

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

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Edited by

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

In memory of Wilhelm Foissner (1948–2020)

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Preface, authorship, acknowledgements, and funding

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

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

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

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

Salzburg
January 2025

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Abstract

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

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

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

Chapter 2

Spathidiida Foissner & Foissner, 1988 (Ciliophora, Litostomatea, Haptoria): a brief introduction¹

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Abstract

The taxon Spathidiida Foissner & Foissner, 1988 is a rather large group of haptorids originally characterised as follows: “Cytostome apical, round or slit-like, in suborder Didiniina on top of cone-like proboscis; rhabdos made of three microtubular components: transverse ribbons originating from the nonciliated kinetosomes of the oral dikinetids, nematodesmal bundles originating exclusively from the same source, and bulge microtubules; somatic ciliation uniform or limited to dense bands which, however, rest within longitudinally running kineties composed of nonciliated kinetids; dorsal brush composed of 2 to many kineties; toxicysts localized, typically in or near oral area; free-living.” According to the most recent revision by Foissner & Xu (2007), the following families are assigned: Spathidiidae Kahl in Doflein & Reichenow, 1929; Apertospathulidae Foissner, Xu & Kreutz, 2005; Arcuospathidiidae Foissner & Xu, 2007; Pharyngospathidiidae nov. fam.; Protospathidiidae Foissner & Xu, 2007. In the present chapter a very brief overview about the spathidiids is given. The other chapters of this book deal with the genera of the family Spathidiidae Kahl in Doflein & Reichenow, 1929 (9 genera; Chapters 3–11) and with the new family Pharyngospathidiidae nov. fam. (2 genera; Chapter 12). The very large genus *Spathidium* Dujardin, 1841 is only briefly reviewed and only 15 species are described in detail (Chapter 3).

¹ This chapter should be referenced as follows: Berger H., Xu K. & Foissner W. (2025): Spathidiida Foissner & Foissner, 1988 (Ciliophora, Litostomatea, Haptoria): a brief introduction. – Ser. Monogr. Cilioph. 6: 25–32. For notes on “Material and methods”, see Chapter 1 (Berger et al. 2025).

Spathidiida Foissner & Foissner, 1988²

1988 **Spathidiida nov. ord.** – Foissner & Foissner, Arch. Protistenk. 135: 229 (original description; see nomenclature).

Nomenclature: Foissner & Foissner (1988) established this order after Jankowski (1980, p. 104) has characterized the new suborder Spathidiina. Article 36 of the ICZN (1985), the relevant code for Foissner & Foissner (1988), deals with the principle of coordination of family names. According to Article 36(a), “A name established for a taxon at any rank in the family group is deemed to be simultaneously established with the same author and date for taxa based upon the same name-bearing type (type genus) at other ranks in the family group, with appropriate mandatory change of suffix.” Since the ICZN does not deal with ranks above the family (ICZN 1985, Article 1(b)(4)), the principle of coordination does not have to be applied to higher ranks, e.g., orders. Thus, we preliminary accept Foissner & Foissner (1988) as authors of the “order Spathidiida”. However, there is no doubt that it would be wise to apply the principle of coordination for all ranks.

Diagnosis (from Foissner & Foissner 1988): Cytostome apical, round or slit-like, in suborder Didiniina on top of cone-like proboscis; rhabdos made of three microtubular components: transverse ribbons originating from the nonciliated kinetosomes of the oral dikinetids, nematodesmal bundles originating exclusively from the same source, and bulge microtubules; somatic ciliation uniform or limited to dense bands which, however, rest within longitudinally running kineties composed of nonciliated kinetids; dorsal brush composed of 2 to many kineties; toxicysts localized, typically in or near oral area; free-living.

Remarks: This chapter shall only serve as very brief overview about the history of this higher taxon. Foissner & Foissner (1988) included three suborders in this taxon (see below), while it is listed as synonym (pro parte) of the Haptoria Corliss, 1974 in the revision by Lynn (2008, p. 367). Vďačný et al. (2014), Rajter & Vďačný (2016), and Barmshuri et al. (2023) discussed that the phylogeny of this group is difficult to follow. Rajter & Vďačný (2016, p. 220) concluded that “Due to the lack of morphological synapomorphies for molecular clades, we recommend to keep the existing morphology-based generic classification of spathidiids proposed by Foissner (1984) and Foissner & Xu (2007), but stress that *Spathidium*, *Epispathidium* and *Arcuospathidium* are artificial collective groups.” Thus, much more detailed research on spathidiid species is needed to get a better insight into the phylogenetic relationships of this large taxon. The description of several new species in the present book shows that a large amount of the spathidiid diversity is still unknown. The book should be a stimulus for other researchers to re-study known species more detailed, including molecular features. In addition, further new regions in all continents should be investigated to get a better overview about the true diversity of this group of ciliates.

Foissner & Foissner (1988, p. 230) provided the following characterization for the “suborder Spathidiina Jankowski, 1980”: “Cytostome apical, round, oval or slit-like, in some genera covering the “ventral” body margin; somatic ciliation usually uniform.”

Suborders originally included: Spathidiina Jankowski, 1980 (nominotypical suborder); Belonophryina Jankowski, 1980; Didiniina Jankowski, 1978.

² The chapters Spathidiida and Spathidiidae were not included in the raw manuscript by W. Foissner. They have been written by H. Berger and provide only a brief overview, mainly about the history of these higher taxa.

Families included by Foissner & Xu (2007, p. 56): Spathidiidae Kahl in Doflein & Reichenow, 1929; Apertospathulidae Foissner, Xu & Kreutz, 2005; Arcuospathidiidae Foissner & Xu, 2007; Pharyngospathidiidae nov. fam.; Protospathidiidae Foissner & Xu, 2007.

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

(from Foissner & Xu 2007, p. 56)

A simple key to the taxa of the *Spathidiida* is impossible, that is, proper classification needs protargol preparations. See Figures 1, 4–12 in Foissner & Xu (2007) for an explanation of the features used. For a key to 57 well described and most common spathidiid species, see Hlúbíková & Tirjaková (2002).

- 1 Cytopharynx permanent, appearing as a comparatively distinct opening in the centre of the oral bulge in vivo and in preparations Pharyngospathidiidae (p. 367)
 - Cytopharynx temporary, usually not recognizable in vivo; appears as a minute, fibrillar, obconical depression near dorsal bulge end in protargol preparations 2
- 2 Circumoral kinetofragments separated from each other by minute gaps 1–3 dikinetids wide (*Protospathidium* pattern). Most species small and/or narrow with oral bulge shorter than widest trunk region Protospathidiidae (Foissner & Xu 2007, p. 57)
 - Circumoral kinetofragments arranged to a continuous circumoral kinety. Most species of ordinary to huge size with oral bulge at least as long as widest trunk region 3
- 3 Ciliary rows separated from circumoral kinety and curved dorsally on both sides of the body Arcuospathidiidae (Foissner & Xu 2007, p. 155)
 - Ciliary rows connected with circumoral kinety (*Spathidium* pattern) or their anterior ends so strongly curved that the circumoral kinety is seemingly doubled (*Epispathidium* pattern). Circumoral kinety closed or open ventrally 4
- 4 Circumoral kinety open. Ciliary pattern often not unequivocally determinable Apertospathulidae (Foissner & Xu 2007, p. 330)
 - Circumoral kinety closed. *Spathidium* or *Epispathidium* ciliary pattern Spathidiidae (p. 27, in part)

Spathidiidae Kahl in Doflein & Reichenow, 1929

1929 **Spathidiidae Kahl** – Doflein & Reichenow, Lehrbuch der Protozoenkunde, p. 1171 (original description; see nomenclature).

1930 **Spathidiidae fam. n.³** – Kahl, Arch. Protistenk. 18: 349 (establishment as new family; see nomenclature).

1930 **Spathidiidae Kahl, 1930** – Kahl, Tierwelt Dtl. 18: 148 (revision of ciliates; 11 genera assigned).

1943 **Spathidiidae Kahl⁴** – Kahl, Infusorien, p. 24 (revision of ciliates).

³ Kahl (1930a) provided the following diagnosis: “Prostome Holophryidae mit spaltigem Munde, der sich auf dem mehr oder weniger ventralwärts abfallenden und mehr oder weniger lateral zusammengedrückten Vorderpol entlang zieht; er ist auf beiden Seiten von einem unbewimperten, mit Trichocysten bewehrten Wulste begleitet, der fast stets eng zusammengedrückt ist und den Schlundeingang nur als schmale, seichte Furche erkennen läßt. Stets ist eine dreireihige, meist kurze Dorsalbürste vorhanden.”

⁴ Kahl (1943) provided the following diagnosis: “Prostome Arten, deren Schlundwandung vorn vorgewölbt ist und einen unbewimperten, mit Toxizysten bewehrten Wulst bildet. Fast alle Arten der Familie ernähren sich räuberisch.”

- 1979 **Spathidiidae** Kahl in Doflein & Reichenow, 1929⁵ – Corliss, Ciliated protozoa, p. 216 (familial revision of ciliates; 16 genera included, one as incertae sedis).
 2007 **Spathidiidae** Kahl, 1929 – Jankowski, Phylum Ciliophora, p. 563 (generic revision of ciliates; 20 genera included).
 2008 **Spathidiidae** Kahl in Doflein & Reichenow, 1929⁶ – Lynn, Ciliated protozoa, p. 369 (familial revision of ciliates; 30 genera assigned, three genera as incertae sedis).

Nomenclature: The name Spathidiidae was first published in Doflein & Reichenow (1929). Since they wrote “Spathidiidae Kahl” it is clear that A. Kahl provided them his data. Shortly after, Kahl (1930a) formally established this family (see list above). However, since the publication in Doflein & Reichenow (1929) is accompanied by a characterization, this work is the original description.

Diagnosis: Spathidiida with closed circumoral kinety. *Spathidium* or *Epispathidium* ciliary pattern.⁷

Type genus: *Spathidium* Dujardin, 1841.

Genera originally assigned: *Spathidium* Dujardin, 1841 (name-bearing type genus); *Legendrea* Fauré-Fremiet, 1908.

Genera treated in present book: *Spathidium* Dujardin, 1841 (name-bearing type genus, only few species reviewed); *Apospathidium* Foissner et al., 2002; *Centrospathidium* nov. gen.; *Epispathidium* Foissner, 1984; *Latispathidium* Foissner et al., 2005b; *Schmidingerophrya* nov. gen.; *Semibryophyllum* nov. gen.; *Semispathidium* Foissner et al., 2002; *Supraspathidium* Foissner & Didier, 1981.

Remarks: The list of synonyms is likely not complete. Alfred Kahl established this family, comprising only two genera, namely *Spathidium* and *Legendrea*, in the monumental work by Doflein & Reichenow (1929). The classification of *Legendrea* in the spathidiids, accepted by Corliss (1979) and Jankowski (2007), was recently supported by molecular data (Pomahač et al. 2023, Weiss et al. 2022; see also Barmshuri et al. 2023, p. 8/13). By contrast, Lynn (2008, p. 367) classified *Legendrea* in the Actinobolinidae Kent, 1881 (p. 630; original spelling Actinobolidae; emended by Kahl 1930b, p. 138).

Spathidium Dujardin, 1841

- 1841 *Spathidium*⁸ – Dujardin, Zoophytes, p. 457 (original description; see nomenclature). Type species (by monotypy): *Spathidium hyalinum* Dujardin, 1841.
 1889 *Spathidium* Dujard. 1841 – Bütschli, Protozoa, p. 1680 (revision; estimated that two or three species belong to this genus).

⁵ Corliss (1979) provided the following characterization: “Cytostome slit-like, generally located apically on nonciliated ridge of body, facilitating ingestion of large prey; body often flask- or sack-shaped, flattened, with truncate anterior end.”

⁶ According to Lynn (2008, p. 370), the main features of the Spathidiidae are: “...; circumoral dikinetids as proliferated anterior fragments of somatic kineties, which may exceed the number of somatic kineties, and which may remain as separated groups after stomatogenesis; ...”

⁷ Note by H. Berger: I did not find a recent, published diagnosis of the Spathidiidae. The diagnosis presented above is from the key in Foissner & Xu (2007, p. 56; see also above).

⁸ Dujardin (1841) provided the following diagnosis: “An. à corps oblong, plus épais et arrondi en arrière; plus mince, élargi et tronqué obliquement en avant.”

- 1930 *Spathidium* Dujardin, 1841 – Kahl, Tierwelt Dtl. 18: 149 (detailed revision of ciliates).
1979 *Spathidium* Dujardin, 1841 – Corliss, Ciliated protozoa, p. 216 (familial revision of ciliates).
1984 *Spathidium* Dujardin, 1841⁹ – Foissner, Stapfia 12: 70 (detailed description of several spathidiids).
2007 *Spathidium* Dujardin, 1841 – Jankowski, Phylum Ciliophora, p. 564 (generic revision of ciliates).
2008 *Spathidium* Dujardin, 1841 – Lynn, Ciliated protozoa, p. 370 (familial revision of ciliates).

Nomenclature: The genus-group name *Spathidium* is obviously a composite of the Greek noun *he spathe* (spatula, sabre, sword; Hentschel & Wagner 1996, p. 551) and the Greek suffix *-idium* (used for genus-group names of small animals; Werner 1972, p. 47), obviously meaning (shaped like) a small spatula (see also Foissner & Xu 2007, p. 92). The name *Spathidia* was first mentioned by Dujardin (1840, p. 285), however, without description. Note that *Spathidium* Dujardin, 1841 is the senior homonym of *Spathidium* Looss, 1899 (p. 605), a trematode. *Spathidium* is of neuter gender (Aescht 2001, p. 300).

Diagnosis (from Foissner 1984, translated): Spathidiidae whose circumoral kinety are not or only indistinctly separated from somatic kineties. Anterior ends of somatic kineties with normal or slightly condensed ciliature, on left side slightly pointing ventrally, on right side clearly pointing dorsally. Oral bulge in top view very differently shaped (elliptical, dumb-bell-shaped, orthogonal, wedge-shaped), distinctly set off from body proper, little to strongly slanted to ventral side. Row 3 of dorsal brush not shortened to significantly shortened.

Remarks: The brief introduction on the genus *Spathidium* is incomplete and serves, like the brief reviews on the higher taxa Spathidiida (p. 26) and Spathidiidae (p. 27), only as brief overview about the history of this rather old and species-rich genus. The list of synonyms comprises only few entries. A detailed revision of this genus is urgently needed.

For description/redescription of some *Spathidium* species, see Chapter 3, that is, Foissner et al. (2025).

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⁹ Foissner et al. (1984) provided the following diagnosis: “Spathidiidae, deren circumorale Kinete von den Somakineten nicht oder nur undeutlich getrennt ist. Anteriore Enden der Somakineten mit normaler oder leicht verdichteter Ciliatur, weisen links leicht nach ventral, rechts deutlich nach dorsal. Mundwulst in Aufsicht sehr unterschiedlich geformt (ellipsoid, hantelförmig, orthogonal, keilförmig), deutlich vom Körper abgesetzt, wenig bis stark nach ventral geneigt. Reihe 3 der Bürste nicht bis deutlich verkürzt.” (For translation, see above).

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Index

Systematic index

The index contains all ciliate names mentioned in the book, including vernacular names for example, haptorids. Designations as, for example, “haptorid ciliates” are mentioned under the corresponding vernacular name, that is, “haptorids” in present example. Names in singular (e.g., haptorid) are mentioned under the plural version (e.g., haptorids). The index is two-sided, that is, species appear both with the genus-group name first (for example, *Apospathidium atypicum*) and with the species-group name first (*atypicum*, *Apospathidium*). Valid (mainly in W. Foissner’s judgement) species and genera treated in detail are in boldface italics print. Valid taxa not treated in detail in the present book, invalid taxa, junior homonyms, synonyms, outdated combinations, incorrect spellings, and nomina nuda are not in bold. Suprageneric taxa are represented in normal type, valid ones treated in detail in the present work in boldface. A boldface page number indicates the beginning of the description of a valid taxon. “T” indicates the location of the table with the morphometric characterisation; “K” marks a key (e.g., of the genus *Apospathidium*) and the page where a taxon is mentioned in a key. The names on the slide figures and the names of the subchapter “Summary of nomenclatural acts and taxa described in Chapters 1–13” (see Chapter 1, pp. 18–20) are not included.

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