TOXISARCON SYNSUCIDICA N. GEN., N. SP., A LARGE MONOPTHALAMOUS FORAMINIFERAN FROM THE WEST COAST OF SWEDEN

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ABSTRACT

A new foraminiferan, Toxisarcon synsuicidica n. gen., n. sp., is reported from clay bottoms of Kosterfjorden (Sweden). The species is characterized by a large irregular cell body covered by an organic lining to which foreign particles are attached. It resembles an irregular clump of detritus or sediment aggregation and it can therefore easily be overlooked. Marine biologists who have worked intensively with benthic fauna in the area have never observed it despite the fact that it is quite common. The peculiar feature of the new species is its capacity to stock toxic products that can be harmful to itself if accidentally released.

INTRODUCTION

The foraminiferal fauna of the west coast of Sweden has been extensively studied. Sandahl (1857), Goës (1894), Höglund (1947, 1948), Nyholm (1950, 1952, 1953, 1954, 1955a, 1974), Nyholm and Gertz (1973), Dahlgren (1962, 1964), and Cedhagen and Mattson (1991) described several new species from this area. In particular, twenty-four new monothalamous foraminifers were isolated and described by them from the Skagerak area, particularly Kosterfjorden and Gullmarsfjorden. The foraminiferan fauna from this area is characterized by the presence of numerous agglutinoids. It comprises also some large agglutinated species, among which the most common are Astrorhiza limicola and P.larosa arborescens (Cedhagen, 1993). Naked foraminifers were also reported by Sandahl (1857), Nyholm (1950), and Cedhagen and Tendal (1989).

Collecting large foraminifers from sieved fractions, one of us (T.C.) noticed the presence of a peculiar organism, which resembled a clump of detritus. Closer examination of it using a stereomicroscope revealed the presence of an amoeboid cell hidden under an organic theca covered by loosely attached mud and mineral particles. The microscopic examination of isolated specimens showed the presence of granuloreticulopodial extensions suggesting that the organism belongs to the group Foraminiferida. As such a foraminiferan had not been reported, to our knowledge, from this area or from any other locality, a new genus and species are erected.

MATERIAL AND METHODS

The specimens were isolated from sediment samples collected in the Koster area, west coast of Sweden: from the SW corner of Yttre Vattenholmen, 70–30 m depth, in September 1997, November 1998, October 1999, August 2000, June 2001; from Stenbrottet close to Kosterstenen (80–50 m depth), in November 1998; and from N of Tegelskär (80–30 m depth) in June 2001. The samples were taken with an epibenthic sledge intermediate in design between that of Ockelmann (1964) and that of Hessler and Sanders (1967). The bottom material was clay with silt, sand and gravel. An additional 19 Van Veen grab samples (0.1 m² area) were collected along a depth transect south of Yttre and Inre Vattenholmarna on October 18, 1999, with a starting point of 59°00.52 N and 11°00.53 E (85 m depth), and an end point of 58°52.557 N and 11°06.709 E (21 m depth).

The sediment samples were brought to the laboratory and carefully sieved in seawater retrieved from 36 m depth in Kosterfjorden. All foraminifers from the sieved fraction larger than 2 mm were picked from a white plastic container under a strong light. The foraminifers from fractions 1 mm and finer were picked under a Wild M5 stereomicroscope. Living individuals were kept in Petri dishes with clean natural seawater, stored in a refrigerator (4–8 °C), and observed using a Wild M5 stereomicroscope. The pseudopodia were observed using Nikon Diaphot inverted microscope.

Twelve specimens were fixed in Bouins fluid (Romeis, 1968) or in 3 % glutaraldehyde buffered with 0.1 M sodium cacodylate. They were then dehydrated in alcohol, embedded in Epon and cut with an ultramicrotome (R. Jung, Heidelberg) in 2 and 3 µm thick sections which were stained in 0.1 % aqueous toluidine blue solution with 0.1 % borax (disodiumtetraborate) for 2 minutes, differentiated in 96 % ethanol, mounted in XAM Neutral Medium (Gurr) and studied using a Leitz Dialux compound microscope.

Formalin-fixed specimens were transferred to acetone and dried in a critical point dryer (EMS850), mounted on stubs, and coated with Au-Pd in a sputter coater. The test surface and organic lining were then observed using a CamScan MaXim 2040 S.

DNA was extracted using DNeasy kit (Qiagen). The PCR amplification, cloning and sequencing were performed as described in Pawlowski (2000). A fragment of ribosomal rRNA gene was amplified using primers s14F3 and s17 (Pawlowski, 2000). The sequence obtained was analyzed using maximum likelihood method as implemented in the PHYLO_WIN program (Galtier and Gouy, 1996).

SYSTEMATIC DESCRIPTION

Order Astrorhizida Jirovec, 1953

It has not been possible yet to define the position of the new genus within the Order Astrorhizida on the basis of molecular evidence.

Genus Toxisarcon Cedhagen and Pawlowski, n. gen.

Diagnosis. Cell body large (up to several centimeters diameter), either covered by agglutinated test or entirely naked and resembling an amoeba. Where present, test is free with central inflated region giving rise to several branches that generally taper and multifurcate terminally.
Test wall agglutinated with little particle selectivity and poorly cemented. Thick masses of agglutinated material attach to the thick organic lining, which is brown or brownish with a violet tinge. 

Type species: Toxisarcon synsuicidica n. sp. 

Remarks. In addition to the type species, the new genus includes Toxisarcon alba Wilding, described elsewhere in this volume.

Toxisarcon synsuicidica n. sp. 

Figs 1–3

Diagnosis. Species of Toxisarcon in which the cell body is usually covered by a weakly agglutinated test up to 20 mm diameter.

Type material. The holotype is a large intact specimen with test. (SMNH Type Collection 5490). Paratypes comprise microscopic preparations of several specimens with and without agglutinated test deposited in the Natural History Museum, Stockholm, Sweden.

Type locality. Sweden, Bohuslän, Kosterfjorden, on the SW corner of Ytter Vattenholmen, 60–30 m depth, clay bottom with silt, sand and gravel.

Description. The test is free, irregular, monothalamous with a central inflated region from which branches extend in all directions (Fig. 1A–L). The test is uneven, loose, very soft, and droops when picked above the water surface. The organism consists of a cell covered by a brownish proteinaceous organic lining (Fig. 1M) to which foreign particles, detritus, small mineral particles or organic flecks adhere. Some of these particles easily detach when the organism is handled. A thin layer of sediment covers the central region of the test. Branches generally taper and multifurcate terminally (Fig. 2B), although these terminations may be broken in preserved specimens. Some branches can also anastomose (Fig. 1M). The shape of the test changes when the cell abandons it (Fig. 3A–E and text below). It is more branched when it is “intact” (Fig. 1).

The test is irregular in shape and measures up to 20 mm (Fig. 4A–L). There is no distinct aperture but numerous pseudopodia protrude through small invisible openings on the test surface. Randomly winding cytoplasmic strings extend in all directions and taper within the outer branches ending in the branch tips as typical granuloreticulopodia (Fig. 2H–J). The pseudopodia can be extended several cm in all directions on the bottom of the Petri dish or tubular plankton chamber (Fig. 2F–G). Typical bidirectional streaming of granules can be observed.

The cytoplasm is yellowish white when alive, and yellowish brown when fixed in formalin, alcohol, glutaraldehyde, or Bouin’s fluid. A large nucleus up to 80 μm in diameter occurs in the central part of the cell. Some specimens seem to possess more than one nucleus, but this remains to be confirmed by further cytological study. The granular nuclei have a lobated outline and are surrounded by a distinct nuclear envelope (Fig. 2J–K). Large numbers of small nucleoli appear at the periphery of nucleus (Fig. 2K). Large masses of material resembling food residues were observed in various areas of the cytoplasm, although only a few pennate diatom frustules were identifiable.

Observed habitat. West coast of Sweden, on silt clay bottoms between 20 and 80 m depth.

Etymology. Toxi(k)on (Gr.) means toxin or poison; sarc- comes from sarx (Gr.) meaning flesh or protoplasm (sarcode) in protists; the suffix –on indicates a unit, but can also augment the force or meaning of the previous. The Greek prefix syn- means together. The word suicide was really coined in English, but on a French or modern Latin model. Skeat (1963) refers its etymology “as a monstrous formation”, which makes its use even more suitable for the new organism.

Taxonomic position. Based on morphology, the genus Toxisarcon most closely resembles the subfamily Astrorhizinae (Astrorhizidae: Textulariidae) (Loeblich and Tappan, 1987). It possesses the morphological features specified for this subfamily, such as a unilocular agglutinated test with a central inflated region from which arms extend in many directions. Its test, however, is much softer and looser than a typical astrorhizid test and is branched in a different way. When Toxisarcon leaves its test, its naked cell resembles a naked granuloreticulosean belonging to the class Athalamida (Bovee, 1985), such as Reticulomyxa Nauss, 1949; Pontomyxa Topsent, 1892, or the naked form of Astrorhiza limicola (Cedhagen and Tendal, 1989).

Molecular phylogenetic analysis based on partial small subunit ribosomal DNA (SSU rDNA) shows that T. synsuicidica belongs to a clade of monothalamous species that branch as a sister group to the radiation of the Textulariida (Fig. 5). The other monothalamous species branch in a poorly resolved radiation at the base of the foraminiferal tree. Molecular data do not confirm traditional morphology-based separation between soft-walled (membraneous or proteinaceous) agglutinates and agglutinated astrorhizids (Loeblich and Tappan, 1987). The phylogenetic analysis of RNA data indicates rather that similar types of test have been formed several times in the evolution of foraminifera (Cedhagen and others, 2002, this volume).

According to the molecular data, the closest relative to T. synsuicidica is T. alba (Wilding, 2002, this volume). Their sequences differ by 0.8 % in the rDNA sites selected for phylogenetic analysis. For comparison, similar sequence divergence is observed in other pairs of species belonging to the same genus: Allagromia laticollaris / Allagromia sp. (0.4%), Critinnithonia delacai / Critinnithonia granum (0.3%), Notodendrodrya hyalinosphaera / Notodendrodrya antarcticus (1.7%). Morphologically, both species have very similar cells and differ only by the fact that T. alba does not seem to build an agglutinated test. There are also some differences in the behavior of the two species. T. synsuicidica has never been observed to form a spheroid form (Wilding, 2002, this volume). On the other hand, T. alba was not observed to accumulate the toxic compound (see below).

Among other monothalamous foraminiferans, T. synsuicidica is most closely related to the genera Cylindrogullmia Nyholm, 1974 and Gloiogullmia Nyholm, 1974 (Fig. 5). Superficially, there are striking differences between Toxisarcon on one hand and Cylindrogullmia and Gloiogullmia on the other. The tests of Cylindrogullmia and Gloiogullmia are regularly elongated with one and two terminal apertures, respectively, unlike that of Toxisarcon. However, there are also some morphological similarities. The test in Cylindrogullmia is smooth, glossy, and often surrounded by a loose covering of detrital particles, a structure called a secondary test (see Cedhagen, 1996). Such particles usually also surround Gloiogullmia with the difference that they adhere to the test surface and give an uneven surface. Toxisarcon resembles Gloiogullmia in this respect, but the tendency to attach detrital particles is further developed.

The general morphology of the test of Toxisarcon resembles some other monothalamous foraminiferans. The branches and some of the test surface of the new species resemble the rhizome-like structures of the lower parts of Pelosina (see Höglund, 1947; Cedhagen, 1993) as well as the long branches of Globipelorhiza subtilitoralis described by Cedhagen and Mattson (1991). Its cytoplasmic strings, however, are not tubular like those of G. subtilitoralis or other komokiaceans. Like some allogromids, T. synsuicidica has the ability to detach its test and live, at least for some time, as a naked amoeba. This feature is shared with Astrorhiza limicola (syn. Meganoemobryxa argillibio) (Schultz, 1915; Nyholm, 1950; Cedhagen and Tendal, 1989) and some marine testaceans (Page, 1983). The naked forms of A. limicola and T. synsuicidica are, in fact, very difficult to distinguish based only on external morphology.

Finally, the nuclear apparatus of T. synsuicidica resembles that described in some allogromids. The nucleus of T. synsuicidica is surrounded by a nuclear envelope and a lining, which resembles the exonuclear vacuome in Ovaminina opaca (Dahlgren, 1967) and similar structures in G. eurystoma (Nyholm 1974) and in A. limicola (Cedhagen unpubl.). The granular nucleus of T. synsuicidica contains numerous nucleoli that are located on the inner side of the nuclear envelope. Nucleoli in a similar position were observed also in O. opaca (Dahlgren, 1967), G. eurystoma (Nyholm, 1974: fig. 3), A. crassilifera (Dahlgren, 1962: pl. II, figs. 2–3), Hippocrepinella alba (Dahlgren, 1967: fig. 1) and Nemogullmia longeviariabilis (Nyholm, 1956: fig. 9, and pls. 2–3).

OBSERVATIONS ON LIVING SPECIMENS

Behavior

The specimens isolated and placed in the Petri dishes usually leave their tests within 24 hours and live at the bottom as large yellowish-white naked amoebas. Some of them are nearly 10 mm in diameter and round, oval or bulging in shape (Fig. 2, C–E). Usually, the cell leaves the test through one area (Fig. 3, A, E), but sometimes, different parts of the cell protrude, simultaneously from different areas including the arms tips. Thin strands of granuloreticulopodia, some of
them up to 30 mm long, extend in all directions around the cell (Fig. 2, F–G).

The test of *Toxisarcon* can easily change its shape. When the freshly isolated individuals are put in a Petri dish and left in a refrigerator, the test contracts into a rounded clump with a much smoother surface than in the freshly isolated specimens (Fig. 3, A, E). This is particularly apparent in specimens with only a little attached sediment. Later, the cell usually detaches from the test and continues to live as a naked form. Sometimes, the amoeboid form divides by fragmentation of the cytoplasm into several small individuals (Fig. 3, B–D). Naked specimens move short distances, a few cm per day. Such movements are often initiated by the formation of a lead pseudopod that is thick, straight,
**FIGURE 3.** *Toxisarcon synsucidica* n. gen., n. sp. A: Cell creeping out of the test. The irregular test morphology is re-shaped into a round soft detritus mass. B–D: Cell undergoing irregular division (multiple fission). E: Specimen leaving its modified test (right) and forming a lead pseudopod (Lp) in the direction of movement. F: Specimen (Ts) creeping on the sediment surface (Ct = creeping track) in an aquarium after detaching its test, 23 August 2000. Scale bar = around 5 mm. (Photo 3F: Sam Bowser).

**FIGURE 4.** *Toxisarcon synsucidica.* Number of individuals in the 2 mm sieve fraction of 19 Van Veen grab samples along a transect south of Yttre and Inre Vattenholmarna, Kosterfjorden.

non-branching, and can reach a length of about 1 cm before branching into typical granuloreticulopodia (Fig. 3, E (Lp)). The entire cell contents are transferred along this lead pseudopod to the new position. Specimens placed in an aquarium with natural sediment, as designed by Cedhagen (1992), creep along the bottom up to 5 cm per day leaving a track behind (Fig. 3, F). While moving, the specimen pushes the sediment aside producing a loose burrow along the track.

**TOXICITY**

A peculiar behavior of *T. synsucidica* was observed in July–September 1997. When an individual was touched with forceps or a pipette, a dark blue or gray-blue spot appeared immediately where it was touched. The spot gradually extended in diameter and additional smaller blue spots appeared on various parts of the cell. Within less than a minute, the entire specimen was dark blue and dead. Simultaneously, a toxic compound was released into the water. This compound induced the same blue spots in all other individuals in the Petri dish leading to their death within a few minutes. If the Petri dish was kept on a white background it was possible to see that the water acquired a slight yellowish tinge and a weak but distinct smell could be noticed. Water from a Petri dish where individuals had released the toxic compound was tested on other organisms: harpacticoid copepods, ostracodes and small polychaetes (Syllidae). All animals were immediately paralyzed by the toxic water. The
FIGURE 5. Phylogenetic position of *Toxisarcon synsuicidica* and *Toxisarcon alba* based on 647 unambiguously aligned sites of the SSU rDNA, inferred by neighbor-joining method using K2 distances. Numbers above branches are bootstrap support values higher than 90% respectively for neighbor-joining and maximum-likelihood analyses. GenBank accession number of *Toxisarcon synsuicidica* sequence is AJ315955. The accession numbers of all other sequences are given in Pawlowski and others (2002, this volume).

toxic effect, however, completely disappeared within a day and most of the animals recovered rapidly.

Our attempts to repeat these observations in November 1998 and October 1999 failed. This made it impossible to examine precisely the composition of the toxin. It allows us, however, to speculate about its origin. If the toxin was produced by the organism itself, and was used for protection or during predation, one would expect to find it throughout the year, or at least during the seasons when the organisms are most active. Conversely, the fact that the toxic reaction in the naked forms could be induced only during certain periods indicates that the toxin is not produced by the organism itself but taken up from the environment. Its source was most probably toxic algae such as dinoflagellates that accumulated on the bottom after plankton blooms. *Toxisarcon synsuicidica* seems capable of ingesting large quantities of the algae without being affected by their toxic contents, but the individuals became extremely fragile. The slightest injury under laboratory conditions, such as puncture of the cell membrane, can provoke the release of the toxin inducing the death of the cell and eventually the "collective suicide" of other individuals. In nature, however, *T. synsuici-
dica* is probably able to handle and break down the toxins and so contribute to the detoxification of the natural sediments.

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