Abstract An important function of symbiont-bearing benthic foraminifera is to provide their endosymbiotic microalgae with light. At the same time, these foraminifera have to resist hydrodynamic forces. Foraminifera match these demands by constructing shells (tests) functioning as glasshouses. In shallowest regions of oligotrophic tropical seas, at the one end of the scale, foraminifera with spherical and thick lenticular tests develop special fixing mechanisms to resist extreme water motion. In the deepest euphotic zone, at the other end of the scale with extremely weak light and quiet water, foraminifera with flat discoid and blade-shaped tests possessing a high surface/volume-ratio position their symbionts just beneath the transparent test walls, intensifying the weak light through elevated test surface structures. Between these two extremes, foraminifera react to decreasing light intensity and water motion by the transition in shell form from spherical to extremely flat tests. A second way in test form from high energetic shallow water to less, but still energetic water is the transition from spherical to fusiform tests, again raising the surface/volume-ratio but not in the same degree as performed by test flattening.

Keywords larger foraminifera, symbionts, test shape, hydrodynamics

Introduction

Foraminifera as single-celled organisms inhabit today most environments of the marine realm. Besides their long geological history with the first appearance in the Late Cambrian (ca. 500 million years ago), the increasing complexity of shells (tests) during earth history makes them excellent indicators of marine environments today and in the past.

The normal size of foraminiferal shells is between 100 μm and 2 mm. In the abyssal, some foraminifera get size of a few cm, but their walls are simple (mainly agglutinated foreign particles loosely fixed by organic cements) and tests are not distinguished by higher complexity.

This is in contrast to shallow water foraminifera living in oligotrophic tropical and warm-temperate seas (Hallock 1999). The test walls consist of secreted calcium carbonate and shells can get sizes that are enormous for single celled organisms. The largest living representative *Cycloclypeus carpenteri* attains 13 cm (Koba 1978). In contrast to large deep sea forms, tests of these shallow living foraminifera show high complexity. All derived from a spiral arrangement of chambers (Fig. 1), where chambers have been originally tubular in the suborder Miliolina or spherical in the suborder Rotaliina. This leads to the
question, why these shallow living benthic foraminifera get such size and in which way they construct their shells to fulfill the main demands for life in oligotrophic waters of tropical and warm temperate seas (Hallock 1985).

These large foraminifera harbor symbiotic microalgae, which ranges from Rhodophyta (Porphyridium) in the foraminiferal family Peneroplidae, Chlorophyta (Chlamydomonas) in Archaeeisnidae, dinoflagellates (Symbiodinium) in Soritidae to diatoms (various genera) in Alveolinidae, Amphisteginidae, Calcarinidae and Nummulitidae. Therefore, the different foraminiferal families harboring symbionts are specified to higher categories of microalgae (Leutenegger 1984; Lee and Anderson 1991; Lee 1998).

In this symbiosis, the profit of the foraminiferal host is the availability of organic food, mainly glycerol and lipids, produced by the microalgae through photosynthesis, thus symbiont-bearing benthic foraminifera (shortened here as SBBF) are mixotrophic organisms. When harboring diatoms, up to 80% of glycerol that is released into the surrounding medium by the algae can be directly digested by the foraminifer. Therefore, diatom-housing foraminifera get independent from external food uptake to a high degree, becoming rather autotrophic organisms similar to lichens. In this case, the minimum necessity of food uptake from outside - mainly bacteria - is to provide the microalgae with inorganic nutrients.

Beside protection of the symbiont through the host by the shell, the major profit of the microalgae is the service of inorganic nutrients by the host. Furthermore, the microalgae obtain inorganic carbon ions necessary for photosynthesis through the calcification process of the foraminiferal test (McConnaughey and Whelan 1997), because the alkaline oligotrophic tropical seas are depleted in carbon dioxide.

The main aspects leading to the construction of tests for benthic foraminifera housing symbiotic microalgae are

1) function
2) building material and
3) construction plan (= bauplan)

where the functional aspect influencing the general shape of shells will be discussed in detail. First, the role of the building material relieving the functional demands together with the limits given by the bauplan will be shown.

**Building material**

The above mentioned suborders Miliolina and Rotaliina differ in wall mineralogy. Extremely small high-magnesium calcite rods (length ca. 1.5 micrometer, diameter ca. 0.5 micrometer) that are randomly oriented in the test walls characterize the Miliolina (Debeney et al. 2000). Light will be reflected by disorientation of the optical axes resulting in white test color. This porcelaneous wall structure allows life in extremely illuminated shallow tropical seas because of protection from UV irradiation. To gather light for symbiotic algae, some test parts have to become transparent in Miliolina, which is done by an extreme thinning of wall parts. These parts are called pits (peneroplids), grooves (alveolinids) and windows (archaiasinids, soritids).

Walls of the Rotalina are constructed by layers of low-magnesium rhombohedra calcite crystallites united in larger crystal blocks. Optical axes of the larger crystal units within the parallel to the surface attached layers (lamella) are oriented either perpendicular or at 45° to the surface making test walls transparent (hyaline walls). This allows gathering of light for symbionts in less illuminated environments.

**Bauplan**

The basic construction plan of a multi-chambered foraminifer living in an environment influenced by hydrodynamics is a series of planispirally coiled chambers (Fig. 1). Low expansion rates of the spiral results in lenticular shells (Dendritina, Archaias, Palaeonummulites, Operculinella). Lenticular tests in Amphistegina and Calcarina results from a flat trochospiral chamber arrangement approximating the planispiral coiling.

Raising the expansion rate of the spiral coil induces blade-shaped tests in Peneroplis, Heterostegina, Planoperculina and Planostegina. Chambers of the last 3 genera are subdivided into chamberlets. Spanning the complete former test by a single chamber subdivided into cham-
berlets leads to annular tests (Fig. 1), where a series of chambers is built within a single growth step (cyclic foraminifera). The circumference of these shells corresponds to a circle. Cyclic tests are characteristic for *Cyclorbiculina*, *Parasorites*, *Sorites*, *Amphisorus* and *Marginopora* in Miliolina and for *Cycloclypeus* and *Heterocyclina* in Rotaliina.

Another method to raise the surface/volume-ratio based on planispiral coiling is by elongation of chambers along the coiling axis leading to spindle-shaped tests (Fig. 1). Again, chambers are subdivided into chamberlets by septula. Today such test forms are verified only in the Miliolina (*Borelis, Alveolinella*).

**Function**

Additionally to the general functions of a protist cell, like the decomposition of complex organic molecules into basic components and assembling them into endogenous macromolecules, further the assemblage of inorganic substances into structural components like skeletons or shells together with reproduction, SBBF must provide their microalgae with inorganic nutrients originating from defecation of the host and with inorganic carbon ions gained by the calcification of the test wall. The number of algae has to be restricted by regulated service with inorganic nutrients; furthermore, the algae should be transported to specific places within the test construction to attain optimum light for photosynthesis (Leutenegger 1984), but have to be transported to safer places - normally located in the test center - in case of unfavorable conditions.

In spherical tests, symbionts living beneath the test surface obtain more light than microalgae living in the test center. Therefore, the rise of the surface/volume-ratio (Haynes 1965) allows positioning of more microalgae just beneath the test wall to gather the most intense light. Special structures – so-called egg-holders (Hottinger 1977) – are developed in some SBBF at the inner surface of the test wall to protect algae from the main cytoplasm streaming in the chamber center.
Raising the surface/volume-ratio with constant volume is performed in two ways. The test shape of SBBF can be described in general form by an ellipsoid, where $L$ is the longest, $I$ is the intermediate, and $S$ is the shortest diameter. A sphere is characterized by $L = I = S$.

Shortening of axes $I$ and $S$ leads to an ellipsoid $L > I > S$ raising the surface/volume-ratio under constant volumes. Two special cases can be found in many SBBF shells (Fig. 1). The relation $L = I > S$ characterizes discoid forms (oblate ellipsoid of revolution), mostly found in the families Amphisteginidae and Nummulitidae, while the relation $L > I = S$ determines a prolate ellipsoid, where spindle-shaped (fusiform) tests are typical for the Alveolinidae and the Paleozoic Fusulinidae (Fig. 1).

The raise of the surface/volume-ratio depending on proportions between the three axes can be represented in the dimensionless Zingg-diagram (Zingg 1935) with the coordinates $S/I$ and $I/L$ (Fig. 2). Checking surface/volume-ratios (Fig. 3A) demonstrates the strong raise of this ratio by oblate ellipsoids when reducing the $S$-axis, which represents the thickness of a foraminiferal shell. In analyses of larger foraminiferal tests, this ratio is well known as the T/D-ratio (Larsen and Drooger 1977; Hallock 1979; Renema 2005). According to the Zingg-diagram, the T/D-ratio is only accessible for lenticular tests with circular circumference, found in amphisteginids (*Amphistegina*), thick lenticular nummulitids (*Palaeonummulites, Operculinella, Operculina*), involute peneroplids (*Dendritina*) and archaiasinsids (*Laevipeneroplis, Androsina, Archaias*); circular circumference is verified in the large annular (cyclic) nummulitids *Heterocyclusina* and *Cycloclypeus*.

The shape of non-lamellar, cyclic archaiasinsids (*Cyclorbiculina* and *Parasorites*) and soritids (*Sorites, Amphisorus* and *Marginopora*) cannot be modeled by oblate ellipsoids.
ellipsoids but by cylinders with concave bottom surfaces. Concavity becomes pronounced with growth because tests start with a spherical or ellipsoidal embryonic apparatus. Therefore, soritids and cyclic archaiasinids must be modeled by oblate ellipsoids at the embryonic apparatus, changing to cylinders with concave bottom areas at later growth stages. The surface/volume-ratios between oblate ellipsoids and cylinders become insignificant at S/I-values <0.25.

Extreme surface/volume-ratios can be found in soritids (from 14 in large Amphisorus to 20 in Parasorites) and in the cyclic nummulitids Cycloclypeus and Heterocyclina (ratio ca. 15). The smaller amphisteginids with oblate ellipsoidal shells are much thicker, thus demonstrating lower surface/volume-ratios (Fig. 3A). Nevertheless, the often mentioned trends in test flattening combined with a deeper habitat can be verified within the lessonii-group of Amphistegina from A. lobifera Larsen(ratio 5.4) to A. lessonii d’Orbigny (5.6) to A. bicirculata Larsen (6.4) and in the radiata-group from A. radiata (Fichtel and Moll) (5.6) to A. papillosa Said (7.8). In the extremely shallow living calcarinids only the genera Neorotalia (5.4) and Calcarina (5.3) possess oblate ellipsoidal shells, while the deeper living Baculogypsinoidea and the very shallow Baculogypsinoid show spherical tests with surface/volume-ratios <5.

A remarkable trend from oblate ellipsoids to blade-shaped ellipsoids can be found in peneroplids, which is coupled with test flattening. The thick involute Dendritina (ratio 5.6) behave similar to A. lessonii, while test flattening raises this ratio from 6.1 in Peneroplis antillarum d’Orbigny to 7.6 in P. planatus (Fichtel and Moll). Similar tendencies can be found in the much larger nummulitids except the annular genera. The genera Palaeonummulites and Operculinella with similar test shape belong to oblate ellipsoids with surface/volume-ratios of 6 for the shallower Palaeonummulites and 7 for the deeper Operculinella.Nummulitids with high expansion rates of the spiral chamber arrangement develop ellipsoidal, blade-like tests. Raising the expansion rate of the spiral chamber arrangement is coupled with test flattening, forcing the surface/volume-ratio from 8.5 in Heterostegina depressa d’Orbigny to 9.5 in Operculina complanata (Defrance) attaining 16 in the genera Planoperculina and Planostegina.

Both latter genera settle today in the deepest euphotic zone.

The third group of ellipsoidal tests allowing raise of the surface/volume-ratio are prolate ellipsoids. Today fusiform or spindle-shaped tests can be found only in Alveolinidae with the genera Borelis and Alveolinella. The maximum ratio of 8 characterizes large specimens (L=4 cm) of Alveolinella quoyi (d’Orbigny).

As mentioned above, raising the surface/volume-ratio is almost correlated with depth. This was first demonstrated for the lessonii-group of Amphistegina (Hansen and Buchardt 1977; Larsen and Drooger 1977), where test flattening is obtained by reducing lamellar thickness keeping the diameter/thickness of chamber volumes constant (Hallock and Hansen 1979). Therefore, test diameter is constant with increasing depth, which could also be found in Amphistegina radiata (Hohenegger et al. 1999). In nummulitids, on the contrary, test flattening is mainly caused by increasing the diameter/thickness-ratios of the chamber volumes with water depth, found in all Operculina species (Pecheux 1995; Yordanova and Hohenegger 2004) and in Heterostegina depressa (Röttger and Hallock 1982).

The weak light at the deeper euphotic zone is intensified by so-called papillae reflecting the scattered light to the test surface, thus enabling active net-photosynthesis for the symbiotic diatoms (Hottinger 2006). Papillae of Amphistegina radiata, A. papillosa, Operculina ammonoides (Gronovius) and O. complanata increase in number/surface-ratio and height with depth. Similar test surface structures like elevated septa and septula found in the deep living Planoperculina and Planostegina have the same effect.

Raising the surface/volume-ratio by flat oblate ellipsoids or long prolate ellipsoids to get optimum light for the symbionts has the disadvantage of becoming strongly affected by hydrodynamics. The slope in coastal regions of seas is characterized by a strong positive correlation between irradiation and hydrodynamics mainly caused by wind induced waves, both showing an exponential decrease with depth (Lalli and Parsons 1997; Bearman 1999). The effect by water motion on test form can also be demonstrated in Zingg-diagrams (Fig. 3B). In this case, the isolines represent settling velocities of ellipsoids
Fig. 3 Zingg-diagrams. A) isolines represent surface/volume-ratios of triaxial ellipsoids with identical volumes. The surface/volume-ratio of a sphere is 4.836. B) isolines represent settling velocities expressed as percentages of the velocity of an equivalent sphere. Species are represented as trajectories indicating changes by growth, starting from a spherical proloculus (dotted line), ranging (thick line) from smallest (arrow) to largest individuals (circle) within a population.

expressed as percentages of the velocity of a sphere with the same volume and density. Settling velocities are important to calculate thresholds of friction velocities that initiate motion in a unidirectional laminar flow. Flow velocities above this threshold keep tests in suspension and they are transported (Yordanova and Hohenegger 2006).

Water energy is often extreme in the very shallow coastal areas of tropical seas that are unprotected by barriers, thus all SBBF tests, also spherical forms, will be entrained when no special fixing mechanisms are developed. While SBBF with spherical tests are little damaged by orbital wave transport because acting like rounded sand grains, the flat, disc-shaped forms will be completely destroyed.

According to the Zingg-diagram, oblate ellipsoids with high surface/volume-ratios are easily transported as well as prolate ellipsoids with long L axes (Fig. 3B), therefore they cannot resist high water motion just by test form. This explains the restriction of genera with flat tests to quiet water, which can be found in deeper parts of the slope or in coastal areas (reef moats or lagoons) that are protected by coral reefs or sand barriers.

Flat large nummulitids thus cannot live in shallow water environment. First they are destroyed by hydrodynamics in wave exposed environments because they cannot fix to the substrate, second the transparent test walls expose the cell nucleus to dangerous UV-irradiation in quiet shallow waters of lagoons and moats. However, large disc-shaped soritids settle in quiet shallow water. They fix with a special glue (Langer 1992) to flat and smooth surfaces found in see-weeds (Langer 1993), thus hindering entrainment. Additionally, they are protected against UV-irradiation by housing zooxanthellae as symbionts degrading dangerous irradiation by the production of aromatic aminoacids (Jokiel and York 1981).

Shells of peneroplids and amphisteginids are much smaller compared to other SBBF families. They protect themselves against high water energy and irradiation by hiding within a net of small filamentous algae (peneroplids) or in small holes of rocky substrate (amphisteginids). Their complex or multiple apertures allow additional strengthening of fixation by multiplying the attachment through a bundle of pseudopods.

Calcarinids are extremely exposed to water energy when living on the reef crest. Additional to a strong glue for fixation (Röttger and Krüger 1990), all possess spines enabling anchoring between filamentous algae. With both mechanisms they resist highest water energy even during tropical cyclones.

Fusiform alveolinids avoid the highest energetic zone, but also cannot be found in quiet shallow water behind barriers. They live in higher energetic shallow water on sandy bottom or hiding in small holes of a rocky surface. Coarse grained sands that are typical for the upper slope are settled by SBBF with thick lenticular tests, like *Amphistegina radiata*, *A. lessonii*, *Operculina ammonoides* and *Palaeonummulites venosus* (Fichtel and Moll). When buried during a tropical storm, these thick lenticular tests facilitate digging to the bottom surface.

These transport possibilities of SBBF are important for sedimentologists, which have to explain the accumulation of empty SBBF tests in fossil sediments by comparing the present situation with the geological past (Yordanova and Hohenegger 2006).

**Conclusion**

Gathering enough light for endosymbionts under differing hydrodynamic conditions is the main functional demand of symbiont-bearing benthic foraminifera. Optimal light can be served, when symbiotic microalgae are positioned just beneath the test wall. Large surface/volume-ratios obtained by flat discoidal or long fusiform tests match this demand. But those tests cannot resist the high water energy of wind induced waves in shallowest regions with highest illumination. Here, spherical and thick lenticular forms developing special fixing mechanisms resist entrainment. In case of being entrained, these tests are not damaged and individuals can survive after fixing again to the substrate. Otherwise, individuals with spherical and thick lenticular tests cannot live in light depleted environments at the deepest euphotic zone. Here, extremely flat disc- or blade-shaped tests with transparent hyaline walls are able to position all their symbionts just beneath the test walls, additionally concentrating the weak and dispersed light to the test surface through papillae or...
other elevated test surface structures. Therefore, the general test forms approximated by ellipsoids and attained by the bauplan of foraminifera explains the distribution of symbiont-bearing larger foraminifera in oligotrophic tropical and warm temperate marine environments.

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