SYNOPTIC CHECKLIST AND BIBLIOGRAPHY
OF THE XENOPHYOPHOREA (PROTISTA), WITH A
ZOOGEOGRAPHICAL SURVEY OF THE GROUP

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ABSTRACT
A list of all described xenophyophore taxa is given, with citation of each original description, type material information, and all significant subsequent references. The development in knowledge of the general distribution of the group is described in some detail. Important areas of contemporary ecological work are pointed out.

INTRODUCTION
Recognition of the xenophyophores as a well defined group at a high taxonomic level within the rhizopods dates back to Schulze's report (1907a) on the material from the Valdivia Expedition. The basis of the classification still in use was, however, created by Haeckel 1889, who treated the large Challenger Expedition (1972-76) collection. He believed he had discovered a new group of horny sponges living in the deep sea in symbiosis with hydroids. The "Deep-Sea Keratosa" turned out to be a compositum mixtum of agglutinating foraminifers, sponges with a sand skeleton, and the new protozoan group which Schulze (1904) named Xenophyphora. Schulze's redescription of the group and his addition of a number of new species (1906, 1907a,b) exited some interest during the
next few years. However, after 1907 only Neviani (1909) assigned one new species to the group, which after a while seems largely to have lost the interest of zoologists. This happened despite the fact that both the “Deep-Sea Keratosa” and the xenophyophores were included in some of the important handbooks of the period (Delage & Hérouard 1899, Minchin 1900, 1912, Lister 1909, Rhumbler 1923, Dolfini & Reichenow 1952, Loeblich & Tappan 1964). The early history of the study of xenophyophores has been treated in detail by Tendal (1972).

The Danish Galathea Expedition 1950-52 brought back a great and very varied collection of xenophyophores, most of which, when first sorted out, were considered sponges. This material, together with the collections described by Haeckel and Schulze from the Challenger, Valdivia, and Siboga Expeditions, numerous undescribed samples from many Vitiaz Expeditions, as well as single samples from a number of other expeditions, formed the basis of a revision and extension of the group (Tendal 1972). The appearance of this monograph in the Galathea Report made colleagues working in the deep sea aware of the existence of the group; it was, so to speak, revived. This, and not least the introduction in deep-sea work of new investigation methods, allowed numerous xenophyophore specimens to be recognized during the following decades, in samples from all over the world. New species were described, and much information on zoogeography and ecology was gathered.


The aim of the present survey is to facilitate further advances in our knowledge of this intriguing group, which among its friends is nicknamed “xe-nos”. An attempt is made here to list all described species, with the information legalizing them according to the “International Code of Zoological Nomenclature”, to bring together in one place the varied literature which has appeared on the xenophyophores during the last 25 years, and to summarize the knowledge of the zoogeography of the higher taxa.

SCOPE AND ARRANGEMENT OF THE LIST

The higher classification of Protista is still debated, and the xenophyophores as a group has at different times been placed at all levels from family to phylum, and even been given up as “Incerta sedis” (Corliss 1984, 1994, Levine et al. 1980, Lister 1909, Margulis et al. 1989, 1993, Poche 1913, Schulze 1907a, 1912, Tendal 1972). The group is here considered a class in that wider context of taxa which form rhizopodean granuloreticulate pseudopodia. A discussion of this problem as well as a reevaluation of some of the xenophyophore taxa is currently in progress and will appear elsewhere.

The classificatory arrangement follows Gooday & Tendal (in press) for orders, families, and genera. In principle, an effort is made to give all known references to individual species and genera. However, a certain restriction to include only those publications where some kind of new information is provided or where the taxon in question is brought into a context that might shed new light on its classification or life circumstances, has been considered reasonable.

For each taxon the original bibliographic citation and subsequent citations is given. Citations are in chronological order, except where subsequent references to a given author are listed just after the earliest one. For genera, synonyms and the type species are given. For species: synonyms, previous generic placements, holo-, lecto- or syntype location, type locality (most often as a station number that can be found in relevant reports), and published figures showing the type specimen. Within each genus the species are placed in alphabetical order. A key to orders, families and genera is found in Gooday & Tendal (in press).
Abbreviations used

BMNH The British Museum (Natural History), London, England (see also NHM)

IOAN P.P. Shirshov Institute of Oceanology, Moscow, Russia

MNHN Muséum national d’Histoire naturelle, Paris, France

NHRM Naturhistoriska Riksmuseet, Stockholm, Sweden

NHM Natural History Museum, London, England (formerly BMNH)

NZOI New Zealand Oceanographic Institute, Wellington, New Zealand

SMF Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt-am-Main, Germany

ZIL Zoological Institute, Academy of Sciences, St. Petersburg (Leningrad), Russia

ZMA Zoological Museum, University of Amsterdam, Amsterdam, The Netherlands

ZMB Museum für Naturkunde an der Universität Humboldt zu Berlin, Berlin, Germany

ZMUC Zoological Museum, University of Copenhagen, Copenhagen, Denmark

SYSTEMATIC LIST

Class XENOPHYOPHOREA Schulze, 1904

Order PSAMMINIDA Tendal, 1972

Family PSAMMETTIDAE Tendal, 1972

Genus Psammetta Schulze, 1906

Psammetta arenocentrum Tendal, 1972

Tendal 1972: 24-25, pl. 2C-E; 15, 21, 26, 76, 77, 81, 82, 86, 87; Gooday et al. 1993: 2141.

Holotype: ZMUC reg. no. PRO-1. “Galathea” St. 233. Figured in Tendal 1972, pl. 2C-D.

Psammetta erythrocytomorpha Schulze, 1907


Type species: P. globosa Schulze, 1906.

Psammetta globosa Schulze, 1906


type material: ZMA. “Siboga” St. 211. Figured in Schepotieff (1912, pl. 15, fig. 1).

Remarks: DeLaca (1982, 1985) briefly mentioned the species as having been taken in Explorers Cove, McMurdo Sound, Antarctica. According to Gooday et al. (1996, p. 243) it is not a xenophyophore.

Psammetta ovale Tendal, 1972

Tendal 1972: 25-26, fig. 1; 14, 21, 24, 66, 69, 70, 71, 76, 79, 81, 82; Schepotieff 1912: 246, 247-258, 259, 260, 262, 263, 264, 273 (as P. globosa).

Holotype: The material is unaccounted for. Sri Lanka. Pictured in Schepotieff (1912, pl. 15, fig. 1).
Remarks: Schulze (1912, p.39) pointed out that material referred to *Psammetta globosa* by Schepotieff (1912, p.247 ff.) probably represented another, new species. Not being able to locate and reinvestigate the original material, Tendal (1972, p. 25) named and diagnosed *P. ovale* on the basis of Schepotieff’s description and figures.

The existence of the species, however, can be doubted. Schepotieff (1912, p. 246) claimed to have found 2 species of xenophyophores in shallow water on a sandy bottom off Kankesanturai (1-5 m depth), Sri Lanka, and one species on corals off Mahé (about 20 m depth), India. He even claimed to have kept specimens alive for some time in aquaria (l.c., p. 263). It was a surprisingly shallow record since, at that time, xenophyophores had not been taken shallower than 981 m (Schulze 1907b). Also, with today’s knowledge of the bathymetry of xenophyophores – the shallowest record is about 500 m (Tendal 1981) – and the zonation of deep-sea faunas, the record is astonishing.

Schepotieff (l.c., p. 246) stated that he borrowed specimens and preparations from Schulze for comparison. Knowing what material Schulze had at hand, it is my guess that in 1909 Schepotieff can only have seen fragments of *Psammetta globosa* Schulze, 1906, *Cerelasma gyrosphaera* Haeckel, 1889 and *Stannophyllum zonarium* Haeckel, 1889, and these are the three species he claims to have found. His descriptions are in numerous details different from Schulze’s, in some cases unlikely, in others so overdetailed that they are hard to believe. Most figures are very schematic and presented in a most confusing way. Moreover, several dimensions must be given wrongly.

I am inclined to believe that Schepotieff may have used specimens and fragments borrowed from Schulze as a basis for fabricating descriptions, or as support when looking at something else he brought home for example poorly preserved sponges, ascidians, or bryozoans. My mistrust should be seen in the light of a forgery Schepotieff made concerning the description of a new group of Protura (Insecta), which he claimed to have collected during the very same expedition to India in 1908 (Rimsky-Korsakov 1911, p. 165, Tuxen 1931, p. 673). It has not been possible to locate Schepotieff’s material (Dr. V.M. Koltun, St. Petersburg, pers. comm.)

**Genus Homogammina** Gooday & Tendal, 1988


**Homogammina crassa** Gooday, 1991


**Homogammina lamina** Gooday & Tendal, 1988


**Homogammina maculosa**

Gooday & Tendal, 1988


Holotype: BMNH reg. no. 1979:10:15:17. “Discovery” St. 9131. Figured in Gooday & Tendal 1988, fig. 2A.

**Homogammina sp. A**


Remarks: Gooday avoided naming the taxon on the basis of the two specimens taken at abyssal localities not far from each other. Since granellare was not observed, and stercomare only with uncertainty in one case, both specimens may have been dead at the time of sampling.

**Genus Maudammina** Tendal, 1972

Tendal 1972: 21; 19, 25, 27, 67, 68, 72, 74, 75, 76,
Type species: *M. arenaria* Tendal, 1972.

**Maudammina arenaria** Tendal, 1972

Tendal 1972: 22, pl. 1A-C; 15, 21, 66, 67, 68, 72, 76, 81, 82, 87.

Holotype: ZMUC reg. no. PRO-2. “Galathea” St. 200. Figured in Tendal 1972, pl. 1A.

**Family** PSAMMINIDAE Haeckel, 1889

**Genus** Psammina Haeckel, 1889


**Psammoplakina** Haeckel 1889, p. 35.

**Astrorhizinella** Saidova 1970, p. 146.

Type species: *P. nummulina* Haeckel, 1889

Remarks: *Psammoplakina* is discussed by Tendal (1972, p. 33). *Astrorhizinella* was at the time of its erection placed in the foraminiferal family Schizamminidae Nervag, 1961 (Saidova 1970, p. 147; translation 1972, p. 156), later in a family and superfamiily of its own (Saidova 1981, p. 12). Loeblich & Tappan (1988, p. 695) considered it of uncertain status, “not recognizable”. A reinvestigation has confirmed the suspicion, that the organism in question is a xenophyphore (Dr. O.E. Kamenskaya. pers. comm., 1993). Because the short description and the figure of *A. planata* both fit the diagnosis of *Psammina*, the two genera are here synonymized.

**Psammina delicata** Gooday & Tendal, 1988


Holotype: BMNH reg. no. 1979:10:15:5. “Discovery” St. 9132. Figured in Gooday & Tendal 1988, fig. 6A.

**Psammina fusca** Gooday & Tendal, 1988


Holotype: BMNH reg. no. 1979:10:15:18. “Discovery” St. 8540. Figures in Gooday & Tendal 1988, fig. 6D.

**Psammina globigerina** Haeckel, 1889


Lectotype: BMNH reg. no. 1889:12:3:1. “Challenger” St. 220. Designated here; figured by Haeckel 1889, pl. VII, figs. 2A-B.

**Psammina nummulina** Haeckel, 1889


Type material: Unaccounted for. “Challenger” St. 274.

**Psammina placina** Haeckel, 1889

Haeckel 1889: 35-36, pl. VII 1A-D; 9, 34, 37; Schulze 1906: 14; 1907a: 20, 48, 49, 50, 51, 53, 54; 1907b: 160, 161; Schepotieff 1912: 273; Lau-
benfels 1948: 184; Tendal 1972: 13, 27, 32, 33-34, 82, 83, fig. 2; 1994: 52. 
Psammoplaikina discoidea Haeckel, 1889: 35.

Type material: Unaccounted for. “Challenger” St. 331. Figured in Haeckel 1889, pl. VII 1A-B.

Psammina planata (Saidova, 1970)


Remarks: The species is here transferred to Psammina; it seems from the original description that it has great resemblance to P. nummulina.

Psammina sabulosa Gooday & Tendal, 1988

Holotype: BMNH reg. no. 1979:10:15:1. “Discovery” St. 9128. Figured in Gooday & Tendal 1988, fig. 7B-C.

Psammina zonaria Tendal, 1994
Tendal 1994: 50-51, fig. 1A-B; 52, 53.

Holotype: MNHN reg. no. 489 UV. MUSOR-STOM 7, St. DW 620. Figured in Tendal 1994, fig. 1A.

Psammina sp. A

Genus Semipsammina Tendal, 1975
Tendal 1975b: 46; Mullineaux 1987: 175.

Type species: S. fixa Tendal, 1975 (by monotypy).

Semipsammina fixa Tendal, 1975
Tendal 1975b: 47, figs. 1-2; Wolff 1976: 163, fig. 1b; 1979: 119, 120; 1980: 201, 202, fig. 1c.


Genus Cerelpemma Laubenfels, 1936
Laubenfels 1936: 33; Tendal 1972: 19, 27, 34, 84, 85, 86.

Type species: C. radiolarium (Haeckel, 1889)

Cerelpemma radiolarium (Haeckel, 1889)

Lectotype: BMNH reg. no. 1889:12:3:3. “Challenger” St. 272. Designated here; figured in Tendal 1972, pl. 5B.

Remarks: The species is so poorly known that it is not absolutely certain that it is a xenophyophore, although by analogy it seems reasonable.

Genus Galatheammina Tendal, 1972

Type species: G. tetraedra Tendal, 1972.

Genus Galatheammina calcarea (Haeckel, 1889)
Haeckel 1889: 41-42 , pl. VII 5 (Psammopemma calcarea); 9; Schulze 1907a: 28, 48, 49, 50, 51, 53, 54; 1907b: 160, 162 (Psammopemma calcare-
um); Schepotieff 1912: 271, 273 (Psammopemma calcareum); Laubenfels 1936: 33; 1948: 184 (Cerelopemma calcareum); Tendal 1972: 13, 15, 27, 28-29, 34, 66, 67, 69, 72, 76, 81, 82, 83, 84, 87, 88, pl. 3C-D; 1979: 15.

Type material: Unaccounted for. “Challenger” St. 89. Figured in Haeckel 1889, pl. VII 5.

Remarks: Haeckel (1889, p. 42) referred “similar pieces” from other “Challenger” stations in the Indian and the Pacific Oceans to the species, and Tendal (1972) accepted this. The material is unaccounted for or in very bad state, and caution is necessary since the study of material taken by later expeditions has resulted in the use of more subtle species characters than before (Gooday 1991, Gooday & Tendal 1988).

Schulze (1907a, p. 28) mentioned two label names, Psammopemma plakinoides and Psammopemma globigerinum, on material probably belonging to this species. The names may have been invented by Haeckel, but were never used in print. According to Schulze (l.c.) little more could be said than both fragments were xenophyophores.

**Galatheammina discoveryi**

*Gooday & Tendal, 1988*


Holotype: BMNH reg. no. 1979: 10:15:11. “Discovery” St. 9132. Figured in Gooday & Tendal 1988, fig. 3A-B.

**Galatheammina erecta**

*Gooday, 1991*

Gooday 1991: 204-206, figs. 3A-D, 4A-B, pl. V 1-5; 210, 211; 1996: 193, 196, 206, pl. 2 1-6, pl. 3 1-4.

Holotype: SMF reg. no. 1090. “Meteor” St. 233. Figured in Gooday 1991, fig. 3B.

**Galatheammina irregularis**

*Gooday, 1991*

Gooday 1991:202-204 (204: G. lamina erroneously used for *G. irregularis*), pl. IV 1-4; 210, 211; 1996: 196.


**Galatheammina microconcha**

*Gooday & Tendal, 1988*

Gooday & Tendal 1988: 423-424, fig. 4A-D; 414, 415; Gooday 1991: 204.


**Galatheammina tetraedra**

*Tendal, 1972*


**Galatheammina sp. A**


**Genus Reticulammina**

*Tendal, 1972*


Type species: *R. novazealandica* Tendal, 1972.

**Reticulammina antarctica**

*Riemann et al., 1993*


**Reticulammina cretacea** (Haeckel, 1889)

Haeckel 1889: 39, pl. VII 7A-C; 9, 38 (Holopsamma cretacea); Schulze 1907a: 25, 26-27, 48, 49, 50, 51, 53, 54, pl. III 4, 6; 1907b: 160, 162 (Holopsamma cretacea); Schepotieff 1912: 271, 275 (Holopsamma cretaceum); Schulze 1907a: 25, 26-27, 48, 49, 50, 51, 53, 54, pl. I 11 4, 6; Schulze 1907b: 160, 162 (Holopsamma cretaceum); Schepotieff 1912: 271, 275 (Holopsamma cretaceum); Laubenfels 1936: 33; 1948: 184 (Cerelpsamma cretaceum); Tendal 1972: 13, 27, 29, 30, 31, 65, 76, 81, 82, 83, 86, pl. 4D-E; 1975a: 97; Gooday 1991: 207.

Type material: The material is unaccounted for, BMNH reg. no. 1889:12:3:2. "Challenger" St. 70. Figured in Haeckel 1889, pl. VII 7A-B.

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**Reticulammina labyrinthica** Tendal, 1972


Holotype: NZOI. NZOI St. F 913. Figured in Tendal 1972, pl. 3H, 4A.

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**Reticulammina novazealandica** Tendal, 1972


Holotype: NZOI. NZOI St. 903-a. Figured in Tendal 1972, pl. 3E-F.

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**Reticulammina plicata** Gooday, 1996

Gooday 1996: 193, 201, 206, 207, pl. 5 1-6, 6 1-6.


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**Family SYRINGAMMINIDAE** Tendal, 1972

**Genus Syringammina** Brady, 1883


**Type species:** S. fragilissima Brady, 1883.

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**Syringammina fragilissima** Brady, 1883


Lectotype: BMNH reg. no. 1885:10:3:119. “Triton” St. 11. Lectotype chosen and figured in Tendal 1972, pl. 6A-B.

Remarks: The lectotype designation was overlooked by Adams et al. (1980, p. 3), as was also the
transferring from the foraminifera to the xenophyophores (Tendal 1972, p. 35).

**Syringammina minuta** Pearcy, 1914


Remarks: The original material may turn up in some foraminiferal collection. Since no new material has been found, there is as yet no particular need for a reference specimen, and the formal designation of a type should wait. Pearcey’s figure is too generalized to be recommended as the base of the species.

**Syringammina reticulata** Gooday, 1996

Gooday 1996: 193, 201, 203, 206, pl. 7 1-4, 8 1-4; 1991: 210, 211, pl. 7 (Occultammina sp. A); Levin 1994: 35, fig. 2a-b (Occultammina sp.).


**Syringammina tasmanensis** Lewis, 1966


Holotype: NZOI reg. no. 19. NZOI St. D 227. Figured in Lewis 1966, fig. 1A-C.

**Syringammina sp.**


Remarks: The citations above seem not to refer to the same species.

**Genus Occultammina** Tendal et al.,1982


Type species: *O. profunda* Tendal, Swinbanks & Shirayama, 1982.

**Occultammina profunda** Tendal et al., 1982


**Occultammina sp.**


Non *Occultammina* sp., Levin 1994: 35 (Syringammina reticulata).

**Genus Aschemonella** Brady, 1879


*Araschemonella* Rhumbler 1913: 440, fig. 15.

Type species: *A. scabra* Brady, 1879.

Remarks: Goody & Nott (1982, p. 601) discovered that *Aschemonella ramuliformis* Brady, 1884 is a xenophyophore and with some hesitation placed it in the family Syringamminidae. *A. scabra*, the type species, is also a xenophyophore.
(Gooday 1983, p. 15, Loeblich & Tappan 1988, p. 726), while the third often mentioned species, A. *catenata* (Norman), may be a foraminifer. Because intraspecific variation has not been well documented there is much confusion in the literature as to the use of the names *A. scabra*, *A. ramuliformis* and *A. catenata*; some examples are given by Gooday (1996, p. 203), and to these can be added Tendal (1985, p. 264), who mixed up *A. scabra* and *A. catenata*.

Since the genus requires revision, and because the study of the actual specimens will be necessary, the bibliography of the 3 species given below applies the names as used by each author. In order to avoid further confusion, no attempt is made to clear up any misunderstandings.

Rather few species have been assigned to *Aschemonella*, but they all need reinvestigation in order to determine whether they are xenophyophores or foraminifers. The names with reference to the original descriptions are given here, but a full bibliography would seem premature: *A. amata* (Goes, 1896) (p. 29), *A. calcarea* Rhumbler, 1913 (p. 468), *A. delicata* Saidova 1975 (p. 54), *A. cushmani* Saidova, 1975 (p. 368), and *A. composita* Schroder, Medioli & Schott 1989 (p. 41). *A. cushmani* is a new name for the material described by Cushman (1921, p. 64, pl. 6 5) and identified as *A. catenata*.

*Aschemonella catenata* (Norman, 1876)


Type material: BMNH. Further details unknown.

*Aschemonella ramuliformis* Brady, 1884


Type material: BMNH. Further details unknown.

*Aschemonella scabra* Brady, 1879


Remarks: Brady (1884, p. 271) synonymized *A. catenata* and *A. scabra*, but Barker (1960, p. 54), Loeblich & Tappan (1964, p. 215), and all following authors maintain them as separate species.

*Aschemonella sp.*

*A. catenata* cf. sp., Stschedrina 1936, p. 55. “... at least two other undescribed xenophyophore-like species of *Aschemonella ...*”, Gooday 1983, p. 16.

**Family CERELASMIDAE** Tendal, 1972

**Genus Cerelasma** Haeckel, 1889

Type species: *C. gyrosphaera* Haeckel, 1889.

**Cerelasma gyrosphaera** Haeckel, 1889


Non *Cerelasma gyrosphaera*, Schepotieff 1912, p. 263 (see *Cerelasma sp.*).

Lectotype: BMNH reg. no. 1889:12:3:11. “Challenger” St. 271. Designated by and figured in Tendal 1972, pl. 7A.

**Cerelasma lamellosa** Haeckel, 1889

Haeckel 1889: 9, 46, 47-49, pl. VI 6-7; Schulze 1907a: 24-25, 26, 48, 49, 50, 51, 53, 54, pl. III 3; 1907b: 160, 161; Schepotieff 1912: 263, 275; Laubenfels 1948: 183; Tendal 1972: 13, 31, 39, 40-41, 76, 81, 83, pl. 7B.

Lectotype: BMNH reg. no. 1889:12:3:12. “Challenger” St. 216A. Designated here; figured in Tendal 1972, pl. 7B.

**Cerelasma massa** Tendal, 1972


Holotype: ZMUC PRO-7. “Galathea” St. 234. Figured in Tendal 1972, pl. 8A-B.

**Cerelasma sp.**


Material: Unaccounted for. India.

Remarks: Tendal (1972, p. 41) pointed out that although the material according to the description of Schepotieff (1912, p. 263-265) undoubtedly belongs to *Cerelasma*, it differs in so many respects from *C. gyrosphaera* that it can not be classified as belonging to this species. (Further, see remarks to *Psammetta ovule*, p. 82).

**Order Stannomida Tendal, 1972**

**Family STANNOMIDAE** Haeckel, 1889

**Genus Stannoma** Haeckel, 1889


**Stannoplegma** Haeckel, 1889: 74; Tendal 1972: 42.


Type species: *S. dendroides* Haeckel, 1889.

Remarks: Church (1970, p. 25) investigated specimens taken in deep water in the East Atlantic, and identified by others. The specimens were small and looked like “black fuzz balls” (Church, pers. comm. 1986); they were probably komokiaceans (Tendal & Hessler 1977), and certainly not xenophyophores.

**Stannoma coralloides** Haeckel, 1889

Haeckel 1889: 73-74; 9, 72, 74, 77, pl. III 5; Schulze 1907a: 35, 36, 48, 49, 50, 52, 53, 54, pl. IV 4; 1907b: 148, 151-152, 156, 157, 160, 162; Schepotieff 1912: 276; Laubenfels 1948: 185; Tendal 1972: 13, 14, 42, 43-44, 74, 76, 77, 81, 84, 85, 87, pl. 8D; Lemche et al. 1976: 271, pl. 4d-e.


**Stannoma dendroides** Haeckel, 1889

1948: 185; Tendal 1972: 13, 14, 15, 43, 66, 68, 69, 70, 71, 73, 74, 76, 77, 79, 81, 84, 87, 90, pls. 8C, 14B-D; Lemche et al. 1976: 271, pl. 4b-c.


Remarks: Haeckel (1889, pl. III 1) provided a drawing, but it cannot be established if this shows the specimen chosen as lectotype.

Genus Stannophyllum Haeckel, 1889


Psammophyllum Haeckel, 1889: 49-50; 7, 8, 19, 20, 43, 44, 54, 55, 56, 59; Schulze 1907a: 5, 28, 43; Neviani 1909: 265, 266; Schepotieff 1912: 269, 271; Laubenfels 1936: 33; 1948: 184, 185; Tendal 1972: 44.


Non Stannarium, Church 1970: 25.


Type species: Stannophyllum zonarium Haeckel, 1889.

Remarks: Concerning Stannarium mentioned by Church 1970, see remarks on Stannoma.

Stannophyllum alatum (Haeckel, 1889)

Haeckel 1889: 70-71, pl. III 6-9, 9, 81 (Stannarium alatum); Schulze 1907a: 45-46, 49, 50, 52, 53, 54 (Stannarium alatum); 1907b: 155-156, 157, 160, 162; Schepotieff 1912: 278; Laubenfels 1948: 185 (Stannarium alatum); Tendal 1972: 13, 14, 44, 45, 57-58, 61, 62, 74, 76, 81, 84, 86, 87, 88, pl. 11E.


Stannophyllum concretum (Haeckel, 1889)

Haeckel 1889: 71, pl. III 10-14, 9, 70 (Stannarium concretum); Schulze 1907a: 46, 49, 50, 52, 53, 54; 1907b: 160, 162 (Stannarium concretum); Schepotieff 1912: 276 (Stannarium concretum); Laubenfels 1936: 33; 1948: 185 (Stannarium concretum); Loeblich & Tappan 1964: 790 (Stannarium concretum); Tendal 1972: 13, 44, 45, 57, 58, 61, 62, 76, 77, 81, 85, 87, pls. 11F, 12A.

Lectotype: Designated here as the specimen figured in Haeckel 1889, pl. III 13-14. “Challenger” St. 270. The material itself seems lost (BMNH; see Tendal 1972, p. 58).

Stannophyllum flabellum Haeckel, 1889

Haeckel, 1889: 60. Nomen nudum.

Stannophyllum flustraceum (Haeckel, 1889)

Haeckel 1889: 51-52, pl. IV 5-6, V 5; 9, 16, 45, 49, 77 (Psammophyllum flustraceum); Schulze 1907a: 44, 49, 50, 52, 53, 54; 1907b: 160, 162; Schepotieff 1912: 278; Laubenfels 1936: 33; 1948: 184; Tendal 1972: 13, 44, 45, 57, 58, 60, 61, 62, 63, 67, 74, 76, 81, 85, 87, pl. 12B.


Stannophyllum fragilis Tendal, 1972

Tendal 1972: 53-54, fig. 12, pl. 10D-E: 15, 44, 45, 51, 57, 58, 61, 62, 63, 67, 74, 75, 76, 81, 83, 85, 86, 87.

Holotype: ZMUC PRO-8. “Galathea” St. 200. Figured in Tendal 1972, pl. 10E.
**Stannophyllum globigerinum** Haeckel, 1889


Syntype material: BMNH reg. no. 1889:12:3:28-34. “Challenger” St. 271. No lectotype has been chosen because of fragmentation.

**Stannophyllum granularium** Tendal, 1972


**Stannophyllum mollum** Tendal, 1972


Holotype: ZMUC PRO-10. “Galathea” St. 231. Figured in Tendal 1972, pl. 12E.

**Stannophyllum pertusum** Haeckel, 1889

Haeckel 1889: 65-66, pl. I 3A-B; 9, 58, 61, 64; Schulze 1907a: 36, 42, 49, 50, 53, 54; 1907b: 160, 162; Schepotieff 1912: 277; Laubefels 1948: 185; Tendal 1972: 13, 44, 45, 55-56, 57, 61, 62, 63, 74, 76, 77, 81, 85, 87, pl. 11A.

Syntype material: BMNH reg. no. 1889:12:3:25. “Challenger” St. 271. No lectotype has been chosen because of fragmentation.

**Stannophyllum radiolarium** Haeckel, 1889


**Stannophyllum indicatum** Tendal, 1972

Tendal 1972: 56-57, pl. 11C-D; 15, 44, 45, 53, 61, 62, 68, 76, 77, 81, 84, 87, 90.

Holotype: ZMUC PRO-9 “Galathea” St. 232. Figured in Tendal 1972, pl. 11C.

**Stannophyllum laciniatum** (Neviani, 1909)

Neviani 1909: 265, 266 (Psammophyllum laciniatum).

Type material: Unaccounted for. Japan.

Remarks: The nature of the species is uncertain. Neviani obviously did not know Schulze’s works, and in his short description follows closely Haeckel’s diagnosis of species of his “Deep-Sea Keratosa” genus *Psammophyllum* (1889, p. 49 ff.). It is nowhere stated what depth the single specimen came from. It should be noted that *Stannophyllum* species are known from off Japan, but only at depths greater than 5000 m (Tendal 1972).
**Stannophyllum setosum** Tendal, 1980


**Stannophyllum venosum** Haeckel, 1889

Haeckel 1889: 67-68, pl. I 4; 9, 51, 52, 58, 61, 64, 66, 80; Schulze 1907a: 36, 42, 49, 50, 52, 53, 54; 1907b: 160, 162; Schepotieff 1912: 277; Laubenfels 1948: 185; Tendal 1972: 13, 44, 45, 56, 57, 61, 62, 63, 66, 76, 77, 81, 85, 87, pl. 11B.


**Stannophyllum zonarium** Haeckel, 1889


_Psammetta annectens_ Haeckel, 1889: 52-54, pl. IV 1-4; 49, 50; Schulze 1907a: 3, 36, 37, 43, 45, 46, 49, 50; 1907b: 160, 162; Schepotieff 1912: 270, 276; Laubenfels 1948: 185; Tendal 1972: 45, 50. Lectotype: BMNH reg. no. 1889:12:3:15. “Challenger” St. 244. Designated here.


Non _Stannophyllum zonarium_ Schepotieff 1912, p. 258.

Lectotype: BMNH reg. no. 1889:12:3:19. “Challenger” St. 271. Designated here; seems to be figured in Haeckel 1889, pl. I 1A.

**Remarks:** The first to describe, albeit informally, this, the widest known of all xenophyophore species, was Alexander Agassiz in a vivid letter written onboard the Steamer “Albatross” and dated March 14, 1891 (Agassiz 1891, p. 191; partly also 1892, p. 78).

**Stannophyllum sp.**

Schepotieff 1912: 246, 258-263, 264, 265, pls. 15 72-73, 16 1-44 (Stannophyllum zonarium); Tendal 1972: 14, 60-61, 70, 79, 80, 81, 84.


**Remarks:** Tendal (1972, p. 60) pointed out that although the material according to the description of Schepotieff (1912, p. 258-263) undoubtedly belongs to _Stannophyllum_, it seems to differ in so many respects from _S. zonarium_ that it can not be classified as belonging to this species. (Further, see remarks to _Psammetta ovale_, p. 82).
The distribution of the Xenophyophorea

Schulze (1907b, table 1-3 and map) knew of 33 localities where xenophyophores were taken, and showed them to be distributed in all the three large oceans, with 24 localities in the Pacific, 6 in the Indian and 3 in the Atlantic Ocean. He noted that all finds were made between 40°N and 40°S, and almost all of them in the narrow tropical belt between 10°N and 10°S, especially in the East Pacific. No explanations were offered at the time, but we now know that both the Challenger- and the Albatross Expeditions hit upon the relatively highly productive, narrow area around the Equator, stretching west from Central America into the Central Pacific. Schulze noted only 3 stations shallower than 2000 m (981-1668m), all the rest having depths between 2000 m and 5353 m, 3 of them being deeper than 5000 m.

Tendal (1972, table 1, p. 10, fig. 14, p. 82, and Fig. 1 herein) added 45 new or hitherto unnoticed localities, and showed the xenophyophores to live abundantly also far outside the low latitudes. New areas found to be rich in xenophyophores were the Northwest Pacific, the Indian Ocean coast of Southern Africa, and around New Zealand. Records from the Atlantic Ocean were still astonishingly few, numbering only 6. The number of stations shallower than 2000 m was increased to 14; half of them were situated on the bathyal rises around New Zealand, the others were scattered all over the world, two of them being in the North Atlantic, west of Scotland. It was possible to list 17 localities deeper than 5000 m, 12 of them in the Japan-, Kurile-Kamchatka- and Aleutian Trench areas. Four stations just exceeded 6000 m, being located in the transition between the abyssal and hadal zones, but xenophyophores were recognized in photographs from 7900 m in the New Britain Trench (Tendal 1972, p. 87 and analyzed in detail by Lemche et al. 1976).

In modern times the number of stations (one station: one operation at a given position), which yielded xenophyophores or information on them, amounts to hundreds. It is difficult to count precisely, because a) in some investigations sampling is repeated time after time at the same spot or in very close by areas, for example as series of box-core samples or trawlings (Gooday 1991, 1996; Kaufmann et al., pers. comm.); b) information about single operations is often not readily available; they may be very numerous, as in the case of Russian investigations in the Pacific, where xenophyophores (and Komokiacea) were said to be rep-

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Fig. 1. Areas from which xenophyophores have been reported. Open circles: From Tendal 1972. Closed circles: Investigated later or not recognized in 1972. Small circles: One or a few operations. Large circles: Five or more operations. Compiled from many different sources, mainly references given in the list, but also unpublished information.
resented at 315 stations (Kamenskaya 1987, p. 16); c) it is a question whether photographic series and submersible operations are to be counted in the same way as other sampling operations.

The map (Fig. 1) marks about 500 single operations, published and unpublished, and even if this is an estimate it represents a pronounced increase from the 78 known in 1972. Areas with many new records are the North Atlantic, the South Atlantic, the East Equatorial Pacific, and off eastern and southern Australia.

**The North Atlantic**

There are numerous records from the western North Atlantic, but the sources are of different kinds and quality, and the fauna has not been adequately studied (Cushman 1920, B. Haecker, pers. comm., Levin 1991, Maciolek et al. 1987, Schröder 1986, Schröder et al. 1988, 1989, Swift et al. 1985, Tendal 1975b, 1988, Vinogradova et al. 1984). It seems to be mainly species of Syringammina and Asclerina that are represented. In this area, xenophyophores have been found from about 800 m to nearly 5800 m.

The eastern North Atlantic fauna has become well investigated, thanks especially to strong British, but also French and German efforts, and many very fragile species have been described (Tendal & Gooday 1979, 1981, Tendal 1980a, 1985, Gooday 1991, 1996, Gooday & Tendal 1988). They are mostly representatives of the genera Homogammina, Psammina, Galatheammina, and Reticulammina. The shallowest record is a Syringammina from 850 m in the Faroe-Shetland Channel and the deepest a Reticulammina from 6050 m off West Africa (Tendal 1972, Tendal & Gooday 1981).

The fact that the order Stannomida is poorly represented in the North Atlantic, with only a few records of a Stannophyllum species in the near equatorial region (Tendal 1980a), is unexplained. It cannot be a sampling artifact, because members of this order are much more solid than most Psamminida, and all depths have also been sampled.

**The Caribbean**

No xenophyophores have so far been reported with certainty from the area. Young et al. (1985, p. 275, fig. 3) interpreted lebensspuren photographed at 5000 m depth in the Venezuela Basin as the possible traces of a Psammetta-type xenophyophore, referring to earlier interpretations of more or less similar traces (Lemche et al. 1976, Tendal 1972, Thiel 1973, 1975). Later developments in bottom photography allows for different interpretations of this type of traces, leaving the present one uncertain. During the 14th Cruise of the “Akademian Kurchatov” in 1973 a number of rather heavily damaged specimens belonging to the order Psamminida were taken at depths between 1000 and 3000 m; they have not yet been taxonomically described.

**The Mediterranean**

The only report of a xenophyophore comes from 760 m depth off Corsica (Soetaert et al. 1991). The species is infaunal, and was found 0.5-2 cm under the sediment surface. It is probably an Occultamina sp. The presence of the species in the Mediterranean rises the question of spreading of xenophyophore species, since the sill of the Gibraltar Strait is only 280 m deep (Bouchet & Taviani 1992).

**The South Atlantic**

Only three records of named species exist from the South Atlantic (the Antarctic region excluded)(Bra- dy 1884, Tendal 1972). During a transatlantic transect at 36°-31°S, the “Academician Kurchatov” took close to 50 trawl and dredge samples; 28 of these, from depths greater than 2500 m, contained xenophyophores, some of them in a very high proportion of the total biomass (Kamenskaya 1988). The taxonomic composition of this important material is not known.

**The Arctic Seas**

Asclerina has been found in the entrance area to the Davis Strait (Norman 1876) and off Northeast Greenland (Cushman 1948). An ?Asclerina sp. has been reported from the Kara Sea, at 78°N (Stshedrina 1936). While the first record is from 3200 m depth, the two others are shallow, the one from the Kara Sea only 276 m. Although description of new material or reinvestigation of the old material is necessary to be certain, the records can for the time being be taken as an indication that xenophyophores may occur also in the Arctic, the 78°N record being the most northerly known.
The Antarctic Sea

Four named records are known from this region (Heron-Allen & Earland 1922, Riemann et al. 1993, Tendal 1972, Tendal & Gooday 1981), one from 1450 m, the others from 3400 to 4800 m. Although there have been comparatively few deep-sea investigations around Antarctica, it seems that xenophyophores are rare in the region. This point of view is supported by Russian investigations around the South Shetland and South Sandwich Islands where xenophyophores were found in only 5 out of a large number of samples from between 1730 and 4200 m, and represented low biomass values (Kamenskaya 1988).

The east equatorial Pacific

As mentioned above, it has long been known that the East Equatorial Pacific is eutrophic and houses a rich and abundant fauna of xenophyophores. Recent Russian investigations have confirmed this and showed that in some areas they constitute the major part of the biomass (Kamenskaya 1987). It would be of great taxonomic interest to have this material worked up, because many of Haeckel's (1889) poorly known species came from the area.

The region off southern and eastern Australia

No xenophyophores have been identified from the general area, except for interpretations in photographs from the New Britain and New Hebrides Trenches, and samples from New Zealand bathyal depths (Lemche et al. 1976, Tendal 1972, 1981, Tendal & Lewis 1978). Russian investigations showed high abundance and high biomass of these protists in the deep part of the Tasman Sea and in the South Fiji Basin (Kamenskaya 1987).

The number of known xenophyophage species

In 1889, when Haeckel invented his "Deep-Sea Keratosa", he described as new 9 genera and 26 species. Seven genera and 21 species were transferred to the xenophyophores by Schulze (1906 and 1907a), and he further erected one genus and described two new species. Thus, the total number of xenophyophage species at the time of the demarcation of the group was 22 as shown in Table 1; one species is not counted, because it was later considered of doubtful nature (Tendal 1972, p. 65). With an intervening number of 36 species in 1972, the number of described species is now 58 (Table 1), a figure that is based both on newly described species and on some species having been transferred from Foraminifera to Xenophyophorea. The number of genera recognized at present is 14, including some taxa transferred from the Foraminifera (Syringammina and Aschemonella).

How many species of xenophyophores are there?

Although needless to say the answer can only be a guess, an estimate of around 100 sounds, on the basis of the considerations given below, reasonable:

Table 1. Genera of xenophyophores and the numbers of species assigned to them, 1907-1996. The number of species per genus reflects contemporary generic placements and takes no account of subsequent transfers.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Schulze 1907a</th>
<th>Tendal 1972</th>
<th>Total 1996</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maudammina</td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Tendal, 1972</td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Ptsamnetta</td>
<td>2</td>
<td>4</td>
<td>4</td>
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<td>Schulze, 1906</td>
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<tr>
<td>Homogamonina</td>
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<td>3</td>
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<td>G. &amp; T., 1988</td>
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<tr>
<td>Galatheammina</td>
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<td></td>
<td></td>
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<tr>
<td>Tendal, 1972</td>
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<td>2</td>
<td>6</td>
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<tr>
<td>Reticulammina</td>
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<tr>
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<td>4</td>
<td>7</td>
</tr>
<tr>
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<tr>
<td>Semipsamnina</td>
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<tr>
<td>Tendal, 1975</td>
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<tr>
<td>Cerelasma</td>
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<tr>
<td>Laubefels, 1936</td>
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<tr>
<td>Stannophyllum</td>
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<td>13</td>
<td>14</td>
</tr>
</tbody>
</table>

Number of species recognized 22 36 58
1) Undescribed samples from different parts of the world are stored in several institutions, such as the P.P. Shirshov Institute, Moscow (Kamenskaya 1987, 1988, 1993, Turpaeva 1984, Vinogradova et al. 1978, 1984, 1990a, 1990b, Zezina 1978), the Southampton Oceanography Centre, Southampton (collection in charge of A.J. Gooday, with perhaps 15 undescribed species (A.J. Gooday, pers. comm. 1996)), and the Zoological Museum, Copenhagen (collection in charge of the author, probably 10 undescribed species).

2) In 6 genera there are taxa that could not be adequately characterized, and were therefore designated "sp.". Because there are also cases where such informal taxa have later been fully described when more material became available (Galatheammina discovery: Gooday & Tendal, 1988, and Syringammina reticulata Gooday, 1996), it is to be expected that at least some of them may eventually be formally named.

3) The discovery by Gooday & Nott (1982) that some species hitherto classified as arenaceous foraminifers (Aschemonella), are in fact xenophyophores opened up a new perspective, viz. that of the existence of an unrecognized fauna of small-sized xenophyophores. Thus, there seems to be a hitherto overlooked fauna of small infaunal species (A.J. Gooday, pers. comm. 1996), and there are indications that other small morphological types are found on special kinds of substrate, such as plant remains (Tendal 1975) and manganese nodules (Riemann 1983, 1985; Mullineaux 1987).

4) In some fauna lists and surveys "sp."s are very briefly mentioned, and only preliminarily assigned to genera (e.g., Kamenskaya 1988, p. 18 (Cerelasma), Levin & Thomas 1988, p. 2011 and Levin 1994, p. 33 (Stannophyllum), Levin & Gooday 1992, p. 96, 97 (Reticulammina, Psammina, Syringammina), and Mullineaux 1987, p. 175 (Semipsammina, Syringammina, Stannoma, Stannophyllum)). These are not considered detailed enough to be separately included in the present checklist, but there is at least in the cases used as examples no reason to doubt their identification as xenophyophores, and some of them may turn out to be new species.

5) Some of the modern sampling equipment, notably boxcorers and multicorers, sometimes used from submersibles, have yielded material of very fragile species in good condition (Gooday 1991, 1996, Levin et al. 1986, Levin & Thomas 1988, Mullineaux 1987, Rieman et al. 1993, Tendal et al. 1982). Such specimens might have been totally lost in towed gear, or at least have been heavily and unrecognizably fragmented. As can be seen from Table 1, the majority of species described between 1972 and 1996 (in fact 15 of 22) belong to such fragile taxa, viz. Homogammina, Galatheammina, Reticulammina, and Psammina.

6) The extensive use of sea-bottom photography over the last 25 years has shown the occurrence of xenophyophores in many deep-sea areas, sometimes in such abundance that they are considered dominant components of the fauna (Kaufmann et al. 1989, Lemain et al. 1976, Levin & Thomas 1988, Levin & Gooday 1992 (review), Rice et al. 1979; Tendal & Gooday 1981, Tendal & Lewis 1978, Thiel et al. 1992). In photographs it may be difficult to distinguish between xenophyophores and representatives of other groups, e.g. certain sponges and bryozoans, but nevertheless the majority of the published statements seems to be correct as far as the identification to xenophyophore is concerned. To go further is more demanding, and it is nearly impossible to identify to more than generic level without samples from the same area at hand; even in such cases there may be problems (discussed in Tendal & Gooday 1981). The extreme case is a possibly undescribed species so fragile that it is only known from photographs (Gooday & Tendal 1981). A number of photographs show supposed xenophyophores, which cannot be identified further because they do not seem to possess the morphology of any known genus or species; accordingly, these may well represent undescribed species (examples are seen in Ewing & Davis 1967, Foell et al. 1986; Fujioka et al. 1989, Pautot & Hoffert 1979, Tendal & Gooday 1981, and Zenkevich 1970).

**Xenophyophore ecology**

The study of bottom photographs and the invention of box- and multicorers have yielded a wealth of information on the lifestyle of xenophyophores and their role in bottom communities in various kinds of topographic, hydrographic and trophic settings. The work has mainly been initiated and carried through by Andrew J. Gooday and Lisa A. Levin, and their collaborators, and is reviewed in several magnificent surveys (Levin 1991, 1994, Levin & Gooday 1992).
In the broad context of xenophyophore ecology there are several more special lines of ongoing work, which should be mentioned:

1) Investigations on seamounts have shown xenophyophores to be an important faunal constituent. A particularly fruitful area of investigation is the relations of these protists to different patterns of water movement and trophic conditions (Kaufmann et al. 1989, Levin et al. 1986, Levin & Thomas 1988, Levin et al. 1991, Rogers 1994, Tendal 1994).

2) Xenophyophores occur regularly in manganese nodule fields, both on the nodules and between them (Foell et al. 1986, Mullineaux 1988, Pautot & Hoffert 1979, Thi el et al. 1992, Titol 1992). They are supposed to play some kind of role in the growth of the nodules, together with other protists (Kamenskaya 1987, Riemann 1983, 1985).

3) Xenophyophores seem to occur around hydrothermal vents, thus maybe showing special biochemical adaptations (Sagalevitch et al. 1992).

4) The biochemistry of xenophyophores is poorly known, but at least one feature is very characteristic, viz. the presence in the plasma of numerous barite crystals (BaSO4) (Schulze & Thierfelder 1904, Tendal 1972). Modern methods (scanning electron microscopy in combination with an energy dispersive x-ray microanalyser (EDAX)) have confirmed the nature of the crystals in some species (Gooday & Nott 1982, Riemann et al. 1993, Tendal 1994), and more information can be expected.

5) Although xenophyophores are probably neither easily fossilized nor recognized as fossils, there is a growing number of suggestions as to the nature of objects that might throw light on the early history of the group. Swinbanks (1982) was the first to call attention to the similarity between specimens of the infaunal genus Occulatammina and trace fossils widely known as Paleodictyon, an interesting thought which would give xenophyophores a fossil record back to the Ordovician. Zhiravlev (1993) suggested that a number of Ediacaran fossils (Cambrian) might represent xenophyophores. Maybury & Evans (1994) reinterpreted what were considered phylloid algae fossils from the upper Carboniferous as xenophyophores. Kuhnt & Kaminski (1989) mentioned two Aschemonella species from Late Cretaceous. A review is given by Levin (1994).

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