Xenophyophores (Protozoa, Sarcodina) in the diet of *Neopilina galatheae* (Mollusca, Monoplacophora)

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ABSTRACT

Xenophyophore fragments occur in the intestinal contents of *Neopilina galatheae,* and marks resembling radula traces are seen on the surface of the xenophyophore *Stannophyllum zonarium* from the same locality. These finds are taken as indications that *N. galatheae* utilizes, perhaps even specializes on, xenophyophores as food. It is rendered probable that the widely held belief that monoplacophores are detritus feeders moving around on the ooze is too much of a generalization.

INTRODUCTION

Many specimens in the material of the xenophyophore *Stannophyllum zonarium* Haeckel, 1889, taken by the Galathea Expedition in the East Pacific, show damage resembling scrape marks (Tendal 1972). The marks can have been made by a species with a rather large radula, and an examination of the list of species from the locality (Wolff 1961, and the expedition journal) points to *Neopilina galatheae* Lemche, 1957, as a possibility.

Inspection of two sectioned specimens of *N. galatheae* and the intestinal contents of a third specimen revealed xenophyophore fragments that with reasonable certainty could be identified as originating from *Stannophyllum zonarium* (Tendal 1979).

RESULTS

The marks

The damage interpreted as possible scrape marks is of varying form, from more or less rounded to triangular and oblong (Pl. 13A). The basic shape is that of a "thick half-moon", up to 3 mm long and 1.5 mm wide. While the 1-2 mm thick, leaf-shaped body of *Stannophyllum* is pierced in a few cases, most marks are rather superficial depressions with a cleaned bottom layer of linellae (thin threads consisting of proteinaceous matter (Tendal 1972, Hedley & Rudall 1974) and constituting most of the organic part of the test in some xenophyophores).

Presumed scrape marks are seen in at least one third of the about 50 more or less intact specimens of *Stannophyllum.* Generally the marks are found only on one side of the body, but in a few cases on both. The number of marks per specimen varies from a few to many. Apart from a faint tendency to follow the zones where the body is thickest, there is no obvious pattern to be seen in the distribution of the marks.

The intestinal contents

The intestinal contents of *Neopilina galatheae* include "a high proportion of radiolarians, scattered centric diatoms, etc., mixed up with much undefined detritus matter" (Lemche & Wingstrand 1959, p. 63, fig. 168 on pl. 56). This description is correct, and can be extended with the fact that the "etc." comprises components that can be identified as parts of a xenophyophore. Such fragments are found in all three available specimens from "Galathea" St. 716 (9°21'N, 89°12'W, 3570 m; one damaged and two sectioned specimens) (Pl. 13B).

Most common, and apparently unaffected by the passage through the intestine, are pieces of stercomare, which are masses of waste materials ("fecal pellets") bound in a mucoid membrane (Pl. 13C). More rare are parts of granellare, which is the plasma that contains crystals of barite and is surrounded by a thin organic tube (Pl. 13D). The appearance of granellare changes with its position in the intestine; in the first coil it is recognizable also by the plasma, whereas in the parts found more posteriorly the plasma has presumably been digested and only the organic tubes with the contained barite crystals remain (Pl. 13E). Linellae are found here and there as small pieces; they are difficult to find and to identify as linellae because they are thin, and also because they are poorly stained in the sections.

A fourth kind of intestinal component probably originating from xenophyophores comprises fragments or intact specimens of radiolarian shells like those present in the agglutinated xenophyophore test; however, it is not possible to distinguish these from shells that might originate directly from the sediment.

Also the intestine of a fourth specimen of *N. galatheae* (taken at the *Vermillion* Sea Expedition St. 16, 22°32.5'N, 109°40.8'W, 2780-2810 m; sectioned specimen) contained pieces of a xenophyophore. Stercomare fragments are rather common, granellare pieces are rare, and linellae are not seen at all. Solid components in the contents are mineral grains with some sponge spicules and radiolarian tests.

DISCUSSION

The identification of the xenophyophores

The presence of recognizable fragments of stercomare and granellare with intact membranous covering shows the xenophyophore origin of these components of the intestinal contents. The presence of plasma in some of the pieces of granellare is a strong indication that the fragments were taken directly from a xenophyophore and not collected by *Neopilina* from the sediment, viz. as scattered dead remains of a xenophyophore. The presence of linellae refers the species in question to the family Stannomidae.

Eight species of xenophyophores have been recorded in the Pacific east of 120°W (Tendal 1972). Seven of these use radiolarian shells as the foreign parts of their agglutinated test, and six belong to the family Stannomidae. *Stannophyllum zonarium* Haeckel, 1889 has been taken many more times and in much larger numbers than any of the other species. Moreover, although two other xenophyophore species also were recorded, *S. zonarium* is the absolutely dominating species of xenophyophore in the catch from "Galathea" St. 716. Accordingly, it seems safe to refer the xenophyophore fragments found to this species[1].

In the specimen of *N. galatheae* taken further to the north, it is not possible to identify the xenophyophore with certainty. Because of the general appearance of the fragments, the seeming lack of linellae, and the domination of mineral grains among the solid components of the intestinal contents, it does not seem to be *S. zonarium,* although this species is reported from the area. It is more like *Psammina nummulina* Haeckel, 1889, a widespread but rarely recorded species.

The food of *Neopilina galatheae*

Whether based on investigations of sections (Lemche & Wingstrand 1959, 1960; McLean 1979) or fecal pellets (Menzies et al. 1959), or judging from the appearance of the intestine (Filatova et al. 1968; Rokop 1972; Filatova et al. 1974), there is agreement among authors that recent monoplacophores are detritus feeders.

In the three examined specimens of *N. galatheae* from "Galathea" St. 716 the xenophyophore *Stannophyllum zonarium* comprises a very large share of

1. Of the other two species, *Psammina nummulina* has no linellae, and *Stannophyllum radiolarium* was represented by only a single fragment and seems on the whole to be a rare species.

the diet, and at least one specimen of *N. galatheae* contains so many remains of this species that *S. zonarium* seems to have been the only food at the time the intestine was filled. The fact that the specimen of *N. galatheae* taken at another locality contains remains of what seems to be a different xenophyophore species might indicate that *N. galatheae* is specialized on xenophyophores for food.

The radula of recent monoplacophores is large in proportion to body size and relatively weak (McLean 1979). Among other features it is characterized by a broad, somewhat membranous, comb-like first marginal tooth supposed to have a brushing function (Wingstrand 1985).

In many xenophyophores, and especially within the Stannomidae where the linellae bind the test together, the xenophyae are loosely attached. Working on the surface of *Stannophyllum zonarium*, the fringed teeth of the neopilinid radula will probably sweep together xenophyae, other accumulated matter, and the superficial parts of stercomare and granellare. The radula is probably not able to cut the numerous tough linellae found in this species, but will rather clean them and leave them exposed as is seen in most of the scrape marks.

The position of *Neopilina galatheae* on the bottom

There has been some debate about the position of *N. galatheae* and related species on the substratum (Lemche 1957; Younge 1957, 1960; Lemche & Wingstrand 1959; Menzies et al. 1959; Wolff 1961). Although no monoplacophore appears to have been recognized on *in situ* photographs (see Wolff 1961 for a discussion of the photograph presented by Menzies et al. 1959), there is now substantial evidence for a limpet-like lifestyle[1]. Thus, monoplacophores from two different areas (Filatova et al. 1968; Lowenstam 1978; McLean 1979) have been secured attached to rocks, and other samples are reported to have contained both monoplacophore specimens and hard substratum, although the animals were not attached (Rokop 1972; Filatova et al. 1974). Nevertheless, several species of monoplacophores are reported to come from soft bottoms without hard material, as was also the case for *Neopilina galatheae* (see Lemche & Wingstrand 1959, Wolff 1961).

This species may obtain a temporary hard bottom on *Stannophyllum zonarium*. Strangely enough, the very common (in the East Pacific) *S. zonarium* has never been identified on bottom photographs, but there is evidence that it lives on the sediment surface (Tendal 1972), as seems to be the case for other species of *Stannophyllum* (Lemche et al. 1976; numerous photographs from different sources). Utilization of *S. zonarium* as a hard substratum would at least temporarily bring *N. galatheae* into a position where fouling of the gills with particles brought in by the ventilating current from the sediment-water interface was reduced. This would also explain the weakness of the foot, as it is used only for slowly moving around, and not for firm adherence by sucking.

In a broader context, it is striking that there is a certain accordance between the scattered information about the life style of some species of monoplacophores and the recent subdivision at the family level of the class Monoplacophora (Moskalev et al. 1983). Available data suggest that the families Vemidae and Neopilinidae comprise soft-substrate species, whereas the species taken attached to rocks are placed in Laevipilinidae and Monoplacophoridae.

1. The specimen of *Neopilina (Vema) ewingi* shown in upside down position in a habitat illustration by Menzies et al. (fig. 8-8, p. 240, 1973) appears to have been drawn so in order to show the characteristic ventral side of the animal.

CONCLUSION

Monoplacophores are usually considered to be deposit-feeders that "presumably feed as they move slowly over the ooze" (Marshall 1979). The find that *Neopilina galatheae* may be more or less specialized on xenophyophores for food calls for a renewed investigation of the intestinal contents of more species of monoplacophores[2]. A detailed comparison of the mouth region structures, the radulae, the kinds of food taken, and the substrate choice in different species may in the end allow for a more differentiated view of both the ecology and taxonomy of the group.

2. I have investigated sections from two specimens of *Neopilina (Vema) ewingi* taken in the Milne-Edwards Trench without finding xenophyophore remains in the intestines.

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PLATE 13

A. Part of *Stannophyllum zonarium* with numerous scrape marks. Bar represents 1 cm. Arrows point to some of the scrape marks.

B. Cross section of first intestinal coil of *Neopilina galatheae.* Spec. III. Bar represents 100 μm. s, stercomare fragment. g, granellare fragment.

C. Section of stercomare fragment from first intestinal coil. Numerous xenophyophore fecal pellets (stercomata) surrounded by membrane (clearly seen to the right). Bar represents 100 μm.

D. Section of granellare from first intestinal coil. Xenophyophore plasma containing numerous barite crystals (granellae) and surrounded by membrane. Bar represents 20 μm.

E. Section of granellare from fourth intestinal coil. Granellae in nearly empty granellare membrane. Bar represents 50 μm.