FORAMINIFERANS AS FOOD FOR CEPHALASPIDEANS (GASTROPODA: OPISTHOBRANCHIA), WITH NOTES ON SECONDARY TESTS AROUND CALCAREOUS FORAMINIFERANS

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ABSTRACT

The food of four species of Cephalaspidea (*Philine aperta*, *Philine denticulata*, *Philine scabra* and *Cylichna cylindracea*) was studied in animals collected on silty clay bottoms at 20-35 m depth on the west coast of Sweden. The specimens were dissected. Only calcareous foraminiferans were found in the gizzard. Very small amounts of foreign particles were ingested. The foraminiferans were crushed in the gizzard and dissolved during their passage through the intestine and no remains of them could be identified in the fecal pellets. The three dominant foraminiferans in the habitat were one calcareous species, *Ammonia batavus* and two agglutinating species, *Ammoscalaria pseudospiralis* and *Ammotium cassis*. The test (shell) material of the latter two species was sand grains (quartz). It was inferred that the gastropods avoid agglutinating foraminiferans as food. Many calcareous but not agglutinating foraminiferans surround themselves with a "secondary test", a cyst or covering of foreign particles around the test. This structure has earlier been called a "reproductive cyst" or "feeding cyst" in some species. "Secondary tests" are primarily connected with feeding, but might also be a preadaptation for other purposes. It might, in species like *Ammonia batavus*, have become a kind of antipredatory device or mimicry. A predator might conceive such a species as an agglutinating species and neglect it. The secondary test is a delicate structure in most species and is easily destroyed by the rough sampling and handling methods conventionally used. This structure is therefore not very well known.

INTRODUCTION

Foraminiferans are numerous in most marine habitats and are probably more important in the food webs than they have been traditionally considered to be. Many species have a high metabolic rate, a short generation time, and can give a quick response to an input of organic food matter (Lipps 1983; Cedhagen 1988; Gooday *et al.* 1992). Foraminiferans are important bacterial and detritus feeders, and some species are also able to take up dissolved organic matter (DeLaca *et al.* 1980, 1981). They are an important source of food for many other organisms (*e.g.*, Fauchald & Jumars 1979; Lipps 1983, 1988; Arnold *et al.* 1985; Cedhagen 1992; Gooday *et al.* 1992; Svavarsson *et al.* 1993). This makes them an important link between the bacterial degradation process and the food chains (Cedhagen 1992; Gooday *et al.* 1992).

Several cephalaspideans are selective predators on foraminiferans (*e.g.,* Hurst 1965; Horikoshi 1967; Rudman 1972a,b; Rasmussen 1973; Thompson 1976, 1988; Shonman & Nybakken 1978; Berry 1988; Berry & Thomson 1990; Chester 1993).

The fact that the foraminiferans are so diverse, and that many organisms prey upon them, suggests that they might have developed strategies to avoid or reduce predation on them. I have found that some cephalaspideans are selective predators on calcareous foraminiferans, and that these foraminiferans usually surround their tests with a covering, cyst or cocoon of foreign particles here called secondary test. I intended to study the specificity of these predators, and if the secondary test of some calcareous foraminiferans implies a protection against predation.

Very little has been reported on the "secondary tests" and other mud structures in foraminiferans, but it is a common phenomenon in many species (own obs.). The reason why this phenomenon is largely unknown, seems to be that the structures in question usually are destroyed by the rough methods of sampling and sieving commonly used.

The secondary test does not hamper the feeding activity of those foraminiferans that are capable of extrathalamous or extracellular digestion, *i.e.*, in those species whose pseudopodia gather and digest food particles outside the test or cell membrane (see *e.g.*, Jepps 1942, 1956). The gathering behaviour of foreign particles may then be a preadaptation to other functions.

Secondary tests or "cysts" made of foreign particles by and around foraminiferans have been described and interpreted to have various functions. Jepps (1942, 1956) described a "feeding cyst" around *Elphidium crispum*. Indigestible food remains and mucus were deposited as a cyst on the test. Rhumbler (1911) and Myers (1935) described "reproductive cysts" of foreign particles surrounding individuals of *Patellina corrugata* involved in sexual reproduction, and Myers (1936) described a similar structure in *Spirillina vivipara*. I interpret it as a protective cover that reduces the risk of dilution of the gamete concentration in turbulent water. Myers (1943) described a protective "growth cyst" surrounding individuals of *Tretomphalus bulloides* during the formation of their "float chamber". Bacterial gardening on a sediment substrate has been described in several species (Langer & Gehring 1993; Linke & Lutze 1993; Cedhagen 1996; but see also Bernhard & Bowser 1992). Agglutinated tubes also serves as a support for structures like the pseudopodia extended into the water by suspension feeding species (Alexander & DeLaca 1987). Cedhagen (1994) described a structure made of excreted food residues around the test margin of *Hyrrokkin sarcophaga*, which lives parasitically on bivalves. This structure makes the junction between the parasite's test and the bivalve's shell smoother, and was considered to reduce the risk of being removed by the cleaning activity of the bivalve's foot. Richter (1965) interpreted the secondary test of littoral foraminiferans as an adaptation to avoid dispersal during strong wave action. A further function of a secondary test in *Elphidium williamsoni* living in wave-swept environments is to avoid denudation by the grinding action of sand-grains (Cedhagen unpubl.). Altenbach *et al.* (1993) described that *Miliolinella subrotunda* constructs a large detritus tube for a temporary hyperbenthic lifestyle. This was also observed in living specimens of *Biloculinella depressa* (d'Orbigny, 1826) kept in aquarium in Bergen, Norway, by Cand. real. Stefan Mattson (pers. comm.). Linke & Lutze (1993) observed secondary tests in *Elphidium* spp. and *Sphaeroidina bulloides* d'Orbigny, 1826. They discussed various advantages of this structure. Bowser *et al.* (1995) raised the question of weather the agglutinated wall of some foraminiferans should be considered a type of "feeding" or "detritic" cyst, rather than a "true" agglutinated test.

Secondary tests or detritus accumulations have been described in other free-living foraminiferans, *e.g.*, *Triloculina circularis* by Rhumbler (1936); *Elphidium oregonense* by Anderson (1963); *Elphidium incertum* by Wefer (1976); *Turritellella shoneana* by Arnold (1979), *Nonionella iridea* by Gooday (1986); and on the test of foraminiferans living attached, *e.g.*, *Cibicides lobatulus* (by

Brady 1884, Cooper 1965, Dons 1942, Nyholm 1961; Arnold 1979); *Valvulina fusca* and *V. conica* (by Brady 1884, Rhumbler 1938); *Haplophragmium globigeriniforme*, *Textularia aspera*, and *Verneuilina propinqua* by Brady (1884); *Haplophragmium globigeriniforme* and *Miliolina circularis* by Rhumbler (1911); *Rupertina stabilis* by Lutze & Altenbach (1988); and *Cibicidoides wuellerstorfi* and *Planulina ariminensis* by Lutze & Thiel (1989).

MATERIALS AND METHODS

The study was made on the west coast of Sweden, mainly at the Tjärnö Marine Biological Laboratory (Göteborg and Stockholm Universities), with additional studies at the Kristineberg Marine Research Station (Royal Swedish Academy of Sciences and Göteborg University) (Fig. 1).

The following cephalaspideans were investigated; *Philine scabra* (Müller, 1776), *P. aperta* Linnaeus, 1767, *Cylichna cylindracea* (Pennant, 1777) (Fig. 2), and a few *P. denticulata* (Adams, 1800). Most of the samples were collected on silty clay bottoms at about 20-35 m depth, mainly with an epibenthic sledge, intermediate in design between that of Ockelmann (1964) and that of Hessler & Sanders (1967). They were sifted carefully with the sieves submerged in sea water. Some samples were studied alive and others were fixed in 4 % formalin solution buffered with disodium tetraborate (borax). The fixed samples were studied under a stereo microscope. A non-violent sampling and handling technique for living as well as fixed samples was used, because the conventional methods destroy many of the external delicate structures of the foraminiferans.

The shells of the gastropods to be dissected were cracked. The gizzard was easily identified because of its black plates (Fig. 3). It was removed, opened and the foraminiferans were picked out. The intestine was removed, and opened lengthwise with a pair of scissors (designed for eye surgery). Its content was studied under a stereo microscope and an interference contrast microscope (Olympus BH-2).

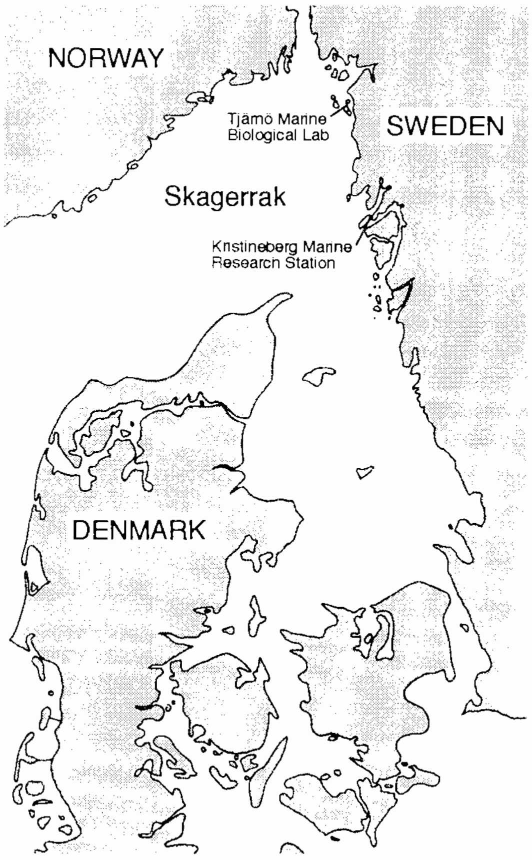

Figure 1. Map of the Skagerrak. The animals studied were collected on the west coast of Sweden, but mainly off the marine biological laboratories indicated.

Nearly 200 cephalaspideans from about 50 samples from several areas in the Skagerrak were dissected between 1981 and 1992.

The food of cephalaspideans was also studied in samples from Kosterhamnen, Kosterfjorden, west coast of Sweden, at 20-35 m depth. Altogether 173 cephalaspideans were immediately fixed after sampling (Oct. 5, 1989) and dissected.

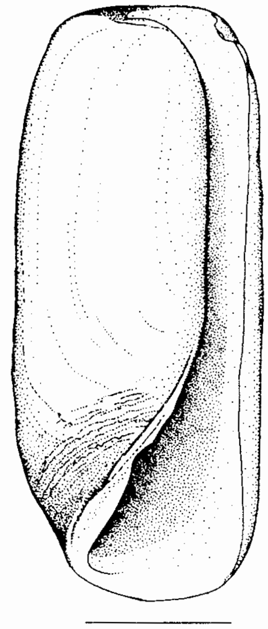

Figure 2. *Cylichna cylindracea*, collected off Hållö (58°23,3'N; 11°09,3'E) on the west coast of Sweden, 47-49 m depth. Scale bar = 1 mm.

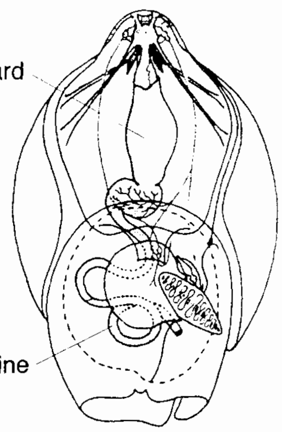

Figure 3. *Philine aperta*. Position and form of gizzard and intestine (Redrawn from Thompson 1976).

Twentyfive *C. cylindracea* and 32 *P. aperta* specimens were collected in the same locality in September 7, 1988. They were kept in clean water in glass jars in a thermostated room. Fecal pellets were collected, squashed

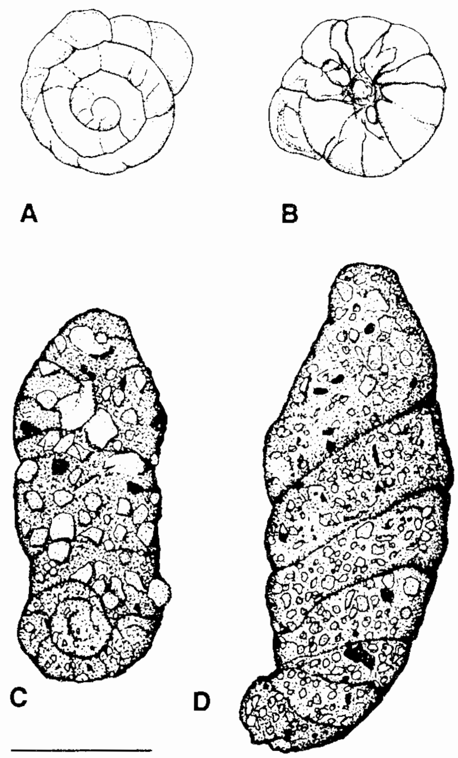

Figure 4. The dominant species of foraminifera in the habitat where the gastropods in Table 1 were collected. A-B. *Ammonia batavus*. C. *Ammoscalaria pseudospiralis*. D. *Ammotium cassis*. Scale bar = 500 μm.

on a microscopic slide, and studied under a microscope to identify residues of prey organisms.

Fourteen *C. cylindracea* and 16 *P. aperta* specimens from the same sample were kept in clean water in an aquarium for over six hours before fixation and dissection, in order to see how soon the food left the intestine.

Predation experiments were made. Cephalaspideans were offered as prey specimens of each of the dominant foraminiferans from their habitat (*Ammoscalaria pseudospiralis*, *Ammotium cassis*, and *Ammonia batavus* with and without secondary test removed).

Secondary tests of foraminiferans were studied in the above mentioned samples, and often observed in other samples from the west coast of Sweden.

Living foraminiferans kept with some sediment were also observed under a stereo microscope in order to study the construction of their secondary tests.

RESULTS

Food and feeding of the cephalaspideans

Only calcareous foraminiferans were found as prey in the nearly 200 cephalaspideans collected at various locations on the west coast of Sweden between 1981 and 1992. The species are listed in Table 1. The dominant prey was *Ammonia batavus*. No agglutinating species were found in any of the gastropods, despite the fact that such foraminiferans were very common in the same areas.

The foraminiferans dissected out from the gastropods collected intensively in a single locality in Kosterfjorden (Oct. 5, 1988) show the same pattern and are listed in Table 2. The dominant foraminiferan species living in this habitat were the calcareous species *Ammonia batavus*, and the arenaceous species *Ammotium cassis* (Parker, 1870) and *Ammoscalaria pseudospiralis* (Williamson, 1858) (Fig. 4).

About 20 % of the foraminiferans in the gizzard were surrounded by small remains of a "secondary test" consisting of foreign particles. Many of the foraminiferans in the gizzard were whole, but in several of them the outer chambers were cracked along the test margin (Fig. 5). As many as five foramini-

Table 1. Calcareous foraminiferans from cephalaspideans at various locations off the west coast of Sweden.

Ammonia batavus (Hofker, 1951)
Bulimina marginata d'Orbigny, 1826
Elphidium spp.
Globobulimina auriculata gullmarensis Höglund, 1947
Globobulimina turgida (Bailey, 1851)
Hyalinea baltica (Schroeter, 1783)
Melonis pompilioides (Fichtel & Moll, 1798)
Nonionellina labradorica (Dawson, 1860)
Quinqueloculina seminulum (Linnaeus, 1758)

Table 2. Frequency of occurrence of food types from the gizzard and upper part of intestine of cephalaspideans collected on the west coast of Sweden, Kosterfjorden, Kosterhamnen, 35-25 m depth, October 5, 1989.

	Cephalaspidean predators		
	Cylichna cylindracea	*Philine aperta*	*Philine scabra*
Food items			
Calcareous foraminiferans			
Ammonia batavus	9	72	16
Globobulimina turgida	2	-	-
Quinqueloculina seminulum	-	3	-
Elphidium sp.	-	1	-
Fragments	2	64	22
Bivalvia			
Mysella bidentata	-	1	-
Mytilus edulis, byssus 3 mm long	-	-	1
Harpacticoida	-	-	1
Ostracoda	-	-	1
"Detritus"	-	16	-
No. of empty predatory specimens	24	7	3
No. of predatory specimens examined	37	107	29

feran specimens were often found lined up in a row in the intestine of *P. aperta*. This shows that the foraminiferans really are a dominant food type, and are not overrepresented only because of their resistance to digestion. The matter found in the end part of the intestine of the cephalaspideans was impossible to identify, except for a few fragments of foraminiferans incompletely broken down.

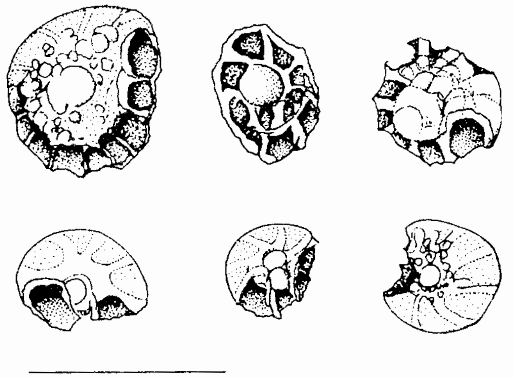

Figure 5. *Ammonia batavus* specimens from the intestine of *Philine aperta* listed in table 1. Several outer chambers have been cracked by the action of the gizzard plates of *Philine*. Scale bar = 500 μm.

Philine scabra seemed to be a less selective predator than *P. aperta* and *C. cylindracea* of the same size. It contained a larger fraction of detritus, mineral grains, and other seemingly indigestible objects than the other two species, and these particles were also larger. The foraminiferans eaten by this species were not cleaned of secondary tests as carefully as in the other two species. The diameter of the intestine in *P. scabra* is larger than in the other species.

The fecal pellets of the cephalaspideans (Sept. 7, 1988) contained nothing identifiable except fine-grained "detritus".

In contrast to the foraminiferans that were fixed immediately, the specimens fixed six hours after sampling in Kosterfjorden contained no food items when dissected, except small amounts of detritus in the end of the intestine. No large, hard structures like mineral grains or sponge spicules were found. This indicates a rapid turnover of the food.

The predation experiment failed. The gastropods starved and died after some days. This reaction might have been a consequence of the fact that the jars used for the experiment lacked sediment.

Observations on the secondary tests of some foraminiferan species
Calcareous foraminiferans often surround themselves with a covering of foreign particles, like mineral grains, detritus, sponge spicules, calcareous fragments, *etc.* Such structures are here called secondary tests. If removed, the secondary test of *Ammonia batavus* was usually remade, normally within 15 minutes to 1 hour. The diameter of the secondary test is up to three times as large as that of the primary test. No agglutinating foraminiferans in this study were surrounded by such structures.

Calcareous and hyalinous foraminiferans in the Skagerrak, other than those mentioned, were often found to build secondary tests of various shapes (Fig. 6 and Table 3). *Nemogullmia* sp. mentioned in Table 3 is an undescribed, violet-coloured species of more than 10 mm in length from 90-110 m depth in Gullmarsfjorden. Agglutinating suspension or deposit feeding foraminiferans were found to normally gather large amounts of foreign particles, planktonic algae, etc. around their apertures (Tab. 4). *Gromia oviformis* Dujardin, 1835 (syn. *Allogromia marina* Nyholm & Gertz, 1973 (S. S. Bowser & A. J. Gooday, pers. comm.)) exhibit a similar behaviour. It gathers detritus around the apertural end and fills its transparent, organic test with detritus.

Table 3. Foraminiferans from the Skagerrak often found to build secondary tests of various shapes.

Calcareous species:
- *Bulimina marginata* d'Orbigny, 1826
- *Cassidulina laevigata* d'Orbigny, 1826
- *Cibicides lobatulus* (Walker & Jacob, 1798)
- *Cibicides refulgens* Montfort, 1808
- *Cornuspira foliacea* Philippi, 1844
- *Elphidium excavatum* (Terquem, 1875)
- *Elphidium williamsoni* Haynes, 1973
- *Globobulimina auriculata gullmarensis* Höglund, 1947
- *Globobulimina turgida* (Bailey, 1851)
- *Hyalinea baltica* (Schroeter, 1783)
- *Nonionellina labradorica* (Dawson, 1860)
- *Paromalina coronata* (Parker & Jones, 1857)
- *Pyrgo williamsoni* (Silvestri & Zangheri, 1942)
- *Rosalina globularis* d'Orbigny, 1826
- *Spirillinoides circumcinctus* Rhumbler, 1938
- *Uvigerina peregrina* Cushman, 1923

Hyalinous species:
- *Hippocrepinella alba* Heron-Allen & Earland, 1932
- *Gloiogullmia eurystoma* Nyholm, 1974
- *Nemogullmia longevariabilis* Nyholm, 1953,
- *Nemogullmia* sp.
- *Phainogullmia aurata* Nyholm, 1955

Table 4. Suspension or deposit feeding agglutinating foraminiferans from the Skagerrak often found to gather large amounts of detritus around their apertures.

- *Ammoscalaria pseudospiralis* (Williamson, 1858)
- *Astrorhiza limicola* Sandahl, 1857
- *Bathysiphon* spp.
- *Dendrophrya erecta* Str. Wright, 1861
- *Globipelorhiza sublittoralis* Cedhagen & Mattson, 1991
- *Hyperammina* spp.
- *Liebusella goesi* Höglund, 1947
- *Marsipella* spp.
- *Pelosina* spp.
- *Radicula limosa* Christiansen, 1958
- *Rhabdammina cornuta* (Brady, 1879)
- *Technitella legumen* Norman, 1878
- *Vanhoeffenella gaussi* Rhumbler, 1935

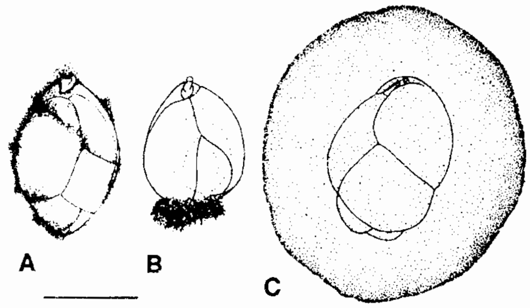

Figure 6. Intact specimens of the calcareous foraminiferans, *Globobulimina auriculata gullmarensis* (A) and *Globobulimina turgida* (B, C), showing their secondary tests (consisting of detritus and clay). Collected in Gullmarsfjorden (58°20,9'N; 11°34,0'E), at 77 m depth, 19 September 1980. Scale bar = 500 µm.

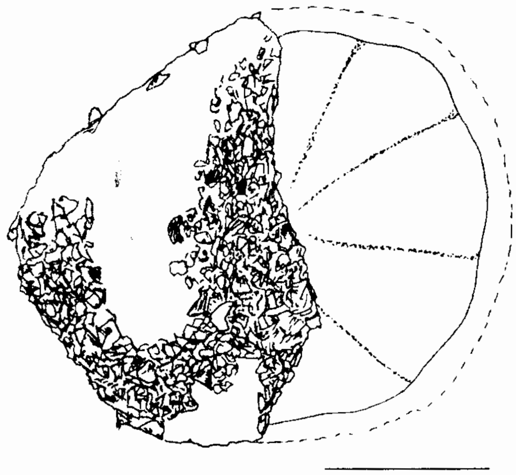

Figure 7. *Elphidium* cf. *incertum*. A calcareous foraminiferan surrounded by its secondary test consisting of mineral grains. Collected at 7 m depth in Gullmarsfjorden, in 1927, at station G28 (Höglund 1947). Redrawn from Dr. Hans Höglund's unpublished pencil drawing. Scale bar = 200 µm.

Höglund (1947) investigated the foraminiferans on the west coast of Sweden. Part of his material was never published, but subsequently handed over to me. He had collected what he believed to be an undescribed saccamminid species from Gullmarsfjorden.

The arenaceous (secondary) test was accidentally cracked, and found to contain a specimen of *Elphidium* cf. *incertum* (Williamson, 1858) (Fig. 7). I have observed the same phenomenon in *Elphidium excavatum*, in which I often found the secondary test to be attached to a mollusc shell fragment several times larger than the size of the foraminiferan.

Goës (1894) figures a foraminiferan that he called *Nonionina scapha arenacea* (p. 105, pl. XVII no. 831). I examined that specimen in the collection of the Swedish Museum of Natural History, and found it to be a specimen of *Nonionellina labradorica* (Dawson, 1860). Its secondary test consists of small mineral particles, and probably also detritus particles.

DISCUSSION

Philine spp. does eat prey other than foraminiferans, such as small metazoans (Thompson 1976, 1988). The reason that foraminiferans constitute such a large portion of the food in this investigation, may be that foraminiferans are of a suitable size for the small sized gastropods.

The cephalaspideans studied by Shonman & Nybakken (1978) had eaten agglutinating as well as calcareous foraminiferans, but the calcareous species dominated. Chester (1993) observed that the cephalaspidean *Acteocina canaliculata* (Say, 1826) feeds on bivalves and various types of foraminiferans. He found that sediment particles appeared to be removed with the jaws of the cephalaspidean. This indicates that these predators dislike the secondary test and so try to avoid it. Many other predators are also quite selective and careful about the quality of their food (*e.g.*, Arnold *et al.* 1985; Mattson & Cedhagen 1989).

The gastropods may avoid agglutinating foraminiferans because these organisms consist largely of mineral particles devoid of nutritional value (see Höglund (1947) and Loeblich & Tappan (1988) for figures on foraminiferans where the volume of the test wall and its contents can be seen). Another reason might be the risk of ingesting a foreign particle, which is too large and cannot be dissolved or passed through the alimentary canal. Such a particle might clog the gut and be fatal. If the predator is unable to evaluate the size of the test particles, it may be better to avoid such prey. This suggestion is supported by the observation that *P. scabra* has a thicker intestine than *P. aperta*, and is less selective in its choise of food.

All of the foraminiferans ingested have a globular or rounded test shape. *Cornuspira foliacea* is a calcareous foraminiferan which lives in areas where the investigated cephalaspideans are common. This species was never found in any cephalaspidean. The reason for this might be that the extremely flat and wide test of this foraminiferan precludes it from being ingested. The same argument can be applied to *Ammotium* and *Ammoscalaria*. Their tests also tend to be wide and flat, but not as extreme as in *Cornuspira*. However, large numbers of other agglutinating species with a globular or rounded shape coexisted with the cephalaspideans in Kosterfjorden and Skagerrak. Such common species were for example *Adercotryma glomerata* (Brady, 1878), *Cribrostomoides crassimargo* (Norman, 1892), *Eggerelloides scabrum* (Williamson, 1958); *Verneuilina europeum* Christiansen, 1958; and *Liebusella goesi* Höglund, 1947. The fact that they were not eaten, suggest that the cephalaspideans really select against agglutinating species. It can also be argued that the predators and their potential prey live in separate microhabitats. This aspect was not studied, but the high numbers and diversity of agglutinating species in the samples indicate that this might be a minor factor.

The secondary test might beside other functions (see introduction) be a kind of protection against predation, a kind of camouflage or mimicry. A calcareous foraminiferan with a secondary test may be neglected or regarded as an agglutinating species by some predators, and therefore avoided. The degree of protection it gives is a field open for future studies. Many cephalaspideans in different parts of the world largely feed on foraminiferans, and some of them are adapted to avoid the secondary test. This suggest that this predator-prey relation is established since a long time ago.

Secondary tests and various mud structures play an important rôle in the life of many foraminiferans. The functions may be diverse, which is a motivation to study the foraminiferans alive.

SUMMARY AND CONCLUSIONS

• The gastropods studied select calcareous foraminiferans as food and ignore agglutinating species.

• The food (test) is entirely broken down during its passage through the intestine.

• The gastropod predator may either select foraminiferans without a secondary test or be able to remove it from the prey.

• I suggest that the secondary test might function as a protection device against predation, either as camouflage or as kind of mimicry.

• The secondary test is related to the feeding activity in many foraminiferans. It might have been a preadaptation for other functions where mud structures are involved.

• Cephalaspideans are common in some Indo-Pacific areas, for example the Andaman Sea (A. Nateewathana, pers. comm.), but as to their way of living poorly known. Their rôle as important predators on foraminiferans, shows that they may be significant in the marine food-webs and turnover of nutrients. This would justify a more intensified study of cephalaspideans in this region.

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