Modern foraminifera: biological and ecological basics

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Abstract. Foraminifera were first described in 1700 by microscopist Antonie van Leeuwenhoek. Today we know they are the most diverse group of shelled microorganisms in modern oceans. Vickerman counted in 1992 about 10.000 species. They are marine sediment-builders and important to help to reconstruct paleo-climates and –temperatures. They can live either planktonic or benthic, build tests with several materials and can populate many different habitats. They are micro-omnivores and have an important position in the nutrition-net.

Biology of modern foraminifera

Systematic

Kingdom	PROTISTA
Phylum	SARCODINA
Class	RHIZOPODA
Order	FORAMINIFERIDA

Suborders: Allogromiina, Textulariina, Fusulinina, Miliolina, Rotaliina

What are foraminifera?

Foraminifera are single-celled marine Organisms. They live either benthic (**Fig.1.**) or planktonic (**Fig.2.**). The soft tissue (protoplasm) is largely enclosed within a harder shell (test). The test can be composed of secreted organic matter (tectin), secreted minerals (calcite, aragonite, opaline silica) or agglutinated particles. The Organism can consist of a single chamber or several chambers. These chambers are mostly less than 1mm across. Each chamber is interconnected with the next by an opening (foramen) or many openings (foramina). This Openings give the animal-class the name.

Foraminifera are known from the early Cambrian until today. The tests can be very abundant in marine sediments, they actually making up the bulk of several rocks. In the geological history foraminifera are important as biostratigraphic indicators in marine rocks, because they were abundant and diverse. Planktonic foraminifera are widespread and have had rapidly evolving lineages. These factors aid the inter-regional correlation of strata. They also help to reconstruct the paleoclimate because the ecological conditions while the lifetime of the organism can be red in the test.

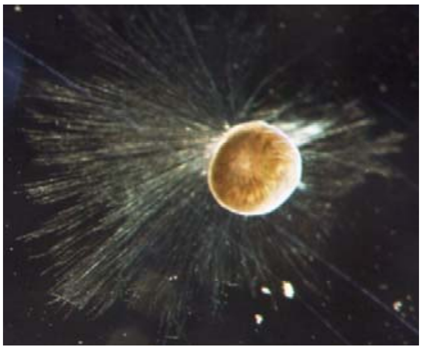

Fig.1. Amphistegina lobifera: Benthic foraminifer with pseudopodial net. (from http://www.mpi-bremen.de)

Fig.2. Planktonic foraminifera: Hantkenina alabamensis; Specimen is about 0.8 mm from spine tip to spine tip. Courtesy of J. H. Lipps, University of California, Davis. Copyright Cushman Foundation for Foraminiferal Research, Inc., 1987

Buildup

The foraminiferid consists of a outer shell filled with protoplasm. This plasma is differentiated into an outer layer of clear ectoplasm and an inner layer of darker, colored endoplasm. The clear ectoplasm surrounds the test and gives rise to lots of thread-like (filose) or branching (reticulose) pseudopodia (**Fig.3.**). With this appendages they draw their food, expel debris, pull the test along and benthic forms use them for anchorage. Pseudopodia are also valuable for construction and maintenance of the test and they even aid in digestion. The endoplasm contains food vacuoles and the nucleus, in many-chambered foraminifera several nuclei can occur together in the cell (multinucleate conditions). In shallow water species the endoplasm can include algal symbionts. The algae are mostly densely packed, in Archaias angulatus they take 75% of the test, even more (till 80%) in Globigerinoides ruber (Nuglisch 1985).

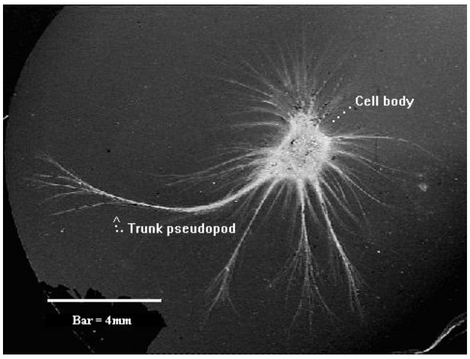

Fig.3. Scanning electron micrograph of the giant Antarctic foraminiferan Astrammina rara with pseudopodia (from http://www.bowserlab.org)

Way of living

Nutrition: Foraminifera trap and engulf small organisms and particles with their sticky pseudopodia (**Fig.4.**). The food requirements vary between different species. This can be: bacteria, diatoms, other protists, small crustaceans, mollusks, nematodes and invertebrate larvae. Few foraminifera are even thought to be parasitic. The engulfed food is digested outside the test in a food vacuole, which is situated in the ectoplasm. These vacuoles and digestion products passing to endoplasm through an aperture in the test. If there is not enough nutrition, the foraminiferid can digest the symbiotic algae (35 – 50%) to get other this food-shortage. The algae show a higher reproduction rate in such times (Nuglisch 1985).

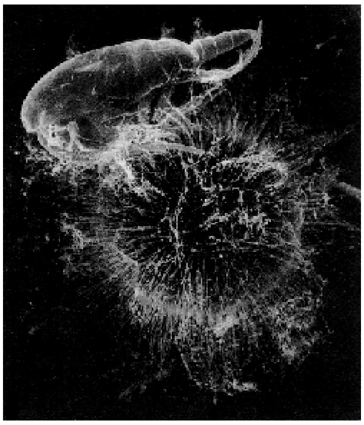

Fig.4. Planktonic foraminifera capturing and breaking down its prey with pseudopodia. (from http://www.bowserlab.org)

Reproduction: The life cycle is characterized by alternation between two generations (**Fig.5.**). There is a gamont generation, which reproduces sexually and the schizont generation reproduces asexually. This cycle may be completed within one year in warm tropical latitudes, in higher latitudes it can take two or more years. This alternation of generations is not always preserved strictly.

Normally the schizont undergoes the asexual reproduction during the winter months. The process begins with the withdrawal of the protoplasm into the test. The plasma splits into numerous tiny daughter cells. Each of them gets a nucleus or several nuclei and if available some symbiotic algae. A reduction division (meiosis) from diploid to haploid has taken place. After the plasma-split begins the chamber formation. The new gamont generation is now released into the water and they come to mature. In the summer months the protoplasm is again withdrawn and divides into haploid daughter cells. These sexual cells (gametes) bear two whip-like flagella. When they are released from the parental generation, two gametes fuse (sexual reproduction) and form the new diploid schizont generation. After this, the parent test is often left empty.

The tests of the two generations are a little bit different in appearance (dimorphic). In general the gamont-tests are more common, smaller and have a large megalospheric initial chamber (proloculus). On the other hand, the schizont tests are larger, have more development stages and a smaller microspheric proloculus.

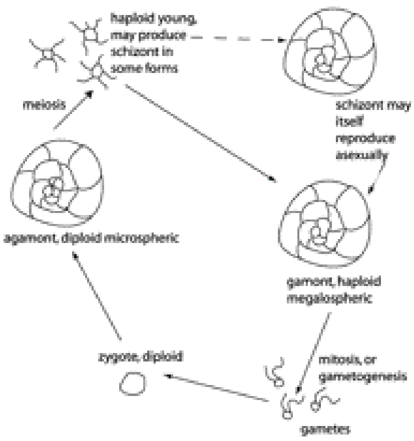

Fig.5. Generalized foraminifera life cycle, showing an alternation between a haploid megalospheric form and a diploid microspheric form. (Redrawn from Goldstein 1999)

The test

Wall structure and composition: There are several materials used in build up the test by several suborders of foraminifera.

The organic-walled forms belong to the suborder Allogromiina. The thin, non-rigid test consists of proteinaceous or pseudochitinous matter. The most hard-tested foraminifera have an similar material as a thin lining to the chambers, this may act as a template for mineralisation.

Textulariina encompasses forms with agglutinated tests(**Fig.6.**). These forms bound organic and mineral matter from the sea floor together, with help of an organic, calcareous or ferric oxide cements.

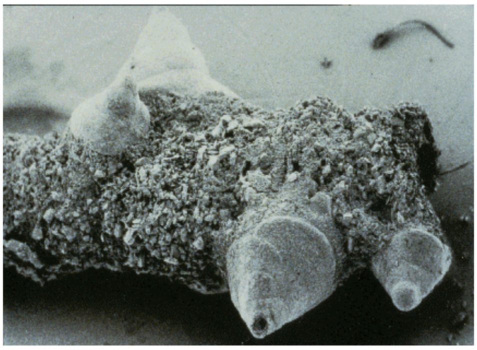

Fig.6. Agglutinated foraminifera: Tritaxis conica. Deep sea near the Walvis Ridge, southeastern Atlantic Ocean. Recent. The view here is about 5 mm wide. Scanning electron micrograph. Courtesy of J. H. Lipps, University of California, Davis. Copyright Cushman Foundation for Foraminiferal Research, Inc., 1987.

Miliolina, Fusulinina and Rotaliina include the forms with a calcareous test. The shell of Miliolina is constructed of tiny needles of high magnesian calcite, which is most randomly arranged. The outer surface is an exception, it is build of horizontally or vertically arranged needles. Fusulinina tests are build of tiny calcareous granules. They can be arranged randomly or normal aligned to test-surface, this gives an fibrous appearance. The granular and pseudo-fibrous layers are often combined. The tests of Rotaliina are generally hyaline, but thick walls, fine dense perforations, granules, spines and pigments may obscure the clarity.

All walls are traversed by small straight pores or branched alveoli, through which fluids may pass. They link ectoplasm and endoplasm.

Chamber development: Foraminifera which consist of one chamber, are called unilocular, when they have two or more, they are multilocular. The chamber growth at unilocular forms proceeds gradually along with protoplasmic growth. The protoplasmic growth in multilocular forms is gradual, but test growth is periodic. A new and larger chamber is being added at regular intervals.

The chamber addition starts with the construction of a loosely bound growth cyst, which is largely composed of food debris. The pseudopodia are withdrawn to occupy the space of the new chamber. First they build an organic wall and then an agglutinated or calcareous one on the outer side.

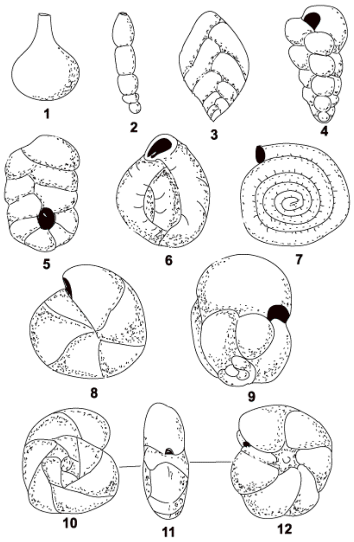

Fig.7. Principle types of chamber arrangement. 1. single chambered; 2. uniserial; 3. biserial; 4. triserial; 5. planispiral to biserial; 6. milioline; 7. planispiral evolute; 8. planispiral involute; 9. streptospiral; 10-11-12. trochospiral (Redrawn from Loeblich and Tappan 1964.)

Apertures and foramina: Apertures are found in the wall of the final chamber, they connect the external pseudopodia with the internal endoplasm. They allow the passage of food and contractile vacuoles, nuclei and release of daughter cells. The position of the aperture remains constant through ontogeny, so each chamber is linked to the next by a foramen or several foramina. Foramina can be secondarily developed by resorption of the chamber walls.

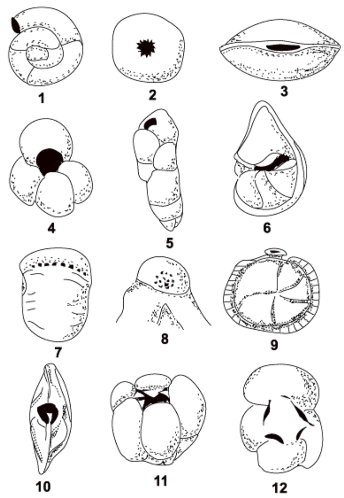

Fig.8. Principle types of aperture. 1. open end of tube; 2. terminal radiate; 3. terminal slit; 4. umbilical; 5. loop shaped; 6. interiomarginal; 7. interiomarginal multiple; 8. areal crbrate; 9. with phialine lip; 10. with bifid tooth; 11. with umbilical teeth; 12. with umbilical bulla. (Redrawn from Loeblich and Tappan 1964.)

Sculpture: On the external surface you can find different appendages, e.g. spines, keels, rugae, fine striae, granules and reticulate sculptures. The surface structure can vary through ontogeny and with environment.

Test function: The test reduces biological, physical and chemical stresses. It decreases the risk of ingestion by deposit feeders or infestation by parasitic nematode worms. The test protects the foraminifera from harmful radiation from the sun, water turbulence and abrasion. It helps to tolerate fluxes in salinity, pH, oxygen and nutrient levels in the water. The protoplasm can be withdrawn into inner chambers, leaving the others as protective lobbies or a detrital plug may close the aperture. Calcareous shells help to buffer the acidity of nutrient-rich and oxygen deficient environments. The test gives stability to the organism. Sculptures may variously assist buoyancy, improve adherence, strengthen test against crushing and help to channel the ectoplasmic flow to and from the apertures, pores and umbilicus.

Ecology of modern foraminifera

Food

Foraminifera are micro-omnivores in marine systems. They feed on small bacteria, algae, protists and invertebrates. Some are also scavengers, feeding on dead organic particles. Foraminifera living on reef and carbonate shoal environments, benefit from endosymbiotic algae. When high-diversity foraminiferid assemblages are found, you can assume that a wide range of food resources is available. This partitioning of resources among species is typical for stable habitats. If there are seasonal fluctuations in food supply it can amount to foraminiferid blooms with low diversity. This opportunistic species reach maturity quick and are small in size. In regions with oceanic upwelling planktonic foraminifera tend to thrive quickly.

Predators

Benthic foraminifera get ingested by worms, crustaceans, gastropods, echinoderms and fish, that browse on the sediments and organisms upon the sea floor.

Substrate

Silty and mud substrates that are rich in organic debris and contain small pore spaces can be good conditions for bacterial blooms. These blooms support large foraminifera populations with thin-shelled, delicate, elongate forms. In sand and gravel substrates we have large pore spaces, they contain fewer nutrients and cause sparser populations. The foraminifera living here are thicker-shelled, heavily ornamented, biconvex or fusiform. Foraminifera can live up to 200 mm below the sediment surface, but the majority are feeding within the top 10 mm. On hard substrates, like rocks, shells, sea-grasses and algae foraminifera are usually attached. These forms have a relatively thin test and a big morphological variability.

Light

The zone of light penetration in the oceans, called photic zone is affected by water clarity and incident angle of the sun rays, so it is deeper in tropical waters. The photic zone is attractive to foraminifera because of primary productions of nutrients by planktonic and benthic algae. The light is preference for algal food sources and association with endosymbiotic algae. Many foraminifera also thrive in protected and food-rich niches around and on algal trouds, roots and sea-grass meadows.

Temperature

Each foraminiferid species is adapted to a certain range of temperature conditions. The narrowest range is found at low-latitude faunas in stable, tropical climates. The bottom waters of the abyssal plains are characterized by cool-water assemblages, that otherwise are found at shallower depths near the poles. Planktonic foraminifera can also be adapted to different ocean layers of particular temperatures and densities. They have fewer buoyancy problems in cooler denser water, so the species living their have a lower test-porosity than forms in warmer or shallower waters. These warm forms improve buoyancy with test-porosity and prominent spines. Deep-water planktonic foraminifera have to cope with the effects of $CaCO_3$-solution, so they build an extra "crust" of radial, hyaline calcite.

Oxygen

Oxygen-requirements of foraminifera are very modest, so O_2 deficiency does not greatly affect them. Regions with anaerobic conditions are typified by small, thin-shelled, unornamented calcareous or agglutinated assemblages. Low oxygen decreases the ability to secrete $CaCO_3$, but it can increase its subsequent chances for preservation, unless conditions are acidic.

Salinity

The majority of foraminifera are adapted to normal marine salinity, under this conditions, we find the highest diverse assemblages. In regions with low salinity of brackish lagoons or marshes low-diversity assemblages of agglutinated foraminifera are domiciled. Hyper-saline waters are dominated by porcelaneous Miliolina.

$CaCO_3$

The solubility of Calcite is less in warm than in cool waters. So, we find thick tests and foraminiferid limestones at lower latitudes. Because of the calcium carbonate compensation depth, populations from abyssal depths are dominated by agglutinated foraminifera.

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