A MONOGRAPH OF THE XENOPHYOPHORIA

(Rhizopodea, Protozoa)

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CONTENTS

I. PREFACE

The present work deals with the almost "forgotten", rarely discussed protozoans, the Xenophyophoria. These protozoans are remarkable for several reasons, the most conspicuous of these being their size; they are by far the largest Protozoa known.

Several reasons can be mentioned as to why this animal group, consisting of large species with a well defined and peculiar organization, has not been more thoroughly investigated.

1. Scarcity of material: Judging from the records known at present, the group is mainly bathyal-abyssal, and one of the most serious problems with deep-sea animals is nearly always the lack of material.
2. Doubt about their real nature: Since the first record in literature, the problem of the xenophyophores' real nature and true affinities has been a puzzle. Some of the species have been described as sponges and others have been described as foraminiferans. The misuse of family and genus names from these groups has led to much confusion with the result being that species belonging to different phyla have been brought together in the same genus.
3. Outer resemblance to other animal groups: From their external appearance many of the species can be mistaken for badly preserved sponges, coelenterates, bryozoans, or ascidians. They have also often been put aside as "mere inorganic concrements" (HAECKEL 1889, p. 41) of foraminiferan or radiolarian tests, sponge spicules, etc. Generally such material will be carefully investigated only if it is scarce as in the case with deep-sea material. If found in shallow water where large quantities of material are usually available, such "badly preserved specimens" are usually disregarded. Perhaps this is the reason for the few (three!) records from coral reefs and other shallow-water localities.
4. Fragility of the species: Some of the species are so fragile that the specimens are totally destroyed when washed in a sieve. Many specimens are damaged during collecting, and even when not washed, such fragments are easily overlooked or recorded as broken, dead sponges.

The rather large and well-preserved collection of xenophyophores from the Danish Galathea Expedition, containing new species (and genera) and new material of poorly known species, forms the basis for the present work. As far as possible specimens from other expeditions have been studied (see Station list), and those from the Challenger Expedition were examined during a visit to the British Museum of Natural History. Descriptions of the xenophyophores in literature are usually quite detailed. However, I found it necessary to borrow the specimens instead of relying on literature, because frequently the terms used in the descriptions were those used for other animal groups. Some of the characteristics that I have used to describe the xenophyophores have been utilized by earlier authors, while others have not appeared in previous literature.

The study is, as must be the case with a deep-sea collection, essentially taxonomical and morphological-cytological; however, whenever possible, non-morphological aspects such as ecology and general biology have been treated.

A large number of people and institutions in many parts of the world have assisted me and have been greatly accommodating in regard to this study. In this way and through the possession of the rich material in the "Galathea" collection, it has been possible to gather a reference collection of xenophyophores in the Zoological Museum of the University of Copenhagen that includes representatives of most of the species, and contains specimens from a considerable number of the known samples.

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II. INTRODUCTION

HISTORICAL REVIEW

1. Expeditions and authors

Our present knowledge of the xenophyophores mainly comes from the reports of a series of the well-known oceanographic deep-sea expeditions (Table 1).

The first xenophyophore was described by BRADY (1883) as a primitive foraminiferan; it was taken by the British Triton Expedition in the North Atlantic in 1882.

Very great numbers of xenophyophores were collected by the Challenger Expedition as early as in 1873, but they were classified on deck by MURRAY as sponges (HAECKEL 1889, p. 2; 1895, p. 35). During the final sorting of the material in England, doubt arose as to the real nature of these strange organisms since several well-known authorities among sponge specialists refuted the earlier classification as sponges, and protozoologists refused to recognize them as rhizopodes. Because of this controversy HAECKEL was asked to make a special contribution on the group in the "Challenger Report". HAECKEL's report appeared in 1889, and after "a very careful study" (1895, p. 35), he classified the enigmatic animals as a group of deep-sea sponges.

In 1892 GOËS described some large, flake-formed organisms taken the preceding year in the East Pacific by the American Albatross Expedition as a special type of agglutinated foraminiferan.

The German Valdivia Expedition collected the first xenophyophores from the area off East Africa in 1899. They were described by SCHULZE together with material from the American Albatross Expedition in the East Pacific 1899-1900. At this time SCHULZE also had most of the "Challenger" collection at his disposal. In his monograph of the group SCHULZE classified the animals as gigantic rhizopodes and named them Xenophyophora. The work was published in 1907, but it was handed to the editor in 1905. SCHULZE always refers to this monograph as "my 1905-work".

In 1906 SCHULZE treated the xenophyophores collected by the Dutch Siboga Expedition to Indonesia 1899-1900, and in 1907 a description of the xenophyophores taken in the East Pacific by the American Albatross Expedition 1904-1905 was printed.

Table 1. Expeditions during which xenophyophores were dredged (in chronological order), number of dredgings containing xenophyophores, and the authors who described them.

Expeditions		No. of dredgings with xenophyophores	Author
"Challenger"	1872-1876	13	HAECKEL 1889
"Triton"	1882	1	BRADY 1883
"Albatross"	1891	3	GOËS 1892
"Valdivia"	1898-1899	2	SCHULZE 1907a
"Albatross"	1899-1900	1	SCHULZE 1907a
"Siboga"	1899-1900	4	SCHULZE 1906
"Scotia"	1903-1904	1	PEARCY 1914
"Albatross"	1904-1905	10	SCHULZE 1907b
SCHEPOTIEFF	1908	2	SCHEPOTIEFF 1912b
"Goldseeker"	1910	1	TENDAL (this paper)
"John Murray"	1933-1934	1	TENDAL (this paper)
"Galathea"	1951-1952	11	TENDAL (this paper)
"Vitiaz"	1954, 1955	16	TENDAL (this paper) and TENDAL (in press)
	1957, 1958		"
	1959, 1966		"
	1969		"
"Vema"	1958	5	TENDAL (this paper)
"Magdalena Bay"	1964	1	TENDAL (this paper)
"Taranui"	1965, 1968	6	LEWIS 1966 (parts) TENDAL (this paper) and TENDAL (in press)

The Russian zoologist SCHEPOTIEFF collected xenophyophores on coral reefs in Ceylon and India in 1908, and in 1912 he published the first description of xenophyophores from shallow, warm water.

A single species belonging to the xenophyophores was collected in the Antarctic by the Scottish Scotia Expedition, and it was described by PEARCY in 1914 as a primitive, agglutinated foraminiferan.

A single species from New Zealand waters was described as a foraminiferan by LEWIS in 1966.

Xenophyophores have also been collected by the following expeditions: The British Goldseeker Expedition in the North Atlantic (1910), the British John Murray Expedition in the Indian Ocean (1934), the Danish Galathea Expedition (1951-1952), the Russian Vitiaz Expeditions in the West, North, and East Pacific (1954, 1955, 1957, 1958, 1959, 1966, 1969), the American Vema Expedition in the East Pacific (1958), the American Magdalena Bay Expedition in the East Pacific (1964), and the New Zealand Taranui Expeditions in the waters around New Zealand (1965, 1968). However, these samples have not been treated previously in the literature.

2. The concept of the nature of the xenophyophores

The first collection large enough to give a general impression of the group was that of the "Challenger", and it was treated by HAECKEL (1889). HAECKEL's conclusion (1889, p. 1) was that the animals were sponges belonging to the Keratosa. These animals were "for the most part modified in a peculiar manner by the symbiosis with a commensal organism which is very probably in most cases (if not in all) a Hydropolyp stock." HAECKEL found (l. c., p. 5) that the state of preservation of all the specimens was very poor as a result of "the sudden change of conditions" during the dredging. He further stated (p. 6): "No trace could be found anywhere of the outer covering pavement-epithelium of the exoderm. The peculiar flagellated epithelium of the entoderm was not distinctly recognizable in most of the specimens, and not fitted for finer examination; in several species, however, its presence could be made out with certainty."

HAECKEL's work was strongly criticized by other zoologists and especially by sponge specialists.

In his survey, WELTNER (1890, p. 228) said that he doubted the sponge nature of all the genera, and placed them (l. c., p. 254) under the designation incertae sedis.

LENDENFELD (1891, p. 177) questioned the sponge nature of one of the families, viz. Ammoconidae (cf. p. 63), but regarded the members of the other families as true sponges; one family was even considered as a synonym of a well-known sponge family.

In a short communication HANITSCH (1893a, p. 365) pointed out the similarity between the organism described as a foraminiferan *(Neusina agassizi)* by GOËS and one of HAECKEL's species of "Deep-Sea Keratosa" *(Stannophyllum zonarium)*. PEARCY, who had at his disposal the whole "Challenger" collection, was of the same opinion as HANITSCH in regard to the identity of the two species. However, he denied (1893, p. 390) that the organisms were sponges and agreed with GOËS in placing them among the foraminiferans. HANITSCH (1893b, p. 439), who had only one specimen *(Stannophyllum zonarium)* at his disposal, preferred to follow HAECKEL; he stated that "... as long as we are not absolutely certain about its cellular structure we are justified in thinking with HAECKEL that general appearance and the presence of oscula, pores, subdermal cavities, horny skeleton, etc., are sufficient to characterize the form as a sponge."

It is undecided whether HAECKEL knew of GOËS' description and PEARCY's objections. He did not refer to these authors when in 1895 and in 1896 he wrote about the "Deep-Sea Keratosa", and his opinion in regard to the nature of the group had not changed. In 1896 (pp. 78, 81, 83) he placed them in his sponge class "Malthosa" and marked them in his phylogenetic tree of the sponges (p. 79).

DELAGE & HEROUARD (1899, p. 197) placed the "Deep-Sea Keratosa" in an appendix to the sponges. They referred to the doubts expressed by LENDENFELD, PEARCY, and SCHULZE (personal communication) and were, like these authorities, compelled to make reservations concerning HAECKEL's conclusions.

MINCHIN (1900, pp. 142, 154) placed the group in the system of sponges under the designation Keratosa (? Foraminifera) incertae sedis (Haeckel, 1889).

The placement of the "Deep-Sea Keratosa" among the sponges was also accepted by LAUBENFELS (1936, p. 32), but he noted that "there is grave doubt in the minds of many students of the items in question as to whether or not they are really sponges at all!" Later (1948, p. 174), he concluded that "members of the subfamily Psammininae [he grouped all the "Deep-Sea Keratosa" together in this subfamily] are not certainly sponges – their flagellate chambers have never been discovered – and they are left in the Porifera only provisionally, partly because of the difficulty of placing them elsewhere. Each is probably an aggregate of organisms of several very diverse sorts." Furthermore (p. 180): "It is here suggested that some of them may have been primarily Protozoa, others primarily coelenterate and possibly some of them genuinely Porifera, but all are extremely uncertain, and at the present time cannot be regarded as finally classified."

A second, large collection of the group containing new as well as old representatives was treated by SCHULZE in his monograph (1907a). He came to the conclusion that the "Deep-Sea Keratosa" constituted an independant group of gigantic Rhizopoda at the order level.

LISTER (1909, p. 286) provisionally placed the xenophyophores as a family within the foraminiferans. His reasons were as follows (p. 285): "In the absence of any information concerning the early stages of development, or of the character of the pseudopodia in the members of this family, it is difficult to assign to them their proper systematic position". Furthermore: "In the absence of a calcareous skeleton the family differs from all the higher and more differentiated families of Foraminifera, but nevertheless the affinities of the family are greater with this class than with any other Protozoa."

After a survey of the organization of the group, MINCHIN (1912, p. 238) concluded: "The affinities of the Xenophyophora are seen to be with the Foraminifera."

On the basis of his investigations on xenophyophores from shallow water, SCHEPOTIEFF (1912b, p. 266) concluded "..., dass die Xenophyophoren nur mit den Myxomyceten zu vergleichen sind." He placed the group in a system including the more or less well-known groups of rhizopod-like organisms most of which can be designated "Rhizopodes douteux ou Champignons inférieurs" (GRASSÉ 1953, p. 492). In another work (1912c, p. 232) he stated: "In den Xenophyophoren, Myxomyceten, Clamydomyxa und Urnatella haben wir wahrscheinlich eine besondere Gruppe von vervandten Organismen, die sich den Rhizopoden anschliessen."

SCHEPOTIEFF's view was opposed by SCHULZE (1912, p. 41) and POCHE (1913, p. 203), who both regarded the xenophyophores as having a special organization at the order level within the "true" rhizopodes.

RHUMBLER placed the group among the rhizopodes but said (1923, p. 105) that "F. E. Schulze ... begründete ... in eingehender Bearbeitung die Ansicht, dass es sich wahrscheinlich um Rhizopoden handele, die in die Nähe der Foraminiferen als selbstständige Gruppe zu stellen seien. Bei dem Ausstehen der Beobachtung lebenden Materials ist diese Auffassung noch heutetags hypotetisch, wenn auch durchaus warscheinlich."

Doflein & Reichenow (1952, p. 746) arranged the xenophyophores as an addition to the foraminiferans and said: "Die Deutung dieser Organismen, welche früher zu den Spongien gerechnet wurden, als den Foraminiferen verwandte Rhizopoden, ist durchaus hypotetisch, da noch keine lebenden Exemplare untersucht worden sind."

Hadži (1963, p. 355) made the following proposal to solve the zoological problem quite effectively: "Zoologists should rather agree to exclude these forms from the animal world and thus to leave them to be studied by botanists or by protistologists who specialize in them."

METHODS

The methods used for a general investigation of the specimens are the same as those used for smaller Metazoa. Measuring, dissecting, and cutting pieces for cytological work was done under the microscope while the specimens were immersed in alcohol.

The pieces for the cytological investigations were embedded in paraffine (tissue-mat) and cut with a steel knife. Ideally 5 μ, 10 μ, and 20 μ thick sections were to be cut, and in many cases there were no difficulties in obtaining good sections. In other cases, however, the many xenophyae (foreign bodies) led to displacement; nevertheless, it was usually possible to get a few good sections from these specimens. In species with very numerous or very thick xenophyae, the only way to get any information was by the help of squash-preparations. In some cases calcareous xenophyae were dissolved with diluted HCl or acetic acid before cutting.

Staining of all species was performed with hematoxylin-eosin (in some cases orange G was used together with eosin). In most species slides were also stained with Heidenhain's azocarmine-anilin blue stain (Azan), Mallory Heidenhain stain (Jane E. Cason), and periodic acid Schiff (PAS). Other stains were used for special purposes, and are referred to in the proper places in the general part.

Short diagnoses are made for each taxonomic category. I have tried to avoid the repetition in lower levels of those characters utilized in the diagnoses of higher categories, but this has not been entirely possible. New diagnoses for nearly all the species have been necessary since most of them originally were described as belonging to other animal groups (sponges, foraminiferans, etc.) by the terms appropriate for these groups.

The descriptions of the material may in some cases seem rather extensive, but this has been willfully done for taxonomic reasons, since knowledge of the xenophyophores can be expected to be greatly enlarged on in the future. The finer differences noted can perhaps prove to be of value as a good demarcation of the species and for a satisfactory systematic division of the group.

The list of synonyms and authors under the heading of each species is thought to be complete. Only authors who actually had material at hand are referred to, and if authors who had not seen the material are cited in connection with a synonym, this will be clearly indicated.

MATERIAL

The greater part of the material is preserved in alcohol and a smaller number of specimens are dried (parts of the "Challenger" and "Galathea" collections and all the specimens taken by the "Triton", the "Goldseeker", and the "Albatross" in 1891). The preservation is rather good in many of the samples, especially when the circumstances during dredging in the deep-sea are taken into consideration. In general there is some shrinking of the plasma, and the more fragile specimens are usually more or less damaged.

The most important fact in connection with the quality of the preservation seems to be the length of time passed before fixation after the animals are brought on deck. No doubt they are killed by the high temperatures in the surface layers of the sea, and the plasmatic parts decay rapidly.

The location of the investigated material is mentioned on the following pages.

LIST OF STATIONS AND KNOWN SAMPLES OF XENOPHYOPHORIA

The following survey of the expeditions during which xenophyophores were dredged is arranged chronologically. The information is intended to include the following: name and year(s) of the expedition; investigated area; references to station list and hydrography; any earlier publications based on the material concerned; present location of the material; and a list of the stations with position, depths, date, bottom type, bottom temperature, and recorded species. Material marked * has been at my disposal during this investigation.

Challenger Expedition, 1872-1876

Area: Circumnavigation.
Station list: MURRAY (1895).
Publications: HAECKEL (1889), SCHULZE (1907a).
Location of material: British Museum of Natural History, London.

St. 70. Central Atlantic (38°25′N, 35°50′W), 3065 m, 26 Jun. 1873, Globigerina ooze, 2.4°C.
Reticulammina cretacea

St. 89. Off West Africa (22°18′N, 22°02′W), 4392 m, 23 Jul. 1873, Globigerina ooze, 2.6°C.
Galatheammina calcarea

St. 198. Celebes Sea (2°55′N, 124°53′E), 3935 m, 20 Oct. 1874, blue mud, 4.0°C.
**Stannophyllum reticulatum*

St. 211. Sulu Sea (8°00′ N, 121°42′E), 4072 m, 28 Jan. 1875, blue mud, 10.3°C. The material was not mentioned by HAECKEL or SCHULZE and it is likely that a mislabelling has occurred.
**Stannophyllum alatum*

St. 216A. North of New Guinea (2°56′N, 134°11′E), 3660 m, 16 Feb. 1875, Globigerina ooze, 1.9°C.
**Cerelasma lamellosa*

St. 220. North of New Guinea (0°42′S, 147°0′E), 2013 m, 11 Mar. 1875, Globigerina ooze, 2.3°C.
Galatheammina calcarea
**Psammina globigerina*

St. 241. North Pacific (35°41′N, 157°42′E), 4209 m, 23 Jun. 1875, red clay, 1.7°C.
Stannophyllum flustraceum

St. 244. North Pacific (35°22′N, 169°53′E), 5307 m, 28 Jun. 1875, red clay, 1.8°C.
**Stannophyllum zonarium*

St. 270. Central Pacific (2°34′N, 149°9′W), 5353 m, 4 Sep. 1875, Globigerina ooze, 1.4°C.
Galatheammina calcarea
Cerelpemma radiolarium
Stannophyllum concretum

St. 271. Central Pacific (0°33′S, 151°34′W), 4438 m, 6 Sep. 1875, Globigerina ooze, 1.4°C.
?*Galatheammina calcarea*
Cerelpemma radiolarium
**Cerelasma gyrosphaera*
**Stannoma dendroides*
**Stannoma coralloides*
**Stannophyllum zonarium*
**Stannophyllum globigerinum*
**Stannophyllum radiolarium*
**Stannophyllum pertusum*
**Stannophyllum venosum*

St. 272. Central Pacific (3°48′S, 152°56′W), 4758 m, 8 Sep. 1875, radiolarian ooze, 1.7°C.
**Cerelpemma radiolarium*
Stannoma dendroides
Stannoma coralloides
**Stannophyllum alatum*

St. 274. Central Pacific (7°25′S, 152°15′W), 5033 m, 11 Sep. 1875, radiolarian ooze, 1.7°C.
Psammina nummulina
Cerelpemma radiolarium

St. 331. South Atlantic (37°47′S, 30°20′W), 3138 m, 9 Mar. 1876, Globigerina ooze, 2.0°C.
Psammina plakina

Triton Expedition, 1882

Area: North Atlantic.
Station list: JEFFREYS (1883).
Publications: BRADY (1883, 1884).
Location of material: British Museum of Natural History, London.

St. 11. Faroe Channel (59°39.3′N, 7°13′W), 1016 m, 28 Aug. 1882, ooze, 7.5°C.
**Syringammina fragilissima*

Albatross Expeditions, 1891, 1899-1900, 1904-05

Area: East Pacific.
Station list: TOWNSEND (1901), BOWERS (1906).
Publications: GOËS (1892), SCHULZE (1907 a, b).
Location of material: 1891: Naturhistoriska Riksmuseet, Stockholm; 1899-1900 and 1904-1905: unaccounted for.

St. 3399. 1°07′N, 81°04′W, 3184 m, 24 Mar. 1891, green ooze, 2.2°C.
Stannophyllum zonarium

St. 3414. 10°14′N, 96°28′W, 4085 m, 8 Apr. 1891, green mud, 2.1°C.
Stannophyllum zonarium

St. 3415. 14°46′N, 98° 40′W, 3438m, 10 Apr. 1891, brown mud and Globigerina ooze, 2.2°C.
**Stannophyllum zonarium*

St. 3684. 0°50′N, 137°54′W, 4504 m, 17 Sep. 1899, grey yellowish Globigerina ooze, 1.7°C.
Stannoma dendroides
Stannoma coralloides
Stannophyllum zonarium
Stannophyllum globigerinum

St. 4647. 4°33′S, 87°42.5′W, 3669 m, 9 Nov. 1904, very light grey Globigerina ooze, 1.9°C.
Stannophyllum zonarium
Stannophyllum globigerinum

St. 4649. 5°17′S, 85°19.5′W, 4090 m, 10 Nov 1904, grey mud, very few globigerinas, 1.9°C.
Stannoma dendroides
Stannophyllum zonarium

St. 4651. 5°41.7′S, 85°59.7′W, 4066 m, 11 Nov. 1904, fine, grey sand, 1.9°C.
Stannophyllum zonarium

St. 4653. 5°47′S, 81°24′W, 981 m, 12 Nov. 1904, dark, brown-grey mud with many diatoms, 5.2°C.
Stannophyllum zonarium

St. 4656. 6°54.6′S, 83°34.3′W, 4066 m, 13 Nov. 1904, fine, green mud, 1.8°C.
Stannophyllum zonarium

St. 4658. 8°29.5′S, 85°35.6′W, 4334 m, 14 Nov. 1904, fine, green mud and manganese nodules, 1.8°C.
Stannophyllum zonarium

St. 4666. 11°55.5′S, 84°20.3′W, 4758 m, 18 Nov. 1904, light grey ooze with flocculent debris, 1.6°C.
Stannophyllum zonarium

St. 4717. 5°11.0′S, 98°56.0′W, 3937 m, 13 Jan. 1905, many diatoms and many radiolarians filled with black mineral particles, 1.8°C.
Stannoma dendroides
Stannophyllum zonarium
Stannophyllum globigerinum

St. 4721. 8°07.5′S, 104°10′W, 3814 m, 15 Jan. 1905, Globigerina o oze, 1.7°C.
Stannoma dendroides
Stannophyllum zonarium
Stannophyllum globigerinum

St. 4742, 0°0.4′N, 117°0.7′W, 4243 m, 15 Feb. 1905, great many radiolarians and diatoms, 1.2°C.
Stannoma dendroides
Stannoma coralloides
Stannophyllum zonarium
Stannophyllum globigerinum
Stannophyllum alatum

Valdivia Expedition, 1898-1899

Area: Atlantic – Indian Ocean.
Station list: SCHOTT (1902).
Publication: SCHULZE (1907a).
Location of material: Zoologisches Museum der Humboldt-Universität, Berlin, DDR.

St. 240. Off East Africa (6°12.9′S, 41°17.3′E), 2959 m, 14 Mar. 1899, Globigerina ooze, 2.0°C.
Stannophyllum globigerinum

St. 250. Off East Africa (1°47.8′S, 41°58.8′E), 1668 m, 24 Mar. 1899, Globigerina ooze and blue mud, 3.8°C.
**Psammetta erythrocytomorpha*

Siboga Expedition, 1899-1900

Area: Indonesia.
Station list: TYDEMANN (1903); hydrography: RIEL (1956).
Publication: SCHULZE (1906).
Location of material: Zoölogisch Museum, Amsterdam.

St. 211. South of Celebes (5°40.7′S, 120°45.5′E), 1158 m, 25 Sep. 1899, coarse, grey mud, *c.* 4.0°C. (after "Snellius" St. 186).
**Psammetta globosa*
**Psammina globigerina*
**Stannophyllum globigerinum*

St. 221. Molluccan Sea (6°24′S, 124°39.0′E), 2798 m, 4 Nov. 1899, solid, bluish-grey mud with foraminiferans, *c.* 3.1°C. (after "Snellius" St. 201).
**Stannophyllum globigerinum*

St. 227. Molluccan Sea (4°50.5′S, 127°59′E), 2081 m, 13 Nov. 1899, grey mud with an upper layer of brown mud with both mixed with sand, *c.* 3.3°C. (after "Challenger" St. 195)
**Psammina globigerina*

St. 295. Timor Sea (10°35.6′S, 124°11.7′E), 2050 m, 24 Jan. 1900, fine, grey mud 3 cm thick, upper layer more liquid, brown with black stripes, *c.* 3.4°C. (after "Snellius" St. 155)
Stannophyllum globigerinum

Scotia Expedition, 1903-1904

Area: Antarctic.
Station list: PEARCY (1914); hydrography: DEACON (1937).
Publication: PEARCY (1914).
Location of material: material unaccounted for.

St. 420. Weddell Sea (69°33′S, 15°19′W), 4795 m, 21 Mar. 1904, glacial clay, −0.8° - −0.5°C.
Syringammina minuta

Schepotieff, personal collection 1908

Area: Ceylon and the west coast of India.
Station information and publication: SCHEPOTIEFF (1912b).
Location of material: material is unaccounted for.

1. Kankesanturai. North point of Ceylon, 1-5 m, spring 1908, sand, *c.* 25°C.
Psammetta ovale n. sp.
Stannophyllum sp.
2. Mahé. Malabar Coast, India, about 20 m, spring 1908, corals, *c.* 25°C.
Cerelasma sp.

Goldseeker Expedition, 1910

Area: North Atlantic.

Station list: HERON-ALLEN & EARLAND (1913); hydrography: BRADY (1883).

No publication.

Location of material: British Museum of Natural History, London.

Haul 8108. Faroe Channel (59°41'N, 8°W), 850 m, 1910, sand and ooze, *c.* 7.7°C.

**Syringammina fragilissima*

John Murray Expedition, 1933-1934

Area: Indian Ocean.

Station list: SEWELL (1935).

No publication.

Location of material: British Museum of Natural History, Lopdon.

St. 119. Off E. Africa (6°29'24''S, 39°49'54''E to 6°32'00''S, 39°53'30''E), 1204 m, 19 Jan. 1934, *c.* 5°C. (after "Galathea" St. 229)

**Psammetta globosa*

Galathea Expedition, 1951-1952

Area: Circumnavigation.

Station list: BRUUN (1959); hydrography: KIILERICH (1964).

No publications.

Location of material: Zoological Museum, Copenhagen.

St. 190. Off S. W. Africa (29°42'S, 33°19'E), 2720 m, 3 Feb. 1951, Globigerina ooze, *c.* 0.4°C. (after St. 186)

**Psammetta globosa*

**Galatheammina calcarea*

St. 192. Off S. E. Africa (32°00'S, 32°41'E), 3430 m, 5 Feb. 1951, Globigerina ooze, *c.* 1.6°C. (after St. 200)

**Galatheammina tetraedra* n. gen., n. sp.

St. 198. Off S. E. Africa (30°32'S, 34°27'E), 2700 m, 15 Feb. 1951, *c.* 0.1°C. (after St. 200)

**Galatheammina calcarea*

**Galatheammina tetraedra* n. gen., n. sp.

St. 200. Off S. E. Africa (29°39'S, 37°01'E), 5110 m, 18 Feb. 1951, Globigerina ooze, 0.54°C.

**Maudammina arenaria* n. gen., n. sp.

**Stannophyllum fragilis* n. sp.

St. 231. Off E. Africa (8°52'S, 49°25'E), 5020 m, 7 Mar. 1951, *c.* 0.3°C. (after St. 232)

**Stannophyllum reticulatum*

**Stannophyllum mollum* n. sp.

St. 232. Off E. Africa (9°03'S, 49°22'E), 4930 m, 8 Mar. 1951, 0.3°C.

**Stannoma dendroides*

**Stannophyllum indistinctum* n. sp.

St. 233. Off E. Africa (7°24'S, 48°24'E), 4730 m, 9 Mar. 1951, *c.* 0.3°C. (after St. 229)

**Psammetta arenocentrum* n. sp.

**Stannophyllum mollum* n. sp.

St. 234. Off E. Africa (5°25'S, 47°09'E), 4820 m, 10 Mar. 1951, Globigerina ooze, *c.* 0.8°C. (after St. 236)

**Cerelasma massa* n. sp.

**Stannophyllum mollum* n. sp.

St. 235. Off E. Africa (4°47'S, 46°19'E), 4810 m, 11 Mar. 1951, Globigerina ooze, *c.* 0.8°C. (after St. 236)

**Cerelasma massa* n. sp.

**Stannoma dendroides*

**Stannophyllum globigerinum*

**Stannophyllum indistinctum* n. sp.

**Stannophyllum mollum* n. sp.

St. 238. Off E. Africa (3°23'S, 44°04'E), 3960 m, 13 Mar. 1951, Globigerina ooze, *c.* 1.3°C. (after St. 236)

**Psammetta globosa*

**Stannoma dendroides*

**Stannophyllum globigerinum*

St. 716. Off Costa Rica (9°23'N, 89°32'W), 3570 m, 6 May 1952, dark, muddy clay, *c.* 1.9°C. (after WOLFF 1961)

**Psammina nummulina*

**Stannophyllum zonarium*

**Stannophyllum radiolarium*

Vitiaz Expeditions, 1954, 1955, 1957, 1958, 1959, 1966, 1969

Area: Pacific, mostly the north-western part.

Station list and other information: KOLTUN (pers. comm.); hydrography: KNUDSEN (pers. comm.).

No publication, except for mention of a few genera names by BELJAEV (1966).

Location of material: Zoological Institute, Leningrad.

St. 3156. Off Japan (39°57'N, 165°08'E), 5515 m, 28 Sep. 1954, red clay with pumice and concretions, 1.6°C.

**Stannophyllum radiolarium*

St. 3166. Kuril-Kamchatka Trench (44°43'N, 153°49'E), 5017 m, 3 Oct. 1954, brown alluvium with pebbles, 1.6°C.

**Stannophyllum granularium* n. sp.

**Stannophyllum mollum* n. sp.

St. 3198. E. of Japan (39°03′N, 151°51′E), 5345-5757 m, 15 Oct. 1954, reddish-brown clayey silt with pumice, 1.6°C.
Stannophyllum granularium n. sp.
**Stannophyllum mollum* n. sp.

St. 3232. E. of Japan (33°18′N, 149°46′E), 6116 m, 6 May 1955, brown clayey silt, 1.6°C.
**Stannophyllum granularium* n. sp.

St. 3359. Aleutian Trench (51°30′N, 172°05′E), 5000 m, 8 Jun. 1955, silt, 1.5°C.
**Stannophyllum granularium* n. sp.

St. 3363. E. of Kamchatka (48°12′N, 169°33′E), 6272-6282 m, 10 Jun. 1955, brown silt with pumice, 1.7°C.
**Stannophyllum granularium* n. sp.

St. 3575. Japan Trench (38°02′N, 146°33′E), 5450-5475 m, 8 May 1957, fine mud with pumice and pebbles, 1.6°C.
**Stannophyllum granularium* n. sp.
Stannophyllum mollum n. sp.

St. 3593. Japan Trench (40°55′N, 144°53′E), 6380 m, 22 May 1957, mud with pebbles
**Stannophyllum mollum* n. sp.

St. 4213. Off San Francisco (34°54′N, 123°56′W), 4231-4200 m, 16 Dec. 1958, green-brown clayey silt
**Stannophyllum zonarium*

St. 4265. Off Mexico (24°58′N, 113°25′W), 3260 m, 13 Jan. 1959, brown clayey silt
**Stannophyllum zonarium*

St. 4495. Banda Sea (7°06′S, 126°04′E), 4365 m, 19 Oct. 1959
**Stannophyllum granularium* n. sp.

St. 5617. Kuril-Kamchatka Trench (42°32′N, 153°46′E), 6710-6675 m, 6 Aug. 1966
**Stannophyllum granularium* n. sp.

St. 5623. Kuril-Kamchatka Trench (45°26′N, 154°59′E), 5045-4995 m, 19 Aug. 1966
**Stannophyllum granularium* n. sp.

St. 5624. Kuril-Kamchatka Trench (45°26′N, 154°12′E), 5200 m, 20 Aug. 1966
**Stannophyllum mollum* n. sp.

St. 5625. Kuril-Kamchatka Trench (45°28′N, 153°46′E), 6215-6205 m, 21 Aug. 1966
**Stannophyllum granularium* n. sp.

St. 6088. Aleutian Trench (53°58.5′N, 157°36′W), 5740 m, 4 May 1969
**Stannophyllum granularium* n. sp.

Vema Expedition, 1958

Area: East Pacific.
Station list: EMERSON (pers. comm.); hydrography: TOWNSEND (1901), WOLFF (1961).
No publication.
Location of material: American Museum of Natural History, New York.

St. 15-44. 9°23′N, 89°06′W, 3498 m, 20 Nov. 1958, 1.9°C.
**Stannophyllum zonarium*

St. 15-49. 9°24′N, 89°27′W, 3563 m, 22 Nov. 1958, 2.1°C.
**Psammina nummulina*

St. 15-50. 9°18′N, 89°32′W, 3502 m, 22 Nov. 1958, 2.1°C.
**Stannophyllum zonarium*

St. 15-55. 12°45′N, 88°38′W, 3950 m, 24 Nov. 1958, *c.* 2°C.
**Cerelasma gyrosphaera*
**Stannophyllum zonarium*

St. 15-64. 6°08′S, 82°41′W, 4051 m, 5 Dec. 1958, 1.9°C.
**Stannophyllum zonarium*

Magdalena Bay Expedition, 1964

Area: East Pacific.
Information: LOWENSTAM (pers. comm.).
No publication.
Location of material: California Institute of Technology, Pasadena.

St. A-36. Off southern Baja California (24°45.2′N, 113°25.0′W to 24°21.3′N, 113°16.8′W), 3333-3535 m, Feb. 1964.
**Stannophyllum zonarium*

NZOI, 1965, 1968

Area: New Zealand waters.
Station list: LEWIS (pers. comm.); hydrography: GARNER & RIDGWAY (1965).
Publications: LEWIS (1966, parts).
Location of material: New Zealand Oceanographic Institute, Wellington.

St. D 227. West of Cook Strait (39°50′S, 169°43′E), 711 m, 1965, Globigerina ooze, *c.* 7-8.5°C.
**Syringammina tasmanensis*

St. D 228. West of Cook Strait (39°08′S, 170°17′E), 664 m, 1965, Globigerina ooze, *c.* 7-8.5°C.
**Syringammina tasmanensis*

St. E 417. Off Dunedin (45°12′S, 171°49′E), 860 m, 13 Oct. 1965, detrital, sandy mud with shells and foraminiferans, *c.* 6-7°C.

**Syringammina fragilissima*

St. E 903 a-b. West of North Island (37°33′S, 172°05′E), a: 960 m, b: 984 m, 27 Mar. 1968, volcanic rock with thin covering of foraminiferal sand, *c.* 7°C.

**Reticulammina novazealandica* n. gen., n. sp.

St. F 881. East of North Island (37°07′S, 177°14′E), 1253 m, 4 Oct. 1968, foraminiferal sand with sand and glauconite, *c.* 5°C.

**Reticulammina lamellata* n. gen., n. sp.

St. F 913. North of North Island (34°43.5′S, 174°31.5′E), 743 m, 11 Oct. 1968, foraminiferal sand with detrital mud, *c.* 7°C.

**Reticulammina novazealandica* n. gen., n. sp.

**Reticulammina labyrinthica* n. gen., n. sp.

TERMINOLOGY

The structures covered by the terms used in the descriptive part are discussed in detail in the general part.

General terminology.

Most of the terms are the same and are used in the same sense as within other protozoan groups, especially the Foraminifera. These terms are dealt with in Boltovskoy (1956) and Loeblich & Tappan (1964, p. 58 ff.).

Special terminology.

The special terminology of the xenophyophores was created and compiled by Schulze (1907a). It includes terms defined by Haeckel (1889), Rhumbler (1894), and Schaudinn (1899).

The following list consists of short definitions of the terms generally used in the descriptions. References to the more detailed discussions in the general part are given in the parentheses.

Granellae: crystals of barium sulphate (barite) found in large numbers in the cytoplasm (p. 70).

Granellare: the plasma body ("protoplasm") of the animal together with its surrounding tube. It is yellowish and branched in varying degrees (p. 68).

Linellae: long, thin threads composed of a cement-like matter. They are found outside the granellare and are regarded as an organic part of the test (p. 74).

Stercomes: fecal pellets (p. 73).

Stercomare: masses, usually formed as strings of stercomes lumped together in large numbers and covered by a thin membrane (p. 72).

Xanthosomes: reddish-brown or yellowish, rounded, and often aggregated bodies found between the stercomes in stercomare (p. 74).

Xenophyae: the foreign bodies of which the inorganic part of the test is composed (p. 76).

III. SYSTEMATIC PART

THE PLACE OF THE XENOPHYOPHORIA WITHIN THE PROTOZOA

Schulze (1912, p. 42) regarded the group as an order of the class Rhizopodea. Poche (1913, p. 202), Rhumbler (1923, p. 105), Loeblich & Tappan (1961, p. 318; 1964, p. 789), and Corliss (1962, p. 67) agreed with this viewpoint.

In the two most recently proposed classifications of the Sarcodina, the xenophyophores are placed in somewhat different positions. Honigberg *et al.* (1964, p. 13) agreed with Schulze in regarding the group as an order side by side with the Foraminiferida (and Athalamida), and placed it in the subclass Granuloreticulosia. Bovee & Jahn (1965a, p. 36; 1965b, p. 297) also regarded the group as an order, but they placed it together with the Mycetozoida ("true slime molds") in the subclass Alternatia within their class Hydraulea.

Which of these classifications one prefers to use is at present merely a matter of opinion.

The taxonomic proposal of Honigberg *et al.* (The Committee of Taxonomy and Taxonomical Problems of the Society of Protozoologists) concerns the whole classification of the Protozoa and to a great degree has its roots in the more or less accepted systems set up during the last fifty years (cf. Hall 1953, p. 106 ff., and Grassé 1952, 1953). The innovations presented result from the co-operative work done by numerous experts, also from outside the Committee (Honigberg *et al.* 1964, p. 7), and this classification is thus a compromise of different views. Considering the amount of experience that formed the basis for this classification, the inevitable future changes will have to be well-founded.

The taxonomic proposal of BOVEE & JAHN concerns only the Sarcodina and breaks with many classical concepts, especially on the order level. The first proposal of the system (JAHN & RINALDI 1959, and especially JAHN, BOVEE & SMALL 1960) was somewhat hesitating, but JAHN and his co-workers have since several times argued for their views (BOVEE & JAHN 1960, 1964, 1965a, 1965b, 1967; JAHN & RINALDI 1963). Decisive new investigations do not seem to have been published, but supporting results have come from JAHN (1964) and JAHN, RINALDI & BROWN (1964). The main division of this system has been adopted by LOEBLICH & TAPPAN (1964). Objections and reservations have come from CORLISS (1962, p. 48), WOHLFARTH-BOTTERMANN (1962, pp. 20, 22), SANDON (1963, p. 167), and HEDLEY (1964, pp. 28, 29).

Classification according to HONIGBERG *et al.* (1964, p. 12):

Superclass Sarcodina
- Class 1. Rhizopodea
  - Subclass (1) Lobosia, with two orders: Amoebida and Arcellinida
  - Subclass (2) Filosia, with two orders: Aconchulinida and Gromiida
  - Subclass (3) Granuloreticulosia, with three orders: Athalamida, Foraminiferida, and Xenophyophorida
  - Subclass (4) Mycetozoia, with three orders: Acrasida, Eumycetozoida, and Plasmodiophorida
  - Subclass (5) Labyrinthulia, with one order: Labyrinthulida
- Class 2. Piroplasmea
  - Order Piroplasmida
- Class 3. Actinopodea
  - Subclass (1) Radiolaria, with two orders: Porulosida and Oculosida
  - Subclass (2) Acantharia, with two orders: Acanthometrida and Acanthophractida
  - Subclass (3) Heliozoia, with three orders: Actinophryida, Centrohelida, and Desmothoracida
  - Subclass (4) Proteomyxidia, with one order: Proteomyxida.

In the present paper the xenophyophores are regarded as a subclass instead of an order (cf. diagnosis and remarks, p. 20), and with this modification the classification of HONIGBERG *et al.* is as follows:

Superclass Sarcodina
- Class 1. Rhizopodea
  - Subclass (1) Lobosia
  - Subclass (2) Filosia
  - Subclass (3) Granuloreticulosia
  - Subclass (4) Xenophyophoria
  - Subclass (5) Mycetozoia
  - Subclass (6) Labyrinthulia
- Class 2. Piroplasmea
- Class 3. Actinopodea
  - Subclass (1) Radiolaria
  - Subclass (2) Acantharia
  - Subclass (3) Heliozoia
  - Subclass (4) Proteomyxidia

Classification according to BOVEE & JAHN (1965b, p. 296):

Subphylum Sarcodina
- I. Class Autotractea
  - A. Subclass Actinopodia, with two orders: Heliozoida and Acantharida
  - B. Subclass Filoreticulosia, with four orders: Hyporadiolarida, Radiolarida Granuloreticulida, and Filida
- II. Class Hydraulea
  - A. Subclass Cyclia, with two orders: Lobida and Acrasida
  - B. Subclass Alternatia, with two orders: Mycetozoida and Xenophyophorida

Conforming with the view of the xenophyophores' pseudopods expressed in this paper (p. 71), I have transferred the group from the class Hydraulea to the class Autotractea. With this alternation and with the xenophyophores regarded as a subclass instead of an order the classification of BOVEE & JAHN is as follows:

Subphylum Sarcodina
- I. Class Autotractea
  - A. Subclass Actinopodia
  - B. Subclass Filoreticulosia
  - C. Subclass Xenophyophoria
- II. Class Hydraulea
  - A. Subclass Cyclia
  - B. Subclass Alternatia.

HITHERTO USED CLASSIFICATIONS OF THE XENOPHYOPHORES

The basis of the systematic divison of the xenophyophores is the classification made by HAECKEL (1889) for the "Deep-Sea Keratosa". He worked with eight genera distributed in three families:[1]

Family	Genus
Psamminidae	*Psammina*
	Holopsamma (=*Reticulammina* pars)
	Psammopemma (=*Galatheammina* pars and *Cerelpemma* pars)
Spongelidae	*Cerelasma*
	Psammophyllum (=*Stannophyllum*)
Stannomidae	*Stannophyllum*
	Stannarium (=*Stannophyllum*)
	Stannoma

This system was without modifications followed by DELAGE & HÉROUARD (1899) and MINCHIN (1900), although the latter was obviously in doubt about the placement of the genera which HAECKEL assigned to Spongelidae.

SCHULZE (1907a) modified HAECKEL's system by distributing his members of the sponge family Spongelidae in other families. In his arrangement eight genera are distributed in two families:

Family	Genus
Psamminidae	*Psammetta*
	Psammina
	Cerelasma
	Holopsamma (*in sensu* HAECKEL 1889)
	Psammopemma (*in sensu* HAECKEL 1889)
Stannomidae	*Stannoma*
	Stannophyllum
	Stannarium

SCHEPOTIEFF (1912b), who was the most recent author to actually work with a relatively large collection of xenophyophores, followed SCHULZE's classification, as did POCHE (1913), RHUMBLER (1923), and LOEBLICH & TAPPAN (1961, 1964). Other authors grouped all the genera in one family (LISTER 1909; LAUBENFELS 1936) or even in one subfamily (LAUBENFELS 1948).

1. Actually, he listed four families of "Deep-Sea Keratosa", but one of them presumably did not contain xenophyophores (see further p. 63).

PROPOSED CLASSIFICATION OF THE XENOPHYOPHORES

The system of the xenophyophores presented here follows the main divisions of SCHULZE (1907a) (although these are given a higher taxonomic rank in some cases), but many of the details are new. Definitions of the taxonomic categories are given in the descriptive part.

Subclass Xenophyophoria n. subcl.
- 1. Order Psamminida n. ord.
  - 1. Family Psammettidae n. fam.
    - Genus *Maudammina* n. gen.
    - Genus *Psammetta* Schulze, 1906.
  - 2. Family Psamminidae Haeckel, 1889.
    - Genus *Galatheammina* n. gen.
    - Genus *Reticulammina* n. gen.
    - Genus *Psammina* Haeckel, 1889.
    - Genus *Cerelpemma* Laubenfels, 1936.
  - 3. Family Syringamminidae n. fam.
    - Genus *Syringammina* Brady, 1883.
  - 4. Family Cerelasmidae n. fam.
    - Genus *Cerelasma* Haeckel, 1889.
- 2. Order Stannomida n. ord.
  - 1. Family Stannomidae Haeckel, 1889.
    - Genus *Stannoma* Haeckel, 1889.
    - Genus *Stannophyllum* Haeckel, 1889.

DESCRIPTIVE PART

High-level classification according to HONIGBERG *et al.* (1964).

Phylum Protozoa
Subphylum Sarcomastigophora
Superclass Sarcodina
Class Rhizopodea

Subclass Xenophyophoria n. subcl.

Synonymy: Domatocoela Haeckel, 1889, p. 8; Abyssospongea (pars) Delage & Hérouard, 1889, p. 197; Xenophyophora Schulze, 1904, p. 1387; 1906, p. 1; 1907a, p. 5; 1907b, p. 145; 1912, p. 38; Xenophyophoridae Lister, 1909, p. 286; Xenophyophora, SCHEPOTIEFF 1912b, p. 267; Psamminidea Poche, 1913, p. 202; Arxenophyria Rhumbler, 1913, p. 339; Xenophiophorae Chatton, 1925, p. 76; Psamminidae Laubenfels 1936, p. 32; Psammininae Laubenfels 1948, p. 180; Xenophyophorida Loeblich & Tappan 1961, p. 318; 1964, p. 789; CORLISS 1962, p. 67; HONIGBERG *et al.*, 1964, p. 13; BOVEE & JAHN 1965a, p. 297.

Diagnosis: The subclass includes animals with a multinucleate plasmodium (granellare) enclosed by a branched tube system composed of a transparent cementlike organic substance. The pseudopodia extend through the free ends of the tubes. The plasma contains numerous barite crystals (granellae). The fecal pellets (stercomes) are retained outside the plasma and organic tube system as dark strings or masses (stercomare). A test consisting of stercomare and foreign matter (xenophyae) in varying proportions surrounds the granellare. Non-granular filopods (reticulopods?) are presumably present.

Remarks: It is well-known that it is often difficult to refer a group of Sarcodina to the proper subclass and order with certainty. This is mainly due to the difficulties in finding and establishing a set of exact and constant characteristics for practical use. The most serious problems in this respect have been discussed by CORLISS (1959, p. 169). Groups of high taxonomical rank have in some cases (out of necessity) been established on the basis of only one character. The distribution of the naked forms of amoebas in several distinct orders within three different subclasses exemplifies this because the pseudopod type served as the sole basis for this classification (cf. e. g. GRASSÉ 1953 and HONIGBERG *et al.* 1964).

The raising of the order Xenophyophorida Schulze, 1907 to the subclass level is justified by its following special set of characteristics: 1) the organization as a plasmodium within a distinct, strongly branched tube-system; 2) the constant presence of granellae in the plasma; 3) the retention of the stercomes in voluminous masses. The generally large size (at least in all known mature individuals) and the distinctive test structure are also very characteristic of the group, although they are perhaps not quite unique. When the current classification of the Sarcodina (classification based mainly on pseudopod type) is taken into consideration, it becomes apparent that the xenophyophores are difficult to place in the succession of subclasses within the system since their pseudopodia are very poorly known. (For further discussion of the characters mentioned and comparisons made with other rhizopod groups, the reader is referred to the general part.)

Key to the orders

Without linellae; body more or less rigid .... Psamminida
With linellae; body flexible .... Stannomida

Order *Psamminida* n. ord.

Diagnosis: Xenophyophores without linellae. The body is rigid.

Remarks: The order Psamminida includes xenophyophores of rather varying appearances distributed in the four families Psammettidae n. fam., Psamminidae Haeckel, 1889, Syringamminidae n. fam., and Cerelasmidae n. fam. This order is sharply distinguished from the other order in the subclass by the absence of linellae. When present, the linellae can be easily observed with the naked eye, and they seem to be very useful in identification since similar structures are as yet unknown in any other protozoan (cf. GRIMSTONE 1961; NOIROT-TIMOTHÉE 1963; PITELKA 1963, 1969).

Scope of the order: The families in the order are defined and distinguished according to the arrangement of the xenophyae and the development of cement in the test. On this basis they can be placed in a series with increasing test complexity.

In the Psammettidae the xenophyae are cemented together without any obvious order. Members of the family are built as more or less massive lumps.

In the Psamminidae the xenophyae are cemented into one or more layers; loosely lying xenophyae may or may not be found between these layers. The body form varies greatly from simple, lumpy forms to free-branched or reticulate forms.

The Syringamminidae are built of well-cemented tubes with the xenophyae strictly limited to the wall. The tubes are organized in a rather complicated system indicative of a phylogenetic distance from the other three families.

The Cerelasmidae are distinguished by the development of great amounts of cement, and the family is difficult to place in relation to the other three. The xenophyae are arranged without any obvious order, and there seems to be a tendency toward reduction in their role as test components.

Key to the families

1a. Xenophyae cemented together without any obvious order; amount of cement varying from small to large 2
1b. Xenophyae cemented together in plates, in a distinct surface layer, or in the walls of tubes 3
2a. Xenophyae cemented together at points of contact by small amounts of cement; body lumpy .... Psammettidae
2b. Xenophyae lying singly and each fully enclosed in a cement layer; body composed of anastomosing branches .... Cerelasmidae 38
3a. Xenophyae cemented together as tube walls without xenophyae in the interior Syringamminidae 35
3b. Xenophyae cemented together in plates, or forming a distinct surface layer covering a mass of loose xenophyae .... Psamminidae 27

Family **PSAMMETTIDAE** n. fam.

Diagnosis: The test is massive and strongly built. The xenophyae are apparently haphazardly arranged and are cemented only at the random points of contact. There is no specialized surface layer and there are no large openings in the test.

Remarks: The two genera *Maudammina* n. gen. and *Psammetta* Schulze, 1906 are referred to this family. The creation of a special family for these genera is based solely on the test characteristics; with regard to construction, the test is considered to be the most primitive within the xenophyophores.

Maudammina may be regarded as the more primitive of the two for the following reasons: 1) the irregular body form; 2) the use of only one type of xenophyae during the whole life span; 3) the large amount of xenophyae in relation to the amount of protoplasm.

It should be noted that quite young specimens of *Psammetta* are difficult to distinguish from *Maudammina.*

Key to the genera and species

1a. Body irregular, platelike; consistency very firm.......... *Maudammina arenaria*
1b. Body form a circular disc or nearly spherical lump .... *Psammetta* 2
2a. Body form a circular disc.......... *P. erythrocytomorpha*
2b. Body form a nearly spherical lump 3
3a. Body oval with flat lower surface and arched upper surface; primary xenophyae: sponge spicules and foraminiferan tests .... *P. ovale*
3b. Body spherical 4
4a. Primary xenophyae: sand grains .... *P. arenocentrum*
4b. Primary xenophyae: foraminiferan tests .... *P. globosa*

Genus ***Maudammina*** n. gen.[1]

Diagnosis: The body is flattened and of irregular form with or without ridge-like crests. The consistency is very firm. The xenophyae are all of the same type and cemented only at the random places of contact, therefore numerous small interstices are left in between.

Remarks: *Maudammina* has been established to receive *M. arenaria* n. sp. which is the type species by monotypy.

Maudammina differs from *Psammetta,* the other genus of the family, in the following: 1) *Maudammina* has an irregular body form while this is well-defined and regular in *Psammetta.* 2) *Maudammina* has only one type of xenophyae while *Psammetta* has two, one type being found predominantly in the younger stages and the other predominantly in the later stages. 3) There is a higher ratio of xenophyae to protoplasm in *Maudammina* than in *Psammetta.* 4) *Maudammina* has a firm consistency due to the quartz while *Psammetta* is felty because of the use of sponge spicules. The last characteristic may not be very useful as a genus character, however, since the consistency depends on the type of xenophyae used.

1. The genus is named after my wife, MAUD.

Maudammina arenaria n. sp.
Pl. 1 A-C.

Material:

"Galathea" St. 200. – 3 specimens and a fragment. As holotype was selected the largest, measuring 45 × 26 × 6 mm.

Diagnosis: The body is flattened, more or less irregularly bent, and has a few plate-like ridges on the one side. It is up to about 45 mm long and 4-8 mm thick; 6 mm is the most common thickness. The colour is yellowish brown and the consistency is very firm. The xenophyae are sand grains.

Morphology: The largest specimen measures 45 × 26 mm and the thickness varies from 5-8 mm. On one surface are found four more or less well-developed ridges 11-30 mm long, 4-9 mm high, and 4-6 mm thick. The long ridge is bent in an obtuse angle and may consist of two ridges, each one being about 15 mm long.

Another specimen (Pl. 1 B) is a strongly bent, partly twisted disc with a single ridge that is up to 13 mm high. The third and smallest specimen is a strongly bent disc without ridges; this indicates that ridges first appear at a certain age and size. If straight, the small specimen would measure about 30 × 15 mm, and it is about 5 mm thick.

The undamaged surfaces are yellow-brown in colour. When the rather thin outermost layer of xenophyae without stercomare is scraped off, the colour is almost black due to stercomare which is found both as independent pellets and as strings. (The former have presumably been scattered when the surface was damaged since the strings of stercomare are very fragile.)

Cytology: Due to the consistency of the test, the minute amount of protoplasm, and the numerous silicious xenophyae, it has been impossible to make a detailed cytological investigation.

The yellowish granellare branches are dichotomously divided and measure 30-90 μ in diameter. Granellae are numerous; they are elongate, rounded, and measure 1-4 μ in length.

The dark strings of stercomare are strongly dichotomously branched and most of the branches are short and bulbous. They measure 50-190 μ in diameter. There are few xanthosomes; those present are scattered, yellowish-brown or reddish-brown, rounded or elongate bodies, 7-12 μ in diameter.

Grains of quartz of many different sizes are the main xenophyae; small numbers of other mineral particles are, however, also found.

Remarks: The smallest, and therefore presumably the youngest specimen, was cross-sectioned in order to see whether the oldest part could be distinguished. However, no area proved to be emptier or looser than any other, and no different types of xenophyae were found.

Occurrence: Known from one dredging off S.E. Africa, at 5110 m, on Globigerina ooze, and at 0.5° C.

Genus *Psammetta* Schulze, 1906

Psammetta Schulze, 1906, p. 1.

Diagnosis: The body is regular and is either a spherical to ellipsoidal lump or a circular disc. Excrescences are not formed. The consistency is felt-like, and the surface is faintly shaggy. In most species there are xenophyae of two types; the youngest part of the body contains primary xenophyae and the remainder of the body contains secondary xenophyae. In all the known species the secondary xenophyae are silicious sponge spicules.

Remarks: SCHULZE did not diagnose the genus, but SCHEPOTIEFF (1912b, p. 273) characterized it as follows: "Körper stellt eine kreisrunde, bikonvexe Scheibe ohne Rindenschicht dar." The statement is incorrect since one species, also referred to by himself, is spherical and another is biconcave.

SCHULZE referred to *P. erythrocytomorpha* already in 1906; it was, however, a nomen nudum at that time since no description appeared until 1907. *P. globosa* Schulze is the type of the genus.

Psammetta globosa Schulze, 1906
Pls. 1 D-E; 2 A-B

Psammetta globosa Schulze, 1906, p. 1, pl. I, 1-10, pl. II, 1-11.
non *Psammetta globosa,* SCHEPOTIEFF 1912b, p. 247, pl. 15, 1-71.

Material:

"Siboga" St. 211. – About 50 specimens.
"John Murray" St. 119. – 28 specimens.
"Galathea" St. 190. – 1 specimen.
"Galathea" St. 238. – 14 specimens.

Diagnosis: The body is spherical and measures 5-25 mm in diameter. Large specimens are sometimes slightly ellipsoidal. The colour is dark brown, and the consistency varies from felty to firm. Primary xenophyae are foraminiferan tests; secondary xenophyae are sponge spicules.

Since the material from the three expeditions differs somewhat, a special description will be given for each.

The "Siboga" material (Pl. 1E)

Most of the individuals are between 15 and 20 mm in diameter. Many have one or more slightly developed flattenings on the faintly shaggy surface. These flattenings are, however, presumably artifacts, caused by pressure from neighbouring specimens during fixation. The colour is dark brown and the consistency is that of thick felt. The yellow granellare branches are conspicuous on the surface.

The smallest and youngest specimens in the sample are spherical and measure about 5 mm in diameter. In these specimens the test consists almost entirely of foraminiferan tests which are the primary xenophyae. In specimens about 7 mm in diameter, the lump of foraminiferan tests is covered by a thin layer of sponge spicules which are the secondary xenophyae. In still larger and older individuals, the layer of sponge spicules is thicker, while the central lump of foraminiferan tests remains unaltered in size.

Cytology: Granellare branches are spreading irregularly through the animal, and they possibly anastomose. In cross-section the branches are circular, and measure 30-120 μ in diameter. Granellae are numerous; they are rounded or elongate, and are 1-4 μ in length. There are numerous spherical nuclei measuring 2.5 μ in diameter. The plasma seems subdivided into rounded lumps (fixation artifact?). Some smaller lumps contain numerous small nuclei about 0.8 μ in diameter. These lumps often give the impression of being subdivided into cell-like structures, since there is a light area around each nucleus. They are interpreted by SCHULZE (1906, p. 10) as possible stages of swarmers.

The initial plasma found in the centre of the animal was observed by SCHULZE (1912, p. 39), but he did not comment on it. It is thin, looks transparent, and contains scattered stercomes, granellae, and xanthosomes.

Stercomare extend radially as anastomosing strings and have a circular cross-section with a diameter of 100-360 μ. Xanthosomes are scattered; they are rounded, yellow-brown, and measure 1-12 μ in diameter. SCHULZE (1906, p. 7) noted that they are irregularly distributed.

Xenophyae are chiefly silicious sponge spicules and foraminiferan tests. The latter are concentrated around the centrally located initial plasma, and are 10-30 in number. Outside this centre the test is composed of cemented spicules, between which foraminiferan and radiolarian tests are only occasionally found.

The "John Murray" material (Pl. 2A-B)

All the specimens are nearly perfect spheres in form, and they measure 16-25 mm in diameter, most of them being 20-24 mm. The colour is dark brown, and the consistency is very firm. The surface is bristly. The yellow branches of granellare can be seen but are not conspicuous.

Cytology: The seemingly anastomosing branches of granellare measure 60-90 μ in diameter. Granellae are numerous; they are elongate, slightly angular, and measure 1-5 μ in length. The numerous nuclei are spherical or ellipsoidal and measure 2-3 μ in diameter. Small nuclei, about 0.8 μ in diameter, are observed as scattered clusters.

The initial plasma was not seen. The central part of the animals is very loose. The only structures of cytological interest seen are scattered stercomes. Presumably the centre dies when the animal reaches about 20 mm in diameter.

The anastomosing strings of stercomare measure 75-450 μ in diameter but the wall is often poorly limited. There are no xanthosomes.

There are numerous, tightly packed xenophyae which are sponge spicules. Scattered foraminiferan tests and test fragments are found among them. A tight lump, 4-7 mm in diameter, of large foraminiferan tests and test fragments is found in the centre of the animals intermingled with a small number of sponge spicules.

The "Galathea" material (Pl. 1D)

Most of the specimens are spherical with a diameter of about 14 mm, but all are more or less damaged. The largest nearly intact specimen is faintly ellipsoidal and measures 18 mm in length. Another specimen, which is greatly damaged, may have been 22-24 mm in length. The colour is dark brown and the consistency is that of heavy felt. The surface is shaggy. The yellow granellare branches are conspicuous.

Table 2. Comparison of some characters of the species of *Psammetta*.

	P. globosa			*P. arenocentrum*	*P. ovale*	*P. erythrocytomorpha*
	"Siboga"	"John Murray"	"Galathea"			
Body form	spherical	spherical	spherical	?	oval with arched top-side and flat underside	circular, biconcave disc
Size	5-25 mm	16-25 mm	12-24 mm	6-?9 mm	1-15 (20) mm	5-12 mm × 20-30 mm
Granellare diameter	30-120 μ	30-90 μ	40-210 μ	60-120 μ	330 μ	90-120 μ
Nucleus diameter	2.5 μ	2-3 μ	2.5 μ	?	3-7 μ	2-3 μ
Stercomare diameter	100-360 μ	75-450 μ	90-270 μ	110-160 μ	330 μ	150-300 μ
Primary Xenophyae	foraminiferan tests	foraminiferan tests	?	sand grains	sponge spicules, foraminiferan tests	no differentiation, all are sponge spicules
Secondary Xenophyae	sponge spicules	sponge spicules	sponge spicules	sponge spicules	sponge spicules, sand grains, shell fragments	

Cytology: The diameter of the granellare branches is 40-210 μ, most of them being between 90 and 125 μ. The numerous granellae measure 0.5-5 μ in length. The nuclei are spherical and 2.5 μ in diameter. Lumps of plasma with small nuclei, 0.8 μ in diameter, are also present.

The initial plasma is found in the centre of the specimens. It is loose, whitish, and has scattered stercomes and many granellae. Sponge spicules are also found here, but are fewer in number than in the other parts of the test. The diameter of the initial plasma is between 2 and 5 mm, but it is not well demarcated. In some cases a hollow instead of the initial plasma is found, and this is presumably due to the death of the plasma.

The stercomare branches are 90-270 μ in diameter. Xanthosomes are rare; they are yellow-brown, rounded, and 0.8-8.5 μ in diameter.

The xenophyae are sponge spicules and foraminiferan tests. The latter are evenly distributed in the test and are not more concentrated in the central parts. In some specimens a hollow is found in the centre (in one case measuring about 5 × 3 × 3 mm), while in others the test is just much looser than it is in the rest of the body. It was impossible to determine the exact nature of the primary xenophyae; possibly they are sponge spicules.

Remarks: SCHEPOTIEFF (1912b, p. 273) gave the following diagnosis: "Körper kreisrund; Xenophyen fast nur Foraminiferenschalen." Both statements are incorrect since the body is spherical and the xenophyae are mainly sponge spicules.

As can be seen from the above descriptions (cf. also Table 2), the samples here referred to *P. globosa* have the same primary taxonomic characteristics. However, the following minor differences should not be disregarded because they may reflect genetic variations between different populations: differences in dimensions of granellare, presence or absence of xanthosomes, and differences in consistency. Availability of building material may, however, be the cause of the differing consistencies.

Distribution: Known from four dredgings, one in the Indonesian area and three off East Africa, at 1158 to 3960 m depth, on Globigerina ooze and grey mud, and at 0.4 to about 5° C.

***Psammetta arenocentrum* n. sp.**

Pl. 2C-E

Material:

"Galathea" St. 233. – 2 specimens. The holotype is the largest of the two, but presumed, however, to be juvenile.

Diagnosis: The subspherical body is at least 9 mm in diameter. The colour is light grey, and the consistency is firm. Sand grains and sponge spicules are the xenophyae in the centre and periphery, respectively.

Morphology: The largest specimen is a little flattened and measures 9 mm in length. The central, arenaceous part is globular and measures about 4 mm in diameter. There is a sharp demarcation between the two body parts, even though some sponge spicules are found in the centre. The other specimen (Pl. 2E) is a little flattened too, and measures 6 mm in diameter. Its test is mainly made of sand grains, but numerous sponge spicules are found among the grains, especially on the surface.

Cytology: The whitish granellare branches measure 60-120 μ in diameter. Granellae are numerous; they are elongate or rounded, 1-5 μ in length, most of them being about 3 μ.

The initial plasma was not observed. It must have been in the centre of the arenaceous lump of xenophyae, where granellare and stercomare are not well-developed.

The dark grey strings of stercomare measure 110-160 μ in diameter. Xanthosomes seem to be scattered; they are rounded, yellow-brown bodies, and the observed ones measured 7-9 μ in length.

The xenophyae in the centre are loosely packed sand grains. In the periphery there are many types of silicious sponge spicules cemented at the points of contact.

Remarks: The two specimens are presumably juvenile and the mature stage is unknown. The test of the youngest specimen (6 mm) is made of sand grains; when preserved, the animal was probably about ready to start using sponge spicules as xenophyae. The larger animal had already entered this stage and has a thin layer of spicules surrounding the arenaceous centre.

P. arenocentrum differs from *P. globosa* and *P. ovale* in using sand grains instead of foraminiferan tests as primary xenophyae. Whether or not there are differences in the body form cannot be determined at present. *P. arenocentrum* differs from *P. erythrocytomorpha* in that the former uses both sand grains and sponge spicules as xenophyae while the latter uses only sponge spicules.

It should be noted that the specimens would have greatly resembled *Maudammina* if they had been collected at a younger stage since the one type of xenophyae would dominate. Other distinguishing genus characteristics such as body form, consistency and the relative amounts of plasma and xenophyae could have been determined only with great uncertainty.

Occurrence: Known from one dredging off E. Africa, at 4730 m, and at *c.* 0.3°C.

Psammetta ovale n. sp.
Fig. 1

Psammetta globosa, SCHEPOTIEFF 1912b, p. 247, pl. 15, 1-71.

SCHEPOTIEFF coll. – Several specimens which are now unaccounted for. The type for the species is the specimen on SCHEPOTIEFF's pl. 15, fig. 1.

Diagnosis: The body is oval, flat on the underside, arched on the topside, 1-15 (20) mm in diameter, and is olive-green to greyish-brown in colour. There is a small cavity on the underside around which the primary xenophyae are found; these are silicious sponge spicules and foraminiferan tests. The secondary xenophyae are silicious sponge spicules, sand grains, and test fragments.

Morphology: The smallest individuals, 1 mm in diameter, are spherical. Specimens 2 mm or more in diameter have a marked underside. The small specimens are yellowish, while the large ones are olive-green to greyish-brown. The surface is even but is somewhat shaggy.

Cytology: Granellare extend radially as irregular dichotomous branches. They are circular in cross-section, measure about 330 μ in diameter, and have numerous short side branches, the lengths of which do not exceed the diameter of the headbranch. The branch walls are up to 2 μ thick. Granellae are numerous; they are angular or rounded and are 1-25 μ long. Nuclei are numerous throughout the plasma; they are spherical, bubble-like, and measure 5-7 μ in diameter.

SCHEPOTIEFF described (1912b, p. 252) some plasma inclusions, and these are commented on in the general part, p. 71.

The initial plasma is formed as a ring or semi-circle 0.5-1.5 mm in diameter, and is found around the cavity on the flat side. When in the form of a ring, the initial plasma appears circular in cross-section; but when in the form of a semi-circle, the plasma appears greatly flattened. Nuclei are numerous; they are oval or spindle-shaped, and are 3-5 μ long.

Stercomare extend radially as dichotomous strings about 330 μ in diameter. Stercomes are ellipsoidal and measure 10-200 μ in length. Xanthosomes are

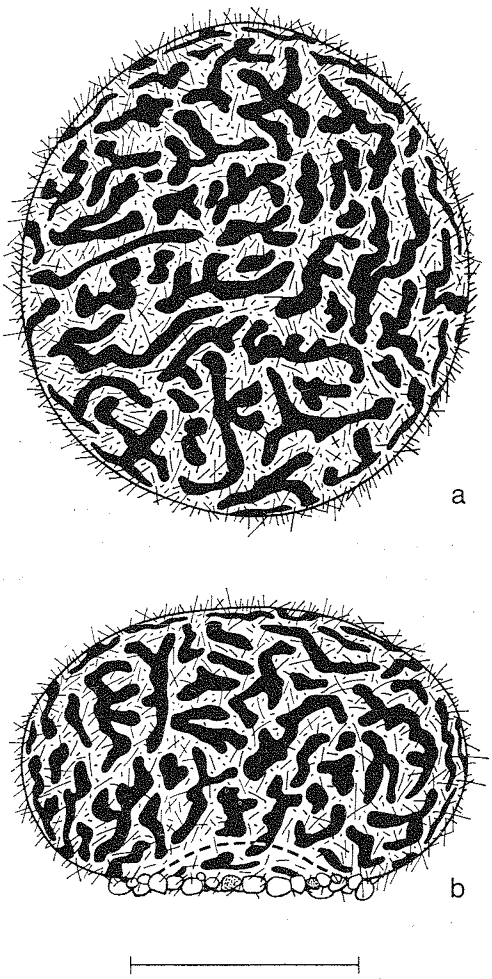

Fig. 1. *Psammetta ovale* n.sp. Body form; a, top view; b, side view. The figure is based on SCHEPOTIEFF's (1912b) figures and text.

numerous; they are yellow or reddish, spherical, 3-10 μ in diameter, and lie singly or aggregated.

SCHEPOTIEFF (1912b, pp. 254, 255) described one more formation in stercomare which he called spherocrystals. These were elongate, rounded, opaque bodies, 15-20 μ in length.

Remarks: It was already pointed out by SCHULZE (1912, p. 39) that the specimens referred to *Psammetta globosa* by SCHEPOTIEFF probably represented a new species. *P. ovale* which I have established here is distinguished by its special body form (Table 2, p. 24). The fully developed body form in *P. arenocentrum* is unknown, but *P. ovale* differs from this species in the type of primary xenophyae present and in the xenophyae arrangement.

Occurrence: Known from one locality at Kankesanturai (North Ceylon), at 1-5 m, on sand, and at *c.* 25°C.

Psammetta erythrocytomorpha Schulze, 1907
Pls. 2F; 16A; 17B-C

Psammetta erythrocytomorpha Schulze, 1906, p. 2. Nomen nudum.

Psammetta erythrocytomorpha Schulze, 1907a, p. 6, pl. I, 1-19, pl. II, 1-4.

Material:

"Valdivia" St. 250. – 2 specimens; originally there were several.

As lectotype I selected the largest of the two, which is intact and measures 26 mm in diameter.

Diagnosis: The body is a circular, biconcave disc, 20-30 mm in diameter and 5-12 mm high. The thickness at the centre of the disc is about half that at the edge. The two faces are alike. The colour is greenish-brown, and the consistency is that of heavy felt. Xenophyae are silicious sponge spicules.

Morphology: The edge is equally thick along the entire periphery. Large specimens show the above mentioned difference in thickness between the edge and the centre, but the difference in smaller specimens is not as marked and the two faces can be nearly parallel. Some specimens have a thin, transparent surface layer (SCHULZE's "Rindenschicht"). This layer is, like the rest of the test, composed of cemented sponge spicules.

Cytology: The yellow granellare branches extend irregularly and do not anastomose. Free ends are commonly seen along the edge, but they are less common on the faces. The swollen ends of short side-branches, mentioned by SCHULZE (1907a, p. 14) are generally discernible. Many branches have severed ends opening into the plasma, but it is impossible to decide whether this is the natural condition or if it is due to damaging. The branches are circular in cross-section and are 90-120 μ in diameter. Granellae are numerous in the plasma; they are rounded or elongate and 1-7 μ in length, most of them being 1-3 μ. The numerous, spherical nuclei are 2-3 μ in diameter.

Stercomare extend radially as dichotomous dark strings but do not anastomose. They are circular to slightly ellipsoidal in cross-section, and measure 150-300 μ in diameter. Yellow-brown or reddish-brown xanthosomes are numerous. They are spherical, 3-15 μ in diameter, most of them being about 6 μ, and they often form aggregations.

The xenophyae are mainly different types of silicious sponge spicules. Some foraminiferan tests, radiolarian tests, and mineral particles are also found.

Remarks: One specimen was dissected in an attempt to locate the oldest part. No xenophyae differentiation was found. The granellare seem to be less developed in the centre than at the periphery.

It should be noted that the young stages of *P. erythrocytomorpha* do not possess a special type of xenophyae as do the other species of the genus, but use the same type of xenophyae during the whole life span. In this respect *P. erythrocytomorpha* resembles *Maudammina;* it differs from this genus, however, in its distinct body shape.

Occurrence: Known from one dredging off E. Africa, at 1668 m, on Globigerina ooze, and at 3.8° C.

Family **PSAMMINIDAE** Haeckel, 1889

Psamminidae Haeckel, 1889, p. 32; DELAGE & HÉROUARD 1899, p. 200; MINCHIN 1900, p. 154; SCHULZE 1907a, p. 6; 1907b, p. 147; LISTER 1909, p. 286; SCHEPOTIEFF 1912b, p. 272; POCHE 1913, p. 203; LOEBLICH & TAPPAN 1961, p. 319; 1964, p. 792.
Psamminae Lendenfeld, 1886, p. 589 (nomen nudum).
Psamminidae, LAUBENFELS 1936, p. 32 (pars).
Psammininae, LAUBENFELS 1948, p. 180 (pars).

Diagnosis: The test is usually solid, but it can be fragile. The external xenophyae are arranged in a surface layer, and in some cases there are several layers. Very little cement is used.

Remarks: The family was established by HAECKEL (1889) with his genus *Psammina* as the type. He included the following three genera in the family: *Psammina* Haeckel, *Holopsamma* Carter, and *Psammopemma* Marshall. SCHULZE (1907a) added *Cerelasma* Haeckel and *Psammetta* Schulze to the *Psamminidae.* LAUBENFELS (1936) placed all the genera of Xenophyophora in this family. Later (1948) he classified it as a subfamily within the sponge family Halisarcidae.

In this paper *Cerelasma* and *Psammetta* are placed in other families and *Holopsamma* (= *Cerelpsamma*) is excluded from the system since its real nature is enigmatic.

At present the family Psamminidae contains four genera: *Galatheammina* n. gen., *Reticulammina* n. gen., *Psammina* Haeckel, 1889, and *Cerelpemma* Laubenfels, 1936 (= *Psammopemma* as used by HAECKEL 1889).

Of the four genera *Galatheammina* can be regarded as the most primitive, having a hard surface layer, a loose interior, and a rather simple body form. A hard surface layer is also found in *Reticulammina,* but this genus has a more specialized body form with anastomosing branches.

In *Psammina* the presence of xenophyae is more or less limited to the two hard plates which form a

Key to the genera and species

1a.	Xenophyae cemented in layers	2
1b.	Xenophyae form a distinct surface layer surrounding a mass of loose xenophyae	4
2a.	Body lumpy, consisting of a stack of numerous layers of cemented xenophyae (radiolarian tests) .... *Cerelpemma radiolarium*	
2b.	Body plate-like, consisting of two plates of cemented xenophyae between which granellare and stercomare are found as a soft layer .... *Psammina*	3
3a.	Xenophyae: radiolarian tests .... *P. nummulina*	
3b.	Xenophyae: foraminiferan tests .... *P. globigerina* but compare also *P. plakina*	
4a.	Body lumpy or with free branches .... *Galatheammina*	5
4b.	Body consisting of anastomosing branches .... *Reticulammina*	6
5a.	Body lumpy .... *G. calcarea*	
5b.	Body shaped like a four-branched star .... *G. tetraedra*	
6a.	Branches distinctly lamellar	7
6b.	Branches nearly circular in cross-section	8
7a.	Branches 1-2 mm wide; xenophyae: sand grains .... *R. lamellata*	
7b.	Branches 4-6 mm wide; xenophyae: Globigerina tests .... *R. cretacea*	
8a.	Branches circular in cross-section, 1-2 mm in diameter .... *R. labyrinthica*	
8b.	Branches often somewhat flattened, 3-7 mm in diameter .... *R. novazealandica*	

sort of box around the animal. In *Cerelpemma* the test is formed as a stack of plates between which are narrow cavities.

The two different arrangements may, if supported by new material, form the basis for a future division of the Psamminidae.

Genus *Galatheammina* n. gen.

Diagnosis: The body is compact, lumpy or branched. The interior consists of a loose accumulation of xenophyae with granellare and stercomare. A hard surface layer of firmly cemented xenophyae forms the outermost layer of the test. In some places the surface is provided with small pores.

Remarks: The genus *Galatheammina* is established to receive the two species, *G. tetraedra* n. sp., the type of the genus, and *G. calcarea* (Haeckel).

The differences between this genus and *Reticulammina* are discussed on p. 29.

Galatheammina resembles *Psammina* in the presence of a hard surface layer and a loose interior. The main differences are as follows: 1) The surface layer in *Galatheammina* surrounds the whole animal as a coherent test without larger openings, whereas in *Psammina* the test is composed of two hard plates, and there are smaller or larger openings where these plates meet. 2) The interior of *Galatheammina* contains numerous loose xenophyae but lacks connecting cemented pillars between the two opposite sides of the body; *Psammina* has few xenophyae in the interior, and the plates are connected by varying numbers of solid cemented pillars.

There is very little plasma in relation to the amount of xenophyae present in *Galatheammina*.

Galatheammina tetraedra n. sp.
Pl. 3 A-B

Material:

"Galathea" St. 192. – 2 specimens, the largest of which is the holotype.
"Galathea" St. 198. – 1 specimen.

Diagnosis: The body is shaped as a four-branched star with the tips of the arms placed in the corners of a tetrahedron. The diameter of the whole animal is 10-18 mm. The colour is white, and the consistency is hard. Xenophyae are exclusively large foraminiferan tests and test fragments, the former being in the surface layer and the latter in the interior.

Morphology: The largest specimen (St. 192) measures 18 mm from tip to tip of the two longest branches. The lengths of each of the branches measured from the centre of the animal are 10 mm, 8 mm, 7 mm, and 7 mm. The two shortest arms seem to be slightly damaged in the outermost tip. The diameter of the branches is 5-6 mm at the centre and 2-3 mm at the tip. The two other specimens are of about the same size, and measure approximately 10 mm from tip to tip of the longest branches.

The test is composed of large foraminiferan tests. On the surface whole tests are cemented into a hard layer 0.5-1 mm thick. Some fine-grained calcareous matter is loosely attached between the tests. The foraminiferan tests are fragmented in the interior, and the fragments lie loosely associated with granellare and stercomare.

Whether or not there are pores in the surface cannot be definitely determined since there are numerous spaces between the foraminiferan tests. Granellare and stercomare protrude through some of these spaces at the branch tips.

Cytology: The light yellow granellare branches measure 30-60 μ in diameter. Granellae are numerous; they are rounded or elongate, 1-5 μ long, most of them being 3-4 μ. The spherical nuclei are 2-3 μ in diameter.

Stercomare masses appear as dark, loosely coherent strings 50-150 μ in diameter, extending randomly and anastomosing. Xanthosomes are scattered; they are light yellowish or nearly transparent rounded masses 6-10 μ in diameter.

Remarks: *G. tetraedra* differs clearly from *G. calcarea* in body shape and in the presence of more uniform xenophyae in the external test layer.

Distribution: Known from two dredgings, both off eastern Africa, at 2700 to 3430 m depth, on Globigerina ooze and between 0.1 and 1.6° C.

Galatheammina calcarea (Haeckel, 1889)
Pl. 3 C-D

Psammopemma calcareum Haeckel, 1889, p. 41, pl. VII, 5; SCHULZE 1907a, p. 28.
Cerelpemma calcareum, LAUBENFELS 1936, p. 33 (LAUBENFELS did not have access to any material).

Material:

"Galathea" St. 190. – 1 specimen and numerous fragments.

"Galathea" St. 198. – 3 specimens and numerous fragments.

Other records (the material is unaccounted for):

"Challenger" St. 89.

"Challenger" St. 220.

"Challenger" St. 270.

Some pieces from "Challenger" St. 271, mentioned by SCHULZE (1907a, p. 28), may also belong to this species.

Diagnosis: The body is massive and lumpy, and forms rounded, occasionally somewhat irregular masses, 6-25 mm in diameter. The colour is white and the consistency is hard. Xenophyae are exclusively calcareous foraminiferan tests.

Morphology: The shape of the largest specimen in the collection (St. 198) is between that of a thick disc and a flattened ball. It measures 12 mm in diameter. The smallest and youngest specimen (St. 190) is nearly spherical and measures 6 mm in diameter. One of the other two specimens is spherical and the other is irregularly rounded.

The test is made of cemented calcareous foraminiferan tests. Externally there is a very hard 0.5-1.5 mm thick layer with small tests cemented into the spaces left between the larger ones. Internally there are loosely associated, whole and fragmented tests.

The surface has numerous small pores and occasionally granellare and stercomare protrude through these.

Cytology: The yellowish granellare are strongly branched but do not anastomose, and the branches measure 25-80 μ in diameter. Granellae are numerous, rounded or elongate and up to 5 μ in length. Nuclei are seemingly spherical and measure about 3 μ in diameter.

A clear lump of plasma is often seen in the tips of the side branches. Apparently these outer plasma parts do not have granellae.

The dark masses of stercomare form anastomosing strings of varying thickness, measuring from 25-120 μ in diameter. Xanthosomes were not seen with certainty, but they are perhaps represented by some scattered, irregular, reddish-brown grains 1-2 μ in diameter.

Remarks: SCHEPOTIEFF (1912b, p. 273) listed *Holopsamma turbo* Carter, 1885 and *Sigmatella turbo* (Lendenfeld, 1889) as synonymies for *G. calcarea*. The material which was described as a sponge by CARTER (1885, p. 213) and later by LENDENFELD (1889, p. 617) was not well-preserved, but there is no reason for doubting its being a keratose sand-incrusting sponge. Even if it were regarded as a xenophyophore, it could not belong to *Galatheammina calcarea* since the xenophyae are sand grains and sponge spicules.

Distribution: *Galatheammina calcarea* has been taken in five dredgings: one in the Atlantic Ocean, two in the Indian Ocean, and two in the west and central Pacific Ocean. Thus, it is the xenophyophore with the widest known distribution. It has been taken at 2013 to 5353 m depth on Globigerina ooze, and between 0.1 to 2.6°C.

Genus *Reticulammina* n. gen.

Diagnosis: The body is lumpy and has numerous anastomosing branches. The consistency is friable. A thin, distinct, hard layer of cemented fine granular matter with some xenophyae is found externally in the branches. The interior contains xenophyae loosely associated with granellare and stercomare.

Remarks: The genus *Reticulammina* has been established to receive four species: *R. novazealandica* n. sp., the type species, *R. labyrinthica* n. sp., *R. lamellata* n. sp., and *R. cretacea* (Haeckel).

Reticulammina is clearly distinguished from the other genera of the family by its anastomosing branches. The genus that resembles *Reticulammina* most is *Galatheammina*. The surface layer in *Reticulammina* is quite distinct due to the fine-grained building material, but it is relatively weak. *Galatheammina*, on the other hand, has a less distinct but stronger surface layer.

There is little plasma in relation to the amount of xenophyae in *Reticulammina*.

Reticulammina novazealandica n. sp.

Pl. 3E-G

Material:

NZOI St. E. 903-a. – 1 specimen.

NZOI St. E. 903-b. – 1 specimen.

NZOI St. F. 913. – 1 fragment.

The holotype is from St. 903-a. It measures about 60 mm in diameter and is kept at NZOI, Wellington, New Zealand.

Table 3. Characteristics of the test of species of *Reticulammina.*

	R. novazealandica	*R. labyrinthica*	*R. lamellata*	*R. cretacea*
Form	rounded lumpy	rounded lumpy	flattened lumpy	irregularly rounded lumpy
Max. known diameter	60 mm	23 mm	32 mm	50 mm
Colour	light grey	whitish	grey	white
Consistency	friable	friable	rather friable	friable
Form of the cross-section of the branches	flattened	mostly circular	lamellate	lamellate
Width of the branches	3-7 mm	1-2 mm	1-2 mm	4-6 mm
Form and diameter of the open spaces	circular or oval 2-10 mm in diameter	circular or oval 1-8 mm in diameter	large irregular	circular 8-12 mm in diameter
Xenophyae	foraminiferan tests	foraminiferan tests	sand grains	Globigerina tests

Diagnosis: The body is rounded, lumpy, and measures up to 60 mm in diameter. The lamella-like branches measure from 3 to 7 mm in width although most of them are about 5 mm. The open spaces in the network are circular or oval in cross-section, and are 2-10 mm wide. The colour is light grey and the consistency is friable. The internal xenophyae are for the most part loose aggregations of foraminiferan tests; externally there is a well-cemented layer of fine calcareous matter with only a few foraminiferan tests.

Morphology: Both of the specimens are somewhat damaged so their real size is unknown. The largest specimen is flattened on one side and thus it appears roughly hemispherical; this is perhaps the normal body form for the species. The other specimen is irregularly shaped and measures 33 mm in breadth at the widest point.

The branches are flattened and anastomose frequently. Neither the branches nor the spaces between them vary in dimension in different body parts. A few of the latter have, however, been found to measure up to 20 mm at the widest point. It was impossible to distinguish any particular branching pattern, and the oldest part of the animal cannot be discerned.

Cytology: The reddish-brown granellare strings are 40-60 μ in diameter. Granellae seem to be scarce; they are rounded, elongate, and 1-3 μ in length. Nuclei range from spherical to slightly ellipsoidal and are 3-5 μ in diameter.

The dark stercomare strings anastomose and are 40-150 μ in diameter. They are most numerous near the surface of the branches. Xanthosomes are found scattered; they are rounded, dark brown, and 1-5 μ in diameter. There are a large number of small, 1-2 μ in diameter, round, yellow-brown grains, and these are perhaps also xanthosomes.

Remarks: *R. novazealandica* strongly resembles *R. labyrinthica* (Table 3). The major differences between the two are the different dimensions and branch forms. However, the fact that these two characteristics remain constant in each species indicates that they are actually two different species instead of two different stages within the same species.

Distribution: Known from two dredgings, both in New Zealand waters, from 743 to 984 m depth on foraminiferal sand with mud and rock, and at a temperature of about 7°C.

Reticulammina labyrinthica n. sp.
Pls. 3H; 4A

Material:

NZOI St. F. 913. – 2 specimens. The holotype is the largest of the two. It is kept at NZOI, Wellington, New Zealand.

Diagnosis: The body is rounded, lumpy, and measures up to 23 mm in diameter. The branches are circular or flattened in cross-section, and are 1-2 mm wide. The open spaces in the network are circular or oval and are 1-8 mm wide. The colour is whitish, and the consistency is friable. Xenophyae are foraminiferan tests. The surface is covered by a well-cemented thin layer (about 0.3 mm thick) of fine, granular calcareous and silicious material.

Morphology: The two specimens measure 23 and 17 mm in diameter, and both are somewhat damaged. The characteristic body form of the species is presumed to be that of a rough hemisphere since they are somewhat flattened on one side.

In cross-section most of the branches are circular or nearly circular, and they form an open network. The branches and the open spaces have the same dimensions throughout the body, and it was impossible to distinguish the oldest part.

Cytology: The granellare branches measure 25-60 μ in diameter. Granellae are rare; they are rounded and measure up to 5 μ in diameter. The nuclei range from spherical to slightly ellipsoidal in shape, are 3-5 μ in diameter, and have a chromatin net-like structure.

The often anastomosing dark stercomare strings measure 25-160 μ in diameter. Xanthosomes are rare; they are yellow-brown, rounded, 7-15 μ in diameter.

Remarks: See *R. novazealandica.*

Occurrence: Known from one dredging off New Zealand, at 743 m, on foraminiferal sand with detrital mud, and at *c.* 7°C.

Reticulammina lamellata n. sp.
Pl. 4B-C

Material:
NZOI St. F. 881. – 1 specimen. The holotype is kept at NZOI, Wellington, New Zealand.

Diagnosis: The body is somewhat flattened and lumpy, 32 mm in diameter and 15 mm in height. Most of the branches are lamellate and are 1-2 mm wide. Large, irregular cavities are found between the branches. The colour is greyish, and the consistency is rather friable. Xenophyae are sand grains. The surface is covered by a thin layer (about 0.2 mm thick) of sand grains and fine granular matter.

Morphology: The specimen is somewhat damaged. Most of the branches are lamellate, but a few are nearly circular in cross-section and are about 1 mm in diameter. It was impossible to distinguish any particular branching pattern, and the oldest part of the animal cannot be discerned.

Cytology: The yellow-brown granellare branches measure 12-90 μ in diameter. Granellae are up to 5 μ in length.

The stercomare branches measure 50-120 μ in diameter. There are few xanthosomes.

Remarks: *R. lamellata* is clearly distinguished from the other species of the genus by the form and arrangement of the branches and by the type of xenophyae used.

Occurrence: Known from one dredging off New Zealand, at 1253 m, on foraminiferal sand with sand and glauconite, and at *c.* 5°C.

Reticulammina cretacea (Haeckel, 1889)
Pl. 4D-E

Holopsamma cretaceum Haeckel, 1889, p. 39, pl. VII, 7A-C; SCHULZE 1907a, p. 26, pl. III, 4 and 6.
Cerelpsamma cretaceum, LAUBENFELS 1936, p. 33. (LAUBENFELS had not seen any material).

Material:
"Challenger" St. 70. – 1 specimen which is unaccounted for.

Diagnosis: The body is irregular, rounded, lumpy, and is 20-50 mm in diameter. The branches are lamellate, 4-6 mm in width. The open spaces are conical depressions and 8-12 mm in diameter. The surface of the branches is perforated by small pores. The colour is white and the consistency is friable. Xenophyae are Globigerina tests.

Cytology: Hardly anything is known. There is very little plasma and a small amount of cement. SCHULZE (1907a, p. 26) observed granellare with granellae and the apparently anastomosing stercomare strings.

Remarks: SCHULZE reexamined HAECKEL's specimen and found that the organism was definitely a xenophyophore. Due to poor preservation, it could not be referred to any of the known genera. Externally it resembles *Cerelasma lamellosa* because of the anastomosing lamellate branches, but there are no further similarities between the two. It seems more reasonable to place the species in *Reticulammina,* but further information is needed to make a final decision.

Occurrence: Known from one dredging in the Central Atlantic, at 3065 m, on Globigerina ooze, and at 2.4°C.

Genus ***Psammina*** Haeckel, 1889

Psammina Haeckel, 1889, p. 34.
Psammoplakina Haeckel, 1889, p. 35.

Diagnosis: The body is discoidal with large pores along the margin. The test is composed of firmly cemented xenophyae in the form of two hard plates. Some xenophyae appear internally as pillar-like structures between the two plates. Branches of granellare and strongly developed stercomare strings are found around the pillars.

Remarks: HAECKEL described the following three species of *Psammina: P. nummulina, P. globigerina,* and *P. plakina* but did not denote any species as the type. His statement that *P. plakina* "is a very remarkable form, which differs from the following typical species of the genus ...", could reasonably have lead to the selection of *P. globigerina* as the type. However LAUBENFELS, the first reviser (1936, p. 33), chose *P. nummulina* as the type while LOEBLICH & TAPPAN (1964, p. 792), apparently unaware of LAUBENFELS' survey, invalidly designated *P. globigerina.*

Psammina nummulina Haeckel, 1889
Pls. 5A; 14A

Psammina nummulina Haeckel, 1889, p. 37, pl. VII,3.

Material:
"Galathea" St. 716. – About 500 fragments.
"Vema" St. 15-49. – About 20 fragments.

Other records (the material is unaccounted for):
"Challenger" St. 274.

Diagnosis: The body is of irregular circular shape with either a swollen or a tapering edge perforated by pores. The two plates have small, scattered pores. The diameter of the disc is 12-15 mm, and it is 0.6-1.4 mm thick. The colour of undamaged surfaces is light grey and the consistency is very brittle. The two plates can be easily detached and then granellare and stercomare can be clearly seen. A few connecting pillars are found between the plates. Xenophyae are radiolarian tests.

Morphology: Most fragments measure 4-7 mm in diameter, and are between 0.6 and 1.4 mm thick. The largest fragment ("Vema" St. 15-49) measures 8×9 mm. Many specimens are slightly bent and some have long, low ridges and thickenings on the surface. The plates have usually been damaged to some extent and the dark colour of stercomare then predominates. The edge thickness is the same or thinner than that of the rest of the body, and in most cases the edge has been broken. The two hard plates are very thin in comparison with the interior body part; both plates are similar, and both have scattered small pores.

Cytology (Pl. 14A): The yellowish granellare branches are usually circular in cross-section; near the plates they are often more oval. Their diameter is 30-60 μ. Granellae are numerous in the plasma; they are either round and 1-3 μ in diameter, or are more elliptical and about 1×3 μ. Numerous spherical nuclei, 3-4 μ in diameter, are distributed in the plasma.

A lump of plasma without granellae was on one occasion observed in the end of a granellare branch.

Stercomare are seen as conspicuous, radially extending, sometimes anastomosing, dark masses. The cross-section is approximately circular and is 40-180 μ in diameter, usually 150-160 μ. The surrounding membrane is thick and measures 1-5 μ. No xanthosomes were found.

The xenophyae are mainly radiolarian tests and mineral particles. Fragments of silicious sponge spicules are also common and occasional foraminiferan tests can be found on the external side of the plates.

Remarks: In his diagnosis of the species, HAECKEL made the following statement (1889, p. 37): "Gastral cavity chambered." He did not elaborate on this, and the statement's meaning is unclear. It should be noted, however, that viewed in tangential sections, the branches of the thick-walled stercomare appear as a row of chambers.

Distribution: Known from three dredgings, all in the central and eastern Pacific, at 3563 to 5033 m depth, on radiolarian ooze and dark clay with diatom, radiolarian, and pelagic foraminiferan remains, and at temperatures from 1.7 to 1.9°C.

Psammina globigerina Haeckel, 1889
Pls. 4F; 16E

Psammina globigerina Haeckel, 1889, p. 36, pl. VII, 2A-D; Schulze 1906, p. 12, Pl. II, 12-15, Pl. III, 1-2; 1907a, p. 18.

Material:
"Challenger" St. 220 – 2 fragments.
"Siboga" St. 211. – About 10 specimens and fragments.
"Siboga" St. 227. – About 8 specimens and fragments.

Diagnosis: The body is either nearly circular or of more irregular form. It is flat or displays varying degrees of bending, and is 20-30 mm in diameter and 1.5-3 mm thick. The edges are rounded and tapered, and they have a row of pores 0.5-1 mm in diameter and 1-2 mm apart. Smaller pores are found in both plates. Strong pillars are found between the plates and they can form longer or shorter walls. The xenophyae are foraminiferan tests.

Morphology: Since the plates are fragile, it is often difficult to distinguish between the fragments and the damaged specimens. Some of the smaller pieces seem to be whole individuals, and the samples may therefore include animals as small as 10 mm in diameter. The small specimens are regular in form with an almost even surface, while the larger specimens are irregular, slightly bent, and have a granulate surface. The two largest animals measure 25 × 20 mm (St. 211) and about 28 × 20 mm (St. 227) (Pl. 4F).

The plates are 0.5-1 mm thick, and have small, scattered pores. There is about 1 mm between the two plates. Many conspicuous, strong columns of cemented foraminiferan tests are found between the plates in the small, discoidal, regular specimens, while there are often longer or shorter walls between the plates in the larger and more irregular specimens. In the larger specimens the body layer appears chambered, but the walls are quite irregular and there is no real division into chambers.

Cytology: The yellowish granellare branches do not anastomose. The diameter is 40-90 μ. Numerous granellae are found in the plasma; they are oval and 1-8 μ in the longest direction. It has been impossible to find definite nuclei, but some spherical bodies 2.5-4 μ in diameter are occasionally observed, and these could be nuclei. Some other bubble-like formations 6-7 μ in diameter with small, dark grains lying in pairs along the periphery somewhat resembled nuclei (in division?). Very few of these two kinds of bodies were observed.

Stercomare are well developed and form a network through the animal. The diameter of the branches is 125-180 μ. The surrounding membrane is thin (< 0.5 μ), but it seems to be unusually strong. Xanthosomes are scattered; they are yellow-brown, rounded, sometimes spherical, and measure 5-8 μ in diameter.

Xenophyae are mainly foraminiferan tests cemented tightly together. Here and there a few radiolarian tests, mineral particles, fragments of silicious sponge spicules, and pieces of mollusc shells are found.

Distribution: Known from three dredgings, all in the Indonesian Archipelago, at 1158 to 2081 m depth on a bottom of Globigerina ooze and grey mud mixed with sand, and at temperatures of 2.3° to 3.7°C.

Psammina plakina Haeckel, 1889
Fig. 2

Psammina plakina Haeckel, 1889, p. 35, pl. VII, 1A-D.
Psammoplakina discoidea Haeckel, 1889, p. 35, pl. VII, 1A-D.

Material:
"Challenger" St. 331. – 2 specimens. The material is now unaccounted for.

Diagnosis: The body is subcircular, faintly convex-concave. It measures 5-12 mm in diameter and is 1.5-2.5 mm thick. The peripheral margin curves somewhat upwards and has 10-12 pores. The upper concave plate has pores. Xenophyae are foraminiferan tests and test fragments. The xenophyae are numerous in the middle layer which is partly subdivided into chambers.

Remarks: The diagnosis of *Psammina plakina* given by Haeckel is practically identical with his diagnosis of *Psammina globigerina*. It is impossible to know what he really meant about the relationship of the two species. He wrote (p. 35): "*Psammina plakina* is a very remarkable form, which differs from the following typical species of the genus

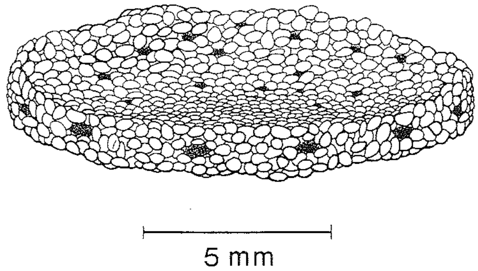

Fig. 2. *Psammina plakina* Haeckel. Body form; surface view. The figure is based on HAECKEL's (1889) figures and text

(P. globigerina) in such essential points that it may perhaps be better described as the representative of a new genus, *Psammoplakina*." (By a peculiar lapse he gave it the specific name *discoidea*). However, later on (p. 37) he said that "*P. globigerina* is very similar to the preceding *P. plakina*, and may be perhaps identical with it".

LOEBLICH & TAPPAN (1964, p. 792) were not able to shed any more light on the problem. They referred to HAECKEL (1889) and SCHULZE (1907a) and concluded: "The description of *P. plakina* stated that it differed sufficiently from the two typical species of the genus to be the type of a new genus. *Psammoplakina discoidea* is thus an objective synonym of *Psammina plakina*. *P. plakina* and *P. globigerina* are congeneric."

As stated by SCHULZE (1907a, p. 20), there is some reason to believe that *P. plakina* and *P. globigerina* are identical, the two forms being the juvenile and the adult stages of the same species.

The possibility that HAECKEL's specimens of *P. plakina* actually were sponges cannot be excluded. They were described as having no "symbiontic Spongoxenia" (i. e. granellare and stercomare), and it is unlikely that these would have been overlooked had they been present. Generally the stercomare are very conspicuous. If *P. plakina* is a sponge, it is of a rather special type. The similarity between HAECKEL's figure of *P. plakina* (1889, pl. VII, 1C) and SCHULZE's figure (1880, pl. XX, 4) of the sponge *Plakina monolopha* is striking. The skeletal type and and the skeletal material are almost the only differences between the two animals.

Occurrence: Known from one dredging in the South Atlantic, at 3138 m, on Globigerina ooze, and at 2° C.

Genus *Cerelpemma* Laubenfels, 1936

Cerelpemma Laubenfels, 1936, p. 33.

Diagnosis: The body is lumpy and is made of numerous thin plates or layers of xenophyae arranged in a stack. Flat cavities with granellare and stercomare are between these layers.

Remarks: The diagnosis as given here is based on the only available specimen of the type species.

The genus *Cerelpemma* was established by LAUBENFELS for two species that were described by HAECKEL (1889) and referred to the sponge genus *Psammopemma* Marshall, 1880. LAUBENFELS selected *C. radiolarium* as the type for the genus. The other species, *C. calcareum*, has been transferred to the new genus *Galatheammina* in this paper.

Cerelpemma radiolarium (Haeckel, 1889)
Pl. 5B-C

Psammopemma radiolarium Haeckel, 1889, p. 41, pl. VII, 4A-B; SCHULZE 1907a, p. 27.

Material:
"Challenger" St. 272. – 1 specimen, which is selected as lectotype.

Other records (the material is unaccounted for):
"Challenger" St. 270.
"Challenger" St. 271.
"Challenger" St. 274.

Diagnosis: The body is more or less irregular, in the form of rounded, subspherical, clavate or turbinate masses 5-25 mm in diameter. The colour is light grey, and the consistency is friable. The xenophyae are exclusively radiolarian tests and these are cemented into numerous thin layers each consisting of but one layer of Radiolaria. The spaces between the layers are of approximately the same thickness as the layers themselves.

Morphology: The specimen available is the turbinate one diagrammed by HAECKEL (1889, pl. VII, 4A-B). The only specimen available to SCHULZE (1907a) was a little, brown fragment, and the only conclusion he could make from this was that it was a xenophyophore belonging to Psamminidae (in sensu SCHULZE 1907a). The collecting locality of the fragment is unknown.

Cytology: The dried specimen does not have any definite features. Some scanty, broken, thin strings could perhaps be granellare. No traces of stercomare are observed.

Distribution: Known from four dredgings, all in the central Pacific, at 4438 to 5353 m depth, on Globigerina and radiolarian ooze, and at temperatures of 1.4 to 1.7°C.

Family **SYRINGAMMINIDAE** n. fam.

Diagnosis: The test is fragile and constructed of tubes that are made of xenophyae tightly cemented together. The xenophyae are restricted to the tube walls, and only granellare and stercomare are found in the interior.

Remarks: The family has been established to receive the genus *Syringammina* Brady which was originally described as a foraminiferan.

The Syringamminidae is here regarded as one of the higher developed families within the order Psamminida since the test has a distinct building plan with a particular, characteristic xenophyae arrangement.

Genus ***Syringammina*** Brady, 1883

Syringammina Brady, 1883, p. 155.
Arsyringammum Rhumbler, 1913, p. 345.

History: *Syringammina* was classified by BRADY as a foraminiferan. Different authors have referred it to different families and subfamilies, but it was always placed in the more primitive part of the foraminiferan classification. The following list gives a survey of the previous placements:

Author	Family	Subfamily
BRADY 1884, p. 242.	Astrorhizidae	Astrorhizinae
RHUMBLER 1895, p. 83.	Rhabdamminidae	Girvanellinae
RHUMBLER 1904, p. 224. / RHUMBLER 1913, p. 345.	Rhabdamminidae	Astrorhizinae
CUSHMAN 1927, p. 14. / CUSHMAN 1948, p. 88.	Hyperamminidae	Dendrophryinae
GALLOWAY 1933, p. 78.	Astrorhizidae	Hyperammininae
CHAPMANN & PARR 1936, p. 146.	Hyperamminidae	Dendrophryinae
LOEBLICH & TAPPAN 1964, p. 192.	Astrorhizidae	Dendrophryinae
LEWIS 1966, p. 115. / LEWIS 1970, p. 10	Astrorhizidae	Dendrophryinae
EADE 1967, p. 15.	Astrorhizidae	Dendrophryinae

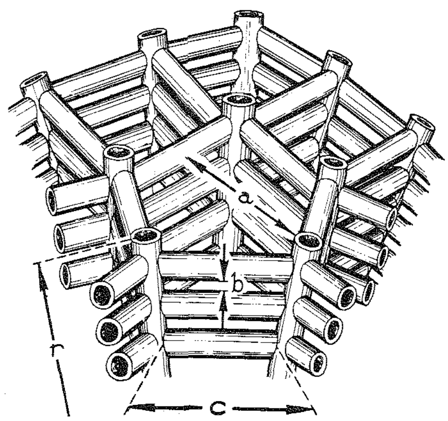

Fig. 3. *Syringammina*. Diagram of radial tubes joined by network of connecting tubes; a, diameter of open space in network of connecting tubes; b, space between consecutive networks of connecting tubes; c, connecting tube; r, radial tube. After LEWIS 1966.

Diagnosis: The body is lumpy, rounded, and made of numerous radiating tubes that are connected by side branches. The tube walls are tightly cemented xenophyae and the outer surface varies in roughness while the interior surface is smooth.

Remarks: The synonym *Arsyringammum* was created by RHUMBLER in his attempt to establish a more consistent foraminiferan nomenclature (1913, p. 333).

The genus *Syringammina* contains three species; *S. fragilissima* Brady (the type species), *S. minuta* Pearcy, and *S. tasmanensis* Lewis.

LEWIS found (1966, p. 117) that in the building plan of *Syringammina* it is possible to distinguish radial tubes (fig. 3) that project from a common centre and connecting tubes that branch off and form consecutive layers perpendicular to the radial tubes.

Key to the species

1a. Xenophyae: calcareous foraminiferan tests .... *S. tasmanensis*
1b. Xenophyae: sand grains 2
2a. Tube diameter 0.5 mm maximum; tubes form an irregular network (test attached, up to 4 mm in diameter) .... *S. minuta*
2b. Tube diameter 0.5-1 mm; tubes form an irregular network in the interior, extending more regularly at the periphery (test free, up to about 40 mm in diameter) .... *S. fragilissima*

Syringammina fragilissima Brady, 1883
Pl. 6A-E

Syringammina fragilissima Brady, 1883, p. 158, pl. 2: 1-5, pl. 3: 6-8; 1884, p. 242.

Material:
"Triton" St. 11. – 2 specimens. The unbroken specimen was selected as lectotype.
"Goldseeker" Haul 8108. – 1 specimen.
NZOI St. E 417. – 1 fragment.

Diagnosis: The body is a fragile, rounded, greyish mass up to 38 mm in diameter. In the centre the tubes are contorted and irregular, while nearer the periphery they extend radially and the anastomosing lateral branches form consecutive layers. The distance between these layers varies from 1.3-2.5 mm and is smallest in the centre and largest at the periphery. The tube diameter varies from 0.5 mm near the centre to more than 1 mm at the surface. The tube wall thickness is about 0.13 mm. The external surface of the tubes is granulate and the interior is smooth. Xenophyae are fine sand grains and small foraminiferan tests.

The specimens from the Faroe Channel (the "Triton" and "Goldseeker" material) (Pl. 6A-B):

There were originally two specimens collected by the "Triton" (Brady, 1883, p. 156), one of which was fragmented into eleven pieces. Brady assumed that if undamaged, the animal would have appeared as a sphere. It seems, however, that the form could have just as well been hemispheric, and it would thus resemble *S. tasmanensis*. This opinion was also stated by Lewis (1966, p. 121). A somewhat similar specimen was dredged by the "Challenger" at 1830 m depth off the Azores, but it was broken in the sieve (Brady, 1883, p. 159; 1884, p. 244).

Cytology: Since the specimens are dried, few cytological observations can be made. Several headbranches of granellare are peripherally arranged in each tube (Pl. 6C), and there is only a single, centrally placed stercomare string.

It is worth noting that the "Goldseeker" specimen has many foraminiferan tests as xenophyae and thereby somewhat resembles *S. tasmanensis* in external appearance.

The New Zealand specimen (Pl. 6D-E):

The specimen is described separately since it was taken far away from the type locality. I cannot, however, find any characteristics that distinguish it from the North Atlantic material.

The specimen is a nearly spherical fragment about 9 mm in diameter. The colour is grey and the test is very fragile. The anastomosing lateral radial tube branches are arranged in relatively conspicuous consecutive layers 0.9-2.8 mm apart. The diameter of the tubes is 0.5-1.6 mm. Tubes with different diameters intermingle and it is impossible to determine the youngest and the oldest part in the present fragment. The wall is 0.11-0.19 mm thick. The external surface of the tubes is nearly smooth, and the interior is quite smooth. The interior surface and the innermost xenophyae layer is yellowish due to a cement covering.

Cytology: The tubes contain granellare and stercomare. Three to six peripheral longitudinally extending headbranches of granellare and one centrally placed, thick stercomare string are in each tube.

The yellowish granellare branches measure 20-140 μ in diameter. The plasma looks granular. Granellae are oval or rounded and up to about 3 μ in diameter; most of them are, however, less than 1 μ.

The dark stercomare strings measure 200-540 μ in diameter, and connect within the tubes. Xanthosomes were not seen.

The xenophyae are tightly packed sand grains, mineral particles, and some very fine-grained material.

Table 4. Characteristics of the test of the species of *Syringammina*.

	S. fragilissima (Faroe Channel)	*S. fragilissima* (New Zealand)	*S. minuta*	*S. tasmanensis*
Form	Rounded mass	Subspherical fragment	Oval mass	Hemispherical mass
Maximal diameter	38 mm	9 mm	4 mm	44 mm
Colour	Grey	Grey	Light grey	Light grey
Consistency	Fragile	Very fragile	Extremely fragile	Extremely friable
Tube form	Central: irregular Peripheral: more regular	Relatively regular	Irregular	Central: irregular Peripheral: regular
Distance between consecutive layers	1.3-2.5 mm	0.9-2.8 mm	?	0-0.6 mm
Open space	1-2 mm?	0.5-2.5 mm	?	1.5-2.9 mm
Tube diameter	0.5-1 mm	0.5-1.6 mm	Max. 0.5 mm	1.1-1.5 mm
Wall thickness	0.13 mm	0.11-0.19 mm	Average 0.08 mm	0.23-0.43 mm
Tube surface: Exterior	Granular	Nearly smooth	Fairly smooth	Coarsely aggregated
Tube surface: Interior	Smooth	Smooth	Smooth	Relatively smooth
Xenophyae	Sand grains and small foraminiferan tests	Sand grains	Sand grains	Foraminiferan tests

Remarks: Only few cytological characteristics at present appear to be of possible taxonomic value in the xenophyophores. In the case of *S. fragilissima* and *S. tasmanensis* such a characteristic may be the granellare and stercomare arrangement in the tubes. In *S. fragilissima* there are several peripherally arranged granellare branches and one very thick, central, stercomare string while in *S. tasmanensis* there is one central granellare branch and several peripheral stercomare strings.

Distribution: Known from two (three?) dredgings in the North Atlantic and one off New Zealand, at 860 to 1556 (1830 m?) depth, on sand, ooze and detrital matter, and at about 6 to 8 °C.

Syringammina minuta Pearcy, 1914
Pl. 6F

Syringammina minuta Pearcy, 1914, p. 997, pl. II, 1-2.

Material:

"Scotia" St. 420. – 2 specimens which are now unaccounted for (cf. EARLAND 1935, p. 12; 1936, pp. 3, 5).

Diagnosis: The attached body is a flattened, oval mass, 4 mm in diameter. The colour is light grey, and the test is extremely fragile. The contorted tubes form an irregular network; the external diameter of these tubes is 0.5 mm maximum and the walls are very thin, about 0.08 mm with the exterior surface fairly smooth and the interior surface smooth. Xenophyae are uniform sand grains and these are intermingled with argillaceous material at the free tube ends.

Cytology: According to PEARCY the tubes "are generally filled with dark olive or yellowish-green granulated sarcode." This statement seems to refer to stercomare.

Remarks: There is a possibility that *S. minuta* and *S. fragilissima* may be the same species. The small body size, the irregular tube arrangement, and the small tube diameter in *S. minuta* greatly resemble the characteristics of the young stages of the two other species within this genus. The only different characteristics (Table 4) are the thin tube walls and the fact that the body was stated to be attached. The wall thickness is relatively unimportant since PEARCY gave the measurement as an average without mentioning the total variation. Whether the body is attached or not may be very important. Attached – not attached is, at least, a frequently used distinguishing characteristic for the agglutinated foraminiferans (cf. CUSHMAN 1948 and LOEBLICH & TAPPAN 1964). PEARCY (pl. II, 1) illustrated one of his two *S. minuta* specimens as being attached to a quartz crystal about one-third greater in diameter than the animal itself. Moreover, he drew tubular off-shoots pressed against the crystal, and noted that they added to the test rigidity. It is difficult to determine whether this is a true case of attachment or merely the animals uptake of an unusually large xenophya. PEARCY's other specimen was so badly damaged that it could not be determined whether it had been attached. The presence of off-shoots in the former specimen indicate that it had been attached, and this, together with the differences in depth and temperature of the collecting localities, leads me still to distinguish *S. minuta* from *S. fragilissima*. Another possible differing characteristic between the two species is the difference in size of the included arenaceous particles. This was noted by PEARCY but was not discussed in detail.

It should be noted that the xenophyophores in general are not attached. The only other case of attachment mentioned was by SCHEPOTIEFF in regard to his *Cerelasma* material (p. 41).

Occurrence: Known from one dredging in the Weddell Sea, at 4795 m, on glacial clay, and at −0.8° to −0.5° C.

Syringammina tasmanensis Lewis, 1966
Pls. 5D-E; 16F

Syringammina tasmanensis Lewis, 1966, p. 114, fig. 1-8; HEDLEY 1966, p. 123, fig. 1.

Material:
NZOI St. D 227. – 4 specimens, one of which is the holotype.
NZOI St. D. 228. – 2 specimens.

Diagnosis: The body is roughly hemispherical and up to 44 mm in diameter. The colour is light grey and the test is extremely friable. The tubes anastomose irregularly in the centre, and more regularly in the periphery where the lateral tube branches form concentrically arranged consecutive layers 0-0.6 mm apart.[1] The diameter of the open spaces in the network is 1.5-2.9 mm. The external diameter of the tubes is 1.1-1.5 mm. The wall is 0.23-0.43 mm thick. The external surface is coarsely agglutinated and rather uneven, and the interior is relatively smooth. Xenophyae are predominantly foraminiferan tests and fine-grained calcareous matter.

Morphology: According to LEWIS (1966, p. 116) all the specimens that are only slightly damaged show the essential species characters. They are or have presumably been roughly hemispherical. The smallest is about 20 mm in diameter. Two specimens (or fragments) are smaller and show only the irregular growth form which is apparently characteristic of the early stages since it is always found in the centre of the animal.

Cytology: One granellare branch in the centre and 2-4 stercomare strings in the periphery are seen in each tube (Pl. 16F).

The yellowish, anastomosing granellare branches measure 115-193 μ in diameter. The plasma contains numerous granellae up to 5 μ in length, and spherical to almost ellipsoidal nuclei 2-3 μ in diameter.

The dark stercomare strings measure 77-460 μ in diameter. Xanthosomes seem to be absent.

Xenophyae are foraminiferan tests, fine-grained calcareous matter, and terrigenous silt. LEWIS (1966, p. 119) stated that the species is non-selective regarding grain size used and that the material was collected mainly from the substrate rather than from descending pelagic debris.

Distribution: Known from two dredgings both off New Zealand, at 664 to 711 m depths, on Globigerina ooze, and at about 7 to 8.5° C.

Family **CERELASMIDAE** n. fam.

Diagnosis: The test is relatively soft and contains varying numbers of xenophyae and large amounts of cement. The xenophyae are in no obvious order and each one is fully encased with cement so that there is no contact between them.

Remarks: The family has been established to receive the single genus *Cerelasma* Haeckel. HAECKEL originally placed the genus in the sponge family Spongelidae, and later on SCHULZE (1907a) transferred it to the xenophyophoran family Psamminidae.

At present it is impossible to say whether or not this family should be regarded as primitive. Primitiveness is suggested by the absence of any system in the xenophyae arrangement, but the strong cement development is most likely a specialized character (the same may be true for the anastomosing branches of the body, cf. diagnosis of *Cerelasma*). In

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1. The measurements were by LEWIS given as 0.3 ± 0.3 mm, 2.2 ± 0.7 mm, 1.3 ± 0.2 mm, and 0.33 ± 0.10 mm.

one species *(Cerelasma massa)*, increase in the amount of cement and decrease in the number of xenophyae (this tendency is also seen in one *C. gyrosphaera* sample) has occurred to such an extent that the cement together with the stercomare has completely assumed the protective and supportive test function.

Genus ***Cerelasma*** Haeckel, 1889

Cerelasma Haeckel, 1889, p. 45.

Diagnosis: The body is lumpy, irregularly rounded, and composed of numerous anastomosing branches.

Remarks: HAECKEL established the genus *Cerelasma* for the two species, *C. gyrosphaera* and *C. lamellosa*. A third species *C. massa* n. sp. is described here. LAUBENFELS (1936, p. 33) selected *C. gyrosphaera* as the type species and LOEBLICH & TAPPAN (1964, p. 792) did the same, being apparently unaware of LAUBENFELS' work.

Key to the species

1a. Xenophyae absent . . . . *C. massa*
1b. Xenophyae present 2
2a. Xenophyae: radiolarian tests . . . . *C. gyrosphaera*
2b. Xenophyae: sponge spicules, mineral particles and fragments of foraminiferan tests *C. lamellosa*

Cerelasma gyrosphaera Haeckel, 1889
Pl. 7A

Cerelasma gyrosphaera Haeckel, 1889, p. 46, pl. VI, 1-5; SCHULZE 1907a, p. 21, pl. II, 5-11, pl. III, 1-2.
Non *Cerelasma gyrosphaera*, SCHEPOTIEFF 1912b, p. 263, pl. 16, 45-65.

Material:
"Challenger" St. 271. – 1 specimen which is selected as lectotype, and many fragments.
"Vema" St. 15-55. – 2 specimens and some fragments.

Diagnosis: The body is lumpy, irregularly rounded, has a convoluted surface, and a diameter of up to 70 mm. The cylindrical anastomosing branches, 1.5-5 mm in diameter, form a network with meshes 1-6 mm in diameter. The colour is grey-brown to very dark brown, and the consistency is firm yet a little elastic. Xenophyae are exclusively radiolarian tests.

Since the two samples are somewhat different, a special description will be given of each.

The "Challenger" material:
The body is a firm, grey-brown lump, 5-70 mm in diameter. The anastomosing branches are circular in cross-section and 3-4 mm in diameter. The meshes in the network are open, 3-6 mm in diameter.

Cytology: The granellare branches are dichotomously divided and presumably anastomose. The cross-section is subcircular, often irregular, and is 25-50 μ in diameter. Granellae are evenly distributed; they are rounded or slightly angular and are 0.8-5 μ in length. Nuclei are numerous. Generally they are spherical or slightly ellipsoidal and look "massive", but in some cases they look more like spherical bubbles. SCHULZE (1907a, p. 23) found lumps of plasma that had numerous small nuclei but were devoid of granellae. His impression was that the small nuclei were derived from bubble-like ones. He occasionally found small, mononucleated cell-like structures about 6 μ in diameter beside these polynucleated plasma lumps.

In small specimens SCHULZE described what may be the initial plasma. The specimens were composed of the usual branches, but did not have the usual granellare and stercomare differentiation. Some specimens had granellare-resembling branches that contained solely or mainly stercomes.

The anastomosing stercomare strings measure 50-150 μ in diameter. Xanthosomes are rare; they are roundish, yellowish, and 3-5 μ in diameter.

The numerous xenophyae (radiolarian tests exclusively) lie in conspicuous sacs of cement associated with the granellare and stercomare walls. Some unassociated xenophyae are found scattered and may, according to HAECKEL, be the most recently incorporated ones.

The "Vema" material:
The largest specimen is irregularly lumpy, 17 mm in length, and somewhat flattened. It is composed of anastomosing, flattened branches 1.5-5 mm in diameter. The meshes in the network are 1-2 mm.

The colour is very dark brown, and the consistency is firm although it is softer than the "Challenger" specimens.

Cytology: The granellare branches are subcircular, somewhat irregular in cross-section, and 17-70 μ in diameter. The plasma is shrunken and lies as a string centrally or along one side of the branch wall. Granellae are numerous and 0.8-5 μ in length. Nuclei are spherical, about 2.5 μ in diameter.

The anastomosing stercomare masses are 70-200 μ in diameter. Xanthosomes are scattered; they are rounded, reddish or brownish, and 0.8-4 μ in diameter.

Xenophyae (radiolarian tests exclusively) are not numerous; there are only about 20 % of the number observed in the "Challenger" material. They are found both with and without a cement mass covering.

Remarks: The major discrepancies between the "Challenger" and the "Vema" material are reflected in the colour difference. The rather light colour of the former is presumably caused by the presence of numerous xenophyae, whereas the dark colour of the latter results from the presence of the relatively stronger developed stercomare masses.

Distribution: Known from two dredgings, one in the E. Pacific and one in the Central Pacific, at 3950 and 4438 m depth, on Globigerina ooze, and at 1.4° to 2.0°C.

Cerelasma massa n. sp.
Pls. 8A-B; 17A, D-E

Material:

"Galathea" St. 234. – 11 specimens and numerous fragments.

"Galathea" St. 235. – 4 specimens and several fragments.

The holotype is from St. 234 and measures 28 × 17 × 17 mm.

Diagnosis: The body is rounded and lumpy with a convoluted surface and is up to 28 mm in diameter. The branches are circular or somewhat flattened in crosssection and measure 2-4 mm in diameter. They are pressed so tightly against each other that meshes in the network are found only occasionally and are 1-3 mm in diameter. The colour is black-brown. The consistency is doughy and the animal can be easily broken. There are no xenophyae.

Morphology: The largest specimen in the collection (St. 234) is 28 × 17 × 17 mm. Most of the specimens are about 25 mm in length and 15-20 mm in breadth and height. There are undoubtedly also smaller specimens in the collection, but they are not easily distinguishable from the fragments.

Cytology (Pl. 17A): The granellare branches have a diameter of 22-35 μ. Granellae are rounded or slightly angular and are 1-6 μ in length. Nuclei are spherical and 3-4 μ in diameter.

The anastomosing dark stercomare masses are 35-250 μ in diameter. Xanthosomes are rare; they measure up to 2.5 μ in diameter.

Xenophyae are rare; the few that are found are either naked or covered by a thin cement layer. Many are found within stercomare, and they cannot therefore be regarded as a part of the test in the usual manner.

Remarks: *C. massa* is distinguished from the two other genus members by the soft consistency and the lack of xenophyae. It resembles *C. gyrosphaera* in having cylindrical branches, and both diverge greatly from *C. lamellosa* which has lamellate branches.

Distribution: Known from two dredgings off E. Africa, at 4810 to 4820 m depth, on Globigerina ooze, and at 0.8°C.

Cerelasma lamellosa Haeckel, 1889
Pl. 7B

Cerelasma lamellosa Haeckel, 1889, p. 47, pl. VI, 6-7; Schulze 1907a, p. 24, pl. III, 3.

Material:

"Challenger" St. 216A. – 1 specimen. Originally there were two specimens.

Diagnosis: The body is irregularly lumpy or nearly spherical and is 7-20 mm in diameter. It is made of anastomosing, lamellar branches, 0.6-2 mm wide. The meshes in the network are 1-2 mm in diameter. The surface is whitish and the interior is brown. The consistency is firm, but the animal is friable. Xenophyae are silicious sponge spicules, foraminiferan test fragments, and mineral particles.

Morphology: The available, somewhat damaged specimen is about 10 mm in diameter. When undamaged, the surface is whitish due to the foraminiferan tests and mineral particles, and it is pierced by small pores. The dark stercomare in the interior are strongly developed.

Cytology: A closer investigation was impossible due to scarcity of material.

Remarks: SCHULZE (1907a, p. 25) noted that *C. lamellosa* further differs from *C. gyrosphaera* both in having less strongly developed granellare and in having larger granellae and stercomes.

Occurrence: Known from one dredging in the W. Pacific, at 3660 m, on Globigerina ooze, and at 1.9° C.

Cerelasma sp.

Cerelasma gyrosphaera, SCHEPOTIEFF 1912b, p. 263, pl. 16, 45-65.

SCHEPOTIEFF coll. – Several fragments.

Since I have not been able to locate the material, the following description is based on SCHEPOTIEFF's report. The measurements are based on his drawing and must be considered with great reservation.

Only fragments were found and one measured about 4 × 5 mm (SCHEPOTIEFF l.c., pl. 16, fig. 45). They were made of anastomosing branches 0.4-1.2 mm in diameter.

Cytology: SCHEPOTIEFF states that the granellare resembled that of his *Psammetta* sample (see p. 25 in this paper) and contained granellae and small nuclei. He also found lumps of protein, crystals, and small grains contained in the granellare.

Stercomare were stated to have resembled that of his *Psammetta* and *Stannophyllum* samples (pp. 25 and 60). Xanthosomes were numerous and occurred as aggregates. The xenophyae were numerous radiolarian tests and most of them were embedded in cement substance.

Remarks: SCHEPOTIEFF's classification of his material as *Cerelasma* was undoubtedly correct. He further referred it to *C. gyrosphaera* because of the cylindrical branches and the type of xenophyae (radiolarian tests). His short description does not allow a thorough comparison of his material with the other material, but the following apparent differences make it highly possible that he had found a new species: 1) The diameter of the branches seems to be distinctly smaller than is usual for *C. gyrosphaera.* 2) SCHEPOTIEFF's reference to *Psammetta* presumably referred to his own sample; in this case, the diameter of granellare and stercomare (especially of the former) is much greater than that of the other two samples. 3) The specimens were attached ("angeheftet") to corals, while the other samples are taken on soft bottom and do not show any signs of having an attaching structure. 4) The specimens were collected in shallow water (coral reef) in a tropical area, whereas the "Challenger" and "Vema" specimens were dredged under abyssal conditions.

Occurrence: Known from one dredging off India, at about 20 m depth, on a coral reef, and at about 25° C.

Order *Stannomida* n. ord.

Diagnosis: Xenophyophores with linellae. The body is flexible.

Remarks: The order Stannomida contains the single family Stannomidae, with two genera, each of which shows a high degree of species uniformity. For further remarks pertaining to the order Psamminida cf. p. 20.

There are different linnellae arrangements, and these are used as taxonomical characteristics.

1) Simple linellae (Fig. 4): There is no connecting substance between crossing linellae, and there are no anastomoses or ramifications. The linellae lie either singly or in bundles with few or many parallel threads.

2) Linellae with fastened crossings (Fig. 5): The linellae crossings are fastened and strengthened with cement. If a central canal is present, it is unbranched.

3) Anastomosing and ramifying linellae (Fig. 6): Linellae usually branch dichotomously but sometimes polychotomously. If a central canal is present it branches also.

Family **STANNOMIDAE** Haeckel, 1889

Stannomidae Haeckel, 1889, p. 54; DELAGE & HÉROUARD 1899, p. 200; MINCHIN 1900, p. 154; SCHULZE 1907a, p. 28; 1907b, p. 147; SCHEPOTIEFF 1912b, p. 275; POCHE 1913, p. 203; LOEBLICH & TAPPAN 1961, p. 319; 1964, p. 790.

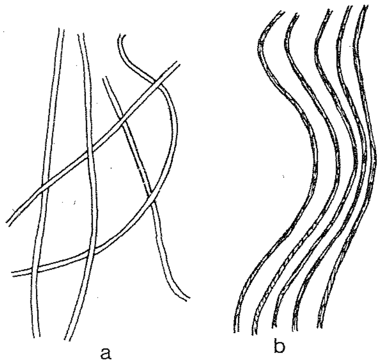


Fig.4

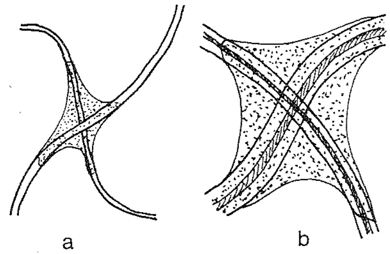


Fig.5

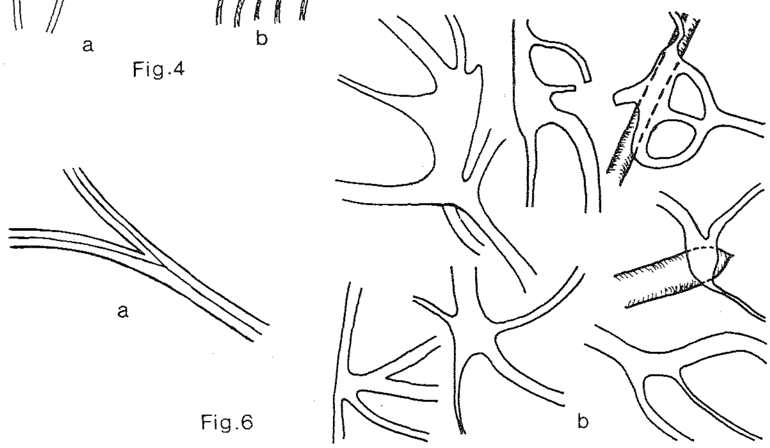


Fig.6

Fig. 4. Simple linellae; a, single linellae; b, linellae bundle.

Fig. 5. Linellae with fastened crossings; a, crossing; b, crossing showing the central canal relations.

Fig. 6. Anastomosing and ramifying linellae; a, dichotomous branching, also of the central canal; b, polychotomous branching linellae.

Spongelidae, HAECKEL 1889, p. 42 (pars); DELAGE & HÉROUARD 1899, p. 199 (pars).
Stannomida Lister, 1909, p. 286.
Neusininae Cushman, 1910, p. 129.
Neusinidae Cushman, 1927, p. 29 (pars).
Psamminidae Laubenfels, 1936, p. 32 (pars).
Psammininae Laubenfels, 1948, p. 180 (pars).

Diagnosis: The body is tree-like branched or flakelike, flexible, and of varying softness.

Remarks: The family was established by HAECKEL for three genera: *Stannoma, Stannophyllum,* and *Stannarium.* The type genus is *Stannoma.* SCHULZE (1907a) incorporated *Psammophyllum* while HAECKEL had placed it in the sponge family Spongelidae. *Psammophyllum* and *Stannarium* are synonyms of *Stannophyllum. Neusina* is another synonym of *Stannophyllum,* and CUSHMAN created the subfamily Neusininae within the foraminiferan family Lituolidae for this genus. Later he ranked it as the type genus of a special foraminiferan family Neusinidae.

At present the family Stannomidae contains two genera: *Stannoma* Haeckel and *Stannophyllum* Haeckel.

Key to the genera

Body tree- or bush-like branched .... *Stannoma*
Body flake-like .... *Stannophyllum*

Genus ***Stannoma*** Haeckel, 1889

Stannoma Haeckel, 1889, p. 72.
Stannoplegma Haeckel, 1889, p. 74.

Diagnosis: The body is tree-like branched with few or many branches.

Remarks: Regarding *Stannoma coralloides,* HAECKEL wrote (1889, p. 74) that "these differences ... might perhaps justify its separation as a peculiar genus *(Stannoplegma)*". Since neither SCHULZE (1907a, p. 35; 1907b, p. 151) nor I find any basis for this proposal, *Stannoplegma* is considered as synonymous with *Stannoma.*

HAECKEL described two species of *Stannoma, S. dendroides* and *S. coralloides*. LAUBENFELS (1936, p. 33) selected the former as type species. LOEBLICH & TAPPAN (1964, p. 790) selected the same species without apparently knowing about LAUBENFELS' work.

Key to the species

Few, free branches .... *S. dendroides*
Numerous, anastomosing branches .... *S. coralloides*

Stannoma dendroides Haeckel, 1889
Pls. 8C; 14B-D

Stannoma dendroides Haeckel, 1889, p. 72, pl. III, 1-4; SCHULZE 1907a, p. 32, pl. IV, 1-3, 5-10; 1907b, p. 148.

Material:
"Challenger" St. 271. – 2 specimens. The largest was selected as lectotype.
"Galathea" St. 232. – 3 specimens.
"Galathea" St. 235. – 2 specimens.
"Galathea" St. 238. – 1 specimen.

Other records (the material is unaccounted for):
"Challenger" St. 272.
"Albatross" St. 3684. – Numerous specimens.
"Albatross" St. 4649. – 1 specimen.
"Albatross" St. 4717. – 1 specimen.
"Albatross" St. 4721. – 3 specimens.
"Albatross" St. 4742. – About 50 specimens.

Diagnosis: The body is tree-like, dichotomously (rarely polychotomously) branched 1-3 times, predominantly planar, up to 8 cm in height, and about 8 cm in breadth. The branches do not anastomose, are circular or slightly flattened in cross-section, and 2-5 mm in diameter. The colour is yellowish to greenish brown. The consistency is soft and the body is very flexible. Linellae are simple, and are 2.5-4 μ in width. Xenophyae are mainly radiolarian tests.

Morphology: The largest specimen ("Galathea" St. 235) (Pl. 8C) is about 5 cm high. In two specimens (both from "Galathea" St. 232) the lower end of the stem is swollen, somewhat flattened, and ends in a linellae tuft intermingled with xenophyae. Two other specimens ("Galathea" St. 235) have inversely conical pointed stem ends and also have a linellae tuft.

Cytology (Pl. 14B-D): The yellowish branches of granellare are 45-135 μ in diameter. The "Galathea" specimens have few, small granellae, but the other specimens have numerous granellae 1-6 μ in length. Nuclei are spherical and 5-7 μ in diameter (cf. Table 6, p. 69).

The dark stercomare masses are 55-120 μ in diameter. Xanthosomes are rare.

Linellae are simple, without anastomoses. Most are between 2.5 and 4 μ in width, but some have been found as thin as 1 μ and as thick as 4.5 μ.

Xenophyae are predominantly radiolarian tests, but many sponge spicule fragments can be seen.

Distribution: Known from ten dredgings, three off E. Africa, two in the Central Pacific, and five in the E. Pacific. It has been found from 3814 to 4930 m depth, on Globigerina or radiolarian ooze, and at 0.3° to 1.9°C.

Stannoma coralloides Haeckel, 1889
Pl. 8D

Stannoma coralloides Haeckel, 1889, p. 73, pl. III, 5; SCHULZE 1907a, p. 35, pl. IV, 4; 1907b, p. 151.
Stannoplegma coralloides, HAECKEL 1889, p. 74.

Material:
"Challenger" St. 271. – 1 specimen.

Other records (the material is unaccounted for):
"Challenger" St. 272. – 1 specimen.
"Albatross" St. 3684. – Several specimens.
"Albatross" St. 4742. – 5 specimens.

Diagnosis: The body is bush-like, most often dichotomously branched in all directions, 2-4 cm high, and about 2-4 cm in diameter. The branches are circular in cross-section and 2-3 mm in diameter. They anastomose and form a network with meshes 2-8 mm in diameter. The colour is yellow-brown. Linellae are simple, 1-2 μ in width, and sometimes with ramifications. Xenophyae are radiolarian tests.

Morphology: The single specimen is in poor condition but is obviously, as mentioned by SCHULZE (1907a) very similar to *S. dendroides* in morphology.

Cytology: The granellare branches seem to measure 25-60 μ in diameter. Granellae are common; they are elongate or rounded, 2-5 μ in length.

Xanthosomes are found scattered in the stercomare; they are rounded, reddish-brown, and 3-7 μ in diameter.

The linellae are generally 1-2 μ in width, but they can occasionally be found up to 7 μ.

Distribution: Known from four dredgings, all in the central and eastern Pacific, from 4243 to 4758 m depth, on Globigerina or radiolarian ooze, and at 1.2°C to 1.7°C.

Genus *Stannophyllum* Haeckel, 1889

Stannophyllum Haeckel, 1889, p. 60.
Psammophyllum Haeckel, 1889, p. 49.
Stannarium Haeckel, 1889, p. 69.
Neusina Goës, 1892, p. 195.

Diagnosis: The body is composed of one or more flake-like parts.

Remarks: Haeckel referred five species to *Stannophyllum: S. zonarium, S. globigerinum, S. radiolarium, S. pertusum,* and *S. venosum*. He referred three species to *Psammophyllum: P. flustraceum, P. reticulatum,* and *P. annectens*. The latter genus was transferred by Schulze (1907a, p. 43) to *Stannophyllum*, and *P. annectens* is here regarded as a synonym of *S. zonarium*. Haeckel referred two species to *Stannarium: S. alatum* and *S. concretum*. Schulze (1907b, p. 155) transferred the former and I transfer the

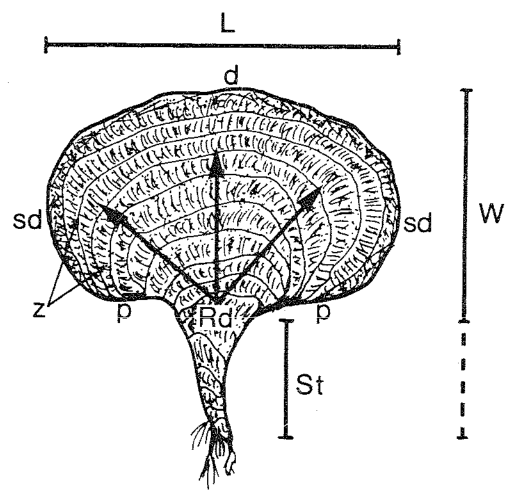


Fig. 7. The body of *Stannophyllum* seen from the surface; L, length; W, width; St. "stalk", proximal prolongation; Rd, radial direction; d, distal edge; p, proximal edge; sd, side edge; z, zonation.

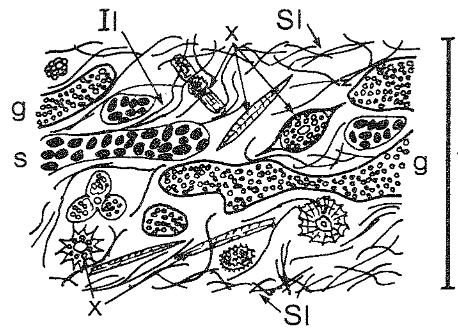


Fig. 8. *Stannophyllum*. Cross-section of the body plate; T, thickness; g, granellare; s, stercomare; Sl, surface layer of linellae; Il, interior linellae; x, xenophyae.

latter to *Stannophyllum*. *Neusina* has long been regarded as a synonym for *Stannophyllum* (cf. p. 45). Four species are described as new here: *S. granularium, S. fragilis, S. indistinctum,* and *S. mollum*.

Laubenfels (1936, p. 33) selected *S. zonarium* as type species. Apparently unaware of this, Loeblich & Tappan (1964, p. 792) selected the same species.

In his remarks on the genus *Stannophyllum*, Haeckel (1889, p. 60) argued for the establishment of several species. However, he mentioned that since there are some transitional forms between these species, and they all are found on the same locality, a "pre-Darwinian" zoologist would have treated them as mere varieties of one species, *Stannophyllum flabellum*. This "species" is in no way defined, and if all of Haeckel's *Stannophyllum* species were united into one, the name should be *S. zonarium*. Following the nomenclature rules *S. flabellum* is a nomen nudum and to avoid future misunderstandings I suggest that it should not be used for any new *Stannophyllum* species.

Since *S. zonarium* is the best known of the species in regard to mention in general zoological literature, the number of known localities, and the amount of available material, I have made a more extensive and detailed description of this species than of the other members of the genus. Many of the general features described and discussed are also found in the other species, but in their descriptions, I have tried to avoid reiterating details of no taxonomic importance. For these reasons the description of *S. zonarium* is presented first even though I regard the species as somewhat specialized (cf. p. 62).

In the diagnosis and descriptions of the species of *Stannophyllum* some terms used need further explanation. Most terms are shown in the figures 7 and 8, and some are also defined below.

Length: The largest measurement parallel to the distal edge, and in case of zonation, also parallel to the zones.

Width: The measurement at right angle to the distal edge (and possible zonation), taken where it gives the largest figure. Where a "stalk" is found, its length is included in the width, but since it is given separately, the dimensions of the body plate proper can be found.

Diameter: Where the length and width cannot be practically used, viz. in case of great damaging or a semicircular outline, the largest diameter is given.

Radial direction: Every direction from the "presumed oldest point" to the distal edge.

Key to the species

1a. Body composed of one leaf 3
1b. Body composed of several leaves 2
2a. One edge of the leaves free; xenophyae: radiolarian tests .... *S. alatum* p. 57
2b. Leaves without free edges but grown together with funnel-shaped cavities between them; xenophyae: foraminiferan tests on the surface, radiolarian tests in the interior .... *S. concretum* p. 58
3a. With ribs 4
3b. Without ribs 6
4a. Ribs only in the proximal part; distal part with concentric zones; xenophyae: sponge spicules, radiolarian tests, and mineral particles .... *S. flustraceum* p. 58
4b. Ribs branching over the whole leaf 5
5a. Ribs distinct; linellae of two sizes (1-2 μ in diameter in the leaf proper, and 6-10 μ in diameter in the ribs) .... *S. venosum* p. 56
5b. Ribs more or less distinct; linellae of one size only (1-3 μ in diameter); body perforated .... *S. pertusum* p. 55
6a. Xenophyae absent; body thick and soft; linellae anastomosing .... *S. mollum* p. 59
6b. Xenophyae present 7
7a. Xenophyae: foraminiferan tests; leaf rather flaccid, sometimes zonated .... *S. globigerinum* p. 51
7b. Xenophyae: not foraminiferan tests 8
8a. Xenophyae: mineral particles, sponge spicules, and a varying number of radiolarian tests; leaf flaccid, sometimes zonated .... *S. granularium* p. 51
8b. Xenophyae: not a combination of mineral particles and sponge spicules 9
9a. Xenophyae: mineral particles exclusively; body fragile; zonation if present, very indistinct .... *S. fragilis* p. 53
9b. Xenophyae: not mineral particles 10
10a. Zonation distinct; well-developed surface layer of linellae; xenophyae: radiolarian tests .... *S. zonarium*
10b. No zonation; no distinct surface layer 11
11a. Linellae anastomosing; xenophyae: sponge spicules .... *S. reticulatum* p. 58
11b. Linellae simple 12
12a. Linellae thin (1-2 μ in diameter); xenophyae: radiolarian tests .... *S. radiolarium* p. 54
12b. Linellae of varying thickness (1-10 μ in diameter); xenophyae: predominantly sponge spicules (this species varies greatly in all characteristics!) .... *S. indistinctum* p. 56

Stannophyllum zonarium Haeckel, 1889
Figs. 9-11. Pls. 8E; 9A-D; 15D; 16C; 17F-G

Stannophyllum zonarium Haeckel, 1889, p. 62, pl. I, 1A-C, pl. II, 1-4; Schulze 1907a, p. 37, pl. V, 1-12, pl. VI, 1-2; 1907b, p. 152.
Psammophyllum annectens Haeckel, 1889, p. 52, pl. IV, 1-4.
Neusina agassizi Goës, 1892, p. 195, pl. I, 1-9.
Non *Stannophyllum zonarium,* Schepotieff 1912b, p. 258, pls. 15, 72-73 and 16, 1-44.

History: *Stannophyllum zonarium* is the species that lead to the discussion mentioned previously (p. 10) on the nature of the "Deep-Sea Keratosa". Unaware of Haeckel's work, in 1892 Goës de-

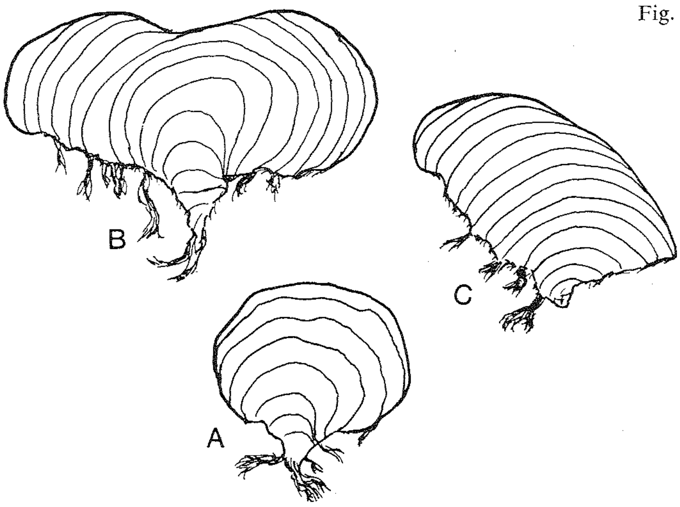


Fig. 9. *Stannophyllum zonarium*. Growth forms A-C.

scribed a leaf-like organism of the same appearance as *S. zonarium* under the name *Neusina agassizi*. The identity of the two species was noted by HANITSCH (1893, p. 365), PEARCY (1893, p. 390), and SCHULZE (1907a, p. 38). Despite this, the species is named *Neusina agassizi* in most of the foraminiferan literature and the many other species described by HAECKEL are not mentioned.

Material:
"Challenger" St. 244. Labelled as *Psammophyllum annectens*. – 1 specimen.
"Challenger" St. 271. – About 10 specimens.
"Albatross" St. 3415. Labelled as *Neusina agassizi*. – Numerous specimens; 1 specimen is available, the others are unaccounted for.
"Galathea" St. 716. – About 100 specimens.
"Vema" St. 15-44. – 3 specimens.
"Vema" St. 15-50. – 1 specimen.
"Vema" St. 15-55. – 10 specimens.
"Vema" St. 15-64. – 2 specimens.
Magdalena Bay Expedition St. A-36. – 2 specimens.
"Vitiaz" St. 4213. – 3 specimens.
"Vitiaz" St. 4265. – 9 specimens.

Other records (the material is unaccounted for):
"Albatross" St. 3399. – Numerous specimens.
"Albatross" St. 3414. – Numerous specimens
"Albatross" St. 3684. – Numerous specimens.
"Albatross" St. 4647. – About 50 specimens.
"Albatross" St. 4649. – About 80 specimens.
"Albatross" St. 4651. – About 50 specimens.
"Albatross" St. 4653. – 1 specimen.
"Albatross" St. 4656. – About 10 specimens.
"Albatross" St. 4658. – 2 specimens.
"Albatross" St. 4666. – 1 specimen.
"Albatross" St. 4717. – 11 specimens.
"Albatross" St. 4721. – 4 specimens.
"Albatross" St. 4742. – About 50 specimens.

Diagnosis: The body is brown, flake-like, reniform, 3-19 cm long, and 1-2 mm thick. The surface is distinctly zonated with zones 3-5 mm in breadth. The consistency is stiff, but the body is somewhat elastic. The linellae are strongly developed; they are simple, without anastomoses or ramifications, and 3-4 μ in width. They form a distinct surface layer and are very often in bundles. Xenophyae are mainly radiolarian tests.

Morphology

The following description is based mainly on the large material from "Galathea" St. 716 since this is presumed to be representative for the actual population. *S. zonarium* has proved to be a very uniform species, and the general comments and conclusions are also valid for the "Albatross", "Vitiaz", and "Vema" samples. A special description of these materials will, therefore, not be given.

The largest "Galathea" specimen measures 7 × 11 cm, the smallest 3 × 2.5 cm. The thickness is 1-2 mm. The colour varies slightly from specimen to specimen, from greenish brown to dark brown. The older body parts are darker than the younger. The organisms are very flexible, and this was also the case when they were brought on deck (Dr. T. WOLFF, personal communication).

Growth forms. From the relatively undamaged specimens from St. 716 (about 30), it is possible to distinguish three growth forms (Figs. 9-10):

Growth form A. Specimens in which the length is nearly equal to the width. This growth form is seen in general in rather small specimens, the largest being 7.5 × 6 cm and the smallest being the smallest specimen in the collection, measuring 3 × 2.5 cm. Two of the specimens in this category are elongated proximally (Pl. 9C). HAECKEL (1889, p. 63) described a "stalk" on a specimen measuring about 6 cm in breadth. GOËS (1892, pl. I, 2) illustrated a specimen measuring about 8 × 7.5 cm. SCHULZE (1907a, p. 37) mentioned that especially the small specimens are often provided with a "pedicle"; his largest specimen of this type measured about 6 cm in breadth.

Growth form B. Specimens in which the length is greater than the width. The largest specimen present with this growth form measures 12.5 × 6 cm. The largest known specimen of *Stannophyllum zonarium* belongs to this form. It is pictured by GOËS (1892, pl. I, 1) and measures 19 × 5 cm (Pl. 8E).

Growth form C. Specimens in which the length is less than the width. The largest specimen in the "Galathea" collection is of this type and measures 7 × 11 cm (Pl. 9A). Specimens of this form are 7-11 cm in width and 5-7.5 cm in length. The tufts of linellae (p. 48) in animals of this growth form are only found along one side edge (in contrast to growth form B, where they are found along both sideedges).

Specimens of growth form A seem to represent the youngest individuals. These have a proximal prolongation which is the oldest part of the animal. The oldest part generally dies when the animal attains a width of about 4-4.5 cm. In some cases it is retained longer, but no individual more than 7 cm in width is known to have this "stalk".

The specimens of growth form B arise from the A form by growing along the distal edge and dying at the proximal edge.

Specimens of growth form C are formed through separation of B animals into two. This happens when the decaying proximal edge reaches the central part of the distal edge, where the growth apparently is slow or has ceased. The legitimacy of this suggestion is indicated by the presence of tufts of linellae along only one side edge. The phenomenon may be regarded as a sort of asexual reproduction.

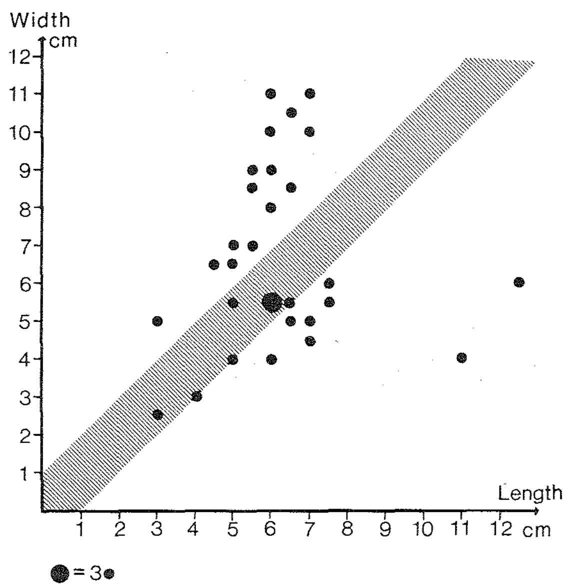


Fig. 10. *Stannophyllum zonarium*. Undamaged specimens (31) from "Galathea" St. 716. Specimens having equal length and width (within 1 cm) are indicated by the hatched area.

Only 31 specimens in the "Galathea" St. 716 sample could be regarded as intact or nearly undamaged, and the distribution of the growth forms in this material gives only an indication of the bottom situation. There are 30 % growth form A, 20 % growth form B, and 50 % growth form C.

Excrescences. Some specimens have leaf-formed excrescences, and these are generally only on one face but in some cases on both. When in natural position on the bottom they must lie parallel to the "mother"-animal (p. 50), as is indicated by the fact that the otherwise free edge is in some cases attached to the "mother"-animal. The excrescences always show zonation, and some or all of the zones pass into zones of the "mother"-animal. The basalline between the "old" and the "young" always extends exactly from one zone furrow to another, and covers 1-6 zones.

This is presumably a sort of budding. In one type of buds where only some of the zones pass into zones of the older animal, the bud is assumed to be released when it reaches a certain size, 20-30 mm in width. Most buds seen are 5-7 mm wide, but there are some larger ones. SCHULZE (1907a, p. 153) reported a specimen where the bud was relatively large. Another type of excrescence where all the zones of the bud pass into zones of the "mother" -animal does not seem to be released. These can be rather large and often nearly of the same size as the "mother"-animal itself.

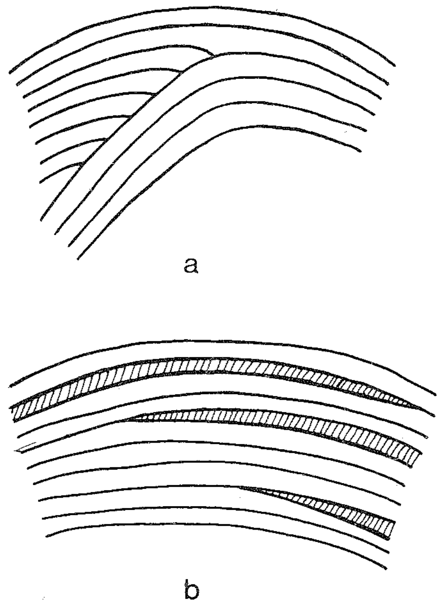


Fig. 11. *Stannophyllum zonarium.* Zonation irregularities; a, zones end oblique to other zones; b, a single zone ends in an acute point within the body plate.

Surface. There is no visible difference between the two body faces. The surface is even; in the older parts it is nearly smooth, and in the younger parts it is more velvet-like. It has numerous pores with a diameter up to about 0.5 mm, but most of them are much smaller. Sometimes 4-7 pores are found in a row, but there is no special orientation with respect to the zones. The pores are found on all parts of the body.

Zonation. The most conspicuous species character is the distinct surface zonation. The zones are concentric, parallel to the distal body edge, and extend from side edge to side edge. Some irregularities are sometimes found where a group of several zones end obliquely to other concentric zones (Fig. 11a), or where a single zone ends in an acute point between two other zones in the middle of the plate (Fig. 11b). The zone breadth varies from 2-7 mm, but it is usually about 3 mm. Each single zone has nearly always the same breadth for its entire length.

When lighted from below the zone limits are seen as light stripes, particularly in the youngest and the oldest body parts. In the largest part they are more faint. Cross-sections show that the zones result from surface depressions; most often these lie exactly opposite to each other on the two sides of the body plate, but they can be found a little displaced. The zone furrows are sometimes more evident in the older body parts due to overlapping of the distal of two neighbouring zones onto the proximal. In cross-section most of the zones are thickest at the zone midline, but, as noted by Haeckel (1889, p. 63), some are thickest in the proximal area. For further discussion regarding zonation, see the general part (p. 67).

The body edges can differ in the following ways:

I. The distal edge where growth takes place (Pl. 9A, a[1], B) is unbroken, even, and sometimes faintly lobed. The outermost 0.5-1 mm is very light and composed of numerous linellae and some xenophyae. Well-limited pores are not seen in this area. Plasma elements were not found. Granellare and stercomare are only weakly developed in the zone next to the distal edge. In specimens of growth form C the distal edge is continuous with a side edge (Pl. 9A, a[2]) which is relatively even and composed of the tightly lying, acutely pointed zone ends.

II. The proximal edge (Pl. 9A, b), where decay occurs, is usually unbroken and even, since it follows a zone furrow. Apparently decay occurs zone by zone and the remains fall off within a short period of time. The well-developed granellare and stercomare can then be easily seen in the next zone.

III. The zones often end in free linellae tufts on both side-edges of the A and B growth form specimens and on the one side-edge of the C form (Pl. 9A, c).

Tufts and tubes. Tufts are mainly made of free linellae which may form thick bundles. The zone passes into the tuft by a tube-like structure that can be of varying length. In some cases the tube originates a few mm behind the zone end within the body plate. Generally each zone ends in a single tube, but the tube can be dichotomously divided with a tuft of linellae in each part. In some cases three tubes were found resulting from a single zone.

The tube diameter is 1-3.5 mm, and the length is up to 7 mm. The tubes and tufts are generally 10-15 mm in length and in some cases up to 20 mm. The tube surface is similar to the body surface and it has pores. Tubes are not found on the youngest zone. In the next youngest zones they are rather flat and are of approximately the same breadth as the zone. The cross-section is more circular and the walls are stiffer in the older zones because of greater numbers of xenophyae. The tube walls pass into the surface layer of the body and into short walls between the zone furrows but they can only be traced a few mm into the body.

Granellare and stercomare are found in the proximal tube part but more rarely in the distal. There are relatively few xenophyae distally, whereas they are more numerous proximally. Sometimes they are so numerous within the outermost range of granellare and stercomare in the proximal part of the tube that they appear to be concentrated here compared with the central body parts.

The tubes and linellae tufts have been interpreted in different ways.

GOËS (1892, p. 196) described them and concluded that "they serve probably as fastenings to the bottom." RHUMBLER (1895, p. 88) regarded them as pseudopodial tubes (Pseudopodialröhren). He had previously (1894, p. 485) described the pseudopodial tubes in the foraminiferan *Saccammina sphaerica* as prolongated parts of the plasma which were surrounded by a wall of test material and from which pseudopodia extend. RHUMBLER considered the pseudopodial tubes to be accumulation centers for test building material either for the individual itself or for the offspring. LÜCKE (1910, p. 27) agreed with him on this matter.

SCHULZE (1907a, p. 38) noted that tufts are not found in the youngest individuals and that if they are found they are only at the narrow end of the "pedicle". He thought they possibly represented decaying zone ends.

GOËS' opinion that the structures serve to anchor the animal has no further support, and nothing in the material at my disposal can be interpreted in this way.

SCHULZE's suggestion that the structures are decaying is feasible, but is contradicted by the presence of the seemingly special organization. Moreover the tubes and tufts are just as well developed in younger parts of the animal as in older parts.

RHUMBLER's conception (1894) of the existence of pseudopodial tubes as a special organelle for the collecting and storing of test material has never been proved and was strongly opposed and criticized by HERON-ALLEN & EARLAND (1913, p. 13). They found that the excrescences in *Saccammina sphaerica* were abnormalities and in some cases might have been simply projecting foraminiferan tests of the *Reophax* type incorporated in the test as building material. Moreover, they stressed that these tubes were not commonly seen in their samples, and that only three of RHUMBLER's numerous specimens had them. LÜCKE (1910, p. 27) described pseudopodial tubes from only one of his *Saccammina sphaerica* specimens.

Pseudopodial tubes were later described in *Pelosphaera cornuta* by EARLAND (1935, p. 54) and HEDLEY (1960a, p. 55). Here again the pseudopodial tubes were only occasionally found and they seemed to be of temporary nature. Structures presumably comparable to the pseudopodial tubes in *Saccammina* and *Pelosphaera,* but of more permanent nature are found in many agglutinated foraminiferans, viz. *Astrorhiza limicola* (BUCHANAN & HEDLEY 1960; HEDLEY 1960a), *Radicula limosa* (CHRISTIANSEN 1958), *Dendrophrya erecta* (WRIGHT 1861; BRADY 1884; CHRISTIANSEN 1958), and *Julienella foetida* (SCHLUMBERGER 1890; BUCHANAN 1960; NØRVANG 1961).

The tube and linellae tuft structure found in *Stannophyllum zonarium* gives the impression of permanency because of its solidity through the strengthening of linellae and its common occurrence in the specimens. Whether or not it is a special functional organelle as proposed by RHUMBLER can presumably only be decided through investigations on living material. Indications thereof may be the presence of granellare (and with this of pseudopodia) and the occasional apparent concentration of xenophyae in the proximal part of the tube. It should be noted that the discussed structures are found only in *S. zonarium,* and not in the other *Stannophyllum* species.

Cytology (Pl. 15D)

The granellare branches are circular to ellipsoidal in cross-section and the diameter is 50-145 μ, but generally about 60 μ. There is no definite branch orientation present. The plasma is hyaline with numerous granellae that can be up to 5 μ in length although most of them are 1-3 μ. The nuclei are ellipsoidal and 5-6 μ in length. In granella-free plasma areas, which are observed only rarely, nuclei with a larger diameter of about 8 μ or possibly more are found.

The stercomare masses form a net-like structure throughout the animal, and are circular to ellipsoidal in cross-section, but can be rather irregular in the older parts. The diameter varies from 90-360 μ. Two different kinds of stercomare are found in most parts of the body and transitions between them are common. The one kind of stercomare is characterized by a thin wall and has loose, uniform, light contents; the other kind has a thick wall and dense, dark contents formed as stercomes. The thin-walled stercomare stage seems to represent the most recently deposited and unfinished masses. It dominates in the youngest body zones and the thick-walled stage dominates in the oldest body zones. Xanthosomes are yellowish, rounded, and measure about 5 μ in diameter. They are few and scattered.

The linellae which often form bundles are generally 3-4 μ in width. They form conspicuous surface layers on the two body surfaces and they are also seen in the interior, especially in the older parts. They often lie closely connected to the walls of the thick-walled stercomare stage.

Xenophyae are radiolarian tests. Sponge spicules, spicule fragments, and occasionally a few mineral particles are found among them. Bundles of linellae often interweave with the xenophyae.

The synonymies

HAECKEL (1889, p. 52) described a species, *Psammophyllum annectens,* with an external appearance similar to *Stannophyllum zonarium*. The only differences between the two species were that the linellae of *P. annectens* possessed numerous ramifications and anastomoses and that the thickest of them enclosed small shells and radiolarian fragments.

Both SCHULZE (1907a, p. 45) and I have re-examined the type specimen of *P. annectens* and have failed to find anything but simple linellae, none of which fit HAECKEL's descriptions. Small xenophyae are often seen "glued" to the surface of linellae, but they are not enclosed, and this characteristic is not unique since it is found in many *Stannophyllum* species. No other differences were found, and *P. annectens* must therefore be regarded as a synonymn of *S. zonarium*.

The specimen of *Neusina agassizi* at my disposal seems to be the one pictured by GOËS (1892) as fig. 1 on his plate. It is dried, measures approximately 17 × 5 cm, and is a little damaged at one end (Pl. 8E). A comparison with both dried and alcohol preserved specimens from the "Challenger", "Galathea", "Vitiaz", and "Vema" collections confirm the identity of *Neusina agassizi* with *Stannophyllum zonarium*.

Remarks on the position of *S. zonarium* on the bottom

The position and possible attachment of *S. zonarium* has been much debated.

HAECKEL (1889, p. 60, pl. I, 1a-1b) presumed that the animal grew vertically, anchored to the bottom by a stalk, and pictured his specimens attached to a stone. There is no foundation for this conception, and HAECKEL's only reason for supposing a vertical orientation was that the two large body faces are identical in structure and appearance.

AGASSIZ (1891, p. 192; 1892, p. 78) described them as: "Foraminifers, forming immense curling sheets attached by one edge to stones or sunk into the mud."

GOËS (1892, p. 196) presumed that the linella tufts served as anchoring structures, but said nothing about the body orientation.

SCHULZE (1907b, p. 153) described a case where a specimen was fixed to the face of another by a long stalk that was flattened at the base and continued: "Dieser letztere Fall scheint mir deshalb wichtig, weil er darauf hindeutet, dass die ganzen Gebilde normaler Weise zunächst wirklich mit der verbreiterten Basis ihres Stieles am Meeresgrunde anderen festen Körpern oder Sandflächen aufsitzen." He thought that the linellae tufts were products of decay formed when the edge of the animal was buried in the mud.

The following facts can be noted in this discussion:

1) In preserved material the body is not stiff enough to stand by itself solidly in a vertical position. Submerged it assumes a half-floating position. As previously mentioned (p. 46) the consistency was unaltered by fixation, but the specific gravity, of course, may have changed when alcohol penetrated the different body parts.

2) "Stalks" are rare and found only on small specimens. This proximal, narrow area is the oldest part of the individual. Morphologically it resembles the rest of the body.

3) All records are from soft bottoms. In no cases are stones reported. (From "Albatross" St. 4658 manganese nodules are mentioned, but not in connection with *S. zonarium*).

4) The surface of many specimens is damaged so that it resembles bites or scrape marks. These are presumably caused by a predator, and they are found on only one side of the body.

5) Other animals, e.g. foraminiferans, small sponges and small crustaceans are quite often attached to *Stannophyllum* species, but they are always found on only one surface.

It seems reasonable to conclude that *Stannophyllum zonarium* lies on one of the large body faces loose or loosely attached (by the pseudopodial tubes?) on or in the surface layer of the bottom.

Distribution

S. zonarium is known from 24 dredgings, 22 in the E. Pacific, one in the Central Pacific, and one in the N. Pacific. They range from 981 to 5307 m and from 1.2 to 5.2°C. The bottom was recorded as Globigerina ooze, red clay, fine sand, and various shore-influenced muds.

Stannophyllum globigerinum Haeckel, 1889
Pls. 9E; 15A-C

Stannophyllum globigerinum Haeckel, 1889, p. 68, pl. I, 5 A-C; Schulze 1906, p. 15, pl. III, 3-4; 1907a, p. 43, pl. VII, 2; 1907b, p. 154.

Material:
- "Challenger" St. 271. – 9 specimens.
- "Siboga" St. 211. – 1 specimen.
- "Siboga" St. 221. – 1 specimen.
- "Galathea" St. 235. – 14 specimens.
- "Galathea" St. 238. – 9 specimens.

Other records (the material is unaccounted for):
- "Valdivia" St. 240. – A few specimens.
- "Siboga" St. 295. – 3 specimens.
- "Albatross" St. 3684 – Several specimens.
- "Albatross" St. 4647. – 1 specimen.
- "Albatross" St. 4717. – 1 specimen.
- "Albatross" St. 4721. – 3 specimens.
- "Albatross" St. 4742. – 16 specimens.

Diagnosis: The body is flake-like, subovate or rounded triangular in outline, 4-9 cm long, and 2-4 mm thick. The colour is whitish to green-brown, depending on the number of xenophyae, and the consistency is flaccid. The linellae are 1.5-6 μ in diameter and form a rather thin and loose surface layer. Xenophyae are foraminiferan tests and test fragments. They are loosely attached and the surface is therefore granulate and friable. Zones are discernable when many xenophyae are removed from the surface.

Morphology: The best preserved "Galathea" specimens are elongate and rounded, but specimens are often irregular in outline due to damaging. The largest intact specimen (St. 235) measures 9 × 6 cm, and is 2-3 mm thick. None of the specimens have a preserved "peduncle" or "Stiel".

Cytology (Pl. 15A-C): The granellare branches measure 35-90 μ in diameter. Granellae are generally numerous in the plasma and are 1-6 μ in length. Nuclei are spherical and 3-4 μ in diameter. For the different nuclei types, see Table 6 (p. 69).

The stercomare masses measure 90-210 μ in diameter. Xanthosomes were not observed in the "Galathea" material. The few xanthosomes in the "Siboga" material are 5-10 μ in diameter.

The linellae vary greatly in thickness from 1.5-6 μ. They form a distinct, thin, loose surface layer; they are also found in the interior of the body. Crossings strengthened with cement seem to be more common in *S. globigerinum* than in the other species without true linella anastomoses, with the exception of *S. granularium* and *S. fragilis*.

Xenophyae are mainly found on the surface; there are few in the interior.

Distribution: Known from 12 dredgings: five in the E. Pacific, one in the Central Pacific, three in the Indonesian area, and three off E. Africa. It has been taken at 1158 to 4810 m depth, on Globigerina ooze or mud with numerous diatoms and radiolarians, and at 0.8° to 4.0°C.

Stannophyllum granularium n. sp.
Pl. 10A-C

Material:
- "Vitiaz" St. 3166. – 16 specimens.
- "Vitiaz" St. 3198. – 4 specimens.
- "Vitiaz" St. 3232[1]. – 1 specimen.
- "Vitiaz" St. 3359. – 4 specimens.
- "Vitiaz" St. 3363[1]. – 3 specimens.
- "Vitiaz" St. 3575. – 3 specimens.
- "Vitiaz" St. 4495. – 2 specimens.
- "Vitiaz" St. 5617. – 3 specimens.
- "Vitiaz" St. 5623. – 2 specimens.
- "Vitiaz" St. 5625. – 4 specimens.
- "Vitiaz" St. 6088. – 2 specimens.

The holotype is from St. 3198. It measures 42 × 40 mm and is in the Zoological Institute, Leningrad.

1. In his book on the hadal fauna, Beljaev (1966, p. 63) lists xenophyophores from this station as *Stannophyllum* sp. 1.

Diagnosis: The body is flake-like, semicircular to reniform in outline, 2.5-10 cm in diameter, and 1.5-3 mm thick. The colour is dark brown and the consistency is rather flaccid. The surface is granular and sometimes has faint zonations. Linellae are simple and are 2-7 μ in diameter, but generally 3-5 μ. They are relatively strongly developed and sometimes form a quite distinct surface layer. Xenophyae are a fixed combination of mineral particles and sponge spicules, and there are a varying number of radiolarian tests present.

Morphology: The type specimen is semicircular to roughly triangular in outline, 42 × 40 mm, and 2 mm thick. The colour is brown and the consistency is flaccid. The surface is granular and has a very faint zonation. The simple linellae form a surface layer and are 3-5 μ in diameter. The xenophyae are restricted to the surface and there are numerous mineral particles with smaller numbers of sponge spicules and radiolarian tests.

The largest specimen in the collection (St. 5625) is 10 × 4 cm and about 2 mm thick, the smallest (St. 4495) 2 × 1.5 cm, and also about 2 mm thick. Many of the specimens are damaged. In two cases the thickness was as great as 4 mm, but this seems to be due to the poor condition of the specimens.

Zonation is seen in the type as well as other specimens (St. 3166, St. 3198, St. 3575, St. 5617 and St. 6088); the zonation is always faint and best seen if the xenophyae are removed. The zones are 3-5 mm broad and can be traced through the whole length of the body. There are often walls made of xenophyae 0.3-0.4 mm thick between the zone furrows. Granellare and stercomare penetrate these walls, but there is a tendency for stercomare to be more strongly developed within the zones and penetrate the wall only in the form of a few strings.

Variation: The specimens from Sts. 3232, 3363, 3575, 5617, 5623, and 5625 closely resemble those from the type locality of St. 3198 (Pl. 10A). Some specimens from St. 3166 resemble the type, but others differ somewhat. The three remaining samples (Sts. 3359, 4495, and 6088) differ in varying degrees from the type. Stations with greatly varying specimens are all (except for St. 4495) situated close to stations yielding specimens resembling the type.

The 16 specimens from St. 3166 are of two different morphological types. Two of them closely resemble the holotype. The remaining 14 specimens are small (2-3 cm in diameter), rather stiff, often provided with thickenings and small leaf-like projections (Pl. 10B). The surface is even and faintly zonated. The xenophyae are restricted to the two surfaces. They are predominantly mineral particles and there are a few radiolarian tests. The linellae measure 1-4 μ (generally 3-4 μ) in diameter, are slightly developed, and are found throughout the whole animal but do not form a special surface layer.

The specimens from St. 3363 are rather stiff, and the immediate impression is that the xenophyae are exclusively radiolarian tests. Nevertheless, numerous minute mineral particles are present.

The specimens from the Banda See (St. 4495) are rather stiff, small, and about 2 cm in diameter. Xenophyae are mainly minute mineral particles of uniform size, and these are also found in the body interior. There are no radiolarian tests. The station is far from the main distribution area in the N.W. Pacific.

The two specimens from St. 6088 are rather stiff and have faint zonation. The xenophyae are mainly mineral particles. There are no radiolarian tests. In comparison with the other samples, there are relatively few sponge spicules.

Cytology: The granellare branches are circular in cross-section and 40-120 μ in diameter. Granellae are numerous and 1-7 μ in length, most of them being 2-3 μ. Nuclei are ellipsoidal and 5-7 μ in length.

The stercomare masses measure 180-ca. 300 μ in diameter. Xanthosomes are numerous, green-brown to yellow-brown, rounded, and 2-15 μ in diameter. A large number of small, yellowish particles measuring about 0.5 μ in diameter are, perhaps, xanthosomes in an early developmental stage.

Linellae are strongly developed. They are simple but crossings strengthened with cement are common. Diameters as great as 10-12 μ are seen, but only rarely. A surface layer is, in some cases, very well developed, while it is hardly detectable in others. Linellae are always found in the body interior.

Xenophyae are generally restricted to the two surfaces. Mineral particles are most commonly seen, but silicious sponge spicules are always present. There are generally fewer radiolarian tests than mineral particles, and in some cases they are almost absent.

Remarks: *S.granularium*'s most distinguishing characteristics are the granulated surface and the combination of mineral particles and silicious sponge spicules as xenophyae. There are usually many radiolarian tests, but the number varies from sample to sample.

The specimens of one of the samples where radiolarian tests were absent (St. 4495) differed also in the following characteristics: small body size, consistency, and type and distribution of xenophyae in the test. On the basis of the two only poorly preserved specimens, it has been impossible to exclude the possibility that they represent a species different from (but closely related to) *S.granularium*.

Stannophyllum granularium resembles *S.fragilis* and *S.globigerinum* most. For a comparison with *S.fragilis*, see p. 54. The resemblances with *S.globigerinum* are the following: flaccid consistency, the granulate surface, the occasionally present zonation, the common occurrence of strengthened linella crossings, and perhaps the distribution of the xenophyae in the test. The greatest differences between the two are the general body outline and the xenophyae type.

Calcareous foraminiferan remnants are almost completely dissolved in depths exceeding 4000-5000 m, a limit that perhaps rises to about 500 m in higher latitudes (cf. BERGER 1967, p. 383; MURRAY & RENARD 1891, pp. 215, 223; KENNETT 1966, p. 192). There is a possibility that *S.globigerinum* uses another type of xenophyae at great depths. *S.granularium* might, therefore, be a variety of *S.globigerinum*. In opposition to this interpretation is the fact that sponge spicules have been available at nearly all the localities in which *S.globigerinum* are reported. Although a few sponge spicules are often found in *S.globigerinum*, they are by no means as regularly distributed or numerous as is characteristic for all the *S.granularium* samples. Furthermore, mineral particles and radiolarian tests are not found in *S.globigerinum* although they must have been available. As long as transition forms between *S. globigerinum* and *S.granularium* are unknown, *S. granularium* must be regarded as a distinct species.

S.indistinctum as well as *S.granularium* have a nearly constant combination of different xenophya types, viz. sponge spicules and radiolarian tests. The two species differ, however, in the body outline and degree of surface granulation. Moreover, *S.indistinctum* is never zonated and does not have a distinct linellae surface layer. The xenophyae differ both in type and in relative abundance. Mineral particles are never found in *S.indistinctum* specimens. Sponge spicules dominate in all the specimens of this species, and radiolarian tests are nearly always present; however, in several cases there are only very few present. A difference, possibly of minor importance, can be seen in the linellae. The strengthened crossings are common in *S.granularium*, but are not, or only rarely, found in *S.indistinctum*.

Distribution: *S.granularium* is known from 11 dredgings, one in the Indonesian area and 10 in N.W. Pacific, at 4365 to 6710 m depth, on clayey, brown silt, and at 1.6° to 1.7°C.

Stannophyllum fragilis n. sp.

Fig. 12. Pl. 10D-E

Material:
"Galathea" St. 200. – 3 specimens and some fragments. The holotype measures 37 × 46 mm.

Diagnosis: The body is fragile, flake-like, semicircular in outline, 4.5-5.5 cm in diameter, and 2-3.5 mm thick. The colour is yellow-brown to dark brown, and the consistency is relatively stiff. The surface is very granular. Linellae are simple and can be 2-40 μ in diameter, but are generally 5-10 μ. They are only slightly developed but are evenly distributed in the test. Xenophyae are exclusively mineral particles (mostly quartz).

Morphology: The largest specimen measures 5.5 × 3 cm, and is about 3 mm thick. When the body is broken, there is a tendency toward breaking in distinct pieces parallel to the distal edge. Therefore, zonation must be present even though it is no timmediately evident because of the numerous xenophyae. In some cases walls made of xenophyae have been found in the fragmentation lines.

Cytology: Due to the numerous silicious xenophyae, little investigation was possible.

The granellare branches seem to be cylindrical and are 90-120 μ in diameter. Where branching occurs, the diameter can reach about 180 μ. Granellae are numerous throughout the plasma; they are elongate, rounded, and 1-4 μ in length.

The strongly developed stercomare masses are loose and 90-210 μ in diameter. Xanthosomes are

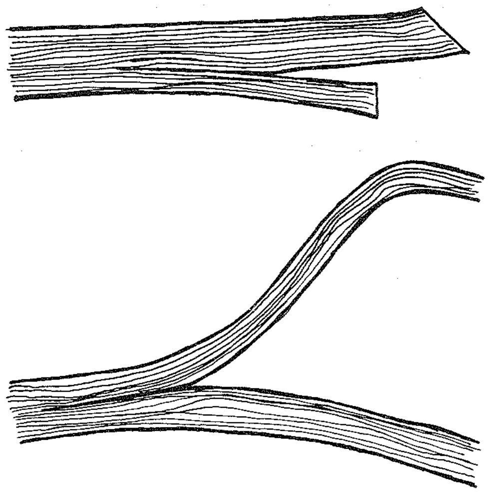


Fig. 12. *Stannophyllum fragilis* n. sp. Division of large linellae bundle.

scattered, yellow-brown to green, elongate, rounded, and up to 8 μ in length.

The rather slightly developed linellae do not form a special surface layer. Those with large diameters (40 μ) are actually bundles of many single linellae. This is not immediately apparent, but can be discerned at the linellae ends or at a rupture. The bundles are unusually stiff and easily broken; they are light brown in colour (in contrast to the usually almost transparent linellae) and this is presumably due to cement between the individual linellae. Ramifications and crossings that are strengthened with cement are common. The ramifications (Fig. 12) seem to be formed by division of the large bundles into two (thus it is not a true ramification according to the definition, p. 41). All linellae thicker than about 10 μ seem to be of the compound type. The remarkable fragility of the species (exceptional among Stannomida) is apparently partly caused by the presence of few linellae and partly by the presence of easily breakable, composed linellae.

The xenophyae are exclusively mineral particles (of varying sizes) and these are generally large (larger than in *S. granularium* - compare Pl. 10C and D). They seem to be concentrated on the surfaces; in the interior they are only found in the walls between the zones. They are numerous and loosely attached.

Remarks: *S. fragilis* resembles *S. granularium* most. The following similarities can be noted: the general body outline, the dimensions, the presence of an indistinct zonation, and the possession of mineral particles as xenophyae. The most important differences are the following: the consistency and degree of fragility, the surface texture, the arrangement and features of the linellae, and the types of xenophyae present (*S. granularium* always has silicious sponge spicules and nearly always radiolarian tests besides mineral particles).

Occurrence: Known from one dredging off S. E. Africa, at 5110 m, on Globigerina ooze, and at 0.5° C.

Stannophyllum radiolarium Haeckel, 1889
Pl. 10F

Stannophyllum radiolarium Haeckel, 1889, p. 65, pl. I, 2A-C; Schulze 1907a, p. 41.

Material:

"Challenger" St. 271. – 5 specimens. As lectotype was selected the largest, intact specimen, measuring 5.5 × 5 cm.
"Galathea" St. 716. – 1 fragment.
"Vitiaz" St. 3156. – 1 specimen.

Diagnosis: The body is rounded, delicate, flake-like, 3-5 cm in diameter, and 1-1.5 mm thick. The colour is whitish to yellow-brown, and the consistency is soft. The surface is nearly smooth and does not have ribs or zones. Linellae are simple and occur singly or in small bundles; they measure 1-3 μ in diameter. Xenophyae are radiolarian tests.

Morphology: Schulze (1907a, p. 42) doubted the validity of the species. For this reason and because the material is small and relatively heterogeneous, a special description will be given of each sample.

"Challenger" material: The specimens are whitish and fit the diagnosis.

Cytology: The granellare branches are circular or irregularly rounded in cross-section and measure 60-90 μ in diameter. The plasma, which is greatly shrunken, contains only few granellae that are up to 3 μ in length, but most of them are 1-2 μ. The numerous nuclei are slightly ellipsoidal and 8-10 μ in length. They are often found singly or grouped in isolated plasma lumps.

Stercomare is slightly developed and poorly preserved; the strings are 35-70 μ in diameter, but presumably reach larger dimensions. Xanthosomes seem to be rare.

The linellae generally are 1-2 μ in diameter, and in a few cases isolated linellae 3-4 μ in diameter were seen. The linellae do not form a surface layer.

Xenophyae are exclusively radiolarian tests, although a few silicious sponge spicule fragments are also seen. They are evenly distributed throughout the test.

"Galathea" material: The fragment is whitish and rather soft. A faint zonation can be distinguished on the surface.

Cytology: The granellare branches are 50-75 μ in diameter. The plasma contains numerous granellae which measure up to 7 μ in length, although most of them are 1-3 μ. Nuclei are difficult to see; they seem to be ellipsoidal and are 4-7 μ in length.

Stercomare are so poorly preserved that no comments can be made.

The linellae are 1-3 μ in diameter. They form a slightly developed surface layer.

Xenophyae are exclusively radiolarian tests, and they are found throughout the test.

"Vitiaz" material: The single specimen measures 2.9 × 2.4 cm and is 0.8-1 mm thick. The colour is yellow-brown and the consistency is soft. On the surface where many xenophyae have fallen off, a faint zonation is seen.

Cytology: Granellare extend radially and have branches 25-60 μ in diameter. Granellae are numerous and 1-3 μ in length. The numerous nuclei are ellipsoidal and 4-6 μ in length. They lie singly or in small groups in small granellae-free plasma areas.

The stercomare branches extend radially and measure 75-240 μ in diameter. Xanthosomes are numerous; they are dark brown, rounded, and 3-7 μ in diameter.

Linellae are 1-2 μ in diameter and of the simple type. They are found throughout the test but do not form a definite surface layer.

Xenophyae are mainly found on the surfaces. They are radiolarian tests, but a fairly high number of silicious sponge spicules and some small mineral particles are also present.

Remarks: As SCHULZE pointed out (1907a, p.42), it is difficult to clearly distinguish between *S.zonarium* and *S.radiolarium,* using HAECKEL's definition of the latter. HAECKEL himself mentioned that *S. radiolarium* is connected with *S.zonarium* and *S. pertusum* by transitional forms, and he found greatest similarity with the former.

New characteristics of taxonomical importance have not been found during the present investigation. The distinguishing ones are, as listed by SCHULZE, 1) the bright colour, 2) the soft consistency, 3) the thin and comparatively few linellae, and 4) the lack of zonation. As SCHULZE also mentioned, all these characteristics are not always found in the same specimen, and they are, with the exception of 3, more or less subjective.

The "Galathea" specimen consists of only one fragment found among about 100 *S.zonarium* specimens, and it is possible that it is a non-typical fragment of a specimen of this species. On the other hand, *S.zonarium* shows a surprisingly high degree of uniformity over its whole distribution area.

As seen from the above description, the "Vitiaz" specimen fits the species diagnosis well. It resembles, however, also *S.granularium,* especially since it has radiolarian tests, sponge spicules, and mineral particles as xenophyae, although the relative amount of these is strongly in favour of radiolarian tests. The important distinguishing characteristics are, in this case, the dimensions of the linellae and body thickness.

Distribution: Known from three dredgings in the E., N. W. and Central Pacific, at 3570 to 5515 m depth, on Globigerina ooze, red clay, and dark, muddy clay, and at temperatures of 1.4 to 1.9°C.

Stannophyllum pertusum Haeckel, 1889
Pl. 11A

Stannophyllum pertusum Haeckel, 1889, p. 65, pl. I, 3A-B; SCHULZE 1907a, p. 42.

Material:

"Challenger" St. 271. – Numerous specimens.

Diagnosis: The body is flake-like, reniform in outline, usually 8-12 cm in length, but some larger specimens can be 20 cm or more. It is about 1 mm thick, and is a little thicker in the ribs. The distal margin is subdivided into a large number of quadrangular lobes. The body is pierced by numerous holes. The colour is light brown and the consistency is very soft. The surface has ribs that radiate from the proximal body part. The linellae are rather few, simple, and measure 1-3 μ in diameter. Xenophyae are radiolarian tests, and these intermingle with foraminiferan tests in the ribs. A few sponge spicules can be seen.

Morphology: The material consists of only fragments in poor condition, but it is possible to find different fragments displaying the species characters: some from the distal edge with the quadrangular lobes, some with the perforations of greatly varying size, and others with the ribs. The ribs are a little lighter in colour than the rest of the body because of the foraminiferan tests.

Cytology: Due to the poor condition of the material, only a few comments can be made.

The granellare branches seem to be empty and they are very irregular in cross-section. The measured diameters are 15-25 μ, but they have presumably been larger in fresh material. Granellae were not seen.

Only small traces of stercomare are left. The xanthosomes are well-developed, yellow-brown, rounded, and 4-6 μ in diameter. They form aggregations here and there and the largest seen are 11 × 15 μ.

Remarks: Characteristics such as the margin lobation and the perforation do not seem to be mere aging phenomenons (cf. SCHULZE 1907a, p. 36). These phenomena are only occasionally seen in the large *Stannophyllum zonarium* material from "Galathea" St. 716 where so many specimens are recorded that it is reasonable to assume that they give a representative sample of the population. No specimens were seen where there were so many lobes or holes that they appeared characteristic. Moreover, lobes and perforations were not found together in the same specimens.

Stannophyllum pertusum and *S. venosum* are practically identical in diagnoses. Moreover, they are both known from only one sample and were taken at the same locality, "Challenger" St. 271. On the basis of the existing descriptions and the preserved material, it is impossible to say if we really have two independent species. The most important characteristics indicating two different species are the rib development on the surface and the presence of one dimension category of linellae in one and of two dimension categories in the other. It should be noted, however, that the species characteristics of *S. venosum* as given by HAECKEL cannot be observed in the material in its present condition.

Occurrence: Known from one dredging in the Central Pacific, at 4438 m, on Globigerina ooze, and at 1.4° C.

Stannophyllum venosum Haeckel, 1889
Pl. 11B

Stannophyllum venosum Haeckel, 1889, p. 67, pl. I, 4; SCHULZE 1907a, p. 42.

Material:
"Challenger" St. 271. – Several specimens.

Diagnosis: The body is broad, flake-like, reniform, up to 25 cm in the largest diameter, and is about 1 mm thick, although somewhat thicker in the ribs. The distal margin is irregularly lobulate and the distal part is occasionally pierced by small irregular holes. The colour is light brown and the consistency is rather soft. The surface has distinct, whitish, thick, branched ribs that radiate from the proximal body part. The linellae are simple; in the body proper they measure 1-2 μ in diameter and in the ribs 6-10 μ in diameter. Xenophyae are radiolarian tests, but in the ribs there are mainly foraminiferan tests.

Morphology: The specimens are only fragments in poor condition. None of the stated specific characteristics can be seen.

Cytology: Due to the poor condition, only very few comments can be made.

The granellare branches are empty except for granellae, more or less circular in cross-section, and presumably 60-180 μ in diameter. Granellae are rather few and 2-4 μ in length.

The linellae are simple and 1-2 μ in diameter.

Remarks: cf. above (comparisons with *S. pertusum*).

Occurrence: Known from one dredging in the Central Pacific, at 4438 m, on Globigerina ooze, and at 1.4° C.

Stannophyllum indistinctum n. sp.
Pl. 11C-D

Material:
"Galathea" St. 232. – About 10 specimens or fragments.
"Galathea" St. 235. – 3 specimens.
The holotype is from St. 232. It measures 4 × about 2.5 cm and has a proximal prolongation of 3.5 cm.

Diagnosis: The body is flake-like, triangular or irregularly rounded in outline, up to 5 cm in length, and 1-3 mm thick. The colour varies from yellow-brown to dark grey-brown. The consistency varies greatly even within the body of a single specimen from very soft to stiff. The surface is smooth to slightly granulate. Linellae are simple and 1-10 μ in diameter. Xenophyae are predominantly sponge spicules.

Morphology: The largest specimen (Pl. 11D) measures about 5 × 3 cm (St. 232), and the smallest is 2 × 1.5 cm (St. 235). In general, they are between 1 and 2 mm thick.

Some of the specimens are roughly triangular in outline and have a long "peduncle". The longest of these prolongations has a soft consistency, measures about 3.5 cm in length, about 2 × 4 mm in cross-section, and ends in a thick tuft of linellae.

One of the specimens has a large flake-like projection.

Cytology: Due to the poor condition of the animals, only a few comments can be made.

The granellare branches are empty. They are rounded, somewhat irregular in cross-section, and measure 40-90 μ in diameter.

Stercomare are seen as vaguely limited masses of differentiated or undifferentiated stercome material. Some yellow-brown, nearly spherical bodies up to 2 μ in diameter are, perhaps, xanthosomes.

The linellae are simple and well-developed. They vary greatly in diameter from 1-10 μ, but most of them are 3-7 μ. They are found uniformly distributed in the test.

The xenophyae are predominantly silicious sponge spicules. Radiolarian tests are found in nearly all specimens, but in varying proportions from one specimen to the other. The specimens from St. 235 all contain many radiolarian tests.

Remarks: *S. indistinctum* possesses only a few distinct, positive species characteristics. It is most easily characterized by the lack of the special characteristics which are found in the following species: *S. zonarium, S. globigerinum,* and *S. granularium* (zonation and linella surface layer, the xenophyae type); *S. fragilis* and *S. radiolarium* (linella dimensions, xenophyae type); *S. pertusum* and *S. venosum* (ribs and perforations, xenophyae type); *S. alatum* and *S. concretum* (growth form, xenophyae type); *S. reticulatum, S. flustraceum,* and *S. mollum* (linella type).

Distribution: Known from two dredgings off E. Africa, at 4810 to 4930 m depth, on Globigerina ooze, and at 0.3° to 0.8° C.

Stannophyllum alatum (Haeckel, 1889)
Pl. 11E

Stannarium alatum Haeckel, 1889, p. 70, pl. III, 6-9; SCHULZE 1907a, p. 45.
Stannophyllum alatum, SCHULZE 1907b, p. 155.

Material:
"Challenger" St. 211. – 1 specimen, not mentioned by HAECKEL (1889) or SCHULZE (1907a).
"Challenger" St. 272. – 1 specimen.

Other records (the material is unaccounted for):
"Albatross" St. 4742. – 3 specimens.

Diagnosis: The body is composed of several flakes. Usually there are two large flakes and sometimes several additional smaller leaves that grow from the primary flake. The distal edges are free and have margins that are rounded or slightly lobulate in outline. The flakes are 3-6 cm in diameter and 1-3 mm thick. The colour is yellow-brown and the consistency is rather stiff. The surface is somewhat felty. The linellae are simple and vary from 2-8 μ in diameter, most being 4-6 μ. Xenophyae are radiolarian tests.

Morphology: The material is in poor condition, but the characteristic growth form can still be seen.

Cytology: Due to the poor condition of the specimens, no comments can be made.

Remarks: SCHULZE (1907b, p. 155) was obviously correct in transferring the species from *Stannarium* to *Stannophyllum.* He preferred to maintain the species although he was in doubt of its possible relations to some of the other *Stannophyllum* species. Since no additional material has been reported, it is impossible at present to investigate the problem further. It should be noted that a growth form closely resembling *S. alatum* is sometimes found in *S. zonarium,* but that the specimens hitherto referred to *S. alatum* have no zonation and no special surface layer of linellae.

Distribution: Known from three dredgings, in the E. Pacific, the Central Pacific, and the Indonesian area, at 4072 to 4758 m depth, on radiolarian ooze or blue mud, and at temperatures of 1.2° to 10.3°C.

Stannophyllum concretum (Haeckel, 1889)
Pl. 11F; 12A

Stannarium concretum Haeckel, 1889, p. 71, pl. III, 10-14; SCHULZE 1907a, p. 46.

"Challenger" St. 270. – Several specimens. The material seems to be unaccounted for. The sample in the "Challenger" collection labelled *Stannarium concretum* resembles a greatly damaged *Stannophyllum globigerinum* fragment. Moreover, the locality is given as "Challenger" St. 271, and *S. concretum* is not reported from this station, whereas *S. globigerinum* was taken here.

Diagnosis: The body is composed of 4-8 flakes of different sizes. They have grown together in such a manner that one or more funnel-shaped cavities have been formed between them. The diameter of the whole animal is 2-5 cm, and the flake thickness is 2-4 mm. The consistency varies and the surface is granulate. The linellae are simple and are 2-8 μ in diameter. They interweave and form bundles surrounding the xenophyae. Xenophyae are foraminiferan tests on the surface, and radiolarian tests in the interior.

Remarks: Without having seen the material, LAUBENFELS (1936, p. 33) and LOEBLICH & TAPPAN (1964, p. 790) selected *S. concretum* as the type species of the genus *Stannarium*. Since the growth form characteristic of *S. concretum* is occasionally found in *Stannophyllum* species (*S. zonarium* and *S. mollum*), there are no good reasons for placing the species in a separate genus when no other distinguishing characteristics have been noted.

Occurrence: Known from one dredging in the Central Pacific, at 5353 m, on Globigerina ooze, and at 1.4°C.

Stannophyllum flustraceum (Haeckel, 1889)
Pl. 12B

Psammophyllum flustraceum Haeckel, 1889, p. 51, pl. IV, 5-6, pl. V, 5.
Stannophyllum flustraceum, SCHULZE 1907a, p. 44.

Material:
"Challenger" St. 241. – 1 specimen.
Since the type material was already lost at the time of SCHULZE's re-investigation of the "Challenger" collection and no additional material is known, the only knowledge of this species comes from HAECKEL's description. The diagnosis given below is HAECKEL's in extended form.

Diagnosis: The brown, flake-like body is reniform, pedunculate, rather thick and soft, and 7-10.5 cm in diameter. The distal margin is lobulate, and the 12-15 large lobes are each subdivided into 2-4 smaller lobes. The surface is felty, presumably has a surface layer of linellae, the distal part has concentric zones 3-4 mm in breadth, and the proximal part has branched ribs radiating from the distal end of the "peduncle". The rib colour is lighter than that of the rest of the body, and is grey or whitish. The anastomosing linellae are strongly developed and form a dense, irregular network; they vary in size from 1-60 μ in diameter. Small xenophyae are enclosed by some of them. Xenophyae are silicious sponge spicules, radiolarian tests, and various mineral particles.

Remarks: Judging from HAECKEL's description, the species seems to possess the following distinctive characteristics: 1) the body is thick and soft, 2) the surface has concentric zones in the distal part and radiating ribs in the proximal part, and 3) the linellae anastomose, are often very thick, and sometimes enclose small xenophyae. Regarding the surprisingly thick linellae, it should be noted that the linellae in *S. zonarium* often form bundles, each of which at first glance appears to be a single, thick linella. In *S. fragilis* this phenomenon is even more distinctive, and the composed, thick linellae are distinguishable from simple linellae only with great difficulty.

Occurrence: Known from one dredging in the N. Pacific, at 4209 m, on red clay, and at 1.7°C.

Stannophyllum reticulatum (Haeckel, 1889)
Pl. 12C

Psammophyllum reticulatum Haeckel, 1889, p. 50, pl. V, 1-4.
Stannophyllum reticulatum, SCHULZE 1907a, p. 44, pl. VI, 3-5.

Material:
"Challenger" St. 198. – 3 specimens.
"Galathea" St. 231. – 1 specimen.

Diagnosis: The body is flake-like, reniform or rounded, up to 90 mm in diameter and 1-3 mm thick. The surface is felty. The colour is brown, and the consistency is soft, and only slightly elastic. The anastomosing linellae are 2-8 μ in diameter. Xenophyae are sponge spicules.

Morphology: The specimen from "Galathea" St. 231 is approximately semi-circular, about 60 mm in diameter and 2 mm thick. The colour is dark brown. The linellae have in some cases a somewhat uneven surface because of small adhering particles. The linellae form a distinct surface layer, but are also found in the test interior. The "Galathea" and the "Challenger" specimens show both true anastomoses and strengthened crossings.

Cytology: The granellare branches measure 60-120 μ in diameter. Granellae are numerous and 2-6 μ long. Nuclei are spherical to ellipsoidal and 4-6 μ in diameter.

The dark stercomare masses are 90-240 μ in diameter. Xanthosomes are found scattered; they are yellow-brown, rounded, and 5-15 μ in diameter.

The linellae are rarely as much as 10 μ in diameter and anastomose strongly in both samples. Where the flattened base of two or more linellae fasten to the same spicule fragment, the spicule can be fully enclosed in linella material.

Xenophyae are mainly silicious sponge spicules and fragments, but occasional radiolarian tests are seen.

Remarks: There are some small differences between the two samples. While the "Challenger" specimens are light brown and rather transparent due to scanty stercomare development, the "Galathea" specimen is dark brown with well developed stercomare. Moreover, it has a distinct linella surface layer not found in the "Challenger" material. Zonation is not developed in either material.

Distribution: Known from two dredgings, one in the Indonesian area and one off E. Africa, at 3935 and 5020 m depth, on blue mud ("Challenger"), and at 0.3° to 4.0°C.

Stannophyllum mollum n. sp.

Pls. 12D-E; 16B

Material:
"Galathea" St. 231. – 7 specimens.
"Galathea" St. 233. – 2 specimens.
"Galathea" St. 234. – 7 specimens.
"Galathea" St. 235. – 14 specimens.
"Vitiaz" St. 3166. – 1 specimen.
"Vitiaz" St. 3198. – 4 specimens.
"Vitiaz" St. 3575. – 13 specimens.
"Vitiaz" St. 3593[1]. – 1 specimen.
"Vitiaz" St. 5624. – 5 specimens.
The holotype is from St. 231 and measures 84 × 68 mm.

Diagnosis: The body is flake-like, semi-circular to irregularly elliptical in outline, 2.5-10.5 cm in diameter, and 4-6 mm thick. The colour is green-brown to dark brown. The consistency is very soft. The surface has fine wrinkles extending in all directions. The linellae are strongly developed, anastomose, and are 2-10 μ in diameter. They form a distinct surface layer. Xenophyae are rare and often absent.

Morphology: The largest known specimen measures 10.5 × 5 cm, the smallest 3 × 2.5 cm. The thickness varies considerably from 3-9 mm. The surface is finely wrinkled, but has no signs of zonation. The degree of wrinkling is not uniform in all specimens; some are rather strongly wrinkled, others are nearly smooth, and in some cases there are differences within the individual specimen.

Several specimens have excrescences in the form of leaves or ridges, and these are always oriented parallel to the animal's width. They do not seem to be released.

Cytology: The granellare branches are subcircular in cross-section and 45-120 μ in diameter. The plasma contains granellae, nuclei, and numerous unidentifiable inclusions. The granellae are numerous and 2-6 μ in length, most being 3-4 μ. The "Galathea" specimens have spherical nuclei that are 5-6 μ in diameter (cf. Table 6, p. 69). They are poorly preserved in the "Vitiaz" material, but are seen as blurred bodies, 3-4 μ in diameter. The plasmatic inclusions appear to be small portions of absorbed bottom material.

Some granellare tubes have no plasma but only

1. In his book on the hadal fauna, Beljaev (1966, p. 63) lists xenophyophores from this station as *Stannophyllum* sp. 2.

stercome-like material, granellae, and occasional xanthosomes.

The stercomare masses make up the greatest body part; they are rounded in cross-section and 80 – about 300 μ in diameter. Not all the stercomes seem to be included in stercomare, since numerous single stercomes are found scattered between the stercomare and granellare branches. Xanthosomes are absent or rare in some specimens and relatively numerous in others. They are yellow-brown to dark brown, rounded, and 3-12.5 μ in diameter.

The frequently anastomosing linellae vary in diameter from 2-10 μ, but each single linella has the same diameter along its entire length. Both true anastomoses and strengthened crossings are found. In many cases small particles seem to adhere to the surface and thus give a somewhat shaggy appearance. The linellae form a distinct surface layer and are also numerous in the test interior.

A few xenophyae (sponge spicules and radiolarian tests) are present in some specimens and absent in others. There are always so few that they cannot have any function in the test construction.

Remarks: The "Galathea" and the "Vitiaz" samples are similar to a great extent, but some smaller differences should be noted. The "Galathea" material is green-brown, 3-6 mm thick, and usually without xenophyae, whereas the "Vitiaz" material is dark brown, 3-9 mm thick, and generally contain a few xenophyae. Moreover, the granellare branch diameter is usually larger in the "Vitiaz" material (90-120 μ) than in the "Galathea" material (45-90 μ).

S. mollum resembles *S. flustraceum* and *S. reticulatum* most, especially since it has linellae with true anastomoses. It further resembles *S. flustraceum* in that the body of both is like a thick, soft leaf, but it differs from this species in lacking lobes along distal edge, zones and ribs on the surface, and xenophyae. Moreover, the dimensions of the linellae are different. *S. mollum* differs from *S. reticulatum* in the presence of a very distinct linella surface layer, in size, thickness, and consistency of the leaf, and in the absence of xenophyae.

The lack of xenophyae may be regarded as a secondary phenomenon. This is indicated by the presence of characteristics that are assumed to be relatively advanced, e.g. the true anastomosing of the linellae and the arrangement of some linellae in a distinct surface layer. As a consequence of reduction in the number of xenophyae, stercomare has become relatively more strongly developed and has, together with the linellae, assumed the entire test function. The few scattered xenophyae found are thus either signs of a "rudimentary tendency" to pick up foreign bodies or they are collected accidentally.

Distribution: Known from nine dredgings, four off E. Africa and five off Japan, at 4730 to 6380 m depth, on Globigerina ooze and fine mud with pumice and pebbles, and at temperatures of 0.3° to 1.6° C.

Stannophyllum sp.

Stannophyllum zonarium, SCHEPOTIEFF 1912b, p. 258, pl. 15, 72-73; pl. 16, 1-44.

SCHEPOTIEFF coll. – several specimens.

Since I have not been able to locate the material, the following description is based on SCHEPOTIEFF's report. Most of the measurements are based on his drawings and must be considered with great reservation.

The specimens were brown, flake-like, and measured several cm in length and width (the largest pictured specimen measures about 2.5 × 4 cm), the thickness generally being 2-3 mm, and in some specimens as much as 5 mm. The surface was distinctly zonated with zones 0.5-3 mm in breadth. The strongly developed linellae were anastomosing, about 5 μ thick and formed a distinct surface layer. The evenly distributed xenophyae were mainly radiolarian- and foraminiferan tests, but sponge spicules, small sand grains, and diatom tests were also found.

Cytology: The granellare branches measured 280-470 μ in diameter, and contained hyaline plasma. The nuclei were spherical or ellipsoidal, and about 5 μ in diameter. The evenly distributed granellae were angular and measured up to 50 μ in length. SCHEPOTIEFF also found large lumps of protein and several types of unidentified inclusions.

Stercomare were stated to resemble that of his *Psammetta* sample (p. 25). Xanthosomes were present.

The anastomosing linellae seem to have shown both fastened crossings and true polychotomous branching.

Remarks: SCHEPOTIEFF's classification of his material as *Stannophyllum* was undoubtedly correct, but the species identification as *S. zonarium* is highly

Table 5. The number of records of *Stannophyllum* species known at different dates.

Species	Author. year			
	HAECKEL 1889	SCHULZE[1] 1905	SCHULZE 1907 b	This paper
S. zonarium	1	5	15	24
S. globigerinum	1	3	10	12
S. granularium	–	–	–	11
S. fragilis	–	–	–	1
S. radiolarium	1	1	1	3
S. pertusum	1	1	1	1
S. venosum	1	1	1	1
S. indistinctum	–	–	–	2
S. alatum	1	1	2	3
S. concretum	1	1	1	1
S. flustraceum	1	1	1	1
S. reticulatum	1	1	1	2
S. mollum	–	–	–	9
S. sp.	–	–	–	1

1. The closing year of the 1907a report.

questionable. His material differed from *S. zonarium* in several characters: the thickness of the body plate in some specimens, the type of linellae, the size of granellae, and the types of xenophyae. Also in the organization of the linella tufts on the sides of the body plate there seem to be differences, since SCHEPOTIEFF's figures show these structures as thin bundles on the proximal part of the zones. Although the substrate of the collecting locality probably was sand, SCHEPOTIEFF states (1912, p. 258) that the specimens were fastened to the bottom by a thin "stalk" and the linella tufts; it is, however, unclear whether he directly observed the animals on the bottom. The specimens were taken in shallow water and at high temperature, which are conditions not known for *S. zonarium,* and further the locality is far from the main distribution area of this species.

Thus it seems highly probable that SCHEPOTIEFF's specimens represented a new species. I hesitate, however, to designate it, as much of the information given seems uncertain and some important characteristics are not stated.

Occurrence: Known from one locality at Kankesanturai (North Ceylon), at 1-5 m, on sand, and at c. 25°C.

The validity of the *Stannophyllum* species

Both HAECKEL (1889, p. 60) and SCHULZE (1907a, p. 36) questioned whether or not there really are as many independent species as had been described by HAECKEL.

HAECKEL himself brought up the following two objections: 1) some of his species were connected by intermediate forms and 2) each species was known from only one sample, and several species were furthermore collected at the same station. However, in the existing "Challenger" collection there are few, if any, specimens so questionable that they can be described as intermediate between two species (although it is true that part of the original material has now disappeared). The fact that many "Challenger" species were taken only once gives of course good reason for doubt. However, as can be seen from Table 5, many of these species are now known from several localities, often widely distributed in the deep-sea. The repeated records have strengthened the impression of validity of some of the species, especially since they are reported by different authors who studied all the material known at the time.

Present knowledge seems to strongly indicate that HAECKEL's following species are valid: *S. zonarium, S. globigerinum* (although doubted by SCHULZE), *S. alatum,* and *S. reticulatum.*

S. radiolarium is somewhat questionable (cf. remarks p. 55), although it has been taken several times.

The problem concerning *S. pertusum* and *S. venosum* is whether or not they are identical. There cannot be much doubt that there is at least one valid species (cf. remarks p. 56).

The original material of HAECKEL's last two species, *S. concretum* and *S. flustraceum,* has disappeared and no new material has been reported.

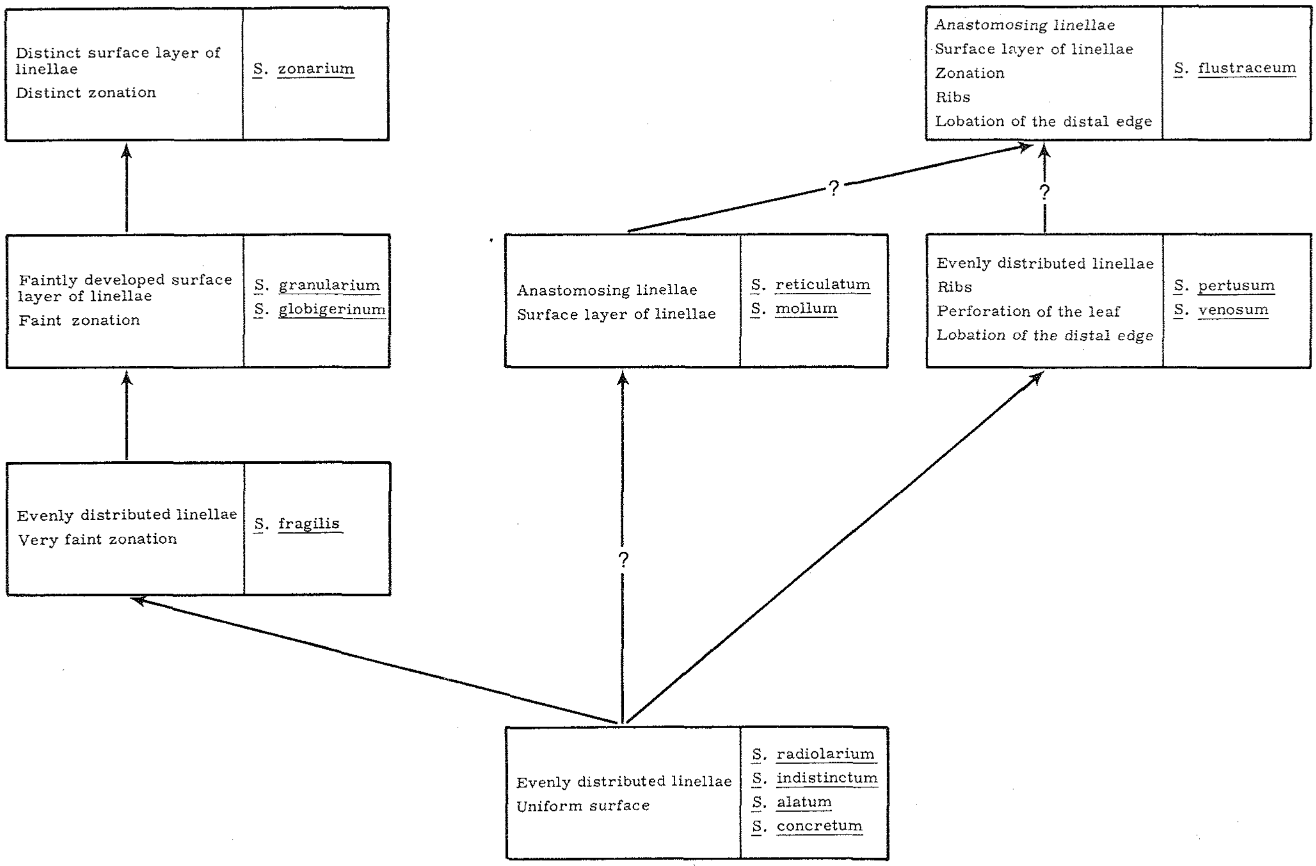


Fig. 13. Diagram showing possible evolutionary trends of morfological variation in the genus *Stannophyllum.* The left part of each box lists the characteristics concerned, and the right gives the species fitting the characteristics.

S. concretum could be identical with *S. globigerinum,* and *S. flustraceum* possibly with *S. reticulatum* even though there are several remarkable characteristics in *S. flustraceum*'s diagnosis (cf. remarks p. 58).

Four new *Stannophyllum* species are described here. One of these, *S. indistinctum,* is perhaps not too well-defined, and although there are thirteen specimens, they were all taken at two neighbouring stations. The species does not have any characteristic features, but it was erected because the material does not correspond to any other material. *S. fragilis* is known from only one station and in three specimens only, but these have such distinctive common characteristics that inclusion in one of the other species (viz. *S. granularium*) would seem quite illogical. The remaining species, *S. granularium* and *S. mollum,* appear well-founded; both have characteristic distinguishing features, and there are numerous specimens from widely distributed stations.

Possible evolutionary trends of *Stannophyllum* character complexes

In addition to body dimensions and form, surface texture, consistency, linella dimensions, and xenophyae types present, some species show other notable characteristics used in the diagnoses, viz. zonation, ribs, development of a special linellae surface layer, linellae anastomoses, body perforations, and lobation of the distal edge.

The condition which seems the most simple may also be assumed to be the most primitive. According this hypothesis, the early *Stannophyllum* species may have had simple linellae evenly distributed throughout the test and a uniform surface. These characteristics are found in *S. radiolarium, S. indistinctum, S. alatum,* and *S. concretum.* The latter two species are perhaps specialized since they have a special growth form. The fact that precisely those species that are assumed to be the most primitive are either little known due to poor condition (*S. indistinctum* and *S. alatum*) or cannot be regarded as quite valid (the two others) is very annoying.

The first step in the development of special characteristics may have been localization of linellae at the surface, giving a more distinct surface layer. Some species are zonated and the origin of this is unexplained other than as a growth phenomenon. These tendencies are found in *S. granularium* and *S. globigerinum,* and a transitional stage is presumably seen in *S. fragilis.* Full development of a distinct surface layer and zonation is found in *S. zonarium* (Fig. 13).

Another evolutionary line may be illustrated by the presence of ribs, body perforations, and lobation of the distal margin, as is found in *S. pertusum* and *S. venosum.* Further development of these three characteristics would lead to *Stannoma*-like forms. On the other hand, continued development of *Stannoma*'s anastomosing branches in one plane could lead to *Stannophyllum*-like forms. The former of these two possibilities is the most simple. *Stannoma*'s early growth stages could possibly cast some light on the problem, but they are not available.

Anastomosing linellae are regarded here as a specialized characteristic since they presumably put greater demands on the pseudopodia function than simple linellae do. Anastomosing linellae always seem to be found together with a linellae surface layer. The species possessing these two characteristics seem to fall into two groups, one without further notable characteristics (*S. reticulatum* and *S. mollum*), and one with a series of special features (*S. flustraceum*).

POSSIBLE AND EARLIER PROPOSED XENOPHYOPHORE SPECIES

This section is intended to correct some mistakes made by different authors and to draw attention to some interesting deep-sea organisms with a systematic position doubtful even with respect to phylum.

The single species (in some cases genera and families as well) are discussed below in the chronological order of appearance in the literature in connection with the xenophyophores.

The following species are considered from HAECKEL's report (1889) on the "Deep-Sea Keratosa": all the species of his family Ammoconidae (p. 23 ff.), *Holopsamma argillaceum* (p. 39), and his reference to *Psammopemma porosum* (p. 46).

HAECKEL listed four families of "Deep-Sea Keratosa". Three of these were xenophyophores, whereas the fourth cannot even be referred to phylum. No additional material has been reported, and the types are unaccounted for; they were presumably totally ruined during HAECKEL's investigation since they were few and small. Even at the time of publication, there was great doubt about their position; both WELTNER (1890, p. 228) and LENDENFELD (1891, p. 177) denied their sponge nature. SCHULZE (1907a, p. 5) mentioned them only briefly.

In the following survey I have altered the diagnoses in such a way that references to phylum are avoided.

Family **AMMOCLATHRINIDAE** nom. nov.

Ammoclathrinidae nom. nov. pro Ammoconidae Haeckel.

Diagnosis: The body is composed of tubules which are single or branched with free or anastomosing branches. The wall has simple pores. The tubule is hollow centrally, and there is a single, large opening at one end in some cases. The wall is mainly formed by radiolarian and foraminiferan tests, sand grains, and fragments of sponge spicules which are connected by a homogeneous ground substance.

The family contains five species in three genera.

Genus ***Ammoclathrina*** Laubenfels, 1948

Ammoconia Haeckel, 1889, p. 30.
Ammoclathrina Laubenfels, 1948, p. 183.

The name *Ammoconia* was preoccupied (for a lepidopteran). The name *Ammoclathrina* was given by LAUBENFELS (1948) who had previously (1936, p. 33) selected *A. aulopegma* as the type species.

Diagnosis: The tube system is reticular and forms a network of anastomosing, porous tubules without larger openings.

Ammoclathrina aulopegma (Haeckel, 1889)

Ammoconia aulopegma Haeckel, 1889, p. 31, pl. VIII, 4.

The body is shaped like *A. sagenella* and is 12-16 mm in diameter. The branches are about 0.5 mm in diameter; their walls are calcareous, and made of agglutinated Globigerina shells.

After dissolving the calcareous matter with acid, HAECKEL found a delicate membrane remaining. It contained what looked like small stellate cells and a few dark, large cells. HAECKEL saw flakes of a possible epithelium composed of minute granular cells on the inside of the wall.

Record: "Challenger" St. 89, tropical Atlantic (22°18'N, 22°02'W), 4392 m, 23 July 1873. Bottom: Globigerina ooze.

Ammoclathrina sagenella (Haeckel, 1889)
Pl. 13A

Ammoconia sagenella Haeckel, 1889, p. 31, pl. VIII, 5 A-B.

The tubes form a loose network, 12-20 mm in diameter. The branches are 1-2 mm in diameter, and there are 2-4 mm between the meshes. The branch walls are silicious and made of sponge spicule fragments or sharp-edged or rounded sand grains.

Record: "Challenger" St. 256. North Pacific (30°22'N, 154°56'W), 5399 m. 21 July 1875. Bottom: red clay.

Genus *Ammolynthus* Haeckel, 1889

Ammolynthus Haeckel, 1889, p. 27.

Diagnosis: The body is simple, unbranched, tubular or urceolate, attached to the substrate by a slender, cylindrical "peduncle" with a broadened basal plate. The distal end of the tubule has a simple opening.

LAUBENFELS (1936, p. 33) selected *A. haliphysema* as the type species.

Ammolynthus haliphysema Haeckel, 1889
Pl. 13B

Ammolynthus haliphysema Haeckel, 1889, p. 28, pl. VIII, 2.

The body is ovate, 15-20 mm in total length, and 5-8 mm in greatest diameter. The "peduncle" is 10-12 mm long and 1-1.2 mm in diameter. The single opening is 2 mm in diameter. The wall is made of calcareous foraminiferan tests and test fragments.

After dissolving the calcareous matter with acid, a thin membrane with numerous small pores remains (the pores are shown on the figure, but could not be seen in the intact animal). On the inside of the wall, HAECKEL found what looked like fragments of a possible epithelium, composed of small granular cells.

Record: "Challenger" St. 270. Central Pacific (2°34'N, 149°09'W), 5353 m, 4 Sep. 1875. Bottom: Globigerina ooze.

Ammolynthus prototypus Haeckel, 1889
Pl. 13C

Ammolynthus prototypus Haeckel, 1889, p. 27, pl. VIII, 1 A-C.

The body is urceolate, 6-10 mm in length and 1-1.2 mm in diameter. The "peduncle" is 0.3 mm in diameter. The large opening is 0.5 mm, and the numerous small pores are 0.03-0.04 mm in diameter. The wall is made of radiolarian tests.

On the inside of the wall HAECKEL described fragments of a possible epithelium. In the wall he found what looked like numerous small stellate cells, a few larger amoeboid cells, and eggs. The latter are described as naked amoeboid cells 100-200 μ in diameter and with a distinct nucleolus in the nucleus.

Record: "Challenger" St. 271. Central Pacific (0°33'S, 151°34'W), 4438 m, 6 Sep. 1875. Bottom: Globigerina ooze with many radiolarians.

Genus *Ammosolenia* Haeckel, 1889

Ammosolenia Haeckel, 1889, p. 29.

Diagnosis: The body is branched and has single, tubular branches with a large, distal opening in each.

Ammosolenia rhizammina Haeckel, 1889
Pl. 13D

Ammosolenia rhizammina Haeckel, 1889, p. 29, pl. VIII, 3.

The diameter of the whole organism is 8-12 mm. The free, cylindrical branches are 0.8-1.2 mm in diameter and are equally thick for the entire branch length. The body length is 10-16 mm. The wall is composed of Globigerina shells.

After dissolving the calcareous matter with acid, a thin membrane with pores remained. Possible fragments of an epithelium were observed among the pores.

SCHEPOTIEFF (1912b, p. 246) reported specimens of *Ammosolenia rhizammina* from shallow, warm water, classifying the species as a sponge, but making no reference to literature. Later (p. 270) he mentioned that he had not completed his investigations, the results of which were apparently never published. His material is unaccounted for.

Records: "Challenger" St. 216 A. Tropical Pacific (2°56'N, 134°11'E), 3660 m, 16 Feb. 1875. Bottom: Globigerina ooze.

SCHEPOTIEFF coll. Mahé, Malabar Coast, India, coral reef, about 20 m, spring 1908. Temp.: about 25°C.

Remarks: HAECKEL himself referred repeatedly to the similarities between the members of this family and some of the larger arenaceous foraminiferans. Based on literature, but not on specimens, he compared *Ammoclathrina (Ammoconia)* with *Sagenella* Brady, *Ammolynthus* with *Rhabdammina* Sars, and *Ammosolenia* with *Rhizammina* Brady, intimating that these foraminiferans might, in fact, be sponges.

Genus ***Cerelpsamma*** Laubenfels, 1936

Holopsamma Carter, 1885, p. 211 (pars); HAECKEL 1889, p. 38 (pars); SCHEPOTIEFF 1912b, p. 275 (pars); LOEBLICH & TAPPAN 1964, p. 792 (pars). *Cerelpsamma* Laubenfels, 1936, p. 33.

Diagnosis: The body is massive, lumpy, and has free branches, each with a large, single opening at the tip. The test is hard and solid. Xenophyae are held together by only small amounts of cement.

Remarks: *Holopsamma* Carter is a sponge genus (LENDENFELD 1885, p. 23; 1889, p. 629; LAUBENFELS 1936, p. 97). LAUBENFELS erected the genus *Cerelpsamma* for two species described by HAECKEL, *C. argillaceum* which LAUBENFELS selected as type species, and *C. cretaceum* which is transferred here to the xenophyophoran genus *Reticulammina*.

Cerelpsamma argillaceum (Haeckel, 1889)
Pl. 13E

Holopsamma argillaceum Haeckel, 1889, p. 39, pl. VII, 6 A-B.

Diagnosis: The body is made of irregular, rounded bulbous masses and is 12-22 mm in diameter. The colour is red-grey and the consistency is hard. The surface is porous. Xenophyae are abyssal clay particles intermingled with sponge spicules and their fragments. There is only very little plasma.

Record: "Challenger" St. 294. South Pacific (39°22'S, 98°46'W), 4154 m, 3 Nov. 1875. Bottom: red clay. Temp.: 2.6°C. – 1 specimen, which is unaccounted for.

Remarks: It is impossible to say whether this organism is a sponge or a xenophyophore. In many "Deep-Sea Keratosa" HAECKEL had mentioned "symbiotic Spongoxenia" which were, in reality, the granellare and stercomare in xenophyophores. He did not, however, describe any of these here, so it is conceivable that the organism could be a sponge. LOEBLICH & TAPPAN (1964, p. 792) thought *C. argillaceum* was possibly a synonym of *Holopsamma laevis* Carter, 1885. LENDENFELD (1889, p. 640) showed that the latter species is a sponge and is presumed to be synonymous with *Psammopemma densum* Marshall, 1881.

HAECKEL briefly noted (1889, p. 46) that *Psammopemma porosum,* described as a keratose sponge by POLEJAEFF (1884, p. 48), might belong to *Cerelasma,* and this was assumed by SCHEPOTIEFF (1912b, p. 274). I have seen the type specimen in the British Museum (Natural History), and there is no doubt that it is a sponge.

On the basis of HAECKEL's report, DELAGE & HÉROUARD (1899, p. 200) mentioned that the genus *Sarcocornea* Carter, 1885, might belong to the "Deep-Sea Keratosa" (although the single record of *S. nodosa* did not originate from the deep-sea). This genus was first referred by LENDENFELD (1885, p. 23) to the sponge genus *Dysidea* and later (1889, p. 670) to *Spongelia.* LAUBENFELS (1936, p. 30) regarded both *Sarcocornea* and *Sponglia* as synonyms of *Dysidea.* The only specimen of the single species known, *Sarcocornea nodosa* Carter, was dried and the choanocyte chambers could not be described. Nevertheless, there are no valid reasons for not considering it to be a sponge.

SCHEPOTIEFF (1912b, p. 274) regarded a series of species referred to the sponge genus *Psammopemma* as xenophyophores, and he further listed some "Zweifelhafte Arten, deren Angehörigkeit zu den Xenophyophoren nur nach nochmaliger Untersuchung erklärt werden kann." At least in some of the species listed, the choanocyte chambers have been described (LENDENFELD 1889, p. 629ff.), but there are few specimens of many species, and these are often dried and fragmented. Strange structures are described in some of these, and investigations of the old material, if it still exists, and of new, well-preserved material would undoubtedly show many interesting features. On the sole basis of the existing descriptions, I cannot accept any of the species listed by SCHEPOTIEFF as xenophyophores.

IV. GENERAL PART

A. EXTERNAL APPEARANCE OF THE XENOPHYOPHORES

1. Body form and dimensions

CORLISS (1962, p. 40) stated that body form and dimensions are often of minor or dubious importance within the protozoan systematics, but can be legitimately reliable sometimes at a given lower taxonomic level and are generally applicable in separating certain major groups.

The body shape of the xenophyophores is very often characteristic for the species, and in many cases the rough body outline is characteristic for the genus. This is exemplified in *Psammetta, Reticulammina, Psammina,* and *Stannoma.* There are, on the other hand, some cases where the rough outline is characteristic of the genus, but the single species does not have a characteristic body shape, as, for example, in *Cerelasma* and *Stannophyllum.* The two known species in *Galatheammina* differ greatly in shape, and there is no common genus body outline.

Many different, specific body forms are seen within the xenophyophores, and the most striking are the biconcave disc of *Psammetta erythrocytomorpha,* the sphere of *P. globosa,* the tetrahedron of *Galatheammina tetraedra,* and the tree-like form of *Stannoma dendroides.* Very characteristic, but perhaps more difficult to accurately describe, are the flattened ball of *Galatheammina calcarea,* the reticulate bodies of the *Reticulammina* species, the plate-like form of the *Psammina* species, and the flake-like bodies of some of the *Stannophyllum* species. Species without an easily characterized body form are *Maudammina arenaria* and *Cerelpemma radiolarium* (only a few specimens of these species are known).

In comparison to most other Protozoa, the xenophyopnores are giants. The largest preserved specimen is a *Stannophyllum zonarium* measuring about 190 mm in length, about 50 mm in width, and 1-2 mm in thickness. The largest specimen reported is a *S. venosum* that measured 250 mm in greatest diameter (HAECKEL 1889, p. 67). The smallest specimens reported are young stages of *Psammetta ovale,* about 1 mm in diameter (SCHEPOTIEFF 1912b, p. 247). Adult xenophyophores usually range from about 15 mm to 70 mm at the largest body part.

The maximum size attained seems to be related to the distance from the central body parts to the body surface. This reflects, perhaps, problems involving transportation of nourishment, oxygen, excretion products, etc. The pseudopodia seem to originate from the granellare branch tips, and transportation to the central parts of granellare probably occurs in the plasma itself. The above-mentioned relationship of body size to distance from the central body part to the surface is exemplified in *Stannophyllum* species where the large flakes always are thin (at maximum 5 mm, but most often less), and in *Cerelasma* and *Reticulammina* where lumps with a large diameter are attained only in reticulate bodies where the distance from the branch centre to the surface never exceeds 2-4 mm. The massive *Psammetta globosa* can be more than 20 mm in diameter, but in these cases, the central, older plasma is generally dead.

2. Colour

The colour varies greatly depending on the relative amount and kinds of xenophyae present.

Where xenophyae are absent, rare, or transparent (radiolarian tests and silicious sponge spicules), the xenophyophore appears brown-black as for example in *Psammetta* species, *Psammina nummulina, Cerelasma* and *Stannoma* species, *Stannophyllum zonarium* and *S. mollum.* The dominating colour is that of the stercomare, and in the Stannomida it is also that of the linellae.

Where the xenophyae are numerous and coloured (foraminiferan tests and mineral particles), the colour varies as for example in the distinctly white tests of *Galatheammina* and *Reticulammina* species and the yellow-brown colour of *Maudammina arenaria.*

3. Surface

The nature and appearance of the surface depends on the type and arrangement of the xenophyae. This is best illustrated in the species that use only rounded, calcareous foraminiferan tests (sometimes test fragments as well) in their tests. The following species are found in a number of genera belonging to different families, but their surfaces are similar (Pls. 3-5 and 9), and are best characterized as granulated: *Galatheammina tetraedra, G. calcarea, Psammina globigerina, Syringammina tasmanensis,* and *Stannophyllum globigerinum.* There are some genera in which all the species have the same surface appearance, viz. *Psammetta, Galatheammina, Reticulammina, Cerelasma,* and *Stannoma,* but all the species within a single genus use the same xenophyae type in these cases. Where the species in a genus use different xenophyae, their surfaces differ, viz. in *Psammina, Syringammina,* and *Stannophyllum.*

The most characteristic surface feature known in the xenophyophores is, without doubt, the distinct zonation found in *Stannophyllum zonarium.* Zonation is more faint in four other species, *S. globigerinum, S. granularium, S. fragilis,* and *S. flustraceum.* At least in the former two species, the zones can be more easily seen if some of the xenophyae are removed.

The zones are 2-7 mm wide, parallel to the distal edge, and separated by narrow surface depressions. Two depressions usually lie exactly opposite to each other on each side of the body-plate. In *S. granularium* the bottoms of the furrows are often connected by xenophyae walls 0.3-0.4 mm thick. In *S. zonarium* and *S. globigerinum* such walls are either absent or at most only occasionally found over a short distance near the side edges. Walls, but not furrows, are found in *S. fragilis.* The condition in *S. flustraceum* is unknown.

A relation seems to exist between variation in zonation and species distribution (recorded at present). There is no variation in the zonation of *S. zonarium* within its rather limited distribution area, whereas great variation in zonation is found in the more widely distributed *S. granularium.* Some variation, although not great, is found in the widely distributed *S. globigerinum.*

GOËS (1892) regarded the zone furrows as "chamber sutures" but did not explain this interpretation. Later authors (HANITSCH 1893a, b; SCHULZE 1907a; SCHEPOTIEFF 1912b) have called them growth lines. They can presumably (as briefly mentioned by GOËS 1892) be compared to a similar phenomenon in the large foraminiferan *Jullienella foetida* Schlumberger where distinct growth lines are found without marked influence on the interior organization (SCHLUMBERGER 1890; BUCHANAN 1960; NØRVANG 1961; CALVEZ 1963, and own observations).

SCHEPOTIEFF (l.c., p. 263) described the early development of a *Stannophyllum* species and figured quite young specimens consisting of only the first zone. The following zone was to have been formed by parts of granellare protruding from the edge of the first zone. It is difficult to discern the zone development in the present material, but the observations seem to agree with SCHEPOTIEFF's. The distal 1-2 mm of the body is transparent, consisting of numerous linellae and few xenophyae; plasma elements are generally either absent or only weakly developed here. This condition is found in many *Stannophyllum* species, both with and without zonation.

In some genera there are numerous, small, scattered, pore-like openings. These "pores" are indistinct where the test is made of randomly cemented xenophyae as in *Maudammina* and *Psammetta,* but are usually more well-defined where the surface layer is more perfectly built, viz. *Galatheammina calcarea, Psammina nummulina, P. globigerinum,* and *Stannophyllum zonarium.* The "pores" in the above species seem to be a permanent structure while in, e.g., *Reticulammina* species they are not regularly found and are, perhaps, only periodically formed. These "pores" are presumably openings from which pseudopodia extend. Fixation conditions, damaging during dredging, and natural surface structure (loose in *Cerelasma* and *Stannophyllum* species) may explain the fact that the pore-like openings are not seen in many other species.

4. Consistency

The consistency varies greatly within the xenophyophores, from *Maudammina arenaria,* which resembles sandstone, to *Stannophyllum mollum,* which resembles a wet rag. There is a distinct difference between the two orders; the members of Psamminida are in general stiff and friable, and the members of Stannomida are flexible and soft. The consistency in the Psamminida depends on the xenophyae type and the relative amount of xenophyae, cement, and stercomare. Where there are numerous, firmly cemented xenophyae and only moderate amounts of stercomare, the consistency is very hard as in *Maudammina arenaria* and the *Galatheammina* species. When there is little cement, as in *Reticulammina, Psammina,* and *Syringammina,* the consistency is friable. Where large amounts of cement are developed together with large amounts of stercomare and the xenophyae are relatively few, the consistency is softer and varies from firm to doughy as in *Cerelasma.*

The consistency of the Stannomida is due to the numerous linellae. The varying consistency of the different species depends mainly on the relative amount of xenophyae since cement, linellae, and stercomare are developed to about the same degree in all the species. The consistency of the Stannomida is the same after fixation as it was when brought on deck (Dr. T. WOLFF, personal communication).

B. ORGANIZATION OF THE XENOPHYOPHORES

1. The general condition of the material and its suitability for cytological investigation

A small part of the available material is dried and is, therefore, completely useless for cytological work. Most of the specimens are preserved in alcohol (70 %), and the condition of these specimens varies greatly due to differing storage time (varying from a few months to about 100 years) and differing lengths of time spent on deck before fixation.

The best preserved samples are found in the youngest collections, i. e., the "Taranui", "Vema", and "Galathea" collections. The "Taranui" material is, however, difficult to work with because of the numerous xenophyae and extreme fragility. Even in these samples, some plasma shrinkage is found. Since alcohol is the sole fixative, some of the generally used cytochemical stains can give ambiguous results.

An attempt was made to obtain information about the most general cytological features in all the species, and the results are presented in the descriptive part and in Tables 6-8. For further investigations, special stains were used on the best preserved material of the following species:

Psammetta globosa	"Siboga" St. 211 "J. Murray" Exp. St. 119 "Galathea" St. 238
Psammetta erythrocytomorpha	"Valdivia" St. 250
Psammina nummulina	"Galathea" St. 716
Psammina globigerina	"Siboga" St. 211
Cerelasma gyrosphaera	"Vema" St. 15-55
Cerelasma massa	"Galathea" St. 234
Stannoma dendroides	"Galathea" Sts. 232, 235
Stannophyllum zonarium	"Galathea" St. 716 "Vema" St. 15-55
Stannophyllum globigerinum	"Siboga" St. 211 "Galathea" St. 235
Stannophyllum indistinctum	"Galathea" St. 232
Stannophyllum mollum	"Galathea" Sts. 231, 235

2. Granellare (Table 6)

This name was created by SCHULZE (1907a, p. 8).

a. General features

Granellare are seen as yellowish, irregularly extending, dichotomously divided tubes (the organic test), containing plasma. Because of the different test components, it is difficult to follow a single string for a distance. The strings are generally freely branched, but in at least some cases, anastomoses are found *(Psammina nummulina, Cerelasma gyrosphaera, C. massa, Syringammina fragilissima,* and apparently *Psammetta globosa* and *Stannophyllum mollum).* It should be noted that anastomoses are difficult to distinguish from mere crossings.

The granellare branch diameter varies from 12-210 μ, but is usually from about 30 μ - about 90 μ. The largest diameters are found in the ramifications. The branch cross-sections are generally circular, but they can be oval. The granellare tube wall is generally very thin, less than 0.5 μ. When unstained it is a thin, yellowish, transparent, relatively solid membrane, and it is often slightly wrinkled (artifact?). Little is known about the chemistry of the tube wall (p. 75).

The granellare constitute only a small part of the total body volume; the largest part of a xenophyophore is dead matter, consisting of stercomare and xenophyae. It has not been possible to express the relationship between the living and dead body parts exactly. It appears to differ from genus to genus, but not within species of the same genus. Some of the genera have weakly developed granellare, viz. *Maudammina, Galatheammina,* and *Reticulammina,* whereas others have strongly developed granellare, viz. *Psammetta, Cerelasma, Syringammina,* and *Stannoma.*

The most obvious, characteristic bodies in the

Table 6. Granellare.

Species	Branching	Diameter of branches (μ)	Diameter of nuclei (μ)			
			Type 1	Nucleolus	Type 2	Type 3
Psammetta globosa	possibly anastomosing	30-210	2-3	+	4-5	0.5
Psammetta ovale	dichotomous	about 330	3-5	?	5-7	+[2]
Psammetta erythrocytomorpha	dichotomous	90-120	2-3	+	?[1]	+[1]
Galatheammina tetraedra	?	30-60	2-3	+	.	.
Galatheammina calcarea	dichotomous	25-80	3	+	.	.
Psammina nummulina	anastomosing	30-60	3-4	+	.	.
Psammina globigerina	dichotomous	40-90	2-4 (?)	.	6-7 (?)	.
Syringammina tasmanensis	anastomosing	115-193	2-3	.	.	.
Cerelasma gyrosphaera	anastomosing	25-70	2-4	+	5[1]	1-2 ?
Cerelasma massa	anastomosing	22-35	3-4	+	.	0.5
Stannoma dendroides	?	45-135	5-8	+	8-9	1
Stannophyllum zonarium	?	50-145	4-7	.	6-9	0.5 ?[1]
Stannophyllum globigerinum	dichotomous	35-90	3-4	+	6-7	1
Stannophyllum radiolarium	?	60-90	8-10	(+)	.	.
Stannophyllum reticulatum	dichotomous	60-120	4-6	.	.	.
Stannophyllum mollum	apparently anastomosing	40-90	4-6	.	(6-7)	0.5

1. Observed by SCHULZE (1907), but could not be verified by a new investigation.
2. All information about *P. ovale* is from SCHEPOTIEFF (1912b).

plasma are nuclei and granellae. The cytoplasmic ground substance itself is seen as a hyaline, homogeneous mass, but it is greatly shrunken in many samples. Sometimes it appears to contain a large number of small bubbles and in a few cases numerous, small, mostly unidentifiable inclusions.

b. Nuclei

When the material is well-preserved, nuclei are numerous and evenly distributed in the plasma (Pls. 14B, 15A, and 16B). In some samples, shrinking has led to the splitting of the plasma into lumps containing smaller or larger numbers of nuclei.

In a number of species three types of nuclei can be distinguished (Table 6). This phenomenon was seen by SCHULZE in *Psammetta globosa* (1906) and in *P. erythrocytomorpha, Cerelasma gyrosphaera, Stannoma dendroides,* and *Stannophyllum zonarium* (1907a). SCHEPOTIEFF (1912b, pp. 253, 257) reported them in *Psammetta ovale,* and I have found them in *Stannophyllum globigerinum* and *S. mollum* as well as observed them in some of the other species mentioned above (Table 6).

Type 1 (Pls. 14 C-D; 15 C). The most common nuclear type is a spherical or slightly ellipsoidal, easily stainable nucleus that most often has a nucleolus. The diameter is 2-10 μ. In Stannomida there is a tendency to larger nuclei than in Psamminida (Table 6). Aside from the nucleolus, there are generally no other structures found in the nucleus; a diffuse chromatin network sometimes appears, however.

Type 2 (Pl. 14 D). An ellipsoidal, bubble-like nucleus, 4-9 μ in length, is the second most commonly seen nuclear type. Again, it appears (Table 6) that the Stannomida have larger nuclei than the Psamminida. The nucleus is hard to stain, has a diffuse chromatin network, and sometimes has a nucleolus-like concentration in the interior. Nuclei of this type are generally found in small groups and are rarely found singly in the plasma.

Type 3 (Pl. 15B-C). Nuclei are small, 0.5-1 μ (2 μ) in diameter, spherical, and easily stainable. They are not common, but when found, there are always several present in a lump, sometimes in an apparently isolated granella-free plasma part. Often the individual nucleus looks as if it were surrounded by a hyaline plasma area, and the total diameter is then 3-5 μ. It is difficult to give the definite location of these nuclei in the plasma, but they tend to be found near the surface. SCHULZE mentioned that they are found near the surface in some species (1906, p. 10; 1907a, p. 16), in the axial part in others (1907a, p. 23), or that they are scattered in a hyaline plasma part in still others (1907a, p. 40). Perhaps nuclei location differs from species to species or even from genus to genus.

The relationship between the three types of nuclei is of interest both in connection with reproduction and for systematic and phylogenetic reasons.

Since no experiments have been conducted with living animals, all our knowledge is pieced together from occasional observations in the preserved material.

I have seen what appear to be intermediate stages between nuclear types 1 and 2 in *Stannoma dendroides*. This may be indicative of development of the type 1 nucleus to the type 2 nucleus. SCHULZE (1906, p. 10; 1907a, pp. 23, 35, 40) and SCHEPOTIEFF (1912b, p. 253) apparently also assumed that the two types represented different stages of the same nuclear type. Type 3 nuclei are interpreted as gametes or as developmental gamete stages resulting from division of type 2 nuclei. This opinion was first expressed by SCHULZE (1906, 1907a) concerning *Psammetta globosa, P. erythrocytomorpha, Cerelasma gyrosphaera,* and *Stannoma dendroides,* and later by SCHEPOTIEFF (1912b) for *Psammetta ovale*. SCHULZE (1907a, p. 35) interpreted structures in *S. dendroides* as gamete flagella with some hesitation. SCHEPOTIEFF described the *P. ovale* gametes as being 20 μ im length, bi-flagellate, with a small, concentrated nucleus, and with homogenous plasma. No structures resembling flagella have been seen in the material at my disposal.

There are reasons to suppose a further differentiation between the nuclei of types 1 and 2 than is indicated above. Type 1 nuclei are much more numerous than type 2. If all type 1 nuclei eventually become type 2 nuclei, the latter must have a very high turn-over, and a large number of gametes should be found. This, however, is not the impression I have of the deep-sea xenophyophores, and SCHEPOTIEFF does not mention it for his shallow water specimens. A convenient explanation could be that the xenophyophores, or at least some of them, are heterocaryotic in analogy with a series of foraminiferan species (GRELL 1962, 1967, 1968, the first with further literature lists; LEE *et al.* 1965). Nuclei of type 1 would then be somatic, and nuclei of type 2 would be generative. It has been shown in foraminiferans that there is a controlling factor regulating the relative numbers of somatic and generative nuclei (CZIHAK & GRELL 1960, and cf. GRELL 1962, p. 33 and 1968, p. 99) and a similar system could have been developed in the xenophyophores. This theory can be supported by SCHEPOTIEFF's observation (1912b, p. 253) that only type 1 nuclei are found in the initial plasma.

It should be pointed out that only the phenomenon of nuclei diversity can be compared between the foraminiferans and the xenophyophores, since only the agamont shows heterocaryoty in the foraminiferans. Another difference is that in the xenophyophores the presumed generative nucleus has a large diameter and is found in smaller numbers, while in the foraminiferans it is small and more numerous than the somatic nuclei.

c. Granellae

The name was given by SCHULZE & THIERFELDER (1905, p. 3).

A unique, conspicuous, characteristic feature of the xenophyophores is the presence of numerous crystalline bodies, granellae, in the plasma.

SCHULZE & THIERFELDER (1905) showed that the crystals are made of barite ($BaSO_4$), and this has been confirmed by Prof. ARRHENIUS (1968, personal communication). Further comments on the nature of the granellae were given by SCHULZE (1906), SAMOJLOV (1911), SCHEPOTIEFF (1912b), and VINOGRADOV (1953).

Granellae are generally evenly distributed in the plasma, although granella-free areas are sometimes seen. In most cases there are many granellae (Pls. 16A-B; 17A); often they are so numerous that the nuclei are nearly hidden. Granellae were either not observed or were very few and small in some of the poorly preserved samples; this was also the case in a few of the well-preserved samples (*Stannoma dendroides* and *Stannophyllum globigerinum* ("Galathea" St. 235), *Stannophyllum radiolarium* ("Challenger" St. 271), and *Reticulammina labyrinthica*).

The granellae are flat, ellipsoidal, spindle-shaped or rounded (Pl. 16C). They are nearly hyaline, and have a faint greenish tint (this colour phenomenon is probably due to refraction and not absorption color in the common sense). Generally granellae are 2-5 μ in size, but smaller and larger specimens are not uncommon; the largest known are reported by SCHEPOTIEFF (1912b) from *Psammetta* ovale (up to 25 μ) and *Stannophyllum* sp. (up to 50 μ).

ARRHENIUS (1968, personal communication) has investigated barite crystals from sediments and from xenophyophores (*Stannophyllum zonarium;* "Galathea" St. 716). A remarkable feature found in many of the crystals is a central hole in various stages of closure. In a number of the crystals without this perforation, an optical discontinuity can be seen in the centre (Pl. 16C).

A detailed investigation of the chemical composition of the granellae is being undertaken by ARRHENIUS (1963 and personal communication). Besides the main component of $BaSO_4$, about 5 vol. percent of strontium substituting for barium, and minor amounts of chromium, possibly substituting as CrO_4^{-2} for SO_4^{-2}, have been found. About 5 ppm uranium is also associated with the crystals; it is uncertain as yet if this and other trace components occur in solid solution or as inclusions in the barite (see also ARRHENIUS *et al.* 1957).

It is questionable as to whether the crystals are actually formed in the xenophyophore plasma or are concentrated by uptake and retention of naturally deposited crystals in the sediment. The first view is held by ARRHENIUS (1966, p. 166 and personal communication; see also ARRHENIUS & BONATTI 1965, p. 17). They suggest that there can be little doubt about an origin within the xenophyophores for the perforated crystals or those with optical discontinuity. In support of this view is the fact that $BaSO_4$ crystals are absent or rare in what I interpret as the most recently collected bottom material, yet they are numerous in both the plasma and the stercomes, some of which may be exclusively made of granellae. These crystals are, therefore, not only concentrated and retained in the plasma, but are also expelled from it in large numbers. The few crystals found in the bottom material recently taken up by the animal, can hardly be the (only) source of the numerous crystals found in the animals, and the only other possibility is that they are actively secreted in the plasma.

The crystals are not found in vacuoles in the xenophyophores, although they are present here in well-investigated rhizopodes (cf. ANDRESEN 1942, p. 166; 1956, p. 502; PAPPAS 1954, p. 208). This can be explained in two ways; either the vacuole is destroyed at death (ANDRESEN 1942, p. 150), or it becomes less conspicuous during fixation (ANDRESEN 1956, p. 490). Structures resembling the stercomes composed solely of granellae are described in *Chaos chaos*. Here they result from the coalescence of numerous crystal vacuoles (ANDRESEN 1958, p. 498) and they are later expelled.

The granellae function is unknown. SCHULZE (1907a, p. 16) mentioned the possibility that they were comparable to the crystals in the crystal swarmers of some Radiolaria, but there is no further support for this view. Crystals of different types are reported from many Protozoa (cf. BERNHEIMER 1938; ANDRESEN 1956, p. 502), but their function and chemical composition are known in only few cases. GRIFFIN's study (1960) showed that crystals in amoebae were composed of carbonyl diurea, and they were consequently assumed to be a nitrogen excretion product. A case that perhaps resembles the xenophyophores more is the enigmatic deposition of either $CaCO_3$ granules or crystals in the plasma of myxomycetes (GRASSÉ 1953, p. 512).

$BaSO_4$ in crystal form is unknown in animals other than the xenophyophores, but a high barium content has been demonstrated in the cytoplasm of foraminiferans and in the spines of achantharid radiolarians (ARRHENIUS 1963, p. 677). At present, the most likely explanation of the presence of barium in the three rhizopod groups mentioned is either that it is passively concentrated (absorbed accidentally), or unavoidably engulfed with food and then chemically neutralized. Water-soluble barium compounds are poisonous whereas the unsoluble $BaSO_4$ is not.

d. Other plasmatic inclusions

There are numerous evenly distributed grains 0.5-0.8 μ in diameter in the plasma of *Psammetta erythrocytomorpha* (Pl. 16A), *P. globosa, Cerelasma massa,* and *Stannophyllum zonarium*. After staining with Azan they are especially conspicuous and are a strong red in colour.

SCHEPOTIEFF (1912b, p. 252) described the following special plasmatic inclusions in *Psammetta ovale:* 1) whitish, spherical or irregular lumps of protein up to 50 μ in diameter, 2) spherical or elongate, sometimes aggregated, brown, opaque grains composed of organic matter, possibly serving as storage material, 3) small, light yellow or brownish crystals or grains with a jagged or rounded outline, and 4) what he calls trichites, more or less arched, up to 25 μ long, 0.5-1 μ wide, stick-shaped bodies. I have not found anything comparable to (1) and (3) in any of the examined species. (2) could possibly be early stages of xanthosomes. "Trichites", or at least inclusions that somewhat fit the description of these, have been found here and there. They resemble most parts of crustacean skeletons. The designation trichite is misleading since trichites are also structures forming a part of the feeding apparatus in some ciliates (GRELL 1968, p. 31).

e. Pseudopodia

The pseudopodia of the xenophyophores have never been described. SCHULZE (1907a, pp. 14, 34; 1912, p. 40) mentioned hyaline drops of plasma without nuclei at the ends of some granellare branches in *Psammetta erythrocytomorpha* and *Stannoma dendroides* and considered them to be contracted pseudopods. I have been able to confirm SCHULZE's observation in *P. erythrocytomorpha*, and I have seen similar formations in *Galatheammina calcarea* and *Psammina nummulina*. A phenomenon similar to this is described in the enigmatic rhizopod *Cinetidomyxa chattoni* (CACHON & CACHON-ENJUMET 1964, p. 49).

The rough outline of the outstretched pseudopod system is presumably seen on some deep-sea photographs from the West Pacific (Pl. 16D) (PROA Project 1962, Scripps Institution of Oceanography) (LEMCHE et al., in preparation). A *Psammetta*-like organism is very common in a number of these pictures. About 50 % of the individuals are surrounded by a star-shaped figure, which I interpret to be pseudopodia. These are long and slender, often dichotomously branched, and apparently do not anastomose. The diameter of the star-shaped figure is 4-7 times the body diameter, and the single pseudopodium possibly reaches 6-12 cm in length. It often appears that the pseudopodia radiate from two opposite sides, thus giving a bilateral impression. On the largest specimens, which are slightly elliptical (as in *Psammetta*), they extend from the poles determined by the longitudinal axis.

The organism with its surrounding figure is strongly suggestive of the appearance of many foraminiferans with the pseudopodia extended, e.g., *Gromia* (HEDLEY 1962a, p. 125, fig. 3), *Astrorhiza* (HEDLEY, personal communication), and *Iridia* (MARSZALEK 1969, p. 602, fig. 4).

If the observations given above are interpreted as xenophyophore pseudopodia, these can be characterized as follows: slender, hyaline, filamentous, and presumably not anastomosing.

According to this interpretation the method of locomotion must be that of the active shearing mechanism (the two-way streaming) (BOVEE & JAHN 1965a, p. 34; 1965b, p. 294). In their proposal of a new division of the Sarcodina, BOVEE & JAHN (1965a, b) have placed the xenophyophores in their class Hydraulea which contains those Sarcodina which move by a conctraction-hydraulic system. Their reasons for this arrangement seem to be partly that SCHULZE placed the xenophyophores between the foraminiferans and the slime molds, and partly a misinterpretation of the structure and role of the granellare tube wall.

SCHEPOTIEFF (1912b, p. 253) believed that the xenophyophores have no pseudopodia, and that the openings at the tips of granellare branches are due to damaging. As noted by SCHULZE (1912, p. 41), SCHEPOTIEFF fails to explain how the xenophyae are gathered and secured, and how the linellae are formed. Moreover, SCHEPOTIEFF's proposal of method of food uptake seems unlikely (see further p. 78).

3. Stercomare

This name was created by SCHULZE (1907a, p. 8).

a. General features

Stercomare are seen as irregularly extending, dark, dichotomously divided strings within the body. Although it is generally difficult to trace a string for a distance, it was found that the strings anastomose in some species (*Psammetta globosa*, *Galatheammina tetraedra*, *G. calcarea*, *Reticulammina labyrinthica*, *Psammina globigerina*, *Cerelasma gyrosphaera*, *C. massa*, and apparently *Stannophyllum zonarium*). In other species anastomoses are rare or absent (*Maudammina arenaria*, *Psammetta erythrocytomorpha*, *Reticulammina novazealandica*, *Psammina nummulina*, *Stannophyllum globigerinum*, and *S. reticulatum*). The form of the single string can be rather irregular; sometimes it resembles a string of pearls (fixation artifact?).

The string diameter can be from 35-540 μ, and it varies greatly from species to species. In general the cross-section is rounded (Pl. 15A, D). In the newly deposited parts, the covering membrane is thinner than the granellare wall (< 0.5 μ). It is a thin, entirely transparent, very fragile membrane. In older parts of the specimen, the stercomare walls are often thickened due to layers of cement mass. Only little is known about the chemistry of the membrane (p. 75).

In comparison to granellare, stercomare are always strongly developed. The relationship between the volume of xenophyae and stercomare varies. Although it has been impossible to express the relationship exactly (cf. granellare, p. 68), it was found that there is marked variation from genus to genus and less variation among species of the same genus. Slightly developed stercomare are found in *Maudammina*, *Galatheammina*, *Reticulammina*, and *Syringammina*, while strongly developed stercomare are found in *Cerelasma* and *Stannophyllum*. In some cases it totally dominates the body, as in *Cerelasma massa* and *Stannophyllum mollum*. The following species pairs serve as good examples of variation between species within the same genus: *Psammina nummulina* – *P. globigerina*, *Syringammina fragillissima* – *S. tasmanensis*, *Cerelasma gyro-*

sphaera – C. massa, and *Stannophyllum zonarium – S. mollum.*

The characteristic contents of stercomare are stercomes and xanthosomes.

b. Stercomes

The name was given by SCHAUDINN (1899, p. 43).

Stercomes (sometimes called stercomata) are ellipsoidal masses measuring 8-60 μ (200 μ) in length, but are generally 10-20 μ. They are dark brown, and it is their colour that gives the stercomare its dark appearance. They are composed of a mass of unidentifiable, small particles. Fragmented remnants of different items such as sponge spicules, crustacean skeletons, radiolarian tests, and diatom shells can occasionally be observed. The stercomes generally also contain granellae (Pl. 17A). All the particles are held together by a transparent, gel-like mass.

Four types of stercomes can be distinguished in the xenophyophores. These types are characteristic, but transition forms are found.

1) (Pls. 16E; 17D-E). The most common stercomes are uniformly granulated. They fit the above description, and besides the inclusions mentioned, they occasionally contain black grains of unknown nature and of varying size. SCHEPOTIEFF (1912b, p. 254) called the grains "Melanellen", referring the name to SCHULZE; I cannot, however, find it anywhere in SCHULZE's works.

2) (Pl. 16E). The second and rather common stercome type has the general form and size, but contains a large number of small, spherical elements 1–4 μ in diameter and does not seem to contain granellae. The colour is often greenish or yellowish.

3) (Pl. 17E). A third type of stercomes containing exclusively granellae is occasionally found. These stercomes are spherical, about 10 μ in diameter, and occur singly.

4) (Pl. 17B). A characteristic but uncommon stercome type also mentioned by SCHULZE (1907a, p. 12) contains folded membranes of unknown origin.

SCHEPOTIEFF (1912b, p. 254, pl. 15, figs. 64-67) also listed four types of stercomes. He distinguished them on the basis of the number and size of "Melanellen" and granellae. He pointed out that all the types are found at the same time in all parts of stercomare. It is easy to find his types in the present material, but it is just as easy to find transition forms between them. His figures do not give the impression of any clear differences.

Stercomes are the fecal pellets of the animal. They are described in a number of benthonic rhizopods other than xenophyophores, and are referred to by many authors (SCHULZE 1854, p. 21; GRUBER 1884, p. 493; RHUMBLER 1892, p. 420; 1894, pp. 494, 563; 1909, p. 239; 1923, p. 75; SCHAUDINN 1894, p. 18; 1899, p. 43; WINTER 1907, pp. 13, 55; ZARNIK 1907, p. 74; AWERINZEW 1910, p. 425; LÜCKE 1910, p. 46; MINCHIN 1912, pp. 194, 233; SCHEPOTIEFF 1912a, pp. 54, 67; 1912c, p. 229; JEPPS 1926, p. 707; 1956, p. 68; DOFLEIN & REICHENOW 1949, p. 151; 1952, p. 739; HEDLEY & BERTAUD 1962, p. 81; HEDLEY 1962a, p. 131; 1964, p. 21; LOEBLICH & TAPPAN 1964, pp. 64, 87).

When examined with electron microscopy, the stercomes of the foraminiferan *Gromia oviformis* appear to be masses of opaque material largely consisting of plate-like crystalline particles and various fragments (HEDLEY & BERTAUD 1962). The stercomes of *Cerelasma massa* have the same appearance (Pl. 17D).[1] The particles are held together by a substance presumably partly consisting of acid mucopolysaccharide (faint metachromasia with toluidine blue; standard method and Kramer & Windrum, after PEARSE 1961), a condition also found in *Gromia* (HEDLEY & BERTAUD, l.c.).

Different stages in the stercome formation in xenophyophores were seen in several species (*Psammina nummulina, Cerelasma massa* (Pl. 17E), *Stannoma dendroides,* and *Stannophyllum zonarium*) where variously differentiated stercomes were found in or at the edge of an undifferentiated mass of accumulated material in the youngest stercomare parts.

Retention of stercomes in huge masses is characteristic of the xenophyophores. A similar phenomenon, but not on such an extraordinary scale, is found in *Gromia* (cf. e.g. JEPPS 1926 and HEDLEY 1962a). Waste materials in many benthonic foraminiferans are either expelled immediately after formation or after some time of accumulation (RHUMBLER 1923, p. 75; JEPPS 1956, p. 68; LOEBLICH & TAPPAN 1964, p. 87). Parts of the large arenaceous foraminiferan tests are in some cases permanently filled with dark material (BRADY 1884, p. 244; RHUMBLER 1894, p. 571; CALVEZ 1938a. p. 84) that is presumably waste material in a form

1. The EM pictures were made by Dr. A. DIBOLL and placed at my disposal by the courtesy of Dr. I. R. KAPLAN, University of California.

other than that of stercomes. The problems of uptake of bottom material as food, digestion, and excretion of waste products seriously need to be investigated in these different rhizopod groups.

The function, if any, of these enormous masses of stercomes in the xenophyophores has never been explained. In the species where stercomare are strongly developed, it seems reasonable to presume that they, together with the xenophyae, have a protective and supportive function as test components. Extreme examples of stercomare development are the cases where xenophyae are absent and the stercomare have assumed the entire test function as in *Cerelasma massa* and *Stannophyllum mollum*. In *Maudammina, Galatheammina* and *Reticulammina* species, only small amounts of stercomare are found in the test, and they cannot, therefore, have any function as a test component. This is probably representative of a primitive state within the xenophyophores, and the tendency to incorporate fecal pellets in the test instead of expelling them, has probably evolved from this condition.

c. Xanthosomes

The name was created by RHUMBLER (1894, p. 566).

The xanthosomes of the xenophyophores are rounded, generally spherical, single or aggregated bodies, 0.8-15 μ in diameter but generally 1-7 μ (Pls. 16E; 17C). The colour is reddish, orange, yellowish, or brownish. They are found scattered among the stercomes and vary greatly in number even in different samples of the same species. In many cases they seem to be absent.

Xanthosomes are described in a number of rhizopodes other than xenophyophores (RHUMBLER 1894, p. 566; 1909, p. 236; 1923, p. 75; SCHAUDINN 1899, p. 47; WINTER 1907, p. 54; ZARNIK 1907, p. 73; AWERINZEW 1910, p. 426; LÜCKE 1910, p. 47; SCHEPOTIEFF 1912a, p. 67; 1912c, p. 229; JEPPS 1926, p. 708; 1942, p. 629; 1956, pp. 69, 71, 75; CALVEZ 1938b, p. 267; 1953, pp. 166, 169, 171; DOFLEIN & REICHENOW 1949, p. 151; HEDLEY & BERTAUD 1962, p. 81; HEDLEY 1962a, p. 131; 1964, p. 21; LOEBLICH & TAPPAN 1964, pp. 65, 87).

It is generally agreed that the xanthosomes are excretion products. Little is known about their composition, and it is likely that chemically different products are included under this designation. SCHULZE (1906, p. 8) showed the presence of an iron compound in the xanthosomes of *Psammetta globosa*. I have (with Pearl's method, after PEARSE 1961, p. 931) confirmed the observation on this species and found organically bound iron in a number of other species too (*Psammetta erythrocytomorpha, Psammina globigerina, Cerelasma massa, Stannoma dendroides, Stannophyllum zonarium,* and *S. mollum*). It is remarkable that RHUMBLER (1894, p. 570) could not detect iron in the xanthosomes of *Saccammina*. An electron microscopical investigation (HEDLEY & BERTAUD 1962) showed the xanthosomes of *Gromia oviformis* to be built of dense, opaque spheres, arranged in concentric layers.

It is unclear whether the xanthosomes of the xenophyophores are formed within the plasma in granellare or not. They are only rarely seen in the plasma. In a few species, especially in *Cerelasma massa,* indistinct bubble-like formations containing a small number of minute grains reacting positively to the iron test were found. These could be early xanthosome stages. The formation of xanthosomes in vacuoles is possibly known in *Gromia,* where ZARNIK (1907, p. 74) described some grains, "Kinetochondren", in vacuoles. AWERINZEW (1910, p. 425) presumes that they are, in fact, xanthosomes.

4. Linellae

The term was created by SCHULZE (1907a, p. 28).

The linellae are extracellular threads that have a supportive and strengthening role in the test (Pls. 14B; 15A, D). These threads are characteristic of the order Stannomida and are always present in large numbers. As previously mentioned (p. 20), similar structures are hitherto unknown in other protozoa.

The single linella measures several mm in length, but it has been impossible to trace any one thread from end to end. The width seems to be constant during the entire thread length. In the single species (and specimens) linellae of different widths are found, but in many cases the variation is rather limited and can be used as a supporting taxonomical criterion. The following species exemplify this variation: *Stannoma dendroides* (2.5-4 μ wide), *S. coralloides* (1-2 μ), *Stannophyllum zonarium* (3-4 μ), *S. radiolarium* (1-2 μ), *S. pertusum* (1-3 μ), *S. alatum* (4-6 μ), *S. fragilis* (2-40 μ) and *S. flustraceum* (1-60 μ) (regarding the very thick linellae of the two latter, cf. p. 53 and p. 58). *S. venosum* can be mentioned as a special case; thin linellae (1-2 μ) are found in the leaf proper, and thick linellae (6-10 μ) are found in the surface ribs.

The ends of linellae are broadly flattened and are fastened to xenophyae, other linellae, or to the granellare and stercomare walls. Where linellae cross each other, the crossing is often strengthened with cement. In some cases it is difficult to distinguish the fastening of a linella on a free part of another linella from a true dichotomy. This depends at least partly on the linellae thickness. As SCHULZE (1907a, p. 29) has also pointed out, the thinnest linellae appear quite hyaline, while the thicker linellae seem to have an axial canal or "marrow".

The linellae vary from species to species, both with respect to quantity and arrangement and to dimensions. They are always numerous, but it is obvious that *Stannophyllum zonarium,* for example, has more linellae than *S. globigerinum* and *S. fragilis.* Although linellae are usually numerous in the test interior, some species also have a very distinct linellae surface layer: *S. zonarium, S. globigerinum,* and *S. mollum.*

The composition of the linellae is poorly known. SCHULZE & THIERFELDER (SCHULZE 1907a, p. 30) found N, S, and I compounds, and got a positive reaction to some protein tests. A rather strong PAS reaction is commonly found, and this together with the protein content indicates the presence of mucopolysaccharides. If this is the case, they do not seem to be of the acid type since tests with toluidine blue (Standard method and Kramer & Windrum, after PEARSE 1961) and Alcian blue were negative.

According to HEDLEY (personal communication), an electron microscopical investigation of linellae from *Stannophyllum zonarium* ("Galathea" St. 716) and *S. mollum* ("Galathea" St. 235) has revealed a structure of concentric (spirally coiled?) alternating layers of high and low electron density (Pl. 17 F-G).

HAECKEL (1889, p. 56ff.) believed that the linellae were comparable to the enigmatic fibers known in the sponges of the genus *Ircinia* (=*Hircinia*), but this was denied by both SCHULZE (1907a, p. 31) and SCHEPOTIEFF (1912b, p. 261). A short communication on the submicroscopical structure of the *Ircinia* fibers has been given by LÉVI (1965, p. 12, fig. 3), and a comparison with the linellae structure emphasizes the differences, one of the most striking of these being the organization of the linellae in concentric layers in contrast to the fibrillar arrangement in the *Ircinia* fibers.

Although no observations exist, it can hardly be doubted that the linellae are formed by pseudopodia. This seems to be the only possible explanation, and SCHEPOTIEFF (1912b, p. 253), who denied the existence of pseudopodia in the xenophyophores, failed to explain linellae formation. On the other hand, his view (p. 262) that the linellae represent the end product of differentiation of the cement substance seems reasonable, at least at present.

5. Cement and granellare and stercomare walls

The individual xenophyae are connected by cement, and these agglomerations are again connected with cement to the linellae and the granellare and stercomare walls. The cement is seen as smaller or larger irregular masses. The amount of cement used varies greatly from genus to genus. There is little cement found in *Maudammina, Galatheammina, Reticulammina,* and *Psammina,* large quantities in *Cerelasma,* and only moderate amounts in *Stannoma* and *Stannophyllum.*

At present hardly anything is known about the composition of the cement mass, the membrane surrounding stercomare, and the granellare tube walls, and none of these can be chemically determined. A positive PAS reaction indicates the presence of polysaccharide, and since mucopolysaccharide is presumably a component of the linellae and is found in the cement and shell of a number of rhizopodes (ANGELL 1967, p. 305; BUCHANAN & HEDLEY 1960, p. 554; CALVEZ 1953, p. 152; DEFLANDRE 1953, p. 110; HEDLEY 1958, p. 574; 1960b, p. 282; 1962b, p. 379; 1963, p. 436; 1964, p. 19; PAPPAS 1954, p. 204; PIERCE *et al.* 1968, p. 244) it seems logical to presume that it is also found here. If the substance is a mucopolysaccharide, it does not seem to be of the acid type; the tests with toluidine blue and Alcian blue were negative. This was also the case in *Haliphysema* (HEDLEY 1958, p. 574) and *Thecamoeba* (PAPPAS 1954, p. 204).

The presence of organically bound iron has been shown in the cement of many rhizopodes (CALVEZ 1953, p. 151; DEFLANDRE 1953, p. 110; HEDLEY 1960b, p. 282; 1963, p. 438; 1964, pp. 6, 13; VINOGRADOV 1953, p. 165). It was searched for but not found in *Allogromia* (PIERCE *et al.* 1968, p. 245). Iron has been detected in the xenophyophores in *Syringammina tasmanensis* (HEDLEY 1966, p. 123). During the present investigation a number of species were treated using Pearl's method (PEARSE 1961, p. 931), but they gave poor results, presumably because of improper fixation (PEARSE l. c., p. 683). Iron was found in the granellare walls (faint reaction) and in the thickened stercomare mem-

Table 7. Xenophyae types in the species of xenophyophores.

Species	Number of types present				Xenophyae types				
	0	1	2	Several	Foraminiferan tests	Radiolarian tests	Sponge spicules	Mineral particles	Fine-grained matter
Maudammina arenaria	.	x	.	.	.	.	.	x	.
Psammetta globosa	.	x[1]	.	.	x	.	x	.	.
Psammetta arenocentrum	.	x[1]	.	.	.	.	x	x	.
Psammetta ovale	.	.	.	x	x	.	x	x	.
Psammetta erythrocytomorpha	.	x	.	.	.	.	x	.	.
Galatheammina tetraedra	.	x	.	.	x	.	.	.	(x)[2]
Galatheammina calcarea	.	x	.	.	x	.	.	.	.
Reticulammina novazealandica	.	.	x	.	x	.	.	.	x
Reticulammina labyrinthica	.	.	x	.	x	.	.	.	x
Reticulammina lamellata	.	.	x	.	.	.	.	x	x
Reticulammina cretacea	.	x	.	.	x	.	.	.	.
Psammina nummulina	.	x	.	.	.	x	(x)	(x)	.
Psammina globigerina	.	x	.	.	x	.	.	.	.
Cerelpemma radiolarium	.	x	.	.	.	x	.	.	.
Syringammina fragilissima	.	.	x	.	x	.	.	x	(x)
Syringammina minuta	.	x	.	.	.	.	.	x	(x)
Syringammina tasmanensis	.	.	x	.	x	.	.	.	x
Cerelasma gyrosphaera	.	x	.	.	.	x	.	.	.
Cerelasma massa	x	.	.	.	.	.	.	.	.
Cerelasma lamellosa	.	.	.	x	x	.	x	x	.
Stannoma dendroides	.	x	.	.	.	x	(x)	.	.
Stannoma coralloides	.	x	.	.	.	x	.	.	.
Stannophyllum zonarium	.	x	.	.	.	x	(x)	(x)	.
Stannophyllum globigerinum	.	x	.	.	x	.	.	.	.
Stannophyllum granularium	.	.	.	x	.	x	x	x	.
Stannophyllum fragilis	.	x	.	.	.	.	.	x	.
Stannophyllum radiolarium	.	x	.	.	.	x	.	.	.
Stannophyllum pertusum	.	.	x	.	x	x	(x)	.	.
Stannophyllum venosum	.	.	x	.	x	x	.	.	.
Stannophyllum indistinctum	.	x	.	.	.	(x)	x	.	.
Stannophyllum alatum	.	x	.	.	.	x	.	.	.
Stannophyllum concretum	.	.	x	.	x	x	.	.	.
Stannophyllum flustraceum	.	.	.	x	.	x	x	x	.
Stannophyllum reticulatum	.	x	.	.	.	.	x	.	.
Stannophyllum mollum	x	.	.	.	.	(x)	(x)	.	.

1. The species uses two types of xenophyae, but type usage is strongly influenced by age.
2. (x) indicates that this type of xenophyae is irregularly used or rare.

brane, but not in the cement proper in *Cerelasma massa*.

Secretion of the cement and the membrane surrounding stercomare must be performed by pseudopodia. The granellare tube wall is presumably secreted from the surface of the plasma.

6. Xenophyae

The name was created by HAECKEL (1889, p. 19).

Xenophyae are foreign bodies taken up from the substratum and used in the test formation. The bodies concerned are generally silicious sponge spicules, foraminiferan or radiolarian tests, and mineral particles. As test components, the xenophyae have a protective and supportive function. The amount of xenophyae taken up varies greatly. All transition forms are found and animals looking like sandstone (*Maudammina*) or friable limestone (*Galatheammina*), due to uptake of a large amount of xenophyae can be found, as well as animals that feel like a doughy lump (*Cerelasma massa*) or a wet rag (*Stannophyllum mollum*), due to total absence of xenophyae.

From the descriptions (Table 7) it appears that most species are strongly selective with respect to the type of xenophyae used. This selectivity is even more apparent when it is considered that several

Table 8. Diversity of xenophyae in xenophyophore species taken at the same station.

Expedition, St. no., depth	Sediment type	Species recorded	Type of xenophyae				
			Foraminiferan tests	Radiolarian tests	Sponge spicules	Mineral particles	No xenophyae
"Challenger" 271 4438 m	Globigerina ooze	*Cerelpemma radiolarium*	.	x	.	.	.
		Cerelasma gyrosphaera	.	x	.	.	.
		Stannoma dendroides	.	x	(x)[1]	.	.
		Stannoma coralloides	.	x	.	.	.
		Stannophyllum zonarium	.	x	(x)	(x)	.
		Stannophyllum globigerinum	x	.	.	.	.
		Stannophyllum radiolarium	.	x	.	.	.
		Stannophyllum pertusum	x	x	.	.	.
		Stannophyllum venosum	x	x	.	.	.
"Siboga" 211 1158 m	Coarse, grey mud	*Psammetta globosa*	x	.	x	.	.
		Psammina globigerina	x	.	.	.	.
		Stannophyllum globigerinum	x	.	.	.	.
"Galathea" 235 4810 m	Globigerina ooze	*Cerelasma massa*	.	.	.	.	x
		Stannoma dendroides	.	x	(x)	.	.
		Stannophyllum globigerinum	x	.	.	.	.
		Stannophyllum indistinctum	.	(x)	x	.	.
		Stannophyllum mollum	.	.	.	.	x
"Galathea" 238 3960 m	Globigerina ooze	*Psammetta globosa*	x	.	x	.	.
		Stannoma dendroides	.	x	(x)	.	.
		Stannophyllum globigerinum	x	.	.	.	.

1. (x) indicates that there are few of this type of xenophyae.

species utilizing different types of xenophyae are often found at the same station (Table 8, further examples can be found in the list of stations) and therefore in all probability on the same type of sediment. In this connection it should be kept in mind that sediment, especially "Globigerina ooze", is a mixture of many constituents, and thereby offers a series of alternatives in the selection of building material for agglutinated tests.

Lewis (1966, p. 119) showed *Syringammina tasmanensis* to be non-selective of grain size through comparison of the size ranges of the particles in the test and from the substratum of the collecting locality.

Selectivity with respect to properties other than size is reflected in the presence of large numbers of species which apparently select predominantly only one type of xenophyae (Table 7). Important factors in the selection could be chemical composition, density, specific gravity, and surface texture of the particles. A chemical distinction is likely where species distinguish between calcareous matter (foraminiferan tests) and silicious matter (sponge spicules and radiolarian tests). It seems rather unlikely that these animals can distinguish chemically between sponge spicules and radiolarian tests; another selective characteristic is probably more decisive here.

The species where two types of xenophyae are used at different stages or in different positions in the test are of special interest and demonstrate the ability of some species to distinguish very clearly between different xenophyae. *Psammetta arenocentrum* uses two silicious types (Pl. 2D): sand grains as young, and sponge spicules as mature, and *P. globosa* uses two types of different chemical composition (Pls. 1E, 2B): foraminiferan tests as young, sponge spicules as mature. In these cases the selectivity for the two different types of xenophyae is connected with development. In other species differentiation can be found in mature animals. Thus, in *Reticulammina novazealandica* and *R. labyrinthica* the tests are mainly composed of foraminiferan tests, but the surface is covered with a distinct layer of fine-grained calcareous matter (Pl. 3 G-H). A somewhat similar distribution of two different xenophyae types (radiolarian and foraminiferan tests) is found in *Stannophyllum pertusum*, *S. venosum*, and *S. concretum* (these three species are, however, poorly known).

C. NUTRITION

SCHEPOTIEFF (1912b, p. 253) interpreted the organization of the xenophyophores in a strange way: "Der Ernährungsmodus der Xenophyophoren bleibt (also) noch unklar. Der Mangel an Pseudopodien und die Kontinuerlichkeit der Membran lassen das Bestehen einer pflanzlichen Nahrungsassimilation durch die Membran hindurch vermuten, nicht aber eine unmittelbare Aufnahme von Organismen durch Pseudopodien oder Cilien, wie dies bei vielen Protozoen der Fall ist." This view was strongly opposed by SCHULZE (1912, p. 41) who stated that "Mir erscheint eine Assimilation nach Art der Pflanzen in den lichtlosen Tiefen undenkbar, und ich wüsste nicht, wie die Materialien zu dem ausserhalb der Granellare liegenden Xenophyagerüst herbeigeschafft und verkittet werden, und die gleichfalls ausserhalb der Granellare befindlichen Linellen hergestellt werden könnten, wenn nicht nacktes Plasma aus den Granellaren mindestens zeitweise austreten könnte."

During the present investigation the following observations have been made: 1) No particles are found in the plasma proper that have an apparent nutritive value. 2) Particles presumed to be nutritive are accumulated between the granellare and stercomare branches. 3) It is possible to find stages of increasing differentiation of the material, from loose accumulations to the fully formed stercomes (Pl. 17 E).

My conclusion is that particles from the surface or the uppermost layer of the surrounding substrate are collected through pseudopodial activity and carried to accumulation sites. Here, the first or possibly all stages of digestion occur outside the organic test (extratestally), and the utilizable matter is transported to the plasma inside granellare. The remnants in the accumulation sites are converted into stercomes and these are, at least in some species, used in the further test development.

Extratestal and/or extracellular digestion is known in four foraminiferans. In *Astrorhiza limicola* (BUCHANAN & HEDLEY 1960, p. 559) there is no accumulation of the nutritive matter before the digestive processes begin, in contrast to the following three species:

JEPPS (1942, p. 625) described the mechanism in *Elphidium crispum* whereby food particles (diatoms) are collected by the pseudopodia and form a feeding cyst covering the animal within a few hours. Digestion continues inside the cyst and the pseudopodia are withdrawn. After some time, the pseudopodia extend again and the animal begins to move, leaving the cyst behind.

The test in *Discorbis patellifera* (CALVEZ 1953, p. 205) is fixed; food particles accumulate between the test and the substratum, and digestion is performed here.

In *Allogromia laticollaris,* LENGSFELD (1969) has shown that food particles are collected by the reticulopods and transported extracellularly into lacunes (which are not vacuoles) inside the test. Here digestion takes place extracellularly and the nutritive matter is absorbed by numerous fine strands extending from the plasma body into the sea-water filled lacunes. Indigestible food residues are removed by reversal of the collecting processes.

It is likely that the membrane surrounding stercomare in the xenophyophores is comparable to the mucus-like covering which is part of the feeding cyst in *Elphidium.* Moreover, it is of interest that many (about 50 %) of the animals seen on some deep-sea photographs interpreted to be xenophyophores (LEMCHE *et al.,* in preparation) have the pseudopodia withdrawn. It is tempting to interpret the xenophyophores with extended pseudopodia as being in "collecting phase", and those with withdrawn pseudopodia as being in the "digestive phase". Since about 50 % of the animals have withdrawn pseudopodia, the digestion process is possibly of rather long duration.

The exact type of nutritional material utilized by the xenophyophores remains to be shown. Only indications can be given here. There seems to be some sort of selectivity with respect to the particle size. Undamaged structures are never observed and the largest components seen are diatom and radiolarian fragments (Pl. 17 A). The majority of the material is composed of particles of colloidal sizes. There is no visible difference between the particles in the accumulations and in the stercomes other than the fact that they are often more concentrated in the latter. Bacteria adhering to the particle surface are presumably the most important nutritional material in matter of this character. It has been shown that bacteria occur in large numbers in the uppermost sediment layer in some deep-sea localities (ZOBELL & MORITA 1959, p. 150; KRISS 1961, p. 26ff.). Although much more information about water movements in the deep-sea, the amount of organic matter reaching the ocean floor, etc., is necessary before a reliable estimation of the production of bacterial substance can be made, there is little doubt that these organisms play an important role in the nutrition of many bottom-living animals (MARSHALL 1954, p. 148; BRUUN 1957, p. 651; ZoBELL & MORITA 1959, p. 151; KRISS 1961, p. 433; JØRGENSEN 1966, p. 260ff.). The xenophyophores have almost always been taken in areas known to have a high surface production or areas that are terrestrially influenced, which would also indicate that they rely partly or solely on a bacterial diet.

The advantages of extratestal digestion of adhering nutritive material on accumulated particles instead of merely a few particles at a time may be that the digestive processes are more efficient. In this manner it is possible to treat a greater volume of material than is possible inside granellare; there is probably also better utilization of the enzymes.

A possibly secondary advantage of this nutritional source is that test-building material is available in nearly unlimited quantities.

D. REPRODUCTION AND DEVELOPMENT

Little is known about the xenophyophores' reproduction; knowledge of this important part of their biology can presumably only be obtained if living animals are experimented with or if regular collection of shallow water species can be conducted.

SCHULZE (1907a, pl. VII, 4; no text comments) proposed the following hypothetical life cycle: Isogametes (monoflagellated?) unite (in pairs?) and form an initial plasma ("Plasmatar"), which differentiates into granellare and stercomare during a vegetative growth phase. After a certain time interval, parts of granellare ("Sporular") break up into gametes.

SCHEPOTIEFF (1912b) assumed that there was a complicated life cycle in the xenophyophores which involved alteration of generations, but he did not, unfortunately, go into details about the succession of the stages. He described, however, some parts of the reproductive cycles in *Psammetta, Cerelasma,* and *Stannophyllum* species:

In *Psammetta ovale* (l. c., p. 257), gametes are formed in specialized granellare parts that look like small, swollen side-branches ("Fruchtkörper"). The gametes are bi-flagellated and measure about 20 μ in length. SCHEPOTIEFF also described small amoeba-like structures, and assumed them to be developmental stages that had accidentally stayed behind among the granellare branches. It is unclear whether he meant that these structures had some connection with the gametes. Juvenile *Psammetta* were described as small horseshoe-shaped plasmodia covered by xenophyae. These organisms were found together with mature specimens.

SCHEPOTIEFF (l. c., p. 264) found reproductive granellare parts in only a few cases in *Cerelasma* sp. Here they were in the form of stalked bubbles. Gametes were apparently not observed. Small amoeba-like structures containing one nucleus were found in some granellare parts.

SCHEPOTIEFF (l. c., p. 262) described two types of reproductive granellare parts in *Stannophyllum* sp. Since both were never found in the same specimen he assumed that there was an alteration of generations. The first stages in gamete formation were observed in a specimen that was in poor condition. Among mature specimens (some of which lived about one week in an aquarium) he found some juvenile stages. The earliest stages were clusters of amoeba-like organisms, which were, perhaps, predecessors of small xenophyae-covered plasmodia. SCHEPOTIEFF presumed that these developed into young *Stannophyllum* specimens.

The present investigation on deep-sea specimens did not yield further information, but has confirmed SCHULZE's (1906, p. 10; 1907a, pp. 16, 23, 35, 40) observations that amoeba-like structures can be found inside granellare, and parts of the plasma here seem to disintegrate into them. SCHEPOTIEFF (l. c., p. 265) also described this phenomenon in a shallow water species.

The present knowledge of the xenophyophores' reproduction can be summarized as follows:

1) The xenophyophores reproduce by gametogamy, the single specimen having several gamete-producing periods during its life span.
2) The gametes have two flagella as is typical for rhizopods.
3) Amoeba-like stages are found in one or perhaps two stages of the life cycle.
4) There is a juvenile period with profound changes.

SCHULZE (1907a) indicated that xenophyophores reproduce by gametogamy in *Stannoma dendroides,* and this was proved by SCHEPOTIEFF (1912b) in *Psammetta ovale* and *Stannophyllum* sp. In Table 6 are listed species in which the nuclei presumed to be stages in the gamete formation are found. Although the gametes described in *P. ovale* are of the usual rhizopod type, it should be noted that for example in *Cerelasma* sp., amoeba-like structures are described as being produced from parts of the plasma. Here, we might have to do with amoeboid gametes, indicating either autogamy or gamontogamy, as in foraminiferans (GRELL 1967, pp. 180, 181; 1968, pp. 179, 183). The latter phenomenon is perhaps seen on some deep-sea photographs which show pairs of specimens of an organism interpreted as a *Psammetta* lying between single specimens.

In *Stannophyllum* sp. (SCHEPOTIEFF 1912b), amoeba-like structures found outside granellare seem to be zygotes developing either singly or in clusters into plasmodia and presumably then into initial plasma.

The initial plasma, or its location, could be pointed out in some species of *Psammetta, Syringammina,* and *Stannophyllum.* The initial plasma is especially distinct in *Psammetta,* because the xenophyae in this stage are of another type than in later stages. It could not be distinguished in the remaining seven genera either because of uniform test construction or because the oldest parts had perished.

During growth from initial plasma to mature stages, a series of remarkable features that differ from genus to genus is distinguishable. In *Maudammina* and *Psammina* the young specimens are regularly shaped whereas the older ones are irregular, with thickenings, ridges, and bends. The very sharp limit between the types of xenophyae used in juvenile and mature *Psammetta* stages has already been mentioned. A particular growth process must take place in *Galatheammina* and *Reticulammina* since the hard surface layer has to be moved outward from the growth area. Presumably this occurs at least partly through xenophyae rearrangements as is the case in the large arenaceous rhizopod *Discobotellina biperforata* Collins (STEPHENSON & REES 1965, p. 222). In *Syringammina* the juvenile part of the tube system is irregular, whereas the older parts are regular. A most interesting growth phenomenon in *Stannophyllum* is the zonation found in several species; the environmental circumstances or internal physiological conditions related to this zonation are unknown.

The individual stages and their order in the life cycle are very poorly known. Although I cannot explain SCHEPOTIEFF's (1912b) observation in a *Stannophyllum* species of two types of reproductive granellare parts, I do not regard it as a good foundation for his assumption of a complicated cycle with alternating generations. If alternating generations are found at all in the cycle as they are in foraminiferans, the life cycle may presumably better resemble that proposed by ARNOLD (1966) for *Gromia oviformis.*

E. DISTRIBUTION

Zoogeographical surveys were given by SCHULZE (1907a, b), but the present, extended knowledge of the xenophyophores has profoundly altered the picture.

1. Horizontal distribution

Table 9 and Fig. 14 show that the subclass Xenophyophoria is known from the three main oceans and the Antarctic; but within these regions, large areas exist where representatives of the group have hitherto not been reported. In some of these areas deep-sea investigations have been performed (the Arctic, the eastern Atlantic, the Mediterranean Sea, and the Antarctic), and xenophyophores may have been taken by several expeditions, but during the sorting of the samples they have been put aside as "incertae sedis" on the shelves of zoological museums, as was e. g., the case with the "John Murray", "Vema", and part of the "Galathea" material. In other areas (the South Atlantic, the central part of the Indian Ocean, the western part of the Central Pacific, and the South Pacific) no deep-sea investigations have been performed.

Besides the deep-sea areas mentioned above, it should also be noted that large, important parts of the continental slope with depths less than about 1000 m have never been investigated (e. g., the coasts of South America, of southern Africa, and of Australia).

Of the two orders of xenophyophores, Psamminida is the most widely distributed since it is represented in the three main oceans and in the Antarctic. Stannomida appears to be strictly Indo-Pacific in distribution (fig. 14).

The very poor representation of the xenophyophores in the Atlantic and the Antarctic is remarkable. The scanty and uncertain finds of Psamminida in the two areas can, perhaps, be explained by the reasons mentioned on p. 8. The total absence of records of Stannomida can, however, hardly be explained in the same way since the representatives of this order are large, solid, and often sponge-like. One would expect that they would have been indentified either as HAECKEL's "Deep-sea Keratosa" or as SCHULZE's xenophyophores because the sponge and the foraminiferan faunas are relatively well-

Table 9. Survey of the geographical and bathymetrical distribution of the xenophyophores.

Species	Number of finds in					Temperature range (C. °)	Bathymetrical range (m)	Total no. of records	No. of finds in						
	Atlantic	Indian O.	Pacific												
			West	Cent.	East				0-100 m	600-700	700-1000	1000-2000	2000-4000	4000-6000	6000-7000
Maudammina arenaria	.	1	.	.	.	0.54	5110	1	.	.	.	.	.	1	.
Psammetta globosa	.	4	.	.	.	0.4-*c.* 5	1158-3960	4	.	.	.	2	2	.	.
Psammetta arenocentrum	.	1	.	.	.	0.3	4730	1	.	.	.	.	.	1	.
Psammetta ovale	.	1	.	.	.	ca. 27	1-5	1	1	.	.	.	.	.	.
Psammetta erythrocytomorpha	.	1	.	.	.	3.8	1668	1	.	.	.	1	.	.	.
Galatheammina tetraedra	.	2	.	.	.	0.1-1.6	2700-3430	2	.	.	.	.	2	.	.
Galatheammina calcarea	1	2	1	1	.	0.1-2.6	2013-5353	5	.	.	.	.	3	2	.
Reticulammina novazealandica	.	.	2	.	.	*c.* 5-7	743-984	2	.	.	2	.	.	.	.
Reticulammina labyrinthica	.	.	1	.	.	*c.* 7	743	1	.	.	1	.	.	.	.
Reticulammina lamellata	.	.	1	.	.	*c.* 5	1253	1	.	.	.	1	.	.	.
Reticulammina cretacea	1	.	.	.	.	2.4	3065	1	.	.	.	.	1	.	.
Psammina nummulina	.	.	.	1	2	1.7-1.9	3563-5033	3	.	.	.	.	2	1	.
Psammina globigerina	.	2	1	.	.	2.3-3.7	1158-2081	3	.	.	.	1	2	.	.
Cerelpemma radiolarium	.	.	.	4	.	1.4-1.7	4438-5353	4	.	.	.	.	.	4	.
Syringammina fragilissima	3	.	1	.	.	*c.* 6-8	850-1016 (1830)	4	.	.	2	2	.	.	.
Syringammina minuta	1[1]	.	.	.	.	-0.8--0.5	4795	1	.	.	.	.	.	1	.
Syringammina tasmanensis	.	.	2	.	.	*c.* 7-8.5	664-711	2	.	1	1	.	.	.	.
Cerelasma gyrosphaera	.	.	.	1	1	1.4-2.0	3950-4438	2	.	.	.	.	1	1	.
Cerelasma massa	.	2	.	.	.	0.8	4810-4820	2	.	.	.	.	.	2	.
Cerelasma lamellosa	.	.	1	.	.	1.9	3660	1	.	.	.	.	1	.	.
Cerelasma sp.	.	1	.	.	.	*c.* 25	20	1	1	.	.	.	.	.	.
Stannoma dendroides	.	3	.	2	5	0.34-1.9	3814-4930	10	.	.	.	.	3	7	.
Stannoma coralloides	.	.	.	2	2	1.2-1.7	4243-4758	4	.	.	.	.	.	4	.
Stannophyllum zonarium	.	.	.	2	22	1.2-5.2	981-5307	24	.	.	1	.	11	12	.
Stannophyllum globigerinum	.	6	.	1	5	0.8-4.0	1158-4810	12	.	.	.	1	7	4	.
Stannophyllum granularium	.	1	10	.	.	1.6-1.7	4365-6710	11	.	.	.	.	.	7	4
Stannophyllum fragilis	.	1	.	.	.	0.54	5110	1	.	.	.	.	.	1	.
Stannophyllum radiolarium	.	.	1	1	1	1.4-1.9	3570-5515	3	.	.	.	.	1	2	.
Stannophyllum pertusum	.	.	.	1	.	1.4	4438	1	.	.	.	.	.	1	.
Stannophyllum venosum	.	.	.	1	.	1.4	4438	1	.	.	.	.	.	1	.
Stannophyllum indistinctum	.	2	.	.	.	0.34-0.8	4810-4930	2	.	.	.	.	.	2	.
Stannophyllum alatum	.	1	.	1	1	1.2-10.3	4072-4758	3	.	.	.	.	.	3	.
Stannophyllum concretum	.	.	.	1	.	1.4	5353	1	.	.	.	.	.	1	.
Stannophyllum flustraceum	.	.	.	1	.	1.7	4209	1	.	.	.	.	.	1	.
Stannophyllum reticulatum	.	2	.	.	.	0.3-4.0	3935-5020	2	.	.	.	.	1	1	.
Stannophyllum mollum	.	4	5	.	.	0.3-1.6	4730-6380	9	.	.	.	.	.	8	1
Stannophyllum sp.	.	1	.	.	.	*c.* 25	1-5	1	1	.	.	.	.	.	.

1. *Syringammina minuta* was found in the Antarctic part of the Atlantic Ocean.

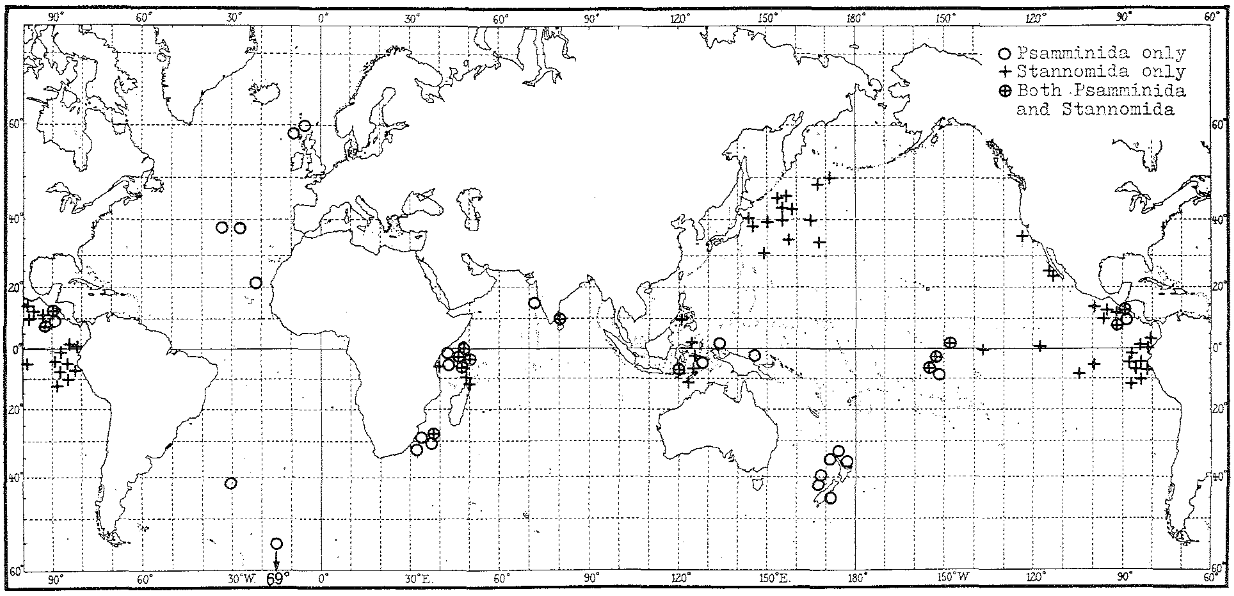


Fig. 14. Distribution of the localities from which xenophyophores have been obtained.

investigated, at least in the North Atlantic and the Antarctic.

Only two species, *Galatheammina calcarea* and *Syringammina fragilissima,* are reliably reported from the Atlantic. I have not seen the Atlantic material of the former, but the species has been taken in several dredgings in other oceans, both by the "Challenger" and the "Galathea" (Fig. 16). I have seen the *Syringammina fragilissima* material of the two North Atlantic records (Fig. 17), one of which comprises the type specimen, while a presumed record of the species off the Azores remains unverified.

Reticulammina cretacea from the central North Atlantic (Fig. 16) and *Syringammina minuta* from the Antarctic (Fig. 17) are known only from the type localities. I have not been able to re-examine the materials, but the former can be referred with certainty to the order Psamminida, and the latter is no doubt placed in the correct genus.

The occurrence of a *Psammina* (*P.plakina*) in the South Atlantic is uncertain in so far as the species cannot be referred to the xenophyophores with certainty, and this record will, therefore, be left out of the zoogeographical discussion.

In the Indo-Pacific Stannomida has only been

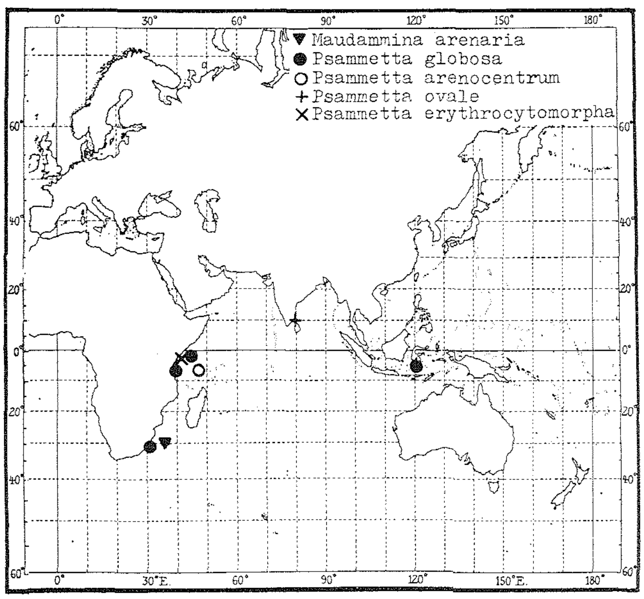


Fig. 15. Distribution of Psammettidae.

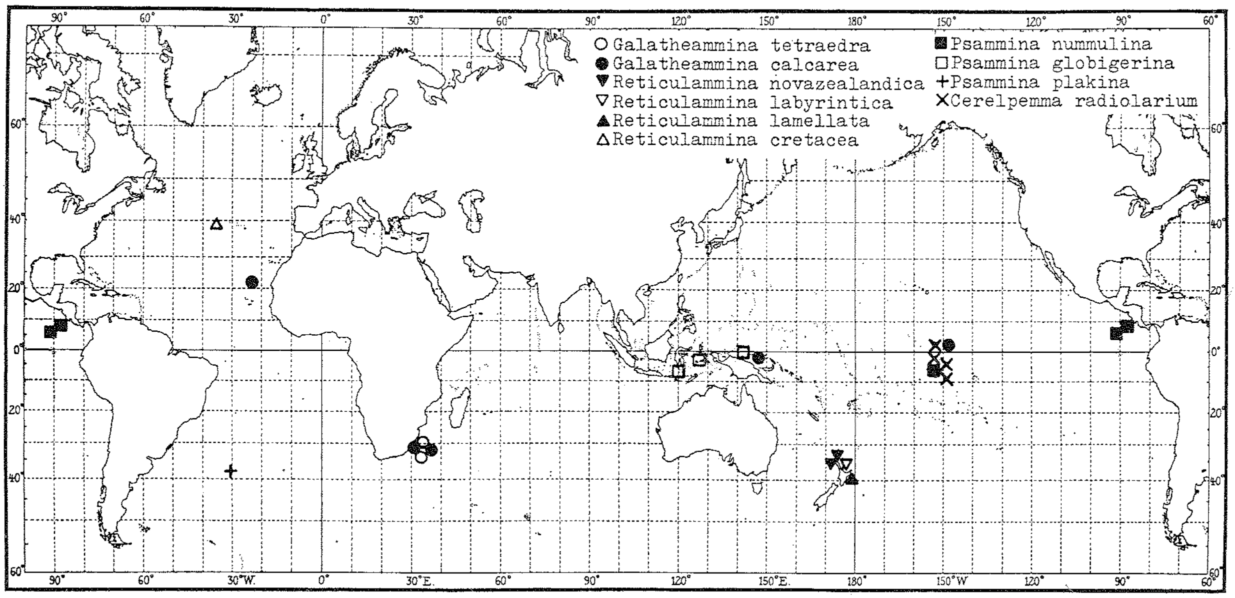


Fig. 16. Distribution of Psamminidae.

found north of 10° S, with the exception of the single record of *Stannophyllum fragilis* at about 30° S off South Africa. The distribution is remarkable in comparison with Psamminida, which in the Pacific has only been recorded south of 10° N (Fig. 14). It should, however, be noted that relatively few deep-sea investigations have been performed south of 10° S, and some expedition materials are, perhaps, not finally sorted out.

In the Peru-Chile Trench in the East Pacific, xenophyophores have not been found (Dr. O. BANDY, personal communication).

The following can be noted about the distribution of the xenophyophore families: Psammettidae seems restricted to the Indian Ocean – Indonesian Archipelago (Fig. 15), Cerelasmidae and Stannomidae seem strictly Indo-Pacific in distribution (Figs. 17-20), whereas Psamminidae is found in the Indo-Pacific as well as in the Atlantic (Fig. 16). Syringamminidae (Fig. 17) is recorded from the Atlantic, the Atlantic part of the Antarctic, and the West Pacific (New Zealand); this discontinuous distribution may be explained by lack of investigations.

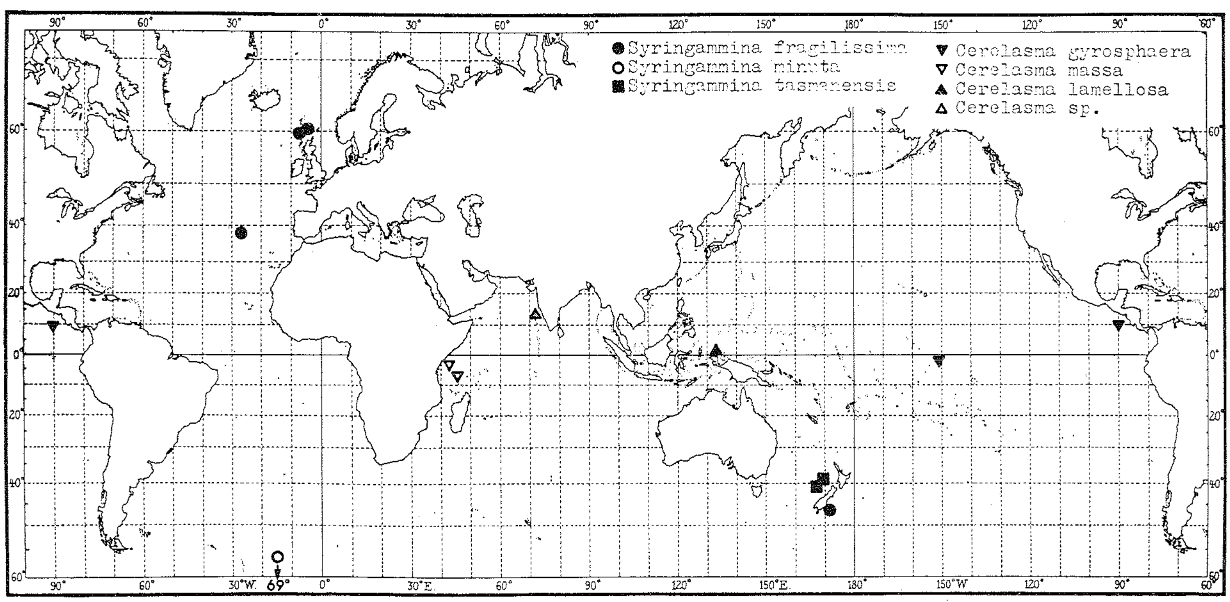


Fig. 17. Distribution of Syringamminidae and Cerelasmidae.

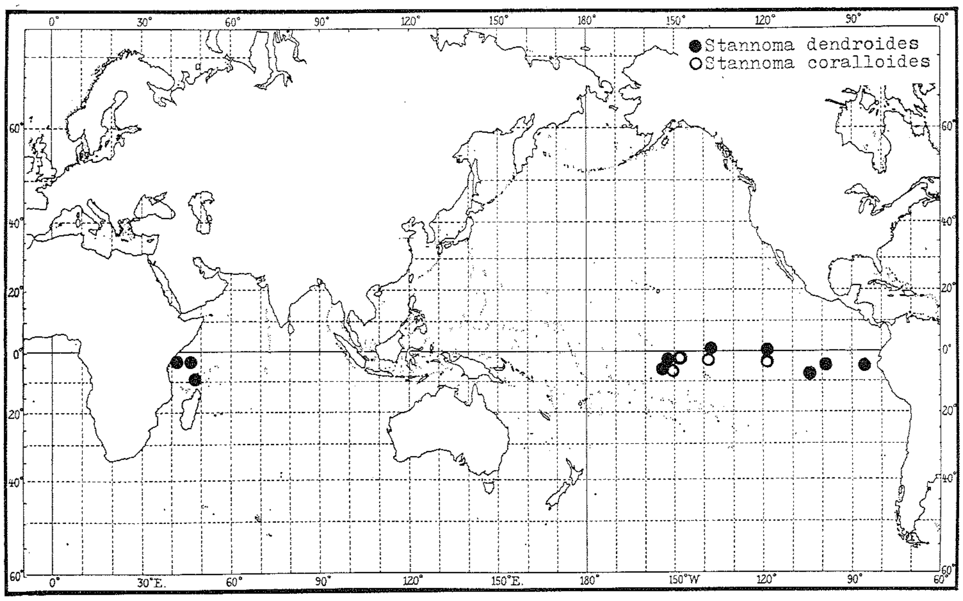


Fig. 18. Distribution of Stannomidae I. *Stannoma.*

Of the ten genera known in the five xenophyophore families, two are monotypic: *Maudammina* (1 find off East Africa) and *Cerelpemma* (4 finds in the Central Pacific). The remaining eight genera contain from two to thirteen species (Table 9) and all the genera are known from at least five finds. Only *Galatheammina* is distributed in all three main oceans, but about half the genera have a distribution in all three main regions of the Indo-Pacific (Table 9).

Only ten of the xenophyophore species have been recorded four times or more; therefore the pattern of species distribution can be only incompletely evaluated. The following five species have a wide distribution: *Galatheammina calcarea* (Fig. 16) 5 finds distributed in all three main oceans; *Stannophyllum globigerinum* (Fig. 19), 12 finds scattered over the three main regions of the Indo-Pacific; *S. alatum* (Fig. 19), 3 finds in the Indonesian Archipelago and in the Central and East Pacific; *Stannoma dendroides* (Fig. 18), 10 finds off East Africa and in the Central and East Pacific; and *Syringammina fragilissima* (Fig. 17), 4 finds in the North Atlantic and the West Pacific.

A zoogeographical barriere in the western Central Pacific (cf. MADSEN 1961b, p. 212; HANSEN 1967, p. 490; KNUDSEN 1970, pp. 193, 196) is, per-

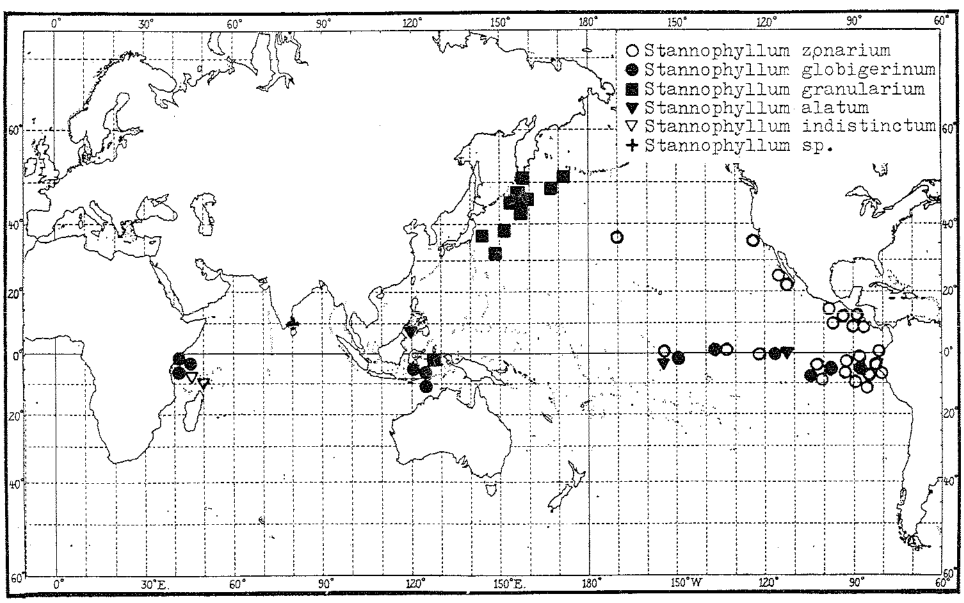
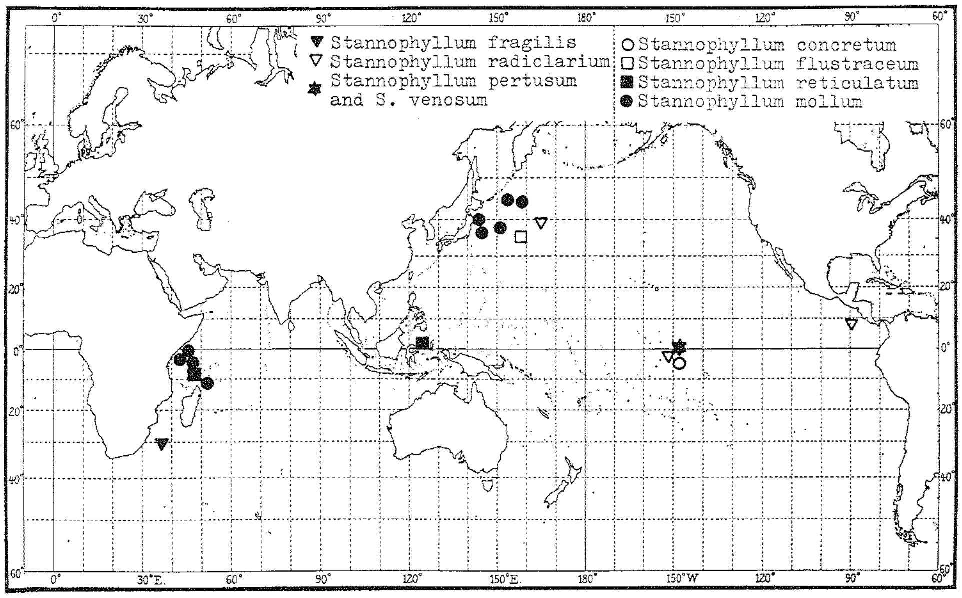


Fig. 19. Distribution of Stannomidae II. Some species of *Stannophyllum.*

Fig. 20. Distribution of Stannomidae III. Some species of Stannomidae.



haps, indicated by a number of species of which all records are from either east or west of the postulated barrier:

Indo-West Pacific:
Psammina globigerina (3 finds, Fig. 16)
Stannophyllum granularium (11 finds, Fig. 19)
Stannophyllum reticulatum (2 finds, Fig. 20)
Stannophyllum mollum (9 finds, Fig. 20)
Central-East Pacific:
Psammina nummulina (3 finds, Fig. 16)
Stannoma coralloides (4 finds, Fig. 18)
Stannophyllum zonarium (24 finds, Fig. 19)

2. Vertical distribution

Both Xenophyophoria orders, Psamminida and Stannomida, are recorded from littoral to very great depths (5353 m and 6710 m respectively) and, judging from deep-sea photographs (Pl. 16 D; LEMCHE *et al.*, in preparation), both also occur at least down to about 7700 m.

The single families of the Xenophyophoria show a wide vertical distribution too:
Psammettidae: 1 (-5)-5110 m (1158-5110 m[1])
Psamminidae: 743-5353 m
Syringamminidae: 664-4795 m
Cerelasmidae: 20-4820 m (3660-4820 m[1])
Stannomidae: 1 (-5)-6710 m (981-6710 m[1])

The four families, Psammettidae, Psamminidae, Syringamminidae, and Cerelasmidae have their present known lower occurrence at about 5000 m, viz. the transition zone between the upper and lower abyssal (MADSEN 1961b, p. 198; VINOGRADOVA 1962, p. 248). The Stannomidae range further down to the lower part of the transition to the hadal zone at about 6800 m (WOLFF 1960, p. 100; 1970, p. 984).

The known representation of xenophyophores in the different depth zones of the sea (the oceanographic terms are used according to the definitions in WOLFF 1962, p. 16; cf. however, MADSEN 1961b, pp. 180, 197ff.) can be summarized as follows:

Eulittoral zone: *Psammetta, Stannophyllum.*
Sublittoral zone: *Cerelasma.*
Bathyal zone: *Psammetta, Reticulammina, Psammina, Syringammina,* and *Stannophyllum.*
Abyssal zone: *Maudammina, Psammetta, Galatheammina, Reticulammina, Psammina, Cerelpemma, Syringammina, Cerelasma, Stannoma,* and *Stannophyllum.*
Hadal zone: *Stannophyllum.*

Eulittoral and sublittoral zones:

The three finds are from the west coast of India and the north coast of Ceylon. It is on this basis alone, of course, impossible to say anything in general about the occurrence of xenophyophores in shallow water, but the records suggest that the group is represented in the Indonesian Archipelago too. This region has the richest species diversity in the world, and precisely this fact could be the reason that the xenophyophores have been overlooked here.

1. Depth range, if SCHEPOTIEFF (1912b) is excluded.

Table 10. The relation of the numbers of finds and species of xenophyophores to the percentage area of different depth zones in the abyssal.

Depth interval (m)	Atlantic + Indian + Pacific Oceans	Indian Ocean	Pacific Ocean	Number of records of xenophyophores	Number of species of xenophyophores
2000-3000	6.2[1]	7.4	5.0	10	5
3000-4000	20.4	24.4	19.1	27	11
4000-5000	36.6	38.9	37.7	47	18
5000-6000	26.2	19.9	28.8	21	11
6000-7000	1.2	0.4	1.8	5	2

1. Percentage figures from SVERDRUP, JOHNSON & FLEMING 1942, p. 21.

Bathyal zone:
Syringammina tasmanensis, 664-860 m, 6-8.5°C., 2 finds.
Reticulammina labyrinthica, 743 m, *c.* 7°C., 1 find.
Reticulammina novazealandica, 743-984 m, *c.* 7°C., 2 finds.
Syringammina fragilissima, 850-1016 m, 6-*c.*8°C., 3 finds.
Reticulammina lamellata, 1253 m, *c.* 5°C., 1 find.
Psammetta erythrocytomorpha, 1668 m, 3.8°C., 1 find.
Stannophyllum zonarium, 981 m, 5.2°C., 1 find.
Stannophyllum globigerinum, 1158 m, *c.* 4°C., 1 find.
Psammina globigerina, 1158 m, *c.* 4°C., 1 find.
Psammetta globosa, 1158-1204 m, *c.* 4-*c.* 5°C., 2 finds.

Of these ten species the first six are truly bathyal, although *P. erythrocytomorpha* is, perhaps, better classified as abyssal because of temperature conditions. The remaining four species have all been taken under definite abyssal conditions too. The only genus of a possible purely bathyal occurrence is *Reticulammina,* since the abyssally recorded *R. cretacea* (p. 31) is of dubious taxonomic position.

The fifteen finds from bathyal depths are geographically very widely spread: North Atlantic, off East Africa, the Indonesian Archipelago, New Zealand, and off Peru. A geographically wide-spread bathyal occurrence still holds, even if we omit those records which because of temperature conditions (4°C. or below) are better classified as abyssal.

Abyssal zone:

By far the main part of the records of xenophyophores are from the abyssal zone. The number of records and species in the region varies slightly depending on the definition of the abyssal:

	Records:	Species:
2000-6000 m $\leqq$ 4°C.	104	28
2000-7000 m $\leqq$ 4°C.	109	28
1000-6000 m $\leqq$ 4°C.	108	29
1000-7000 m $\leqq$ 4°C.	113	29

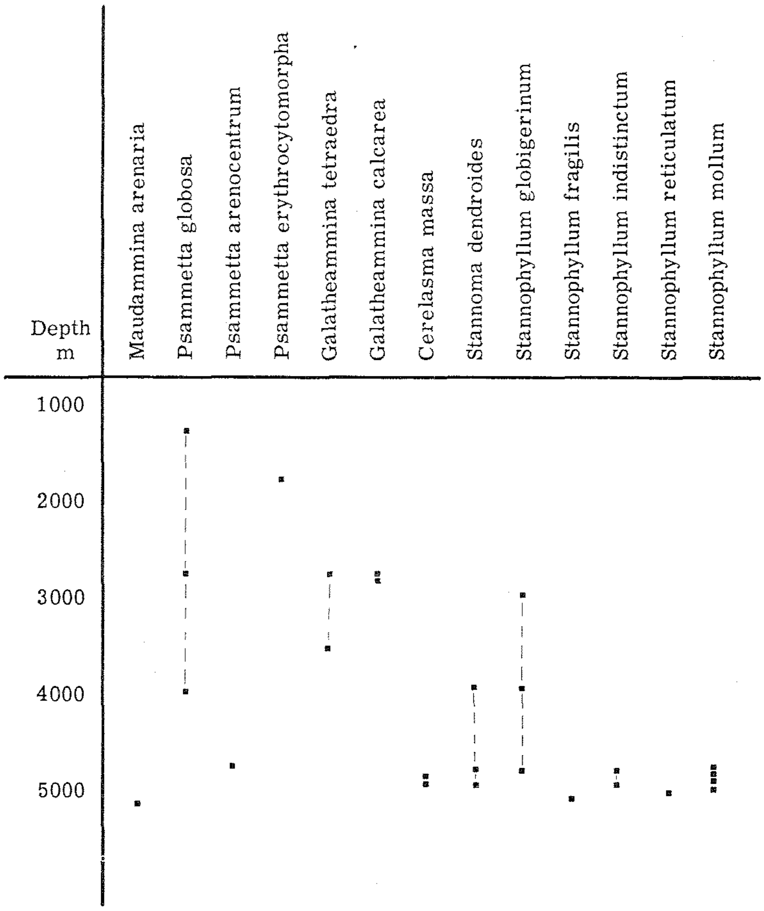
It should be noted that one record of *Stannophyllum alatum* ("Challenger" St. 211) is from the Sulu Sea at 4072 m depth, but at a temperature of 10.3°C., showing that the species, although it has hitherto only been recorded from 4072-4758 m (3 finds), is able to cross the surrounding thresholds which have a maximum depth of less than 1000 m. Cf., however, the list of stations (p. 13).

All ten xenophyophore genera are represented in abyssal depths (Table 9) except for, perhaps, *Reticulammina* (cf. above). Four are exclusively abyssal: *Maudammina* (1 sp.), *Galatheammina* (2 spp.), *Cerelpemma* (1 sp.), and *Stannoma* (2 spp.).

The number of finds and of different species within different depth intervals in the abyssal zone (Table 9) are in close agreement with the percentage area of each depth interval (Table 10). Most dredgings have been done in limited geographical areas (Fig. 14) and most xenophyophore species are known in only few finds; it is, therefore, difficult to decide whether this relation of record/species number to percentage area is a mere reflection of the dredging activity, or whether the large number of species in the 4000-5000 m interval indicates a transition zone between an upper and a lower abyssal xenophyophore fauna.

The species that are found only at depths greater than about 4500 m are *Maudammina arenaria* (1 find), *Psammetta arenocentrum* (1 find), *Cerelpemma radiolarium* (4 finds), *Syringammina minuta* (1 find, cf., however, p. 37), *Cerelasma massa* (2 finds), *Stannophyllum granularium* (11 finds), *S. fragilis*

Fig. 21. The vertical distribution of the xenophyophores taken off East Africa.



(1 find), *S. indistinctum* (2 finds), *S. mollum* (9 finds), and the rather dubious species: *S. pertusum, S. venosum,* and *S. concretum* (all known from 1 find only). Furthermore, a number of species are known from about 4000 m and downwards: *Cerelasma gyrosphaera* (2 finds), *Stannoma dendroides* (10 finds), *S. coralloides,* (4 finds), *Stannophyllum alatum* (3 finds), *S. flustraceum* (1 find), and *S. reticulatum* (2 finds).

Since some of the areas where dredging has been done have prevailing depths greater than about 4000 m (for example the central and western Pacific), the list of species taken does not say much about possible existence of a special lower abyssal xenophyophore fauna. The existence is, however, indicated from the distribution of the xenophyophore species off East Africa. Here dredging has been done at different depths, and many records of xenophyophores are available (Fig. 21). The temperature range is small, and the sediments are classified as Globigerina ooze at all stations (except a few where the sediment type is not stated). Moreover, the number of stations is almost equal in the upper and lower abyssal zones. Nevertheless, eight species are solely known from depths greater than about 4500 m. Most of these species have been taken only off East Africa and are known from only one or two finds; but one species is known from many records, also in other regions: *Stannophyllum mollum,* 4 records off East Africa (4730-5020 m) and 5 records off Japan (5017-6380 m).

Hadal zone:

There are four finds of *Stannophyllum granularium* and one of *S. mollum* from depths greater than 6000 m but not exceeding 6800 m and thus within the transition region between the abyssal and hadal zones (Wolff 1960, 1970).

Indications of xenophyophores living in true hadal depths are, however, found on films from the northern flank of the New Britain Trench (about 5°50′S, 152°32′E) at 7665-7710 m depth. A large number of organisms resembling *Psammetta* and a few resembling *Cerelasma* and *Stannophyllum* are seen on some of the pictures (Lemche *et al.,* in preparation).

3. Some factors possibly deciding the distribution

a. Temperature

Being members of a distinct cold water fauna, the deep-sea animals are restricted in their upper distribution by a certain temperature, or rather by a certain temperature variation (MARSHALL 1954; BRUUN 1957; MADSEN 1961b; MENZIES 1965).

Many of the xenophyophores show a temperature dependence like that known in other deep-sea animal groups, for instance the sea star family Porcellanasteridae (MADSEN 1961b). Some species that have been taken in many dredgings thus show a wide horizontal and a wide vertical distribution (mainly upper abyssal), but they are only recorded within a narrow temperature range. Examples from Table 9 are: *Galatheammina calcarea, Stannophyllum zonarium,* and *S. globigerinum*. Other frequently recorded species with a wide horizontal distribution and a more restricted vertical distribution (mainly lower abyssal) are found in an even more narrow temperature range, viz. *Stannophyllum granularium* and *S. mollum*. The highest temperature at which a deep-sea xenophyophore species is reported is 10.3° C., viz. a sample of *Stannophyllum alatum* (cf., however, list of stations p. 13), and the lowest temperature is -0.8°--0.5°C (reported for *Syringammina minuta*).

b. Pressure

Although hydrostatic pressure is generally attributed less importance than temperature and is difficult to distinguish from temperature in its effects, it is attributed a role as a significant ecological factor in the deep-sea by most authors (MARSHALL 1954; BRUUN 1957; WOLFF 1960, 1962, 1970; MADSEN 1961b; MENZIES & WILSON 1961; MENZIES 1965; KNIGHT-JONES & MORGAN 1966; HANSEN 1967; MORITA 1967). Only very little is known regarding the pressure influence on the metabolism of deep-sea organisms, since investigations in animals on this point generally have been performed on species from shallow water (BRUUN 1957; MENZIES & WILSON 1961; MENZIES 1965; MORITA 1967), and only in a few cases on meso- and bathypelagic species (GILLEN 1971; TEAL & CAREY 1967).

Bacteria, which are the only organisms where investigations of the role of pressure have been carried out on samples from both the deep-sea and shallow water, proved to be very heat and pressure sensitive (ZOBELL & OPPENHEIMER 1950; ZOBELL & MORITA 1959; MORITA 1967). It is interesting that a damaging effect of high hydrostatic pressure was found in the synthesis of protein, RNA, and DNA in bacteria (ALBRIGHT & MORITA 1968).

Some of the results obtained in shallow water animals may, because they concern fundamental processes, be of a general importance for the xenophyophores as well as for all other animals in the deep-sea. In *Arbacia* and *Paracentrotus* eggs (Echinodermata), the first cleavage was inhibited under exposure to 450 atmospheres (MARSLAND 1938, pp. 60, 66; cf. also ZIMMERMAN & MARSLAND 1964). When the pressure was released the eggs passed directly to the four-cell stage, the divisions afterwards continuing at normal rate. Apparently, nuclear divisions had taken place without cell division while the eggs were exposed to high pressure. In amoebae (and in *Arbacia* eggs) it has been shown that high hydrostatic pressure (up to about 700 atmospheres) decreases the viscosity of the cytoplasm (BROWN & MARSLAND 1936, p. 162; LANDAU *et al.* 1954, p. 224), and pseudopodial movement ceases (MARSLAND & BROWN 1936, p. 168; LANDAU *et al.* 1954, p. 215; MARSLAND 1964, p. 177). *Arbacia* eggs continued to synthesize DNA during exposure to pressure (about 340 atmospheres), although in some phases the process was greatly delayed (ZIMMERMAN 1963, pp. 43, 48).

These results show that living under high hydrostatic pressures requires a pronounced adaptation. Important aspects of life, such as metabolic processes and reproduction, are strongly influenced, and a logical conclusion is, therefore, that a species with a large vertical distribution in the sea, consists of individuals, or populations, each adapted to only a given pressure range (a restricted vertical range).

An estimation of this range can only be reliably founded on investigations of deep-sea animals. The studies referred to concern, however, fundamental biological features essentially identical in all animals, and the results may, therefore, be of general application. Although Table 11 ought to be considered with greatest reservation, the physiological reactions agree fairly well in having a maximum pressure range tolerance from 1 to 200-300 atmospheres, corresponding to a depth range of about 2000-3000 m. It seems impossible at present to estimate the extent of this conclusion; it is, for example, not known whether an animal once adapted to a high pressure has a larger or a more narrow pressure tolerance when compared with a shallow water animal.

Table 11. The reaction of different biological processes to increased pressure.

Species	Process investigated	Temp. (C.°)	Pressure (atm.)	Results	Process reversible	Authors and references
Amoeba proteus	pseudopodia and movement	25	136-204	pseudopodia more slender than usual, movement definitely reduced	+	LANDAU *et al.* 1954, pp. 214, 215, 218.
		25	204-272	pseudopodia drastically reduced both as to length and diameter, movement stopped	+	
		25	272-408	no pseudopodia, no movement	+	
		10	c. 204	no pseudopodia, no movement	?	
Arbacia punctulata eggs	mitotic apparatus	20	c. 136	chromosomal movement retarded	+	ZIMMERMAN ? MARSLAND 1964, p. 297.
		20	c. 272	chromosomal movement stopped	+	
	DNA synthesis	20	c. 340	strong delay of some phases of the process	+	ZIMMERMAN 1963, p. 48.
	cleavage	20	340-408 (30 min.)	cleavage delayed	+	ZIMMERMAN 1963, p. 45.
		20	340-408 (60 min.)	no cleavage occurs or there are numerous abnormalities	–	
Chaetopterus pergamentaceus (Annelida) eggs	cleavage	20-25	220-270	cleavage blocked	?	MARSLAND 1956, p. 187. PEASE & MARSLAND 1939, p. 408.
Cumingia tellenoides (Mollusca) eggs	cleavage	20-25	270-330	cleavage blocked	?	
Solen siliqua (Mollusca) eggs	cleavage	20-25	230	cleavage blocked	?	
Ciona intestinalis (Tunicata) eggs	cleavage	20-25	200	cleavage blocked	?	

In the evaluation of the range, the role of the temperature was ignored. It is, however, important to note that a close relationship exists between the effects of temperature and pressure. ZOBELL & OPPENHEIMER (1950, p. 777) found in bacteria that a lethal or inhibitory effect of pressure is more pronounced at 10°C. than at 25°C. MARSLAND (1950, p. 220) investigating *Arbacia* eggs, and LANDAU *et al.* (1954, p. 218) who investigated *Amoeba proteus* found concurrently that temperature and pressure have opposite effects on the sol-gel equilibrium in the plasma. A temperature decrease of 5°C. is approximately equivalent in effect to an increase in pressure of about 68 atmospheres. (In Table 11 this effect is illustrated in *Amoeba proteus*.) Thus, there is still one more problem and source of error in the estimation of the pressure tolerance range: the animals used in the experiments were all warm water species, and it is not known if animals living in cold water would react likewise. Investigations on Arctic and Antarctic animals (some of which penetrate into the deep-sea) could presumably throw more light on the problem of pressure adaptation. The few investigations on meso- and bathypelagic animals indicate perhaps that in these species there is less interaction between pressure and temperature than in species from shallow water (GILLEN 1971; TEAL & CAREY 1967).

Table 12. The species and number of specimens of xenophyophores and various other groups of benthic animals dredged on some deep-sea localities by the "Galathea".

Animal group	St. 235[1]		St. 238[1]		St. 716[2]	
Xenophyophoria (species and number of specimens)	*Cerelasma massa* 4 *Stannoma dendroides* 2 *Stannophyllum globigerinum* 14 *Stannophyllum indistinctum* 3 *Stannophyllum mollum* 14		*Psammetta globosa* 14 *Stannoma dendroides* 1 *Stannophyllum globigerinum* 9		*Psammina nummulina c.* 500 fragments *Stannophyllum zonarium c.* 100 *Stannophyllum radiolarium* 1 fragment	
	No. of species	No. of specimens	No. of species	No. of specimens	No. of species	No. of specimens
Porifera	.	.	2	3	3	*c.* 41
Coelenterata	5?	numerous	6	54	15	*c.* 137
Annelida	1	1	.	.	*c.* 20	*c.* 310
Mollusca	7	10	8	32	14	168
Crustacea	12	97	12	59	*c.* 32	*c.* 170
Echinodermata	7	*c.* 350	10	*c.* 620	30	1171
Tunicata	1	3	4	31	6	45
Pisces	8	20	4	9	9	66

1. Data of Sts. 235 and 238 are taken from the expedition journal, and the numbers given are too low, especially regarding the species numbers.
2. Data of St. 716 are from WOLFF (1961, and personal communication).

c. Food

The xenophyophores seem to require a relatively large food supply. This is indicated by the distribution of the group (Fig. 14) since most records are from areas having a high surface production or being terrestrially influenced (it must, however, not be overlooked that deep-sea investigations are relatively scanty in relation to the large area under consideration, and many dredgings have been purposely done where rich life on the bottom could be expected). Moreover, a very rich and varied animal life is usually recorded in stations where xenophyophores are found (Table 12).

F. PHYLOGENETIC CONSIDERATIONS

The organization of the xenophyophore body as a free-living, pseudopodia forming, multinucleate plasmodium enclosed by an organic and an agglutinated test, and reproducing by biflagellate gametes and syngamy places the xenophyophores within the class Rhizopodea (classification of HONIGBERG *et al.* 1964).

Hitherto the xenophyophores have been placed either between the Foraminiferida and the Mycetozoia (as an order of Granuloreticulosia) (SCHULZE 1912; HONIGBERG *et al.* 1964), or close to the Mycetozoia (and Labyrinthulia) and separated from the other rhizopods (SCHEPOTIEFF 1912b; BOVEE & JAHN 1965b).[1]

Because they posses a set of characters that are unique and a set of characters with special development, the xenophyophores are placed in a subclass of their own, Xenophyophoria, within the class Rhizopodea in the present work. The characters concerned are enumerated on p. 20, and they are discussed in detail in the general part.

Within the Rhizopodea five subclasses are recognized: Lobosia (most of the naked amoebae and the testate amoebae), Filosia (some naked amoebae and the gromiids), Granuloreticulosia (some naked amoebae and the foraminifers), Mycetozoia (the Acrasida, the "true slime molds", and the Plasmodiophorida), and Labyrinthulia.

A comparison of these subclasses and the Xenophyophoria is attempted in Fig. 22. The unequal importance of the characters and the problem of primitiveness versus derivation are not considered

1. The classifications of SCHEPOTIEFF and BOVEE & JAHN are possibly not quite comparable. Without giving it rank in the classification, SCHEPOTIEFF introduced the term "Myxozoa" to embrace the present day Xenophyophoria, Mycetozoia, Labyrinthulia, and some Proteomyxida. It seems that he was of the opinion that the group had an independent origin from flagellates.

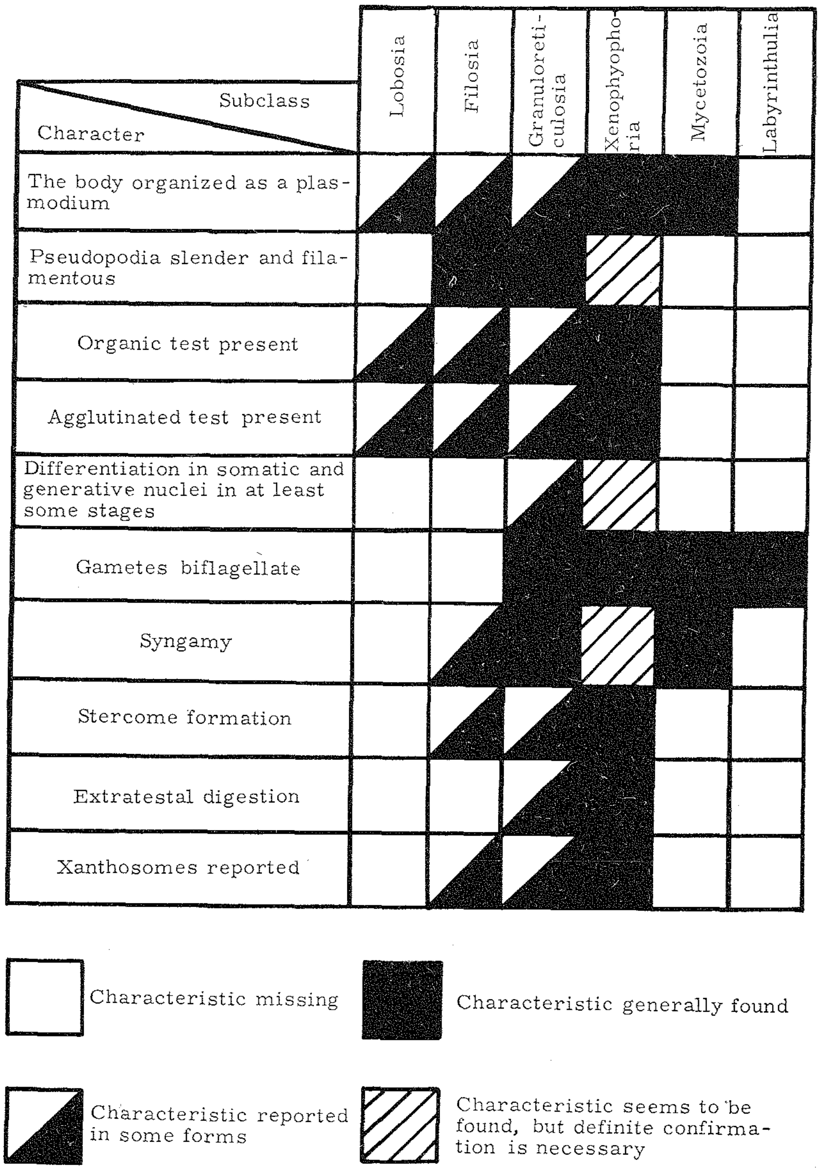


Fig. 22. The distribution of some selected characters of the subclasses of Rhizopodea.

in the diagram, but should appear from the following discussion.

The organization of the body as a multinucleate plasmodium of large size is well known in the Mycetozoia, especially in the order Eumycetozoida, and is common for this group and the xenophyophores. Plasmodial organization is also well-known from a number of amoebae, in some gromiids, and in at least some stages of some foraminifer forms. In these cases very large sizes are not attained with the exception of a number of organisms, commonly placed in the Foraminiferida, that are so large that they can be expected to be plasmodia in spite of the nearly total lack of information about their cytology. Examples of these organisms are species of *Ophiotuba, Radicula, Rhizammina, Dendrophrya, Normanina, Schizammina, Julienella, Saccodendron,* and *Sagenia* (figures and references are found in LOEBLICH & TAPPAN 1964). The mycetozoan plasmodium is organized as a network of tubes of cytoplasm gel containing a sol plasma and connected at the fringe by a continuous protoplasm. The xenophyophore plasmodium is distinctly branched, and each branch is surrounded by an organic tube, which is a secretion, not a part of the plasma. There is no indication of the presence of a sol–gel mechanism taking part in the plasma movements, but it should be noted that experiments and observations have never been performed on living animals.

Thus, although the plasmodial organization is similar in the xenophyophores and the slime molds, this similarity seems to be of only superficial nature. A stronger similarity can presumably be expected to exist with the foraminiferan organisms referred to above, but further observations are also necessary here. The present known organization is found without variations throughout the whole group of xenophyophores, and it seems to represent the original condition within this group.

The scanty knowledge of the xenophyophore pseudopodia indicates a relationship with Granuloreticulosia and Filosia, both in appearence and in mechanism of movement. It has not been possible to definitely decide whether the pseudopodia are filose or reticulose, or if they are granular. Within the Sarcodina, features of the pseudopodial system are generally regarded as very important for the demonstration of the phylogenetic relationships because these features, or some of them, are presumed to represent primitive conditions of the group concerned.

Tests are found within Lobosia, Filosia, Granuloreticulosia, and Xenophyophoria. A common feature of test structure in the four groups is the presence of an organic test that relatively tightly covers the cytoplasm and is presumably secreted from its surface. Agglutinated tests are also found in the four groups, but the present conditions differ greatly in the xenophyophores and the three other groups, although the original condition may well have been the same. At least in primitive forms of Lobosia, Filosia and Granuloreticulosia, agglutinated tests are made by foreign bodies being fixed to the organic test by pseudopodia. In the xenophyophores, the agglutinated test must also be built through action of the pseudopodia, but it is widely separated in space from the organic test and is quite independent of it with respect to morphological form.

The probable heterocaryous condition is discussed on p. 70. This point of similarity between some highly developed foraminifers and the xenophyophores is presumably analagous.

The xenophyophore gametes are of the primitive biflagellated type (pp. 70 , 79) commonly seen in Granuloreticulosia, especially in the primitive forms. Flagellated gametes are not known in Lobosia. Monoflagellated gametes are reported from Filosia (in *Gromia,* HEDLEY & WAKEFIELD 1969), but are usually explained as being a degeneration since there are two basal bodies. In Mycetozoia the gametes are biflagellated, but one flagellum is strongly reduced (ELLIOTT 1948; BONNER 1967). Biflagellate swarmers are described in Labyrinthulia, but there has been no demonstration of sexuality (HOLLANDE & ENJUMET 1955; BONNER 1967).

Stercomes are reported from some bottom dwelling species within Filosia and Granuloreticulosia and in all the known species of xenophyophores. There seems to be a connection between deposit feeding and the accumulation of fecal material in masses. In the gromiids, stercomes are formed in the cytoplasm and are retained inside the test. In the foraminifers concerned, stercomes are also formed within the cytoplasm, but they are expelled immediately or from time to time. In the xenophyophores, stercomes are formed outside the plasma (outside granellare) and are permanently retained between the branches of granellare as the conspicuous stercomare. The phenomenon is a special xenophyophore characteristic, presumably developed in connection with the mode of extratestal digestion. The evolution within the group has led to the use of stercome masses as a part of the agglutinated test; in *Cerelasma* and *Stannophyllum* this has independently led to a condition where stercomes are the only test material.

Xanthosomes are reported from some Filosia, some Granuloreticulosia, and from nearly all the xenophyophore species. Although their presence is not constantly connected with the formation of stercomes, they always seem to be found in animals living as deposit feeding bottom-dwellers. In gromiids the xanthosomes are formed and retained in the cytoplasm. They are left behind inside the organic test at the time of swarming. In Granuloreticulosia the xanthosomes are formed within the plasma, and they are expelled from time to time. In the xenophyophores, xanthosomes are possibly formed outside the organic test at the same time and place as the stercomes. They are retained in stercomare among the stercomes.

My conclusion is that, in light of the present knowledge, the xenophyophores resemble the Granuloreticulosia most. It has been possible to compare only a few characters, but at least the plasmodia organization, the pseudopodial system, the gametes, and the syngamy are features generally attributed importance in protozoan phylogeny. The value of the test construction and the nuclear differentiation in this respect is difficult to outline, but at least they show the specialization of the xenophyophores. The stercomes and the xanthosomes should be considered in connection with the feeding method, and they are presumably of no phylogenetical importance in relation to other groups.

In view of the present knowledge of the xenophyophoran biology, these considerations and conclusions must be considered as tentative. I am, however, convinced of the value of every well-intentioned attempt to clarify phylogenetic relationships within the large, varied assemblage of organisms united under the term "Protozoa". My conclusions and considerations are included here in agreement with "Dougherty's principle" (CORLISS 1963, p. 53): "better to have a working hypothesis, even if based on fragile evidence, than to shrug aside a question of phylogeny as prematurely posed".

V. SUMMARY

The work deals with a marine protozoan group, the Xenophyophoria, which for the last sixty years has only rarely been mentioned in the literature.

A historical account of the expeditions during which xenophyophores have been dredged, and of the authors describing these collections is given. The shifting view in the literature on the true nature of these organisms is presented chronologically.

The work is based on the material obtained by 14 expeditions. The rich and well-preserved collection from the Galathea Expedition has been especially important since it contains a total of 15 species (7 new) belonging to 6 genera (2 new).

At present, xenophyophores have been recorded from 78 localities yielding 128 species samples. Material from 54 localities comprising 84 species samples has been at my disposal, 60 species samples from 39 localities being recorded here for the first time.

The terminology is largely identical with that of other Protozoa, especially the Foraminifera. Definitions are given of the few special terms.

The systematic position of the xenophyophores has varied a good deal in the literature, some species being described as sponges, others as foraminifers. In 1907 SCHULZE separated the group as a taxonomic unity and created the name Xenophyophora.

Within the Protozoa, the xenophyophores have generally been regarded as constituting an order of the class Rhizopodea. In the present work the group is raised to subclass level as Xenophyophoria, and the position is given within two modern rhizopod classifications, that of HONIGBERG *et al.* (1964), and that of BOVEE & JAHN (1965).

According to a new classification, the Xenophyophoria comprises two orders, Psamminida n. ord. and Stannomida n. ord. Psamminida contains four families: Psammettidae n. fam.; Psamminidae Haeckel; Syringamminidae n. fam.; and Cerelasmidae, n. fam. Stannomida contains one family, Stannomidae Haeckel. The family definitions are based on characters not previously used: the xenophyae arrangement and the relative amount of cement in the test.

Eleven genera were previously ascribed to the xenophyophores. Six of these are retained (*Psammetta, Psammina, Cerelpemma, Cerelasma, Stannoma,* and *Stannophyllum*). *Stannarium* was found to be a synonym of *Stannophyllum,* and four genera (*Ammoclathrina, Ammolynthus, Ammosolenia,* and *Cerelpsamma*) are omitted as they were found not to contain xenophyophores. *Syringammina* has been transferred from the foraminifers, and three new genera are described (*Maudammina, Galatheammina,* and *Reticulammina*).

Of the 28 species previously referred to the xenophyophores, 21 are retained, 1 was found to be synonymous with another, and 6 are not xenophyophores. Three species are transferred from the foraminifers, and 12 new species are described.

Keys are prepared for orders, families, genera, and species. In all doubtful cases, alternative characters are given, if possible.

In external appearence the xenophyophores vary greatly. At the species level a large number of body forms are specific, and this is the case also with a series of genera.

The largest xenophyophore known measured about 25 cm in diameter, but was leaf-shaped and only about 1 mm thick. The largest available specimen is also leaf-shaped, measures about 19 cm in diameter, and is 1-2 mm thick. Most species are, however, lumpy and measure from 1.5 to 7 cm in diameter. It is found that the distance from the central parts of the plasma to the nearest part of the body surface never exceeds 2-4 mm. If the body is lumpy, the central part is either dead, or the body is organized as a lattice-work of anastomosing branches, probably because the transport way for oxygen, nourishment, etc. cannot exceed a certain distance.

The colour depends on the type and amount of xenophyae (foreign bodies) in relation to amounts of stercomare (fecal masses) and cement. It is generally a shade of brown, yellow or white. The surface texture depends on the xenophya type and arrangement. The zonation found in some species is regarded as a growth phenomenon, but is otherwise unexplained. The consistency, which also depends on the type and amount of xenophyae in relation to the amount of stercomare and cement, varies greatly from species to species. All transitions from sandstone-like to something resembling a wet rag have been found within the group.

Granellare, the plasma body with its organic test, appears as rather irregularly running, dichotomously branched strings, generally 30-90 μ wide. The volume of granellare is very small compared with the volume of the whole body. Accordingly, by far the largest part of a xenophyophore is dead, composed of the stercomare and the xenophyae.

The homogenous, hyaline plasma contains numerous nuclei and an enormous number of granellae (crystals). Nuclei are evenly distributed in the plasma and in a series of species it is possible to distinguish 3 types: 1) The most common is spherical or slightly ellipsoidal, provided with nucleolus, and easily stained; the diameter is 2-8 μ, the largest being found only in Stannomida. 2) Not very common, ellipsoidal, bubble-like, lacks nucleolus, and is only faintly stained; the diameter is 4-9 μ, the largest being found only in Stannomida. 3) Not common, but when found, several are always present; the diameter is 0.5-1 μ. Type 2 nuclei seem to originate from type 1 nuclei. Type 3 nuclei are interpreted as gamete stages, and are thought to originate from nuclei of type 2. It is proposed that the xenophyophores, or some of them, are heterocaryous, type 1 nuclei being somatic, and type 2 nuclei being generative.

Granellae are crystals of $BaSO_4$ which are found in enormous numbers evenly distributed in the plasma. They are hyaline or faintly greenish, 2-5 μ in length, and of rounded or slightly angular form. Granellae seem to be formed in the plasma and are also found in the stercomes. The function is unknown, but it is proposed that toxic Ba from water soluble compounds is neutralized as the unsoluble $BaSO_4$.

The xenophyophore pseudopodia have never been described. On the basis of structures in the preserved animals, supported by deep-sea photographs assumed to show xenophyophores with outstretched pseudopodia, they can for the present be characterized as slender, filamentous, hyaline, and possibly not anastomosing.

Stercomare, the fecal pellets held together in masses, are seen as dark, irregularly running, dichotomously branched, sometimes anastomosing strings, 35-540 μ wide. Compared to granellare, stercomare is always strongly developed. They contain stercomes and xanthosomes.

The former are dark-brown, ellipsoidal, and 10-20 μ long. They are composed of small unidentifiable particles held together by a transparent, gel-like substance, which apparently contains acid mucopolysaccharide. This retention of fecal pellets in voluminous masses is a characteristic of the xenophyophores. The xanthosomes are rounded, reddish-brown or yellowish bodies, 1-7 μ in diameter. They are found scattered between the stercomes, although this is not the case in all species and in all samples of the same species. They are presumed to be an excretory waste product.

Linellae are extracellular threads, generally 1-6 μ thick and several mm long. They form part of the test in the Stannomida and are thus a characteristic of this order. They seem to contain mucopolysaccharides. Electron microscopy shows that the structure of the cross-section consists of layers of alternately high and low electron density.

Xenophyae are foreign bodies used in the construction of the agglutinated test. The common types are mineral particles, sponge spicules, and foraminiferan and radiolarian tests. Most species are rather strongly selective and some species even use one type in young stages and another in older stages.

The digestion seems to be extratestal. Sediment particles are accumulated in masses on the surface of the body, and in the masses all transitions from undifferentiated material to fully formed stercomes are found. The advantages of extratestal digestion of adhering nutritive material on accumulated particles instead of merely a few particles at a time may be that the digestive processes are more efficient. In this manner it is possible to treat a greater volume of material than inside granellare; there is probably also better utilization of the enzymes.

The present knowledge of the reproduction of the xenophyophores is very scanty. It is known that at least the shallow water species reproduce by gametogamy and have biflagellate gametes. Amoeba-like stages are found in the life cycle, but their role is not definitely decided. The deep-sea species possibly have amoeboid gametes and perhaps gamontogamy. In some species there is a juvenile period with profound morphological changes.

Xenophyophores are known from the three main oceans and the Antarctic. However, from the Atlantic there are only few reliable records, and from the Antarctic only one. The Psamminida has the widest distribution (the three main oceans and the Antarctic), whereas the Stannomida seems restricted to the Indian and the Pacific Oceans. Only one genus is known to be common to the three main oceans, but more than half of the genera are common to the Indian Ocean and the western and eastern Pacific. Since only ten species have been recorded four times or more, the pattern of species distribution can be only sketchily outlined. One species is known from all the three main oceans. Large discontinuities in the distribution of a series of species are presumed to be due to absence of investigations in certain areas. As is also the case for other deep-sea animals, there are indications of the existence of a zoogeographical barrier in the western Pacific.

Both orders are known from the littoral zone down to very large depths (Psamminida to 5350 m, Stannomida to 6710 m). The records from the littoral-sublittoral zone are very few. From the bathyal zone rather numerous and very widely distributed records are known: North Atlantic, off East Africa, Indonesia, New Zealand, and off Peru. By far the largest number of records are from the abyssal zone, and there are indications of the existence of a lower abyssal fauna. Xenophyophores have hitherto not been dredged from depths exceeding 6800-7000 m (the true hadal zone), but photographs from 7700 m indicate that both orders occur in these depths.

The xenophyophores show a temperature dependence resembling that known in other deep-sea animals. Several species with a very wide horizontal distribution are only known within a narrow temperature range. Excluding the shallow water forms, the highest recorded temperature is 10.3° C. (the Sulu Sea) and the lowest is –0.8-–0.5° C. (the Antarctic), both records being from depths exceeding 4000 m.

The role of the hydrostatic pressure for the distribution of deep-sea animals is shortly discussed on the basis of literature. It is generally agreed that it is a significant factor, but on the one hand its effect is difficult to evaluate in itself, and on the other hand it is difficult to distinguish from the effect of temperature. Investigations on amoebae and eggs from different invertebrates suggest that the pressure range tolerance for the single individual (with respect to locomotion, DNA synthesis, cleavage, etc.) is from 1 to 200-300 atmospheres, corresponding to a depth interval of 2000-3000 m. The temperature has a pronounced effect, since it can be shown (in *Amoeba proteus*) that a decrease of 5° C. corresponds to an increase in pressure of 70 atmospheres. Investigations on cold water animals would presumably throw more light on the problems of pressure adaptation.

The accessible food supply seems to be of importance for the distribution, as xenophyophores have nearly always been taken in areas known to have a high surface production or an influence from land, but many investigations have purposely been done in areas where a rich animal life could be expected.

A comparison of the subclasses within the Rhizopodea showed more similarities between the foraminifer-like groups and the xenophyophores than between these and the slime molds.

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