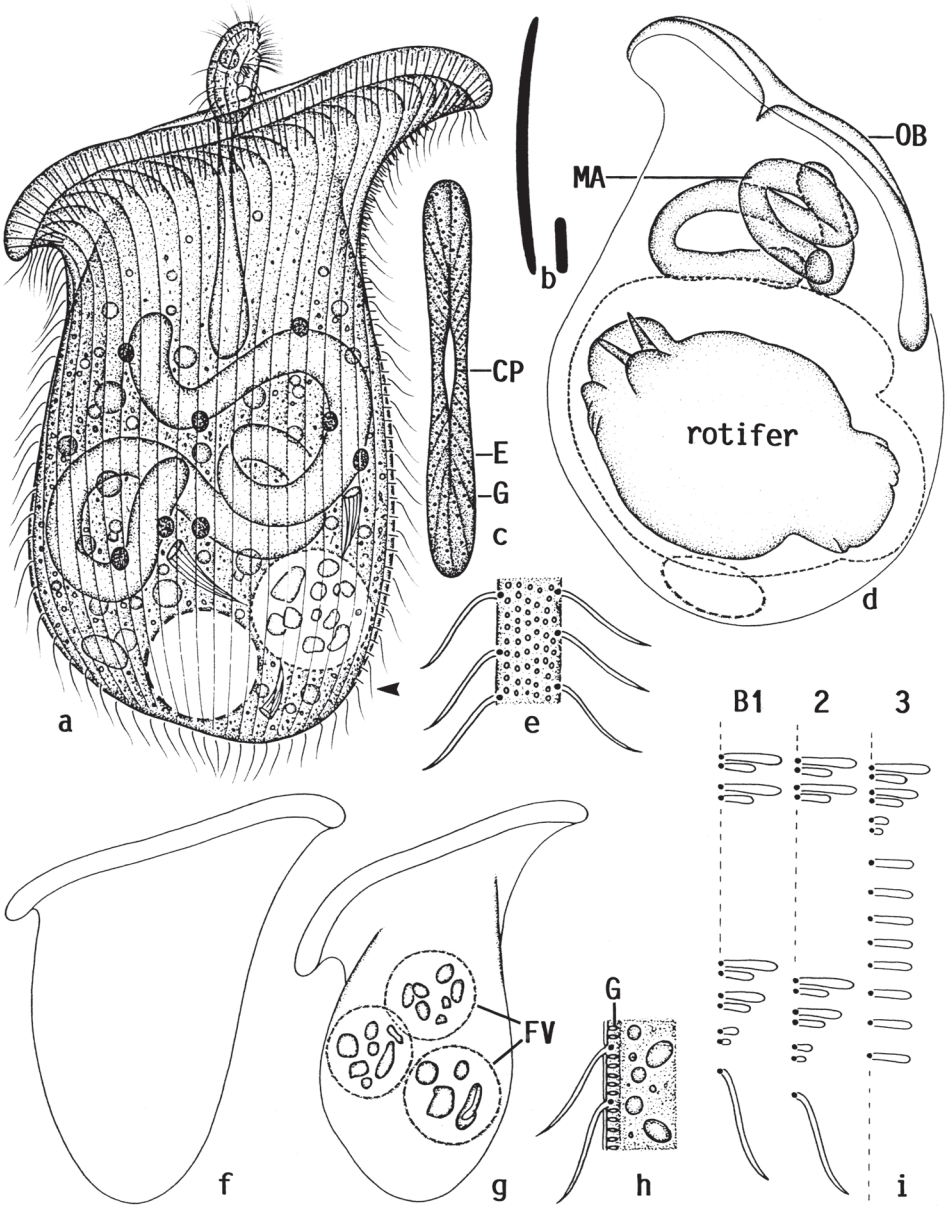



**Fig. 12.1a–i** *Pharyngospathidium longichilum longichilum* nov. subspec. (originals. a–c, e–i, from life; d, protargol preparation). **a:** Left side view of a representative, mushroom-shaped specimen (140 µm) just ingesting a small ciliate, viz., *Drepanomonas revoluta*; when ingestion commences, a long tube forms from the pharyngeal opening to mid-body. **b:** Type I (length 10–14 µm) and type II (2–3 µm) oral bulge extrusomes. **c:** Frontal view of oral bulge showing the central pharyngeal opening. The cortical granules and the extrusomes form rather distinct rows. **d:** A specimen with a large rotifer ingested, length of ciliate 110 µm. **e, h:** Cortical granulation in surface view and optical section. **f, g:** Same specimen before and after feeding, about 100 µm. **i:** Dorsal brush. B1–3 – dorsal brush rows, CP – cytopharyngeal opening, E – extrusomes, FV – food vacuoles, G – cortical granules, MA – macronucleus, OB – oral bulge.

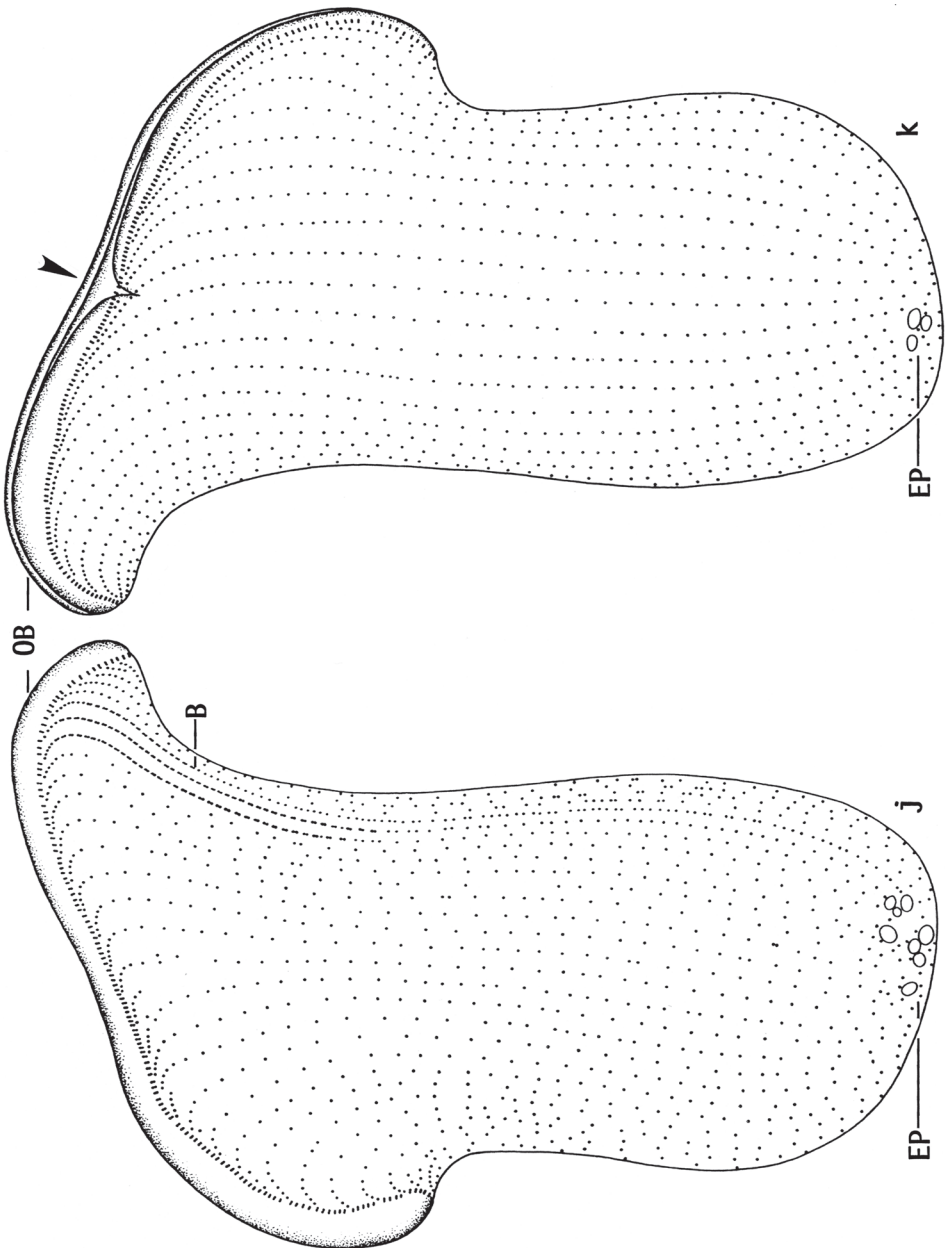



**Fig. 12.1j, k** *Pharyngospathidium longichilum longichilum* nov. subspec. (originals. Protargol preparation). Left and right side ciliary pattern of holotype specimen, 120 µm. Internal details, see Fig. 12.1l, m. Note the *Epispathidium* ciliary pattern and the monokinetidal bristle tail of dorsal brush 3, where the basal bodies are much more narrowly spaced than in the ordinary ciliary rows. The arrowhead marks the pharyngeal opening. B – dorsal brush, EP – excretory pores of the contractile vacuole, OB – oral bulge.

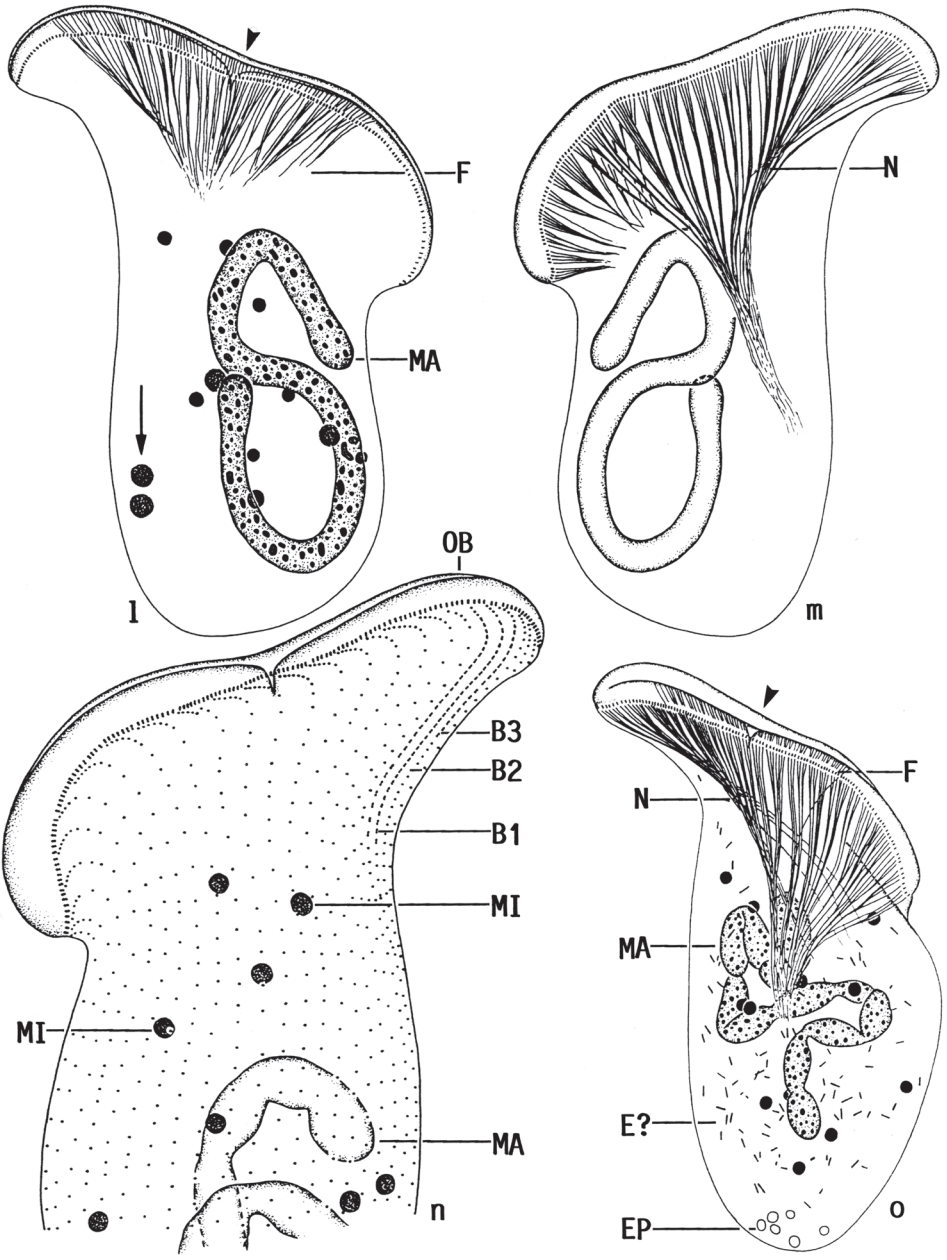



**Fig. 12.1l–o** *Pharyngospathidium longichilum longichilum* nov. subspec. (originals. Protargol preparation). **l, m:** Right and left side view of holotype (for the ciliary pattern, see Fig. 12.1j, k) showing the inner (F) and outer (N) oral basket and the nuclear apparatus, 120 µm. Note some enlarged (reorganizing?) micronuclei (arrow). **n:** Right side view of anterior body half of another specimen, length of oral bulge 80 µm. Note the *Espispathidium* ciliary pattern and the comparatively short dorsal brush. **o:** Body shape and internal details of another specimen, 113 µm. Arrowhead marks pharyngeal opening. B1–3 – dorsal brush rows, EP – excretory pores, E? –extrusomes?, F – fibres composing inner oral basket, MA – macronucleus, MI – micronuclei, N – nematodesmata composing outer oral basket, OB – oral bulge.

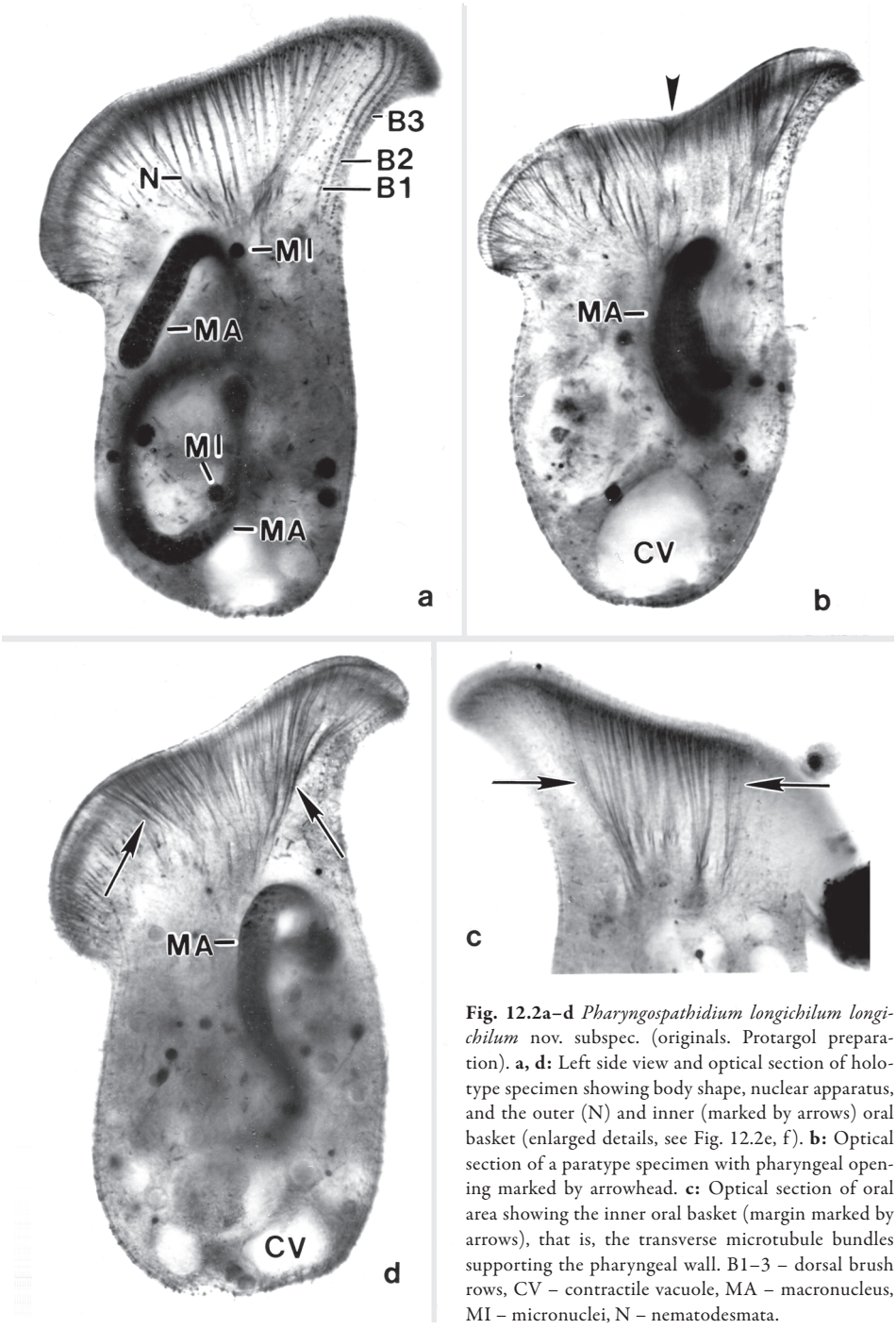



**Fig. 12.2a–d** *Pharyngospathidium longichilum longichilum* nov. subspec. (originals. Protargol preparation). **a, d:** Left side view and optical section of holotype specimen showing body shape, nuclear apparatus, and the outer (N) and inner (marked by arrows) oral basket (enlarged details, see Fig. 12.2e, f). **b:** Optical section of a paratype specimen with pharyngeal opening marked by arrowhead. **c:** Optical section of oral area showing the inner oral basket (margin marked by arrows), that is, the transverse microtubule bundles supporting the pharyngeal wall. B1–3 – dorsal brush rows, CV – contractile vacuole, MA – macronucleus, MI – micronuclei, N – nematodesmata.

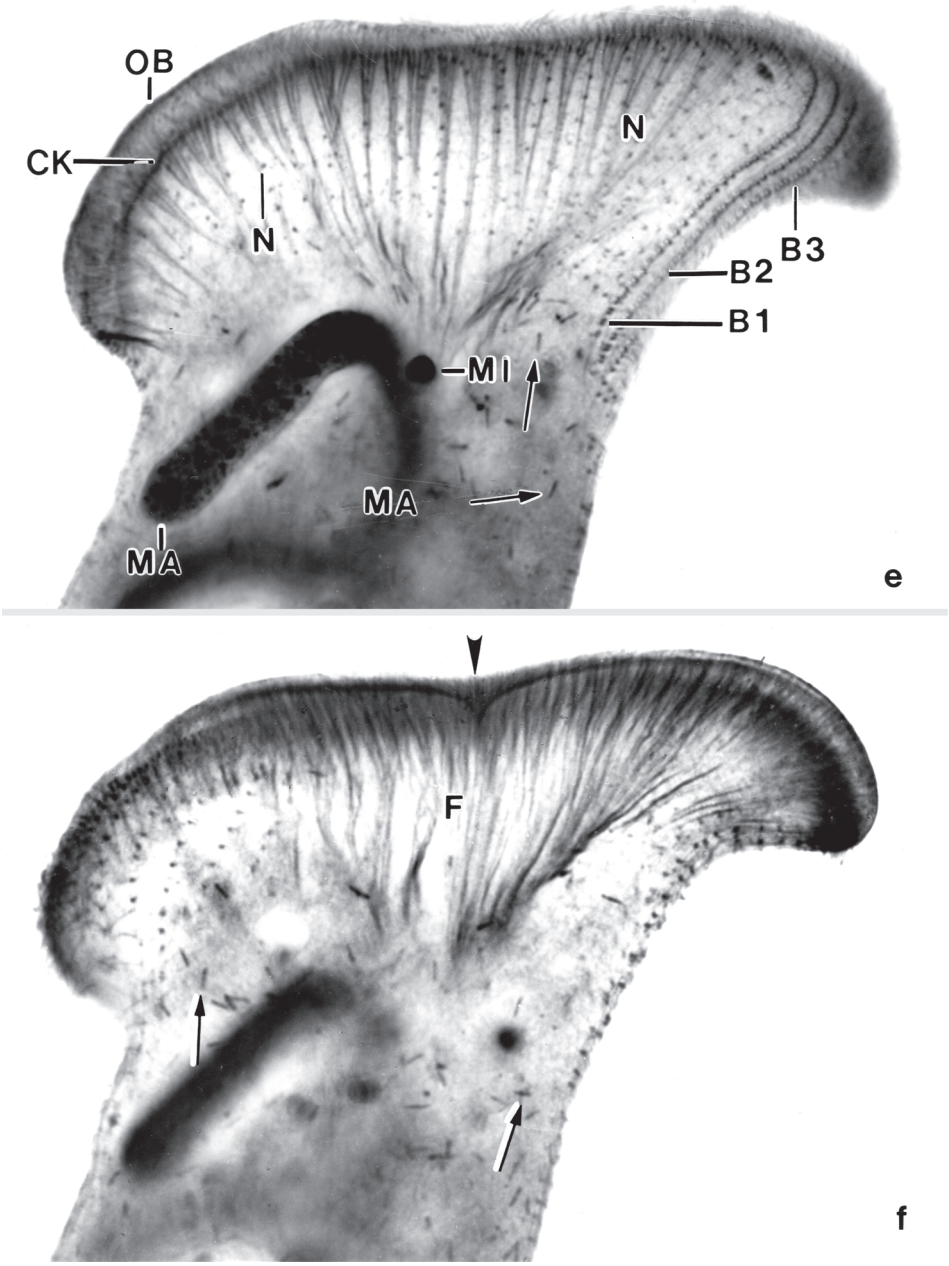



**Fig. 12.2e, f** *Pharyngospathidium longichilum longichilum* nov. subspec. (originals. Protargol preparation). Anterior portion of holotype specimen (overviews, see Fig. 12.2a, d). The inner oral basket is formed by transverse microtubule ribbons (F) originating from the circumoral dikinetids and extending into the pharyngeal wall. The outer oral basket is formed by nematodesma bundles (N) originating from the circumoral kinety. Arrows mark short cytoplasmic rods (extrusomes?). Arrowhead denotes pharyngeal opening. B1–3 – dorsal brush rows, CK – circumoral kinety, F – fibres, MA – macronucleus, MI – micronucleus, N – nematodesmata, OB – oral bulge.

especially in body outline and the large oral bulge. Except for the temporary cytostome, as definitely mentioned by Wang & Nie (1933), *Spathidium macrostomum* differs also by the horseshoe-shaped macronucleus (vs. long and tortuous) and the planktonic, freshwater habitat (vs. saline soil). *Spathidium canadense* is easily distinguished from both subspecies by the macronucleus (scattered nodules vs. tortuous strand) and the ciliary pattern (*Spathidium* pattern, as definitely stated by Wilbert vs. *Epispathidium* pattern).

**Description:** See *Pharyngospathidium longichilum longichilum* nov. subspec. and *Pharyngospathidium longichilum amphoriforme* nov. subspec.

**Occurrence and ecology:** Very likely a terrestrial species. For details, see *Pharyngospathidium longichilum longichilum* nov. subspec. and *Pharyngospathidium longichilum amphoriforme* nov. subspec.

## *Pharyngospathidium longichilum longichilum* nov. subspec.

(Fig. 12.1a–o, 12.2a–f, 12.5i–n, Table 12.2)

2007 ***Pharyngospathidium longichilum longichilum*** – Foissner & Xu, Monogr biol. 81: 18, 21, 22, Fig. 11c–e, 13i, 14g (Fig. 12.1a, c, d, l, m; nomen nudum).

**Nomenclature:** This is the nominotypical subspecies. For derivation of the species-group name, see species. *Pharyngospathidium longichilum longichilum* in Foissner & Xu (2007; see entry in list of synonyms) is a nomen nudum because not accompanied by the explicit fixation of a holotype (ICZN 1999, Articles 16.4.1, 72.3).

**Diagnosis:** Body size about 135 × 55 µm in vivo. Mushroom-shaped with inconspicuously dumbbell-shaped oral bulge about 1.5 times as long as widest trunk region. Macronucleus usually highly tortuous. On average 45 ciliary rows.

**Type locality:** Same as for *Pharyngospathidium longichilum* nov. spec., that is, sandy, saline coastal soil near Punta Pirikiki (about 09°39'29''N 82°45'16''W), circa 54 km south of the town of Limon, Caribbean coast of Costa Rica.

**Type material:** Same as for *Pharyngospathidium longichilum* nov. spec. (see there).

**ZooBank registration:** Same as for species.

**Remarks:** For separation from the subspecies *Pharyngospathidium longichilum amphoriforme*, congeners, and similar species, see remarks to the *Pharyngospathidium longichilum* nov. spec.

**Description:** Body size moderately variable, viz., 100–170 × 45–80 µm in vivo, usually about 135 × 55 µm, as calculated from some in vivo measurements and the morphometric data (Table 12.2). Overall appearance broadly spatulate or mushroom-shaped, though body length:trunk width is only about 2:1, because of the pronounced neck and the long oral bulge distinctly projecting from both sides of the cell; body shape, however, also highly dependent on nutrition state (Fig. 12.1f, g). Trunk cylindroidal to ellipsoidal, laterally flattened up to 2:1, in hyaline neck and oral area up to 4:1; dorsal side considerably longer than ventral, concave anterior end thus distinctly slanted; posterior end broadly rounded, occasionally wrinkled due to the contractile vacuole contained (Fig. 12.1a, f, g, j–o, 12.2a,

for the junior homonym; the name refers to the country (Canada) where the species was discovered (Wilbert 1995, p. 275).

b). Macronucleus in middle body third, long and usually highly tortuous with ends slightly inflated, rarely more or less moniliform; contains many nucleoli up to 2 µm across. On average 16 micronuclei about 3 µm across attached to or far away from macronucleus; occasionally occur some larger (reorganizing?) micronuclei with disintegrated membrane (Fig. 12.1a, l, n, o, 12.2a, b, d). Contractile vacuole in rear body end, many excretory pores in pole area. Two types of extrusomes studded in oral bulge (Fig. 12.1a–c): type I rod-shaped with pointed ends and curved, 10–14 *µm long,* scattered also in cytoplasm; type II rod-shaped and 2–3 *µm long,* recognized only in oral bulge. Oral bulge extrusomes impregnate more or less intensely with Wilbert's protargol method, but are unstained with Foissner's method with which, however, many short cytoplasmic rods impregnate, possibly extrusome developmental stages (Fig. 12.1o, 12.2e, f). Cortex very flexible and 1 µm thick, contains about five rows of colourless, narrowly spaced, approximately 1.0 × 0.7 µm-sized granules between each two ciliary rows. Cytoplasm colourless, depending on nutrition contains few to many lipid droplets up to 10 *µm across* and one to several large food vacuoles with remnants of ciliate (e.g., *Drepanomonas revoluta*) and rotifer prey, which is slowly digested and thus identifiable. Interestingly, a long tube forms as soon as the prey touches the pharyngeal opening (Fig. 12.1a). Movement without peculiarities.

Somatic cilia about 8 µm long in vivo and ordinarily spaced (about 2.5 µm), except of anterior end of rows, where the narrowly spaced cilia produce, together with those of the circumoral kinety, a conspicuous corona; arranged in an average of 45 equidistant, bipolar rows anteriorly forming a typical *Epispathidium* pattern; anteriorly frequently with small irregularities, such as minute breaks and/or supernumerary kinetids outside rows (Fig. 12.1a, j, k, n; Table 12.2). Dorsal brush dikinetidal and strongly heterostichad, moderately conspicuous because occupying about 29% of body length and bristles up to 4 µm long in vivo; all rows commence with some ordinary cilia anteriorly, rows 1 and 2 continue with ordinary cilia posteriorly; two supernumerary dikinetidal rows occur right of row 1 in one out of 42 specimens analysed. Bristles of same appearance in all rows, that is, anterior bristle of dikinetids clavate and up to 4 µm long, posterior rod-shaped and about 2 µm long; bristle length gradually decreases from about 4 µm anteriorly to about 1 µm posteriorly. Brush row 1 composed of an average of 29 dikinetids, slightly shorter than row 2 composed of an average of 36 very narrowly spaced dikinetids; occasionally, some monokinetids interspersed in both rows. Row 3 only about half as long as rows 1 and 2, comprising an average of 18 dikinetids followed by a monokinetidal tail extending to posterior body end and composed of rather closely spaced, rod-shaped bristles about 3 µm long in vivo (Fig. 12.1a, i, j, n, 12.2a, e; Table 12.2).

Oral bulge slanted by about 30°, very conspicuous both in vivo and protargol preparations because (i) about 1.5 times longer than widest trunk region, distinctly set off from body proper, and distinctly sigmoidal, that is, slightly concave at cytopharyngeal entrance; (ii) bright due to the many extrusomes contained; and (iii) up to 5 µm high in lateral view and about 10 µm wide in frontal view, where it is slightly dumbbell-shaped (Fig. 12.1a, l–o, 12.2a–f; Table 12.2). Cytopharynx comparatively inconspicuous, broadly funnel-shaped in lateral and fusiform in frontal view. Circumoral kinety at the base of oral bulge, elongate elliptical with ends slightly widened; continuous and separate from ciliary rows, composed of dikinetids usually more closely spaced laterally than dorsally and ventrally; individual

dikinetids each associated with a cilium about 8 µm long, a long nematodesma, and a faintly impregnated fibre (likely transverse microtubular ribbon) extending into cytopharyngeal wall to form the very distinct (inner) basket composed of bundled fibres. Outer (oral) basket very conspicuous in protargol preparations because composed of distinct, cuneate nematodesma bundles extending to mid-body; central nematodesma bundles usually much longer than marginal ones (Fig. 12.1a, j–o, 12.2a–e).

**Occurrence and ecology:** As yet *Pharyngospathidium longichilum longichilum* was found only at the type locality (see above); it became moderately abundant in the non-flooded Petri dish culture. The sample was a mixture of sandy, highly saline soil (>20‰; pH 7.6), roots, and litter from halophytes under coco palms. *Pharyngospathidium longichilum longichilum* is obviously a carnivorous, litter and/or sand inhabiting species mainly preying on rotifers and ciliates (Fig. 12.1a, d).

## *Pharyngospathidium longichilum amphoriforme* nov. subspec.

(Fig. 6.3c in Foissner et al. 2025b; Fig. 12.3a–t, 12.4a–i, 12.5a–h, o–t, Tables 12.1, 12.2)

1956 ***Spathidium amphoriforme* (Greeff) var. *securiforme* (Kahl) Form B** – Gellért, Acta Biol. Hung. 6: 83, Abb. 2 (Fig. 6.3c in Foissner et al. 2025b; brief redescription with detailed figure; likely a misidentification, see remarks; whereabout of possible voucher material not checked).

**Nomenclature:** The species-group name *amphoriform·is, -is*, *-e* (amphora-shaped) is a composite of the Latin noun *amphora* (vessel, flagon, pitcher, flask, bottle, jar; Brown 1954, p. 86), the thematic vowel *·i-*, and *-form·is*, *-is*, *-e* (Latin adjective [m, f, n]; -shaped; see Hentschel & Wagner 1996, p. 274 at *glómeriformis*), referring to the amphoriform shape of protargol-prepared specimens. *Pharyngospathidium longichilum amphoriforme* in Durán-Ramírez et al. (2015, p. 18) is a nomen nudum, that is, an unavailable name (ICZN 1999, p. 111).

**Diagnosis:** Body size about 160 × 65 µm in vivo. Body spatulate to amphoriform with elongate elliptical oral bulge about 1.2 times as long as widest trunk region. Macronucleus roughly C-shaped or sigmoidal. On average 39 ciliary rows.

**Type locality:** Soil and litter from a *Nothofagus* forest about 30 km south of the town of Pucón (about 39.3°S 71.9°W), Chile.

**Type material:** The slide (Fig. 12.5o, p; accession number 2024/201) containing the holotype specimen (Fig. 12.4a) and two paratype slides (Fig. 12.5q–t; 2024/202, 203) have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI).

**ZooBank registration:** urn:lsid:zoobank.org:act:E95892B7-0396-4028-AF0C-D8260B60DAB3

**Remarks:** For separation from the second subspecies, congeners, and similar species, see remarks to species.

After finishing this chapter, W. Foissner recognized that "*Spathidium amphoriforme* var. *securiforme*" sensu Gellért (1956) is likely identical with *Pharyngospathidium longichilum amphoriforme* (Fig. 6.3c in Foissner et al. 2025b). Except of the smaller size (90–100 µm), all main features match (body and macronucleus shape, 40 ciliary rows), and Gellért (1956) even mentions a "cleft-like oral opening". The small size could be caused by the preparation

continued on p. 382

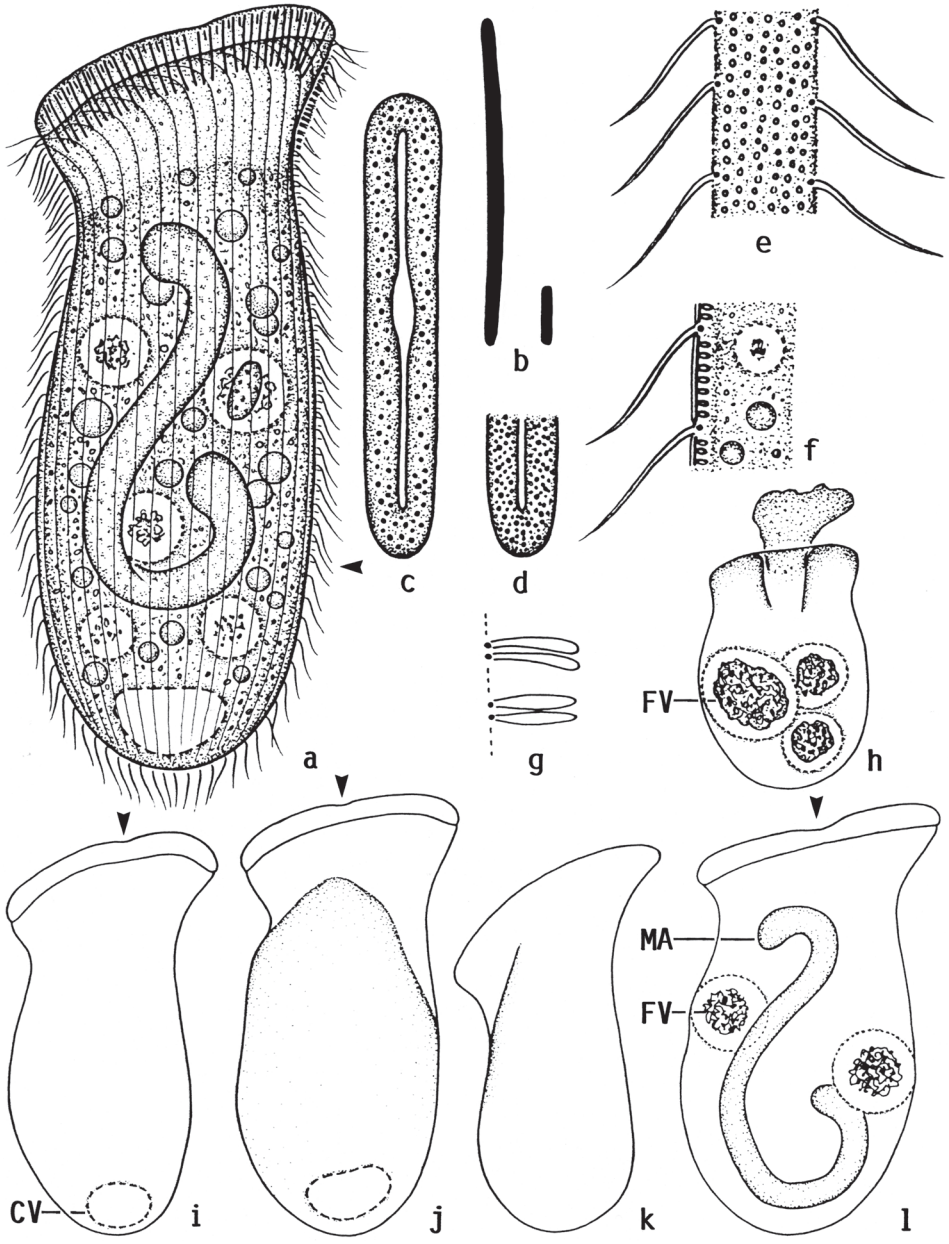



**Fig. 12.3a–l** *Pharyngospathidium longichilum amphoriforme* nov. subspec. (originals. From life; a, i, j, redrawn from video records). **a:** Left side view of a rather slender specimen, 160 µm. Arrowhead marks end of monokinetidal bristle tail of brush row 3. **b:** Type I (10–15 µm) and type II (2.0–2.5 µm) oral bulge extrusomes. **c:** Frontal view of oral bulge. **d:** Ventral end of oral bulge showing cortical granulation. **e, f:** Surface view and optical section showing cortical granulation. **g:** Dorsal brush bristles are up to 3 µm long and clavate or tongue-shaped. **h:** When ingesting a *Gonostomum affine*, specimens may contract by 30%. **i–l:** Outlines of ordinary fed (i, l), well fed (j), and hungry (k) specimens. Arrowheads mark inconspicuous pharyngeal opening. CV – contractile vacuole, FV – food vacuoles, MA – macronucleus.

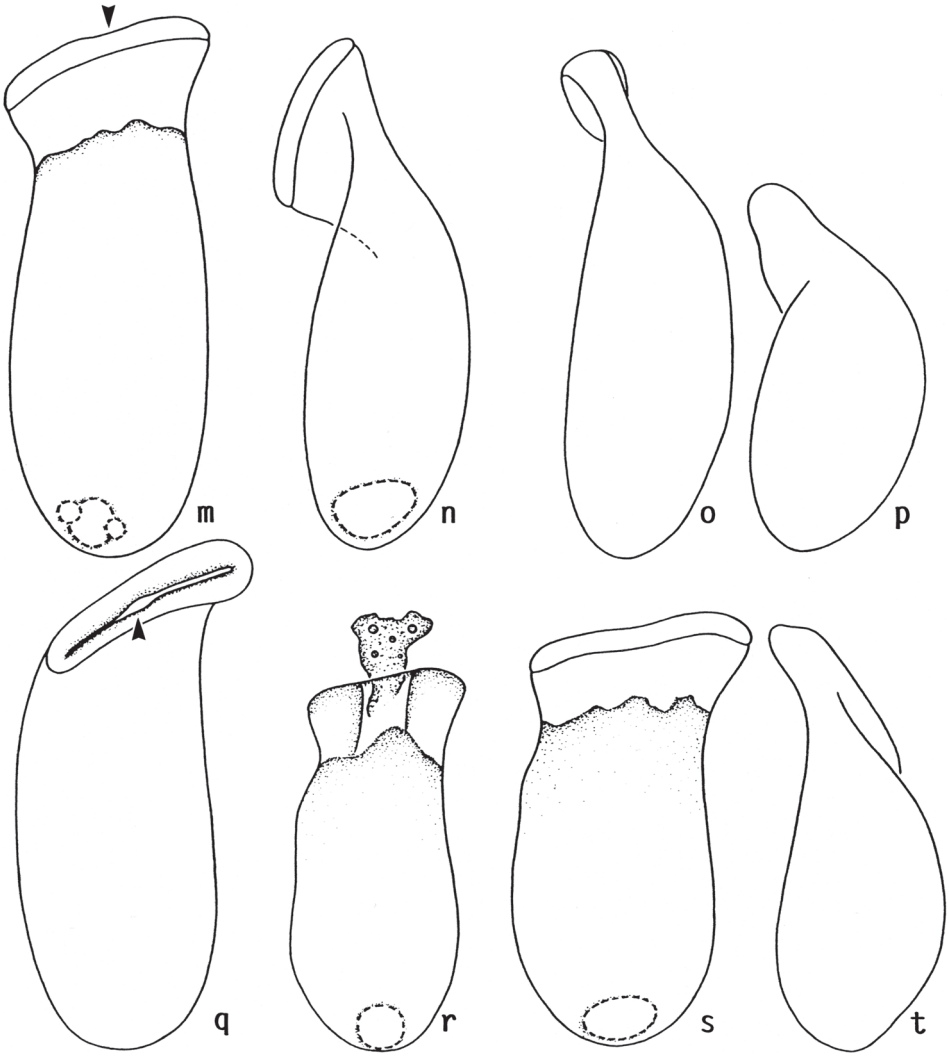



**Fig. 12.3m–t** *Pharyngospathidium longichilum amphoriforme* nov. subspec. (originals. From life, redrawn from video records). **m–q:** Various views of a swimming specimen: left side view (m), dorsolateral view when slightly twisted about main axis (n), dorsal view (o), oblique posterior polar (p) and left side (q) view when oral region is curved laterally at almost right angles. Arrowheads mark inconspicuous cytopharyngeal opening. **r–t:** Various views of a gliding specimen: left side view when feeding on *Gonostomum affine* (r), left side (s) and dorsolateral (t) view when well-fed.

method used (opal-blue), where specimens are air-dried and thus likely shrinking considerably; unfortunately, Gellért (1956) does not mention whether the size values refer to live or prepared specimens. Gellért (1956) discussed that his population is smaller (90–100 µm) as the population described by Kahl (1930a, b), which is 200–300 µm long. Therefore, he designated the population described by Kahl as "Form A" and his Hungarian population as "Form B"; for brief review of the Gellért (1956) population, see below.

continued on p. 386

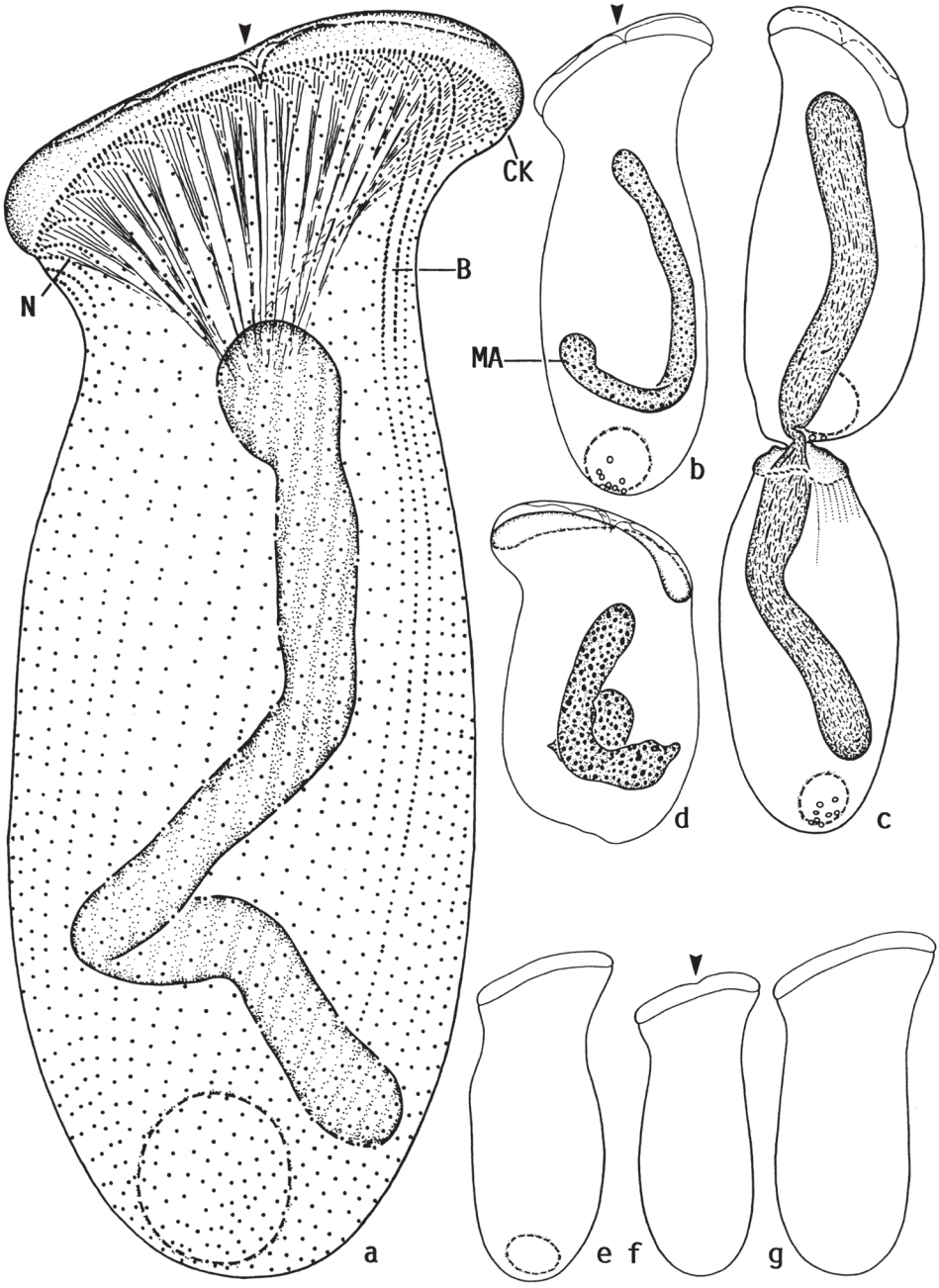



**Fig. 12.4a–g** *Pharyngospathidium longichilum amphoriforme* nov. subspec. (originals. a–d, protargol preparation; e–g, from life, redrawn from video records). Arrowheads mark pharyngeal opening. **a:** Left side view of holotype specimen, length 127 µm. **b:** Specimen with C-shaped macronucleus, length 138 µm. **c, d:** Very late divider (195 µm) and early proter post-divider (80 µm). **e–g:** Outlines of starved specimens. B – dorsal brush, CK – circumoral kinety, MA – macronucleus, N – nematodesmata.

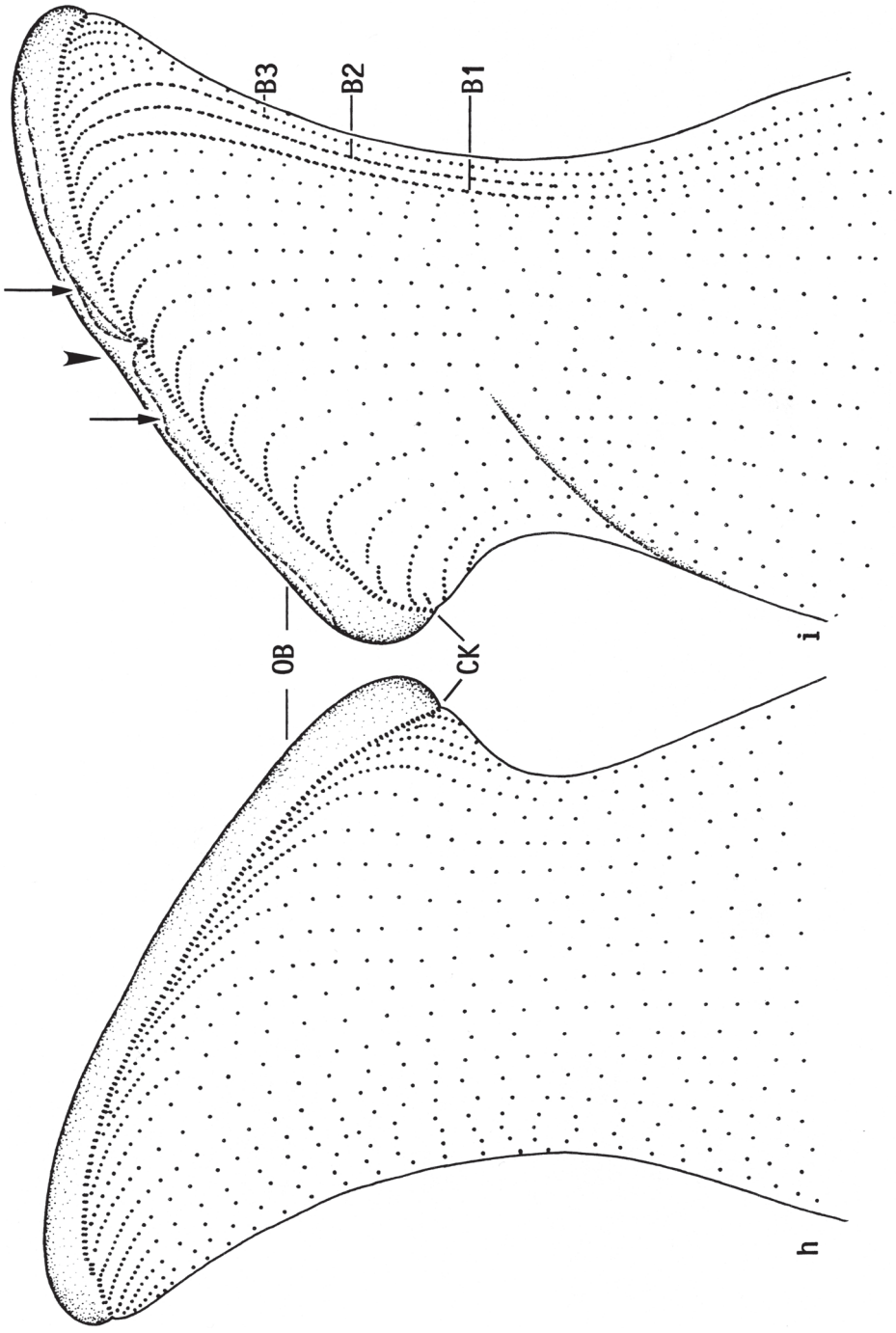



**Fig. 12.4h, i** *Pharyngospathidium longichilum amphoriforme* nov. subspec. (originals. Protargol preparation). Right and left side view of ciliary pattern; oral bulge length 65 µm. Arrows mark wrinkled wall of cytopharyngeal canal. Arrowhead denotes cytopharynx. B1–3 – dorsal brush rows, CK – circumoral kinety, OB – oral bulge.

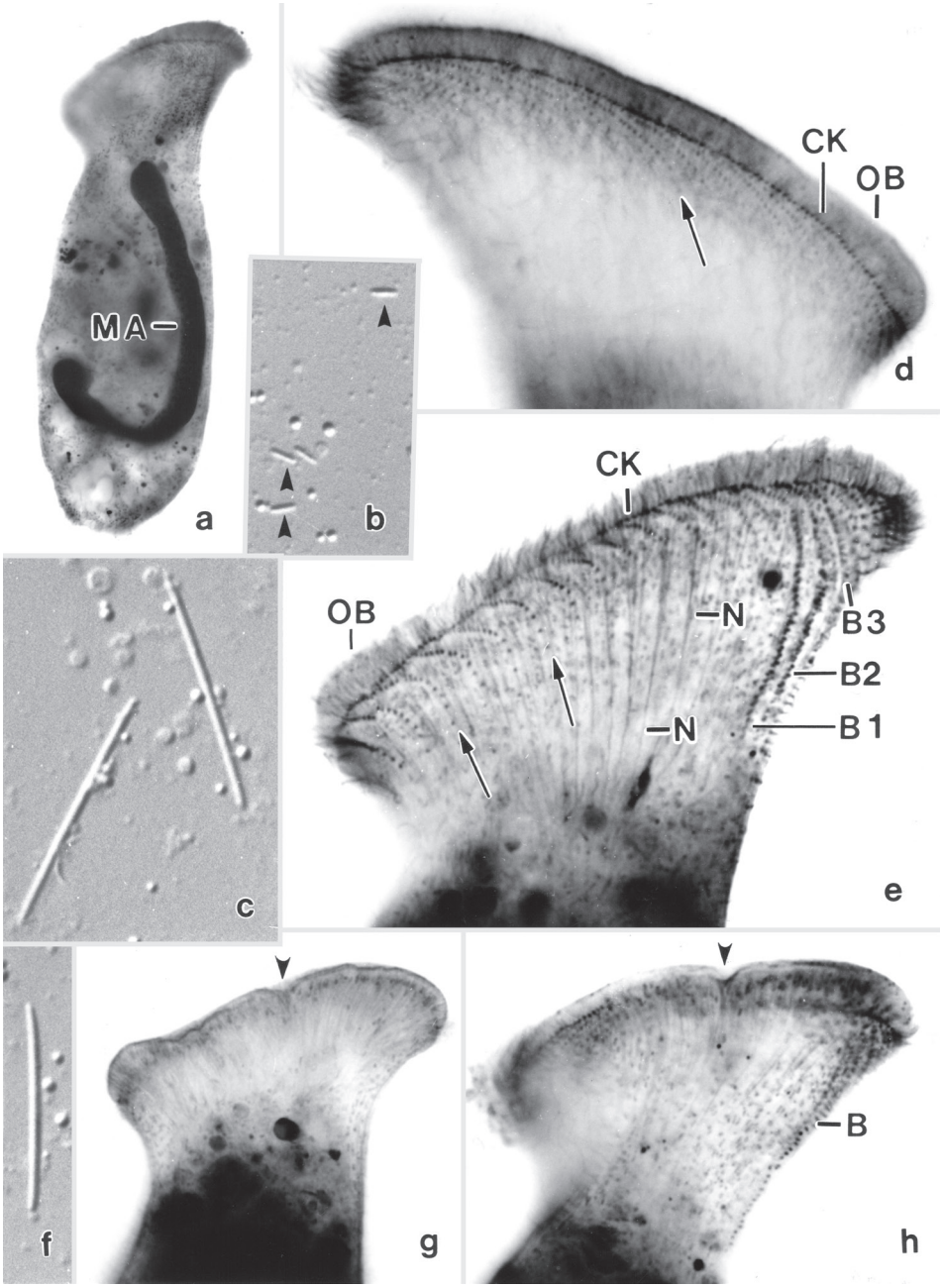



**Fig. 12.5a–h** *Pharyngospathidium longichilum amphoriforme* nov. subspec. (originals. a, d, e, g, h, protargol preparation; b, c, f, from life). **a:** Overview of an *Epispathidium amphoriforme*-shaped specimen. **b, c, f:** The oral bulge contains many short (b, arrowheads) and long (c, f) extrusomes. **d, e:** Right and left side view showing the *Epispathidium* ciliary pattern (arrows). **g, h:** Left side views of oral area with opening of the permanent cytostome marked by arrowheads. B – dorsal brush, B1–3 – dorsal brush rows, CK – circumoral kinety, MA – macronucleus, N – nematodesma bundles, OB – oral bulge.

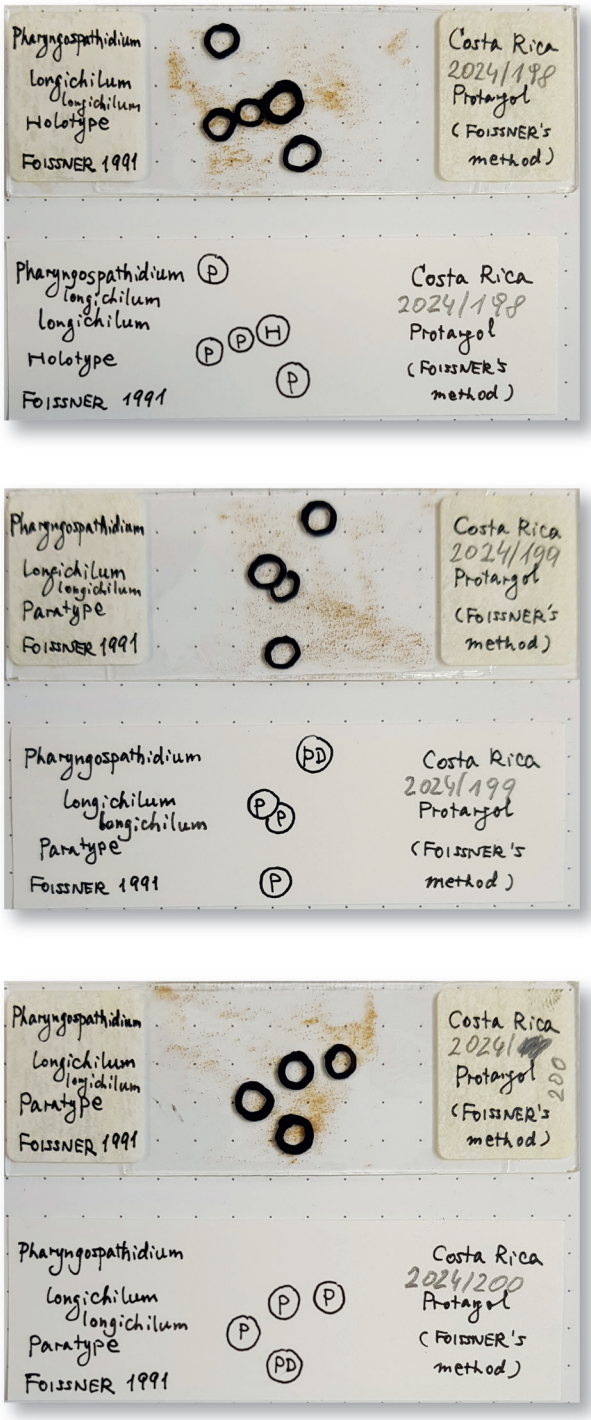
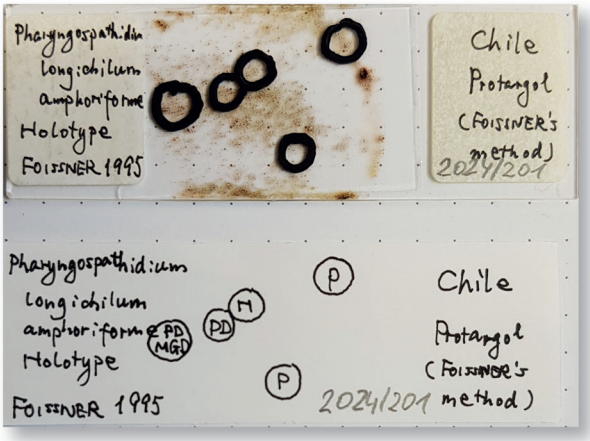


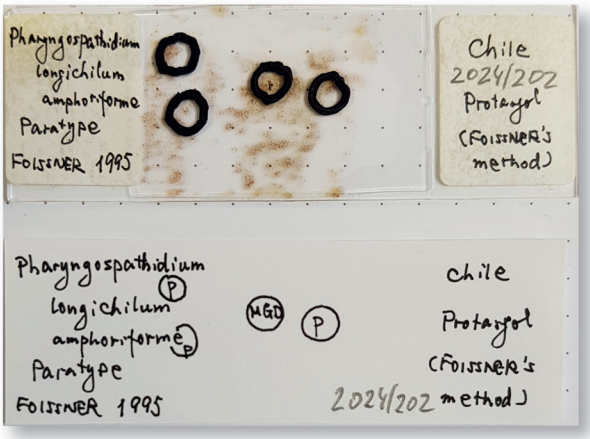

**Fig. 12.5i–n** *Pharyngospathidium longichilum longichilum* nov. subspec. (originals. Protargol slides). **i, j:** Slide (i) and protocol (j) containing holotype (H) and paratypes (P). Accession number (LI): 2024/198. **k–n:** Slides (k, m) and protocols (l, n) containing paratypes drawn (PD) and paratypes (P). Accession numbers (LI): 2024/199, 200.

**Description:** At first the type population from Chile is described in detail. The last paragraph of this chapter deals with the misidentified population described by Gellért (1956).

Type population (Fig. 12.3a–t, 12.4a–i, 12.5a–h; Table 12.2): Body size moderately variable, viz., 120–190 × 40–80 µm in vivo, usually about 160 × 65 µm (length:width ratio about 2.5:1), while 145 × 47 µm (about 3.1:1) in protargol preparations (Tables 12.1, 12.2); thus, neck and trunk width strongly shrunken (~35%) and shape rather different in vivo and protargol preparations, viz., spatulate vs. amphoriform to slenderly amphoriform because oral bulge relative to neck width considerably longer in preparations than in vivo (Table 12.1). Body shape conspicuous also due to the comparatively broadly rounded oral bulge ends and the ability to curve the strongly flattened (up to 5:1) oral bulge area at



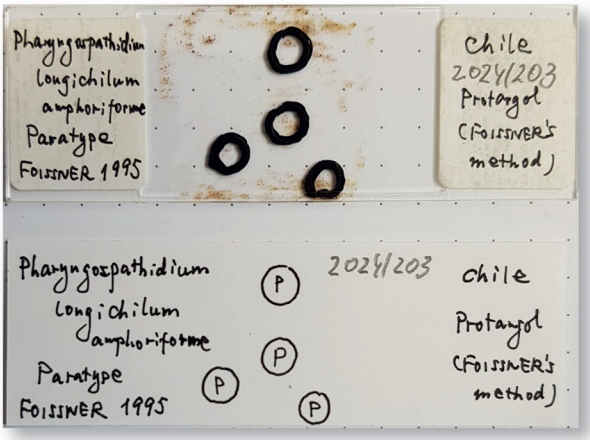

o




p

q

r




s

t

**Fig. 12.5o–t** *Pharyngospathidium longichilum amphoriforme* nov. subspec. (originals. Protargol slides). **o, p:** Slide (o) and protocol (p) containing holotype (H), paratypes (P), paratypes drawn (PD), and morhogenetic stage drawn (MGD). Accession number (LI): 2024/201. **q-t:** Slides (q, s) and protocols (r, t) containing paratypes (P) and morphogenetic stage drawn (MGD). Accession numbers (LI): 2024/202, 203.

right angles to main body axis (Fig. 12.3p, q). Trunk ellipsoidal to almost cylindrical with ventral margin occasionally rugged by large food vacuoles, inconspicuously flattened laterally; dorsal side slightly longer than ventral, slightly convex anterior body end thus inconspicuously slanted; posterior end usually broadly rounded, occasionally bluntly pointed and/or wrinkled due to the contractile vacuole contained (Fig. 12.3a, i–t, 12.4a, b, e–g, 12.5a; Table 12.2). Macronucleus strand in middle quarters of cell, ends slightly inflated, studded with nucleoli up to 2 µm across, shape highly variable (Fig. 12.3a, l, 12.4a, b): in about half of 85 specimens analyzed C- or horseshoe-shaped, in 26% a sigmoidal rod, and in 23% a long, tortuous strand, as in *Pharyngospathidium longichilum longichilum*; one specimen has two rather long strands. Micronuclei not unequivocally identifiable due

to many similarly sized and impregnated cytoplasmic inclusions. Contractile vacuole in rear end, many excretory pores in pole area. Two types of extrusomes scattered in cytoplasm and studded around cytopharynx and, especially, in oral bulge ends (Fig. 12-3a–c): type I inconspicuously curved rods with narrowed ends, 10–15 × 0.7–1.0 μm in size; type II rod-shaped and 2.0–2.5 × 0.4–0.6 μm in size, in protargol preparations forms dotted line above circumoral kinety due to the intensely impregnated posterior end. Many fusiform, developing cytoplasmic extrusomes often strongly impregnate with the protargol method used. Cortex very flexible and near 1 μm thick, contains about six rows of colourless, approximately 0.8 × 0.4 μm-sized granules between each two ciliary rows; granules in oral bulge cortex form short, oblique rows. Cytoplasm colourless, inclusions mainly in trunk leaving blank and hyaline oral area; depending on nutrition, studded with few to many lipid droplets, some apparently empty vacuoles, and large food vacuoles containing remnants of ciliate prey (e.g., the hypotrich *Gonostomum affine*). When feeding, the cell may contract distinctly becoming bursiform, and the cytopharynx opens widely to ingest the lysing prey (Fig. 12.3h, r). Swims moderately rapid, frequently curving laterally oral portion (Fig. 12.3p, q).

Somatic cilia 8–10 μm long in vivo and ordinarily spaced, except of anterior portion of rows, where the densely arranged cilia produce, together with those of the circumoral kinety, a conspicuous corona; arranged in an average of 39 equidistant, bipolar rows forming a typical *Epispathidium* pattern along circumoral kinety; anteriorly occasionally with small irregularities, such as minute breaks and/or supernumerary kinetids outside rows (Fig. 12.3a, 12.4a, h, i; Table 12.2). Dorsal brush dikinetidal and strongly heterostichad, of ordinary appearance, that is, occupies about 26% of body length and bristles up to 3 μm long in vivo; all rows commence with some ordinary cilia anteriorly, rows 1 and 2 continue with ordinary cilia posteriorly. Bristles similar in all rows, viz., clavate to tongue-shaped and about 3 μm long in middle portion of rows decreasing in length to 1–2 μm anteriorly and posteriorly. Brush rows 1 and 2 end at same level, each composed of an average of 37 dikinetids; frequently, dikinetids of row 1 slightly obliquely arranged; row 3 distinctly shortened, comprising an average of only 16 dikinetids followed by a monokinetidal tail extending to posterior third of body and composed of rather closely spaced, rod-shaped, about 1.5 μm long bristles (Fig. 12.3a, g, 12.4a, i; Table 12.2).

Oral bulge slanted by only 20–30°, but conspicuous both in vivo and protargol preparations because (i) 1.2 times longer than widest trunk region and massive, that is, about 6 μm high and 13 μm wide; (ii) ends comparatively broadly rounded and smoothly merging into neck, making anterior region somewhat clavate; and (iii) bright due the many rather long and thick extrusomes contained. Oral bulge elongate elliptical with dorsal end inconspicuously inflated; surface flat to rather distinctly convex, usually with minute indentation in centre where the cytopharynx opens. Cytopharynx comparatively inconspicuous, funnel-shaped in lateral view and fusiform with shallow canals extending to bulge ends in frontal view; wall of opening and canals frequently wrinkled in protargol preparations, an unusual feature not observed in the other members of the family (Fig. 12.3a, c, i–t, 12.4a, b, e–h, 12.5g, h; Table 12.2). Circumoral kinety at base of oral bulge, elongate elliptical with ends slightly widened; continuous and usually distinctly separate from ciliary rows, composed of narrowly spaced dikinetids each associated with a cilium about 10 μm long, a long nematodesma, and a faintly impregnated fibre (likely transverse microtubular ribbon)

extending into cytopharyngeal wall to form an inconspicuous, faintly impregnated (inner) basket. Outer oral basket conspicuous in protargol preparations because composed of distinct, cuneate nematodesma bundles extending to second quarter of cell (Fig. 12.3a, 12.4a, h, i, 12.5d, e).

Population described by Gellért (1956; Fig. 6.3c in Foissner et al. 2025b): The following text is a translation (not verbatim) of the description by Gellért (1956). Body length 90–100 µm (in vivo?), length:width ratio 2:1. Body shape like a "milk pot", flattened; shape constant, but body rather flexible. Oral bulge slightly curved; mouth opening cleft-like, with short trichites; middle portion of oral bulge slightly concave, the dorsal portion somewhat thicker. 40 somatic kineties, cilia short, narrowly spaced. On left side near dorsal region two short brush rows and one which extends along whole body length; brush cilia short, very narrowly spaced. Macronucleus in middle body portion, U-shaped with opening directed anteriorly, ends club-shaped widened. Contractile vacuole terminal, with 6–8 excretory pores; filled via auxiliary vacuoles. Cytoplasm bright with slightly brownish colour. Movement cumbersome, very slow. Feeds on small protozoans. Not common, divides slowly.

**Morphogenesis** (original observations on type population from Chile): A very late divider shows that the oral bulge and the *Epispathidium* ciliary pattern develop post-divisionally; further, the comparatively small, not yet aligned oral kinetofragments suggest post-divisional proliferation of circumoral dikinetids (Fig. 12.4c). An early proter post-divider is identifiable by the small size, a minute projection at posterior end where the daughters separated, and the pointed macronucleus (Fig. 12.4d).

**Occurrence and ecology:** As yet *Pharyngospathidium longichilum amphoriforme* nov. subspec. was found only at the type locality (see above); it was abundant in the non-flooded Petri dish culture (pH 6.1). The sample, kindly provided by Dr. M. Bonkowski (University of Göttingen, Germany) in November 1994, was composed of some black-brown soil and much litter from bamboo understorey.

Gellért (1956) found this (or a very similar?) species in the humus layer formed underneath the lichen *Parmelia saxatilis* collected from the south-western side of the Magoska hill (Tokaj-Eperjes mountains) north-east of the village of Boldogkőváralja, administrative district of Abauj-Torna, Hungary. Durán-Ramírez et al. (2015, p. 20, 23) recorded it from tanks of bromeliads from Coffee plantations in Mexico.

## *Pharyngospathidium pseudobavariense* nov. spec.

(Fig. 12.6a–h, n, o–v, 12.7a–q, Table 12.2)

1953 ***Spathidium bavariense* Kahl 1930** – Wenzel, Arch. Protistenk. 99: 79, Abb. 2 (Fig. 12.6n; brief description of Bavarian population; misidentification).

1987 ***Spathidium bavariense* Kahl, 1930** – Tirjaková & Matis, Acta Fac. Rerum nat. Univ. comen, Bratislava, Series Zoologia 29: 20, figure on p. 25 (Fig. 12.6h; brief description of Slovakian population; misidentification).

1998 ***Spathidium bavariense* Kahl, 1930** – Foissner, Eur. J. Protistol. 34: 209 (misidentification; however, it is uncertain whether all records belong to *Pharyngospathidium pseudobavariense*).

**Nomenclature:** The species-group name *pseudobavariense* is a composite of the Greek *pseudo-* (false, wrong; Hentschel & Wagner 1996, p. 499), the New Latin noun *Bavaria* (https://

continued on p. 392

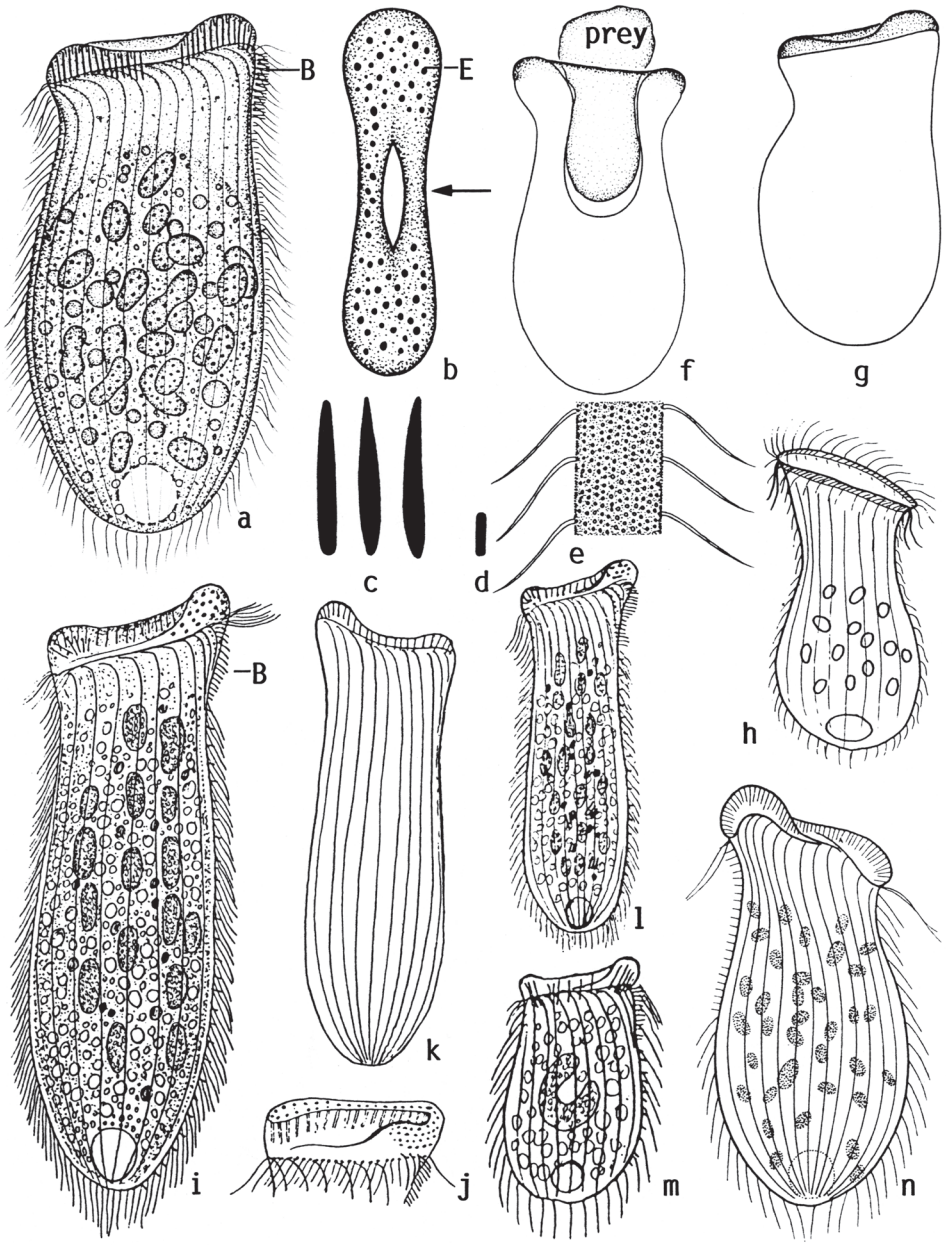



**Fig. 12.6a–h, n** *Pharyngospathidium pseudobavariense* nov. spec. (a–g, originals of type population; h, from Tirjaková & Matis 1987; n, from Wenzel 1953. From life). **a:** Left side view of a representative specimen, length 110 µm. **b:** Frontal view of oral bulge lacking extrusomes at left side of pharyngeal opening (arrow). **c, d:** Type I (length 6 µm) and type II (1.5 µm) extrusomes. **e:** Cortical granulation. **f:** Feeding specimen, length 100 µm. **g:** Shape variant. **h, n:** Slovak (h) and Bavarian (n) specimens, length 110–120 µm, 70 µm. B – dorsal brush, E – extrusomes
**Fig. 12.6i–l** *Pharyngospathidium bavariense* (Kahl, 1930) nov. comb. (from Kahl 1930a, b. From life). Left and right side views and oral bulge, length 160 µm. Note that this species has more ciliary rows on the left (i) than right (k) side.

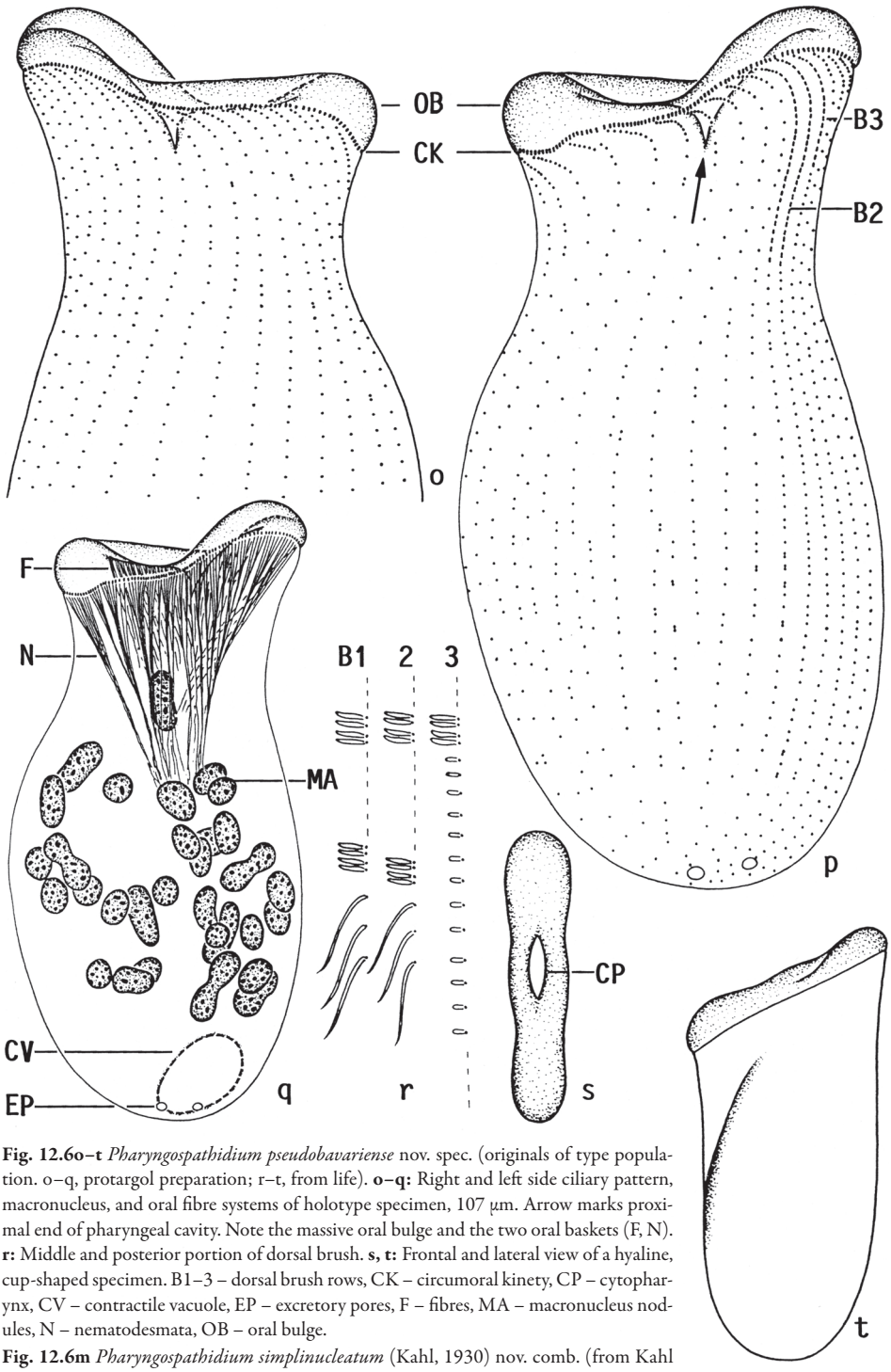



**Fig. 12.6o–t** *Pharyngospathidium pseudobavariense* nov. spec. (originals of type population. o–q, protargol preparation; r–t, from life). **o–q:** Right and left side ciliary pattern, macronucleus, and oral fibre systems of holotype specimen, 107 µm. Arrow marks proximal end of pharyngeal cavity. Note the massive oral bulge and the two oral baskets (F, N). **r:** Middle and posterior portion of dorsal brush. **s, t:** Frontal and lateral view of a hyaline, cup-shaped specimen. B1–3 – dorsal brush rows, CK – circumoral kinety, CP – cytopharynx, CV – contractile vacuole, EP – excretory pores, F – fibres, MA – macronucleus nodules, N – nematodesmata, OB – oral bulge.

← **Fig. 12.6m** *Pharyngospathidium simplinucleatum* (Kahl, 1930) nov. comb. (from Kahl 1930a. From life). This species has a horseshoe-shaped macronucleus, length 90 µm.

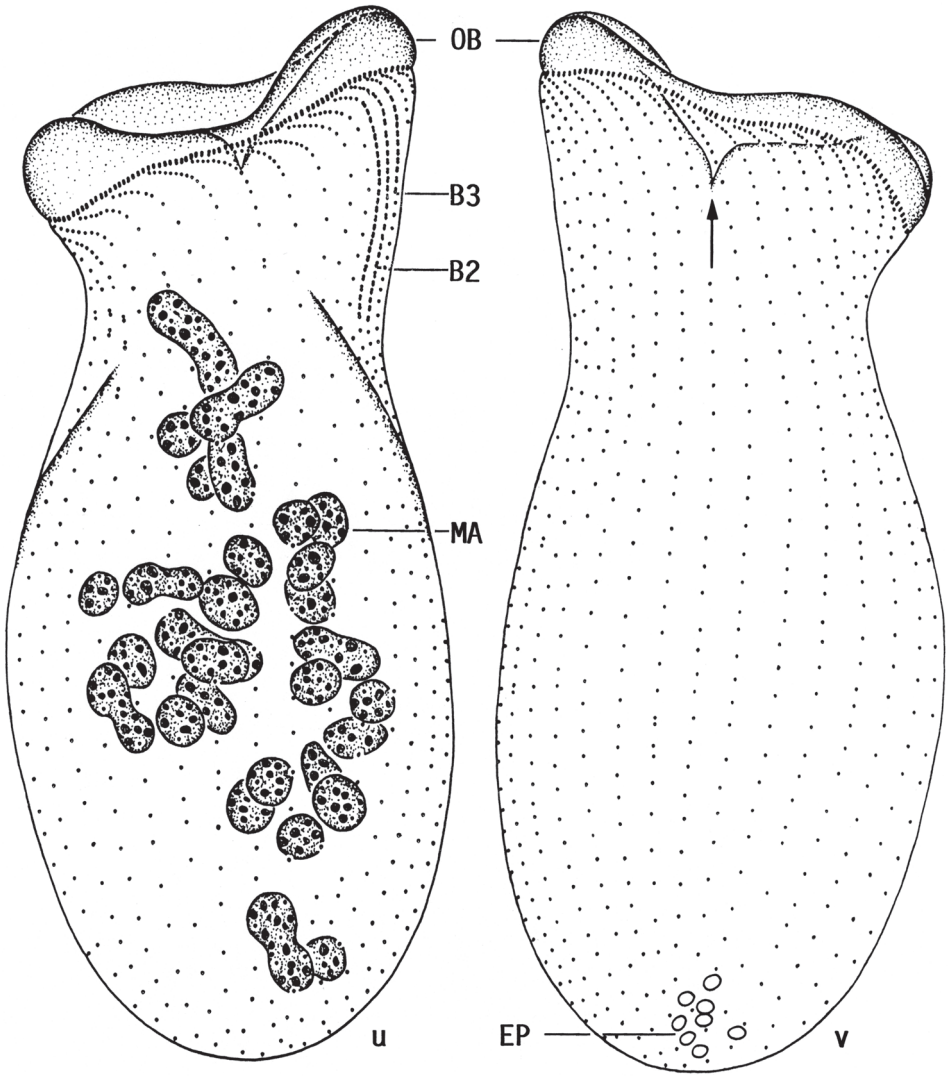



**Fig. 12.6u, v** *Pharyngospathidium pseudobavariense* nov. spec. (originals of type population. Protargol preparation). Ciliary pattern of left and right side and nuclear apparatus of a representative specimen, 98 μm. Arrow in (v) marks proximal end of pharyngeal cavity. B2, 3 – dorsal brush rows, EP – excretory pores of contractile vacuole, MA – macronucleus nodules, OB – oral bulge.

en.wiktionary.org/wiki/Bavaria; accessed 05 Jun 2023), and the Latin suffix *-ens·is, -is*, *-e* ([m, f, n], means for species names the geographical range of life, that is, belonging to Bavaria in present case; Werner 1972, p. 44). The name refers to the similarity with *Pharyngospathidium bavariense* (see below).

**Diagnosis:** Body size about 110 × 50 μm in vivo. Body spatulate to bursiform with slightly oblique, dumbbell-shaped oral bulge about 80% as long as widest trunk region.

continued on p. 395

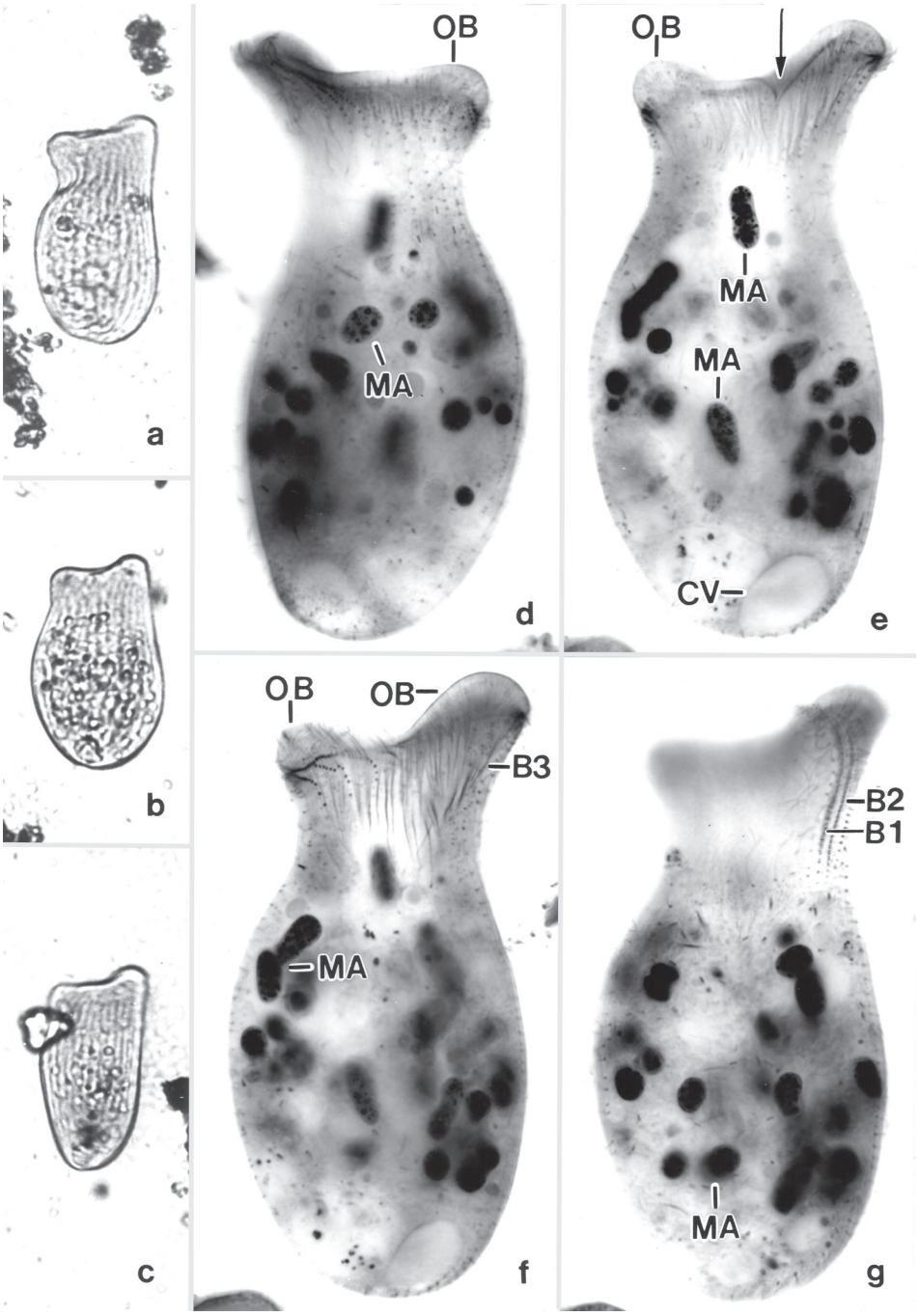



**Fig. 12.7a–g** *Pharyngospathidium pseudobavariense* nov. spec. (originals of type population. a–c, from life; d–g, protargol preparation). **a–c:** Shape variability of freely motile specimens. **d–g:** Same specimen with permanent cytostome marked by arrow. B1–3 – dorsal brush rows, CV – contractile vacuole, MA – macronucleus nodules, OB – oral bulge.

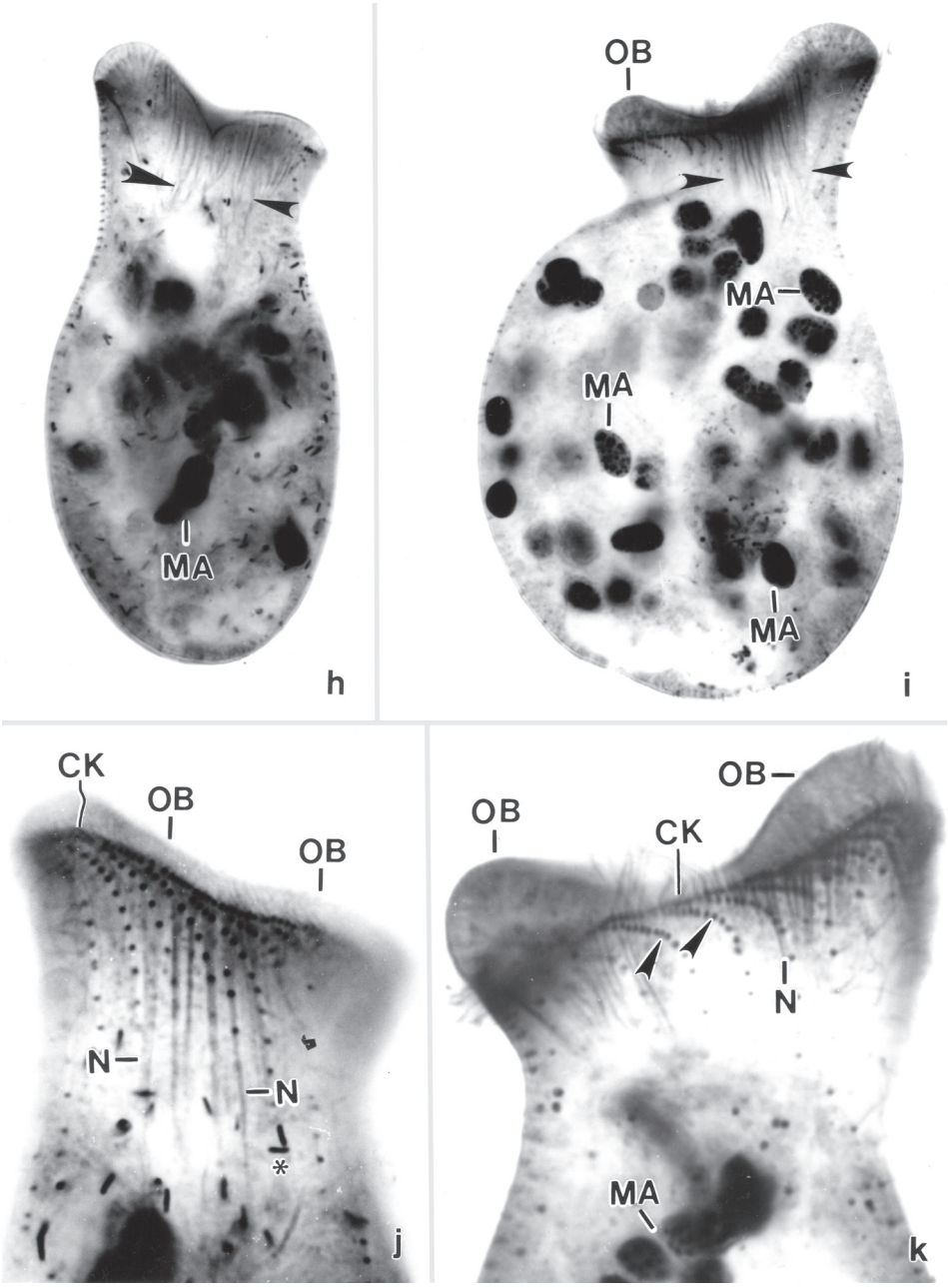



**Fig. 12.7h–k** *Pharyngospathidium pseudobavariense* nov. spec. (originals or type population. Protargol preparation). Ciliary and nuclear pattern. **h, i:** Overviews showing the mighty oral bulge and the fine fibres (arrowheads) lining the permanent cytostome. **j, k:** Right and left side view showing the *Epispathidium* ciliary pattern (arrowheads) and the nematodesmata originating from the circumoral kinety. Asterisk marks cytoplasmic extrusomes(?). CK – circumoral kinety, MA – macronucleus nodules, N – nematodesma bundles, OB – oral bulge.

Macronucleus composed of an average of 30 ellipsoidal, scattered nodules. Two types of extrusomes: type I acicular to fusiform, about 6.0 × 0.8 µm in size; type II rod-shaped and about 1.5 µm long. On average 30 ciliary rows, three anteriorly modified to strongly heterostichad dorsal brush occupying about 25% of body length.

**Type locality:** Soil from a beech forest in the surroundings of the castle of Neuhaus (about 47°48'31"N 13°04'23"E; sea level about 440 m), district Parsch, town of Salzburg, Austria.

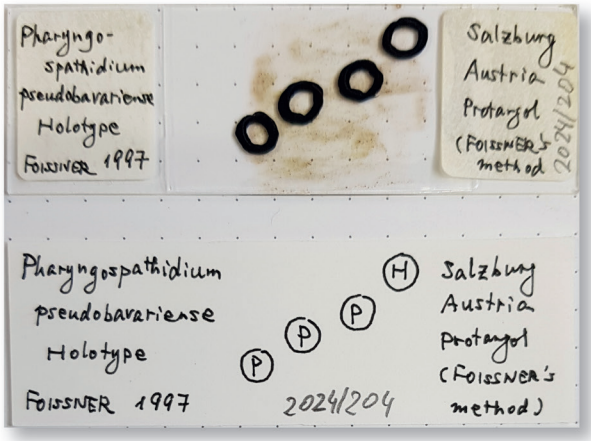
**Type material:** The slide (Fig. 12.7l, m; accession number 2024/204) containing the holotype (Fig. 12.6o–q) and two paratype slides (Fig. 12.7n–q; 2024/205, 206) have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI).

**ZooBank registration:** urn:lsid:zoobank.org:act:0F9FE721-B079-4CB1-A2E8-41F1 6E9F08E1

**Remarks:** The specimens described by Wenzel (1953) and Tirjaková & Matis (1987) have a similar size and shape as *Pharyngospathidium pseudobavariense*, and likely belong to this species because the authors do not mention the specific features of *Pharyngospathidium bavariense* (see below). Indeed, our population is highly similar to *Pharyngospathidium bavariense*, but lacks some of its main features, viz., the large size (≤150 µm vs. 160–200 µm), the asymmetric (vs. symmetric) somatic ciliary pattern, and the duplicated (vs. simple) left oral bulge half. Thus, we consider it as a new species.

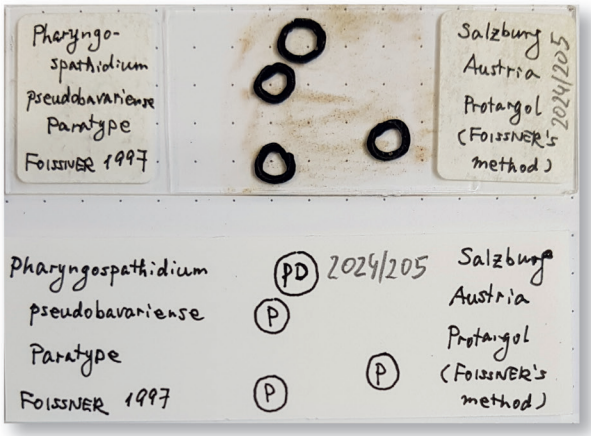
*Pharyngospathidium pseudobavariense* is also rather similar to *Neospathidium africanum* (p. 418) differing from that species by the *Epispathidium* (vs. *Spathidium*) ciliary pattern, the higher number of ciliary rows (30 vs. 20), the longer dorsal brush (on average 26 dikinetids in row 1 vs. 11), and the acicular (vs. rod-shaped) extrusomes. Other multinucleate species, for instance, *Spathidium seppelti* Petz & Foissner, 1997 (their p. 313) and *Epispathidium regium* (see Chapter 6, that is, Foissner et al. 2025b) have a different ciliary pattern and a temporary mouth (vs. permanent cytopharynx), and thus belong to the family Spathidiidae.

**Description of type population:** Body size moderately variable, viz., 90–140 × 35–60 µm in vivo, usually near 110 × 50 µm, as calculated from some in vivo measurements and the morphometric data (Table 12.2). Broadly spatulate to spatulate, rarely bursiform or indistinctly cup-shaped, length:width ratio 1.6–2.6:1 in protargol preparations, on average near 2.2:1 both in vivo and preserved cells, laterally flattened up to 2:1 on both sides. Neck usually more pronounced ventrally and in prepared cells than dorsally and in vivo, except when feeding, where the neck area rather distinctly contracts. Dorsal side slightly longer than ventral, concave anterior (oral) end thus slightly slanted; posterior end invariably broadly rounded (Fig. 12.6a, f, g, h, n, q, t, u, 12.7a–k). Macronucleus pattern rather variable because culture was fixed during exponential, as evident from many (30%) dividers and post-dividers contained in the slides. An average of 30 perfectly scattered macronucleus nodules occurs in the posterior three quarters of 28 out of 35 specimens analyzed (including three very early dividers, which show the true pattern best), while a reticulum of partially fused nodules is found in an early divider and an Y-shaped mass in a mid-divider. Further, one specimen has a tortuous and partially nodulated strand and four cells have a mixture of nodules and short strands; likely, these five specimens are post-dividers, as evident from the studies on *Spathidium turgitorum* Foissner et al., 2002 (p. 244). Individual nodules globular to elongate ellipsoidal or dumbbell-shaped, on



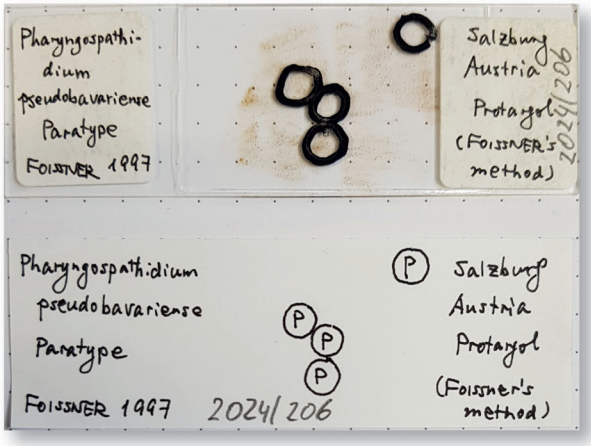

l

m




n

o




p

q

**Fig. 12.7l–q** *Pharyngospathidium pseudobavariense* nov. spec. (originals. Protargol slides). **l, m:** Slide (l) and protocol (m) containing holotype (H) and paratypes (P). Accession number (LI): 2024/204. **n–q:** Slides (n, p) and protocols (o, q) containing paratypes drawn (PD) and paratypes (P). Accession numbers (LI): 2024/205, 206.

average 10 × 5 µm in protargol preparations; each usually contains several nucleoli up to 2 µm across (Fig. 12.6a, q, u, 12.7d–i, k; Table 12.2). Micronuclei likely about 3 µm across, not unequivocally to identify due to many similarly sized and impregnated cytoplasmic inclusions. Contractile vacuole in rear body end, some excretory pores in pole area. Two types of extrusomes scattered in cytoplasm and studded in oral bulge, especially in inflated ends, except for a small, bare area left of pharyngeal opening, where extrusomes are lacking, a curious feature checked in three specimens. Type I extrusomes fusiform to acicular, about 6.0 × 0.8 µm in size; type II thin, about 1.5 µm long rods; oral bulge extrusomes never impregnate with the protargol method used, while cytoplasmic extrusomes impregnate more or less intensely (Fig. 12.6c, d). Cortex very flexible and about 1 µm thick, contains about 10 rows of colourless, approximately 1.0 × 0.2

µm-sized granules between each two ciliary rows; usually impregnates rather strongly, possibly due to the cortical granule layer, except along ciliary rows, which thus appear as white stripes; contains a conspicuous, likely postciliary fibre system. Cytoplasm colourless, usually studded with lipid droplets 2–10 µm across and 1.5–2.0 µm long rods (type II extrusomes? mucocysts?). When feeding on ciliates, the bulge centre opens wide (Fig. 12.6f). Movement without peculiarities, that is, glides and rotates slowly on microscope slide.

Somatic cilia about 10 µm long in vivo and rather narrowly spaced (~2 µm), especially in anterior portion of rows, where they form a conspicuous ciliary corona together with the cilia of the circumoral kinety; arranged in an average of 30 equidistant, bipolar rows anteriorly forming typical *Epispathidium* pattern (indistinct *Spathidium* pattern in one out of 35 specimen investigated) more pronounced on left side than right; rows frequently with small irregularities, such as minute breaks and/or supernumerary kinetids outside rows (Fig. 12.6a, n, o, p, u, v, 12.7j, k; Table 12.2). Dorsal brush dikinetidal and strongly heterostichad, of ordinary appearance, that is, occupies about 25% of body length and has fusiform bristles up to 4 µm long in vivo; all rows commence with some ordinary cilia anteriorly, rows 1 and 2 end at nearly same level and continue with ordinary, but more closely spaced cilia posteriorly; bristles of similar shape and size in all rows, viz., fusiform and 3–4 µm long. Brush row 1 composed of an average of 26 very narrowly spaced dikinetids, slightly shorter than row 2 composed of 27 dikinetids; row 3 only half as long as row 1 and 2, composed of an average of 12 dikinetids followed by a monokinetidal tail extending to posterior body end and composed of rather narrowly spaced, rod-shaped bristles about 2 µm long in vivo (Fig. 12.6a, n, p, r, u, 12.7f, g; Table 12.2).

Oral bulge slanted by 15–30°, occupies about 80% of maximum trunk width in protargol preparations; very conspicuous, especially in preparations because (i) distinctly set off from body proper and large, viz., in vivo about 7 µm high and up to 10 µm wide in frontal view; (ii) markedly concave with conspicuously inflated, bright ends containing many extrusomes, especially the dorsal hump; (iii) left half of humps almost twice as high at right, producing curious outlines in lateral view; (iv) ∞-shaped in lateral and dumbbell-shaped in frontal view, with dorsal portion slightly wider than ventral. Cytopharynx in vivo conspicuous only in frontal view, where it forms a bright, fusiform opening, in preparations distinct also in lateral view, where it appears as a short, broad funnel. Circumoral kinety dumbbell-shaped as the oral bulge, continuous and separate from ciliary rows, composed of narrowly spaced dikinetids each associated with a cilium, a long nematodesma, and a faintly impregnated fibre extending into cytopharyngeal wall to form a rather distinct (inner) basket composed of bundled fibres. (Outer) oral basket conspicuous in protargol preparations because composed of distinct, cuneate nematodesma bundles extending to mid-body (Fig. 12.6a, b, f, n, o–q, s–v; Table 12.2).

**Occurrence and ecology:** As the other members of the Pharyngospathidiidae, *Pharyngospathidium pseudobavariense* is infrequent and rarely becomes abundant in raw cultures. Disregarding the type locality (see above), it has been found with low abundance in mosses from Bavaria (Wenzel 1953) and Slovakia (Tirjaková & Matis 1987). We have a definite record from a floodplain soil from Rio Negro at Manaus (Brazil), where the specimens are only 70–90 µm long.

## *Pharyngospathidium bavariense* (Kahl, 1930) nov. comb.

(Fig. 12.6i–l)

1930 ***Spathidium bavariense* spec. n.**[3] – Kahl, Arch. Protistenk. 70: 384, Fig. 8a–c (Fig. 12.6i–k; original description; no type material available).
1930 ***Spathidium bavariense* Kahl, 1930** – Kahl, Tierwelt Dtl. 18: 165, Fig. 245 (Fig. 12.6l; revision of ciliates).
1943 ***Spathidium bavariense* Kahl** – Kahl, Infusorien, p. 26, Tafel VI, Fig. 4 (brief review of ciliates).

**Nomenclature:** Etymology not given in the original description or a later work. For derivation of species-group name, see *Pharyngospathidium pseudobavariense* (p. 389). The name obviously refers to Bavaria, a state in the south-east of Germany, where the species was discovered. Kahl (1930a, p. 386) established the variety *Spathidium bavariense simplinucleatum*. Thus, he automatically also activated the nominotypical variety *Spathidium bavariense bavariense* Kahl, 1930a, which is identical with the present species. *Spathidium bavariense simplinucleatum* is raised to species rank and transferred to *Pharyngospathidium* in the present work (see below).

**Improved diagnosis:** Body size about 160 × 50 µm in vivo. Body spatulate with slightly oblique, complicated oral bulge approximately as long as widest trunk region and with left bulge half twice as thick as right. Macronucleus in 15–20 ellipsoidal nodules. Extrusomes about 5 µm long and rather thick. Approximately 20 ciliary rows, about 8 on left side and 12 on right. Dorsal brush short, bristles up to 4 µm long, row 3 extends as a monokinetidal bristle tail to rear body end.

**Remarks:** We transfer *Spathidium bavariense* to *Pharyngospathidium* because Kahl (1930a) illustrates an *Epispathidium* ciliary pattern (Fig. 12.6i) and the massive, complicated oral bulge suggests that it belongs to the Pharyngospathidiidae. It is, however, curious that Kahl, although obviously studying the oral bulge very carefully, did not notice a pharyngeal cavity. Thus, we cannot exclude that this species belongs to another family (Spathidiidae) and represents a distinct genus. A detailed redescription is required.

*Pharyngospathidium bavariense* has three distinct features, definitely stated by Kahl (1930a, b) and not found in any other member of the family and, especially, in *Pharyngospathidium pseudobavariense*: large body size (160–200 µm vs. ≤150 µm); asymmetric (vs. symmetric) somatic ciliature, viz., 8 rows on the left side and 12 on right; left half of oral bulge twice as thick as right (vs. both halves of same thickness). As Kahl was a very experienced observer in 1930, we cannot assume that these peculiarities are misobservations. Thus, all populations which lack these features must be referred to other species. This concerns not only the populations of Wenzel (1953) and Tirjaková & Matis (1987), which belong to *Pharyngospathidium pseudobavariense*, but also the records mentioned in Foissner (1998, p. 209).

**Description** (from Kahl 1930a, b; for original German diagnosis, see footnote above): Body size fairly stable, viz., about 160 × 50 µm in Kahl (1930a), while 160–200 µm long in

[3] Kahl (1930a) provided the following diagnosis: "Größe wenig um 160 µ schwankend; Gestalt schlank oval (3–3½:1), hinten kurz bis breit gerundet, zum Wulst etwas halsförmig eingeengt; abgeflacht, rechts flach, links flach gewölbt. Streifung weit, links weiter als rechts (etwa 8 gegen 12 Reihen); Wimpern dicht, sehr zart, etwa 12 µ lang. Kern in zahlreiche längliche Brocken zerteilt (15–20), etwa 10 × 4 µ groß. Micronuclei in ähnlicher, meist etwas geringerer Zahl, ca. 3 µ groß, rund. Plasma farblos granuliert; kontraktile Vakuole terminal. Dorsalbürste vorn etwa 4 µ hoch und dicht; die rechte Reihe zieht sich gelockert und niedriger bis zum Hinterende." For description of oral bulge, see "Description".

Kahl (1930b). Body spatulate to slenderly spatulate, that is, length:width ratio 3.0–3.5:1, oral bulge about as long as widest trunk region, neck inconspicuous. Trunk ellipsoidal, right side flat, left slightly convex; dorsal side inconspicuously longer than ventral, concave anterior (oral) end thus slightly slanted; posterior end narrowly to broadly rounded. Macronucleus composed of about 15–20 scattered nodules, nodules approximately 10 × 4 µm in size; about 10–15 scattered micronuclei approximately 3 µm across. Contractile vacuole in rear body end. Oral bulge extrusomes 5 µm long and rather thick. Cytoplasm colourless and granulated. Glides on right side and rotates on microscope slides.

Cilia about 12 µm long in vivo and densely spaced within rows, arranged in approximately eight rows on left side and 12 on right. Dorsal brush short, bristles about 4 µm long anteriorly, row 3 with monokinetidal tail of minute bristles extending to rear body end.

Oral bulge slanted by about 30°, bright, left half of bulge twice as thick as right, that is, duplicated, as recognizable in rotating specimens showing bulge surface frontally (Fig. 12.6j); bulge ends wart-like projecting and thickened at left, contain many short (5 µm), rather thick trichocysts also laterally, especially the dorsal tubercle whose left side becomes lower along a special contour extending ventrally.

**Occurrence and ecology:** As yet *Pharyngospathidium bavariense* found only at the type locality, which is, however, not described in detail by Kahl (1930a). He found it in limerock moss in Upper Bavaria (= southeastern region of Bavaria); the abundance was high. All later records, including those of Foissner (1998, p. 209), are likely misidentifications (see remarks).

## *Pharyngospathidium simplinucleatum* (Kahl, 1930) nov. comb.

(Fig. 12.6m)

1930 ***Spathidium bavariense* var. *simplinucleatum*** – Kahl, Arch. Protistenk. 70: 386, Fig. 9m (Fig. 12.6m; original description; no type material available).

2025 ***Spathidium simplinucleatum* Kahl, 1930** – Original act (change from variety [= subspecies] to species rank; see nomenclature).

**Nomenclature:** No etymology has been given in the original description or a later work. The name *simplinucleatum* is a composite of the Latin adjective *simplex* (simple, single; Werner 1972, p. 376) and the Latin adjective *nucleat*·us, -a, -um ([m, f, n]; nut kernel-like; Hentschel & Wagner 1996, p. 429) and obviously refers to the single macronucleus.

Kahl (1930a) classified the present taxon as variety. The name has, according to ICZN (1999, Article 45.6.4), subspecific rank (*Spathidium bavariense simplinucleatum* Kahl, 1930a). We classify it as valid species (see list of synonyms) and thus the author name and year do not change (ICZN 1999, Article 50.3.1). The term "stat. nov." should not be used in that case (ICZN 1999, Recommendation 16A). In a further step, we transfer it to *Pharyngospathidium* (see heading).

**Diagnosis:** Not given in the original description. Should await redescription.

**Remarks:** Kahl (1930b, p. 165; 1943, p. 26) did not mention the scientific name of this variety. We consider the variety described and named by Kahl (1930a) as distinct species because (i) its macronucleus pattern is markedly different from that of *Pharyngospathidium bavariense* (p. 398) and from all other described species of the Pharyngospathidiidae; (ii) a

horseshoe-shaped macronucleus occurs in various spathidiids, suggesting that Kahl (1930a) did not investigate a malformed or reorganizing specimen; and (iii) very likely we know only a small portion of the actually existing *Pharyngospathidium* species.

The transfer to the genus *Pharyngospathidium* is based on Kahl's figure and remark that the oral bulge is "exactly as in *Spathidium bavariense*". Of course, *Pharyngospathidium simplinucleatum* needs a detailed redescription with modern methods.

**Description:** Kahl (1930a) provided only a brief description and a single illustration because he classified this species as variety of *Spathidium bavariense*; further, it was rare and thus Kahl could investigate in detail only a single specimen. Data from other sources are not available.

Body length 90–95 µm. Body bursiform with anterior end slightly obliquely truncated and posterior broadly rounded, length:width ratio about 2:1. Macronucleus in centre of cell, horseshoe shaped. Contractile vacuole in rear body end. Extrusomes in oral bulge 5 µm long. About 10 equidistantly spaced ciliary rows on left side. Dorsal brush bristles about 4 µm long anteriorly, brush row 3 has a monokinetidal bristle tail extending to rear body end. Oral bulge as in *Pharyngospathidium bavariense*.

**Occurrence and ecology:** As yet *Pharyngospathidium simplinucleatum* was found only at the type locality, namely, in lime-rock moss from the Zillertal (Ziller Valley; exact sample site not mentioned by Kahl 1930a; northern end of this valley at about 47°23'50"N 11°49'37"E), Tyrol, Austria.

## *Neospathidium* nov. gen.

**Nomenclature:** Composite of the Greek adjective *neos* (new, young, fresh; Hentschel & Wagner 1996, p. 420) and the genus-group name *Spathidium* Dujardin, 1841 (see Chapter 2, that is, Berger et al. 2025b) referring to the conspicuous cytopharynx and the similarity with the genus *Spathidium*. Like *Spathidium* of neuter gender (Aescht 2001, p. 300).

**Diagnosis:** Pharyngospathidiidae with ciliature in *Spathidium* pattern, that is, ciliary rows attached to continuous circumoral kinety and anteriorly curved ventrally on left side and dorsally on right side.

**Type species:** *Neospathidium longinucleatum* nov. spec.

**Species assigned:** *Neospathidium longinucleatum* nov. spec (type species); *Neospathidium africanum* nov. spec.; *Neospathidium brachystichos* nov. spec.

**ZooBank registration:** urn:lsid:zoobank.org:act:2A62DA54-5D50-4CA8-A8B7-7972A6C65C51

**Remarks:** See same chapter at type species.

### Key to species

**1** Macronucleus a tortuous strand ..... **2**
– Macronucleus in about 18 scattered nodules. About 20 ciliary rows ..... ..... *Neospathidium africanum* nov. spec. (p. 418)
**2** On average 31 ciliary rows. Extrusomes rod-shaped, about 10 µm long ..... ..... *Neospathidium longinucleatum* nov. spec. (p. 401)

– On average 12 ciliary rows. Extrusomes rod-shaped, about 4 µm long ..... ..... *Neospathidium brachystichos* nov. spec. (p. 424)

## *Neospathidium longinucleatum* nov. spec.

(Fig. 12.8a–v, 12.9a–w, 12.10a–l, Table 12.3)

**Nomenclature:** The species-group name *longinucleat*·us, -a, -um is a composite of the Latin adjective *longus* (long; Hentschel & Wagner 1996, p. 370), the thematic vowel ·i-, and the Latin adjective *nucleat*·us, -a, -um ([m, f, n]; nut kernel-like; Hentschel & Wagner 1996, p. 429) and refers to the long macronucleus. This is the type species of *Neospathidium*.

**Diagnosis:** Body size about 100 × 50 µm in vivo. Body spatulate with slightly oblique, dumbbell-shaped oral bulge about 60% as long as widest trunk region. Macronucleus long and tortuous. Two types of extrusomes: type I rod-shaped and slightly curved, 10–11 × 0.5 µm in size; type II rod-shaped and about 2 *µm long.* On average 31 ciliary rows, three anteriorly modified to inconspicuous dorsal brush occupying about 21% of body length.

**Type locality:** Bark from *Lonchocarpus capassa* trees at the bank of a river near the village of Tshokwane (about 24.7828°S 31.8596°E) in the Krueger National Park, South Africa.

**Type material:** The slide (Fig. 12.10g, h; accession number 2024/207) containing the holotype specimen (Fig. 12.8m, n) and two paratype slides (Fig. 12.10i–l; 2024/208, 209) have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI). A voucher specimen (Fig. 12.8s–v) is on a paratype slide of *Centrospathidium verrucosum* (see Fig. 5.2m, n in Chapter 5, that is, Foissner et al. 2025d; accession number 2025/236).

**ZooBank registration:** urn:lsid:zoobank.org:act:CC1BCE54-A6D7-4A86-AB15-CA9ED4D499C3

**Remarks:** *Neospathidium longinucleatum* is rather similar to *Neospathidium africanum* nov. spec., especially in size and shape of body, oral bulge, and extrusomes. However, the macronucleus pattern (tortuous strand vs. scattered nodules) and the number of ciliary rows (31 vs. 20) are very different. *Neospathidium brachystichos* nov. spec. has, inter alia, a much lower number of ciliary rows (12 vs. 31). *Neospathidium longinucleatum* nov. spec. differs also distinctly from *Pharyngospathidium longichilum longichilum* nov. subspec. (p. 378) and *Pharyngospathidium longichilum amphoriforme* nov. subspec. (p. 380), though having the same macronucleus type, by the *Spathidium* ciliary pattern (vs. *Epispathidium*) and the markedly lower number of ciliary rows (31 vs. 45). Further, both *Pharyngospathidium* subspecies are distinctly larger and easily recognized by the *Epispathidium*-like overall appearance.

There is some possibility that *Neospathidium longinucleatum* nov.spec. is identical with *Pharyngospathidium simplinucleatum* (Fig. 12.6m) because the preparations from the declining culture contain rather many malformed specimens (see introduction to description!), some of which have a short macronucleus similar to that of Kahl's (1930a) species, while all well-looking individuals have a long, tortuous nucleus (Table 12.3) distinctly different from the horseshoe-shaped macronucleus of *Pharyngospathidium simplinucleatum*. Furthermore, Kahl (1930a) definitely states that the extrusomes are 5 µm long, while they have double length in *Neospathidium longinucleatum*, although both taxa have a very similar body size (about 100 µm). Thus, synonymy of *Neospathidium longinucleatum* nov. spec. and *Pharyngospathidium simplinucleatum* is unlikely, which is sustained by the fact that the

continued on p. 403

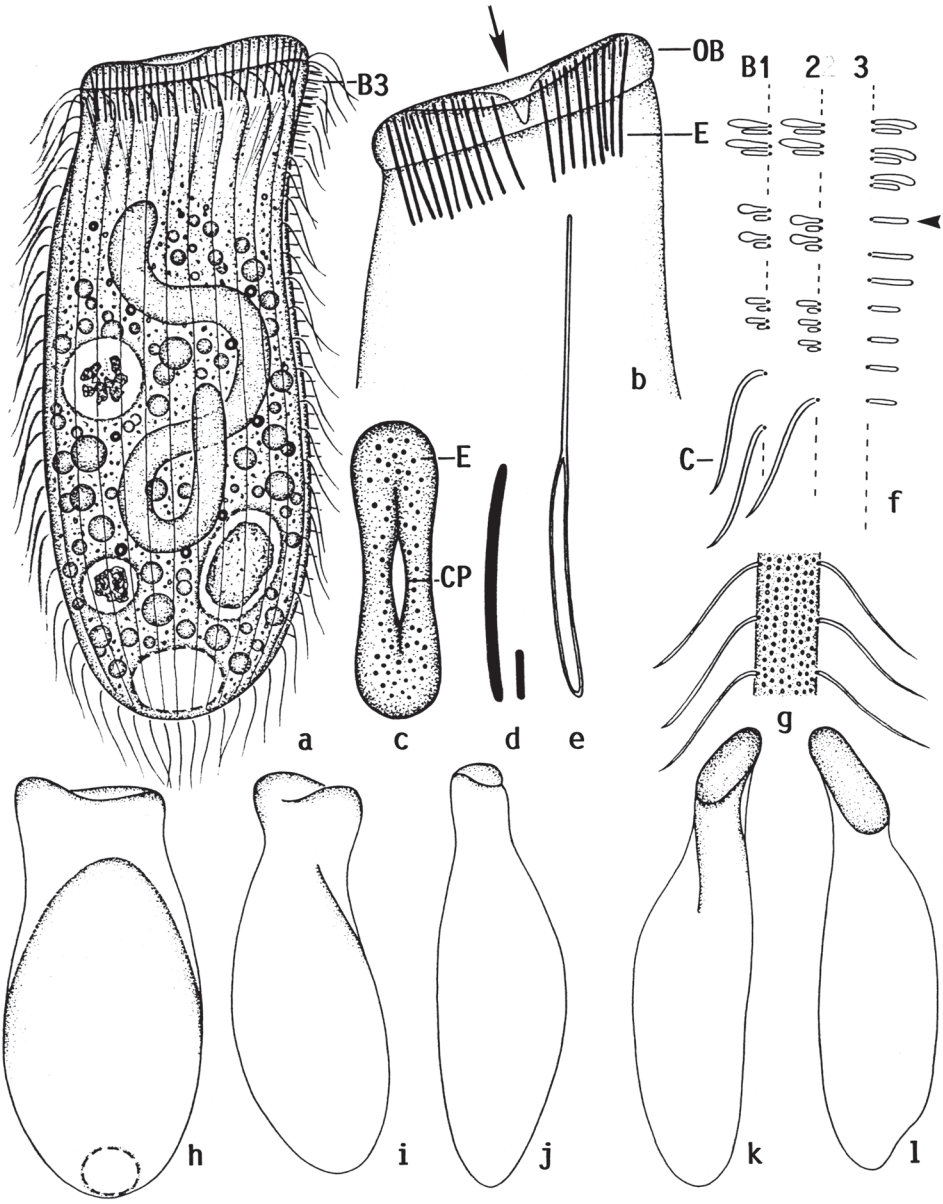



**Fig. 12.8a–l** *Neospathidium longinucleatum* nov. spec. (originals of South African type specimens. From life). **a:** Left side view of a representative specimen, shape redrawn from video records, 100 μm. Note monokinetidal bristle tail of dorsal brush row 3 extending to posterior body end. **b:** Anterior body portion showing extrusomes and cytopharyngeal entrance (arrow). **c:** Frontal view of oral bulge studded with extrusomes. **d:** Oral bulge extrusomes, type I 10–11 μm long, type II about 2 μm. **e:** Exploded type I extrusome. **f:** Dorsal brush with highly differentiated bristles up to 3 μm long (see text). **g:** Surface view showing cortical granulation. **h–j:** Lateral, ventrolateral, and dorsal view of same specimen (redrawn from video records). **k, l:** Ventrolateral views of same specimen (redrawn from video records). B1–3 – dorsal brush rows, C – ordinary somatic cilium, CP – cytopharyngeal entrance, E – extrusomes, OB – oral bulge.

horseshoe-shaped macronucleus pattern of *Pharyngospathidium simplinucleatum* is a distinct nucleus type of *Spathidium* s.l. in general.

*Neospathidium longinucleatum* nov. spec. has a *Spathidium*-like overall appearance and ciliary pattern, and thus shows a close resemblance to several *Spathidium* species, viz., *Spathidium*

continued on p. 414

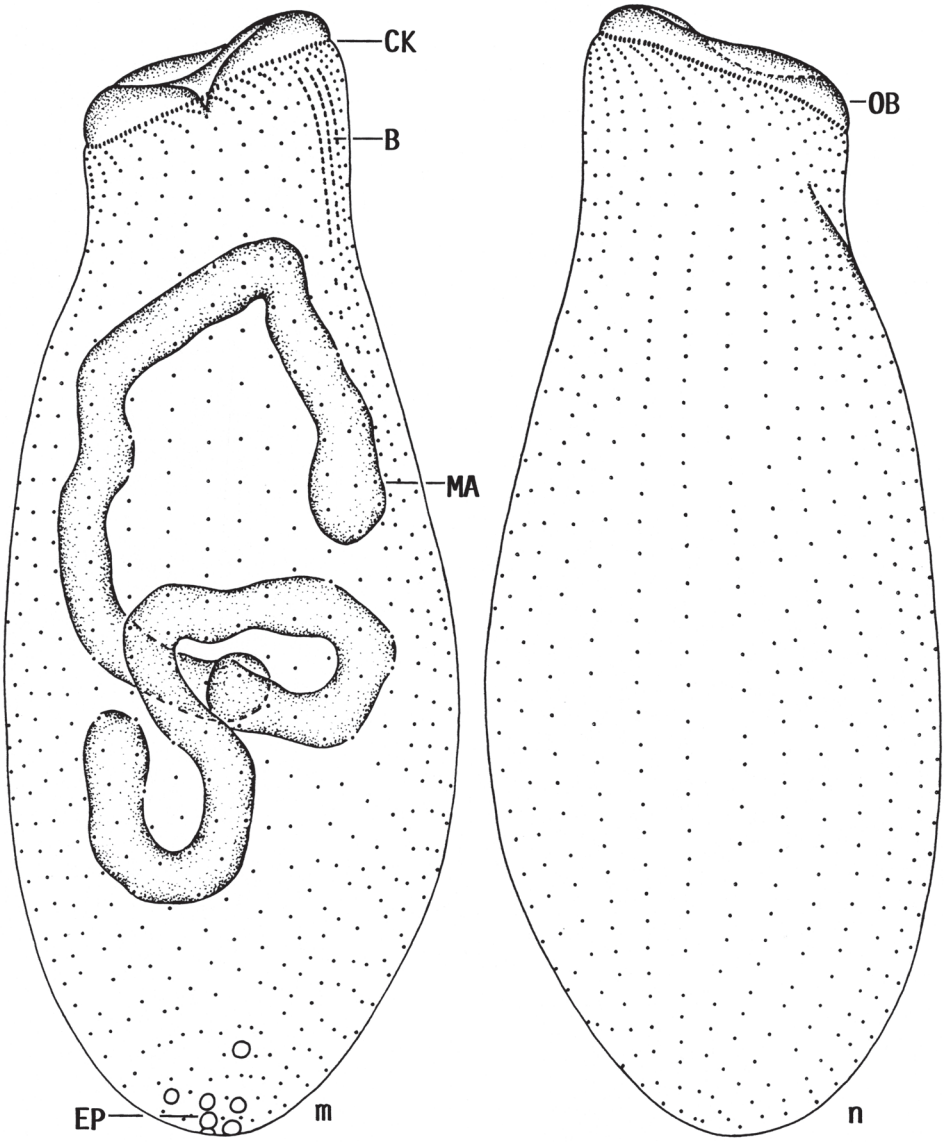



**Fig. 12.8m, n** *Neospathidium longinucleatum* nov. spec. (originals of type population. Protargol preparation). Ciliary pattern of left and right side and nuclear apparatus of holotype specimen (see also Fig. 12.8o), 100 µm. Note the short, inconspicuous dorsal brush (B) which, however, has highly differentiated bristles (Fig. 12.8f). B – dorsal brush, CK – circumoral kinety, EP – excretory pores of contractile vacuole, MA – macronucleus, OB – oral bulge.

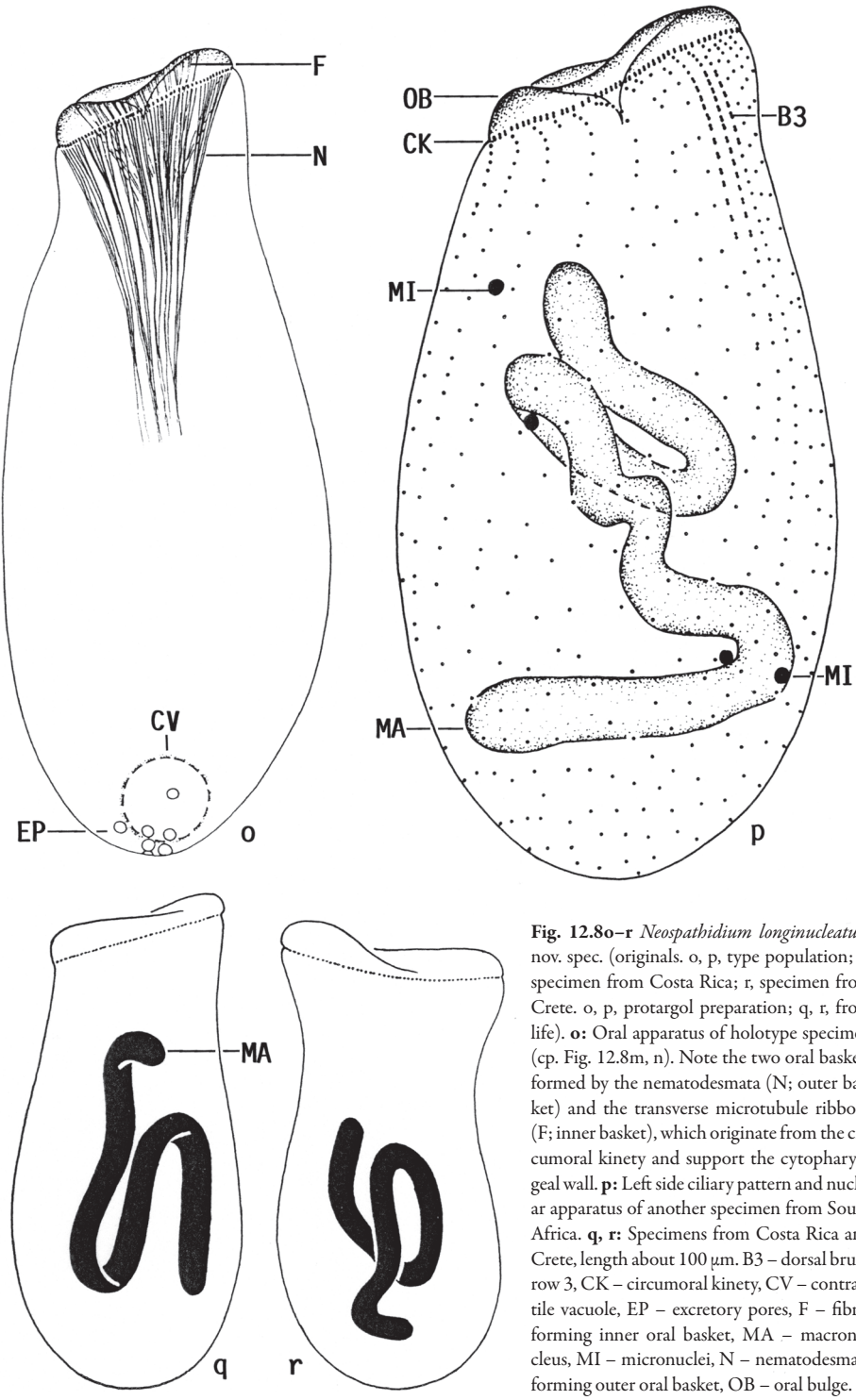



**Fig. 12.8o–r** *Neospathidium longinucleatum* nov. spec. (originals. o, p, type population; q, specimen from Costa Rica; r, specimen from Crete. o, p, protargol preparation; q, r, from life). **o:** Oral apparatus of holotype specimen (cp. Fig. 12.8m, n). Note the two oral baskets formed by the nematodesmata (N; outer basket) and the transverse microtubule ribbons (F; inner basket), which originate from the circumoral kinety and support the cytopharyngeal wall. **p:** Left side ciliary pattern and nuclear apparatus of another specimen from South Africa. **q, r:** Specimens from Costa Rica and Crete, length about 100 µm. B3 – dorsal brush row 3, CK – circumoral kinety, CV – contractile vacuole, EP – excretory pores, F – fibres forming inner oral basket, MA – macronucleus, MI – micronuclei, N – nematodesmata forming outer oral basket, OB – oral bulge.

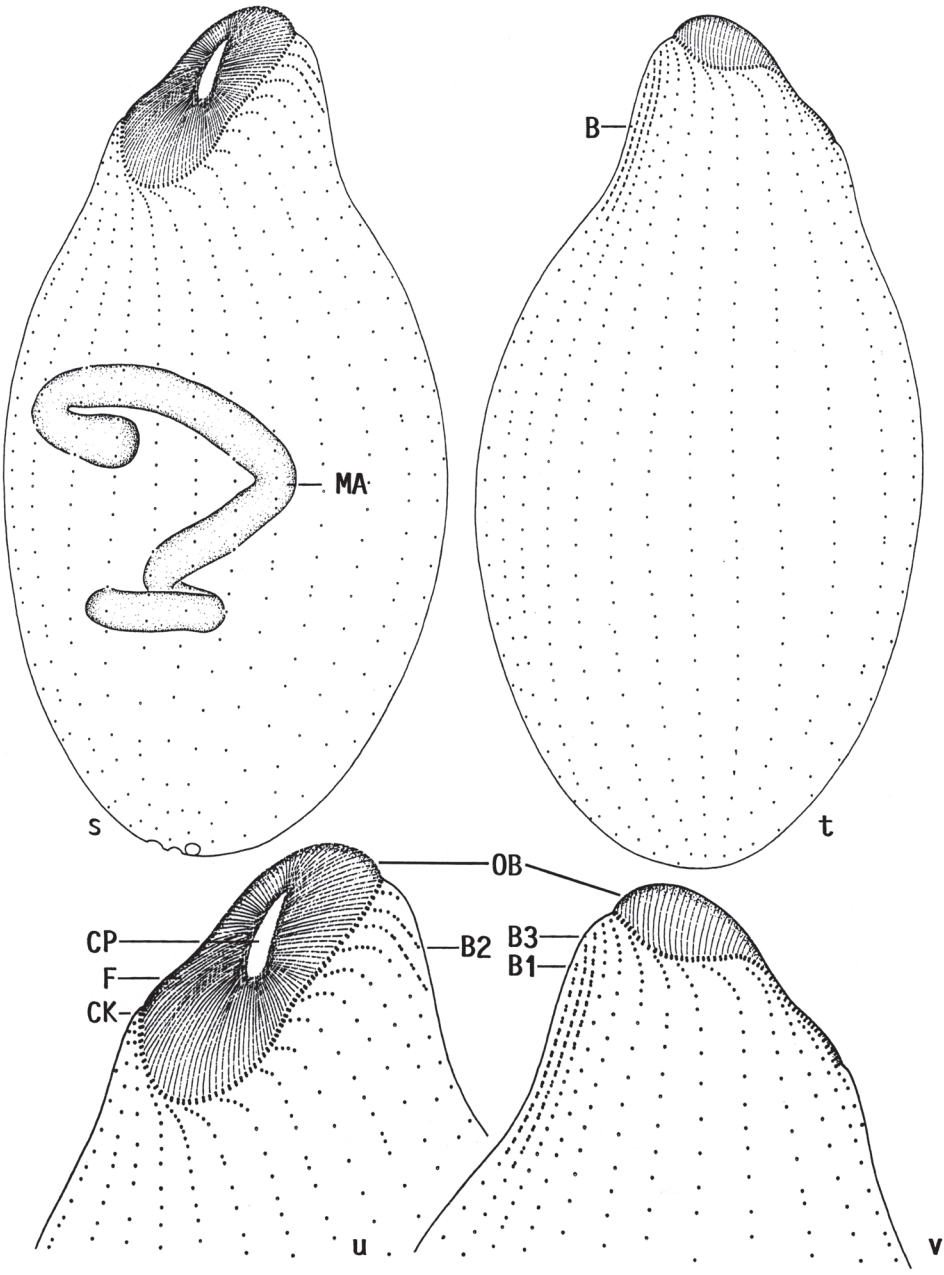



**Fig. 12.8s–v** *Neospathidium longinucleatum* nov. spec. (originals of Australian specimen. Protargol preparation). Ventrolateral (s, u) and dorsolateral (t, v) view showing the somatic and oral ciliature, the oral bulge, and the macronucleus. Note the conspicuous transverse microtubule bundles (F) originating from the circumoral dikinetids and supporting the cytopharyngeal wall. B – dorsal brush, B1–3 – dorsal brush rows, CK – circumoral kinety, CP – cytopharyngeal opening, F – fibres, MA – macronucleus, OB – oral bulge.

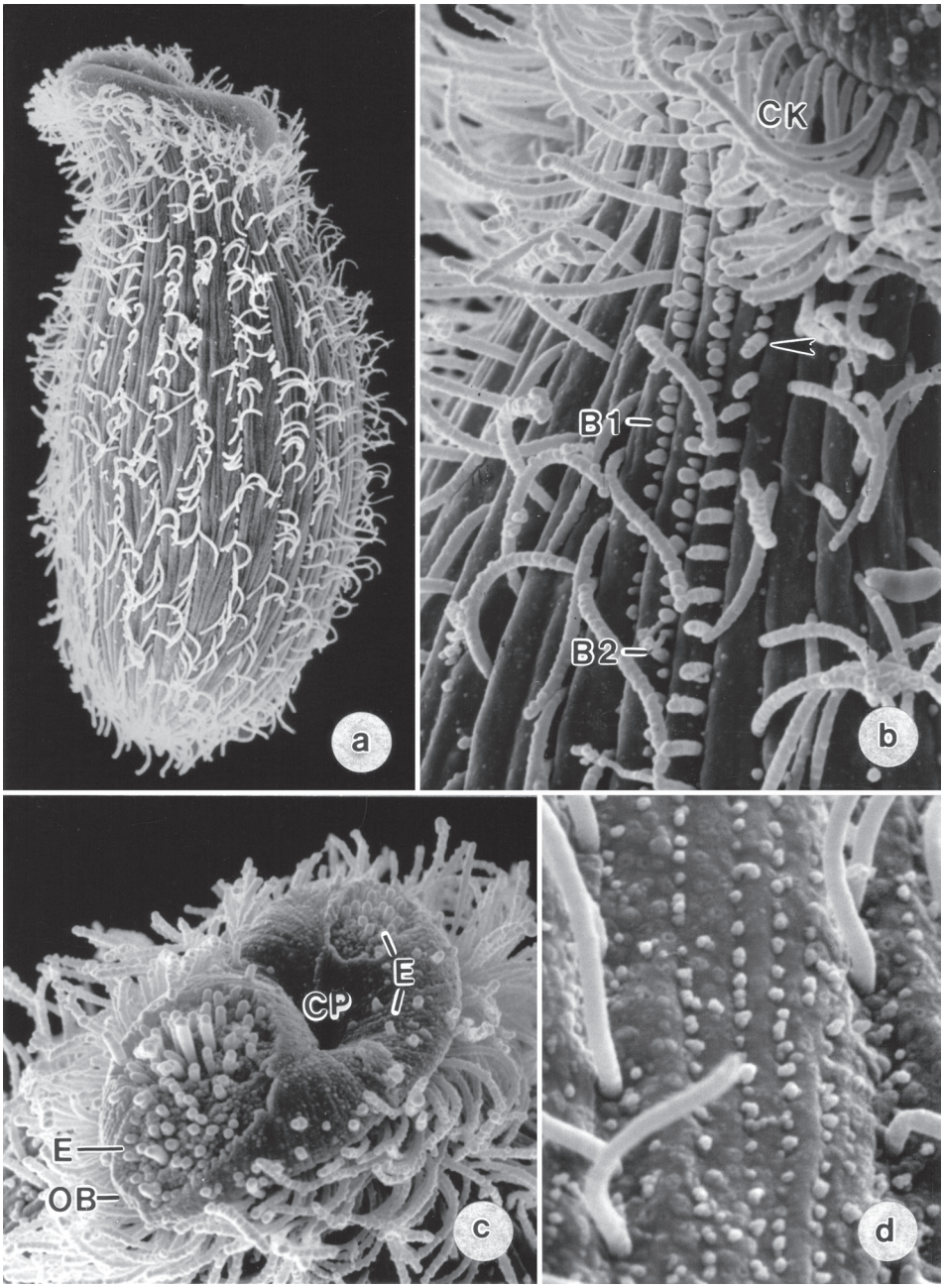



**Fig. 12.9a–d** *Neospathidium longinucleatum* nov. spec. (originals of South African type specimens. SEM). **a:** Right side overview showing the typical, ∞-shaped oral bulge. **b:** The dorsal brush bristles are short (up to 3 μm), but of very different shape and size. Arrowhead marks begin of monokinetidal bristle tail of brush row 3. **c:** A specimen with short, ellipsoidal oral bulge partially demembranated to show the exploding type I extrusomes. **d:** Surface view showing partially extruded cortical granules. B1, 2, – dorsal brush rows, E – exploding type I extrusomes, CK – cilia of circumoral kinety, CP – cytopharyngeal entrance, OB – oral bulge.

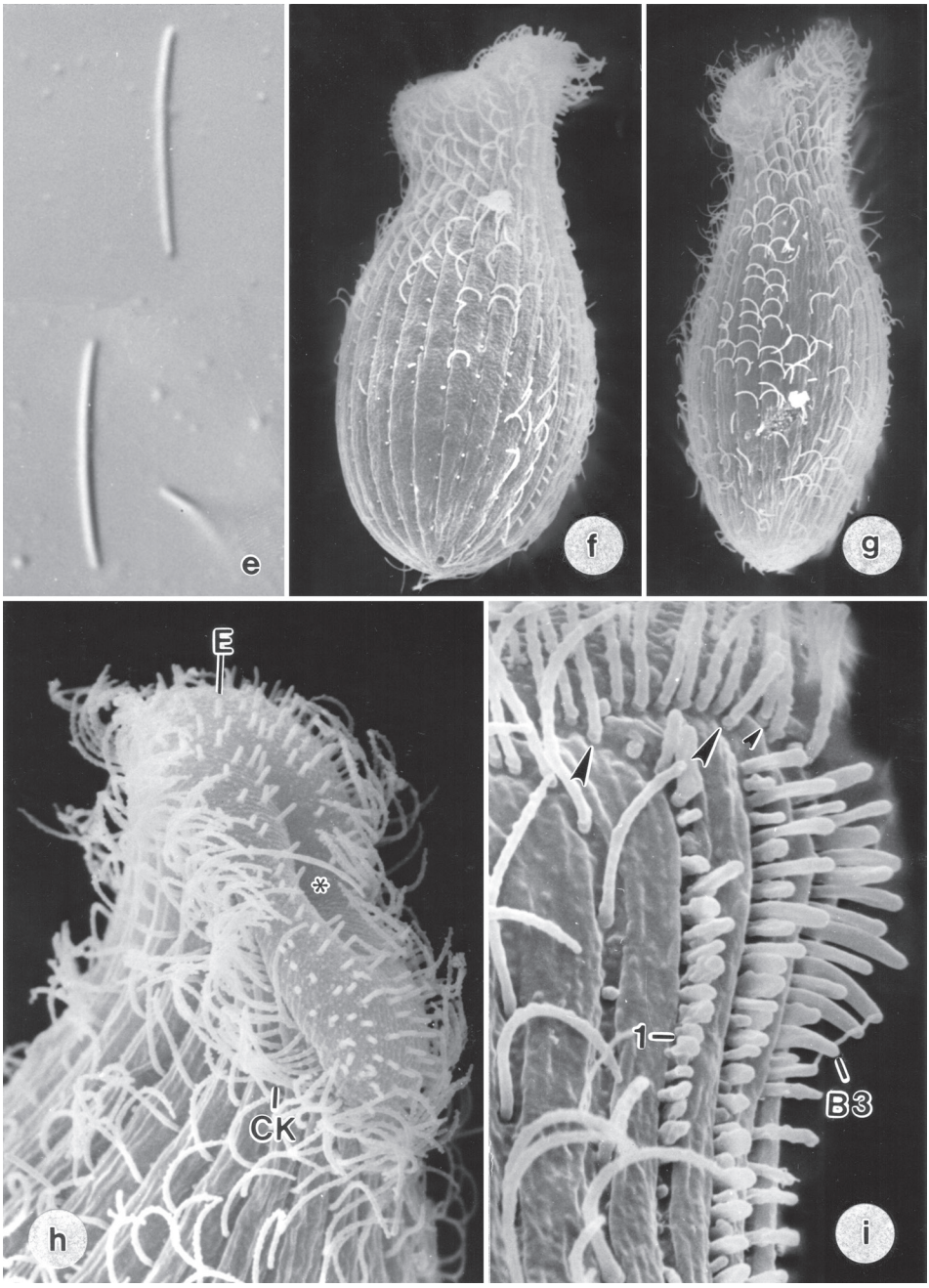



**Fig. 12.9e–i** *Neospathidium longinucleatum* nov. spec. (originals. e, South African type specimen; f–i, specimens from Australia. e, from life; f–i, SEM). **e:** Type 1 extrusomes. **f, g:** Left lateral and ventral overview, showing the central oral bulge concavity and the lateral flattening of the cell. **h:** Ventrolateral view showing the oral bulge with exploding extrusomes and the conspicuous pharyngeal opening (asterisk). **i:** Dorsal brush with ordinary cilia anteriorly (arrowheads). B1, 3 – dorsal brush rows, CK – cilia of circumoral kinety, E – extrusomes.

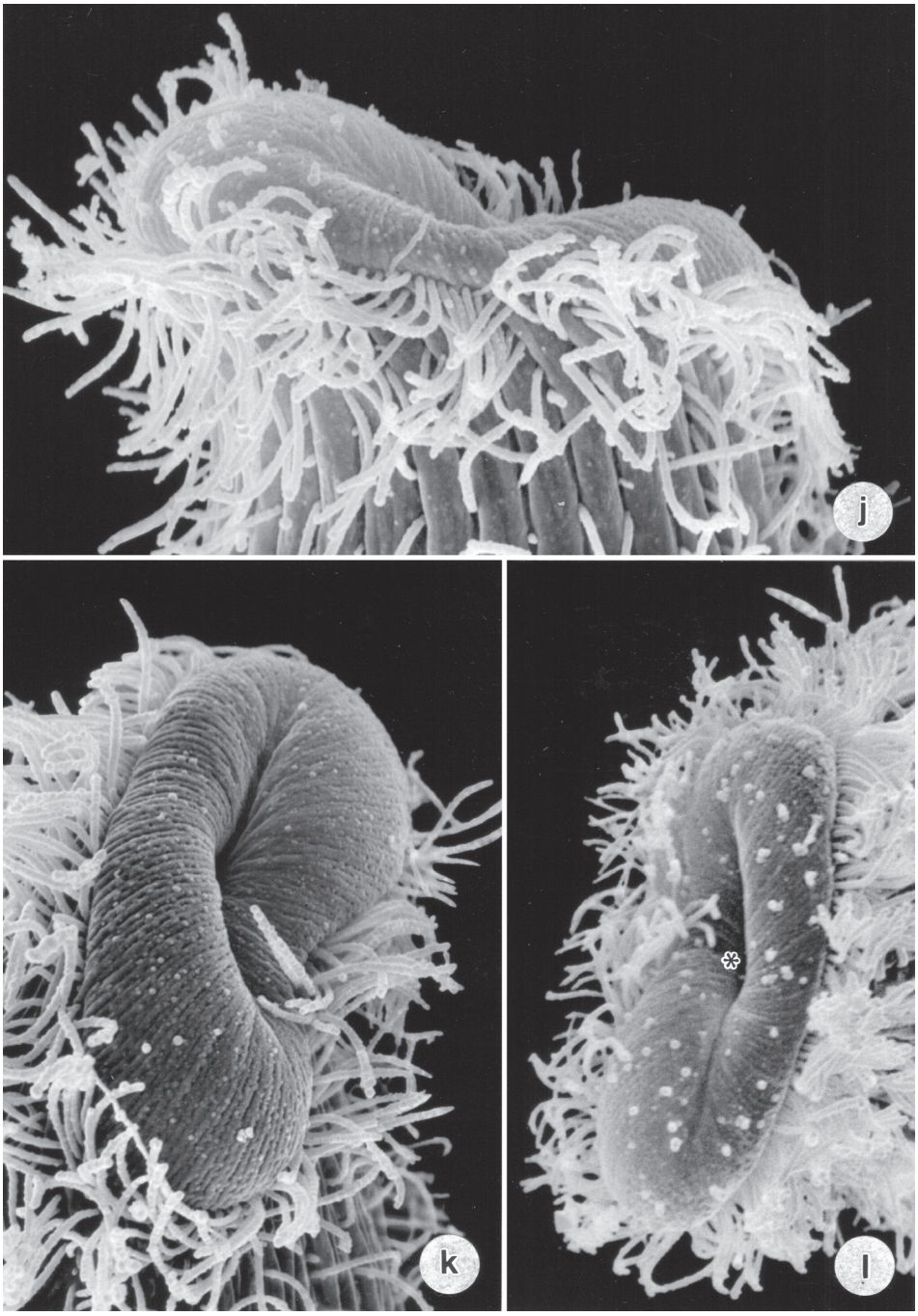



**Fig. 12.9j–l** *Neospathidium longinucleatum* nov. spec. (originals. Australian specimens. SEM). **j:** Lateral view showing the ∞-shaped oral bulge. **k, l:** Frontal views of the conspicuous oral bulge, showing the permanent pharyngeal opening (asterisk in l) and the propeller-like twist of the oral bulge.

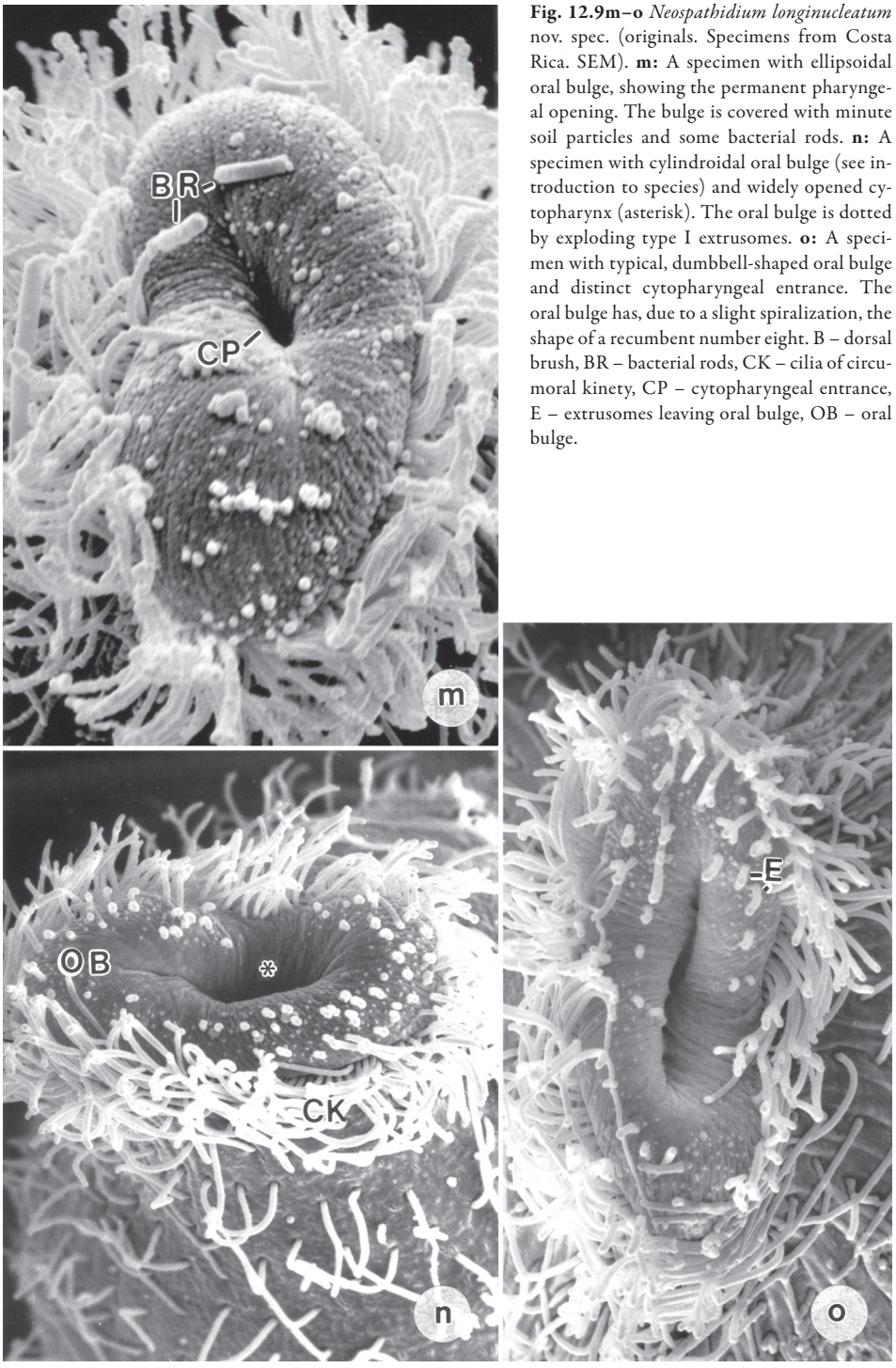



**Fig. 12.9m–o** *Neospathidium longinucleatum* nov. spec. (originals. Specimens from Costa Rica. SEM). **m:** A specimen with ellipsoidal oral bulge, showing the permanent pharyngeal opening. The bulge is covered with minute soil particles and some bacterial rods. **n:** A specimen with cylindroidal oral bulge (see introduction to species) and widely opened cytopharynx (asterisk). The oral bulge is dotted by exploding type I extrusomes. **o:** A specimen with typical, dumbbell-shaped oral bulge and distinct cytopharyngeal entrance. The oral bulge has, due to a slight spiralization, the shape of a recumbent number eight. B – dorsal brush, BR – bacterial rods, CK – cilia of circumoral kinety, CP – cytopharyngeal entrance, E – extrusomes leaving oral bulge, OB – oral bulge.

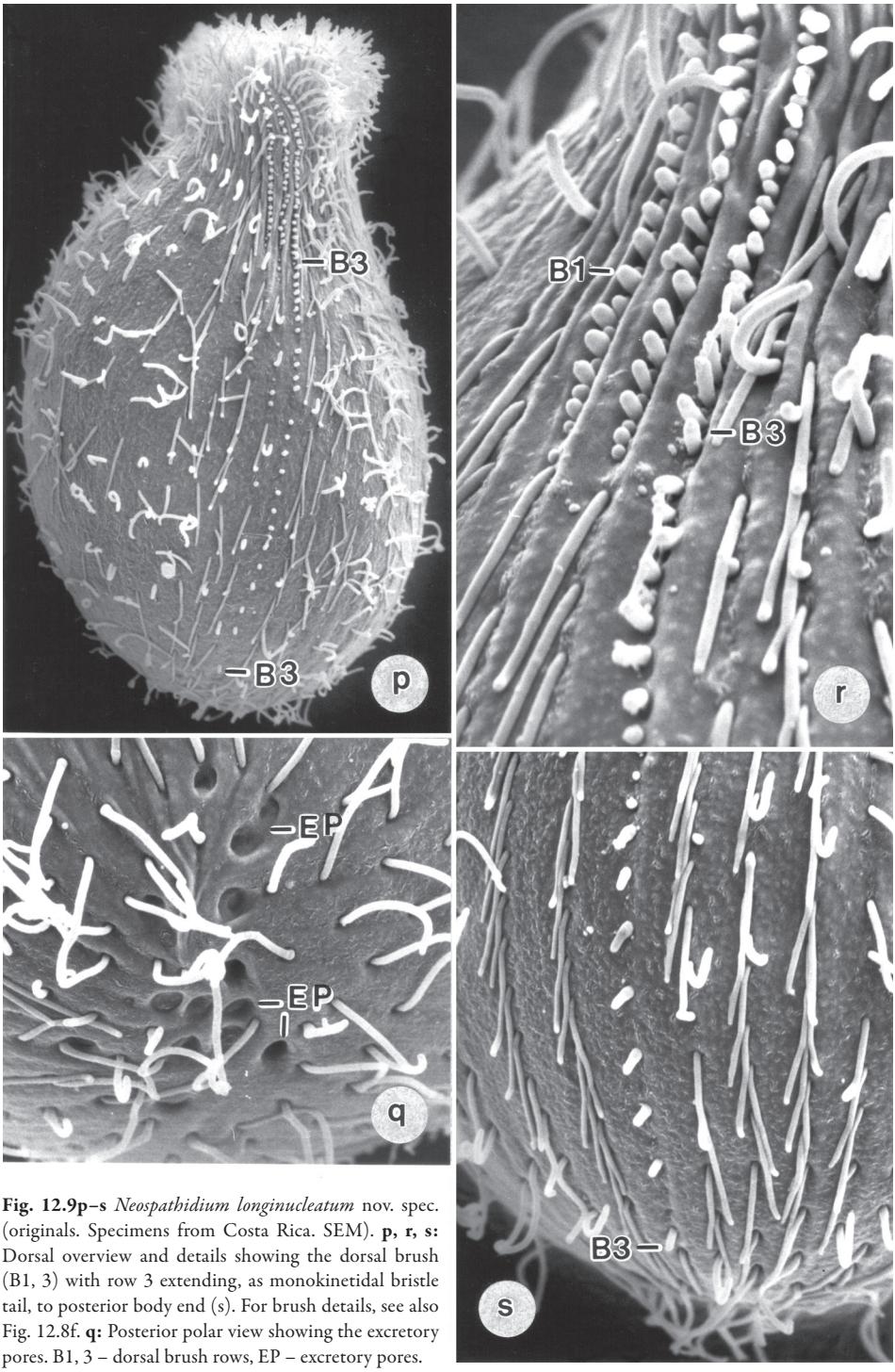



**Fig. 12.9p–s** *Neospathidium longinucleatum* nov. spec. (originals. Specimens from Costa Rica. SEM). **p, r, s:** Dorsal overview and details showing the dorsal brush (B1, 3) with row 3 extending, as monokinetidal bristle tail, to posterior body end (s). For brush details, see also Fig. 12.8f. **q:** Posterior polar view showing the excretory pores. B1, 3 – dorsal brush rows, EP – excretory pores.

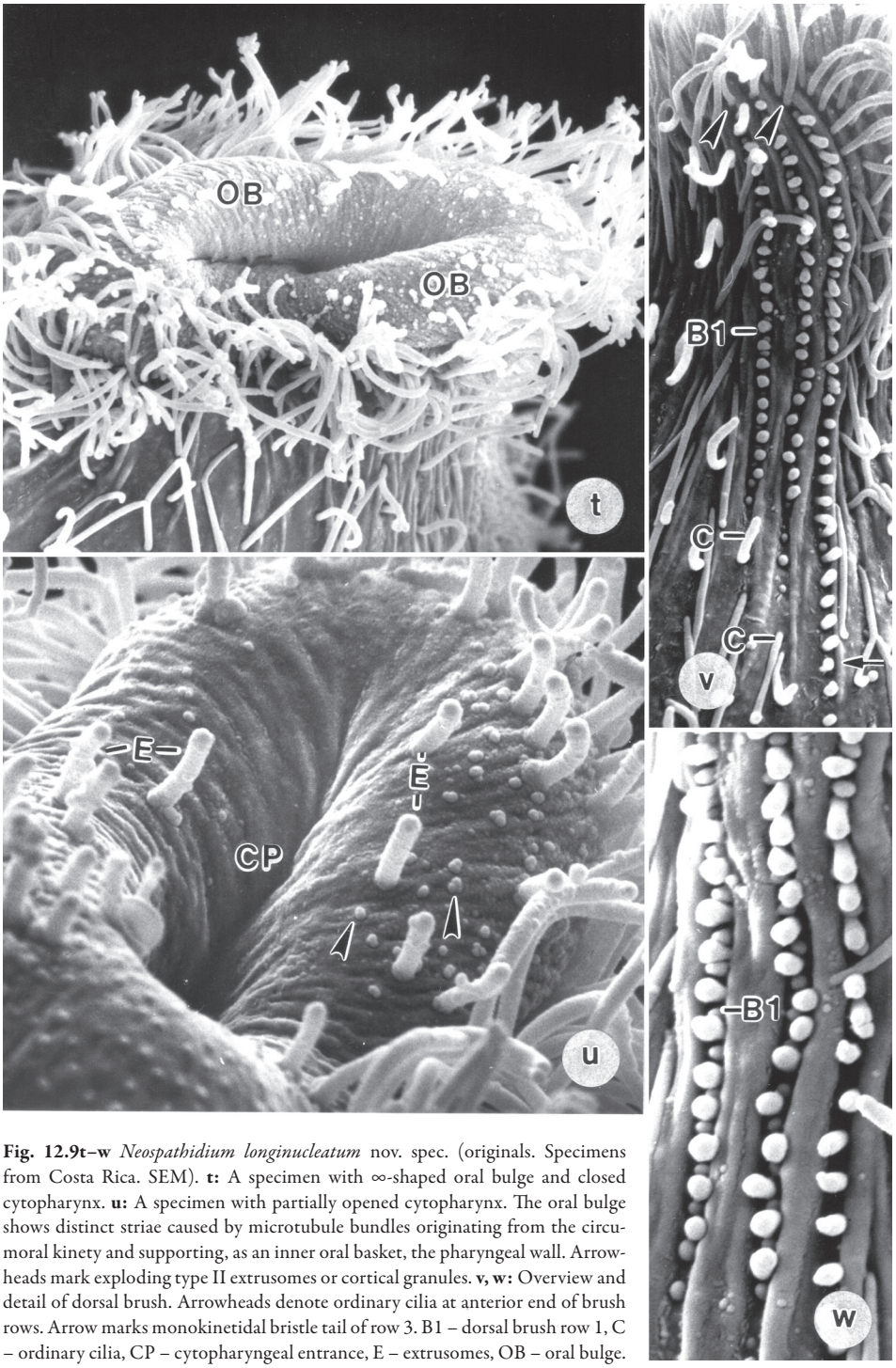



**Fig. 12.9t–w** *Neospathidium longinucleatum* nov. spec. (originals. Specimens from Costa Rica. SEM). **t:** A specimen with ∞-shaped oral bulge and closed cytopharynx. **u:** A specimen with partially opened cytopharynx. The oral bulge shows distinct striae caused by microtubule bundles originating from the circumoral kinety and supporting, as an inner oral basket, the pharyngeal wall. Arrowheads mark exploding type II extrusomes or cortical granules. **v, w:** Overview and detail of dorsal brush. Arrowheads denote ordinary cilia at anterior end of brush rows. Arrow marks monokinetidal bristle tail of row 3. B1 – dorsal brush row 1, C – ordinary cilia, CP – cytopharyngeal entrance, E – extrusomes, OB – oral bulge.

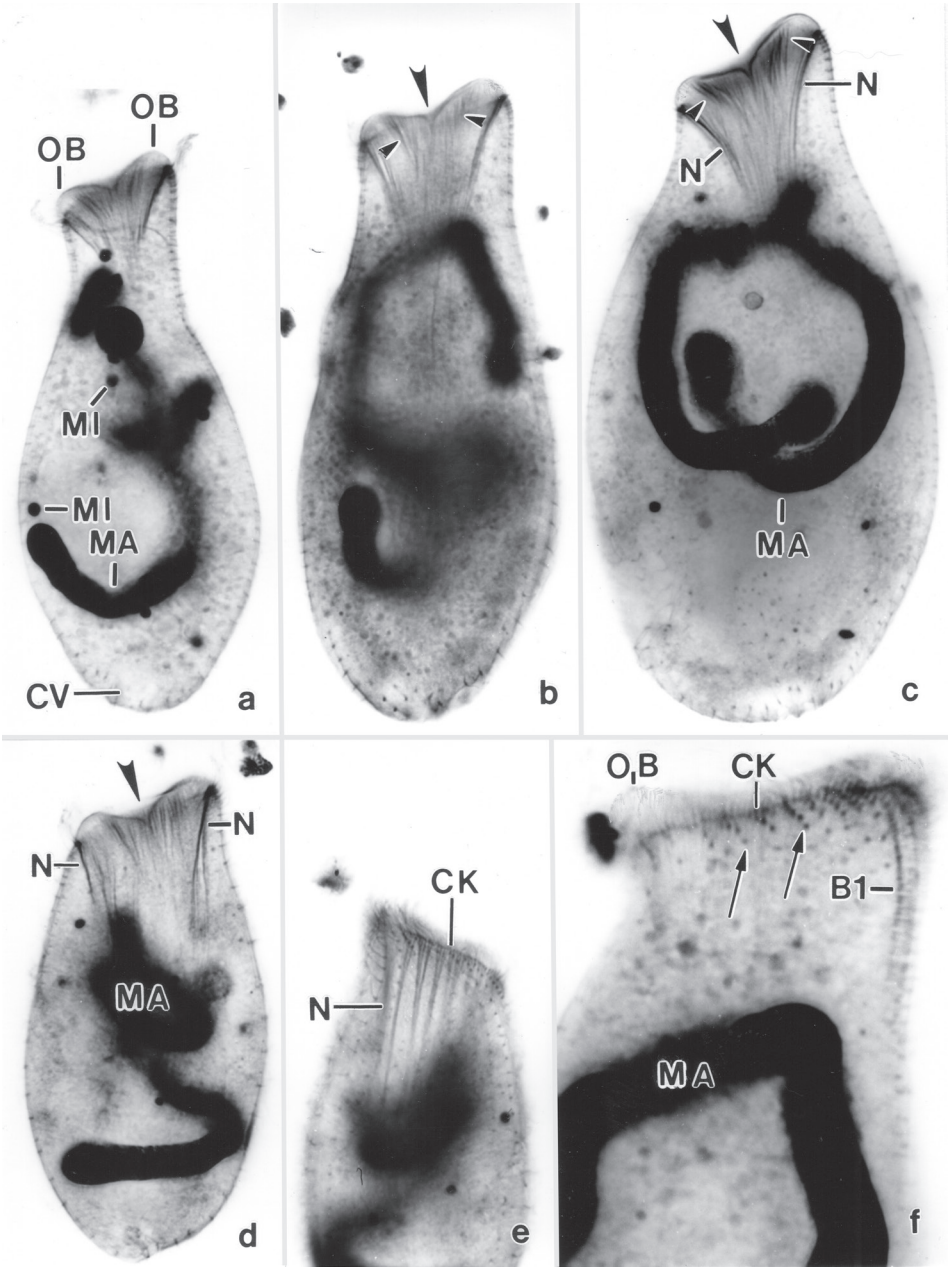



**Fig. 12.10a–f** *Neospathidium longinucleatum* nov. spec. (originals. Australian population. Protargol preparation). **a–d:** Left side overviews showing the long macronucleus and the massive oral bulge with the opening of the permanent cytostome (large arrowheads). Small arrowheads mark fibres supporting the wall of the permanent cytostome. **e:** Right side view showing nematodesma bundles originating from circumoral kinety. **f:** Left side view showing ciliary rows arranged in *Spathidium* pattern (arrows). B1 – dorsal brush row 1, CK – circumoral kinety, CV – contractile vacuole, MA – macronucleus, MI – micronucleus, N – nematodesmata, OB – oral bulge.

**Table 12.3** Morphometric data on *Neospathidium longinucleatum* nov. spec. populations from South Africa (SA1, randomly selected specimens; SA2, selected, typical, *Spathidium*-shaped specimens with flattened oral area and long oral bulge; original data), Australia (AUS; original data), and Costa Rica (CR; original data)[a]

| Characteristic | Pop | Mean | M | SD | SE | CV | Min | Max | n |
|---|---|---|---|---|---|---|---|---|---|
| Body, length | SA1 | 77.5 | 74.0 | 11.7 | 2.5 | 15.1 | 63.0 | 108.0 | 21 |
| | SA2 | 83.4 | 83.0 | 13.4 | 3.2 | 16.1 | 65.0 | 108.0 | 17 |
| | AUS | 101.7 | 106.0 | - | - | - | 86.0 | 113.0 | 3 |
| | CR[b] | 65.0 | 65.5 | 3.2 | 1.0 | 5.0 | 60.0 | 70.0 | 10 |
| Body, width | SA1 | 36.0 | 35.0 | 6.4 | 1.4 | 17.9 | 28.0 | 55.0 | 21 |
| | SA2 | 39.8 | 39.0 | 7.4 | 1.8 | 18.6 | 30.0 | 55.0 | 17 |
| | AUS | 50.7 | 55.0 | - | - | - | 40.0 | 57.0 | 3 |
| | CR[b] | 45.8 | 45.0 | 3.0 | 1.0 | 6.7 | 41.0 | 51.0 | 10 |
| Body length:width, ratio | SA1 | 2.2 | 2.1 | 0.2 | 0.1 | 10.6 | 1.7 | 2.6 | 21 |
| | SA2 | 2.1 | 2.1 | 0.3 | 0.1 | 13.3 | 1.6 | 2.5 | 17 |
| | AUS | 2.0 | 2.0 | - | - | - | 1.9 | 2.2 | 3 |
| | CR[b] | 1.4 | 1.4 | 0.1 | - | 7.1 | 1.3 | 1.7 | 10 |
| Oral bulge, length | SA1 | 15.8 | 15.0 | 4.5 | 1.0 | 28.3 | 10.0 | 26.0 | 21 |
| | SA2 | 22.1 | 21.0 | 2.0 | 0.5 | 9.3 | 20.0 | 26.0 | 17 |
| | AUS | 29.0 | - | - | - | - | 28.0 | 30.0 | 2 |
| | CR[b] | 22.8 | 23.0 | 1.3 | 0.5 | 5.8 | 21.0 | 25.0 | 6 |
| Oral bulge length:body width, ratio | SA1 | 0.4 | 0.4 | 0.1 | - | 21.8 | 0.3 | 0.6 | 21 |
| | SA2 | 0.6 | 0.6 | 0.1 | - | 16.5 | 0.4 | 0.7 | 17 |
| | AUS | 0.6 | 0.6 | - | - | - | 0.5 | 0.8 | 2 |
| | CR[b] | 0.5 | 0.5 | 0.1 | - | 11.8 | 0.4 | 0.6 | 6 |
| Oral bulge, height | SA1 | 2.8 | 2.5 | 0.6 | 0.1 | 21.7 | 2.0 | 4.0 | 21 |
| | SA2 | 3.1 | 3.0 | 0.5 | 0.1 | 16.2 | 2.5 | 4.0 | 17 |
| | AUS | 4.2 | 4.5 | - | - | - | 3.0 | 5.0 | 3 |
| Circumoral kinety to last dikinetid of brush row 1, distance | SA1 | 13.9 | 13.0 | 2.8 | 0.6 | 19.9 | 11.0 | 23.0 | 21 |
| | SA2 | 16.2 | 15.0 | 2.4 | 0.6 | 15.0 | 14.0 | 23.0 | 17 |
| | AUS | 23.0 | 21.0 | - | - | - | 18.0 | 30.0 | 3 |
| Circumoral kinety to last dikinetid of brush row 2, distance | SA1 | 15.0 | 14.0 | 2.9 | 0.6 | 19.6 | 12.0 | 25.0 | 21 |
| | SA2 | 17.9 | 17.0 | 2.4 | 0.6 | 13.6 | 15.0 | 25.0 | 17 |
| | AUS | 23.0 | 22.0 | - | - | - | 18.0 | 29.0 | 3 |
| Circumoral kinety to last dikinetid of brush row 3, distance | SA1 | 8.0 | 8.0 | 1.4 | 0.3 | 18.0 | 6.0 | 11.0 | 21 |
| | SA2 | 9.3 | 10.0 | 1.0 | 0.3 | 11.3 | 7.0 | 11.0 | 17 |
| | AUS | 11.7 | 12.0 | - | - | - | 11.0 | 12.0 | 3 |
| Anterior body end to macronucleus, distance | SA1 | 23.5 | 23.0 | 7.4 | 1.6 | 31.5 | 10.0 | 42.0 | 21 |
| | SA2 | 25.8 | 27.0 | 6.5 | 1.6 | 25.2 | 13.0 | 34.0 | 17 |
| | AUS | 33.0 | 33.0 | - | - | - | 21.0 | 45.0 | 3 |
| Macronucleus figure, length | SA1 | 35.8 | 34.0 | 9.1 | 2.0 | 25.5 | 22.0 | 54.0 | 21 |
| | SA2 | 38.3 | 35.0 | 9.8 | 2.4 | 25.6 | 24.0 | 59.0 | 17 |
| | AUS | 43.3 | 35.0 | - | - | - | 27.0 | 68.0 | 3 |
| Macronucleus, length (spread, thus approximate) | SA1 | 123.3 | 120.0 | - | - | - | 80.0 | 210.0 | 21 |
| | SA2 | 133.8 | 130.0 | - | - | - | 100.0 | 210.0 | 17 |
| | AUS | 93.3 | 90.0 | - | - | - | 80.0 | 110.0 | 3 |
| Macronucleus, width in central third | SA1 | 4.4 | 4.0 | 0.7 | 0.2 | 16.5 | 3.5 | 6.0 | 21 |
| | SA2 | 5.1 | 5.0 | 0.7 | 0.2 | 13.0 | 4.0 | 6.0 | 17 |
| | AUS | 6.3 | 6.0 | - | - | - | 5.0 | 8.0 | 3 |

**Table 12.3** Continued

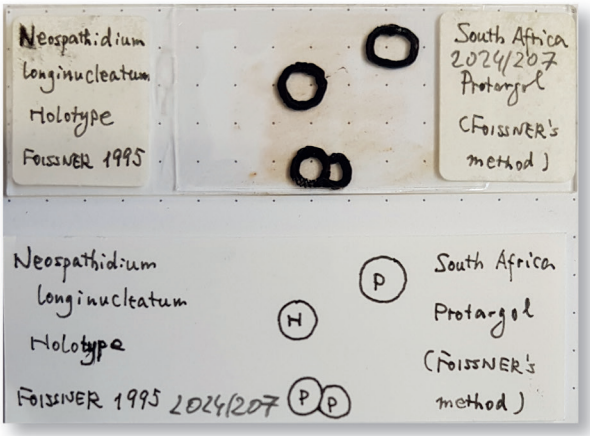
| Characteristic | Pop | Mean | M | SD | SE | CV | Min | Max | n |
|---|---|---|---|---|---|---|---|---|---|
| Macronucleus, number | SA1 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 | 1.0 | 1.0 | 21 |
| | SA2 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 | 1.0 | 1.0 | 17 |
| | AUS | 1.0 | 1.0 | - | - | - | 1.0 | 1.0 | 3 |
| Micronuclei, across | SA1 | 1.7 | 2.0 | 0.3 | 0.1 | 17.3 | 1.0 | 2.0 | 21 |
| | SA2 | 1.9 | 2.0 | 0.4 | 0.1 | 19.0 | 1.0 | 2.5 | 17 |
| Micronuclei, number | SA1 | 16.1 | 15.0 | 4.6 | 1.0 | 28.2 | 9.0 | 23.0 | 21 |
| | SA2 | 15.9 | 15.0 | 4.7 | 1.2 | 29.8 | 6.0 | 24.0 | 17 |
| Somatic kineties, number | SA1 | 29.8 | 30.0 | 2.9 | 0.6 | 9.8 | 24.0 | 38.0 | 21 |
| | SA2 | 31.3 | 31.0 | 2.4 | 0.6 | 7.7 | 28.0 | 38.0 | 17 |
| | AUS | 27.0 | 27.0 | - | - | - | 25.0 | 29.0 | 3 |
| Basal bodies in a right-side kinety, number | SA1 | 28.9 | 29.0 | 5.2 | 1.1 | 18.1 | 20.0 | 43.0 | 21 |
| | SA2 | 33.8 | 32.0 | 5.2 | 1.3 | 15.4 | 27.0 | 43.0 | 17 |
| | AUS | 39.3 | 41.0 | - | - | - | 25.0 | 52.0 | 3 |
| Dorsal brush rows, number | SA1 | 3.0 | 3.0 | 0.0 | 0.0 | 0.0 | 3.0 | 3.0 | 21 |
| | SA2 | 3.0 | 3.0 | 0.0 | 0.0 | 0.0 | 3.0 | 3.0 | 17 |
| | AUS | 3.0 | 3.0 | - | - | - | 3.0 | 3.0 | 3 |
| Dikinetids in brush row 1, number | SA1 | 12.7 | 12.0 | 2.3 | 0.5 | 18.0 | 10.0 | 20.0 | 21 |
| | SA2 | 15.7 | 15.0 | 1.9 | 0.5 | 12.3 | 13.0 | 20.0 | 17 |
| | AUS | 20.7 | 21.0 | - | - | - | 13.0 | 28.0 | 3 |
| Dikinetids in brush row 2, number | SA1 | 14.0 | 13.0 | 2.4 | 0.5 | 17.3 | 10.0 | 20.0 | 21 |
| | SA2 | 17.2 | 17.0 | 1.6 | 0.4 | 9.3 | 15.0 | 21.0 | 17 |
| | AUS | 21.7 | 22.0 | - | - | - | 14.0 | 29.0 | 3 |
| Dikinetids in brush row 3, number | SA1 | 6.3 | 6.0 | 1.2 | 0.3 | 18.2 | 5.0 | 8.0 | 21 |
| | SA2 | 8.4 | 8.0 | 1.1 | 0.3 | 12.7 | 7.0 | 11.0 | 17 |
| | AUS | 9.7 | 9.0 | - | - | - | 9.0 | 11.0 | 3 |

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

[b] Data from SEM micrographs of specimens from a non-flooded Petri dish culture.

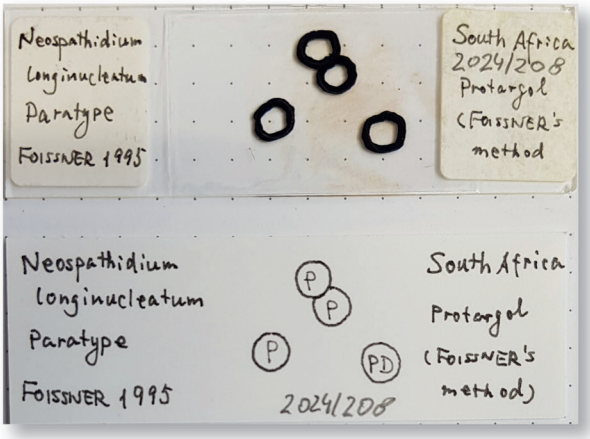
*spathula* (Müller, 1773) Bütschli, 1889, *Spathidium holsatiae* Kahl, 1930a, and *Spathidium lucidum* Kahl, 1930b. Certain populations of *Spathidium spathula*, especially those described by Moody (1912), Foissner (1981, 1984) and Lokot (1987), highly resemble *Neospathidium longinucleatum*, differing mainly by the family-specific oral apparatus (temporary cytostome vs. permanent cytopharynx) and the long (vs. short) macronucleus. *Spathidium holsatiae* has an ellipsoidal macronucleus with an adjacent micronucleus, fewer ciliary rows (15 vs. 31), and a wart-like dorsal oral bulge end studded with extrusomes. *Spathidium lucidum*, which Kahl (1930b) discovered in a pond, has a moniliform macronucleus with 10–12 nodules, fewer ciliary rows (about 7 on one side according to the illustration), and a reddish cytoplasm.

Within the genus *Enchelydium* Kahl, 1930a only *Enchelydium thecatum* (Kahl, 1926) Kahl, 1930a and *Enchelydium blattereri* Foissner et al., 2002 have a similar size and macronucleus



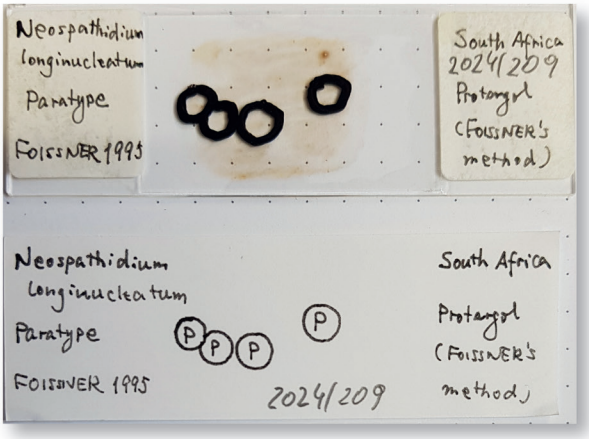

g

h




i

j




k

l

**Fig. 12.10g–l** *Neospathidium longinucleatum* nov. spec. (originals. Protargol slides). **g, h:** Slide (g) and protocol (h) containing holotype (H) and paratypes (P). Accession number (LI): 2024/207. **i–l:** Slides (i, k) and protocols (j, l) containing paratype drawn (PD) and paratypes (P). Accession numbers (LI): 2024/208, 209.

(Foissner et al. 2002; Kahl 1926, 1930a, b). However, both differ from *Neospathidium longinucleatum* nov. spec. by the smaller, roundish oral bulge (vs. *Spathidium*-like and dumbbell-shaped) and the very long extrusomes (>30 µm vs. 5–11 µm). Further, *Enchelydium thecatum* has a mucilaginous body envelope, and *Enchelydium blattereri* possesses 110 (vs. 31) ciliary rows.

**Description:** We studied this species in populations from the Republic of South Africa (type population), Australia, and Costa Rica. The Costa Rican specimens were studied in vivo and in the scanning electron microscope, while the Australian population was investigated mainly in the SEM. Complete data are available only from the South African specimens, viz., from a pure culture, which, however, already declined when fixed for preparations. In protargol and SEM preparations, this species shows two forms in each population,

viz., typical, *Spathidium*-shaped specimens with flattened oral area and long oral bulge (Fig. 12.8m–p, 12.9a, f), and *Enchelydium*-shaped cells with narrow, more or less cylindrical oral region/bulge. The morphometric analysis shows that the two forms differ in size and size-related features, suggesting that the smaller cells with roundish oral area are declining specimens (Table 12.3); however, some increased shrinkage of the oral area relative to the body is likely involved. Thus, the following description is based, if not stated otherwise, on typical, *Spathidium*-shaped specimens and excludes not only the cylindrical variant, but also rather many minute cells with malformed macronucleus and/or dorsal brush contained in the slides from the declining culture.

The three populations match in most important features, for instance, body and oral bulge size and shape, the macronucleus pattern, and the funnel-shaped cytopharynx. Although conspecificity is beyond reasonable doubt, the observations are largely kept separate, and the formal diagnosis and description contain only data from the South African population.

South African type population (Fig. 12.8a–p, 12.9a–e; Table 12.3):[4] Body size highly variable, usually 80–140 × 40–60 μm in vivo, on average near 100 × 50 μm, as calculated from some in vivo measurements and the morphometric data, assuming about 10% preparation shrinkage (Table 12.3); occasionally occur large specimens up to 220 μm long in vivo. Body broadly spatulate to spatulate with a length:width ratio of 1.6–2.5:1 in prepared specimens, on average near 2:1 both in vivo and in protargol preparations; oral bulge about 60% as wide as widest trunk region. Neck inconspicuous to conspicuous, depending on specimen and population (Fig. 12.8o–r), usually more pronounced in vivo than in protargol preparations, where the oral bulge likely shrinks rather strongly (see above). Trunk ellipsoidal with left side almost flat, while right more or less strongly vaulted, laterally thus flattened up to 2:1, in hyaline neck and oral area up to 3:1; dorsal side slightly longer than ventral, anterior (oral) end thus slightly slanted and rather distinctly concave, especially in SEM preparations; posterior end broadly rounded, occasionally wrinkled due to the contractile vacuole contained (Fig. 12.8a, b, h–p, 12.9a, b). Macronucleus in middle body portion, long and tortuous, contains many nucleoli up to 2 μm across. On average 15 micronuclei about 2 μm across near or attached to macronucleus (Fig. 12.8a, m, p). Contractile vacuole in rear body end, many excretory pores in pole area (Fig. 12.8m, o). Two types of extrusomes scattered in cytoplasm and studded around cytopharynx and, especially, in the inflated oral bulge ends (Fig. 12.8a–e, 12.9c–e, h): type I extrusomes rod-shaped with rounded ends and slightly curved, about 10–11 × 0.5 μm in size; type II rod-shaped and about 2.0 × 0.2 μm; both do not impregnate with the protargol method used. Exploded extrusomes of ordinary appearance, about 20 μm long. Cortex very flexible, contains about six rows of colourless granules up to 0.2 μm across between each two ciliary rows. Cytoplasm colourless, contains – depending on nutrition – few to many lipid droplets up to 10 μm across and food vacuoles with ciliate prey (Fig. 12.8a, g); in culture, it feeds on specimens of the *Tetrahymena pyriformis*-complex and the *Sterkiella histriomuscorum*-complex. Movement without peculiarities.

Somatic cilia about 12 μm long in vivo, arranged in an average of 31 equidistant, mostly bipolar, rather loosely ciliated rows abutting on circumoral kinety in typical *Spathidium* pattern; frequently with small irregularities, such as minute breaks and/or supernumerary

[4] Few illustrations mentioned in the following text refer to other populations (see legends for details).

kinetids outside rows; some kineties occasionally slightly spiral in posterior body portion, likely a preparation artifact (Fig. 12.8a, m, n, p, 12.9a; Table 12.3). Dorsal brush dikinetidal and three-rowed, inconspicuous because occupying only about 21% of body length and bristles merely up to 3 µm long; all rows commence with one to several ordinary cilia (Fig. 12.8a, m, p, 12.9c, i, s). Brush rows 1 and 2 end at nearly same level and are composed of a similar number (15, respectively, 17) of dikinetids (occasionally some monokinetids interspersed), both continue with ordinary cilia to posterior body end. Brush row 3 distinctly shorter than rows 1 and 2 comprising an average of only eight dikinetids, but with a monokinetidal bristle tail extending to body end. Brush bristles highly differentiated in vivo (Fig. 12.8f; differentiation only partially preserved in SEM preparations and possibly slightly different in the various populations, Fig. 12.9b, i, o, p, r, s, v, w): dikinetids of anterior quarter of rows 1 and 2 associated with about 3 µm long, tongue-shaped anterior bristles and about 2 µm long, rod-shaped posterior bristles; dikinetids of middle quarters associated with approximately 2 µm long, drumstick-shaped anterior bristles and approximately 1 µm long, rod-shaped posterior bristles; dikinetids of posterior quarter are associated with about 1.5 µm long, rod-shaped anterior bristles, and about 0.7 µm long, rod-shaped posterior bristles. Dikinetids of row 3 associated with about 3 µm long, clavate anterior bristles slightly curved posteriorly and about 2 µm long, rod-shaped posterior bristles; bristles of monokinetidal tail rather closely spaced (compared with ordinary cilia) and rod-shaped, decreasing in length from about 3 µm anteriorly to 2 µm posteriorly (Fig. 12.8a, f, m, p, 12.9b; Table 12.3).

Oral bulge slanted by less than 30°, occupies about 60% of maximum trunk width in protargol preparations, conspicuous both in vivo and preparations because (i) of the distinct cytopharyngeal concavity; (ii) about 4 µm high in lateral and up to 10 µm wide in frontal view; (iii) ∞-shaped in lateral and dumbbell-shaped in frontal view; and (iv) bright due to the many and rather thick extrusomes contained. Cytopharynx conspicuous, funnel-shaped in lateral and fusiform in frontal view (Fig. 12.8a–c, h–p, 12.9a, b). Circumoral kinety of same shape as oral bulge, continuous and more or less distinctly connected with ciliary rows, composed of narrowly spaced dikinetids each associated with an about 15 µm long cilium, a long nematodesma, and a faintly impregnated fibre (likely transverse microtubular ribbon) extending into cytopharyngeal wall to form a rather distinct (inner) basket composed of bundled fibres. Oral (outer) basket recognizable in vivo, very conspicuous in protargol preparations because composed of distinct, cuneate nematodesma bundles extending to mid-body (Fig. 12.8a, m–p, 12.9c, h).

Observations on Australian and Costa Rican specimens (Fig. 12.8s–v, 12.9f–w; Table 12.3): Although morphometry is rather incomplete, the Australian specimens likely are slightly larger than the South African ones, and thus show several size-related differences, for instance, the dorsal brush is slightly longer and composed of more dikinetids. The number of ciliary rows, in contrast, is lower, as also recognizable in SEM-micrographs (Fig. 12.8s–v, 12.9f–i; Table 12.3). Two size types (8–9 µm; about 3 µm) of rod-shaped, cytoplasmic extrusomes impregnate with the protargol method used. Furthermore, the cortex is frequently distinctly furrowed in the SEM preparations, likely by the postciliary microtubule bundles distinct also in protargol-impregnated cells. The oral bulge fibres (likely transverse microtubular ribbons), which originate from the circumoral kinetids and extend into the cytopharyngeal wall, are intensely stained (Fig. 12.8s–v, 12.9h).

In vivo, the Costa Rican specimens match well the South African ones in body shape and size, while specimens prepared for scanning electron microscopy are considerably smaller and stouter, likely due to strong shrinkage (Fig. 12.9m–o; Table 12.3). Only one type of oral extrusomes was recognized in vivo, viz., slightly curved, 8–10 *µm* long rods; likely, the minute, second type was overlooked.

In addition, we observed some specimens each in soils from Hawaii, Crete, and Austria. They all match the South African type population, for instance, in shape and size of the type I extrusomes: indistinctly fusiform to almost rod-shaped with narrowed ends, slightly curved, 7.0–8.0 × 0.5 µm in size (Crete specimens); rod-shaped with narrowed ends, slightly curved, about 5.0–6.0 × 0.5 µm in size (Austrian specimens). Body shape, however, is more distinctly spatulate because the neck is more pronounced, and the oral bulge ends more conspicuously inflated (Fig. 12.8r).

**Occurrence and ecology:** At the type locality (South Africa; bark with pH 7.8 in water; details, see above), *Neospathidium longinucleatum* became abundant in the non-flooded Petri dish culture.

In Australia, it occurred in floodplain soil from the Murray River (landside of Ryans road) near the town of Albury, Australia. According to a note by H. Berger in Foissner (2021, p. 100, footnote 1), this site must be at or near the following point: 36°06'49.342"S, 146°58'13.966"E. This is also the type locality of *Levispatha australiensis* Foissner, 2021 (p. 100) and very likely also the type locality of *Bursaria fluviatilis* Foissner, 2021 (p. 185) and *Pseudofuscheria magna* Foissner, 2021 (p. 113). The sample consisted of dry leaves of *Myriophyllum* and leaves of the red gum tree, with much soil and litter; soil loamy-sandy, middle-brown to yellowish; pH 5.2. The non-flooded Petri dish method was started on 4 May 1998 and it provided a huge number of species.

The Central American population occurred in sandy, saline (>20‰; pH 7.6) coastal soil near Punta Pirikiki (about 09°39'29"N 82°45'16"W; co-ordinates from https:// www.wikidata.org/; accessed 19 Feb 2024), at the village Puerto Viejo, circa 54 km south of the town of Limon, Caribbean coast of Costa Rica. Both populations became rather abundant in the non-flooded Petri dish cultures some days after wetting, and thus could be studied in the scanning electron microscope.

The populations from soils of Hawaii (USA; sandelwood forest in the Volcano National Park; pH 6.1), Crete (Greek island; grassland soil), and Austria (floodplain soil from Beugenau [about 48°07'52"N 16°34'01"E] near Vienna; pH 7.4) occurred with low abundance. Although the last-mentioned populations were not checked in silver preparations, the data suggest that *Neospathidium longinucleatum* is a euryhaline cosmopolitan.

## *Neospathidium africanum* nov. spec.

(Fig. 12.11a–k, 12.12a–l, Table 12.4)

**Nomenclature:** The species-group name *african·us, -a, -um* (Latin adjective [m, f, n]; African, living in Africa; Hentschel & Wagner 1996, p. 68) refers to the continent the species was discovered.

**Diagnosis:** Body size about 100 × 40 µm in vivo. Body spatulate with oblique, dumbbell-shaped oral bulge about 70% as long as widest trunk region. Macronucleus in an average

continued on p. 420

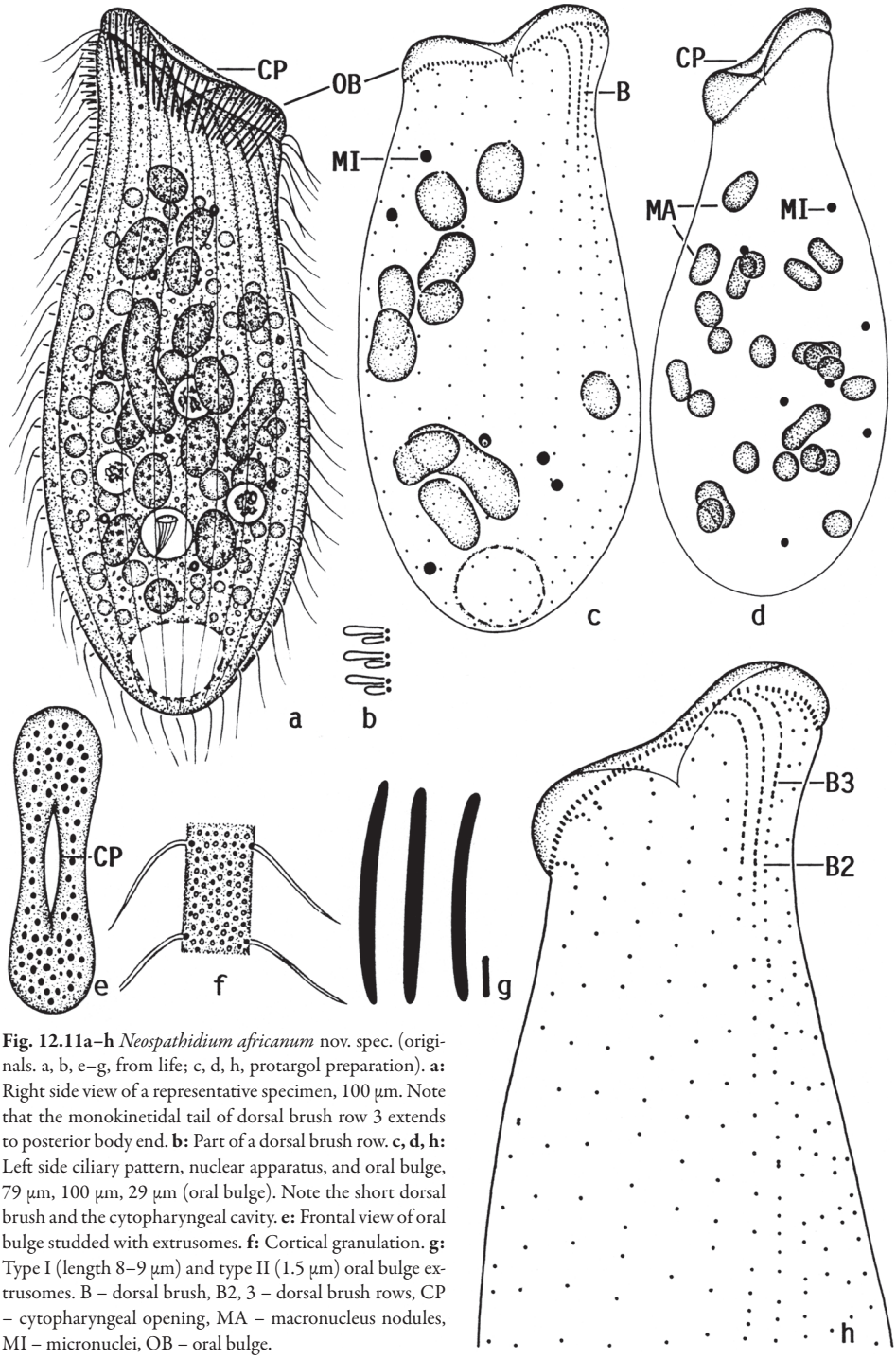



**Fig. 12.11a–h** *Neospathidium africanum* nov. spec. (originals. a, b, e–g, from life; c, d, h, protargol preparation). **a:** Right side view of a representative specimen, 100 µm. Note that the monokinetidal tail of dorsal brush row 3 extends to posterior body end. **b:** Part of a dorsal brush row. **c, d, h:** Left side ciliary pattern, nuclear apparatus, and oral bulge, 79 µm, 100 µm, 29 µm (oral bulge). Note the short dorsal brush and the cytopharyngeal cavity. **e:** Frontal view of oral bulge studded with extrusomes. **f:** Cortical granulation. **g:** Type I (length 8–9 µm) and type II (1.5 µm) oral bulge extrusomes. B – dorsal brush, B2, 3 – dorsal brush rows, CP – cytopharyngeal opening, MA – macronucleus nodules, MI – micronuclei, OB – oral bulge.

of 18 scattered nodules. Two types of extrusomes: type I rod-shaped with narrowed ends and slightly curved, 8.0–9.0 × 0.7 μm in size; type II rod-shaped and about 1.5 μm long. On average 20 ciliary rows, three of them anteriorly modified to inconspicuous dorsal brush occupying about 17% of body length.

**Type locality:** Bark from *Schorsiar* sp. tree (Boer bean) in the Inyata Lodge garden (about 24.77099°S 31.38747°E) at the Sand River, that is, at the south margin of the Krueger National Park, Republic of South Africa. Sample collected on 7 Feb 1995, investigated on 20 Nov 1995.

continued on p. 422

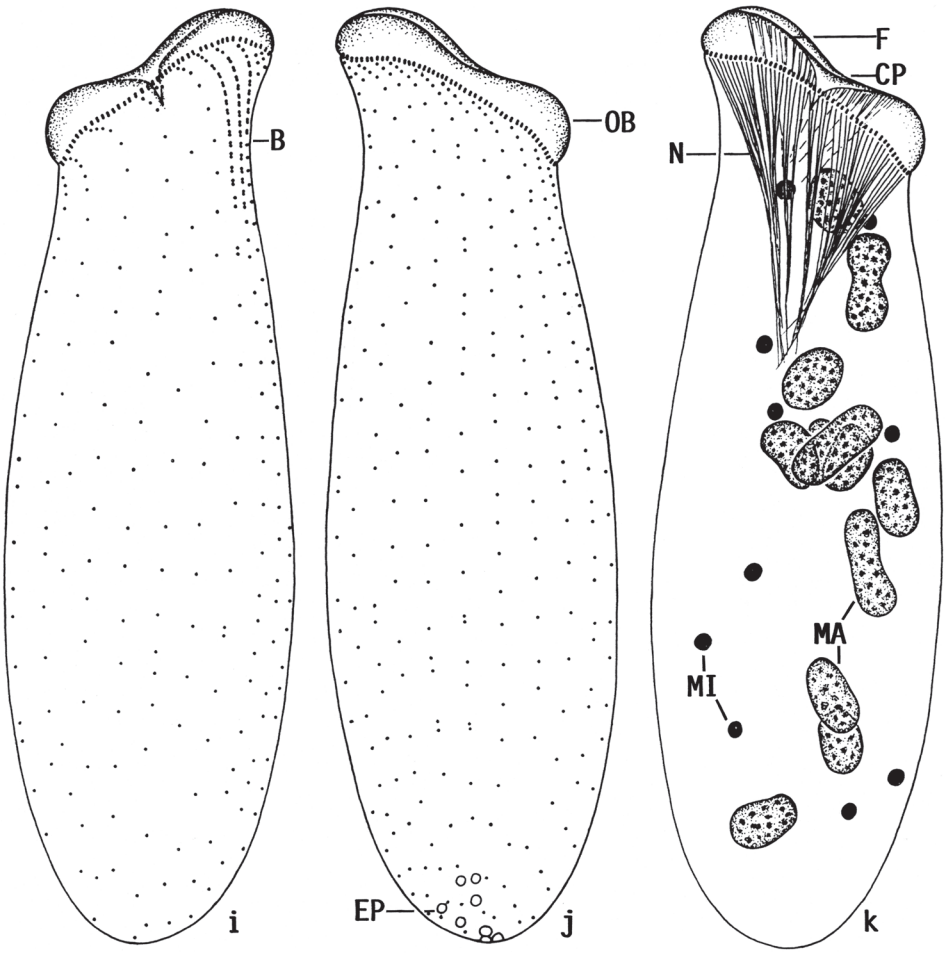



**Fig. 12.11i–k** *Neospathidium africanum* nov. spec. (originals. Protargol preparation). Ciliary pattern of left and right side, oral fibre systems, and nuclear apparatus of holotype specimen. Note the loose ciliation, the short dorsal brush, and the conspicuous oral bulge. B – dorsal brush, CP – cytopharyngeal opening, EP – excretory pores of contractile vacuole, F – fibres supporting cytopharyngeal wall, respectively, forming the inner oral basket, MA – macronucleus nodules, MI – micronuclei, N – nematodesmata supporting the outer oral basket.

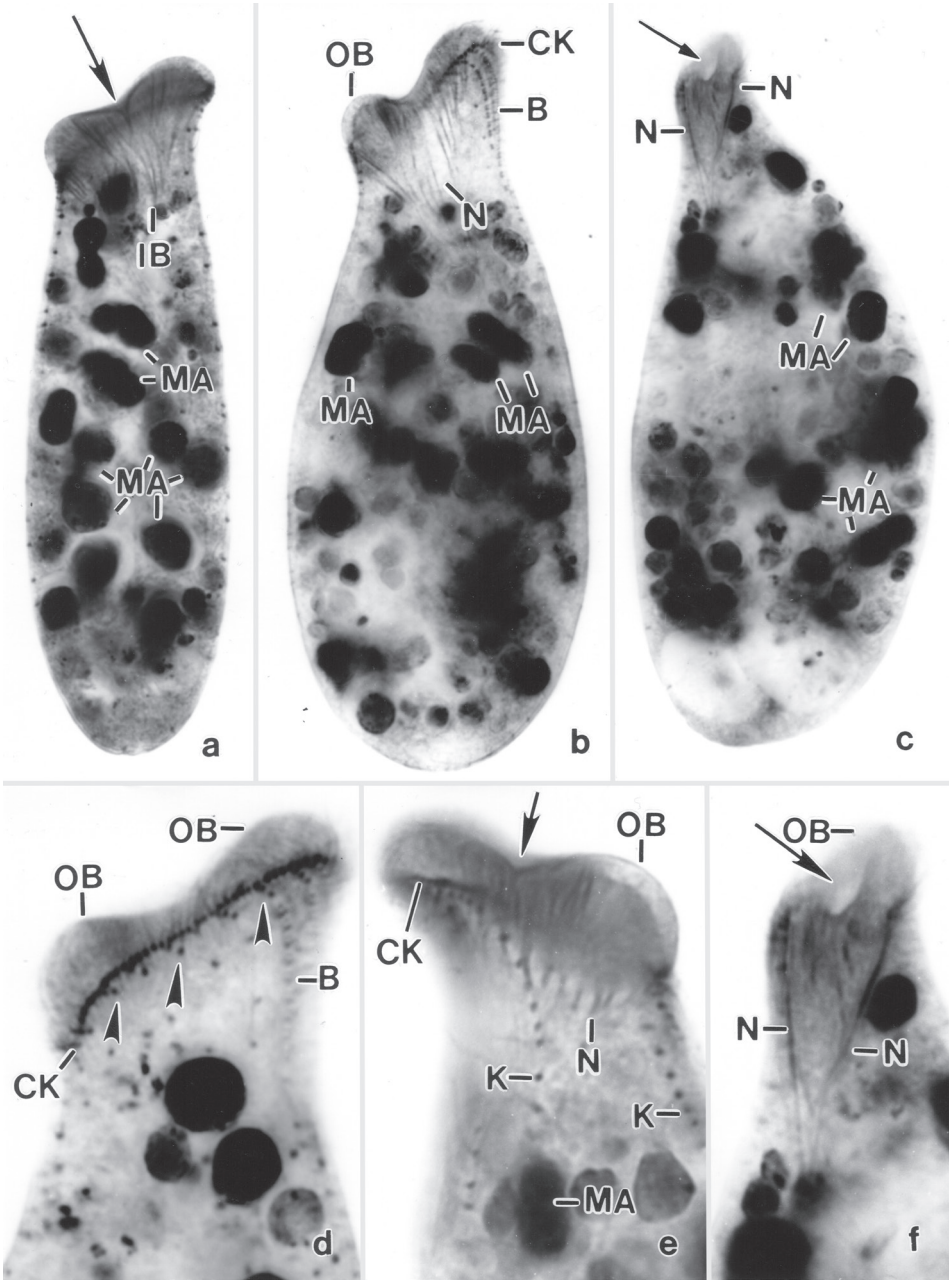
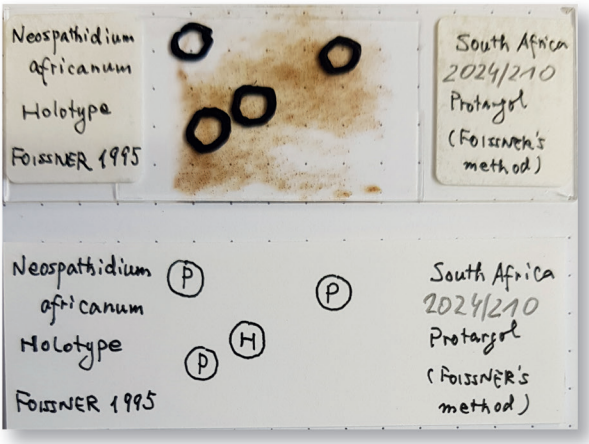
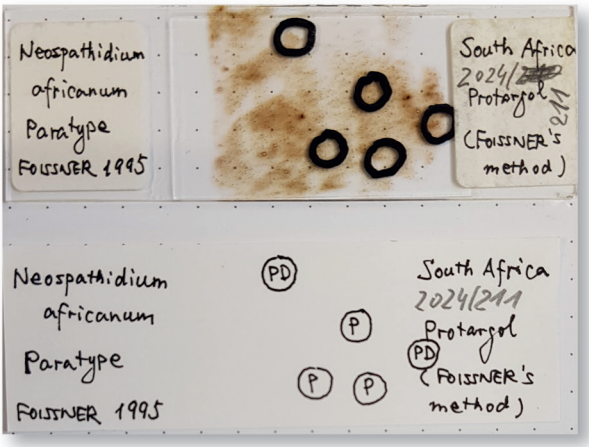



**Fig. 12.12a–f** *Neospathidium africanum* nov. spec. (originals. Protargol preparation). This species is characterized by (i) many macronucleus nodules, (ii) the *Spathidium* ciliary pattern (d; arrowheads), and (iii) the conspicuous, permanent cytostome, well recognizable in lateral (a, e; arrows) and, especially, ventral view (c, f; arrows). The cytoplasm is packed with macronucleus nodules and lipid droplets. B – dorsal brush rows, CK – circumoral kinety, IM – inner basket, K – somatic ciliary rows, MA – macronucleus, N – nematodesmata, OB – oral bulge.



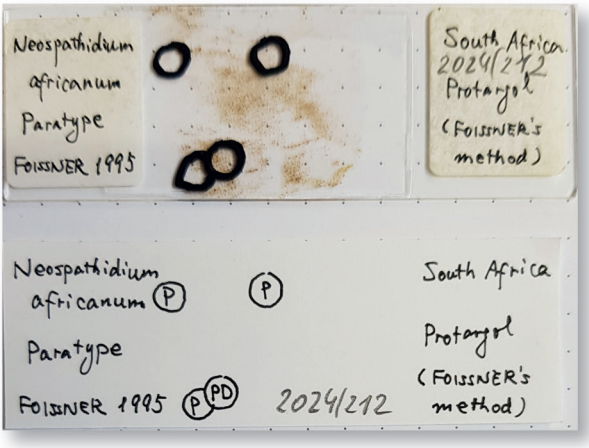

g

h




i

j




k

l

**Fig. 12.12g–l** *Neospathidium africanum* nov. spec. (originals. Protargol slides). **g, h:** Slide (g) and protocol (h) containing holotype (H) and paratypes (P). Accession number (LI): 2024/210. **i–l:** Slides (i, k) and protocols (lj, l) containing paratypes drawn (PD) and paratypes (P). Accession numbers (LI): 2024/211, 212.

**Type material:** The slide (Fig. 12.12g, h; accession number 2024/210) containing the holotype (Fig. 12.11i–k) and two paratype slides (Fig. 12.12i–l; 2024/211, 212) have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI).

**ZooBank registration:** urn:lsid:zoobank.org:act:-E6462619-6C59-486A-9BB5-9B7B76116186

**Remarks:** *Neospathidium africanum* nov. spec. differs distinctly from its congeners *Neospathidium longinucleatum* nov. spec. and *Neospathidium brachystichos* nov. spec. by the macronucleus pattern (scattered nodules vs. tortuous strand). Furthermore, *Neospathidium longinucleatum* is stouter (length: width ratio 2.1 vs. 2.6) and has more ciliary rows (31 vs. 20; Tables 12.3, 12.4); *Neospathidium brachystichos* has only 12 ciliary rows on average (Table 12.4). *Neospathidium africanum* highly resembles *Pharyngospathidium pseudobavariense* (p. 389) in many main features,

especially the macronucleus pattern. However, the ciliary pattern is clearly different (*Spathidium* vs. *Epispathidium*), the number of ciliary rows distinctly lower (20 vs. 30), and the dorsal brush shorter and thus composed of much fewer dikinetids (on average 11 vs. 26 in row 1; Table 12.2).

At first glance, several other spathidiids closely resemble *Neospathidium africanum*, viz., *Spathidium seppelti* Petz & Foissner, 1997 (p. 313), *Spathidium* sp. illustrated by Smith (1978, p. 64), and *Epispathidium regium* (see Chapter 6, that is, Foissner et al. 2025b). Except for the temporal cytostome (vs. permanent cytopharynx), *Spathidium seppelti* differs also by the more slender shape (length:width ratio about 4.0–5.4:1 vs. 2.6:1) and the much higher number of macronucleus nodules (about 65 in *Spathidium seppelti etoschense* Foissner et al., 2002, p. 229 and >100 in *Spathidium seppelti seppelti* vs. 18). The Antarctic population described by Smith (1978) is likely *Spathidium seppelti*, as already discussed by Petz & Foissner (1997). *Epispathidium regium* is considerably larger (about 180 µm vs. 100 µm), has a distinct *Epispathidium* ciliary pattern (vs. *Spathidium* pattern), and possesses much more ciliary rows (on average 41–49 vs. 20) and macronucleus nodules (about 50–100 vs. 18).

**Description:** Body size moderately variable, viz., 80–130 × 30–50 µm in vivo, usually approximately 100 × 40 µm, as calculated from some in vivo measurements and the morphometric data, assuming about 10% preparation shrinkage (Table 12.4). Body spatulate to slenderly spatulate with rather distinct neck, length:width ratio 2.1–3.2:1 in preparations, on average near 2.6:1 both in vivo and protargol slides; oral bulge shorter by about 30% than widest trunk region. Trunk ellipsoidal, laterally flattened up to 2:1, in hyaline neck and oral area up to 3:1; dorsal side slightly longer than ventral, anterior (oral) end thus slightly slanted and distinctly concave, especially in protargol preparations; posterior end broadly rounded (Fig. 12.11a, c, d, h–k). Macronucleus in an average of 18 highly scattered nodules, leaving blank only body ends; exact number, however, often difficult to determine due to many similarly sized and impregnated lipid droplets and food residues. Individual nodules globular, elongate ellipsoidal, or dumbbell-shaped, on average 7 × 5 µm in protargol preparations; each usually contains many globular to lobate nucleoli about 1 µm across. On average eight spherical micronuclei about 1.5 µm across scattered between macronucleus nodules (Fig. 12.11a, c, d, k, 12.12a–c, e). Contractile vacuole in rear body end, some excretory pores in pole area. Two types of extrusomes studded around cytopharynx and, especially, in inflated oral bulge ends: type I extrusomes inconspicuously acicular to rod-shaped and slightly curved, 8.0–9.0 × 0.7 µm in size; type II rod-shaped, about 1.5 µm long and rather thin; both do not impregnate with the protargol method used (Fig. 12.11a, e, g). Cortex very flexible, contains many rows of colourless granules about 0.2 µm across. Cytoplasm colourless, contains few to many lipid droplets up to 8 *µm across* and food vacuoles with colpodid and microthoracid ciliate prey, whose oral baskets are occasionally recognizable (Fig. 12.11a, f). Movement without peculiarities.

Somatic cilia about 10 µm long in vivo, arranged in an average of 20 equidistant, mostly bipolar, loosely ciliated rows abutting on circumoral kinety in pronounced *Spathidium* pattern (indistinct *Epispathidium* pattern in two out of 39 specimens analysed); occasionally occur small irregularities, such as minute breaks and/or supernumerary kinetids outside rows (Fig. 12.11a, c, h–j, 12.12b, d, e; Table 12.4). Dorsal brush dikinetidal and three-rowed, inconspicuous because occupying only about 17% of body length and bristles merely

up to 3 µm long; all rows commence with several ordinary cilia, rows 1 and 2 continue with ordinary cilia posteriorly; a fourth row comprising several dikinetids occasionally beside row 1. Bristles of same appearance in all rows, that is, anterior bristle of dikinetids clavate and about 3 µm long, posterior rod-shaped and only about 1.5 µm long. Brush row 1 slightly shorter than row 2, composed of an average of 11 dikinetids; longest row 2 comprises an average of 15 dikinetids; row 3 distinctly shorter than rows 1 and 2, composed of an average of only eight dikinetids followed by a monokinetidal tail of rather closely spaced, rod-shaped bristles extending to body end (Fig. 12.11a–c, h, i, 12.12b, d; Table 12.4).

Oral bulge slanted by about 30° and occupying about 70% of maximum trunk width, conspicuous both in vivo and protargol preparations because (i) of the distinct cytopharyngeal concavity; (ii) up to 5 µm high in lateral and about 10 µm wide in frontal view; (iii) ∞-shaped in lateral and dumbbell-shaped in frontal view; and (iv) bright due to the many and rather thick extrusomes contained. Cytopharynx conspicuous, funnel-shaped in lateral and fusiform in frontal view (Fig. 12.11a, c–e, h–k). Circumoral kinety of similar shape as oral bulge, continuous and more or less distinctly connected with ciliary rows, composed of narrowly spaced dikinetids each associated with a cilium, a long nematodesma, and a faintly impregnated fibre (likely transverse microtubular ribbon) extending into cytopharyngeal wall and forming a rather distinct (inner) basket composed of bundled fibres. Oral (outer) basket conspicuous in protargol preparations because composed of distinct, cuneate nematodesma bundles extending to second third of body (Fig. 12.11c, h–k, 12.12a–f).

**Occurrence and ecology:** To date *Neospathidium africanum* nov. spec. was found only at the type locality (see above). It was rare in the non-flooded Petri dish culture (pH 6.8 in water).

## *Neospathidium brachystichos* nov. spec.

(Fig. 12.13a–k, Table 12.4; Fig. 8.3o–v in Foissner et al. 2025c)

**Nomenclature:** The species-group name *brachystichos* is an apposition of the Greek *brachys* (short; Hentschel & Wagner 1996, p. 136) and the Greek noun *stichos* (row, line; Werner 1972, p. 390) and refers to the short dorsal brush rows.

**Diagnosis:** Body size about 115 × 35 µm in vivo. Body narrowly spatulate with oblique, oblong oral bulge about 60% as long as widest trunk region. Macronucleus curved-cylindrical and about 50 µm long. Extrusomes rod-shaped with narrowed ends, 3.0–4.0 × 0.7 µm in size. On average 12 ciliary rows, three of them anteriorly modified to inconspicuous, strongly heterostichad dorsal brush occupying about 11% of body length.

**Type locality:** Highly saline (>30‰), circumneutral (pH 7.6) soil from the surroundings of the Pink Lake (centre of lake at about 35.58655°S 139.37820°E), about 12 km north of Meningie, a small town on the east coast of Lake Albert, Australia.[5]

[5] Note by H. Berger: In the raw manuscript, W. Foissner provided the following text for the type locality: "Highly saline (>30‰), circumneutral (pH 7.6) soil from the surroundings of Lake Meningie near the town of Adelaide (S35° E138°40'), Australia." However, a search via Google and Google Maps showed that there exists no "Lake Meningie". The co-ordinates mentioned by W. Foissner ("E138°40' S35°") indicate a forest site few kilometres east of the southern region of the city of Adelaide, about 100 km away from Meningie. Very likely, the sample is from the margin of the Pink Lake near the Princess Highway (about 35.586°S 139.372°E) at the east coast of Lake Albert which is about 100 km southeast of the city of Adelaide. Meningie (35.689°S 139.337°E) is a small town at the east coast of Lake Albert.

The sample was collected on 11 Feb 1987 (likely by Hubert Blatterer, Austria); the original labelling of the sample (= Australian sample P39) was "Adelaide Meningie Salzsee Grasbewachs. Hügel, 11.2.87" (in English: Adelaide Meningie salt lake grass-grown hill, 11 Feb 1987).

**Type material:** The slide (Fig. 8.3o, p in Foissner et al. 2025c; accession number 2024/239) containing the holotype (Fig. 12.13h, i) and three paratype slides (Fig. 8.3q–v in Foissner et al. 2025c; 2024/240, 241, 242) have been deposited in the Biology Centre of the Upper Austrian Museum in Linz (LI).[6]

**ZooBank registration:** urn:lsid:zoobank.org:act:0C1C3B50-B6CA-4B54-80BE-3753BDE957C9

**Remarks:** At first glance, *Neospathidium brachystichos* looks like an ordinary *Spathidium*. However, on more detailed investigation, the permanent cytopharynx becomes recognizable, suggesting classification in *Neospathidium*. *Neospathidium brachystichos* is distinguished from the congeners by many conspicuous features, for instance, the short extrusomes (3–4 µm vs. 8–11 µm), the short macronucleus (vs. long and tortuous or in many scattered nodules), and the markedly lower number of somatic ciliary rows (12 vs. 31 or 20). The macronucleus pattern and the extrusomes of *Neospathidium brachystichos* resemble *Pharyngospathidium simplinucleatum* (p. 399) which, however, is much stouter (about 2:1 vs. 3:1 in *Neospathidium brachystichos*) and has more ciliary rows (about 10 on left side vs. at total of 11–13). *Neospathidium brachystichos* resemble also *Spathidium rusticanum* Foissner, 1981 (see Chapter 3, that is, Foissner et al. 2025a) which, however, has a different oral apparatus (no permanent cytopharynx) and a moniliform macronucleus strand.

**Description:** Body size moderately variable, viz., 90–140 × 25–45 µm in vivo, usually near 115 × 35 µm, as calculated from some in vivo measurements and the morphometric data (Table 12.4). Body narrowly spatulate with moderately distinct neck and a length:width ratio of 2.3–4.2:l in prepared specimens, on average near 3:1 both in vivo and protargol preparations; anterior (oral) end oblique and inconspicuously concave in vivo, posterior usually rounded, widest underneath mid-body. Trunk ellipsoidal with ventral side more distinctly vaulted than dorsal, laterally flattened up to 2: 1 (Fig. 12.13a, h). Macronucleus in middle third of body, usually a curved strand with a spread length of about 50 µm in vivo, rarely elongate reniform or oblong; nucleoli do not impregnate with the protargol method used, not even in over-impregnated specimens (Fig. 12.13a, h). Likely several micronuclei difficult to differentiate from many similarly sized and impregnated cytoplasmic inclusions. Contractile vacuole in rear body end, some excretory pores in pole area. Oral extrusomes rod-shaped with narrowed ends, about 3.0–4.0 × 0.7 µm in size; do not impregnate with the protargol method used (Fig. 12.13a, c). Cortex very flexible, contains colourless, minute granules. Cytoplasm colourless, usually packed with lipid droplets 1–5 µm across (Fig. 12.13a, k). Swims moderately rapid by rotation about main body axis.

Somatic cilia about 7 µm long in vivo, arranged in an average of 12 equidistant, mostly bipolar, ordinarily ciliated rows abutting on circumoral kinety in typical *Spathidium* pattern; occasionally with small irregularities, such as minute breaks and/or supernumerary kinetids outside rows (Fig. 12.13a, g–j; Table 12.4). Dorsal brush dikinetidal and strongly

[6] These slides also contain the holotype and paratypes of *Schmidingerophrya macrothrix* nov. spec. (see Chapter 8, that is, Foissner et al. 2025c).

continued on p. 428

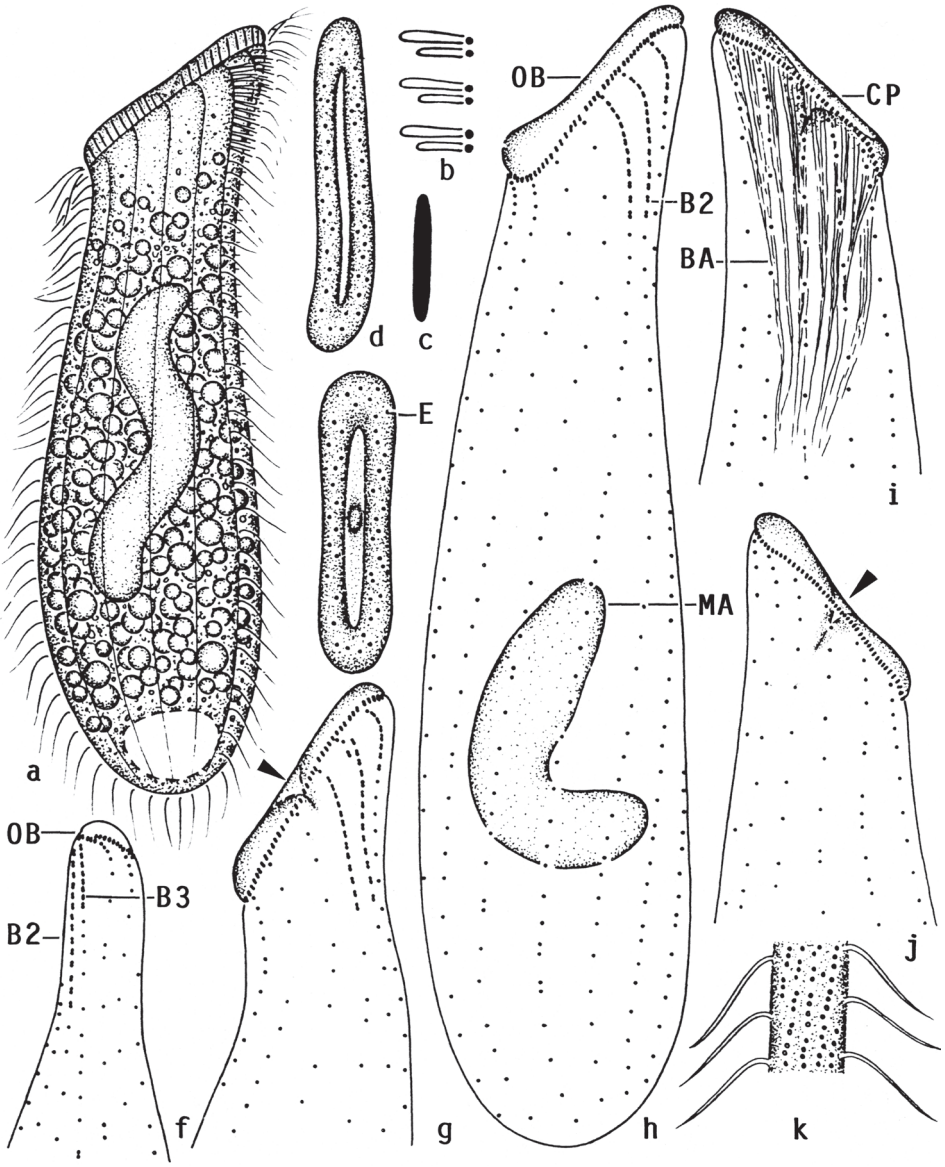



**Fig. 12.13a–k** *Neospathidium brachystichos* nov. spec. (originals. a–e, k, from life; f–j, protargol preparation). **a:** Left side view of a representative specimen, 120 µm. Note the short, slightly curved macronucleus. **b:** Part of dorsal brush, bristles up to 4 µm long. **c:** Oral bulge extrusome, 4.0 × 0.7 µm. **d, e:** Frontal views of oral bulge. **f, g, j:** Ciliary pattern of anterior dorsal (f), left (g), and right (j) side. Arrowheads in (g, j) mark cytopharyngeal entrance. Note the very short brush row 3, a main feature of this species. Length of oral bulge about 20 µm. **h, i:** Ciliary pattern of left and right side and macronucleus of holotype specimen, 95 µm. **k:** Surface view showing cortical granulation. B2, 3 – dorsal brush rows, BA – oral basket, CP – cytopharyngeal opening, E – extrusomes, MA – macronucleus, OB – oral bulge.

**Table 12.4** Morphometric data on *Neospathidium africanum* nov. spec. (original data; upper line) and *Neospathidium brachystichos* (original data; lower line)[a]

| Characteristic | Mean | M | SD | SE | CV | Min | Max | n |
|---|---|---|---|---|---|---|---|---|
| Body, length | 88.5 | 87.0 | 10.6 | 2.3 | 12.0 | 75.0 | 115.0 | 21 |
| | 101.5 | 103.0 | 13.1 | 3.0 | 13.9 | 80.0 | 124.0 | 19 |
| Body, width | 34.1 | 34.0 | 3.7 | 0.8 | 10.9 | 28.0 | 40.0 | 21 |
| | 32.6 | 33.0 | 4.5 | 1.0 | 13.7 | 25.0 | 43.0 | 19 |
| Body length:width, ratio | 2.6 | 2.6 | 0.3 | 0.1 | 12.5 | 2.1 | 3.2 | 21 |
| | 3.2 | 3.2 | 0.6 | 0.1 | 19.3 | 2.3 | 4.2 | 19 |
| Oral bulge, length | 23.5 | 24.0 | 2.6 | 0.6 | 11.1 | 19.0 | 29.0 | 21 |
| | 19.5 | 20.0 | 1.5 | 0.4 | 7.9 | 17.0 | 22.0 | 19 |
| Oral bulge length:body width, ratio | 0.7 | 0.7 | 0.1 | 0.0 | 13.5 | 0.6 | 0.9 | 21 |
| | 0.6 | 0.6 | 0.1 | - | 18.0 | 0.4 | 0.8 | 19 |
| Oral bulge, height | 4.1 | 4.0 | 0.8 | 0.2 | 19.1 | 3.0 | 6.0 | 21 |
| | - | - | - | - | - | - | - | - |
| Circumoral kinety to last dikinetid of brush row 1, distance | 12.0 | 12.0 | 1.6 | 0.3 | 13.0 | 10.0 | 15.0 | 21 |
| | 9.2 | 9.0 | 2.0 | 0.5 | 22.2 | 6.0 | 13.0 | 19 |
| Circumoral kinety to last dikinetid of brush row 2, distance | 15.5 | 15.0 | 1.9 | 0.4 | 12.2 | 12.0 | 20.0 | 21 |
| | 11.5 | 12.0 | 1.7 | 0.4 | 15.2 | 9.0 | 15.0 | 19 |
| Circumoral kinety to last dikinetid of brush row 3, distance | 8.4 | 9.0 | 0.8 | 0.2 | 9.6 | 7.0 | 10.0 | 21 |
| | 5.3 | 5.0 | 0.7 | 0.2 | 14.1 | 4.0 | 7.0 | 19 |
| Anterior body end to anteriormost macronucleus nodule, distance | 18.6 | 17.0 | 4.7 | 1.0 | 25.3 | 11.0 | 30.0 | 21 |
| | - | - | - | - | - | - | - | - |
| Macronucleus figure, length | 60.3 | 59.0 | 9.0 | 2.0 | 14.9 | 49.0 | 85.0 | 21 |
| | 35.9 | 34.0 | 8.5 | 1.9 | 23.6 | 23.6 | 50.0 | 19 |
| Macronucleus nodules, length | 6.9 | 7.0 | 1.9 | 0.4 | 27.8 | 4.0 | 11.0 | 21 |
| | 41.2 | 40.0 | 12.0 | 2.8 | 29.2 | 24.0 | 65.0 | 19 |
| Macronucleus nodules, width | 4.7 | 5.0 | 0.7 | 0.2 | 15.6 | 3.0 | 6.0 | 21 |
| | 6.8 | 7.0 | 0.8 | 0.2 | 12.2 | 5.0 | 8.0 | 19 |
| Macronucleus nodules, number | 18.1 | 17.0 | 7.2 | 1.6 | 39.9 | 9.0 | 42.0 | 21 |
| | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 | 1.0 | 1.0 | 19 |
| Micronuclei, diameter | 1.6 | 1.5 | 0.4 | 0.1 | 21.8 | 1.0 | 2.0 | 21 |
| | - | - | - | - | - | - | - | - |
| Micronuclei, number | 8.5 | 8.0 | 1.9 | 0.4 | 22.1 | 5.0 | 12.0 | 21 |
| | - | - | - | - | - | - | - | - |
| Somatic kineties, number | 20.2 | 20.0 | 1.7 | 0.4 | 8.4 | 17.0 | 24.0 | 21 |
| | 12.4 | 13.0 | 0.8 | 0.2 | 6.2 | 11.0 | 13.0 | 19 |
| Basal bodies in a right-side kinety, number | 28.6 | 28.0 | 6.1 | 1.3 | 21.2 | 21.0 | 44.0 | 21 |
| | 45.3 | 44.0 | 8.5 | 1.9 | 18.7 | 30.0 | 58.0 | 19 |
| Dorsal brush rows, number | 3.0 | 3.0 | 0.0 | 0.0 | 0.0 | 3.0 | 3.0 | 21 |
| | 3.0 | 3.0 | 0.0 | 0.0 | 0.0 | 3.0 | 3.0 | 19 |
| Dikinetids in brush row 1, number | 11.0 | 11.0 | 1.7 | 0.4 | 15.9 | 8.0 | 15.0 | 21 |
| | 11.6 | 12.0 | 1.6 | 0.4 | 13.9 | 9.0 | 15.0 | 19 |
| Dikinetids in brush row 2, number | 15.0 | 15.0 | 2.2 | 0.5 | 14.6 | 11.0 | 19.0 | 21 |
| | 13.8 | 14.0 | 1.9 | 0.4 | 13.5 | 12.0 | 17.0 | 19 |
| Dikinetids in brush row 3, number | 7.9 | 8.0 | 1.1 | 0.2 | 13.5 | 6.0 | 11.0 | 21 |
| | 6.3 | 6.0 | 0.9 | 0.2 | 13.9 | 5.0 | 8.0 | 19 |

**Table 12.4** Continued

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

heterostichad, inconspicuous because occupying only about 11% of body length and bristles merely up to 4 µm long in vivo; all rows commence with few (usually two) ordinary cilia anteriorly and continue as somatic kineties posteriorly. Bristles ordinarily spaced and of similar pattern in all rows, that is, anterior bristle of dikinetids about 4 µm long and slightly inflated, posterior rod-shaped and about 3 µm long. Brush row 1 slightly shorter than row 2, composed of an average of 14 dikinetids; row 3 only about half as long as rows 1 and 2, composed of an average of merely six dikinetids, but followed by a monokinetidal tail of bristles extending to second third of body (Fig. 12.13a, b, f–h; Table 12.4).

Oral bulge slanted by 30–45° and occupying about 60% of maximum trunk width, inconspicuous both in vivo and preparations because only about 2 µm high and thus indistinctly separate from body proper; ∞-shaped in lateral view and oblong to distinctly dumbbell-shaped in frontal view; surface slightly concave and with flat, central groove with cytopharyngeal opening in bulge centre. Cytopharynx moderately conspicuous, funnel-shaped in lateral view (Fig. 12.13a, d, e, g–j). Circumoral kinety of similar shape as oral bulge, continuous, composed of narrowly spaced dikinetids each associated with a cilium, a long nematodesma, and a faintly impregnated fibre (likely a transverse microtubule ribbon) extending into cytopharyngeal wall to form a rather distinct (inner) basket composed of bundled fibres. Oral (outer) basket distinct in protargol preparations because composed of cuneate nematodesma bundles extending over one third of body length (Fig. 12.13a, g–j).

**Occurrence and ecology:** As yet *Neospathidium brachystichos* was found only at the type locality (see above), where it was very rare in the non-flooded Petri dish culture.

## Funding

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

## Acknowledgements

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

## References

Aescht E. (2001): Catalogue of the generic names of ciliates (Protozoa, Ciliophora). – Denisia (Linz) 1: 1–350.

Berger H., Xu K. & Foissner W. (2025a): General section to "Revision of some spathidiid genera (Alveolata, Ciliophora, Spathidiida)", including nomenclatural notes. – Ser. Monogr. Cilioph. 6: 1–24.

Berger H., Xu K. & Foissner W. (2025b): Spathidiida Foissner & Foissner, 1988 (Ciliophora, Litostomatea, Haptoria): a brief introduction. – Ser. Monogr. Cilioph. 6: 25–32.

Brown R.W. (1954): Composition of scientific words. A manual of methods and a lexicon of materials for the practice of logotechnics. Brown, Baltimore. 882 pp.

Bütschli O. (1889): Protozoa. III. Abtheilung: Infusoria und System der Radiolaria. In: Bronn H.G. (ed.): Klassen und Ordnungen des Thier-Reichs, wissenschaftlich dargestellt in Wort und Bild, Erster Band, pp. 1585–2035, Tafeln LVI–LXXIX. Winter, Leipzig.

Claparède É. & Lachmann J. (1859): Études sur les infusoires et les rhizopodes. – Mém. Inst. natn. génev. 6 (year 1858): 261– 482, Planches 14–24.

Durán-Ramírez C.A., García-Franco J.G., Foissner W. & Mayén-Estrada R. (2015): Free-living ciliates from epiphytic tank bromeliads in Mexico. – Eur. J. Protistol. 51: 15–33.

Foissner W. (1981): Morphologie und Taxonomie einiger neuer und wenig bekannter kinetofragminophorer Ciliaten (Protozoa: Ciliophora) aus alpinen Böden. – Zool. Jb. Syst. 108: 264–297.

Foissner W. (1984): Infraciliatur, Silberliniensystem und Biometrie einiger neuer und wenig bekannter terrestrischer, limnischer und mariner Ciliaten (Protozoa: Ciliophora) aus den Klassen Kinetofragminophora, Colpodea und Polyhymenophora. – Stapfia (Linz) 12: 1–165.

Foissner W. (1998): An updated compilation of world soil ciliates (Protozoa, Ciliophora), with ecological notes, new records, and descriptions of new species. – Eur. J. Protistol. 34: 195–235.

Foissner W. (2003): The Myriokaryonidae fam. n., a new family of spathidiid ciliates (Ciliophora: Gymnostomatea). – Acta Protozool. 42: 113–143.

Foissner W. (2021): Taxonomy of soil ciliates (Ciliophora) from Australia and some other parts of the world. – In: Foissner W. & Berger H. (Eds): Terrestrial ciliates (Protista, Ciliophora) from Australia and some other parts of the world. – Ser. Monogr. Cilioph. 5: 55–345.

Foissner W. & Foissner I. (1988): The fine structure of *Fuscheria terricola* Berger et al., 1983 and a proposed new classification of the subclass Haptoria Corliss, 1974 (Ciliophora, Litostomatea). – Arch. Protistenk. 135: 213–235.

Foissner W. & Xu K. (2007): Monograph of the Spathidiida (Ciliophora, Haptoria) Vol. I: Protospathidiidae, Arcuospathidiidae, Apertospathulidae. – Monogr. biol. 81: i–xii, 1–485.

Foissner W., Agatha S. & Berger H. (2002): Soil ciliates (Protozoa, Ciliophora) from Namibia (Southwest Africa), with emphasis on two contrasting environments, the Etosha region and the Namib Desert. – Denisia 5: 1–1459.

Foissner W., Xu K. & Berger H. (2025a): Characterisation of 15 species belonging to the genus *Spathidium* Dujardin, 1841 (Ciliophora, Spathidiidae), including three new. – Ser. Monogr. Cilioph. 6: 33–109.

Foissner W., Xu K. & Berger H. (2025b): *Epispathidium* Foissner, 1984 (Ciliophora, Spathidiidae), a genus where the circumoral kinety is completely separated from the somatic kineties. – Ser. Monogr. Cilioph. 6: 141–211.

Foissner W., Xu K. & Berger H. (2025c): *Schmidingerophrya* nov. gen. (Ciliophora, Spathidiidae), a new genus whose species have only two dorsal brush rows. – Ser. Monogr. Cilioph. 6: 257–280.

Foissner W., Xu K. & Berger H. (2025d): *Centrospathidium* nov. gen. (Ciliophora, Spathidiidae), a new genus whose type species is from Australia. – Ser. Monogr. Cilioph. 6: 127–140.

Gellért J. (1956): Die Ciliaten des sich unter der Flechte *Parmelia saxatilis* Mass. gebildeten Humus. – Acta biol. hung. 6: 77–111 (sometimes cited as Gellért 1955).

Hentschel E.J. & Wagner G.H. (1996): Zoologisches Wörterbuch. Tiernamen, allgemeinbiologische, anatomische, physiologische Termini und Kurzbiographien. Gustav Fischer Verlag, Jena. 677 pp.

ICZN (International Commission on Zoological Nomenclature) (1999): International Code of Zoological Nomenclature, 4th edn. – International Trust for Zoological Nomenclature, London: i–xxx, 306 pp.

Kahl A. (1926): Neue und wenig bekannte Formen der holotrichen und heterotrichen Ciliaten. – Arch. Protistenk. 55: 197–438.

Kahl A. (1930a): Neue und ergänzende Beobachtungen holotricher Infusorien. II. – Arch. Protistenk. 70: 313–416.

Kahl A. (1930b): Urtiere oder Protozoa I: Wimpertiere oder Ciliata (Infusoria) 1. Allgemeiner Teil und Prostomata. – Tierwelt Dtl. 18: 1–180.

Kahl A. (1943): Infusorien (1. Teil). Ein Hilfsbuch zum Erkennen, Bestimmen, Sammeln und Präparieren der freilebenden Infusorien des Süßwassers und der Moore. Buchbeilage zum Mikrokosmos Jahrgang 1942/43, d. h., erschienen in der Reihe "Handbücher für die praktische naturwissenschaftliche Arbeit", Band 31/32, 52 pp. Franckh'sche Verlagsbuchhandlung, W. Keller & Co., Stuttgart.

Lokot L.I. (1987): Ökologie der Wimpertiere im Süßwasser des zentralen Baikalgebietes. Akademia Nauka, Novosibirsk. 152 p. (in Russian).

Lynn D.H. & Small E.B. (2002): Phylum Ciliophora, pp. 371–656. In: Lee J.J., Leedale G.F., Bradbury P. (eds.): An illustrated guide to the Protozoa. Second edition. Organisms traditionally referred to as Protozoa, or newly discovered groups. Volume I. Society of Protozoologists, Lawrence.

Moody J.E. (1912): Observations on the life-history of two rare ciliates, *Spathidium spathula* and *Actinobolus radians*. – J. Morph. 23: 349–407.

Müller O.F. (1773): Vermium Terrestrium et Fluviatilium, seu Animalium Infusoriorum, Helminthicorum et Testaceorum, non Marinorum, Succincta Historia. Heineck and Faber, Havniae and Lipsiae. 135 pp.

Petz W. & Foissner W. (1997): Morphology and infraciliature of some soil ciliates (Protozoa, Ciliophora) from continental Antarctica, with notes on the morphogenesis of *Sterkiella histriomuscorum*. – Polar Rec. 33: 307–326.

Schubert R. & Wagner G. (1979): Pflanzennamen und botanische Fachwörter. Botanisches Lexikon mit einer „Einführung in die Terminologie und Nomenklatur" einem Verzeichnis der „Autorenamen" und einem Überblick über das „System der Pflanzen". Neumann-Neudamm, Melsungen, Berlin, Basel, Wien. 466 pp.

Smith H.G. (1978): The distribution and ecology of terrestrial protozoa of sub-Antarctic and maritime Antarctic islands. – Br. Antarct. Surv. Sci. Rep. No. 95: 1–104.

Tirjaková E. & Matis D. (1987): Ciliates of dry mosses in Bratislava in relation to air pollution. – Acta Fac. Rerum nat. Univ. comen., Bratisl., Series Zoologia 29: 17–31.

Wang C.C. & Nie D. (1933): Report on the rare and new species of freshwater infusoria, part I. – Contr. biol. Lab. Sci. Soc. China, Zoological series 10: 1–99.

Wenzel F. (1953): Die Ciliaten der Moosrasen trockner Standorte. – Arch. Protistenk. 99: 70–141.

Werner F.C. (1972): Wortelemente lateinisch-griechischer Fachausdrücke in den biologischen Wissenschaften. Suhrkamp, Baden-Baden. 475 pp.

Wilbert N. (1995): Benthic ciliates of salt lakes. – Acta Protozool. 34: 271–288.

Xu K. & Foissner W. (2005): Morphology, ontogenesis and encystment of a soil ciliate (Ciliophora, Haptorida), *Arcuospathidium cultriforme* (Penard, 1922), with models for the formation of the oral bulge, the ciliary patterns, and the evolution of the spathidiids. – Protistology 4: 5–55.

# 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*, R*ostrophryides* 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 longichilum*** 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
*Ap ertospathula pelobia* 6
*Apertospathula similis* 6
Apertospathulidae 25, 27
*Apobryophyllum* 143, 206
*Apobryophyllum schmidingeri* 445
*Apobryophyllum vermiforme* 8
*Apocolpodidium Apocolpodidium etoschense* 9
*Apocolpodidium etoschense*, *Apocolpodidium* 9
*Apocolpodidium Phagoon macrostoma* 9
*Apocyclidium obliquum* 4
*Apometopus Apometopus pyriformis* 16
*Apometopus pyriformis*, *Apometopus* 16
***apospathidiforme***, ***Spathidium*** 33, 34, 35, 37, 38, 38T, **43**, 44T, 112, 114, 119, 301
***Apospathidium*** xv, 28, 43, **111,** 112K, 312
*Apospathidium atypicum* 3, 112, 117
***Apospathidium longicaudatum*** 3, 43, 47, 65, 67, 111, 112, 112K 113T, 114, **117**
***Apospathidium terricola*** 111, 112K, **112**, 113T, 119, 343
***arboricola***, ***Latispathidium*** 213, 214, 215K, **229**, 236T, 266
arcuospathidiid 241
Arcuospathidiidae 25, 27, 433
*Arcuospathidium* 11, 12, 26, 85, 143, 149, 206, 214, 281, 283, 286, 336, 362, 445, 447
*Arcuospathidium atypicum* 440
*Arcuospathidium australe* 439, 440, 441, 442, 443
*Arcuospathidium bulli* 41, 85
*Arcuospathidium coemeterii* 443
*Arcuospathidium cultriforme* 446
*Arcuospathidium cultriforme cultriforme* 196
*Arcuospathidium cultriforme lionotiforme* 446
*Arcuospathidium cultriforme scalpriforme* 447
*Arcuospathidium deforme* 6
*Arcuospathidium japonicum* 435, 445
*Arcuospathidium lionotiforme* 446, 447
*Arcuospathidium multinucleatum* 149
*Arcuospathidium muscorum rhopaloplites* 6
*Arcuospathidium namibiense* 11, 12, 214, 233, 235, 258, 266
*Arcuospathidium pelobium* 6
*Arcuospathidium vermiforme* 270
*Arcuospathidium virugense* 7
*Arcuospathidium virungense* 7
*Arcuospathidium vlassaki* 214
*arenicola*, *Protospathidium* 5, 8
*Armatospathula* 7
*Armatospathula costaricana* 7
*Armatospathula periarmata* 7
*Armatospathula plurinucleate* 7
***armatum***, ***Semispathidium*** 311, 312, 313T, 315K, 315, **320**, 328
***armatum***, ***Supraspathidium*** 8, 335, 336, 337, 338K, 344T, 345T, 348, **353**, 360
***ascendens***, ***Epispathidium*** 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 Epispathidium*? 142

*bavariensis*, *Gastrostyla* 15
*bavariensis*, *Gastrostyla Kleinstyla* 14, 15
Belonophryina 26
*Bilamellophrya australiensis* 134
***bimacronucleatum*, *Latispathidium truncatum*** 215, 217T, 219, 220T, 220K, **222**
*binucleate, Parakahliella* 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 amicronucleata*, *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 amicronucleata* 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
*Condylostomides 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
***duschli*, *Spathidium*** 33, 34, 37, 38, 38T, **59**, 60T, 90, 91

*edaphicus*, *Clavoplites* 8
*Edaphospathula brachycaryon* 7, 238, 242
*Edaphospathula fusioplites* 5, 224, 227, 228, 276
*Edaphospathula gracilis* 7, 238, 242
*Edaphospathula inermis* 8
*Edaphospathula paradoxa* 5, 8, 250
*elegans*, *Ilsiella* 9
*elmenteitanum*, *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*, *Semispathidium*** 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
***Epispathidium*** xv, 26, 27, 28, 34, 89, 91, 97, 141, **142**, 224, 290, 336, 367, 368, 369, 372, 374, 385, 395, 401, 423
***Epispathidium amphoriforme*** 141, 142, 143K, 145, 158, 160, 164, **197**, 200T, 211, 368, 372, 385
*Epispathidium amphoriforme amphoriforme* 162
*Epispathidium amphoriforme rectitoratum* 198
*Epispathidium amphoriforme securiforme* 154, 160
***Epispathidium 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*, R*ostrophryides africana* 9
*Etoschophrya oscillatoriophaga* 9
*extensum*, *Spathidium* 35

*falciforme*, *Spathidium* 230, 233
*fastigata*, *Colpoda* 207
***faurefremieti***, ***Spathidium*** 33, 41, **86**, 87T, 337, 358
***faurei*, *Centrospathidium*** 127, 128, 128K, 134, **136**
*faurei*, *Spathidium* 86, 136
*fenestrate*, *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 wolfi*** 33, 34, **85**
gymnostomatid 368
gymnostomes 324

*halophila*, *Parakahliella* 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
*holsatiae*, *Spathidium* 414
*Homalozoon* 359, 360
*Homalozoon vermiculare* 359, 360

*horribile*, *Colpodidium Colpodidium* 8
*hyalinum*, *Spathidium* 3, 28, 38, 160
hypotrichs 83

*Ilsiella 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 loyezae* 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
*lieberkühnii*, *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*, *Wolfkosia* 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*, C*olpodidium 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
*muscicola*, *Protospathidium* 5, 12, 326
*muscicola*, *Spathidium* 41, 61, 196, 197, 443
*muscorum rhopaloplites*, *Arcuospathidium* 6
*muscorum*, *Levispatha* 43, 47, 58
*Myriokaryon* 337, 360, 361
*Myriokaryon lieberkuehnii* 358, 360, 362
Myriokaryonidae 337, 368

*namibicola*, *Protospathidium* 354
*namibicola*, *Spathidium* 346
*namibiense*, *Arcuospathidium* 11, 12, 214, 233, 235, 258, 266
*namibiensis costaricensis*, *Maryna* 9
*namibiensis maldivensis*, *Rostrophrya* 9
*namibiensis namibiensis*, *Maryna* 9
*namibiensis namibiensis*, *Rostrophrya* 14
*namibiensis*, *Kuehneltiella* 9
*namibiensis*, *Maryna namibiensis* 9
*namibiensis*, *Metacineta* 8
*namibiensis*, *Plagiocampa* 9
*namibiensis*, *Rostrophrya namibiensis* 14
*Nassula* 357
*Nassula dragescoi* 8
*Nassula etoschensis* 8
*Nassula granata* 8, 353
*Nassula tuberculata* 14
***Neocultellothrix*** xiii, xv, 213, 214, 241, 433, **434**, 436K
***Neocultellothrix atypica*** 18, 117, 241, 242, 243, 433, 435, 436K, **439**
***Neocultellothrix coemeterii*** 3, 433, 435, 436K, **443**
***Neocultellothrix japonica*** 433, 435, 436K, **445**
***Neocultellothrix lionotiformis*** 289, 433, 435, 436K, 445, **446**
***Neocultellothrix paucistriata*** 433, 435, 436K, **448**
***Neocultellothrix tortisticha*** 245, 433, 435, 436K, **449**

***Neocultellothrix velhoi*** 18, 87, 289, 433, 435, 436K, **436**
***Neospathidium*** xv, 149, 367, 368, 369K, **400**, 400K
***Neospathidium africanum*** 367, 395, 400, 400K, 401, **418**, 427T
***Neospathidium brachystichos*** 265, 266, 267, 400, 401K, 401, 422, **424**, 427T
***Neospathidium longinucleatum*** 129, 134, 367, 400, 400K, **401**, 413T, 422

*obliquum*, *Apocyclidium* 4
*obovate*, *Frontonia angusta* 9
*oscillatoriophaga*, *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
*Parakahliella binucleate 14*
*Parakahliella halophila* 9
*paucistriata*, *Cultellothrix* 7, 435, 448
***paucistriata***, ***Neocultellothrix*** 433, 435, 436K, **448**
*pelobia*, *Apertospathula* 6
*pelobium*, *Arcuospathidium* 6
*pentadactyla*, *Plagiocampa* 9
*periarmata*, *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 lieberkühnii* 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
Protospathiidiidae 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*, *Tetrahymena* 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 fenestrate* 14
*Rostrophrya namibiensis maldivensis* 9
*Rostrophrya namibiensis namibiensis* 14
R*ostrophryides 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 macrothrix*** 257, 258, 258K, **258**, 268T, 272, 275, 425
***securiforme***, ***Epispathidium*** 141, 142, 143, 143K, **154**, 154T, 200T, 201, 372
*securiforme*, *Epispathidium amphoriforme* 154, 160
*securiforme*, *Spathidium* 155, 158
*securiforme*, *Spathidium amphoriforme* 142, 154, 155, 157, 158, 160, 62, 200T, 201, 380
***Semibryophyllum*** xv, 28, 258, **281**, 285K
***Semibryophyllum cultellum*** 281, 282T, 283, 285K, **285**, 291, 293, 303, 306
***Semibryophyllum foliosum*** 281, 283T, 283, 285, 285K, 291, **303**
***Semibryophyllum palustre*** 281, 282T, 283, 285, 285K, **291**, 306, 308
*Semiplatyophrya acrostoma* 9
***Semispathidium*** xv, 28, 143, 207, 311, **312**, 315K
***Semispathidium armatum*** 311, 312, 313T, 315K, 315, **320**, 328
***Semispathidium breviarmatum*** 311, 312, 315K, **325**, 328
***Semispathidium enchelyodontides*** 311, 312, 313T, 315K, **315**, 320, 322, 328
***Semispathidium fraterculum*** 311, 312, 315K,

328, **329**, 330
***Semispathidium lagyniforme*** 311, 312, 313T, 315K, 315, 320, **322**, 328
***Semispathidium longiarmatum*** 311, 312, 315K, **326**, 329, 330
***Semispathidium pulchrum*** 311, 312, 315K, 328, 329, **330**
*Semispathidium* sp. 326
*seppelti etoschense*, *Spathidium* 149, 423
*seppelti seppelti*, *Spathidium* 423
*seppelti*, *Spathidium* 395, 423
*seppelti*, *Spathidium seppelti* 423
*serpens*, *Protospathidium* 12, 250
*serpens*, *Spinispatha* 250
*serranoi*, *Phialina* 1, 15
***simile***, ***Latispathidium*** 213, 214, 215K, 232, **238**, 244T, 443
*similis*, *Apertospathula* 6
***simplinucleatum***, ***Pharyngospathidium*** 367, 369, 369K, 391, **399**, 401, 403, 425
*simplinucleatum*, *Spathidium* 369, 399
*simplinucleatum*, *Spathidium bavariense* 398, 399
sp., *Epispathidium* 211
sp., *Pseudocohnilembus* 270
sp., *Semispathidium* 326
sp., *Spathidium* 221, 423
*Spathidia* 29
spathidiid(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 faurefremieti*** 33, 41, **86**, 87T, 337, 358
*Spathidium faurei* 86, 136
*Spathidium gigas* 336, 361, 362
*Spathidium gigas*, *Pseudoprorodon* 361, 362
*Spathidium holsatiae* 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 wolfi*** 33, **85**, 87T
***Spathidium wolfi* 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
*thecatum*, *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*, *Condylostomides* 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
*virungense*, *Arcuospathidium* 7
*vlassaki*, *Arcuospathidium* 214
*Vorticella astyliformis* 103

***wolfi* group**, ***Spathidium*** 33, 34, **85**
***wolfi***, ***Spathidium*** 33, **85**, 87T
*Wolfkosia loeffleri* 9

## Table index

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