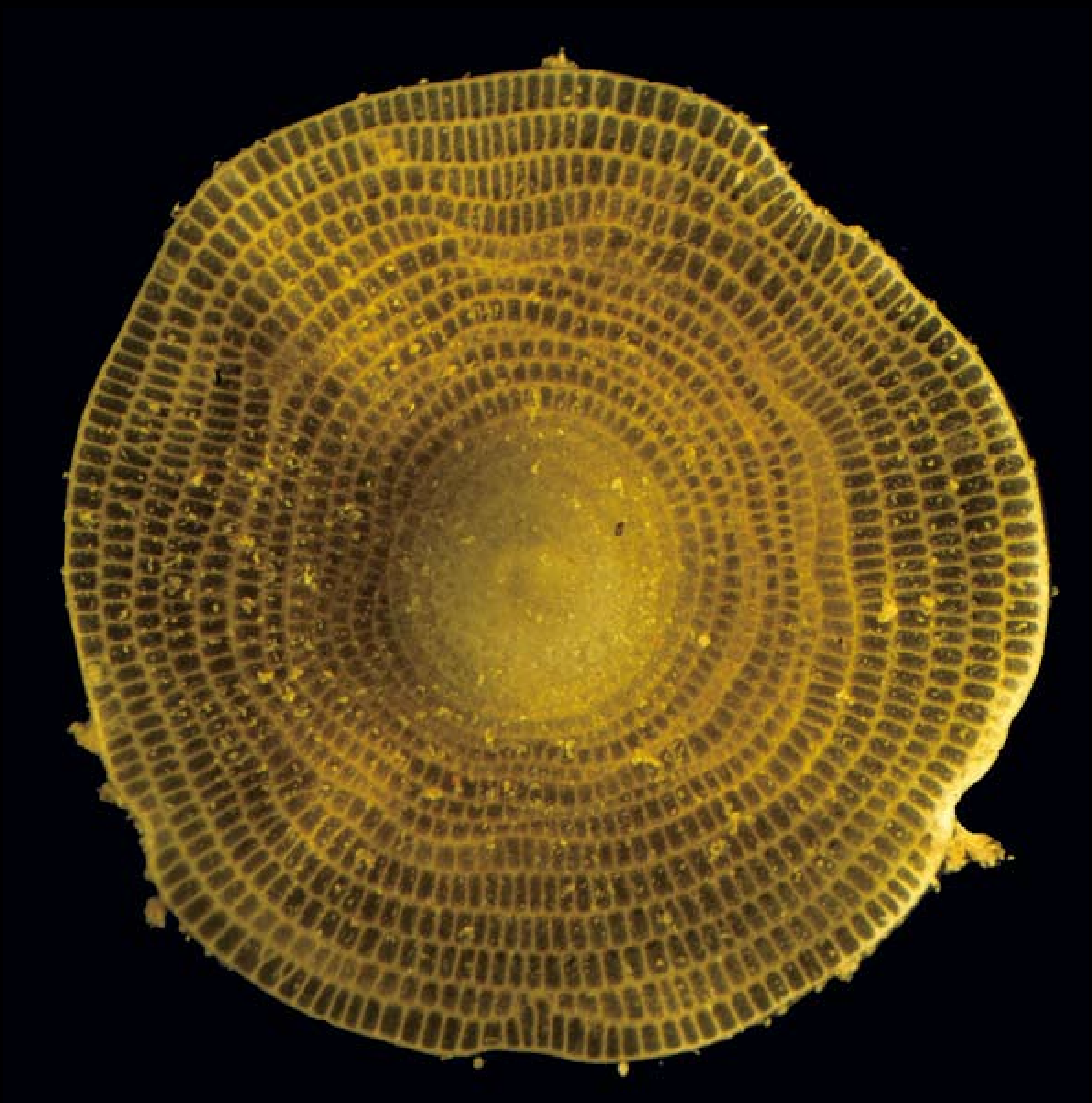
LARGE FORAMINIFERA

GREENHOUSE CONSTRUCTIONS AND GARDENERS IN THE OCEANIC MICROCOSM

JOHANN HOHENEGGER



The Kagoshima University Museum

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Cover Photograph: *Cycloclypeus*

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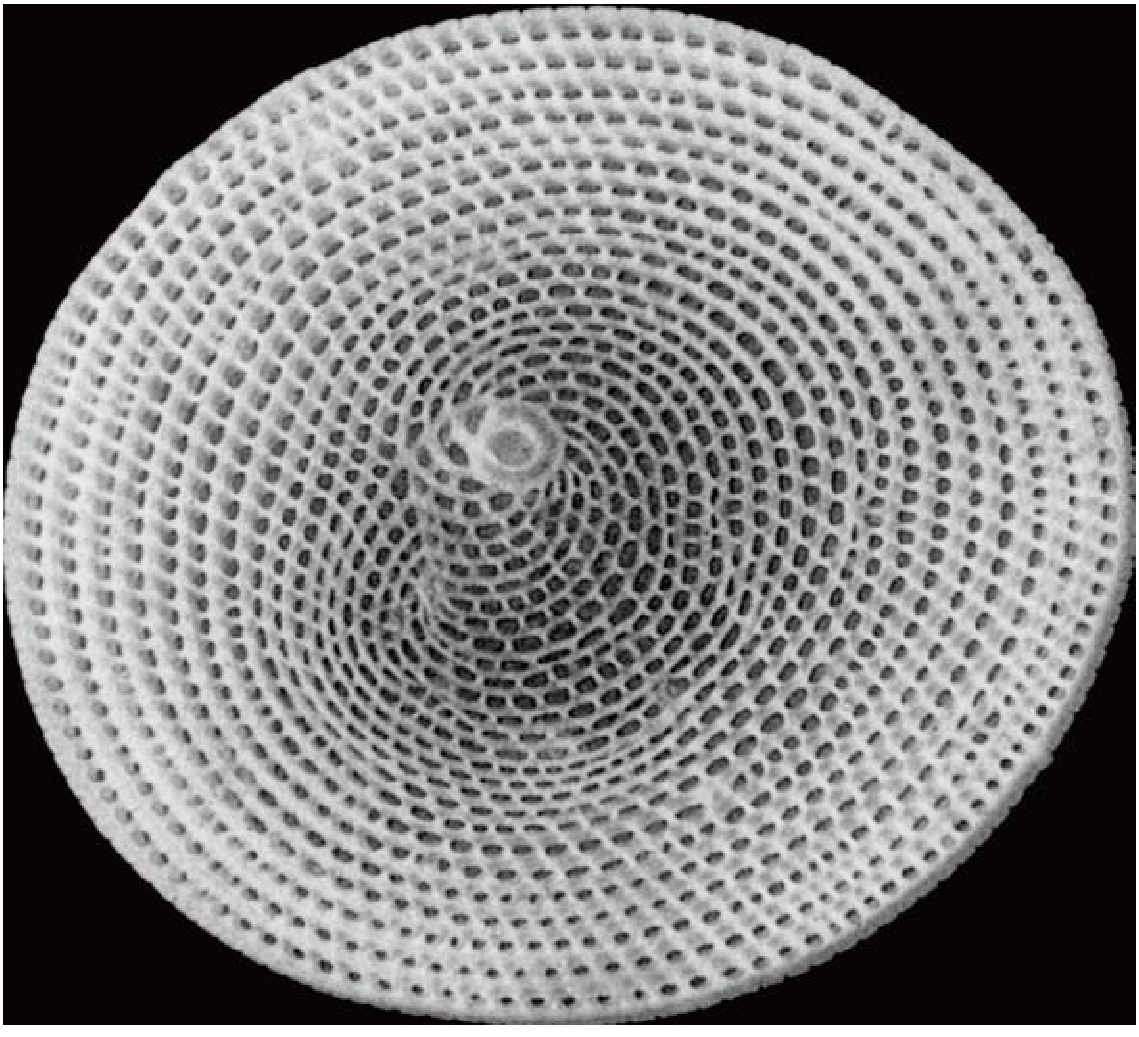

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Photograph on the reverse side: *Parasorites*

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Preface

This book is about microscopic organisms consisting of a single cell, which house microscopic algae as plants and thus construct complex greenhouses of calcium carbonate in tropical shallow water oceans. They have a long geological history of about 350 million years. Today, their empty glasshouses are important components of carbonate sand in tropical shallow water, where they often attain more than 90 % of carbonate sand grains. Beach sands in the tropical Indo-Pacific are named 'living sand' or 'star sand' according to the form of sand grains, which resembles to little stars or sun discs. The knowledge about life and demands of these micro-organisms to the environment is important for the preservation of carbonate sand beaches especially in the Indonesian Archipelago and the tropical West Pacific from the Barrier Reef to the Ryukyu Islands. Therefore, I wrote this book in a non-scientific and, as I hope, generally understandable manner to focus the interest to these organisms and to the problems of preserving carbonate beaches.

There is a lot of institutions and people that helped me during my scientific work and supported the making of this book. First, I have to thank the scientific and technical staff of the Tropical Biosphere Research Center, University of the Ryukyus, Sesoko Station, making a 12 months stay in 1992/ 1993 (director the late Prof. Kiyoshi Yamazato) and a 4 months stay in 1996 (director Prof. Tazunori Takano) as an invited foreign researcher possible. Second, I thank the Kagoshima University (president Prof. Hiromitsu Tanaka) for a 7 months stay in 1997/98 as a visiting professor at the Research Center for the South Pacific (director Akio Inoue) and for participation of a 4 weeks cruise in 1995 on the 'Keiten Maru' to Belau, where I got friendship with many Japanese scientists, but was especially supported by Prof. Akio Hatta (Kagoshima University). Finally, I will thank my good friend Prof. Kimihiko Ōki (director of the Kagoshima University Museum) for providing support of the Japanese Society for the Promotion of Science for many stays at Kagoshima University and for organizing a special cruise to Amami-Oshima, Tanegashima, and a flight to Okinoerabu Jima, where I could take samples to broaden my horizon about larger foraminifera. Last, but not the least, I thank the Kagoshima University Museum for publishing this book.

The Austrian Science Fund (FWF) supported investigations within several projects, where Elza Iordanova (3 projects) and Christian Baal (1 project) were employed. Franz Tatzreiter supported field work in 1996. Discussions with Prof. Rudolf Röttger (Kiel) were useful for understanding the biology of these gardeners and molecular genetic investigations of Maria Holzmann helped to clarify the evolutionary relationships between different species.

All illustrations and most of the photographs were performed by the writer, otherwise the authors, almost Christian Baal and Elza Iordanova, are cited. Finally, I thank M. Stachowitsch for correcting the English text.

Vienna, February 2010

Johann Hohenegger

It is a great pleasure to publish a book “Large foraminifera - Greenhouse constructions and gardeners in the oceanic microcosm”. I became acquainted with Prof. Hohenegger at the fourth International Symposium on Benthic Foraminifera (Benthos ’90) in 1990. I stayed at Vienna University for study of benthic foraminifera at the northern most part of Adriatic Sea for 7 months, 1994. At that time my family was under indebtedness to Professor Hohenegger and his wife. After that Prof. Hohenegger stayed at Kagoshima University in 1995, 1996, 1997~1998, 1998, 1999, 2003 and 2004. He collected bottom sediments and large foraminiferal specimens off Amami-oshima, Tanegashima, Amakusa-shimojima and Okierabu-jima in 1999, 2003 and 2004 with me. I would like to say thanks to a good friend Prof. Hohenegger for giving me this chance.

ŌKI Kimihiko

Director of the Kagoshima University Museum

GREENHOUSE CONSTRUCTIONS AND GARDENERS IN THE OCEANIC MICROCOSMOS

Let's have a look at one of the world's most famous cultural heritages, the pyramids of Gizeh! Located southwest of today's Egyptian capital Cairo, the god-kings (pharaohs) of the first dynasties initiated the erection of these buildings as their mausoleums 4,500 years ago.

At 138.75 m (originally 8 m higher) the pyramid of king Chufu (Cheops) is the tallest one. It was built on a calcareous plateau together with the somewhat smaller pyramid of king Chaefre (Chephren) and the much smaller one of Menkaure (Mykerinos).

The Sphinx in the foreground with the pyramids of king Chaefre (Chephren) to the right and king Menkaure (Mykerinos) to the left.

The pyramid of king Chufu (Cheops).

While the sepulcher of the Cheops pyramid consists of granite blocks originating from quarries near Assuan more then 600 km to the south, the pyramid itself is composed of large limestone blocks that had been crushed in nearby quarries. Thus, the transport distance was not too far.

What are the main components of this limestone?

A closer look at the blocks shows a dense packing of lens-shaped components measuring from 5 mm to 3 cm.

The base of the Cheops Pyramid. The mean height of the limestone blocks is 1 meter.

These components consist of **calcium carbonate** ($CaCO_3$) and are thus calcareous particles and pieces. Each of these components demonstrates a complex internal structure, clearly visible in fractured pieces.

These structures hint to an organic origin, which is not surprising, because more than 90% of all limestone deposited during Earth History originates from organism skeletons or shells.

Details of a block from the Cheops Pyramid.

In the case of the pyramids, these lens-shaped calcareous components can be separated into 2 size groups. The spaces between the larger components (size between 2 and 3 cm) are densely stuffed with lens-shaped grains characterized by sizes between 0.5 and 1 cm.

The surface of a block from the Cheops Pyramid showing the composition of the limestone by small, lens-shaped components of 5 mm size and larger lenses with 30 mm size.

Isolated calcareous lenses (*Nummulites perforatus* Montfort) falling into two size groups (photo C. Baal).

Before the rise of biological sciences in the 17th century and knowledge about fossilization, which means the preservation of organic material or skeletons and shells in rocks or stones, farmers regarded the smaller components as 'petrified lentils' and some people called the large ones 'petrified coins'. Therefore, today's scientific name for these components is '*Nummulites*', originating from the Latin name for small coins, which is '*nummulus*', and the Greek name '*lithion*', which means 'stone'.

The originator of lens-shaped components

We know that organisms can form complex hard structures like vertebrate bones, shells of clams, or skeletons of stony corals by arranging tiny calcareous minerals in different and complex order, leading to these structures. This gives rise to the question: what kind of organisms were responsible for these lens-shaped calcareous objects in the pyramid limestone and where did they originally live?

A further question relates to the function of these calcareous objects:

a. Are these objects **skeletons** used to strengthen the organism's soft body to better resist mechanical forces, much like stony corals do against the strong waves?

b. Are these skeletons used to enable movement by stabilizing soft bodies, like the exoskeleton (surrounding the soft bodies) of insects or the endoskeleton (within the soft body) of vertebrates do?

c. or can these objects be regarded as **shells** to shelter the organism against the environment, by enabling them to retract the body into the shelly cave, like clams and snails do?

To get answers to these questions, we have to investigate these objects in detail.

One investigation method is to make sections of a single object. There are two preferred orientations for sectioning a lens-shaped object, leading to two types of sections.

The first preferred orientation corresponds to the symmetrical plane dividing the lens-shaped object into two equal parts. This plane, called the **equatorial section,** is unique; no other equatorial section is possible (Figure 1).

The second preferred orientation, perpendicular to the equatorial section, runs through the center of the lens-shaped form. The line, which is oriented perpendicular to the equator and runs through the center, is called the axis of rotation; such sections are called **axial sections**. As opposed to the equatorial section, which is unique, an infinite number of axial sections are possible by rotating 360° around the axis.

Making equatorial and axial sections for the smaller and the larger lens-shaped objects reveals their structures and demonstrates similarities and differences between both groups. In equatorial sections of both lens-shaped objects, a chamber is located in the center. This chamber is large in the group of small-sized objects and extremely small in the group characterized by large objects.

Starting from this center, a series of chambers is arranged in a spiral following the equatorial plane. This type of coiling is named **planispiral**. It can be found in living cephalopods, which are related to squids, protecting

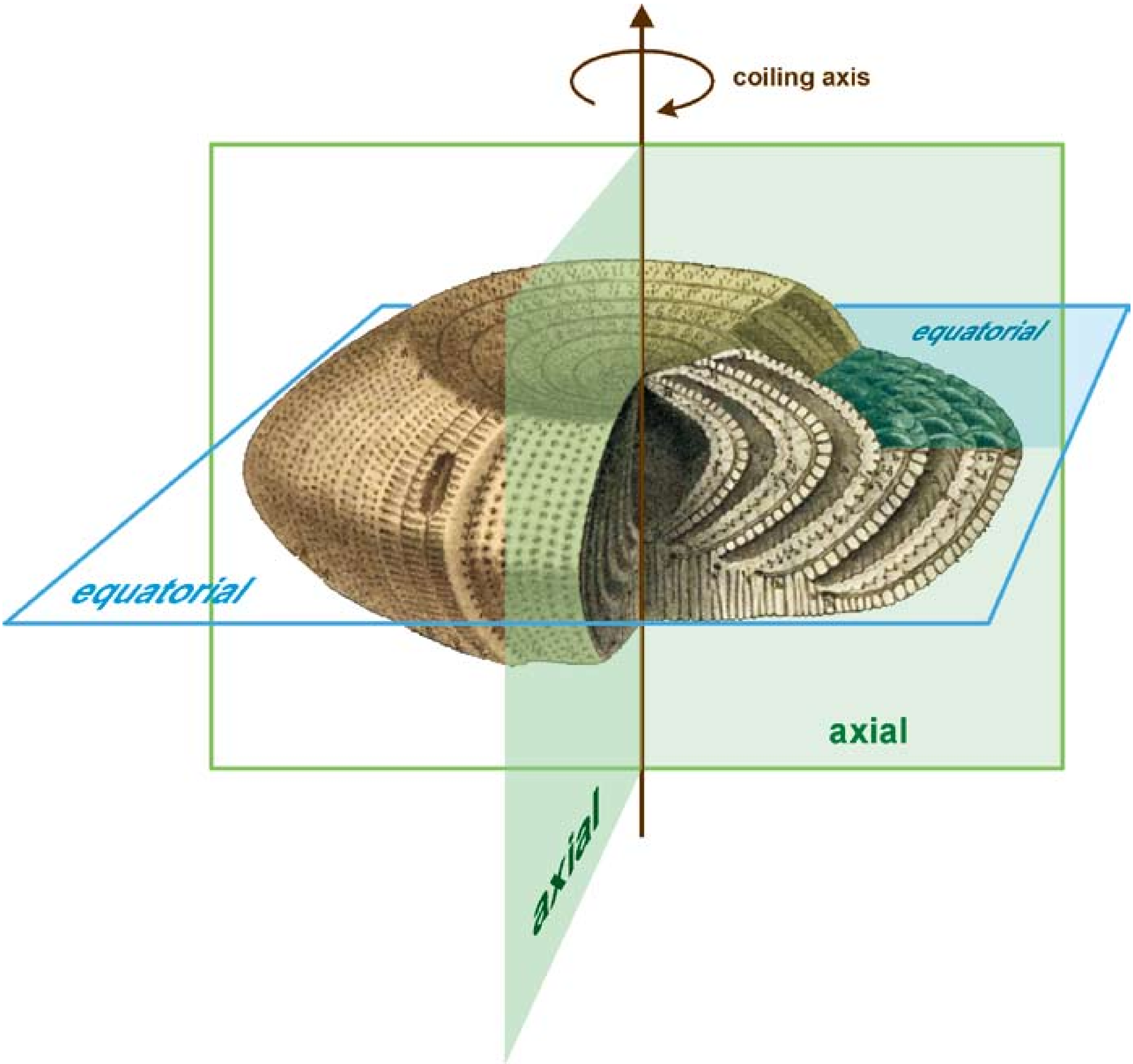


Figure 1. Preferred sections on a planispirally enrolled shell (foraminiferal test after Carpenter 1858).

Equatorial section through a lens-shaped object (size = 12 mm; photo C. Baal)

Axial section through a lens-shaped object (size = 7 mm; photo C. Baal)

Equatorial section (size = 30 mm) of a shell with a small initial chamber and many whorls (photo C. Baal).

Equatorial section (size = 8 mm) of a shell with a large initial chamber and a few whorls (photo C. Baal).

the soft body within beautiful shells (*Nautilus*), as well as in their fossil relatives, the ammonites. When spiral coiling leaves the equatorial plane and moves continuously along the axis of coiling, then it is named **trochospiral**. Trochospirally coiled shells are typical for snails.

Squids and the *Nautilus* live in the sea. This is where we can also find relatives of the objects that produced the shells that make up pyramid limestones. They are much smaller in size than the *Nautilus*. Another difference is the life habit. While cephalopods swim about (**nektonic**), these smaller organisms live on the sea floor. Living on the sea floor is called a **benthonic** or **benthic** habit.

The bodies themselves make up the second difference. Cephalopods are multicellular animals characterized by a set of organs like eyes, jaws, intestines, execratory organs, gonads, and different numbers of tentacles.

The small-sized organisms living on the sea floor do not show such differentiation. From the opening of the shell or test, these organisms spread a bundle of fine threads, which are interconnected much like a spider's net. Each test contains only a single cell. Therefore, these individuals belong to the group of single-celled organisms like amoebas. Similar to the latter, they do not have a fixed body shape like other single-celled organisms, but can change their flexible body, especially in the outer part, for locomotion and feeding. These flexible parts create different foot-like forms, which are called **pseudopods**.

Dissimilar to the amoebas, which move slowly by forming rounded pseudopods (*lobopods*), the threadlike interconnected pseudopods are called **reticulopods**. Besides movement, reticulopods function as organs for nutrition by catching food and transporting it into the inner cell in a process called ingestion.

In the early 19th century, when the first of these organisms were described as living forms from the sea and as fossils, they were regarded as 'cephalopods' because their tests or shells bore a certain similarity. True cephalopods with a chambered shell *(Nautilus* and the fossil ammonites) connect their chambers, which are filled by gas for buoyancy control, with an organic string called '*sipho*'. This creates complex chamber connections. In contrast, test chambers of these single-celled organisms are filled by the cell body and the connections between chambers are simple openings. This led the famous paleontologist Alcide Dessalines d'Orbigny (1802-1854) to differentiate between '*Céphalopodes siphonifères*' (which means 'carrying a sipho') and '*Céphalopodes foraminifères*' ('carrying a *foramen* = opening'). Today, the term **Foraminifera** remained, including all single-celled organisms living (mostly) in the sea, hiding their soft cell bodies in tests and producing reticulopods as organs for movement and food capture.

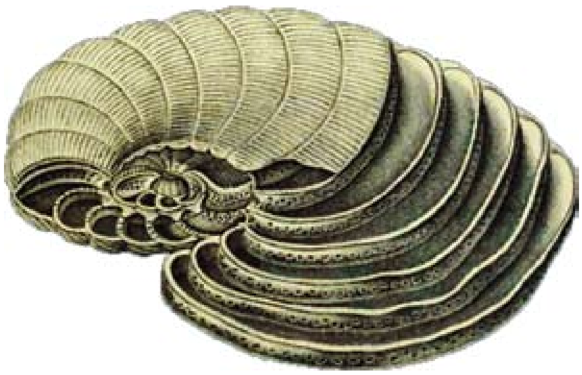
Side and frontal view of a *Nautilus* shell with planispiral enrollment (photo P. Pervesler).

Trochospiral enrollment demonstrated by the land snail *Achatna* (photo P. Pervesler).

A living *Nautilus* – a relative of squids – with large, but simple eyes and many tentacles for catching food.

A living *Peneroplis* (size = 1.2 mm) with pseudopods spreading from the test opening (aperture).

Shell of the cephalopod *Nautilus* (size = 15 cm) cut close to the medium section, demonstrating the body chamber and gas chambers. The body chamber is connected with the embryonic chamber by a tube called siphon (photo P. Pervesler).



Shell of *Peneroplis* (size approximately 2 mm) showing the different chambers that are connected by simple openings = foramina (drawing by Carpenter 1855-1860).

The body

Foraminifera consist of a single cell (Figure 2).

The normal size of foraminifera is between 100 micrometers and 2 millimeters, which is large for single-celled organisms. Sizes of other single celled organisms like diatoms (siliceous algae) or dinoflagellates are much smaller, ranging from 10 to 100 micrometers. Most bacteria are distinguished by a size that is one order of magnitude smaller, between 1 and 10 micrometers.

The foraminiferal cell representing the whole individual is separated from the surrounding water by a membrane. Organic molecules related to the group of fats (**phospholipids**) construct these membranes. These 'fatty' membranes prevent mixture of fluids between both membrane sides. In the case of foraminifera, sea water from outside the cell cannot be mixed with fluids of the inner cell. The membranes do, however, enable penetration of smaller molecules like oxygen and carbon dioxide for respiration by various transport mechanisms.

The liquid within the cell is called **cytoplasm** and consists of water (80-85%), in which organic molecules like amino acids and proteins (10-15%), lipids (2-4%), sugars (0.1-1.5%) along with inorganic molecules and ions (1.5%) are dissolved.

Organic molecules of higher complexity regulate life within the cell. **Proteins** as the most important structures of life mainly act as **structural components**. They can also accelerate processes by transforming simple molecules into larger ones, or, vice versa, disassemble complex molecules into simple ones. This group of proteins is known as **enzymes**. Another important group of proteins are responsible for molecule **transport**. All these processes need energy.

Proteins as chains (macropolymeres) of amino acids are assembled at **ribosomes**, which are tiny grains found in large numbers within the cyctoplasm.

Since proteins cannot be synthesized chaotically all over the cell like in bacteria, especially when these cells are as large as in foraminifera, regulation is necessary. This involves formation and transport of proteins and other organic and inorganic substances at places where they are needed at the moment. Therefore, the inner cell is not a large undifferentiated bottle, but is structured by membranes, the so-called **endoplasmatic reticulum**, where most ribosomes are concentrated.

Beside organic macromolecules, which are synthesized in the cytoplasm, organic and inorganic substances that are needed outside the cell membrane for protection or movement are assembled in separate compartments called **dictyosomes**. Membranes surround these dictyosomes. In one group of foraminifera, tiny calcite-needles 0.5 and 2 micrometers long are formed in dictyosomes and then transported within so-called **Golgi vesicles** to the cell surface.

The reversed mechanism takes place during ingestion of food like bacteria, microalgae or organic waste (**detritus**). Feeding is necessary to obtain organic macromolecules and then disassemble them into more simple organic molecules. This process is termed digestion. Simple organic molecules like sugars, organic acids, and lipids can now be used to assemble larger macromolecules that are specific and necessary for the organism. Parts of the cell membrane, where food is captured, invaginate. This gives rise to bladder structures, the **phagosomes**, where food is digested.

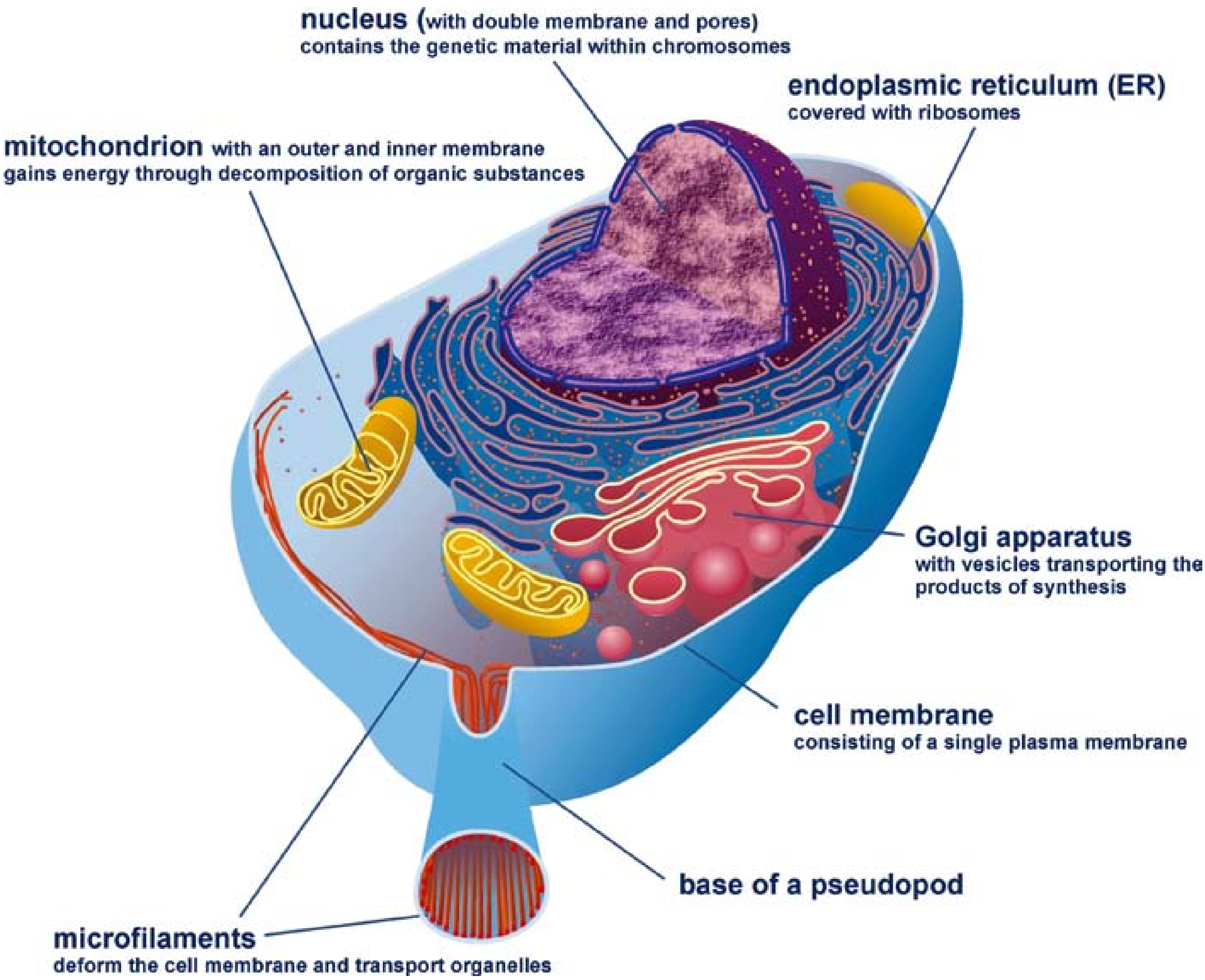


Figure 2. Scheme of a foraminiferal cell (modified after Campell and Reece 2008).

All processes for assembling and disassembling substances need energy. Energy is gained by respiration, representing the one part of metabolic processes that is typical for animals. During respiration, higher organic molecular structures, mainly sugars and fats, are burned with the help of oxygen into inorganic carbon (carbon dioxide). The regained energy is chemically bound in **ATP** (adenosine triphosphate), where it can be used whenever necessary. Respiration takes place in separate cell compartments called **mitochondria**.

All life processes performed by proteins have to be regulated by a special structure, where the information about protein structure and the onset of protein construction is stored. Except bacteria, this information in the form of nucleic acids (DNA = **D**eoxyribo **N**ucleic **A**cid) is bundled as chromosomes within the **cell nucleus**. The nucleus is separated from the other cell parts by a double membrane, allowing regulated penetration of information carriers in the form of proteins into the nucleus and by mRNA (**m**essenger **R**ibo **N**ucleic **A**cid) to the outside.

The cell wall of the foraminifer is not strengthened by organic macromolecules like structure proteins or polymer sugars as in other single celled organisms, where they lead to a fixed and unchangeable cell form. Rather, it demonstrates plasticity due to the flexible cell membrane, where proteinaceous **microfilaments** allow changes in shape by contraction.

Furthermore, the cyctoplasm of the foraminifera is differentiated into a dark inner part of the cell, the **endoplasm**, and a transparent outer part, the **ectoplasm**. While most organelles are located in the endoplasm, making it nontransparent, the ectoplasm is responsible for test construction.

A net-like bundle of **reticulopods** is spread from the ectoplasm, which consists of filamentous and contractible cyctoplasm strings. The main task of reticulipods is **food capture**, **movement**, and **test construction**.

Foraminifera lack flagellae (like in human sperm cells) or cilia (like in *Paramecium*) that function as organs for fast locomotion, which are typical for active swimmers. Instead, they live preferably on the sea bottom, moving slowly on or within the sediment and gathering food. When foraminifera live in the water column as passive swimmers (**plankton**), they develop special mechanisms like globular tests and long inorganic spines to increase frictional resistance. This reduces their sinking velocity. Another way to adapt to planktic life is to reduce test density by incorporating lipids (fats). This helps keep the tests in the upper 200m of the water, where the animals feed on phytoplankton.

Today, siliceous algae – the diatoms – represent the major part of the phytoplankton in the sea. Planktic diatoms are the main food of planktic foraminifera, much like benthic diatoms are the main prey of benthic foraminifera. Living diatoms as food sources, however, are found only in the sunlit uppermost parts of the oceans: they need sunlight as an energy source to transform carbon dioxide and water into carbohydrates. This metabolism process is known as **photosynthesis**. The uppermost water column allowing photosynthesis is called the **euphotic zone**. Benthic foraminifera living below the euphotic zone cannot feed on living micro-algae, but have to use the products of organic decay, the **detritus**.

Reproduction and life span

Foraminifera have a complex life cycle with two alternating generations (Figure 3).

One generation is characterized by a single set of chromosomes (where the information as DNA is stored) that is restricted to the nucleus. Organisms with a single set of chromosomes in the cell nuclei are called **haploid**. The haploid generation of foraminifera is named **'gamonts'** because a single gamont produces hundred thousands of **gametes** by multiple fission of the cell nucleus.

Gametes of foraminifera are small (1.5-2.5μm), possessing 2 or 3 flagella for active motion to find another gamete as a partner for fusion. Sexual differences of gametes like sperm and egg cells are not known; gametes of a foraminiferal species originating from different individuals have the same form and are thus called **isogametes**.

After fusion of two gametes, which unifies the chromosomes in one cell nucleus, the new individual (**zygote**) possesses the double set of chromosomes. Organisms with a double set of chromosomes are so-called **diploid** organisms. Although the zygotes are extremely small, because they result from a fusion of two nuclei and very little additional cell plasma, the cells can become larger than the gamonts before reproduction. This generation is named **'agamonts'** because they reproduce asexually.

The multiple fission of diploid cell nuclei is combined with a reduction fission (**meiosis**) of the chromosomes. This

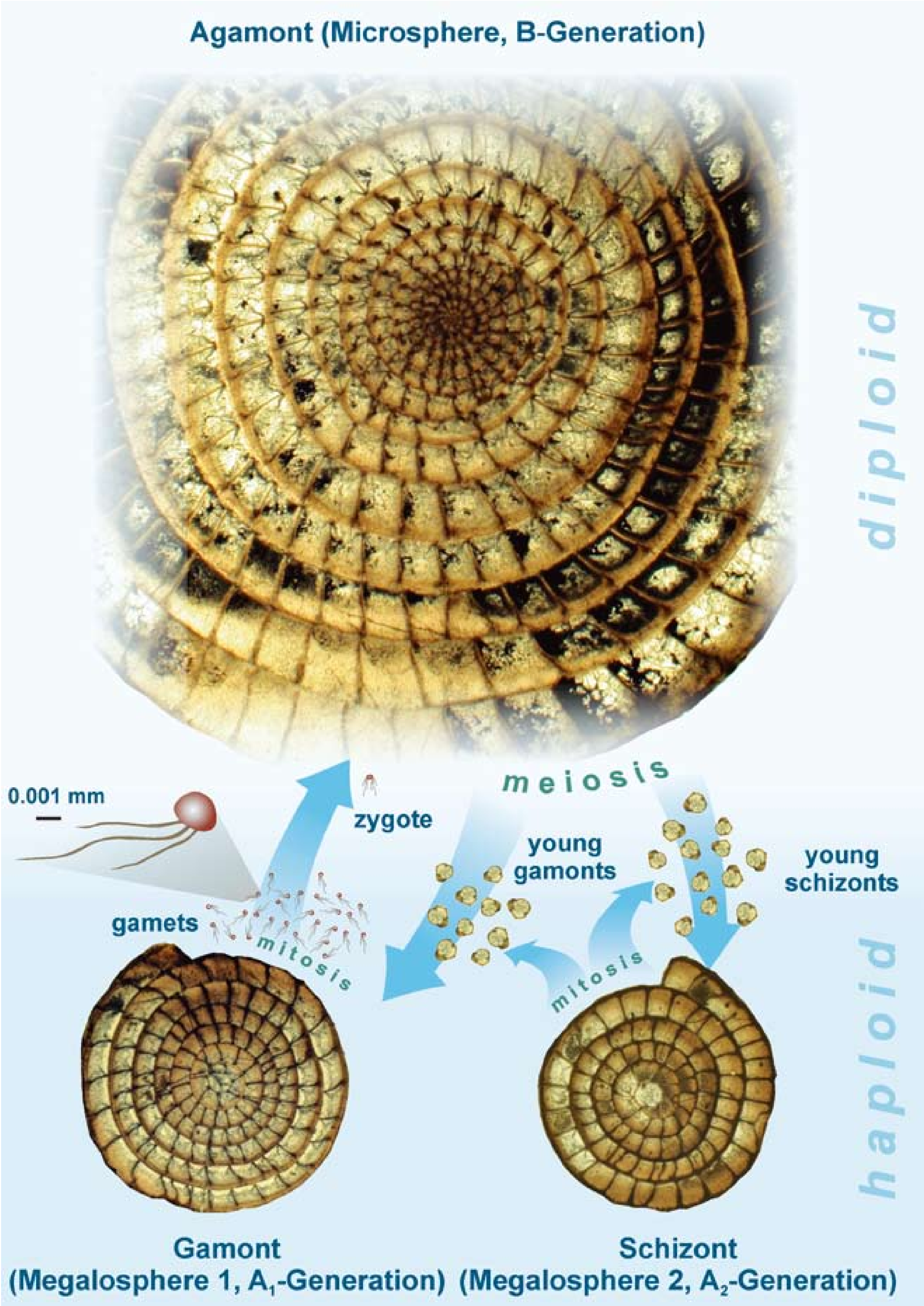


Figure 3. The life cycle in larger foraminifera (size of gametes not to scale).

yields a lesser number (several hundred) of **young gamonts** possessing the single set of chromosomes (haploid) compared to the enormous number of gametes in sexual reproduction.

Reproduction by multiple fission and meiosis normally takes place within the foraminiferal test. The young gamonts remain within the parental test and grow until they develop the first 3 to 4 chambers. After forming the test, the gamonts are released into the seawater.

Every young gamont get parts of the parental cyctoplasm containing all organelles like mitochondria that are necessary for the life of young gamonts.

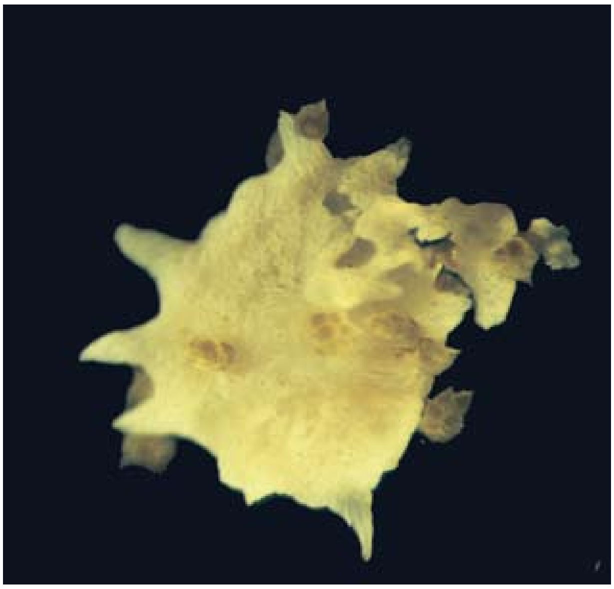
Since young gamonts are sheltered by the parental test until they grow large enough, survival of a young individual released to the seawater is much higher compared to the extremely small and naked zygote. In the latter case, before conjugation, the tiny and naked isogametes have to find a partner, which must not originate from the same parental cell (hindering self-fertilization). Although hundreds of thousands of gametes are released by a single gamont, it is extremely difficult for a gamete to find a partner originating from another gamont.

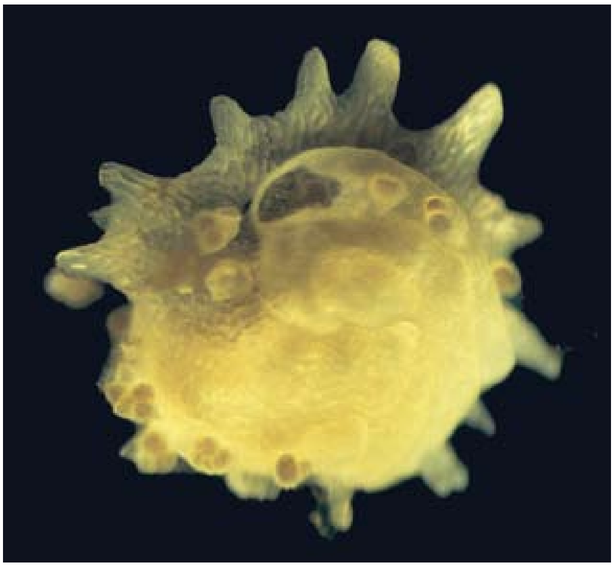
Low settlement densities cause difficulties because they hinder fusion of gametes when distances are too far to detect a partner. Another difficulty is the non-contemporary release of gametes in most foraminifera. Since the survival time of free gametes is restricted to a few days, differences in gamete release of more than one day makes conjugation of gametes originating from different parental organisms improbable even if they may live close together.

The much higher survival rate of young gamonts (compared to the difficulties in finding a conjugation partner for the small isogametes) explains the strong abundance differences in both generations. Adult gamonts are thus much more abundant than agamonts. The proportions between generations depend on the species, but vary from 1 agamont per 100 gamonts down to 1 agamont per 1000 gamonts in larger foraminifera.

The life span of generations differs between and within the species. It ranges from 2 weeks to 1 month in planktic foraminifera, where the individual sinks during this period from the sea surface down to 200 m. After attaining the maximum depth, planktic foraminifera reproduce sexually and the tiny young forms, possessing a few chambers, passively rise to the surface due to their low weight.

Foraminifera living on the shallow sea floor have a life





The foraminifer *Neorotalia* (size = 2.5 mm) with broken brood chamber and hatched offspring.

The foraminifer *Amphisorus* (size = 40 mm) with 4 rings of transparent brood chambers and hatched offspring.

span between 2 and 6 months, whereby diploid agamonts often live longer than haploid gamonts. Reproduction periods depend on season, whereby the first reproduction in spring is caused by high food availability during the bloom of marine microalgae (phytoplankton). High input of organic food and inorganic nutrients due to rainy seasons, when plant debris is swept into the sea by rivers, also promotes reproduction in shallow tropical and subtropical seas.

The life span of deep-sea foraminifera depends on the organic input by the phytoplankton bloom in spring and is thus longer than in shallow-living foraminifera, normally about 1 year. This is caused by a slow-down of life processes that saves energy.

The gardeners

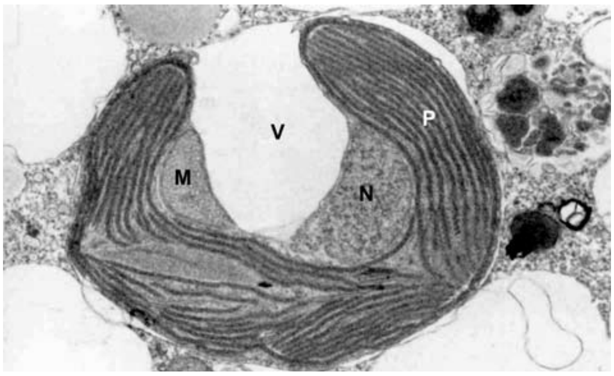
Foraminifera living today in shallow water are characterized by sizes that often considerably exceed the size of normal foraminifera (100 micrometer to 2 mm). While some groups grow to about 4 mm, other forms have tests that measure a few centimeters; the largest species today attains a size between 4 and 12cm. Thus, larger foraminifera are truly the largest single-celled organisms living today!

Beside the cell characters described above, which can be found in all foraminifera, the larger foraminifera also have intensively colored organic grains measuring between 4 and 20 micrometers. While the cytoplasm of a 'normal' foraminifer is uncolored or has an extremely weak brownish color, these tiny particles within the cytoplasm are responsible for an intensive coloring that is visible in every living larger foraminifer.

Based on this color, the identification of larger foraminifera as living individuals is easier compared to 'normal' foraminifera, where differentiation between empty tests and living individuals is difficult (because in those living foraminifera the tests are filled with more or less colorless cyctoplasm). Two methods are available to identify 'normal' foraminifers as living individuals. The first requires looking for activities. If pseudopods are not visible, the foraminifera have to be killed and then the cytoplasm made visible by special colors (i.e. Rose Bengal). This method is not necessary for living larger foraminifera, because they are naturally colored through the above-mentioned small particles.

What's the nature of these particles?

Investigation by high-resolution microscopes using the TEM (transmission electron microscope) has shed light on the nature of these particles.



Transmission electron microscope (TEM) image of a symbiotic microalgae (size = 0.0048 mm) within a foraminiferal cell. The chloroplast (P) responsible for photosynthesis surrounds the nucleus (N) and the mitochondrium (M). A large vacuole (V) is typical for storing the products of photosynthesis like glycerols and lipids (from Leutenegger 1984).

Every particle is separated from the cytoplasm of the foraminifer by a membrane. It possesses an own cell **nucleus** along with so-called **vacuoles**, which are large spaces for the storage of substances that are surmounted by membranes. These cells also contain special laminated organelles that are not found in the cytoplasm of normal foraminifera. These intensively colored organelles, named **plastids** or **chloroplasts**, are typical for plants cells because they are necessary for photosynthesis.

Therefore, every pigmented particle within the cytoplasm of larger foraminifera is a single-celled organism that is capable of photosynthesis. According to the extremely small sizes, these organisms are called **microalgae**.

The life form of microalgae within a larger foraminifer is known as **symbiosis**. Here, the larger foraminifer acts as the host and the small single-celled microalgae are the guests.

In symbiotic life, both partners have to obtain profit.

What's the profit for the host by housing microalgae within the test instead of eating them? To understand this, we have to look at the kind of food that microalgae produce and that foraminifera can use (instead of simply digesting the whole microplant).

How does photosynthesis work?

Plants cells have the capability to transform water (H_2O) and carbon dioxide (CO_2) into simple **carbohydrates**, mostly sugars, which are a balanced combination of carbon, hydrogen, and oxygen. This process needs energy that is gained from the sunlight. The chemical reaction is written as

$$n\,(H_2O) + n\,(CO_2) \xrightarrow{sunlight} n\,(CH_2O) + n\,(O_2)$$

and is called **photosynthesis** (φως = light, *σ ύ ν θ ε σ η* = combination). In a first step of photosynthesis, simple sugars known as **glycerols** (for example glucose with the formula $C_6H_{12}O_6$) are synthesized and later transformed into more complex carbohydrates. Such compounds include starch grains (found in potatoes) or cellulose, which strengthens the walls in plants cells.

Most single-celled algae produce, in a first photosynthetic step, much more glycerols or fats (lipids) than necessary for the life processes of the small algae. Sometimes, up to 80% of the glycerols and lipids are not used by the algae and released into the surrounding medium. When this medium is the foraminiferal cytoplasm (instead of seawater), then the foraminifer can directly use these excess glycerols and lipids as food. This ultimately yields energy by respiration, making the forminifera independent from capturing food.

Why plants have different colored pigments?

Photosynthesis starts with the transformation of sunlight into chemically bound energy. These processes are performed within the chloroplasts by the use of pigments.

Pigments are of different color. The pigment mostly used by plants is **chlorophyll *b***, which is characterized by an intensive green color. The related pigments **chlorophyll *a*** and **chlorophyll *c*** have colors ranging from brownish ocher to bluish to olive green. Other pigments, like **xanthophyllids, phycobilins** and **carotins**, are characterized by brown to purple to red colors.

While most higher plants like mosses, ferns, herbaceous plants, grasses, and trees have an intensive green color in their leaves due to the dominant chlorophyll b, lower plants like multicellular or single-celled algae show a variety of pigments in their cells or **thalli** (leaf-like structures in multicellular algae) and thus have different colors. Especially the large brown algae get their color from xanthophyllid pigments, mainly **fucoxanthin**. The purple color of the red algae is based on the pigment group phycobilin.

Color differences in the thalli or leaves depend on the absorption of light of different wavelengths. Red light with long wavelengths, which is best absorbed by green-colored pigments, penetrates the atmosphere down to the Earth's surface. Nonetheless, the sun's wavelengths change in the sea. The low-energy red light is rapidly absorbed in the uppermost surface water, while high-energy blue-green light with short wavelengths penetrates down to 150 m in clear ocean water. In these deeper parts, light is best absorbed by brownish to purple-colored pigments such as those represented in chlorophyll a, chlorophyll c, fucoxanthin, and phycobilins.

Therefore, multicellular plants living in the sea are distinguished near the ocean water surface by the dominance of green-colored organisms, like sea grass and green algae (for example the well-known sea salad *Ulva*). A transformation from brownish to red colors is characteristic for deeper-living algae (red and brown algae).

The single-celled organisms with chloroplasts that serve as symbionts for the larger foraminifera also show these tendencies. Larger foraminifera working as gardeners and living at different depth have to utilize this capability of their photosynthetic plants.

Therefore, the foraminifera work as gardeners at different depths in illuminated areas of the sea floor. They have to culture those plants adapted (that grow best or produce a maximum of glycerols) to specific light wavelengths.

What's the profit for microalgae living in a foraminiferal test?

Beside carbohydrates as energy resources necessary for life processes, all organisms, even plants, need inorganic molecules to synthesize complex organic macromolecules. The most important elements are nitrogen (chemical symbol ***N***), phosphorus (***P***), and sulfur (***S***).

Nitrogen is an important element in amino acids. Proteins are chains of amino acids having different lengths and structures. Nitrogen is also an important element in organic bases in nucleic acids, which are responsible for storing (DNA) and transporting (RNA) information to those places where the synthesis of inorganic or organic substances via proteins takes place.

Phosphorus is important in all cell membranes because they consist of phospholipids. Nucleic acids (DNA and

RNA) also need phosphoric acid, and phosphorus is an important element of the energetic reservoir ATP (adenosine triphosphate).

Sulfur is an important ingredient in some proteins and coenzymes (functioning together with a protein as an enzyme),

Beside these main inorganic elements, metallic elements like **magnesium** (*Mg*), **potassium** (*Ka*), **calcium** (*Ca*), and **iron** (*Fe*), as well as trace elements, are also essential for life.

Land plants get these important inorganic nutrients from the soil through roots by taking up water. Inorganic nutrients are either completely dissolved in the soil water, or they are bound as complex molecules like ammonium (NH_4) and nitrate (NO_3). Most of these molecules represent disaggregated products of higher organic molecules by animal digestion **(catabolism**). They cannot be used in the further production of the organism-specific organic macromolecules.

When farmers or gardeners culture plants they therefore need to provide sufficient inorganic nutrients. Especially plants growing in monocultures require large amounts of nutrients. Therefore, human gardeners and farmers fertilize the soil either by dunging and manuring or by applying artificial fertilizers.

All plants living in the sea can take up these nutrients directly from the seawater. Most nutrients are transported into the sea by rivers, explaining the rich algal presence in coastal areas.

On the other hand, nutrient uptake is more difficult for plants living in the upper 150 m of the sea, when the sea bottom is below 200 m. Ocean floors, however, lie between 2000 to 4000 m. Here, waste products of catabolism sink to the bottom and cannot be used by the single-celled phytoplankton living in the upper 150 m, where light is not absorbed and photosynthesis is possible. Because phytoplankton does not have 3000-m-long roots to take up nutrients from the sea floor, other mechanisms have to provide them with nutrients.

In polar and subpolar regions of the oceans as well as in 'normal' temperate seas, vertical mixture of cold with warm waters transports nutrient-rich bottom waters to the surface. This is not the case in the subtropics and tropics. Here, no mixture of the water masses occurs, and warm surface waters constantly overlie the cold deeper waters. Phytoplankton is extremely poor in such surface water because of missing nutrients. Therefore, clear and blue ocean waters dominate in the tropics and subtropics, because light penetrates the surface water without being absorbed by inorganic and organic particles. These oceans regions are called 'blue deserts' based on their lack of rich organic life.

Only along the west coast of continents in the subtropics, where trade winds transport the warm surface water westwards towards the ocean center, does cold and nutrient-rich deeper water surge up to the surface. Phytoplankton life is extremely rich in these '**upwelling**' regions, making room for abundant animals that feed either on the phytoplankton and multicellular plants, or feed on smaller animals. Upwelling regions are thus the best fishery sites.

Coastal shallow waters on the east side of continents in the tropics and subtropics are not nutrient-depleted when rivers transport nutrients into the sea, especially during the rainy seasons. Otherwise, coastal regions in the arid zone, where deserts are developed on the continent, lack this nutrient input by rivers. Correspondingly, the shallow waters here are depleted in inorganic nutrients. These regions are found mainly on the eastern side of continents. Examples include the Red Sea to the east of the Nubian Desert or the northeast coast of Australia.

Shallow waters around tropical islands that are located far from the continent are also characterized by poor inorganic nutrients. This is because rivers cannot bring in enough nutrients from the island, although these islands may have dense tropical vegetation.

Thus, unicellular as well as multicellular plants living in the sea have difficulties surviving in 'blue deserts' and must develop alternate strategies to inhabit these regions. Living as symbionts in a host, for example in stony corals, giant clams or a larger foraminiferal cells, provides the microalgae with inorganic nutrients, which are directly obtained from the host as waste products of its digestion.

A further profit for the plant as one partner of the symbiosis is the availability of the inorganic carbon necessary for photosynthesis. Land plants get inorganic carbon directly from the air, which is rich in carbon dioxide. But marine plants have difficulties because carbon dioxide is dissoluble only in cold, acidic seawater. In the alkaline tropical warm surface waters, this molecule is transformed into the unstable **carbon acid** (H_2CO_3), which is dissociated instantly into **hydrogen** (H^+) and **carbonate** (HCO_3^-) ions.

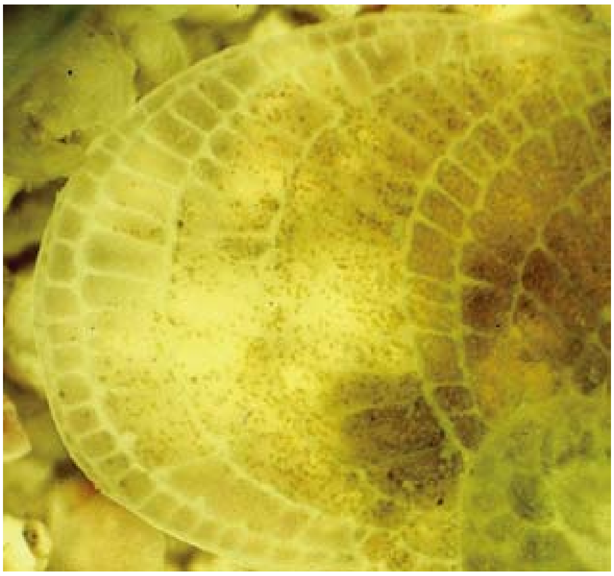
Therefore, warm temperate and tropical surface seawater is rich in hydrogen carbonate (HCO_3^-) and carbonate (CO_3^{2-}) ions, which can be used for the calcification processes of skeletons and shells in animals and plants:

$$Ca^{2+}+2HCO_3^- \Leftrightarrow CaCO_3+CO_2+H_2O$$

During the calcification process of the foraminiferal test, the second inorganic carbon ion that is not bound in the calcium carbonate can be directly used for photosynthesis by the microalgae. This process explains the continuous production of calcium carbonate skeletons of organisms housing symbiotic algae. This may result in enormous skeletons on a macro-scale (stony corals, giant clams) as well as on a micro-scale (larger foraminifera).

Therefore, larger foraminifers as gardeners provide their culture plants with inorganic nutrients and carbon ions in 'blue deserts', where they can grow and reproduce. The foraminifer gains profit from the plants by obtaining food in the form of simple sugars, or by feeding these plants in case of starvation.

The foraminifer *Planostegina* (size = 3 mm) from 90 m depth with retracted protoplasm, which is colored by symbiotic microalgae.



Details of the last chambers of *Planostegina*, where single small microalgae return to the final chambers after being disturbed.

Which plants do the gardeners culture?

There are three requirements for a gardener:

The first requirement is the size of the plant.

The plants have to be small-sized for transport between different test parts. Connections between the chambers of the foraminiferal test are often extremely small. The smallest are at 4μm (=0.004mm), allowing only the smallest microalgae to pass through. All foraminifera retract their cytoplasm to the inner test parts in case of unfavorable conditions of the surrounding seawater. The cytoplasm is then spread to the marginal chambers when conditions become normal.

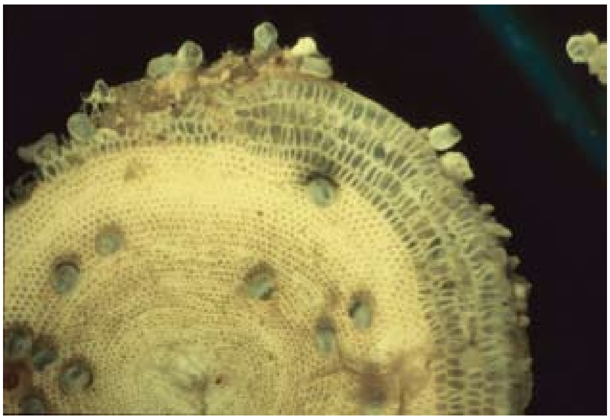
This requires the symbionts to move through small connections between the chambers during cytoplasm retraction and spreading. Only tiny, single-celled microalgae fulfill this condition.

The second requirement is to know which plant grows and reproduces best in the environment in which the foraminifer lives.

Conditions for best growth and reproduction are, on the one hand, optimal wavelengths for the plant to photosynthesize. On the other hand, the plant has to get enough inorganic nutrients like nitrogen, phosphorus, and sulfur for constructing higher organic substances. This requires the gardener to serve these inorganic nutrients to the plant.

How do foraminifera acquire the plants?

The easiest way is by asexual reproduction. After multiple fission of the foraminifers' cell nucleus into several hundred nuclei, every nucleus is surrounded by parental cytoplasm containing all necessary organelles. This process also splits the symbiotic algae such that every young foraminiferal cell obtains a few symbiotic algae; these algae then become the base of the new plant stock of the growing foraminifer.



Reproducing *Amphisorus* (test diameter = 40 mm) with numerous 2-chambered offspring.

Hatched *Amphisorus* (size = 0.15mm) incorporating small symbiotic algae originating from the parental organism.

This transfer is not possible in sexual reproduction, because gametes do not have enough space for organelles outside the cell nucleus, and certainly no space for symbiotic algae. Therefore, the young diploid agamonts have to pick up free-living algae from the seawater and ingest them by phagocytosis.

The foraminifer must then decide which ingested microalgae can be used as symbionts, and which are utilizable as food. The decision process is based on biochemical reactions in which the foraminifer recognizes the appropriate symbiotic algae by specific enzymes.

After recognition as a symbiont, so-called **lysosomes**, i.e. membrane-surrounded bobbles carrying digestive enzymes, do not conjugate with the **phagosome** carrying the microalgae (because in the case of conjugation the microalgae will be digested). The membrane separating the algae from the foraminiferal cytoplasm originating from the phagosome is named **symbiosome**.

The cultivated plants

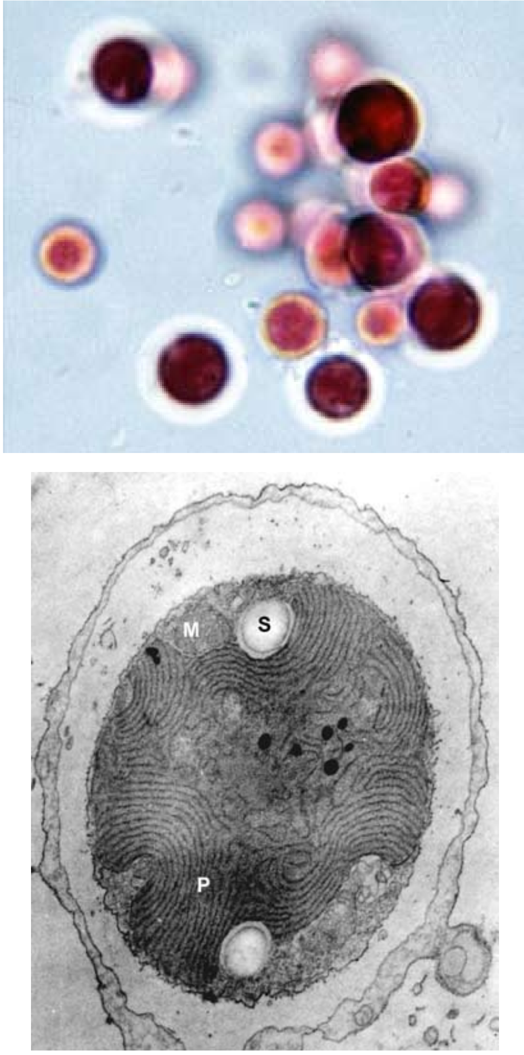
Let's have a look at the different plants the larger foraminifera can decide to harbor:

Red Algae (Rhodophyta)

The first group of marine algae fulfilling these conditions belongs to the group of Rhodophyta, the red algae. Normally, red algae are multicellar plants of different size, growing up to 50 cm. The *Corallinacea*, a group of red algae, show strong calcification between their cells and are responsible for strengthening the skeletons of dead coral branches: they cement both the small and large interspaces between these branches. Therefore, the stability of the reef crest of coral reefs is based mainly on cementation by coralline algae.

Not all red algae necessarily have a red color originating from the photosynthetic pigment group phycobilin: other pigments like chlorophyll a and chlorophyll c are present within the red algae in different proportions, leading to brownish or even dark green colors.

Only a single red algal species named *Porphyridium purpureum* fulfills the requirements for becoming a symbiotic microalgae in foraminifera. This is because the whole individual is a single cell. The size ranges from 5 to 6µm. The pigment phycoerythrin of the plastids, a phycobilin, is responsible for the plant's intensive purple color. Phycobilins reflect red light and absorb blue-green light with short wavelengths, which penetrates down to 200m in clear ocean water. Therefore, *Porphyridium purpureum* works best in energy-rich, short wavelengths. On the one hand, short wavelengths are dominant in deeper water because red light with longer-wavelengths is absorbed at the water surface. On the other hand, the foraminiferal test also absorbs long wavelengths through special test structures in extremely shallow water. In this case, only short wavelengths – meaning blue green light – penetrate the test.



Light microscope and TEM image of the single celled red algae *Porphyridium* (diameter = 0.0036mm). The chloroplasts (P) dominate the cell, where 2 stark grains (S) and mitochondria (M) are visible (from Lee 1990).

Living *Dendritina* (size = 1.2 mm) colored by the purple symbiotic microalgae *Porphyridium*.

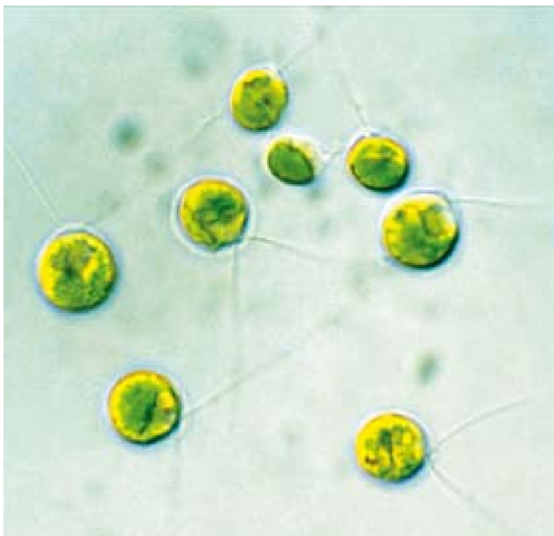
Unlike in other symbiotic microalgae, the symbiosome membrane does not surround *Porphyridium purpureum*. Reproduction of *Porphyridium purpureum* is always asexual through multiple fissions.

Superfluous photosynthates in the form of glycerols are spread into the surrounding medium, but the amount of glycerols is apparently not very high. Therefore, feeding on glycerols produced by red algae is insufficient for the foraminiferal host. The foraminifera culturing this plant have to capture additional food for themselves and also to provide the microalgae with inorganic nutrients.

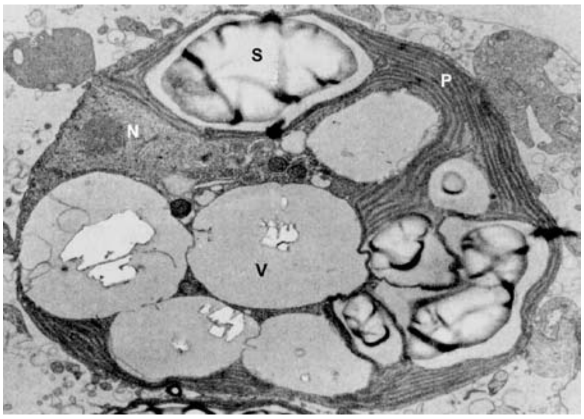
Green Algae (Chlorophyta)

Members of only one genus within the single-celled green algae are used as symbionts in larger foraminifera. All species of the genus ***Chlamydomonas*** possess two flagellae in free-living forms, which allows active movement in the seawater. The size is about 10 micrometers and the flagellae are approximately the same length as the cell body. Reproduction in free-living *Chlamydomonas* is asexual by multiple fissions and sexual by conjugating isogametes, which look identical to normal cells. There are no morphological differences between gametes and normal (vegetative) cells.

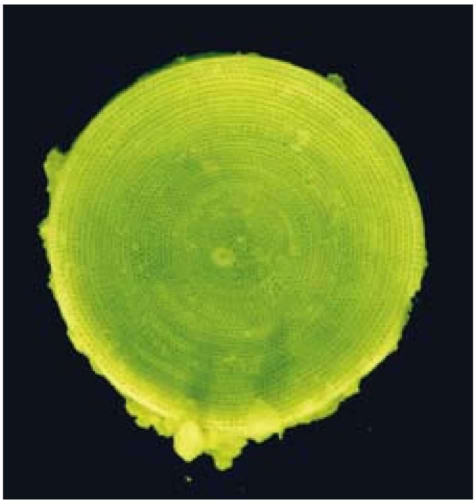
Possessing the pigments chlorophyll *a* and especially chlorophyll *b* in the plastids allows green algae to absorb red light. Therefore, larger foraminifera can use them only in the shallowest sea as “cultures” because photosynthesis in deeper regions, i.e. below 40m, becomes difficult as red light is absorbed in the upper parts by water molecules.



The single celled free living green algae *Chlamydomonas* (body size = 0.015mm) possess 2 flagella for active movement.



TEM micrograph of the endosymbiontic green algae *Chlamydomonas* (diameter = 0.008 mm). Cup shaped chloroplasts (P), the nucleus (N), Vacuoles (V) and stark grains (S) are visible (from Leutenegger 1984).



Living *Parasorites* (size = 4 mm) colored by the green symbiotic microalgae *Chlamydomonas.*

Chlamydomonas loses the flagellae within the foraminiferal body because active movement is unnecessary in the host. Reproduction of *Chlamydomonas* within the cell is always asexual by multiple fissions.

The carbohydrate mannitol released by *Chlamydomonas* into the surrounding medium is a combination of sugar and alcohol. The proportion of superfluous photosynthates that are released into the foraminiferal cyctoplasm is not high. Therefore, the foraminifera housing green algae have to take up additional food.

Furthermore, *Chlamydomonas* cells are characterized by a large amount of starch grains, again a carbohydrate, stored in special vacuoles. The foraminiferal host uses these grains either by dissolving the protective cell membrane of the microalgae and digesting only the starch grains or by totally digesting the tiny plants.

Dinoflagellates (Pyrrhophyta)

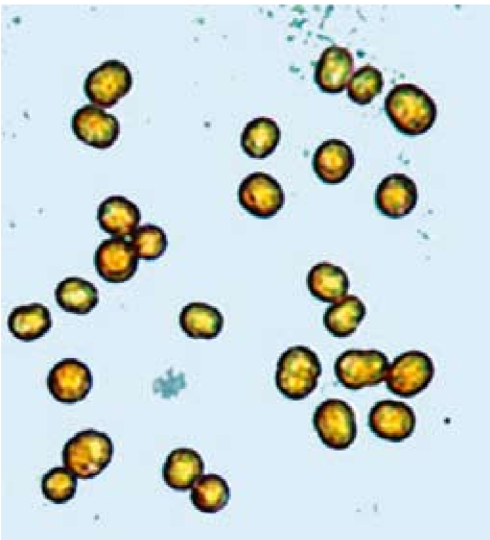
These microalgae are very abundant in the oceans today, representing a high proportion of the phytoplankton. The single-celled individuals possess two flagella, which allows active movement in the water. While one flagellum is responsible for movement, the other surrounds the cell like a girdle, stabilizing the cell during movement.

Why do these small plants need a girdle flagellum for stabilization? This is based on the grotesque form of the cells, which is caused by various cellulose plates covering the cell body. These plates give dinoflagellates the appearance of armored individuals. Free-living dinoflagellates differ in size and form. Chlorophyll *a* and *c* are the main pigments in the plastids, allowing a range of colors from ocher to olive green and bluish, but never the intensive green of chlorophyll *b*.

Many animals living in the tropics use one group of dinoflagellates as symbionts. Especially organisms with strong calcareous skeletons or shells (that do not move or are more or less fixed to the sea-bottom like stony corals or giant clams) exclusively use dinoflagellates as symbionts. In these cases, the microalgae do not inhabit the cell plasma, but live within the tissue of the multicellular organisms. The beautiful color of stony corals or the shell edges of the giant clam originate from the different pigment colors of the microalgae.

The absorption of light by the olive- to bluish-colored pigments chlorophyll *a* and *c* is profitable for photosynthesis in deeper environments, but absorption in the shallowest waters is also possible. Like in humans, permanent exposure to UV-irradiation causes cancer. Dinoflagellates can decompose the highest-energy UV-light into harmless wavelengths using special proteins, much like sun blockers for the human skin. They therefore protect the genetic material of the host, which is concentrated in the nuclei, from this dangerous light. This enables foraminifera, corals and giant clams to live in the shallowest sea directly exposed to the sunlight.

Since dinoflagellates are the dominant symbiont group within multicellular animals, they received the name **zooxanthellae**, a combination of animal (zoon = ζώον) and the yellow color (chansos = ξανσοσ). The zooxanthellae lose their cellulose plates when living in the foraminiferal cell or in animal tissues. The naked cells keep their flagellae for active movement within the tissue or cell, but they often lose these organelles, especially when active movement is unnecessary. This is the case when the zooxanthellae are passively transported by the cytoplasm.

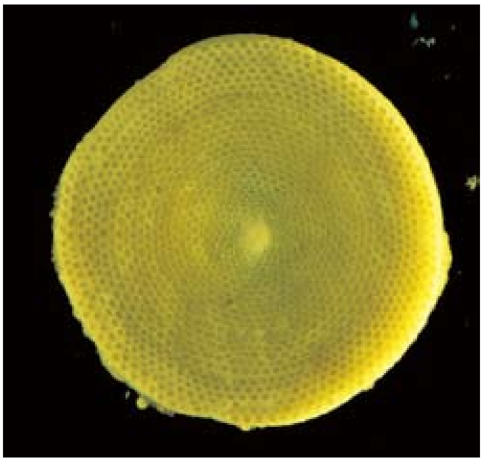


The dinoflagellate algae *Symbiodinium* is used as a micro-symbiont in many invertebrates like stony corals and giant clams (mean body size = 0.012 mm).

TEM micrograph of the endosymbiotic dinoflagellate algae *Symbiodinium* (diameter = 0.007 mm). Chloroplasts (P), the nucleus (N) with chromosomes, vacuoles (V) and the base of flagella (F) are visible (Leutenegger 1977).

Zooxanthellae are much smaller than free-living dinoflagellates, with sizes ranging between 4 and 20 micrometers. Most zooxanthellae belong to the genus ***Symbiodinium***. Larger foraminifera share a single *Symbiodinium* species with stony corals and giant clams, while the remaining two *Symbiodinium* species are restricted to larger foraminifera.

Reproduction in *Symbiodinium* seems to be asexual in the foraminifera, since sexual reproduction has not yet been reported.



Living *Amphisorus* (size = 3.8 mm) colored by the dinoflagellate symbiotic microalgae *Symbiodinium*.

The zooxanthellae produce mainly fats (lipids) as superfluous products of photosynthesis, which are released into the foraminiferal cyctoplasm; glycerols are less important than in the red and green algae. Although the proportion of photosynthates that are set free is higher (~25%) compared to red and green algae, larger foraminifera and all multicellular animals housing dinoflagellates have to take up additional food for respiration and to synthesize complex organic molecules.

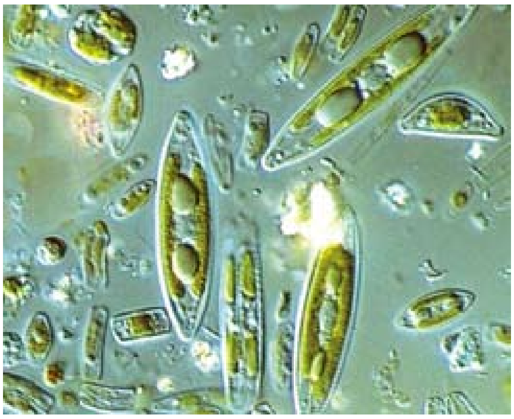
Diatoms (Bacillariophyta)

These small organisms are the most abundant microalgae in today's oceans, representing the highest proportion of phytoplankton. Thus they are the main primary producers - this means that inorganic carbon as represented in carbon dioxide is transformed into organic carbon in the form carbohydrates in the oceans. Diatoms also live on the sea floor. They can cover the bottom with mats in the shallow seas, where light penetrates to the sea floor and enables photosynthesis there.

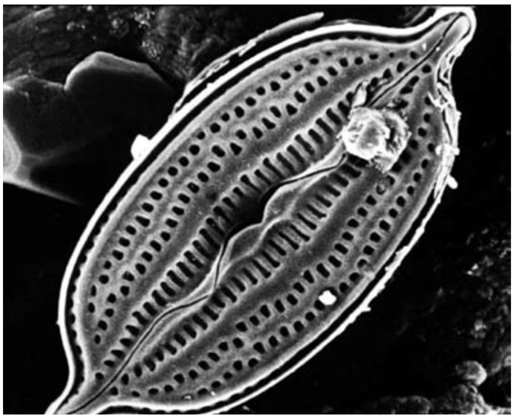
The single-celled individuals protect their cell bodies with box-like shells, called frustula, consisting of siliceous material (silicic acid). Diatoms living on the sea floor (benthic diatoms) possess frustula in the form of shoeboxes, whereas the planktic forms are distinguished by frustula that resemble hat boxes due to their circular form.

The size of a diatom cell is not constant, but changes continuously in becoming smaller during asexual reproduction. Maximum size is between 10 and 100 micrometers, making them useful as symbionts in larger foraminifera.

Pigments of the chloroplasts in diatoms are similar



Free living diatoms of different size.



Scanning electron microscope (SEM) micrograph of a frustulum (= shell) of a diatom (size = 0.022 mm) attached to a foraminiferal shell.

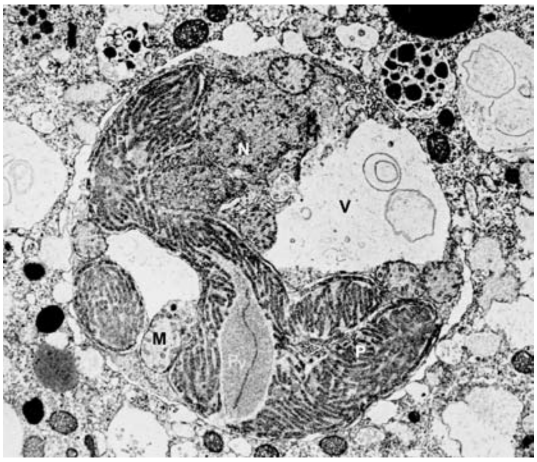
to dinoflagellates, consisting of chlorophyll *a* and *c*, but lacking the green chlorophyll *b*. Ocher to ocher-greenish colors predominate in diatoms, allowing photosynthesis with high-energy blue-green light, which is absorbed by these pigments. Diatoms are the only phytoplankton group that photosynthesizes under extremely weak light. While all other phytoplankton is restricted to the so-called euphotic zone, where the depth limit is round about 150 m in clear, tropical ocean water, diatoms show a positive photosynthetic rate (i.e. the proportion of organic carbon gained through photosynthesis is higher than the loss through respiration) down to 250 m. This zone between 150 and 250 m with extremely weak light is called the **dysphotic** zone.

Especially diatoms living on the sea floor demonstrate different grade of dependence from light intensities. This means that they reproduce best under specific light conditions. Some diatoms prefer the high intensities found near the water surface. Light intensities are measured in Micro-Einstein, counting the number of photons striking a standard area. These intensities change due to seasons, geographical latitudes and the day-night cycle. In the tropics, an optimum of about 2000 Micro-Einstein is attained during summer noon. The absorption of light intensities through water particles in clear ocean water reduces light intensities to 10 Micro-Einstein at 150 m depth during summer noon. Some diatoms prefer these low light intensities, which means that they grow best under extremely low light intensities.

This advantage of partitioning the whole photic zone by diatoms preferring distinct light intensities makes them the ideal symbiotic microalgae, especially for larger foraminifera. As opposed to other algal groups, where only a single genus (the red algae *Porphyridium*, the green algae *Chlamydomonas*, and the dinoflagellate *Symbiodinium*) is used as an endosymbiont, several genera and species of diatoms can be used by larger foraminifera. This depends on the restriction of diatoms to different light intensities. Larger foraminifera that prefer extreme shallow water have to use other diatoms as endosymbionts than foraminifera living in quiet water with low light intensities. This is problematic for those gardeners that try to cover a wide range of light intensities, living from close to the surface down to the deeper, light-depleted parts. Such gardeners have to change the plants. The same species is able to harbor diatoms preferring high light intensities in the shallow zone, and changes to symbionts preferring lower light intensities when inhabiting deeper parts.

Diatoms used as endosymbionts by larger foraminifera do not need frustula for protection, thus they are naked. Transport within the foraminiferal cyctoplasm is passive because the diatoms lack mechanisms for active movement. Reproduction is always asexual by simple fission. Since the endosymbionts are not restricted by a frustulum, they maintain their size during the series of asexual reproduction. Normal size is between 4 and 10 micrometers.

Since they are not longer enclosed by a frustulum, they can change their form, allowing them to pass through the smallest chamber connections with a minimum diameter of 4 micrometers. The different genera and species can be identified by setting the diatoms free and culturing them on an appropriate medium. The free symbionts suddenly build frustula, enabling their identification based on the highly diverse forms of frustula. Representatives of the genera *Fragilaria, Achnanthes, Cocconeis, Amphora, Entomoneis, Navicula,* and *Protokeelia* have hitherto been described. More are expected in the future as research on these micro-plants progresses.



TEM micrograph of an endosymbiotic diatom (diameter = 0.008 mm). Chloroplasts (P), mitochondrium (M), the nucleus (N) and the large vacuoles (V) are visible (from Leutenegger 1977).

Living *Amphistegina* (size = 3 mm) colored by symbiotic diatoms.

Diatoms release the highest amount of produced photosynthates (40 to 80%) into the surrounding medium. These photosynthates consist mainly of lipids (~50%) and glycerols (~10%). Therefore, the foraminiferal host becomes independent of additional food, and food uptake is often restricted to the necessary uptake of inorganic nutrients.

The construction engineers

Larger foraminifera acting as gardeners have to use their houses to protect themselves against the surrounding world, but also as cultivation greenhouses for their 'plants'. Therefore, beside gardeners, they can also be regarded as construction engineers.

Three general principles are important for all constructions, and thus also for microscopic glasshouses:

First, the constructions must be **functional**, fitting all the demands for the life of the foraminifer. Therefore, glasshouses have to be convenient and simplify the life of the host as well as allow the 'gardener' to cultivate 'plants'.

Second, the **building material** of glasshouses is important, on the one hand for strengthening them against destruction by water movement, and, on the other hand, for making parts of the walls transparent to enable the light penetration necessary for the 'plants'.

Third, **constructional** aspects are important to enable accommodation of the glasshouses to the environment and fulfilling all functional demands. Basic constructional plans exist in foraminifera; they have to be modified by the 'gardener' to fulfill the functional requirements for cultivating plants.

The functional aspect

The function of the construction has two main points. The first is to protect the gardener against the environment, hindering being eaten by predators or becoming infected by bacteria or viruses. Large predators can be snails, scaphopods, and fishes, which all consume the whole cytoplasm; examples of small predators that attack only parts of the foraminifera are small worms, predatory relatives (other smaller foraminifera), or ciliates (relatives of *Paramecium*).

The second point is to allow connections between the cell body inside the test and the surrounding seawater, enabling the transport of nutrients and metabolic products. The construction must also be conducive to regulating the metabolism within the test and to providing the microalgae with necessary nutrients in an optimal way. This makes test openings and connections between test parts important.

Construction openings

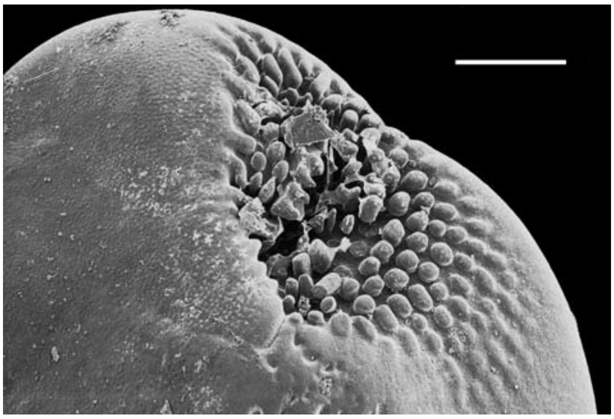
There must be a number of openings between the inner part of the construction, where the foraminifer lives and retracts under unfavorable circumstances, and the outside, allowing the penetration of the cytoplasm to form reticulopods.

The primary role of these foot-like structures in 'gardeners' is to attach the construction to a base, which can be stones, broken and dead coral peaces, sea grass leaves, or thalli of sea weeds. Therefore, additional elements improving the fixation of pseudopods to the substrate are developed around the openings, or these openings are subdivided or multiplied. The fixation of a glasshouse is always temporarily; thus, under poor conditions like low light intensities or inadequate substrate, the larger foraminifer can move to more appropriate places.

Beside this possibility to change localities, it becomes important to dig into or out of the sediment, for example sand (grain size between 0.063 and 2 mm) or silt (0.0039 to 0.063mm). Gardeners living on coarse sand sometimes dig into the sediment to stabilize the construction. In fine-grained sand and silt, digging below the surface helps protect the gardeners against predators. When strong storms dislodge gardeners from hard substrate or transport them in sands, they become suspended in the water column like other sediment grains. This means they are transported by the storm currents and ultimately buried in the sediment. In such cases, the foraminifers have to dig out of the sand using their pseudopods.

The second role of the reticulopods is to capture food. Some 'gardeners' need this type of food (either living microalgae or organic remains known as detritus) additionally to the nourishment they get directly from the symbiotic 'micro-plants' by digesting them or feeding on the excessive photosynthates produced by the plants. Otherwise, uptake of a small amount of food is always necessary for gardeners to provide 'micro plants' with inorganic nutrients like nitrogen and phosphorus. To obtain enough food in large-sized tests (>1 cm), many openings for the penetration of reticulipods are necessary to increase the chances for food capturing.

SEM micrograph of *Dendritina* (scale bar = 0.1 mm) showing multiple test openings (apertures).



SEM micrograph of *Amphistegina lobifera* (scale bar = 0.1 mm) showing a structured aperture.

Therefore, the number, form, and position of openings allowing penetration of the cytoplasm depends on the necessity for fixation to the substrate, movement on or in the sediment, and food capture.

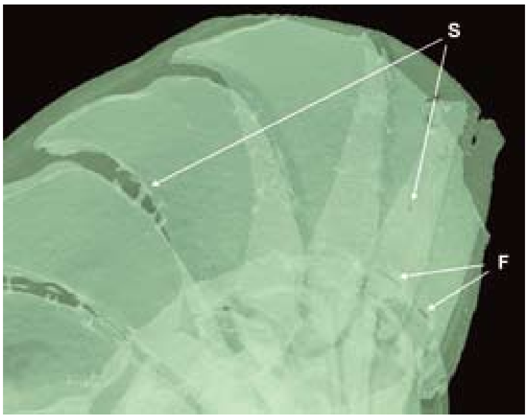
Connections within the construction

Since chemical reactions during metabolic processes are improved in small, delimited volumes of the cytoplasm, constructions that enclose large cytoplasm bodies have to be divided into smaller units. These so-called compartments are separated by walls. Connections between compartments are thus important for the directed cyctoplasm flow.

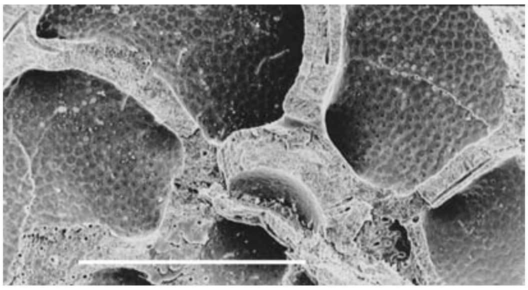
Gas molecules like the oxygen necessary for respiration are transported by that flow to the mitochondria, where ATP-molecules, the energy units, are produced. Subsequently, these energy-carrying molecules have to be transported to those sites where substances are synthesized, because any synthesis requires energy. The carbon dioxide resulting from the respiration process has to be transported to the plants, which can directly use them for photosynthesis.

The information transfer by chemical signals from the environment or any compartment of the glasshouse to the command centers (nucleus), and vice versa, requires a regulated cytoplasm flow within the complex construction. This calls for an organized system of openings connecting the small compartments to enable the shortest route of information flow between any compartment of the cell and the regulation center.

A further important function of the construction is to allocate the algae into an optimal position for gathering light, a prerequisite for photosynthesis. A wide space just below the glassy windows has to be supplied for the microplants, enabling them to attain optimal light. Additionally, tiny caves called 'egg-holders' help fixation of microalgae just below and partly within the test wall. This protects the symbionts from the cytoplasm flow in the compartment centers.



Micro-Computer Tomography of the last chambers of *Operculina* that are connected by foramina (F) at the base of the septa separating the chambers and by stolons (S) randomly distributed on the septal area (photo A. Briguglio).



Sectioned initial chambers of *Operculina* (scale bar = 0.1 mm) showing "egg-holder" structures at the inner chamber surface, where the symbiotic algae are positioned and thus protected from the foraminifers' protoplasm (SEM micrograph by courtesy of L. Hottinger).

The building material

The basic material of constructions like greenhouses made by humans is not restricted to a single type. Any building is composed of various basic materials such as boards, blocks of stones, bricks, concrete or other types of construction material. Most greenhouses constructed by humans consist of iron or wooden beams and girders, where large glass windows close up the inner part of the greenhouse and protect it from weather conditions. Allowing the penetration of sunlight creates an inner climate, whereby different blinds regulate the intensity of sunlight that reaches the plants.

Similar to the buildings erected by humans, the foraminifera are not restricted to a special type of material as basic modules, but use different minerals for constructing test walls. The best material for constructing transparent tests should be silicic acid (SiO_2), which is used by various organisms as skeletal material. Silicic acid – the main component of glass windows made by humans – allows the formation of different skeletons and shells, like the complex frustula of the diatoms, because it can crystallize in an amorphic manner (opal) without preferred crystal axes. Unfortunately, in surface waters of tropical and temperate oceans, organisms can only use silicic acid as an endoskeleton. There, organic cytoplasm in single-celled organisms (like diatoms and radiolaria) or tissue in multicellular organisms (like sponges) protect the mineral from the aggressive seawater. Silicic acid dissolves in contact with the alkaline seawater that dominates the surface ocean waters in warm climates.

The basic material of skeletons and shells used by most organisms in warm, alkaline seawater is therefore calcium carbonate ($CaCO_3$). The basic module of the foraminiferal test consists either of a single, tiny crystal of calcium carbonate. It can also consist of foreign particles, which are taken up from the surrounding sea bottom, fixed by an organic or inorganic cement, then by a calcareous cement. The latter wall structure is similar to concrete material, where stones are also fixed by calcareous cement resulting in compact and firm test walls. The use of organic cements yields more flexible test walls.

Calcium carbonate is not amorphic like opal (SiO_2) but crystallizes along three preferred axes. Light striking perpendicular to the crystal surface is non-refracted only in the direction of the optical axis; otherwise it is refracted due to the high refraction index of calcium carbonate. This is important for the construction of transparent wall structures. Since the single calcium carbonate crystal used by foraminifera for wall construction is extremely small (1 to 5 micrometers), the transparent walls necessary for the glasshouse effect can be obtained through extremely thin walls consisting of only a few layers of calcium carbonate crystals. In another strategy, transparency in thick walls is possible when the tiny crystals are arranged with all optical crystal axes oriented perpendicular to the test surface.

Not all basic modules for test wall constructions developed by foraminifera in their long geological history can be used by larger 'gardening' foraminifera. One condition for the test wall is their composition of calcium carbonate crystals. Because warm surface seawaters are depleted in carbon dioxide, the synthesis of calcium carbonate by the foraminifera improves photosynthesis of the micro-algae by providing the necessary inorganic carbon ions during the calcification process.

Today, such larger gardeners use only two types of basic modules. Both 'bricks' are based on calcium carbonate ($CaCO_3$) in the modification known as **calcite**. They differ, however, in their content of additional magnesium carbonate ($MgCO_3$), which is incorporated in the crystal lattice of the mineral. A proportion of magnesium up to 4% is called **low magnesium calcite**, while **high magnesium calcite** can have a content of 23% magnesium.

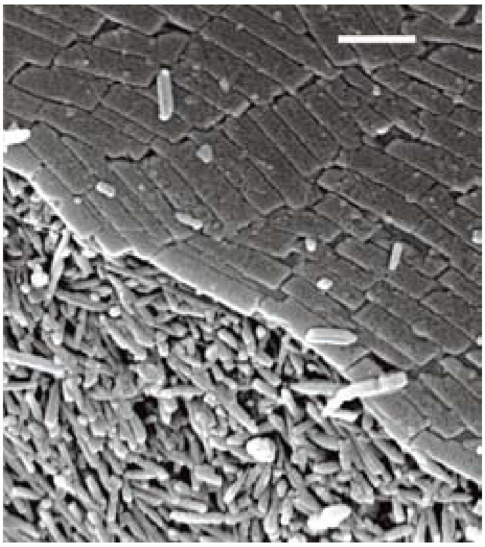
According to these two types of minerals used in test wall construction, foraminifera working as greenhouse gardeners can be differentiated into two groups. Beside differences in the crystals, the formation of these 'bricks' – a process termed **biomineralization** − also differs.

'Bricks' of high magnesium calcite

The single crystal is needle-shaped, where the optical axis corresponds to the longitudinal axes of the needle. Its length is between 1 and 3 micrometers, but each foraminifer using this type of crystal retains a constant length in all crystals. If a foraminifer uses crystals of 1.3-micrometer length, then all crystals used for the test wall are of that precise length. The diameter of the needles can vary between 0.4 and 0.6 micrometers but is also kept constant within one species.

Needles are formed within the foraminiferal cell in dictyosomes and then transported through 'Golgi-vesicles' to the site where a new test wall has to be formed.

The arrangement of these equally sized needles in the wall is completely irregular and chaotic. This is advantageous in two ways. First, the interstices between



SEM micrograph showing the broken test of the porcelaineous foraminifer *Quinqueloculina* (scale bar = 0.001 mm) with irregularly ordered calcite needles of the inner wall and the smoothed surface caused by plate-like needles arranged like a parquet floor (photo C. Baal).

the crystals are filled with organic material, allowing the penetration of gas molecules like oxygen or carbon dioxide. Therefore, no special openings for the interchange of gases during respiration are necessary. Second, the complete disorder of the thousands of optical axes leads to a total light refraction and reduces the penetration of light through thin test walls.

On the inner and outer surface of the test wall, the needle-shaped crystals lose their disorder. Here, a different type of crystal is produced. It results from the ordered arrangement of crystal needles parallel to the surface and from fusion into larger units. The resulting arrangement is similar to a parquet floor, with the same smooth surface but on a micro-scale! This means 10,000 times smaller then the wooden parquet floor in human rooms and halls!

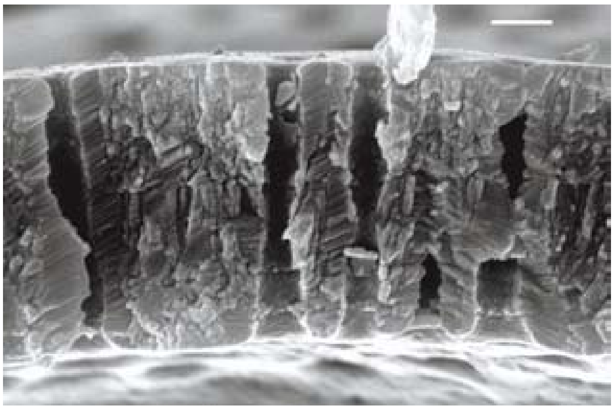
The total reflection of light in combination with a completely smooth surface gives these tests the appearance of porcelain coffee cups at the microcosm level.

This condition allows 'normal' foraminifera with **porcellaneous** walls to live exposed to extreme sunlight, for example in the shallowest seas of the tropics and warm temperate seas. This is because the test wall protects the foraminiferal cell from the injurious UV-light. The greenhouse gardeners with this wall structure must construct stable tests, where light can penetrate through the test walls. They therefore regulate light penetration by thinning the test walls at those test parts where the micro-plants are concentrated. This yields enough light for the symbionts but protects the foraminifera's genetic material. It does this by keeping the cell nucleus, or often a bundle of nuclei, in shadowed areas protected by the thicker test walls or in the center of the test.

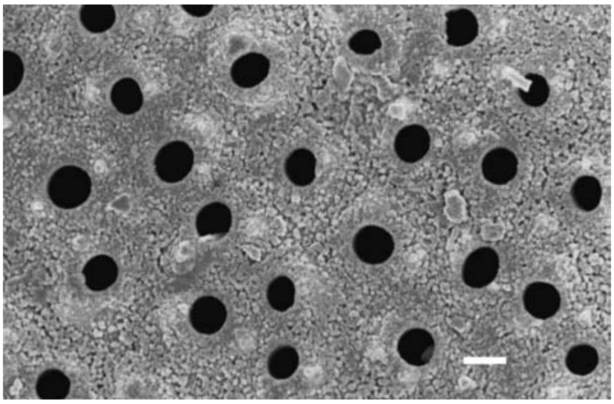
'Bricks' of low magnesium calcite

The single crystal is extremely small and can differ in size. The wall is formed by an ordered arrangement of small crystals to larger crystal units. Within such a unit, all crystals have the same orientation of the axes and their surfaces are in contiguous contact, with no interspaces between the crystals. Therefore, gas exchange between both sides of the wall is impossible and special openings − so-called **pores** − have to be constructed to enable gas exchange.

Low magnesium calcite crystals and crystal units are not formed within the cell in dictyosomes, but crystallize in a space bordered by two organic layers, which form the new



SEM micrograph showing the transparent (hyaline) test wall of the foraminifer *Ammonia* (scale bar = 0.001 mm) broken perpendicularly to the surface with blocks of ordered calcite crystals. Gas exchange between the outside and inner test is provided by pores (photo C. Baal).



SEM micrograph showing the surface of the transparent (hyaline) test wall of the foraminifer *Operculina* (scale bar = 0.001 mm) demonstrating the density of pores.

chamber wall. The inner layer acts as the starting place for the crystallization, and growth of the crystal units continues until the second layer terminates crystal growth.

When all optical axes of crystal units are oriented perpendicular to the surface, incident light can pass in a non-refracted manner through thick test walls. Even thick tests are completely transparent. This so-called **hyaline** wall structure is preferable for gardeners living in deeper regions, where light is weak for photosynthesis by the microalgae. At those light-depleted regions, the gardeners develop special light-intensifying structures.

The construction plan

Although a few foraminifera − some of them live in freshwater lakes − do not develop tests in which to hide, the vast majority construct tests of various forms and sizes (Figure 4).

The basic elements of tests are single tubes or spheres. Tubes are either open at both sides or closed on one side, while globular tests have a simple rounded opening. These test openings are called **apertures**.

Again, a few foraminifera leave those single-chambered tests when they grow larger. They briefly live naked like amoebas, grow, and then construct a new test adapted to their new size.

Most foraminifera overcome this problem of test-leaving during growth by adding a larger chamber to the older test part and keeping the connection between the chambers by openings, the **foramina**. These foramina are the former apertures in simple tests. In most foraminifera with tests, growth leads to chambered forms, whereby the basic chambers can be either tube-shaped or spherical.

Differences in the geometrical order of chambers during growth lead to an extreme variety of test forms. Straight tests are constructed when consecutive chambers are arranged along a straight or slightly curved line. These tests are at a disadvantage in environments with high water energy or sediment motion because they can easily break. Therefore, rounded and more stable test are constructed by different modes of chamber sequence. The arrangement can be irregular like a ball of string (**streptospiral**). More commonly it coils in a plane (**planspiral**) like the cephalopod *Nautilus*, or coils in conical form along an axis (**trochospiral**), comparable to snails.

Starting from this basic construction plan, the gardeners − as architects − have to build greenhouses with a large surface area that enables light penetration for their plants through broad ‘windows’. This is especially important in deeper regions, where light is weak.

A solution to this problem is to construct large and very thin, flat tests that exhibit a high proportion between cell surface and volume. Additionally, these constructions have to be separated into small, equally sized compartments−but with large windows−to support biochemical processes during metabolism.

How can this be done, considering the restriction of possessing only the above basic construction plans? Should a series of chambers be built step by step in an irregular manner, or arranged in a coiling plane, or arranged along a coiling axis? The first and the third solution are inappropriate for constructing flat tests, leaving only a single solution: planispiral enrollment - coiling around an axis in a coiling plane (Figure 5).

The simplest solution is to start with the first chamber, the proloculus. All succeeding chambers are arranged step

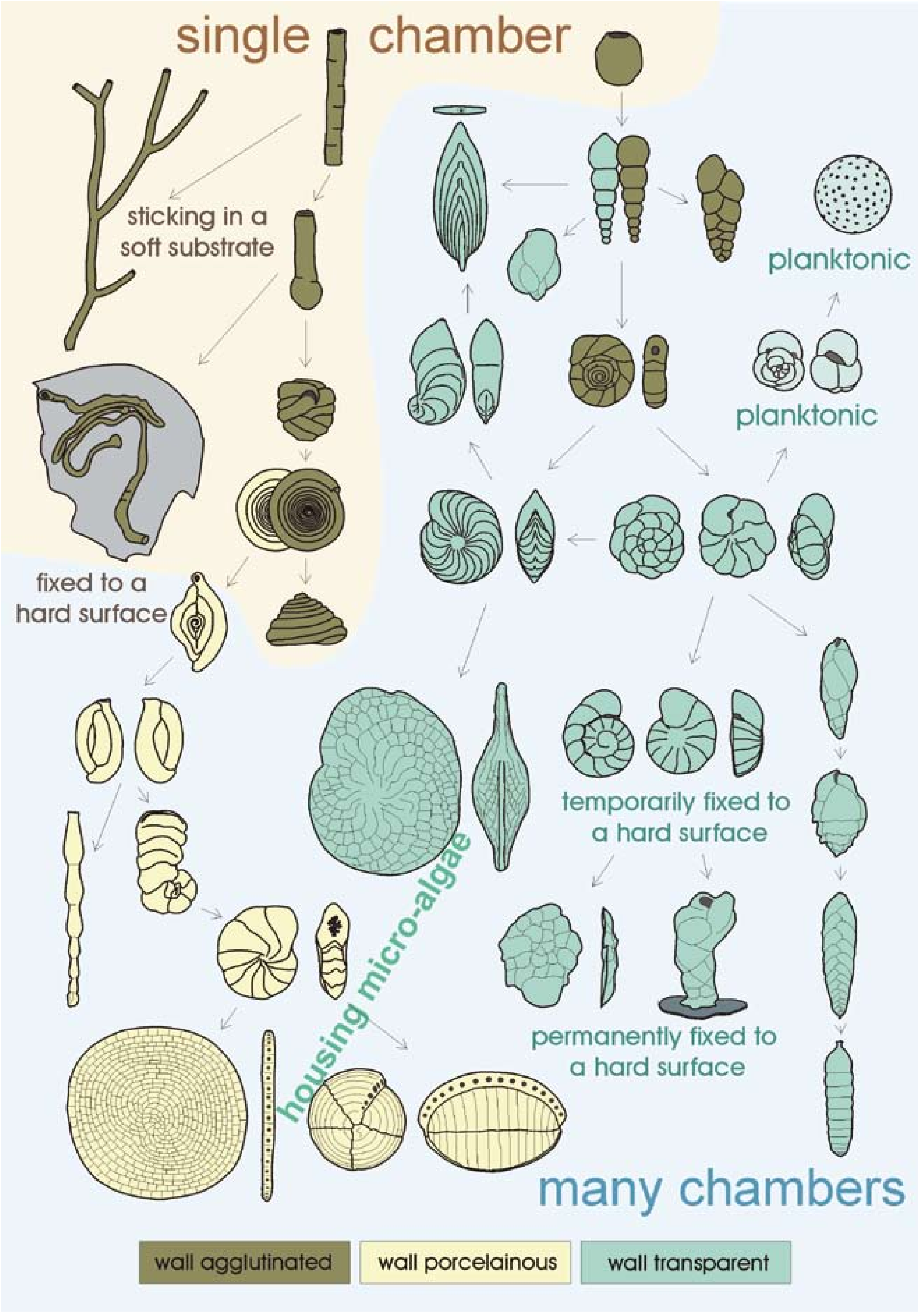


Figure 4. Tendencies in foraminiferal test construction.

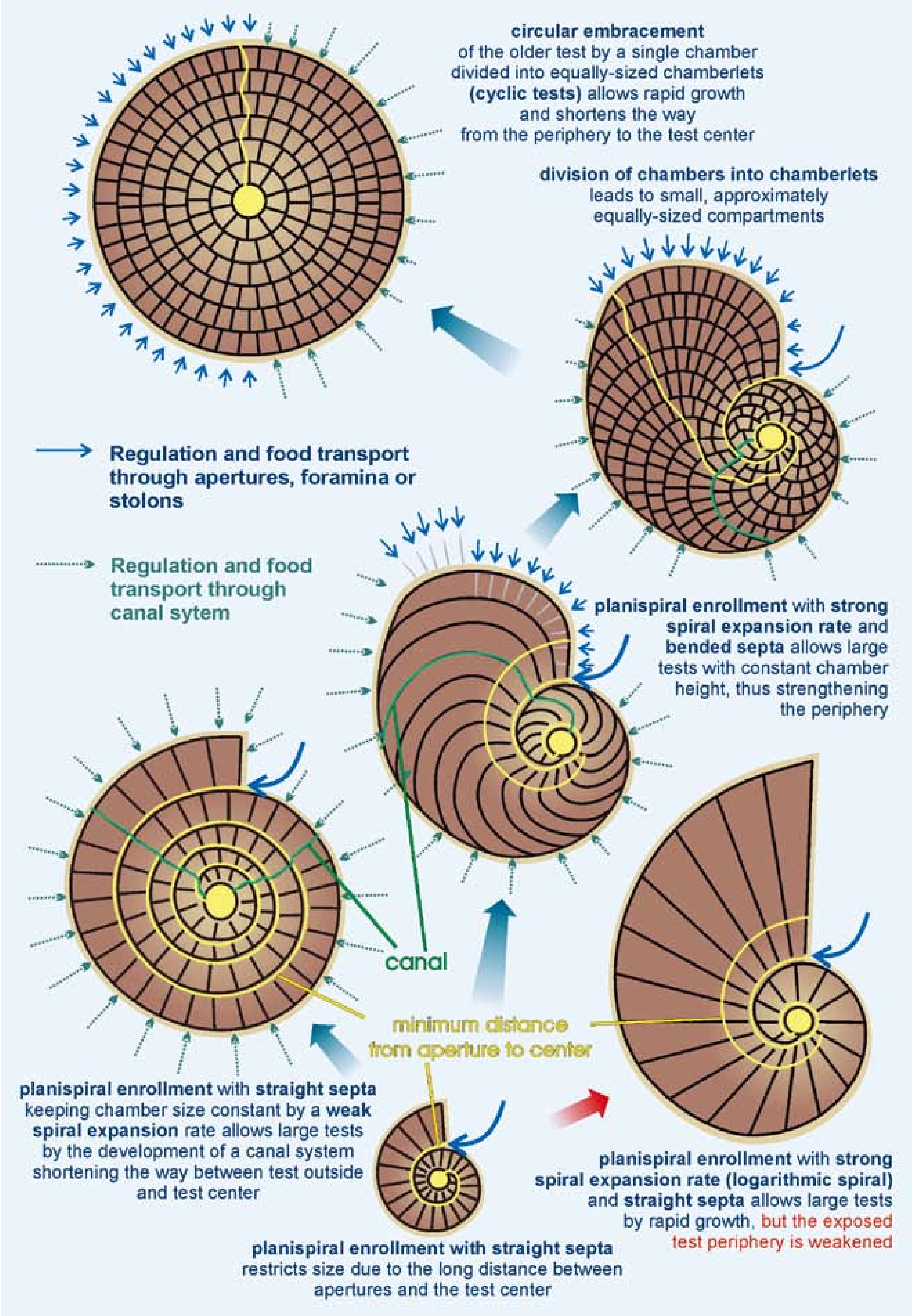


Figure 5. Different ways to construct large tests originating from an planispirally coiled test.

by step around the first chamber in a plane, forming a spiral. After an initial increase of chamber size in the first few whorls, these sizes will be kept constant during further growth. This allows the development of compartments constant in size, but needs an extremely long period of growth. Because of the constant chamber height, the mathematical spiral called 'Spiral of Archimedes' can model the test outline.

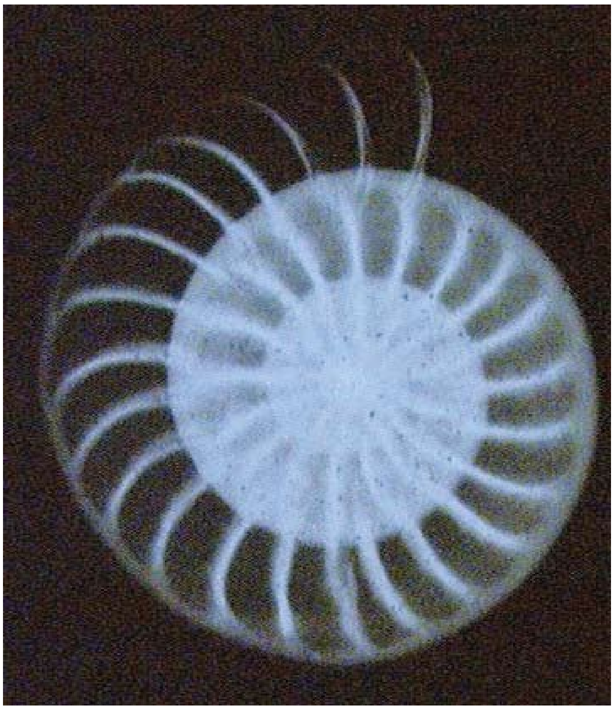
This simple way to construct a glasshouse is complicated by a functional aspect explained above, namely the connections between compartments. The step-by-step growth makes the former aperture of the last chamber, the original connection to the surrounding seawater, into a foramen (the opening between the next-to-last and the new last chamber). Accordingly, foramina are the only connections between chambers, and the aperture is the single connection to the surroundings. This makes the path that information and transport has to take from the outside to the central test and vice versa extremely long. This also hinders a time consistent distribution of information and transport over the compartments.

Therefore, this 'simple' construction method restricts gardeners and architects to small tests (like *Peneroplis pertusus*).

Larger and giant glasshouses were made possible by this method after the invention of a so-called 'canal system'. The invention of this thermion system located within the test wall makes the gardeners into plumbers as well. These tubes represent a complicated system of connections between the chambers, allowing much shorter and direct communication between chambers and the outside.

In contrast to pores, where only gas exchange is possible, the cytoplasm can flow through these canals. This allows the transport of larger molecules like proteins or carbohydrates (sugar polymers), of synthesized organic particles and even symbionts. Therefore, in case of danger, the whole cell plasma can quickly be retracted into the innermost test.

Building new chambers step-by-step is a time-consuming and tedious process, and continuous addition of chambers is impossible. After adding a new chamber, the foraminifer has to rest and take up inorganic nutrients by feeding. Accordingly, test sizes of more than 2 cm take several years. For very large individuals from the geological past, such as those that make up the stones of the Egyptian pyramids, a life span up to 100 years has been estimated, especially for the large *Nummulites* specimens exceeding 10 cm in diameter.

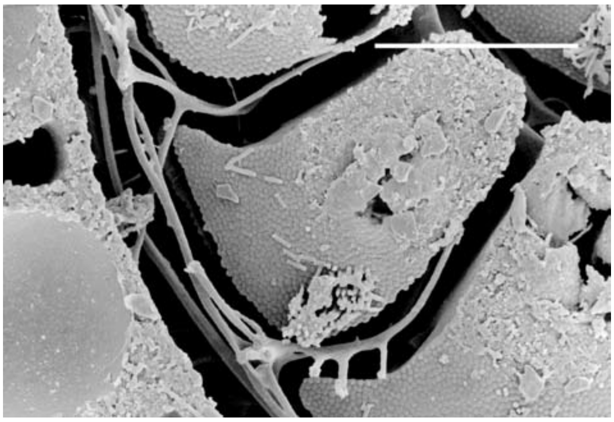


X-Ray micrograph of *Operculina ammonoides* (size = 2.5 mm) with a test following the spiral of Archimedes.

Another construction plan allows faster test growth by constantly increasing chamber heights. The outline of the test follows a so-called 'logarithmic spiral', also found in fossil and recent squids that have a shell like the living *Nautilus* or fossil ammonites.

Growth of chambers with straight septa involves weakness in the peripheral part due to the large space. Such chambers can be easily fractioned by predators like fishes or even through friction by larger sediment particles during intensive water motion. A backward bending of chambers has a strengthening effects: the distances between consecutive chambers remain constant along the whole chamber height, which adds mechanical strength to the peripheral test parts.

This construction plan allows faster growth to large-sized tests, and connections between chambers do not necessarily require additional connections like a canal system. Otherwise, single foramina at the chamber base allow a short and direct connection from the outside to the center, but peripheral chamber parts are less well provided. Multiplication of apertures along the front of the last chambers leads to multiple foramina connecting consecutive chambers; this guarantees consistent information and product transfer to all cell parts.



SEM micrograph showing the canal system within the wall and septa of *Nummulites* (scale bar = 0.1 mm). The test is dissolved by acid, while the empty space of chambers and the canal system running in the wall and septa was filled by resin cast and thus remained.

Logarithmic spiral of *Operculina* (size = 3.5 mm) with straight septa.

Logarithmic spiral of *Peneroplis* (size = 1.5 mm) with bended septa.

This construction plan is the oldest one for obtaining large flat tests. It has been reported for the first time in the Jurassic ~ 190 million years ago.

When test become larger than 1 cm, this construction is not the best solution because the chambers become too high and thus fragile (in flat tests).

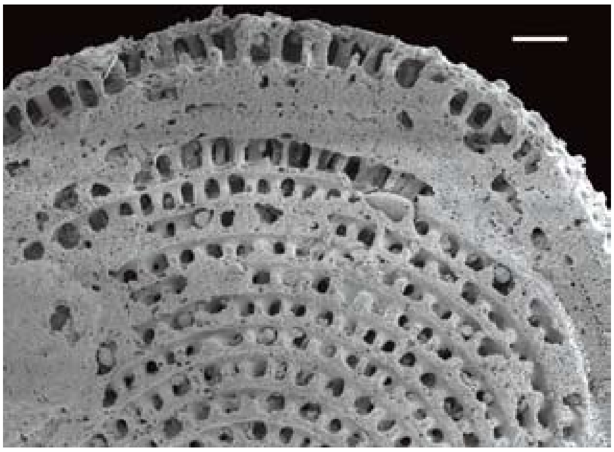
One solution for test strengthening is fitting the chambers with tiny pillars.

Another solution is to divide the chambers into smaller, equally sized compartments by constructing additional walls called **septula**. These small compartments are named **chamberlets** because a chamber is partitioned into smaller units. Since a chamber is formed during a single growth process, a series of chamberlets representing the single chamber is constructed during this short growth process. Such an amplification of equally sized compartments is less time consuming than the step-by-step procedure in the 'Spiral of Archimedes'.

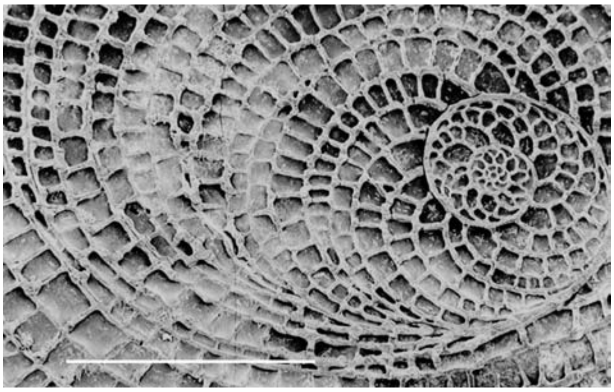
Besides test strengthening, the construction of smaller compartments simplifies metabolic processes in these smaller units. To provide the prompt and short transfer of substances between compartments, a complex system of openings between chamberlets has to be established. These openings do not originate from former apertures and are therefore not called foramina but **stolons**. Since an information transfer from and to the regulation center becomes very complicated in such systems, the cell nucleus −acting as the regulation center−is subdivided into many nuclei. This yields short distances from the multiple regulation centers to those places where metabolic processes occur (mitochondria, secretory vesicles, lysosomes) or substances are synthesized (ribosomes, dictyosomes).

In some foraminifera with backwards-bending chambers and division into chamberlets, an additional canal system is present. It consists of tubes and shortens the product transfer between compartments and the information transfer from and to the regulation center (the nucleus). In this case the regulation center is not divided and is typically located in the test center, the first chamber.

SEM micrograph showing a row of apertures in the last chamber of *Peneroplis* (scale bar = 0.1 mm).



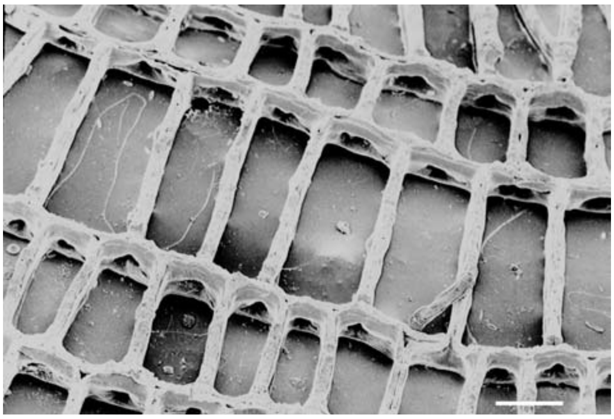
SEM micrograph of a broken test of *Archaias* (scale bar = 0.1 mm) showing pillars that strengthen the chambers (photo C. Baal).



SEM micrograph of the broken test of *Heterocyclina* (scale bar = 1 mm) with a complete division of chambers into chamberlets showing the transition from a logarithmic spiral into a cyclic arrangement of chambers (courtesy by Lukas Hottinger).

To reach extreme sizes (more than 1cm) the backbend of chambers also becomes extreme, leading to envelopment of the whole former test by a single chamber.

Many species exhibit this transition from an initially planspiral arrangement of chambers to a circular arrangement, and the original planispiral construction plan is visible in the inner part. When an enveloping chamber is built during a single growth process, the chamber



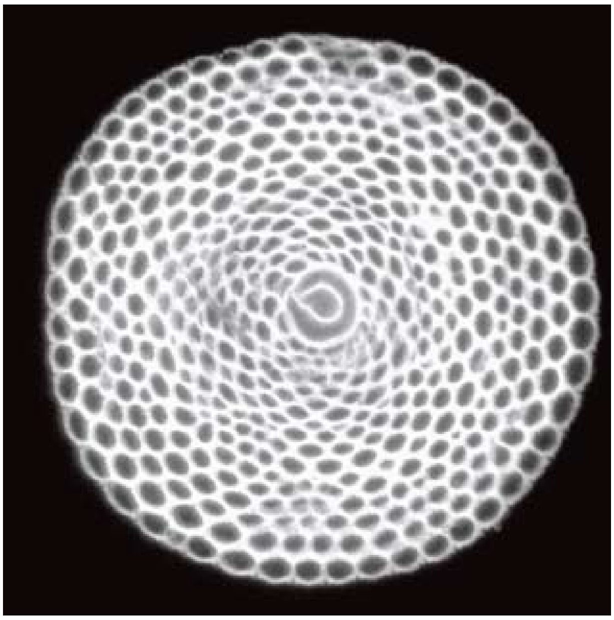
SEM micrograph of a broken test of *Heterocyclina* (scale bar = 0.1 mm) showing openings (stolons) between chamberlets (courtesy by Lukas Hottinger).

arrangement is called **annular**.

When the annular chamber is divided into chamberlets, then this series of chamberlets is constructed during a single growth process, called a cycle. Therefore, such tests are called **cyclic**.

In cyclic tests, a complex system of stolons allows connections between neighboring chamberlets of consecutive growth cycles. In many forms, but not in all cyclic tests, stolons also connect neighboring chamberlets of the same growth cycle.

In some foraminiferan architects, the initial test part shows the original construction plan of the planipiral test, but in many forms, these test parts are simplified by developing initial parts starting with a complex of large chambers that deviates from the ’normal’ chamber in form



X-ray micrograph of *Sorites* (size = 3.4 mm) showing a complete cyclic arrangement of chambers subdivided into chamberlets and an embryonic part (= nepiont) consisting of a spherical first chamber and a tubular second chamber.

and size. These complexes are called **embryonic apparatus** and sometimes **nepiont**.

The advantage of a large embryonic apparatus is that the cyclic construction can start with a large size. This lessens the danger that young individuals will be eaten by smaller predators and enables accelerated growth.

Flat and thin tests are ideal for gardeners living in deeper parts of the ocean, where light intensity is low but still enough for the symbiotic algae to photosynthesize. Such tests, especially the cyclic tests, are inappropriate for shallow water. There are two reasons for this. First, light intensity is too extreme near the surface: the dangerous UV radiation penetrates tropical clear water down to 20 m and damages the DNA in the cell nucleus. Second, the strong water movement can fracture the construction.

Nevertheless, one group of gardeners with cyclic tests surmounts these difficulties. First, extreme irradiation is weakened by the test structure (porcellaneous walls), where the extremely tiny and unordered crystals fraction and partially refract the light. Only a small proportion of the light reaches the cyctoplasm and the microalgae. Second, such tests withdraw from the high water energy by using their pseudopods to attach to flat surfaces like sea grass leaves or the smooth thalli of larger red and brown algae. Smooth and flat rocky bottom are also suitable substrates for cyclic gardeners to attach and escape strong water energy.

Smaller foraminifera with porcellaneous tests that are not endangered by UV light resist water energy by hiding and attaching themselves in the dense network of filamentous algae covering the rocky substrate or in small grooves and holes of the reef crest.

Gardeners with porcellaneous test walls and tests larger than 5 mm developed yet another strategy of constructing glasshouses when living in high energetic environments without the possibility of attaching to smooth and flat surfaces. They use the initial construction plan of a 'Spiral of Archimedes', whereby they maintain the chamber height rather constant after an initial increase. Contrary to the growth mode for becoming flat tests, they elongate their chambers along the coiling axis. This strategy yields spindle-shaped, so-called **fusiform** tests (Figure 6).

These constructions are not adapted to the highest water energy and can be found at the edge of a coral reef and on the reef crest; gardeners with this type of construction live today in holes and grooves at the high energetic reef slope just below the extremely turbulent reef edge (10 to 30 m depth).

Depending on the water energy, which the test has to resist, the length/diameter ratio changes. More rounded forms are abundant in higher energetic regions, while long forms are characteristic for less energetic, but still turbulent waters. Nevertheless, all porcellaneous gardeners are restricted by their test ultrastructure to shallow environments. In clear ocean water, this depth limit is about 60m.

Similar to the flat forms, the fusiform growth leads to an increase in chamber volume, slowing down the biochemical and metabolic processes. This calls for a division of the long chambers into smaller chamberlets, and also requires a system of connections between the neighboring chamberlets and chamberlets of the succeeding chambers. Since each chamberlet of the final chamber opens to the outside, these forms are characterized by a number of apertures.

This spindle-shaped construction is the oldest, first developed ~300 million years ago, when primitive amphibians and the oldest reptiles (long before dinosaurs evolved) lived in woods of ferns and horsetails, the origin of black coal.

We have regarded foraminiferan architects that started with an original construction plan as a series of chambers that are spirally arranged in a plane. As noted above, strepto- and trochospirally coiled tests seem to be disadvantageous for constructing large and flat glasshouses, but this is not completely true for trochospiral tests. In smaller foraminifers we find extremes in the trochospiral form, from extremely high-spirals to a very flat trochospiral coiling, whereby the latter approximates the planispiral coiling.

In trochospiral tests there is a distinction between the spiral side and the umbilical side. All whorls are visible on the spiral side, while only the last whorl can be seen from the umbilical side

Some foraminifers became gardeners despite their trochospiral construction. The low trochospiral tests are size-restricted, but can become very thick by enveloping chambers. This yields so-called involute tests, where only the last whorl is visible from both sides. These lens-shaped tests with a maximum size of 4 mm are appropriate for living in regions of high, but not extreme water turbulence. These forms use pseudopods to attach to the substrate and resist water turbulence by living in small holes or caves of rocky bottoms

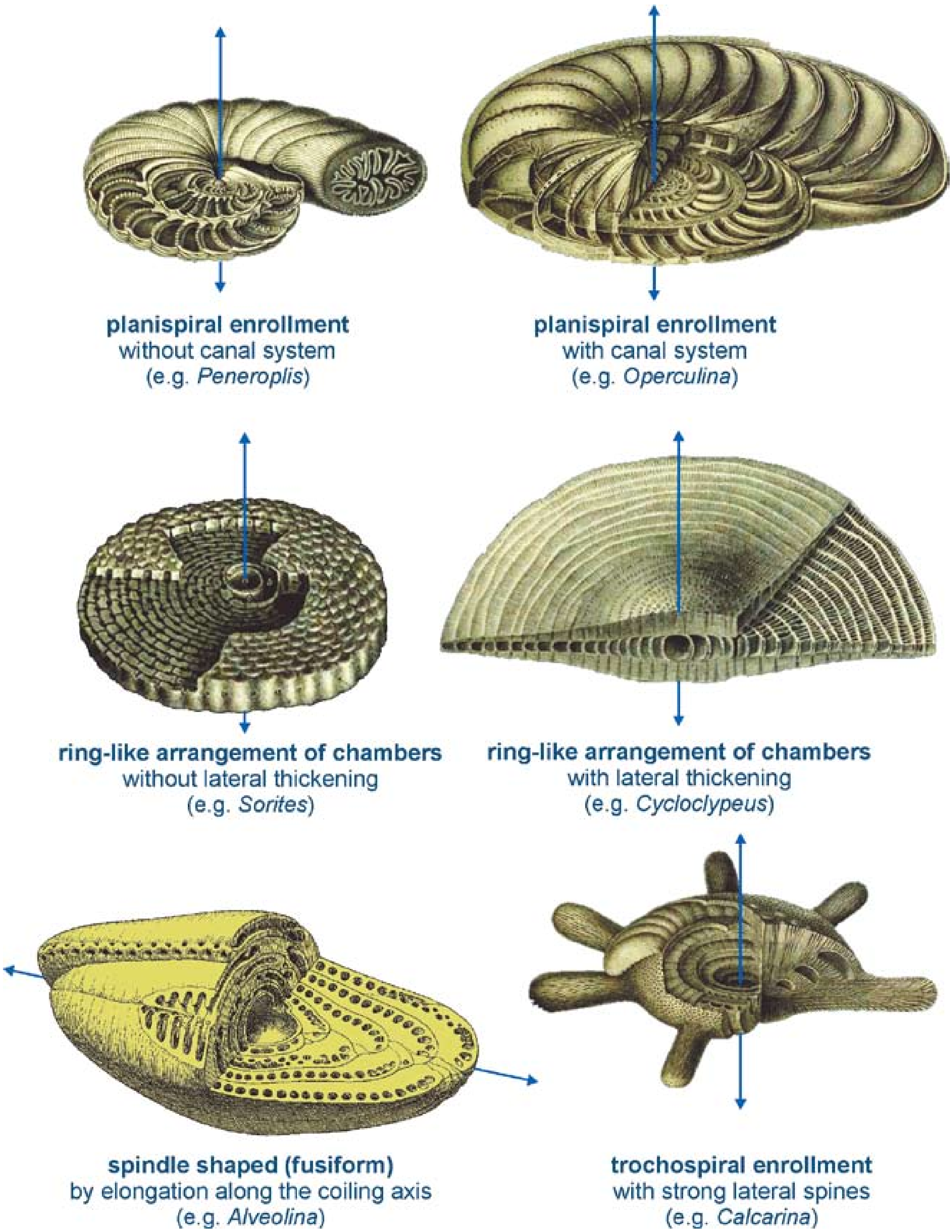
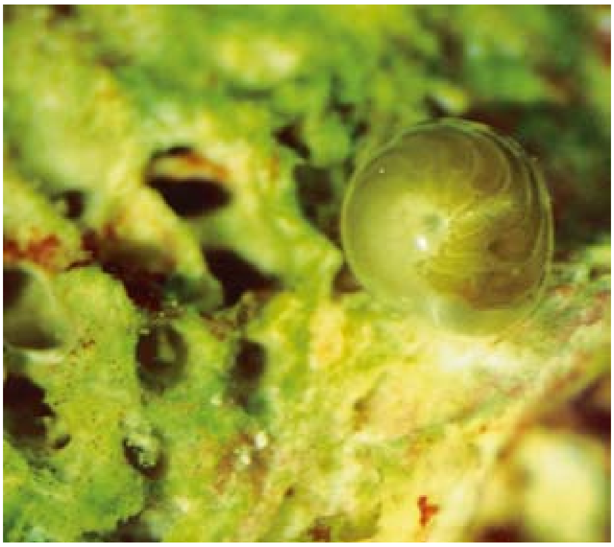


Figure 6. Test constructions in modern larger foraminifera (drawings except *Alveolina* after Carpenter 1858, *Alveolina* modified after Reichel 1936).

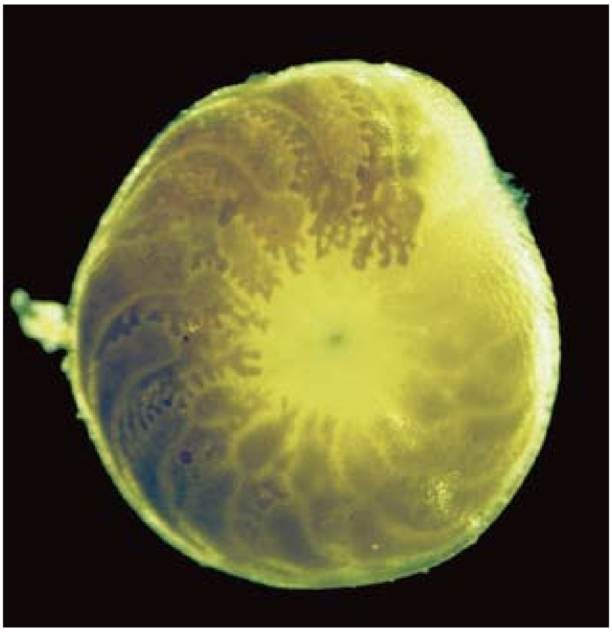


The foraminifer *Amphistegina lessonii* (size = 2.2 mm) with a lens-shaped test fixing to algal mat at 0.5 m depth.

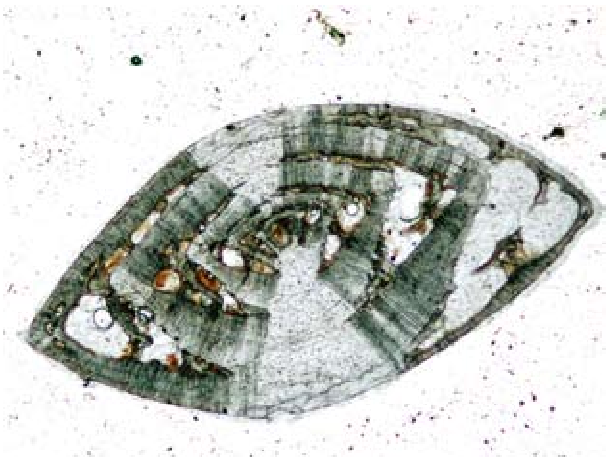
Some forms with extreme flat trochospiral coiling become rather symmetrical with no differences between the spiral and umbilical side. These truly lens-shaped forms prefer sandy bottoms, where they live between the grains. Their lens-shaped tests enable them to easily dig back to the surface if they become buried by tropical storms, which shift and suspend the sand.

The foraminifer *Amphistegina radiata* (size = 3.5 mm) loosely attached to calcareous grains from 30 m depth.

These flat trochospiral forms with thick tests protect themselves against dangerous UV-irradiation by hiding in holes and caves. Since the tests are rather small, not all symbiotic algae that inhabit the cell plasma of the gardener can live in the last whorl. However, only this whorl provides enough sunlight for photosynthesis. The space for microplants is thus too small when it is restricted to the outermost whorl. In this type of construction, in which the chamber wall covers the complete former test during each chamber construction process, the walls are composed of many layers. These are termed lamellae and are especially evident in the central part.



The thick lens-shaped foraminifer *Amphistegina lobifera* (size = 2.1 mm).



Axial thin section through the test of *Amphistegina lobifera* (diameter = 1.8 mm) showing the flat trochospiral enrollment, the porous wall and the large transparent plugs leading light into the test center (photo E. Iordanova).

Because of this construction and due to the high content of organic matter between the lamellae, walls are only transparent at the outermost test part, but become non-transparent in the test center. Therefore, such gardeners develop special constructions for getting light into the innermost whorl. All gardeners living in highly illuminated areas construct a totally transparent, glassy central test part. These so-called plugs are not divided by organic material.

Now, light can penetrate into the inner test and enables photosynthesis for the microalgae living in the inner chambers.

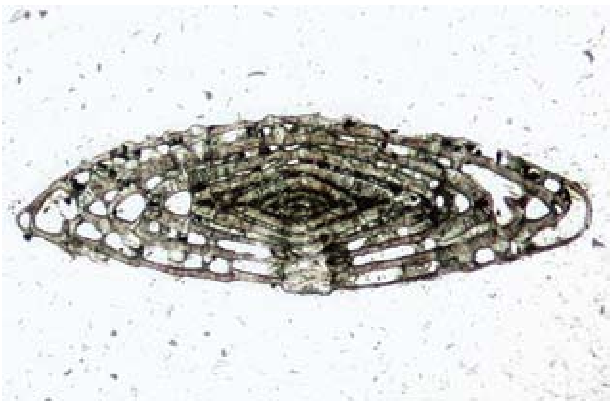
Since gardeners also try to live in deeper regions with extreme low light intensities (but enough for photosynthesis of their microplants), they must provide this weak light for their symbionts. The foraminiferans follow two strategies. First, the lamellae of the wall became extremely thin when covering the former test parts. Since the animal's volume does not change as depth increases and the lamellae become extremely thin, the test diameter also remains the same, but the test itself becomes very flat.

The flat lens-shaped *Amphistegina bicirculata* (size = 1.6 mm)

Axial thin section through the test of *Amphistegina bicirculata* (diameter = 1.5 mm) showing the flat trochospiral enrollment and the thin porous wall (photo E. Iordanova).

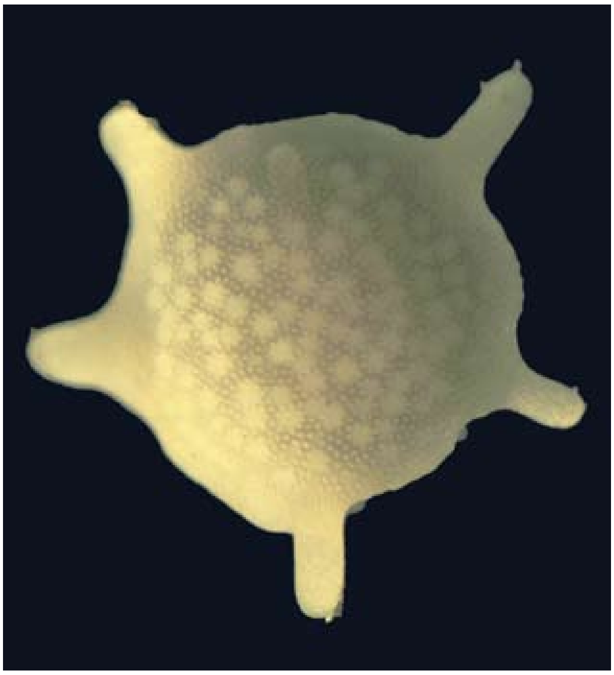
A second way for light gathering is to develop so-called papillae. Papillae are round, hemispherical elevations at the test surface, like pustules, with a glassy, transparent structure. They do not act as lenses to focus light because at depths below 50 m light is not directed, but scattered. Therefore, these papillae reflect the light, which is normally lost in the water, to the test surface.

The flat lens-shaped *Amphistegina papillosa* (size = 1.2 mm)



Axial thin section through the test of *Amphistegina papillosa* (diameter = 1.1 mm) showing the flat trochospiral enrollment, the thin porous wall and the numerous papillae for concentrating dispersed light to the test surface (photo E. Iordanova).

Another group of gardeners prefers to inhabit highly illuminated regions with extreme water turbulence. They also originate from ancestors constructing flat trochospiral tests, but in contrast to the smooth and round tests of the former group, they construct spines for attach and anchor to the substrate (Figure 6). These spines, which can be present in different numbers, forms and lengths, have internal canals in which the cell plasma flows. Beyond the foramina in some forms, these spines provide additional connections to the outside. In a few species lacking foramina, spines are the only connections between the gardener and its surrounding.

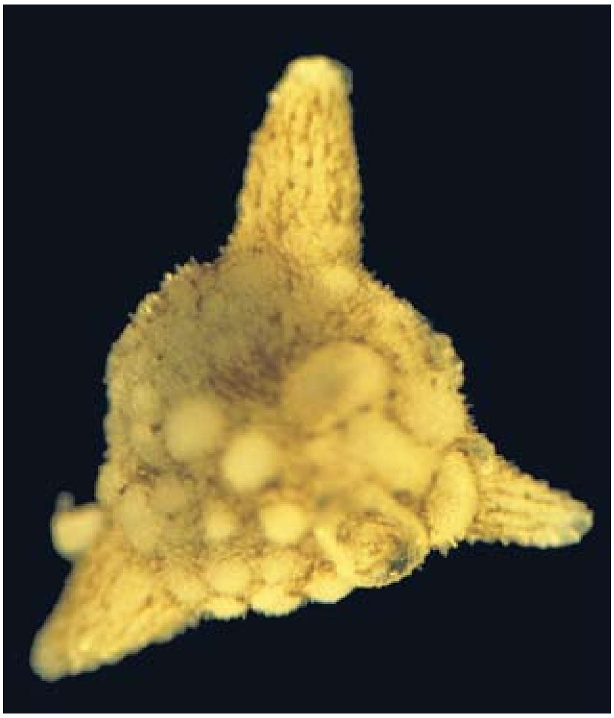


The thick lens-shaped *Calcarina gaudichaudii* (body diameter = 1.8 mm).

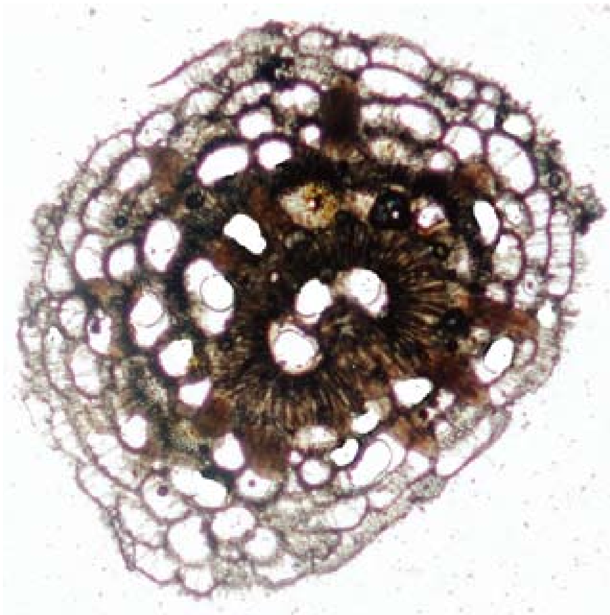
Axial thin section through the test of *Calcarina gaudichaudii* (diameter = 1.8 mm) showing the trochospiral enrollment and the thick porous wall (photo E. Iordanova).

To attach to the substrate, the anchoring spines themselves are additionally equipped with a special glue that attaches the end of the spines to the substrate. The adhesion is strong enough to require force to detach the individuals.

For developing spherical glasshouses, which are advantageous in extremely turbulent water, some of these gardeners, instead of thickening the walls with lamellae, put additional chambers at the spiral and umbilical test side.



The globular *Baculogypsinoides spinosus* (body diameter = 2.5 mm) with 3 strong spines.

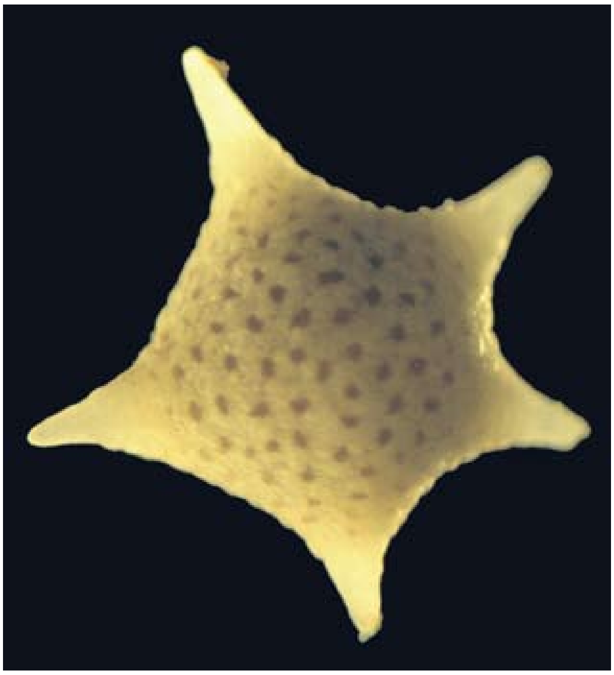


Axial thin section through the test of *Baculogypsinoides spinosus* (diameter = 2.8 mm) showing the trochospiral enrollment of the central part with thick porous wall and the lateral chambers with thin walls (photo E. Iordanova).

Finally, in the most developed architects of this group, the trochospiral arrangement of the main chamber series is abandoned: a cyclic arrangement is initiated after a short initial spiral.

Adding lateral chambers at both sides of the main chamber plane leads to globular, spherical chambers. Only the arrangement of spines signalizes the original coiling plane.

The thick, lamellar walls and abundant organic material makes these tests intransparent, although the walls are hyaline. Thus, only microplants concentrated near the test surface get enough light for photosynthesis, while the inner chambers are light depleted. Such test constructions are therefore characterized by numerous pillars that are totally translucent and penetrate the tests down to the center. This enables photosynthesis also for the microalgae living in the inner test parts.



The globular *Baculogypsina sphaerulata* (body diameter = 1.5 mm) with strong lateral spines ordered in an equatorial plane.

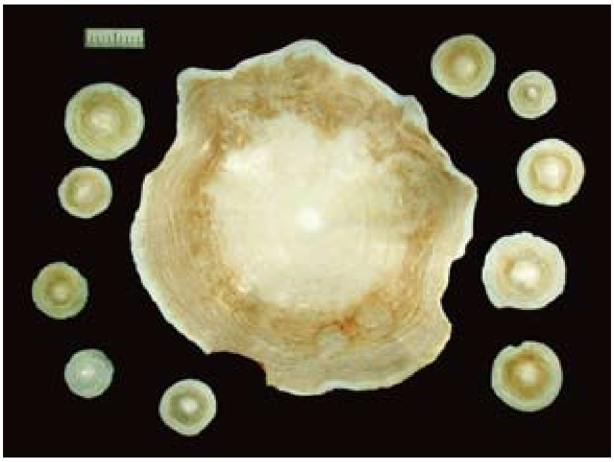
Axial thin section through the test of *Baculogypsina sphaerulata* (diameter = 2.3 mm) showing the flat trochospiral enrollment of the first chambers continuing into an equatorial layer that extends into a spine. Look at the huge number of lateral chambers interrupted by transparent piles extending into the test center (photo E. Iordanova).

The reproduction of greenhouse gardeners (Figure 3)

The building of a complex embryonic apparatus is possible only during asexual reproduction. After division, every nucleus is surrounded by a portion of the parental cytoplasm possessing all the organelles necessary for life. This unit is separated by cell membranes from other nuclei, thus becoming single individuals. Some microalgae also become members of the new daughter cell. This results in the transfer of the symbiotic plants from the parent to the daughter individuals.

These embryonic cells with abundant cytoplasm grow and form the embryonic apparatus by mineralizing the test wall. Afterwards, they leave the sphere of the parental test and start their independent life. The number of juveniles leaving the parental organism ranges from a few hundred to more than 2000 individuals in large-sized species. All have a good chance to survive and to reproduce. The disadvantage of asexual reproduction is the spatial restriction: these large benthic forms that crawl slowly on the sea bottom cannot surmount inconvenient environmental conditions such as lowered light intensities (reduced water transparency due to suspended organic and inorganic material during the monsoon season), lowered temperatures in winter, salinity changes, etc.

To negotiate such environmental barriers and even geographical barriers like the deep ocean bottom between islands, the second type of reproduction – the sexual reproduction – enables individuals to spread more widely. Individuals with the single set of genes grow to adult individuals (**gamonts**) and reproduce, at the end of their lives, tiny **gametes** 20 to 40 micrometers in size. These gametes possess 2 to 3 locomotion organs, each termed a **flagellum**. Such gametes are identical in form and are also known as **isogametes**. One parental individual releases ten to one hundred thousand gametes into the water, where they actively swim using the flagella as propulsion. After conjugation of two gametes, the new individual, called **zygote**, is characterized by the double set of genes. Since the gametes are tiny, the zygote is also extremely small. The new individuals remain small after growing to three-chambered individuals with calcified tests. Their density is lower than that of seawater. Thus, they float in seawater (**plankton**) and can be transported by currents. This explains the broad distribution of benthic larger foraminifera, which are restricted to shallow, warm and clear water environments, over all tropical and subtropical ocean islands, even though the islands can be separated by thousands of miles with deep (~4000 m) ocean bottoms, where the gardeners could never live and survive as full-grown organisms. These individuals with a very small embryonic part are called **agamonts**. They grow much larger compared to the generation with a large embryonic part, especially in large symbiont-bearing foraminifera.



Sexual (small tests) and asexual (large test) generation of *Cycloclypeus* (scale bar = 10 mm; photo C. Baal).

The settlement of greenhouse gardeners

What are the conditions for those larger foraminifera that act as gardeners and that construct greenhouses?

Light

First, gardeners have to live in illuminated water down to those depths where their cultivated plants, the microalgae, can still get a 'positive net production'. A positive net production means that the carbon produced by photosynthesis (main elements of sugars and fats) exceeds the carbon (carbon dioxide) lost by respiration by the algae. The depth at which the rate of respiration is equal to the rate of photosynthesis is called the **compensation depth**. Compensation depths differ between the microalgal groups used by foraminifera and depend on water transparency. In clear water, such as in the tropical and subtropical ocean far away from large land masses or in desert (arid) zones, red algae are characterized by compensation depths more than 300 m, followed by diatoms (~200 m) and dinoflagellates (~150 m), while green algae are restricted to shallower regions (~80 m). When microalgae are unable to get a positive net rate sufficient for the host's metabolism, then the host digests the plants to obtain food. Afterwards, if no food becomes available or the uptake from the outside is insufficient, the host must die.

When there is too much light, plant photosynthesis is reduced, especially in the case of diatoms, dinoflagellates and red algae. Green algae, on the other hand, achieve optimum production rates under strongest light at the surface. At the water surface, the decrease in the photosynthetic rate of diatoms is caused by photoinhibition, mainly through UV-radiation, which damages the photosynthetic system. Dinoflagellates have gained the ability to transform this dangerous short-waved UV-light into harmless wavelengths by special pigments. Therefore, gardeners living at the surface and housing diatoms as plants had to build glasshouses to protect their plants against UV-radiation, while gardeners housing dinoflagellates can be exposed to strongest sunlight.

Temperature

Second, gardeners need warm water, which is found in (warm) temperate to tropical seas. As explained above, temperature is important for the availability of hydrogen carbonate and carbonate ions during the calcification process of the test. Larger foraminifera can survive temperatures below the **minimum survival temperatures** (MinST) up to a few (maximum 2) weeks. The minimum survival temperatures differ between gardeners, but never fall below 14℃. In species restricted to shallow tropical seas, these minimum survival temperatures are about 19℃.

Nothing is known about **maximum survival temperatures** (MaxST) of gardeners. Here we have to differentiate between the MaxST of the gardener and the MaxST of the plants, which can strongly differ. Lengthier temperature increases higher than the MaxST of the micro-algae block photosynthesis and build up products that poison the algae. In such cases, for example when corals act as hosts, they can spit out the symbiotic algae (naked dinoflagellates known as zooxanthellae) and become uncolored. This is the well-known 'coral bleaching' that has damaged coral reefs in the late 1990s. Bleaching is also found in larger foraminifera, but raised temperatures are not the cause. In some foraminifera, high solar irradiation caused by ozone depletion damages the plants, which in this case are diatoms. Contrary to coral polyps, the foraminifer digests all damaged diatoms and becomes partially bleached.

Normally, foraminifera can survive high temperatures (~45℃), especially species with porcellaneous walls.

Therefore, the cultivated plants ultimately define the upper temperature limit of the gardener.

Footing

It is important for all gardeners to move their glasshouses into the best position for light. This can be done, on the one hand, by climbing to sunlit places to gather more light or, on the other hand, by hiding in small holes, caves or beneath larger plant leaves, algal thalli (constructed similar to leaves in larger algae) or rubble to reduce irradiation. Therefore, the substrate for footing of glasshouses differs. It can be organic material like algal thalli and algal rhizomes (whose function is similar to roots in land plants but is restricted to attachment to the bottom). Gardeners avoid living on animal tissue like coral polyps or sponges. Some gardeners rest their tests on rocks, boulders and coarse sand; a very few prefer fine-grained sediments like fine sand and silt.

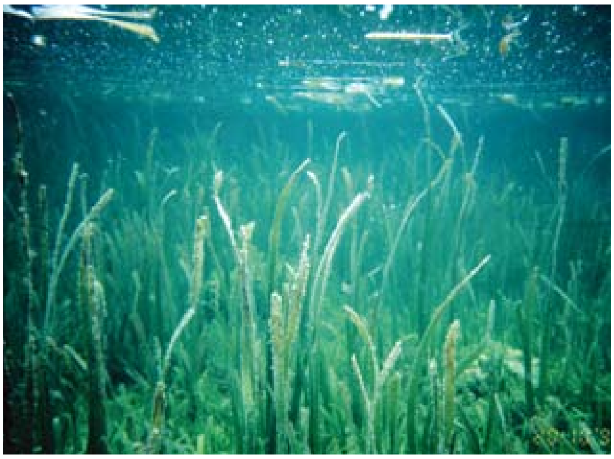
Since water movement by waves and currents is responsible for the development of sediments and also determines the distribution of larger plants, the gardeners have to resist being swept away (entrainment) from the surface by fixing mechanisms in turbulent water.

Let's have a look at some footing possibilities:

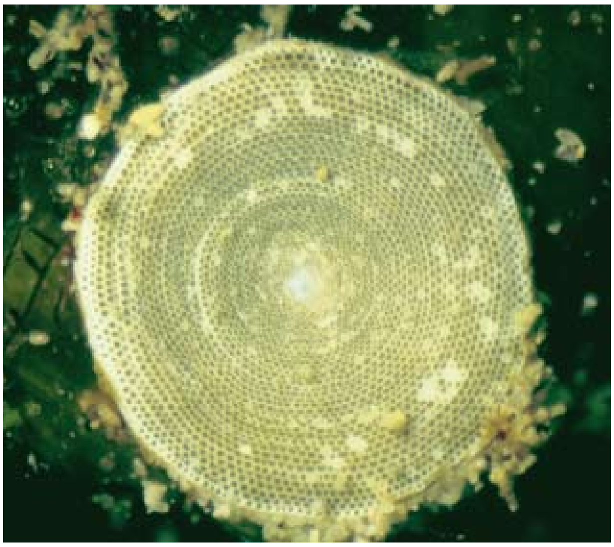
a. Flat and smooth surfaces as found on seagrass leaves or large, smooth algal thalli are inhabited by flat, disc-shaped gardeners.

In that case, the biconcave tests hinder entrainment from the surface by creating negative pressure at the test side oriented to the leaf surface. Additionally, these gardeners fix their tests with gluey pseudopods. These extrude from the numerous apertures at the test periphery and are used to feed on extremely small microorganisms like bacteria and microalgae living on the surface of leaves or thalli.

Shallow lagoon at Peleliu, Belau. The open sea is behind the reef crest right in the background.



Meadows of the sea grass *Enhalus* (leaf length =1,200 to 1,500 mm) in the shallow lagoon at Peleliu, Belau.

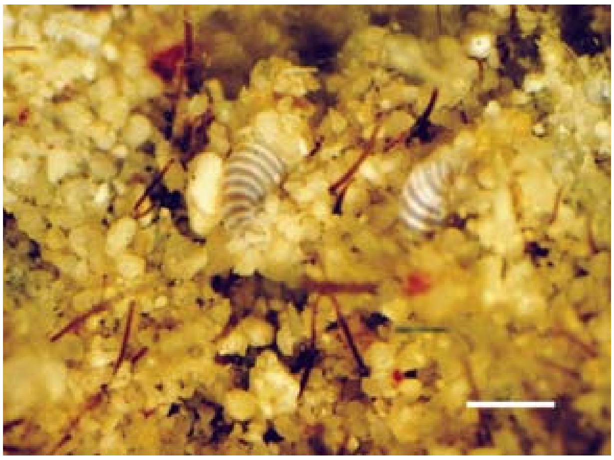


The foraminifer *Amphisorus* (size = 40 mm) attached to the smooth surface of the sea grass *Enhalus.*

b. In the uppermost meters of the sea, light-oriented rock surfaces and boulder are densely overgrown by small, filamentous macroalgae possessing thalli of a few

Fringing reef in front of a rocky coast (Cape Bise, Motobu, Okinawa) during tidal low stand showing the clear zonation from the coast to the reef moat, always covered by water, and to the reef crest that is falling dry during low stand. The waves of the open sea are braking at the reef crown.

Fringing reef in front of a sandy coast NW of Kabira Bay, Ishigaki, Okinawa, Japan showing the transition from the sandy beach to the broad reef moat.



Sand grains caught by fine filamentous red algae, where foraminifera of the genus *Peneroplis* with symbiotic red micro-algae are protecting against light and waves (scale bar = 1 mm).

millimeters length. Sand grains from 100 micrometer to 1 mm in size are trapped within this algal turf. Lens-shaped flat foraminifers settle between the grains, attaching with pseudopods extruding from the multiple apertures to the rocky bottom or algal filaments.

With this life style, these foraminifera resist entrainment under highest water motion and energy.

When these surfaces are more or less flat, then also larger gardeners with flat, disc-shaped biconcave glasshouses can settle, again attaching with gluey pseudopods to the filamentous algal turf.

c. Larger macroalgae with sizes up to 10cm that have a network of filamentous to rod-like thalli can be found at sites with extreme water energy. Gardeners living within these dense networks are distinguished by lens-shaped glasshouses having long, thick spines, giving them the appearance of little stars or sun discs.

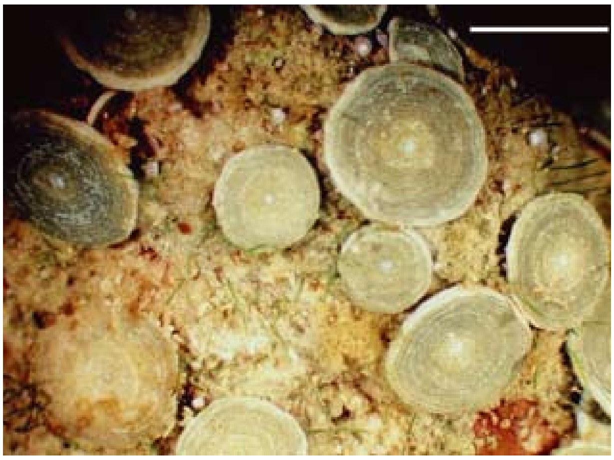
These spines act as anchors within the thalli or between the glasshouses, whereby cyctoplasm extruding from the tips of the spines has a strong glue that fixes the glasshouse to the algae. Water movement alone cannot entrain these gardeners from the algae. Here, forceps or strong mechanical force is required to separate the foraminifer from the algal thallus.

d. The bottom side of boulders deposited in the uppermost meters lacks algal cover; gardeners that are not adapted to extreme irradiation can hide at such more or less weakly illuminated places.

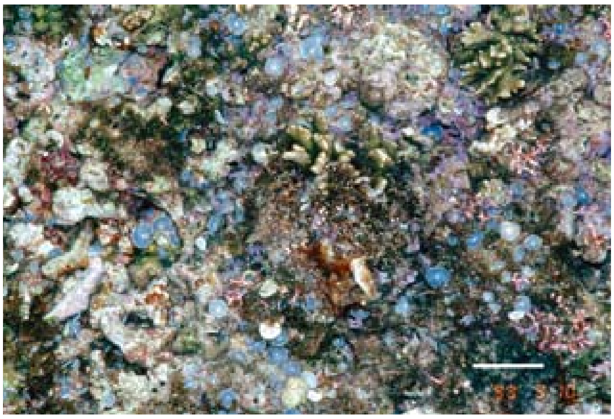
Small gardeners with thick, lens-shaped glasshouses live beneath boulders, using tiny holes as hideaways to resist entrainment by water movement. They weakly attach to the boulders by pseudopods extruding from a single small aperture, and can therefore be more easily entrained. Additionally, they cannot block irradiation like the above-described gardeners living in extremely illuminated regions. This explains life at energy- and light-protected sites.

In the uppermost part of coral reefs that face the open

Shallow reef moat north of Sesoko Island, Okinawa, Japan. The rocky bottom is partly covered with sand, where a few stony corals are living. The filamentous red algae *Jania* covers the bottom, where sea cucumbers and sea urchins are living.



Boulder of the reef moat close to the reef crown with filaments of the green algae *Halimeda* (scale bar = 15 mm), densely settled by large *Amphisorus* and small *Peneroplis.*



Reef moat close to the crest at Kabira Bay, Ishigaki Island, Japan showing the dense settlement of the foraminifer *Amphisorus* on coral rubble (scale bar = 100 mm).

Reef crest NW of Kabira bay at tidal low stand, which is densely covered by filamentous red algae mixed with green algae.

Living foraminifera of genera *Calcarina, Baculogypsina* and *Peneroplis* in the dense meshwork of filamentous red algae from the reef crest (scale bar = 10 mm).

sea, the rocky surfaces are overgrown by red algal crusts (corallinacean algae). These algae are preferred places for larger foraminifera, especially when these rocks are well structured with small holes and caves, where the lens- and cigar-shaped gardeners can best resist the high water energy.

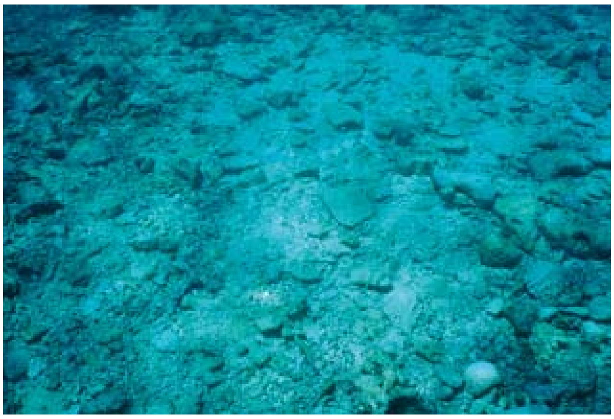
Living sand on the reef crest of Hateruma Island, Japan (scale bar = 10 mm).

Foraminiferal fauna from the reef crest with the star shaped *Calcarina calcar, Calcarina gaudichaudii* and *Baculogypsina sphaerulata,* the thick lens-shaped *Amphistegina lobifera* an the purple *Peneroplis antillarum* (scale bar = 1 mm)

Reef crown of the fringing reef NW of Sesoko Island, Okinawa, Japan consisting mainly of the tabular stony coral *Acropora* resisting extreme water energy.

A 2 m deep groove in the reef crown caused by strong rip currents (speed ~ 2 meters per second) flowing seawards from the surf zone where waves are braking.

e. In areas of the upper reef slope that are protected from strong wave action, sand with large grain size (1-2 mm) is mixed with gravel (> 2 mm). Most sand- and gravel-sized particles are broken coral pieces and corallinacean



Bottom of the groove covered by large boulders of broken corals and rocks.

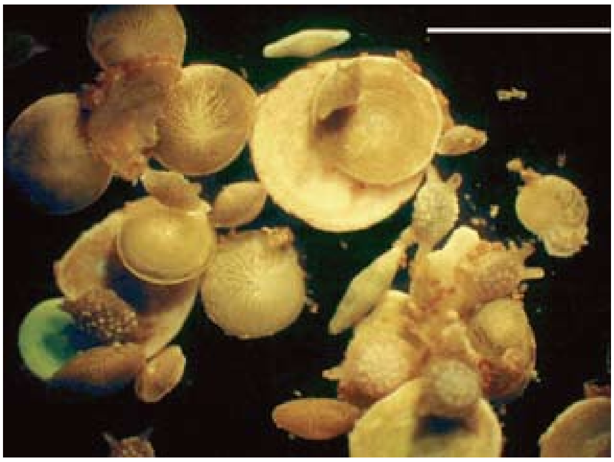
Surface of a boulder, which is totally covered by calcareous corallinaecean red algae. Thick lens shaped foraminifera of the genus *Amphistegina* are hiding in small holes (scale bar = 1 mm)

algae, fractured shells of clams and snails and spines of sea urchins. Therefore, the size of the grains is similar to that of the gardeners. When the slope in front of the reef is gentle, the proportion of sand increases with depth, and the sand becomes finer.

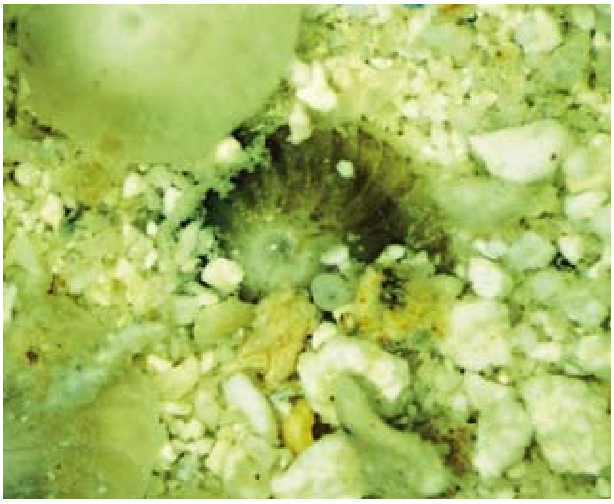
The spindle shaped foraminifer *Alveolinella* (size = 2.5 mm) attached to coral cobble.

Sandy bottom at 5 m depth on the reef slope north of Sesoko Island, Okinawa, Japan. This sand is deposited in quiet regions of the slope.

Rocky bottom at 30 m depth north of Sesoko Island, Okinawa, Japan, which is the base of the coral reef (distance between stripes = 10 cm; photo F. Tatzreiter).



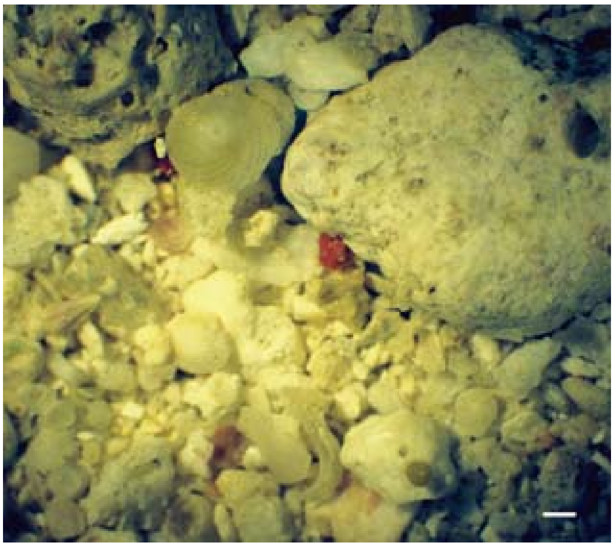
Foraminiferal fauna from the upper reef slope with the star shaped *Calcarina hispida,* the spindle shaped *Alveolinella quoyi*, the lens-shaped *Amphistegina radiata* and the flat disc-shaped *Amphisorus hemprichii* (brown) and *Parasorites orbitolitoides* (green) (scale bar = 10 mm).



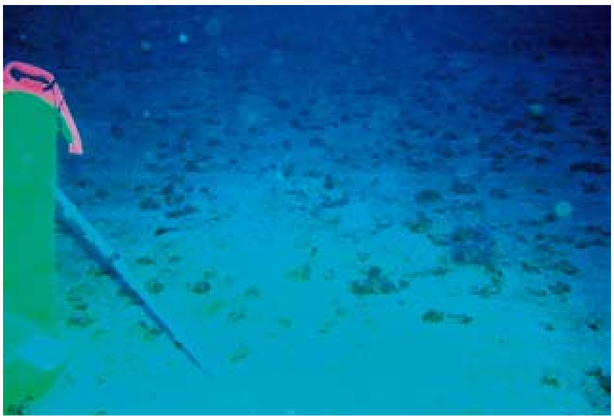
Living *Operculina* (size = 3 mm) burrowing in coarse sand of the fore reef area

The gardeners live on or in the substrate. In the latter case, they use the space between grains, but do not dig too deep into the sand so that they still attain enough light. These glasshouses are always thick lens-shaped. This form makes it easier to climb up to the surface if they become buried by sediment transported by storms.

f. As explained above, the sand becomes finer with increasing depth. Therefore, the grain size of the sediment near the compensation depth in clear ocean water is between 0.063 and 0.25 mm. This sediment type is called 'fine sand'. In this case the sand grains are much smaller than the glasshouses of the gardeners. In contrast to sand grains, which become smaller with increasing depth, the glasshouses become larger with depth in order to gather enough light for their micro-plants. The largest glasshouses with transparent (hyaline) test walls are found here. Today they reach sizes of a few centimeters!

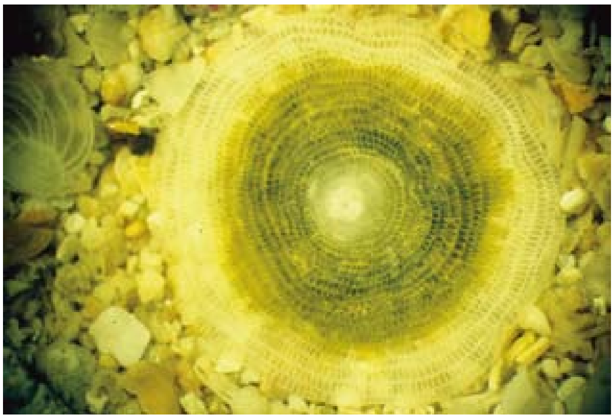


Typical bottom sediment of the upper reef slope at 40 m depth with the living foraminifera *Heterostegina* and *Amphistegina* (scale bar = 1 mm)



Sandy bottom at 50 m depth northwest of Sesoko Island, Okinawa, Japan, that is covered with larger particles, so-called macroids (distance between stripes = 10 cm; photo F. Tatzreiter).

Foraminiferal fauna from the deeper reef slope with the lens-shaped *Amphistegina radiata*, the star-shaped *Baculogypsinoides spinosus* and *Calcarina mayori*, and the flat large planspirally coiled *Operculina complanata* and *Heterostegina depressa* (scale bar = 10 mm).



The disc-shaped *Cyclocyleus carpenteri* (diameter = 15 mm) living at 70 m on sandy bottom.

All gardeners with large, flat tests live on the bottom surface, not in the sediment (where they would be unable to get enough light for their plants). The flat and large tests have the advantage that, after becoming suspended by tropical storms, which affect sediments down to 150 m water depth, the smaller sand particles settle earlier than the plate-like glasshouse after the waning storm. This reduces the threat of becoming buried in the sediment: the gardeners do not have to dig to the sediment surface, which is difficult for forms possessing large and flat tests.

g. Sediment finer than 0.063 millimeter is called silt or mud. These sediments can be found only in the deeper parts of gently inclining slopes facing the open sea, much deeper than the compensation depth, or in protected areas like lagoons. In the first case, no gardeners live at these depths because of insufficient light. Gardeners living in lagoons on or in an extremely fine silt or mud are characterized by lens-shaped tests, similar to the forms found on or in coarse-grained sand. Here, the ability to dig is important: it allows the foraminifera to get the best position in or on the sediment; therefore, lens-shaped tests are advantageous.

The thick lens-shaped *Operculina discoidalis* (size = 2.5 mm) living on muddy bottom at 18 m depth in the lagoon west off Motobu town, Okinawa, Japan.

The clans of gardeners

According to their genetic relationships, which are proven by very complex molecular techniques, we distinguish seven clans of gardeners today. In zoological systematics these clans are called families. Besides molecular relationships, the attribution of a gardener to a clan is supported by wall mineralogy and structure, glasshouse construction, and specification of their cultivated plants, the microalgae.

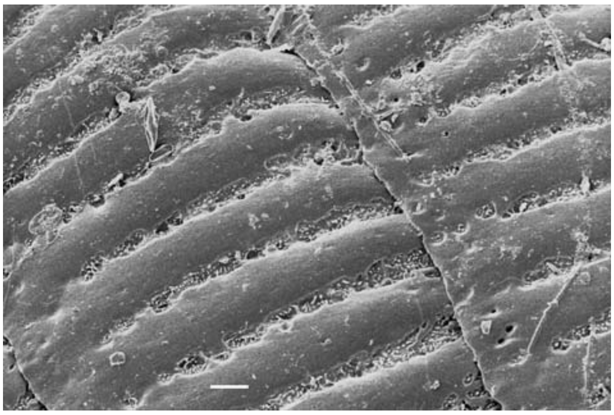
Purple gardeners, scientific name ***Peneroplidae***

This clan of gardeners cultivates single-celled red algae (*Porphyridium*). Living individuals are therefore characterized by an intensive purple color caused by these plants.

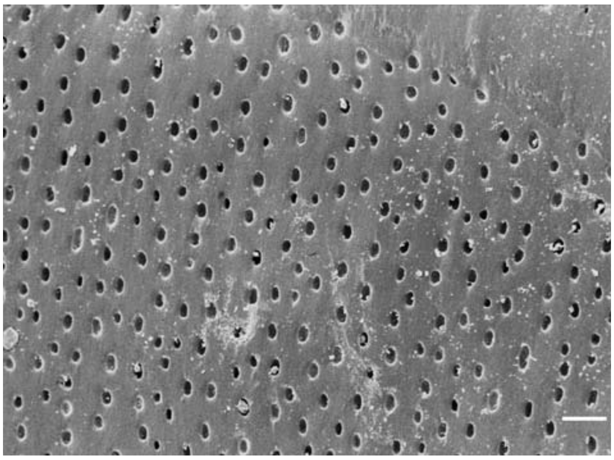
Empty tests are smooth and white, like porcellaneous coffee cups. This is caused by the total reflection of light. The transparency of walls necessary for light penetration is obtained by pits that are arranged in straight grooves.

The construction plan starts with a spherical first chamber and a short tubular second chamber. The following chambers are arranged in a spiral plane. Chamber height is relatively small and does not increase during growth, while chamber width strongly increases in some representatives. Enrollment of the spiral can be weakened in younger tests, resulting in a straight chamber arrangement.

Test openings are irregular in outline and often tree-shaped (*dendritic*) in thick forms, becoming a series of



SEM micrograph of the test surface of *Peneroplis pertusus* showing pseudopores within the striae (scale bar = 0.01 mm).



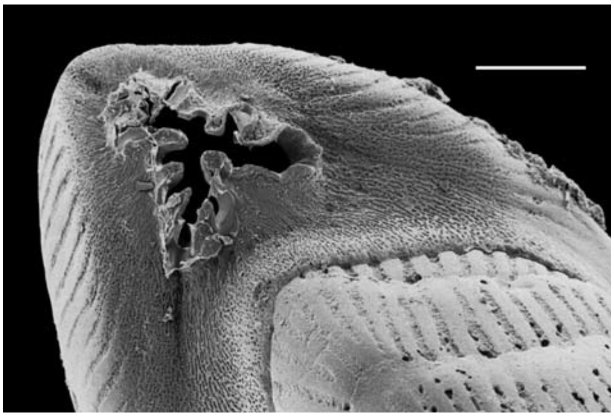
SEM micrograph of the test surface of *Dendritina zhengae* showing pseudopores on the smooth test surface, that do not penetrate the wall (scale bar = 0.01 mm).

rounded openings in flat forms. This promotes spreading of pseudopods and clinging to the substrate, preventing entrainment by strong water movement like waves and breakers.

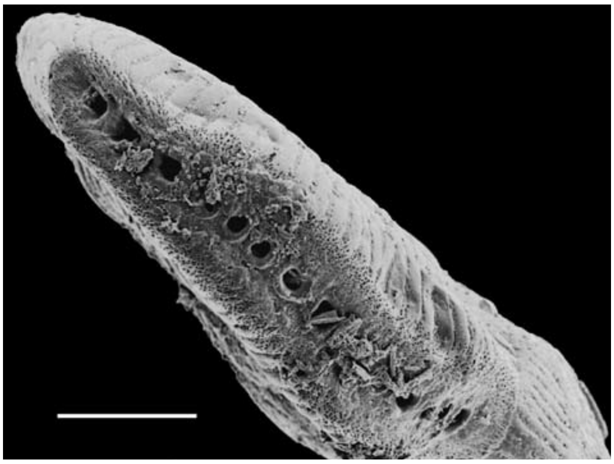
The normal size of 'adult' individuals is between 1 and 2 mm; a few can grow up to 3 mm.

Clan members divide the habitat according to their different requirements (habitat partitioning). Flat forms, in which chambers keep contact with the spiral part even in straight tests, prefer shallow water and prevent entrainment by strong breakers by hiding between and clinging to small filamentous macroalgae covering the reef crest in tropical seas (*Peneroplis antillarum, Peneroplis planatus*).

Gardeners with thick lens-shaped tests avoid extremely shallow water because they cannot resist strong water energy (*Dendritina*). They prefer clear ocean water in the uppermost region from 10 to 40 m depth, where they live between sand grains. They cannot be found on steep reef slopes because sandy sediments are transported to deeper regions, where peneroplids cannot survive.



SEM micrograph showing an irregular opening (aperture) at the end of the final chamber of *Dendritina ambigua* (scale bar = 0.1 mm) remembering a tree (dendros), therefore the name dendritic aperture and the name *Dendritina*.



SEM micrograph showing a row of round openings bordered by a rim at the final chamber of *Peneroplis planatus* (scale bar = 0.1 mm).

In a third group of purple gardeners, both chamber height and width slowly increase with growth: after a short spiral initial part, the chambers are arranged in a linear series and lose contact with the initial spiral part (*Peneroplis pertusus*). Robust tests with this chamber arrangement are rare in energy-dominated regions of the upper breaker zone, becoming more abundant in protected deeper parts down to 40 m depth, preferring rocky bottoms.

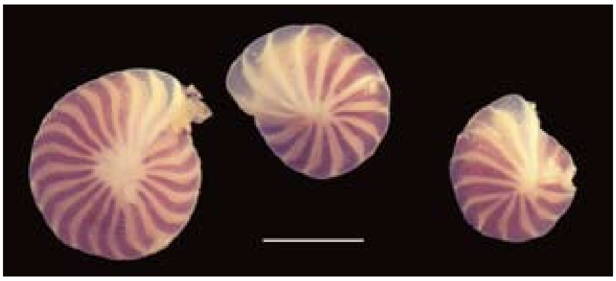
Small and fragile forms are extremely rare and prefer to settle in the most protected parts of the uppermost regions. They would be completely destroyed and fractioned in regions with permanently moving sediment like sands.

Purple gardeners are not restricted to tropical seas, but can also be found in warm temperate oceans, where winter temperatures sink below 14℃. Their geographical distribution is worldwide, whereby their presence throughout the Mediterranean is remarkable.

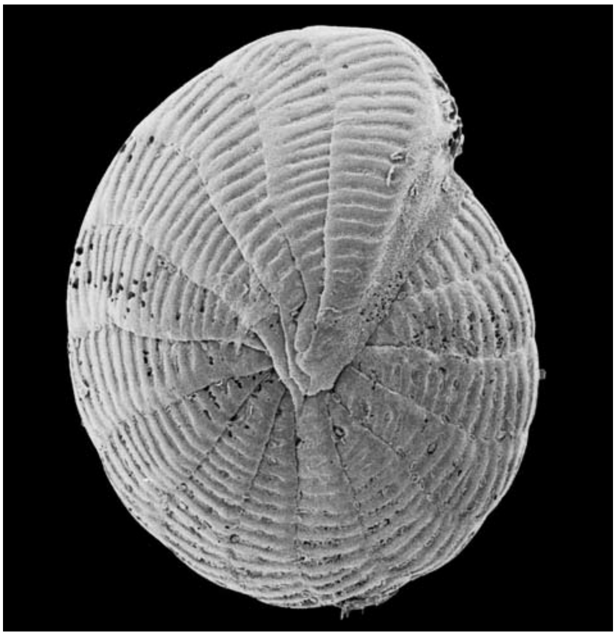
Living *Peneroplis antillarum* colored by purple microalgae (scale bar = 1 mm).

SEM micrograph of *Peneroplis antillarum* (size = 1.2 mm).

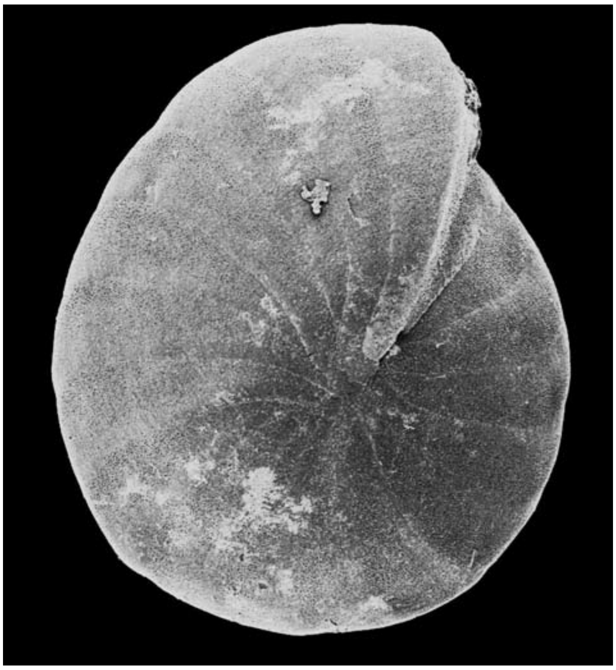
SEM micrograph of *Peneroplis planatus* (size = 1.8 mm).



Living *Dendritina ambigua* colored by purple microalgae (scale bar = 1 mm).

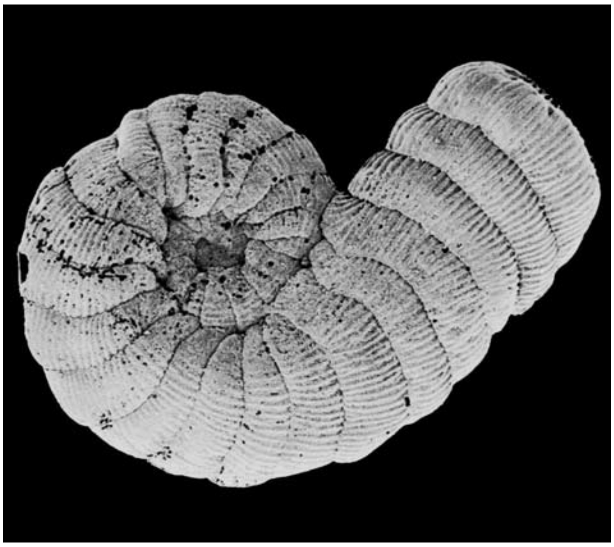


SEM micrograph of *Dendritina ambigua* (size = 1.2 mm).



SEM micrograph of *Dendritina zhengae* (size = 1.4 mm) possessing a smooth porcellaneous shell.

SEM micrograph of *Peneroplis pertusus* (size = 1 mm) showing a weak increase in chamber height and evolute coiling, which means that the inner whorls are visible from outside.



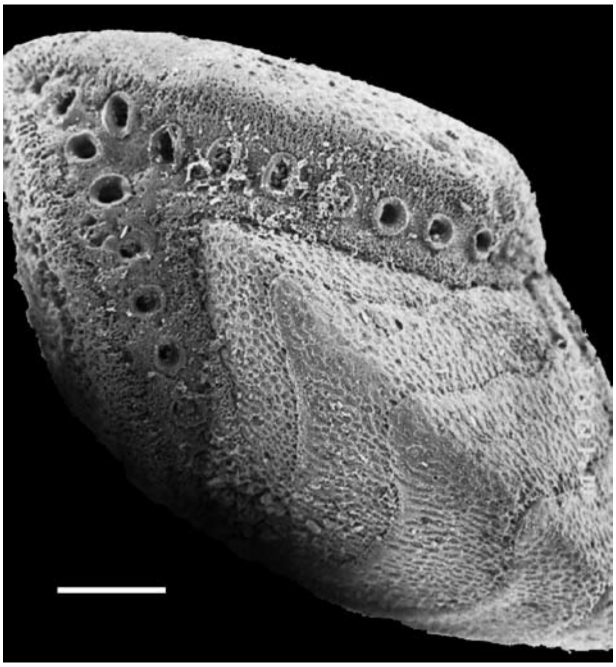
SEM micrograph of *Peneroplis pertusus* with final chambers that are arranged in a straight order (size = 1.4 mm).

Green gardeners, scientific name ***Archaiasinidae***

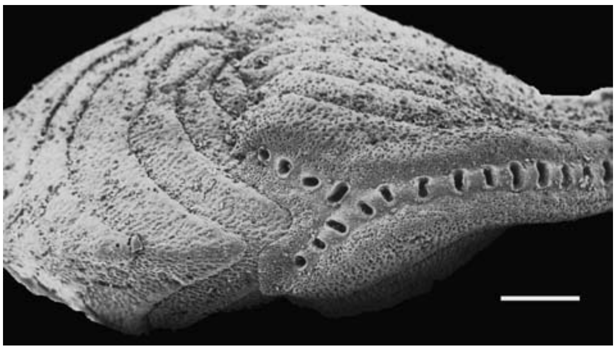
Similar to purple gardeners, the clan members possess white and non-transparent porcellaneous walls. The intensive green color is caused by their symbiotic plants, which are green algae (*Chlamydomonas*). In contrast to purple gardeners, where the openings (aperture) are elongate, oval or irregularly dendritic, these greenhouses always show a series of regular circular to oval openings surrounded by a small rim. Most of these openings become a distinct double row with alternating apertures after an initial single row stage.

Members of this clan show greater variability in their construction plan and size compared to purple gardeners. The simplest constructions are similar to purple gardeners, showing the same planispiral coiling, where chamber height remains constant (*Laevipeneroplis*). The chambers always keep contact with the initial spiral, surrounding the former test when the chamber arrangement becomes straight. In contrast to purple gardeners, tests are smooth, and light penetrates the thick walls through pore-like structures. These structures do not penetrate the thick walls but make them thinner in places.

Clan members showing the initial test construction explained above can grow to more than 3 mm. In large individuals, chambers envelop parts of the older test.



SEM micrograph showing the row of round openings bordered by a rim at the final chamber of *Laevipeneroplis proteus* (scale bar = 0.1 mm).



SEM micrograph showing the row of round openings bordered by a rim at the final chamber of large *Laevipeneroplis proteus* (scale bar = 0.1 mm).

SEM micrograph showing the double row of round openings bordered by a rim at the final chamber of verly large *Laevipeneroplis proteus* (scale bar = 0.1 mm).

These gardeners are restricted to shallow water with weak water movement, for example in wave-protected shallow reef and backreef areas (reef moat) in the Caribbean, where they are abundant. A very few representatives can be found in the central tropical West Pacific.

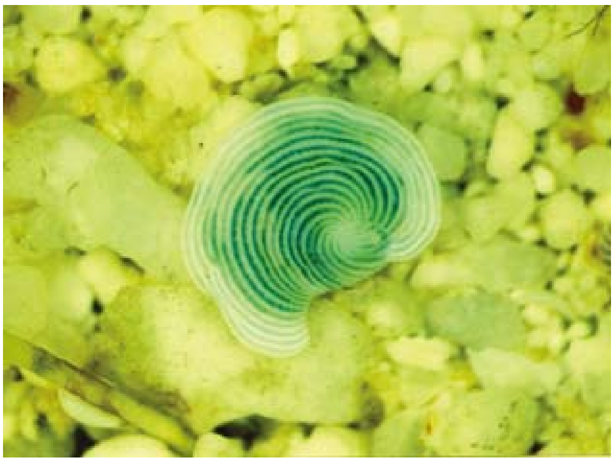
Similar constructions with large flaring chambers are abundant in protected areas of the shallow sea, attaining sizes of up to 4mm. Due to the larger size they have to strengthen their tests with pillars, which divide the chambers into smaller units; a complete separation by septulae, however, is not attained.

Much larger and thicker individuals with lens-shaped tests densely settle on macroalgae of the high-energy reef flats in the Caribbean (*Archaias*). They also strengthen their constructions with pillars, and the strong backbend of chambers is characteristic.

Sea grass meadows of deeper water down to 10 m depth are inhabited in the Caribbean by flat circular tests

SEM micrograph of *Laevipeneroplis proteus* (size = 0.6 mm).

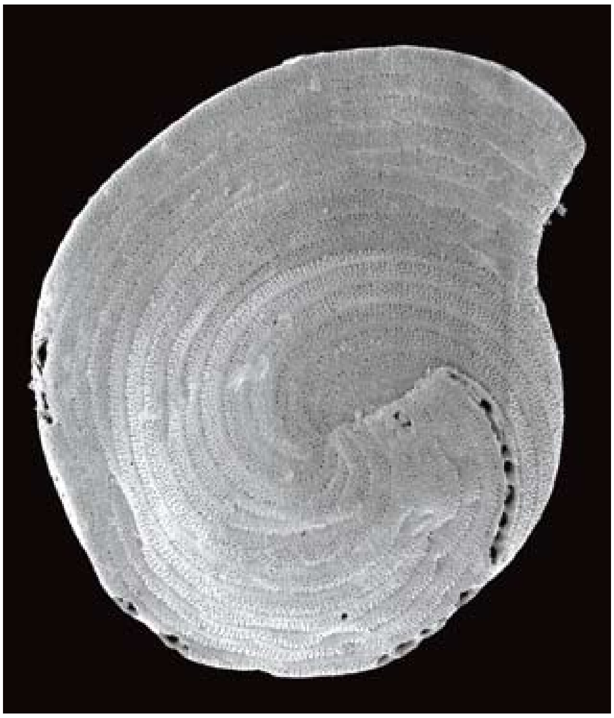
SEM micrograph of *Laevipeneroplis proteus* with chambers embarrassing the former test part (size = 1.2 mm).



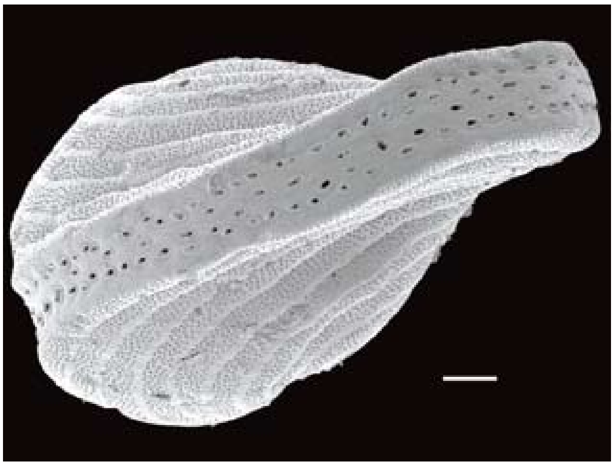
Living *Laevipeneroplis proteus* (size = 2.1 mm) on sandy bottom in the shallow lagoon of Peleliu, Belau.

with a thicker initial part similar to their back reef relatives (*Cyclorbiculina*). The chamber envelopment visible in the relative is completed in these forms. This leads to ring-like (annular) chambers that are divided by pillars. Size often exceed 1 cm.

A quite different construction plan characterizes the last clan member (*Parasorites*). Test construction starts with a flat initial spiral quite similar to flat purple gardeners (*Peneroplis planatus*), immediately transforming into ring-like annular chambers. The distinguishing feature from the three above-described relatives is the complete division of



SEM micrograph of *Archaias angulatus* with chambers embarrassing the former test part (size = 1.5 mm; photo C. Baal).



SEM micrograph of the oval, rimmed openings of *Archaias angulatus* in the final chamber (scale bar = 0.1 mm; photo C. Baal).

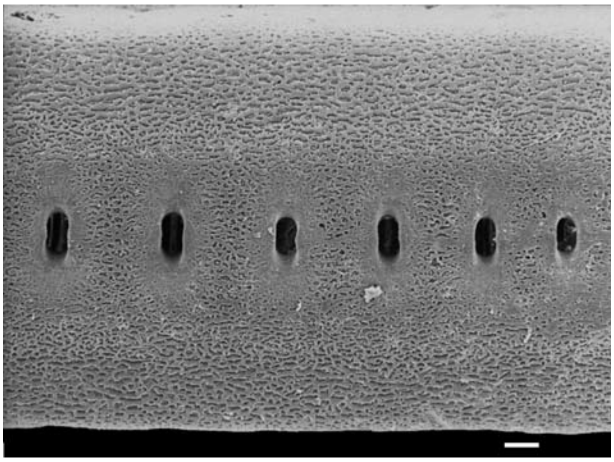
the chambers into chamberlets that are separated by walls called septulae. Additionally, the inner part is not thickened like in other clan members with flaring chambers.

Membership in the clan of green gardeners is also characterized by equally sized pores surrounded by small rims that are arranged in a single row; this leads to double rows in larger (up to 1 cm) tests. The last group again is abundant in the Caribbean, but can also be found in the tropical West Pacific, where it settles in clear ocean water from 30 to 60m. This is extremely deep for gardeners with porcellaneous tests because light is weak at those depths and lacks the red wavelengths that are necessary for photosynthesis of green plants.

SEM micrograph of *Cyclorbiculina compressa* with chambers partly embarrassing the former test part (size = 1.6 mm; photo C. Baal).

Light micrograph of *Cyclorbiculina compressa* (size = 2.4 mm) with chambers totally embarrassing the former test part (photo C. Baal).

Light micrograph of living *Parasorites orbitolitoides* (size = 2.3 mm).

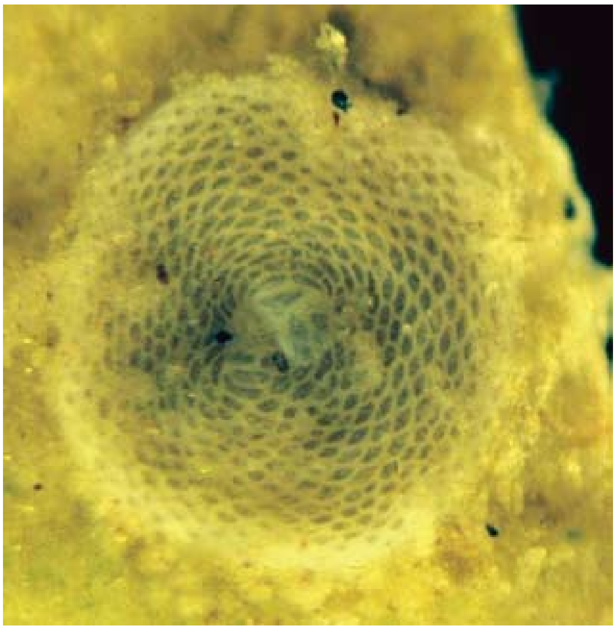


SEM micrograph of the lateral side of *Parasorites orbitolitoides* showing a single row of oval openings without a rim (scale bar = 0.01 mm; photo C. Baal)).

Blue to brownish-violet gardeners, scientific name ***Soritidae***

These gardeners are characterized by large, circular test constructions attaining sizes of up to 3 cm. Walls are porcellaneous and transparency is obtained by an extreme thinning of the wall, which acts like the window panes in glasshouses. Therefore, their test construction is the most similar to glasshouses constructed by human engineers. The large initial chamber is followed by a tubular second chamber, which is then immediately surrounded by rings of chambers with glassy windows.

The bluish to brownish-violet color originates from the microalgae, which are dinoflagellates as in corals. In corals, most of the different colors are caused by symbionts.

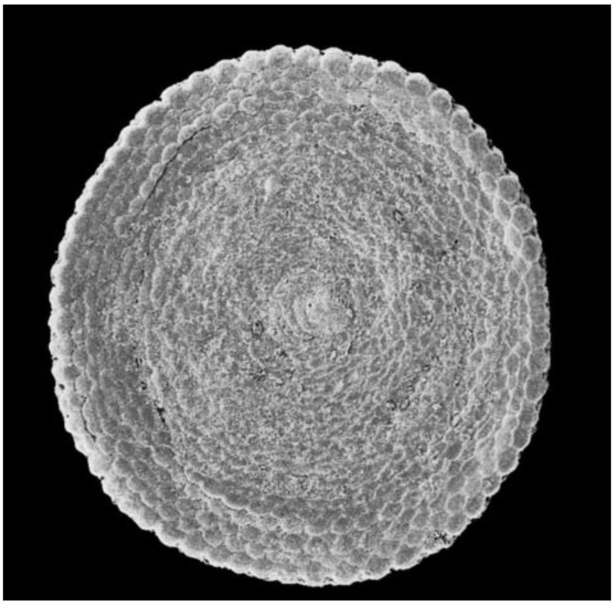


Living *Sorites orbiculus* (size = 1.4 mm) fixed to a coral boulder.

This makes the colors in the soritids also highly variable, differing and changing from place to place.

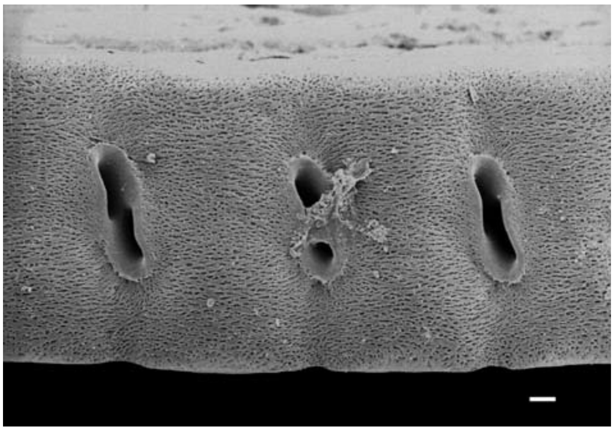
Three main types live in the shallow tropical and warm temperate oceans. The first group (*Sorites*) constructs flat glass houses with a single row of openings.

They live attached to flat and firm substrates like sea grass leaves, larger thalli of macroalgae or on smooth rocky bottom. Especially in the latter case, they adjust their test according to the form of the substrate. Abundance is highest



SEM micrograph of *Sorites orbiculus* (size = 1.5 mm).

Thin section of *Sorites orbiculus* showing the transparent test parts at the chamber surface (size = 1.3 mm; photo E. Iordanova).



SEM micrograph of the lateral side of *Sorites orbiculus* showing a single row of inclined apertures consisting of the openings of contiguous chambers (scale bar = 0.01 mm).

at the surface in quiet waters, living attached to sea grass, but they can survive in clear water down to 50 m depth.

The geographical distribution, similar to purple gardeners, is not restricted to tropical seas but also ranges to warm temperate regions. The northern distribution limits are Florida in the West Atlantic, Sicily in the Mediterranean and Kii Peninsula of Japan in the West Pacific.

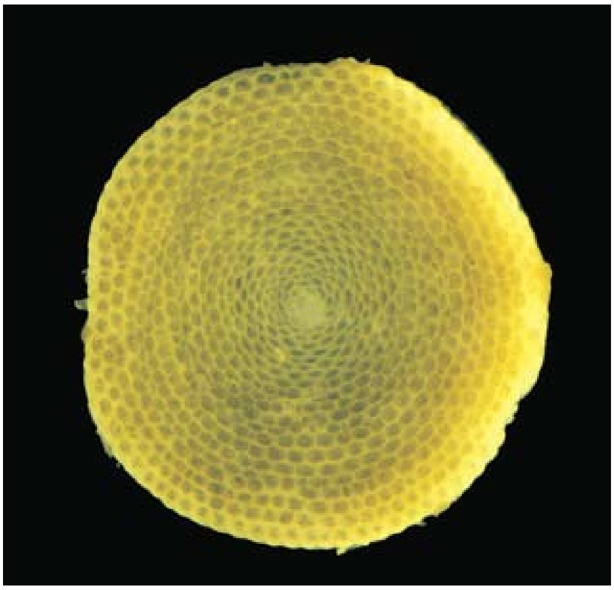
The second group belonging to this clan (*Amphisorus*) shows a construction plan similar to the first group. It differs somewhat in that it becomes larger and thicker by alternating chamberlets, causing increasing thickness during test growth. Therefore, test openings are arranged in a double row.

The shallow-living forms become thicker compared to the deeper-living forms. Thus, a median layer of irregular openings is positioned between the two main rows.

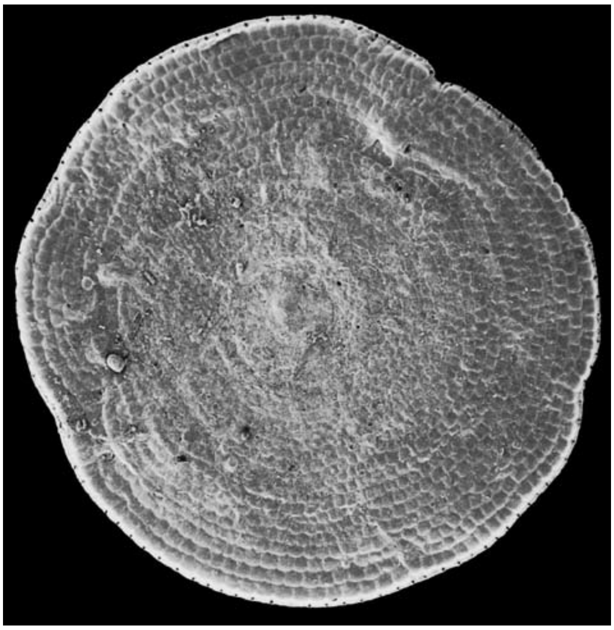
These gardeners can attain extreme abundances in the shallowest region of protected reef areas, where they settle on firm substrate, i.e. attached to the rocky bottom or fixed to small filamentous algae. In lagoonal areas they are extremely common on sea grass leaves or on smooth and flat macroalgal thalli. Abundance decreases with depth, where they can live in clear water down to 50 m. From 5 to 50 m, tests are always thin and do not show intermediate layers of apertures.

The geographical distribution is more restricted compared to its smaller relative. These gardeners are rare in the Atlantic but abundant in the Red Sea, Indian Ocean and Central and West-Pacific as far south as New Guinea.

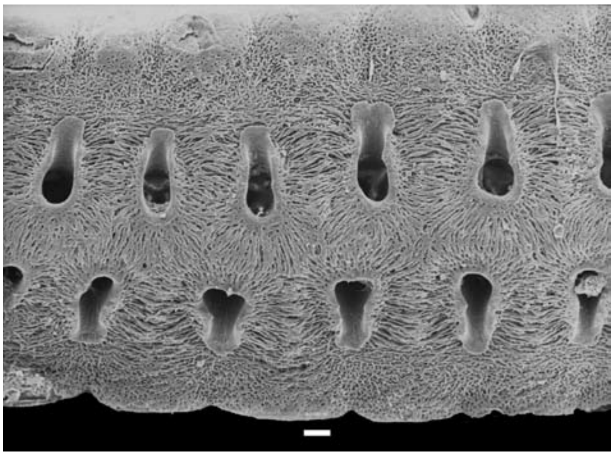
In the Central and SW Pacific a related group with similar test form and size replaces the above gardeners



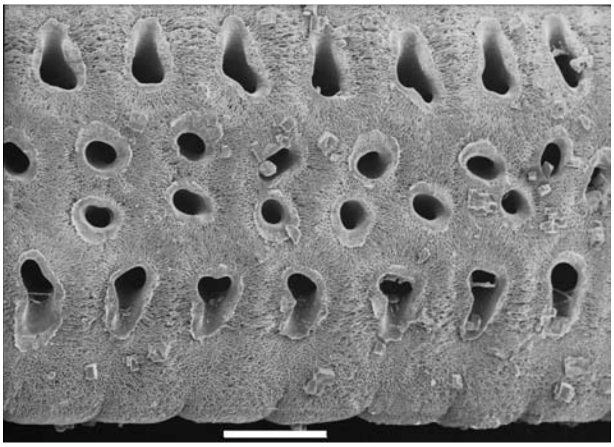
Living *Amphisorus hemprichii* (size = 2 mm).



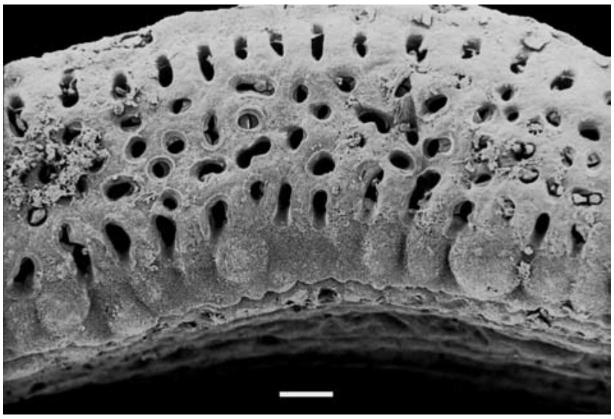
SEM micrograph of *Amphisorus hemprichii* (size = 3 mm).



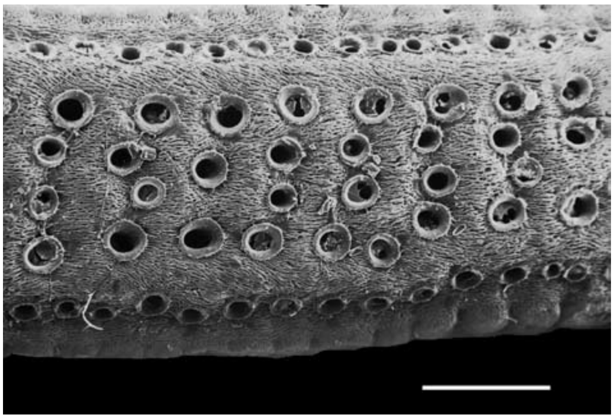
SEM micrograph of the lateral side of *Amphisorus hemprichii* showing a double row of drop shaped apertures, alternating due to the contiguous chambers (scale bar = 0.01 mm).



SEM micrograph of the lateral side of a thick *Amphisorus hemprichii* showing a double row of drop shaped apertures with an additional median layer of double rows (scale bar = 0.1 mm).



SEM micrograph of the lateral side of an extreme thick *Amphisorus hemprichii* showing the double row of drop shaped apertures with an additional median layer of several rows of irregularly formed openings (scale bar = 0.1 mm).



SEM micrograph of the lateral side of *Marginopora vertebralis* showing the double row of rimmed and rounded apertures with median rows of rimmed circular openings (scale bar = 0.1 mm).

(*Marginopora*). Beside chamber construction, the main differences lie in the openings, which are always circular and of the same size, surrounded by a rim and arranged in multiple rows.

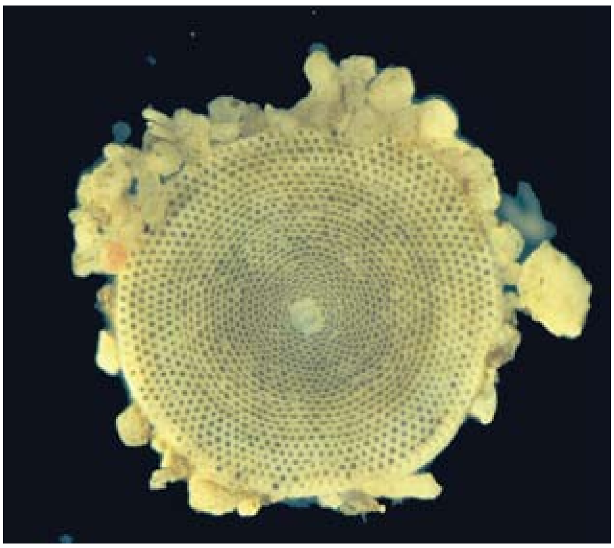
The depth distribution of these gardeners is more restricted compared to its close relative, and they can live in shallow regions down to 10 m.

Ocher gardeners with spindle-shaped greenhouses, scientific name ***Alveolinidae***

These gardeners construct special glasshouses that resemble a spindle. The form and size of the spindle are variable, ranging from approximately globular constructions to very elongate, needle-shaped forms.

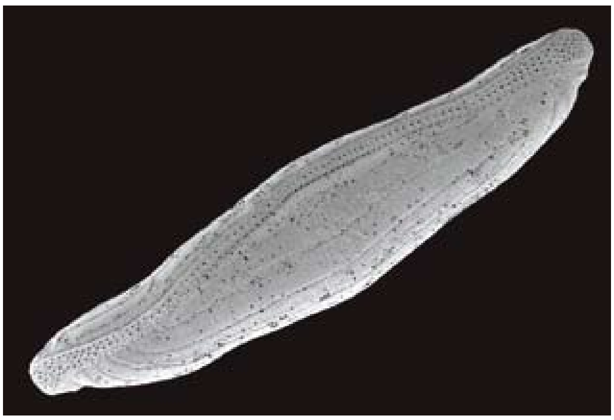
The size also ranges from 2 mm in ‘adult’ globular individuals to 4 cm in the needle shaped forms. The elongated chambers are planispirally arranged and subdivided by septula into chamberlets. Every chamberlet possesses an aperture, becoming the foramen as a connection to the chamberlet of the next chamber. Moreover, the row of chamberlets within one chamber is connected by a specific system of openings, called canals. These canals are openings in the septula running in front of, behind the main chamber wall (septum) or in both directions.

Because the walls are porcellaneous, these gardeners have to make their walls extremely thin in the center of the chamberlet to provide transparency for the symbiotic

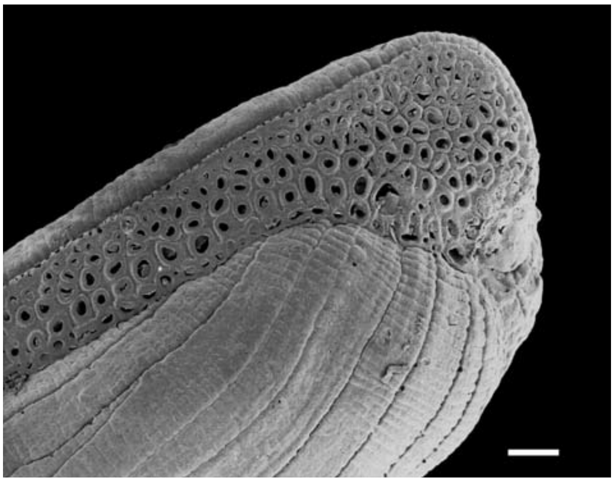


Living *Marginopora vertebralis* (size = 3 mm).

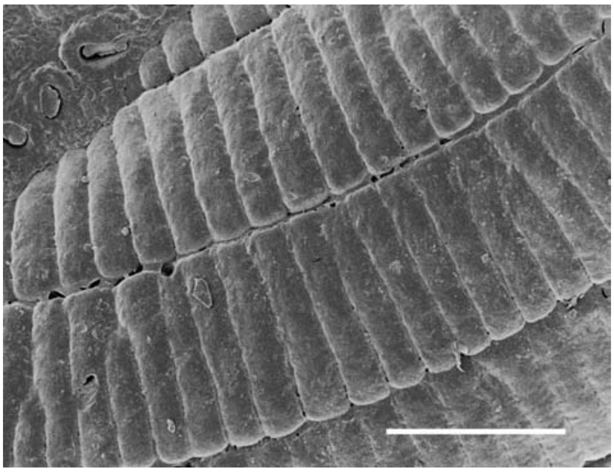
Living *Alveolinella quoyi* (size = 3.8 mm).



SEM micrograph of *Alveolinella quoyi* (size = 4.1 mm).



SEM micrograph of *Alveolinella quoyi* showing the multiplication of rows of rimmed apertures at the spindle edge (scale bar = 0.1 mm).

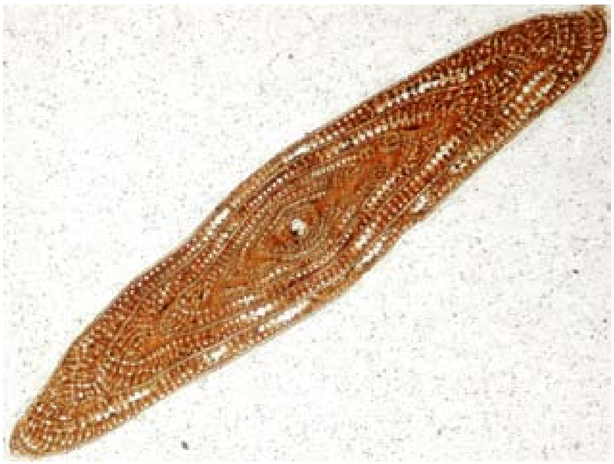


SEM micrograph of *Alveolinella quoyi* showing the grooves at the shell surface enabling light penetration (scale bar = 0.1 mm).

plants, which are diatoms. Housing diatoms as symbionts is unique for the gardeners with porcellaneous walls, while diatoms are the only plants that gardeners with hyaline test can house. Again, transparent wall regions above every chamberlet are called 'windows'. When the gardener is fully active and undisturbed, it attaches the glasshouse to the bottom with pseudopods extruding from one end of the spindle. The cytoplasm of the host transports the microalgae into the last whorl to attain enough light for photosynthesis (because photosysnthesis is hampered in the inner whorl).

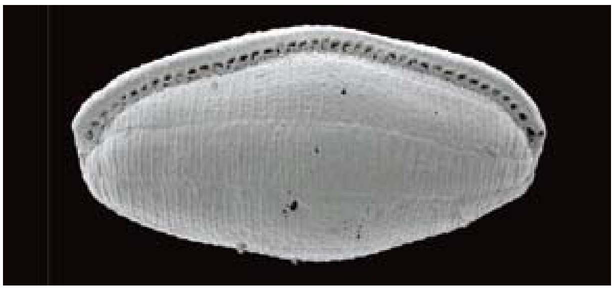
These gardeners do not live in regions with extreme water motion at the reef crest, but also do not prefer quiet shallow water such as is found in the reef moat and in lagoons. They need some water motion, but do not depend on substrate. In regions with higher water motion, e.g. on the upper reef slope, they live in small holes of boulders and reef rock. With decreasing motion they can also live on mobile, coarse sand that is more abundant in deeper regions of the upper slope. Nevertheless, these gardeners need highly transparent water, and the deepest-living gardeners are found in these waters at 50 m depth.

These gardeners with spindle-shaped glasshouses are today not represented in the tropical Atlantic. Globular tests and thick spindles (*Borelis*) are found in the Indian Ocean and the Red Sea, while the long spindle types (*Alveolinella*) are restricted to the tropical West Pacific.



Thin section through the spindle shaped *Alveolinella quoyi* (size = 3 mm; photo E. Iordanova)

Light micrograph of *Borelis melo* (size = 1.3 mm; photo C. Baal)



SEM micrograph of *Borelis melo* (size = 1.4 mm) showing the single row of rimmed apertures (photo C. Baal).

Olive-green gardeners constructing lentil-shaped greenhouses, scientific name ***Amphisteginidae***

These gardeners construct small glasshouses between 1.5 and 4 mm, where the chambers are enrolled similar to a snail shell (**trochospiral**). But these spirals are extremely flat, approximating enrollment in a plane. Only chambers of the last whorl are visible from both sides, making the tests looks like small lentils. On the lower side (scientifically named **umbilical side**) the chamber is partitioned by a septum-like structure. Therefore, the central part of the lower side of the glasshouses looks like small swastikas.

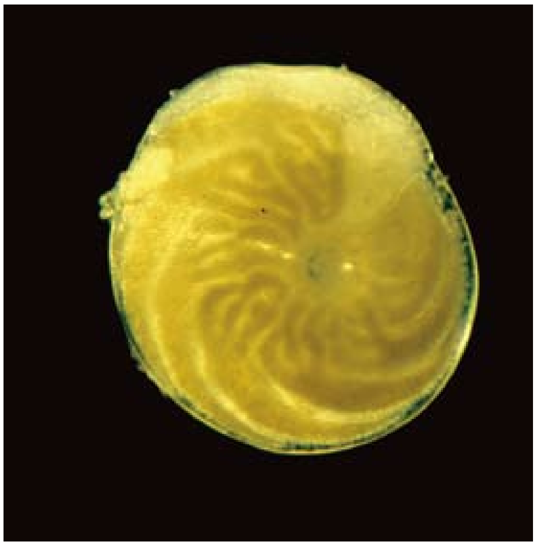
The amphisteginids harboring diatoms as greenhouse plants develop modifications of the initial construction plan. This enables them to live in extremely illuminated environments on the one side, but also in light-depleted environments on the other. Thick glasshouses (*Amphistegina lobifera*) are constructed in shallow regions with high, but not extreme water motion. Here, the amphisteginids fix their glasshouses to filamentous algae or seek protected areas in small holes of boulders or in the reef rock. To provide the microalgae living in the inner whorls of the glasshouse with enough light, these thick constructions show a totally transparent center, which are known as plugs.

Gardeners with completely symmetrical lentil-shaped glasshouses (*Amphistegina radiata*) inhabit shallow ocean regions with high, but not extreme water motion, where coarse sand covers the sea floor. It is difficult to differentiate between the upper and lower side. The glasshouse openings are also located at the lateral side and are not adapted for attachment to firm substrate.

The two groups of gardeners within the Amphisteginidae react to weaker light at deeper regions in different ways. The first-mentioned group (*Amphistegina lessonii*) makes very flat tests without changing size (*Amphistegina bicirculata*). Thus they are restricted to highly transparent water to 90 m depth.

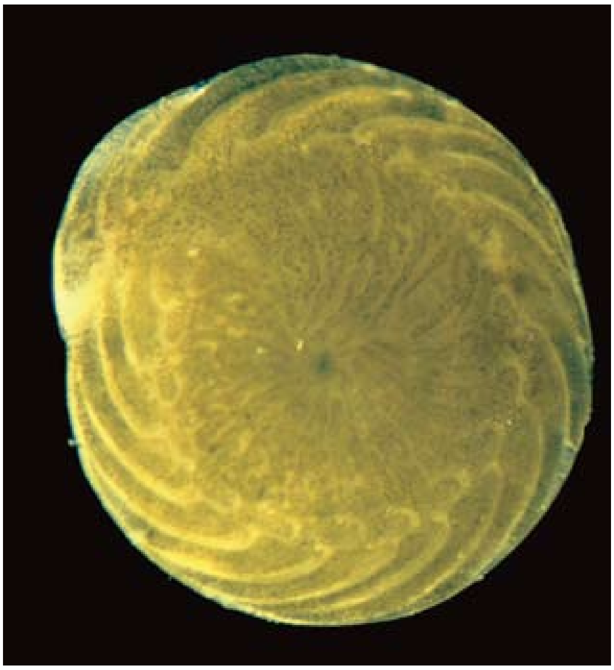
The second group with completely symmetrical test also becomes flatter, but in deeper regions they construct glassy structures on their surface called **papillae** to concentrate the reflected light (*Amphistegina papillosa*). With this mechanism, gardeners can provide their microalgae with enough light for photosynthesis down to 120 m in transparent ocean water.

While members of the first group show a worldwide distribution, tolerating the lowest temperatures of all greenhouse gardeners and thus extending to the warm temperate zone, the second group is restricted to the tropical Indo-Pacific.



Living *Amphistegina lessoni* (size = 1.1 mm), view from the spiral side (upper) with lobate chamber partitions and from the umbilical side (lower) with septal partitions.

Amphistegina lobifera (size = 2 mm) living in shallowest water showing lobate chamber partitions.



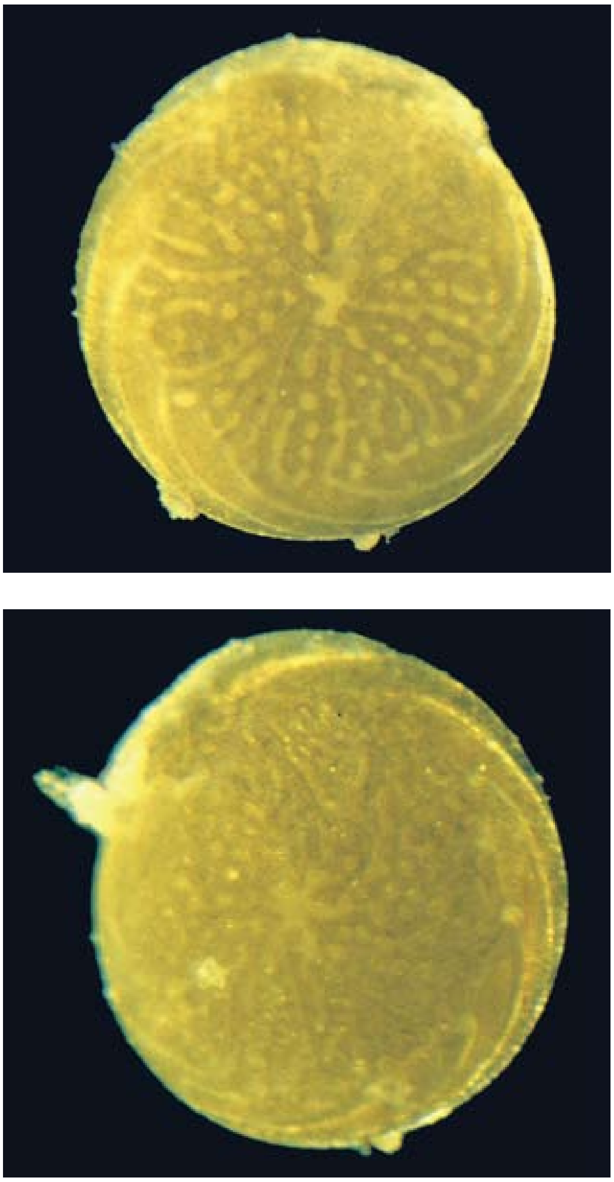
Living *Amphistegina radiata* (size = 1.7 mm), view from the spiral side (upper) and from the umbilical side (lower).

Living *Amphistegina bicirculata* (size = 1.3 mm); view from the spiral side (upper) and from the umbilical side (lower), the latter demonstrating additional partitions by septa.

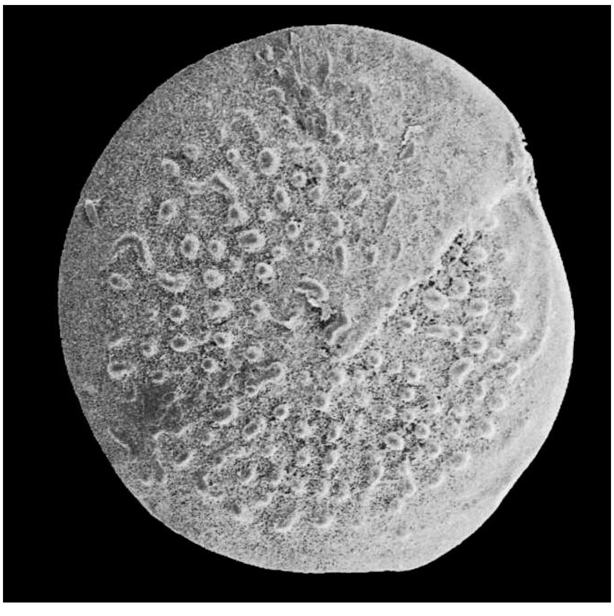
Thin section of *Amphistegina radiata* (size = 2.2 mm; photo E. Iordanova).

Ocher gardeners with star-shaped greenhouses, scientific name ***Calcarinidae***

The calcarinids cultivating diatoms construct glasshouses similar to the former group, with the chamber arrangement in a flat trochospiral and thick walls. The main difference to the former clan is the construction of long spines, giving glasshouses the appearance of little stars or sun discs. Spines act as anchors for fixing the glasshouses to the substrate. Glasshouse size ranges from 2 to 5 mm. Based on this construction, calcarinids often settle in high abundance in regions with extreme water motion. They



Living *Amphistegina papillosa* (size = 0.9 mm), view from the spiral side (upper) and from the umbilical side (lower).



SEM micrograph of *Amphistegina papillosa* (size = 0.7 mm).

therefore populate the reef crest, where they densely cover the bottom. Their size, which is similar to coarse sand grains, and their extreme density, which can be 600,000 per m^2, gives the impression of a sandy floor on the reef flat, but all these sand grains are alive!

Therefore, they are called ’living sand’ or ’star sand’ and often sold as souvenirs filled in small glass-bottles.

The calcarinid gardeners construct different types of glasshouses for settling in shallow regions of the tropical ocean. They need clear ocean water and thus avoid regions with high fluvial input of fine sediment from the land or polluted water. This makes them good indicators for healthy regions of the shallowest tropical seas in the East Indian and West Pacific Ocean.

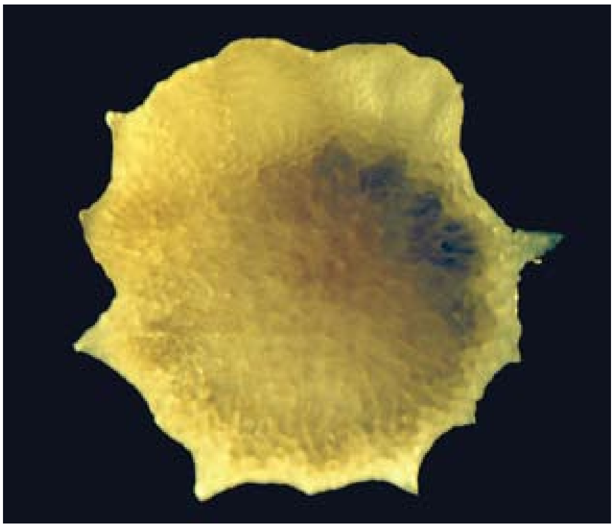
Calcarinids that construct flat trochospiral glasshouses where all chambers are visible, and that possess short spines at the lateral chamber part, are found in the whole tropical Indian Ocean and West Pacific, where they settle in shallow regions with little water motion (*Calcarina calcar*).

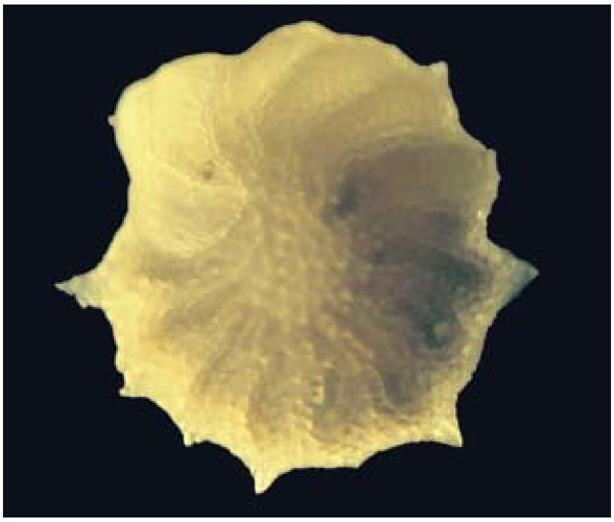
All other calcarinids are restricted to the Indonesian Archipelago and the tropical West and Central Pacific

Calcarinids similar to the former group, where the glasshouses have longer spines that are sometimes furcated,

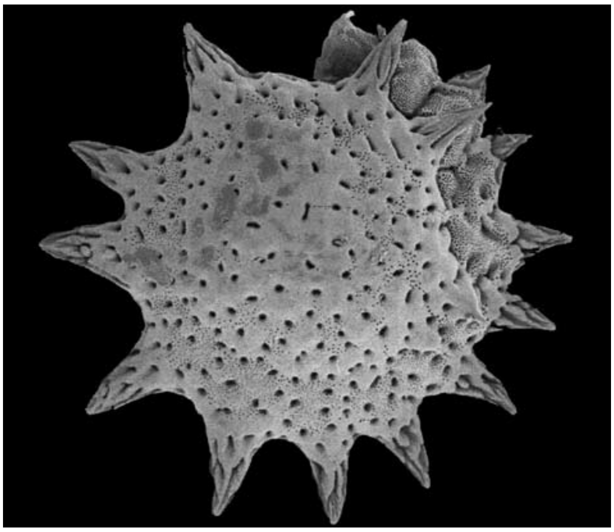
“Living sand” on the reef crest of Hateruma Island, Okinawa, Japan (scale bar = 10 mm).

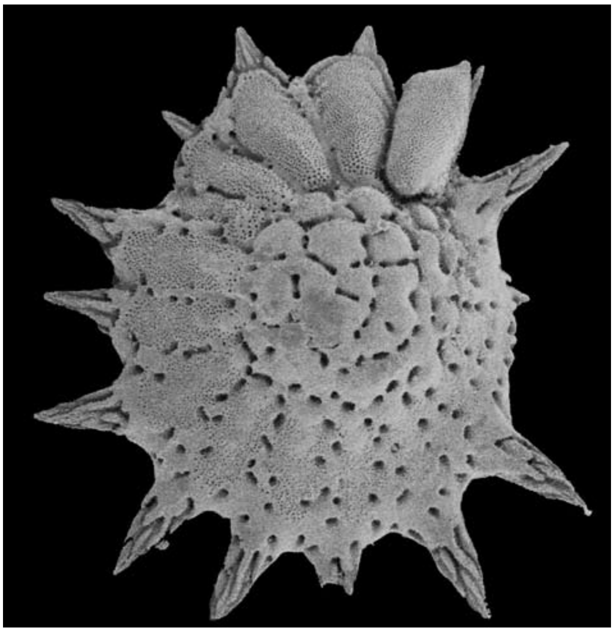
Small glass bottles filled with “Star Sand”. Souvenir from Motobu, Okinawa.





Living *Calcarina calcar* (size = 1.4 mm); view from the spiral side (upper) and from the umbilical side (lower).



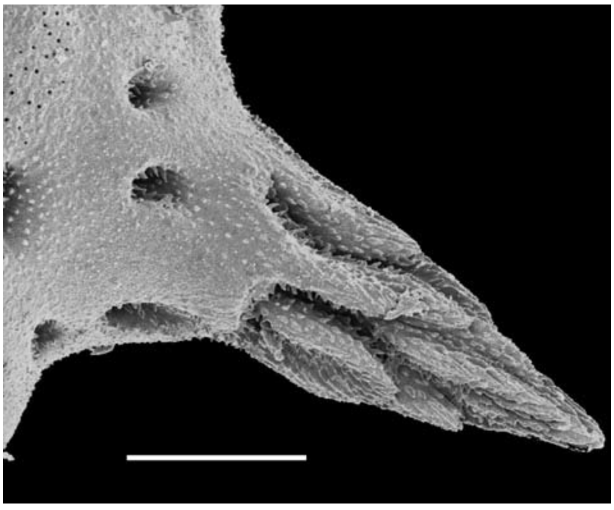


SEM micrograph of *Calcarina calcar* (size = 1.5 mm); view from the spiral side (upper) and from the umbilical side (lower).

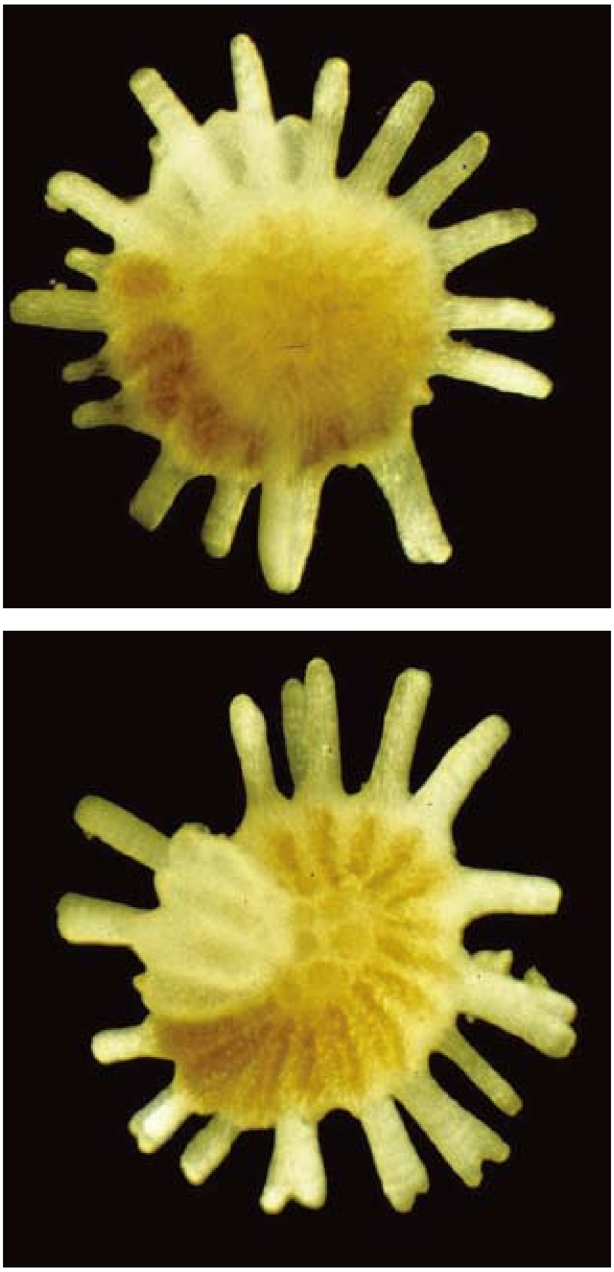
settle in regions similar to the former group (*Calcarina defrancii*). Thus they are found in front of or behind the most extremely turbulent reef crest, clinging to filamentous macroalgae.

Robust and large glasshouses with a few but very strong spines resemble little sun disks (*Calcarina gaudichaudii*). They lack an aperture, and connections to the environment can thus only be found at the tips of spines. These gardeners can resist extreme water motion by clinging to filamentous macroalgae or anchoring together. This makes them one of the main members of the ‘star sand’ living in the highest energetic zone of a Pacific coral reef.

Some gardeners within the calcarinids additionally cover their tests surfaces with spikes that are smaller than spines. Three types of glasshouses are described, which depend on water motion. Glasshouses with short spines similar in length to the long spikes (giving the impression of small sea urchins) are found in the shallowest zone, but



SEM micrograph of a spine of *Calcarina calcar* (scale bar = 0.1 mm).

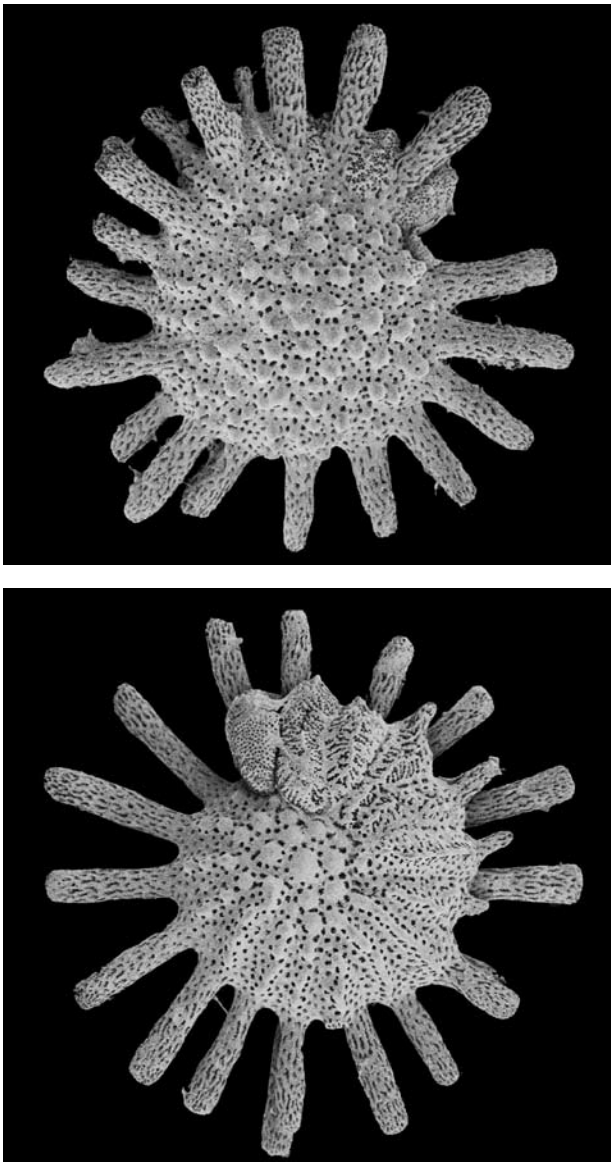


Living *Calcarina defrancii* (size = 1.8 mm); view from the spiral side (upper) and from the umbilical side (lower).

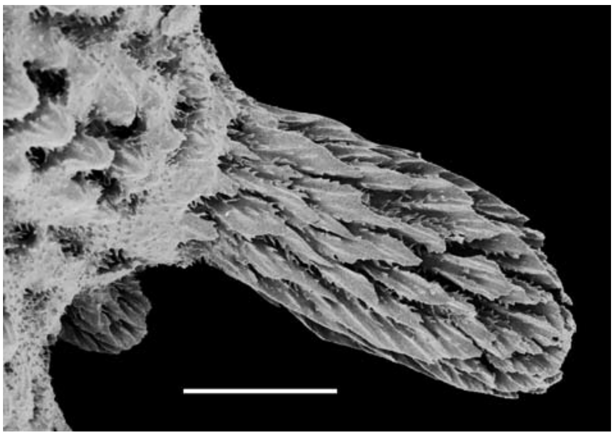
not on the reef crest (*Calcarina quoyi*).

In upper regions of the reef slope down to 30 m, calcarinids with longer and robust spines are abundant (*Calcarina hispida*), while between 20 and 60 m a third group with long, sometimes bifurcated spines is found (*Calcarina mayori*).

The last group of gardeners with additional spikes covering the glasshouse adds additional chambers on the upper (spiral) and lower (umbilical) side of the main chamber spiral (*Baculogypsinoides*). The number of spines, again found as chamber extensions, is reduced to 3. This construction results in approximately globular glasshouses, yielding the largest size (5 mm) within the calcarinids.

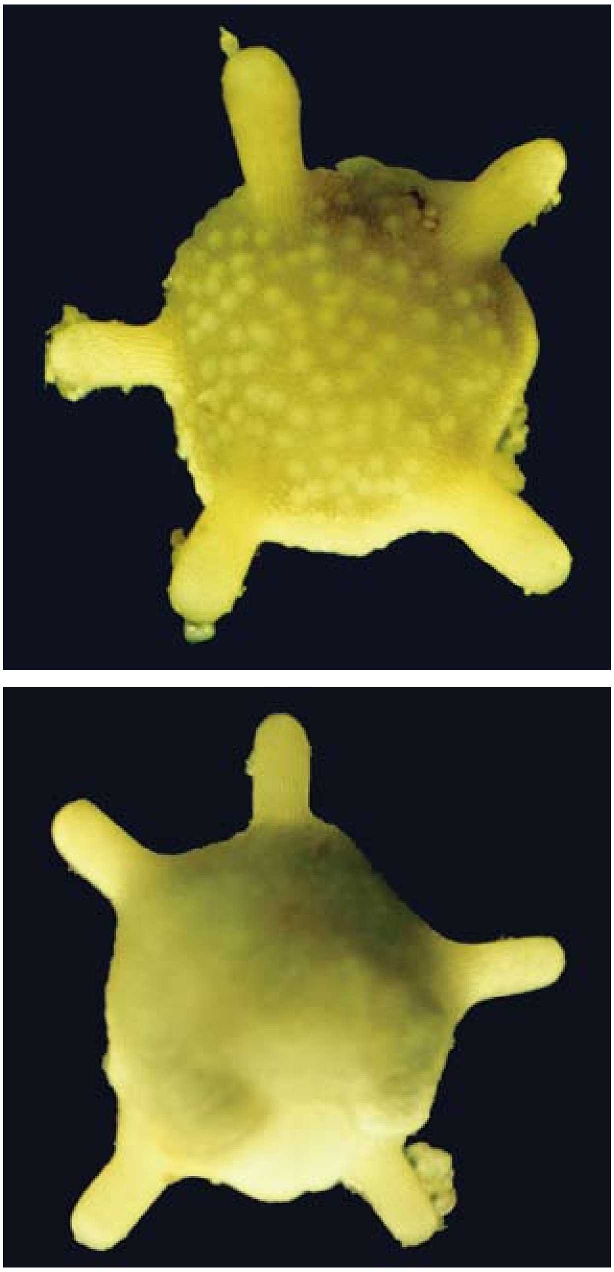


SEM micrograph of *Calcarina defrancii* (body size without spines = 1.2 mm); view from the spiral side (upper) and from the umbilical side (lower).

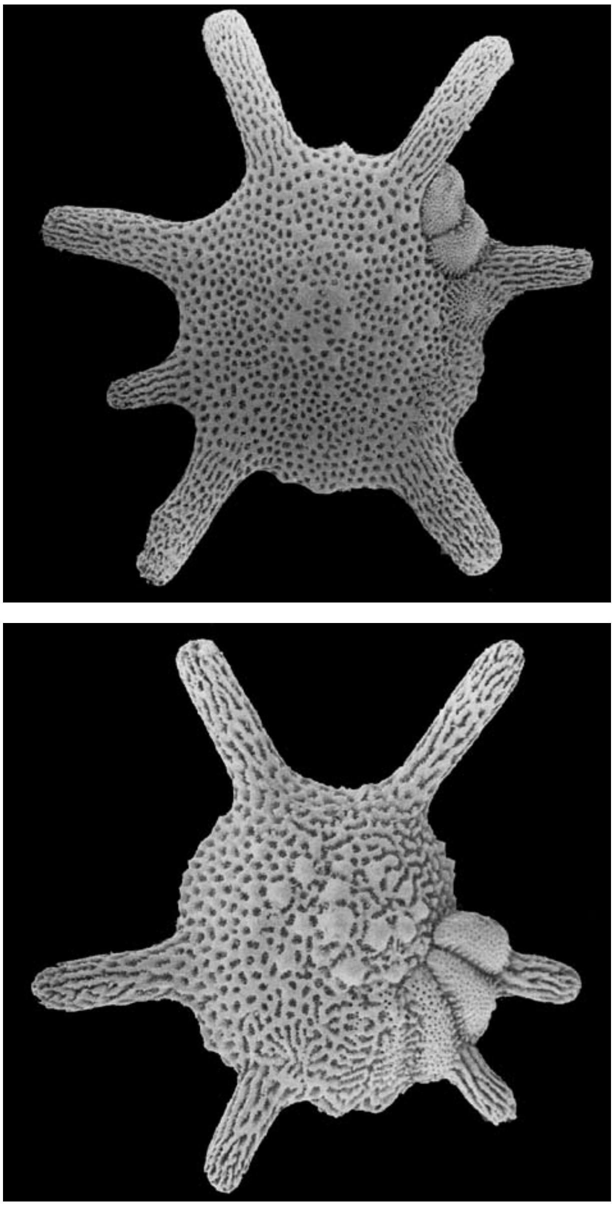


SEM micrograph of a spine of *Calcarina defrancii* (scale bar = 0.1 mm).

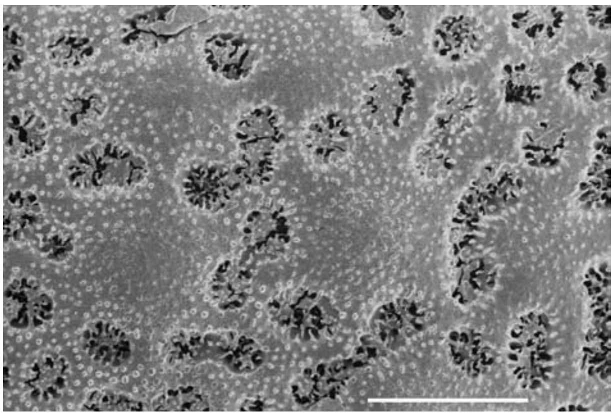
Large pustules, similar to plugs in amphisteginids as completely transparent structures, transmit light into the central test part and thus provide the microalgae living in



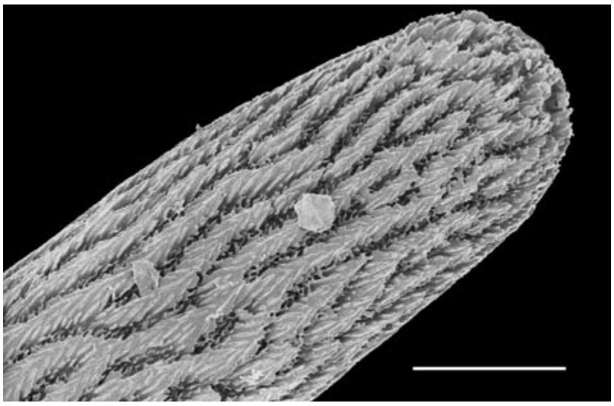
Living *Calcarina gaudichaudii* (size = 2.1 mm); view from the spiral side (upper) and from the umbilical side (lower).



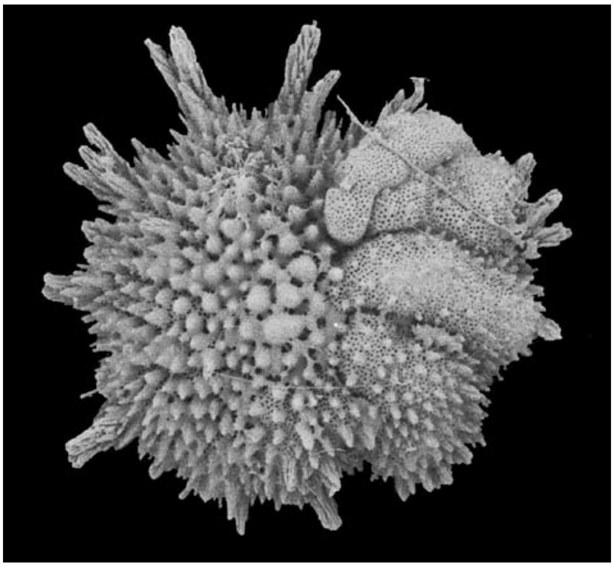
SEM micrograph of *Calcarina gaudichaudii* (body size without spines = 1.2 mm); view from the spiral side and from the umbilical side.



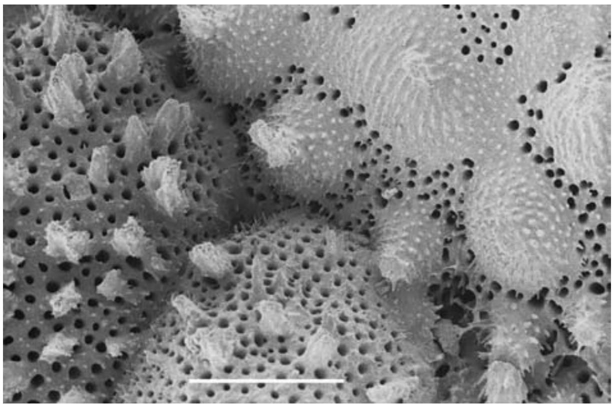
SEM micrograph of the surface of *Calcarina gaudichaudii* showing the protection of pores by small spikes (scale bar = 0.1 mm).



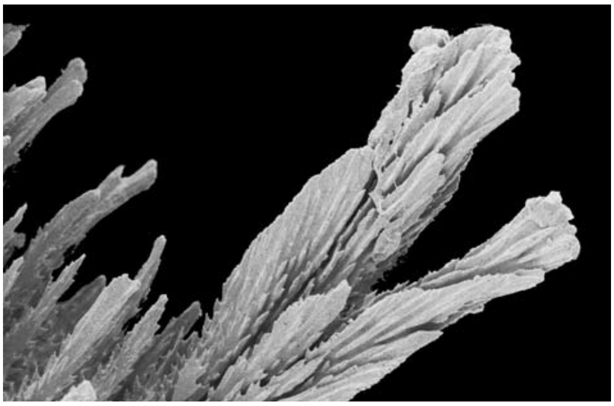
SEM micrograph of a spine of *Calcarina gaudichaudii* (scale bar = 0.1 mm).



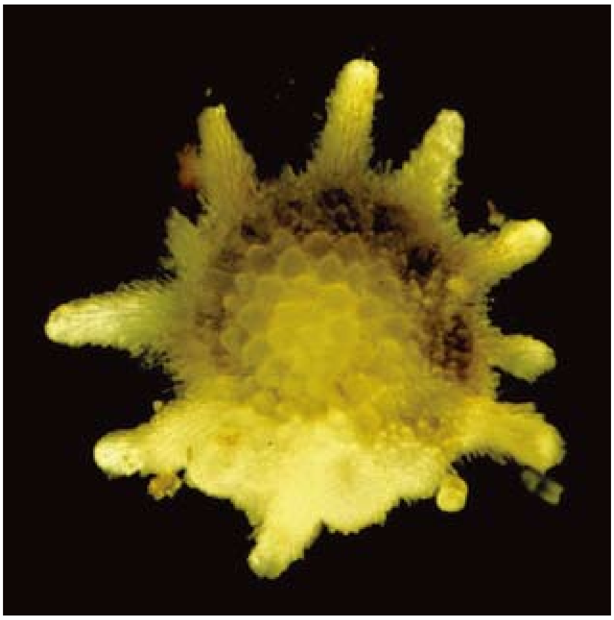
SEM micrograph of *Calcarina quoyi* (size = 1.5 mm); view from the umbilical side.

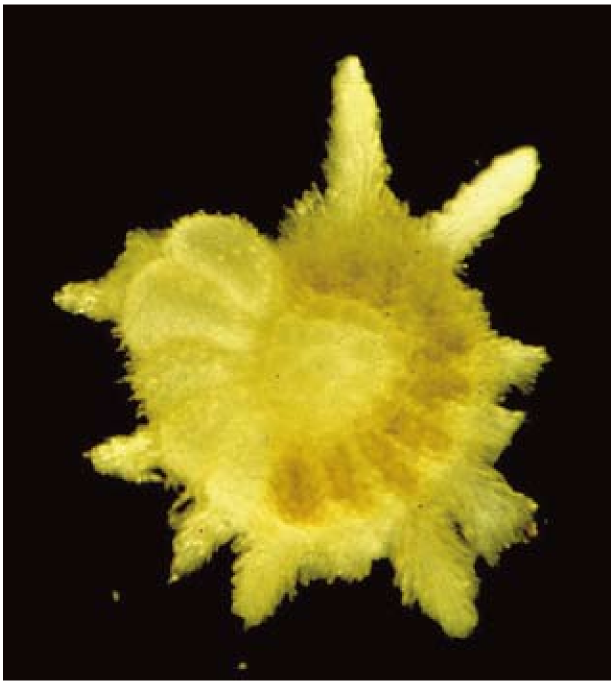


SEM micrograph of the surface of *Calcarina quoyi* showing the protection of pores by small spikes (scale bar = 0.1 mm).

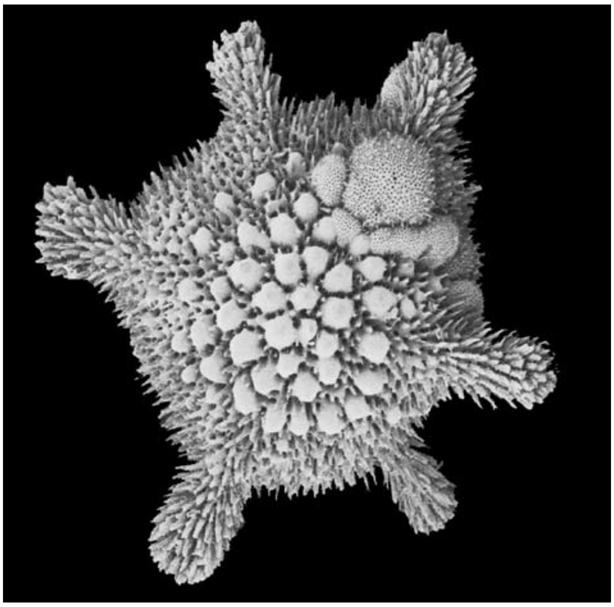


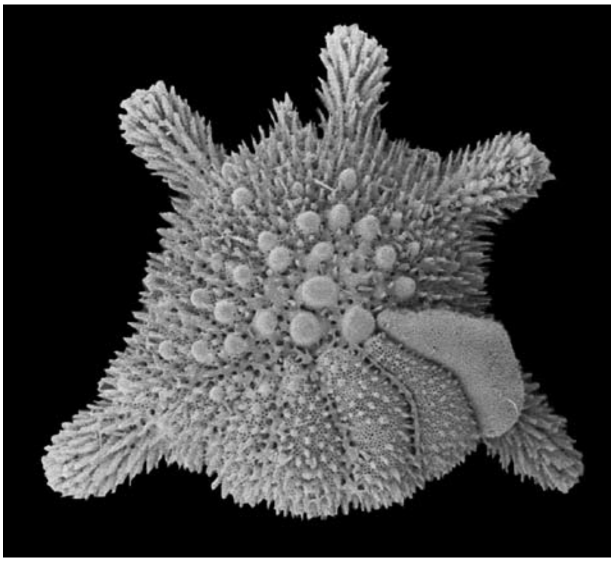
SEM micrograph of a spine of *Calcarina quoyi* (scale bar = 0.1 mm).



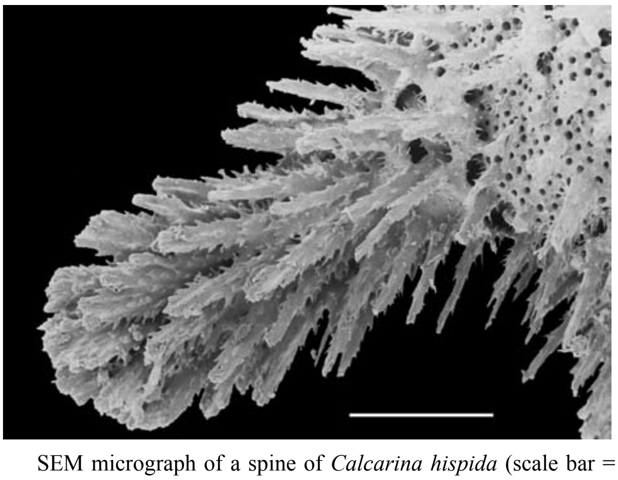


Living *Calcarina hispida* (size = 2.5 mm); view from the spiral side (upper) and from the umbilical side (lower).

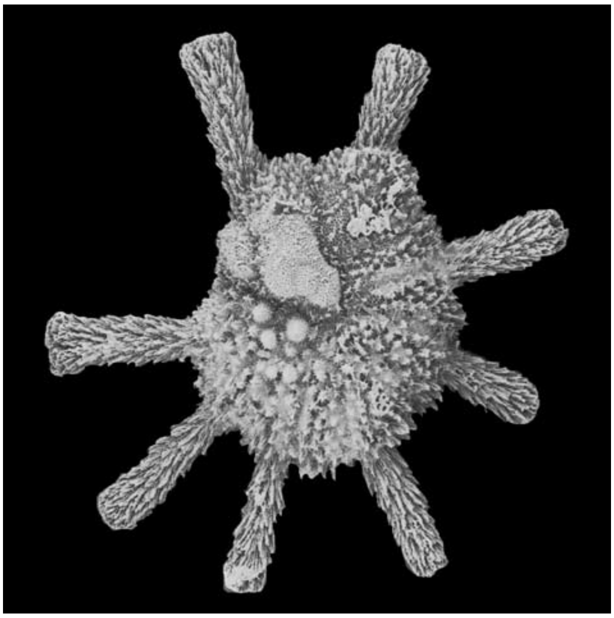




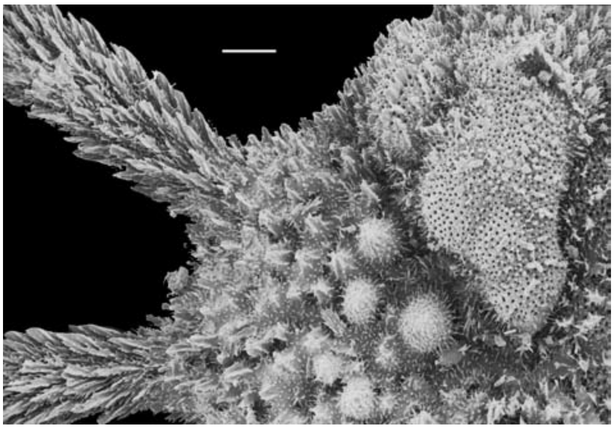
SEM micrograph of *Calcarina hispida*; view from the spiral side (body size without spines = 1.6 mm) and from the umbilical side (body size without spines = 1.5 mm).



SEM micrograph of a spine of *Calcarina hispida* (scale bar = 0.1 mm).



SEM micrograph of *Calcarina mayori* (body size without spines = 1 mm)

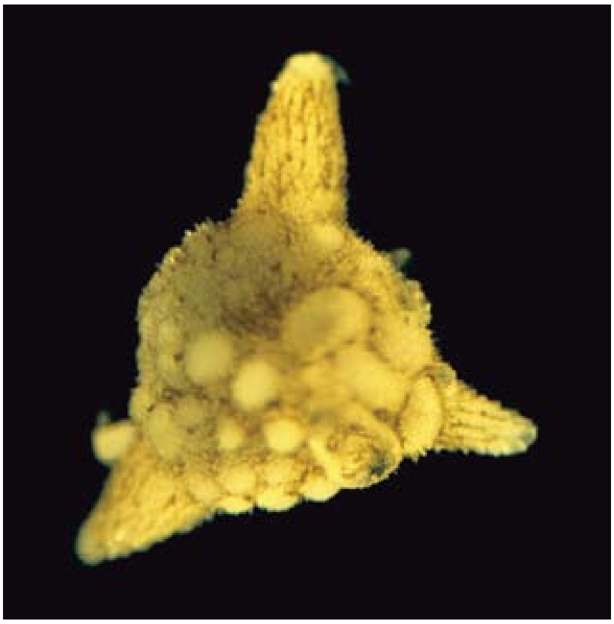


SEM micrograph of a spine and shell surface of *Calcarina mayori* (scale bar = 0.1 mm).

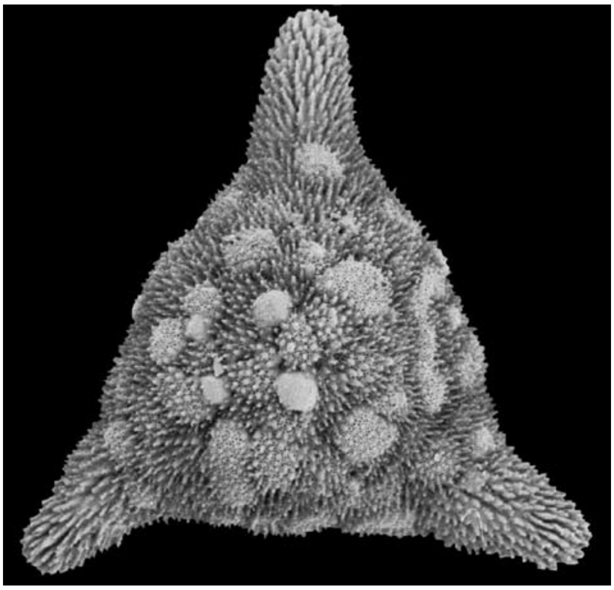
the test center with necessary light.

These gardeners are the only clan members that range into the deeper regions of the well-illuminated reef slope between 30 and 60 m.

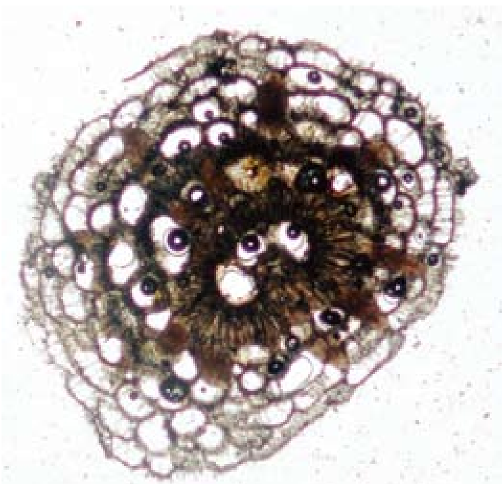
The last two groups of gardeners within the calcarinids construct special glasshouses that deviate from the main trend in calcarinids. The first group (*Baculogypsina*) arranges their chambers, after developing a flat and short spiral, in circular manner around this embryonic spiral. Four to seven spines are developed at the lateral side of this plane. Additional chambers are built at both sides of this median plane, resulting in thick lens-shaped glasshouses with strong spines. Totally glassy pustules allow light to



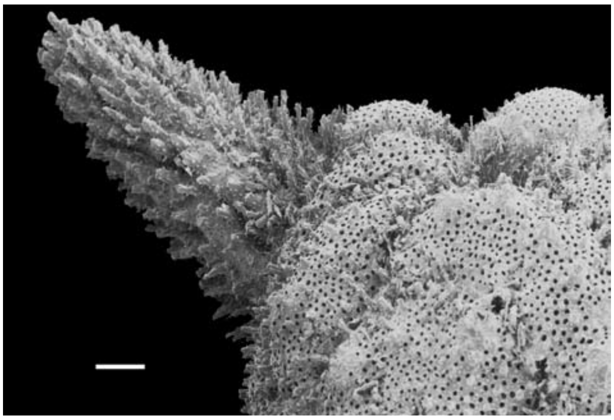
Living *Baculogypsinoides spinosus* (size = 3 mm).



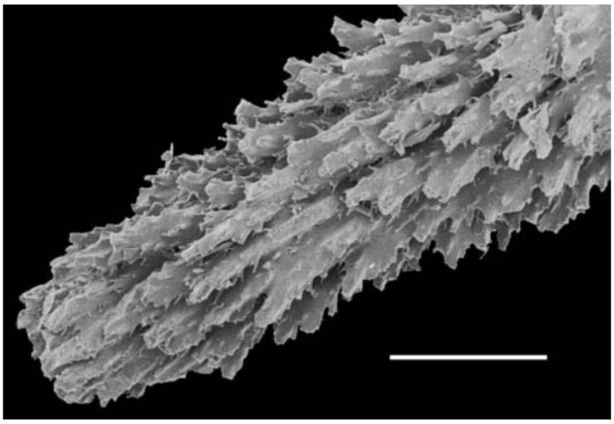
SEM micrograph of *Baculogypsinoides spinosus* (body size without spines = 2 mm).



Thin section through *Baculogypsinoides spinosus* (size = 2.5 mm; photo E. Iordanova).



SEM micrograph of a spine and shell surface of *Baculogypsinoides spinosus* (scale bar = 0.1 mm).



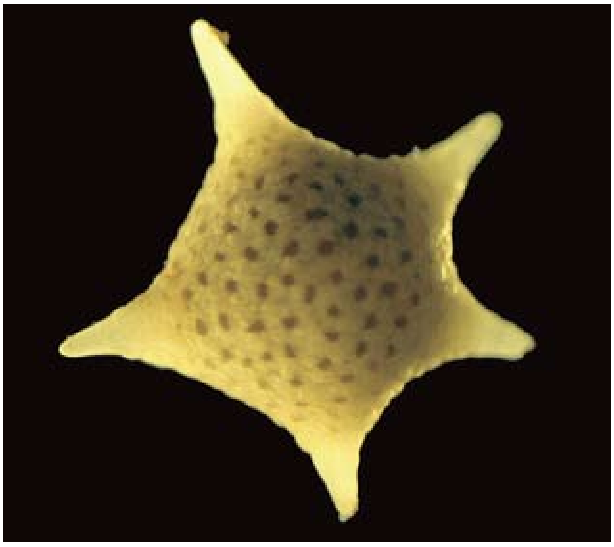
SEM micrograph of a spine of *Baculogypsinoides spinosus* (scale bar = 0.1 mm).

penetrate into the central test part. This construction has the appearance of little stars and makes this group the main components of star-sand in the tropical West-Pacific, where it inhabits regions of extreme water motion.

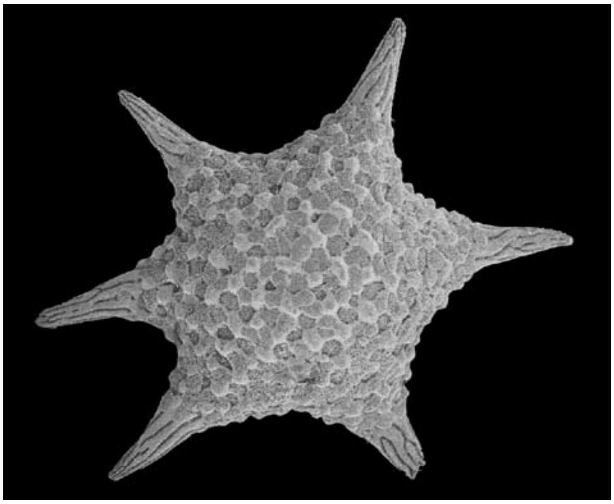
The last and most developed group within the calcarinid gardeners constructs glasshouses similar to the former group with dominating lateral chambers (*Schlumbergerella*). The lack of a planispiral initial chamber arrangement leads to a special construction of tetrahedral glasshouses, where the short but strong spines mark the corners of the tetrahedron. Therefore, these glasshouses resemble concrete breakwaters built by humans. They can be found, similar to the star-sand of the West Pacific, in highest energetic regions of the Indonesian Archipelago.

Ocher to olive-green gardeners with large, often flat greenhouses, scientific name ***Nummulitidae***

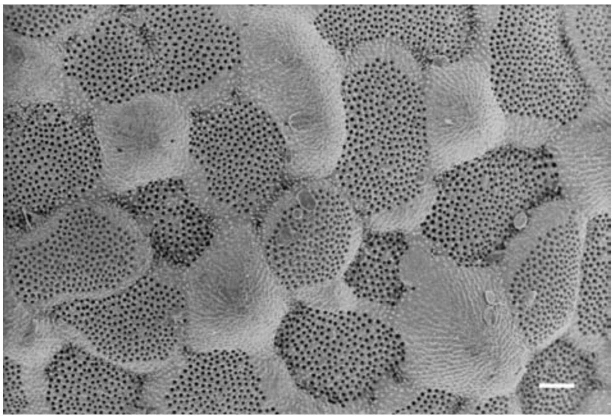
The last clan of today’s gardeners with transparent walls also house diatoms acting as greenhouse plants. In contrast to the calcarinid clan, they prefer the deeper regions of the shallow tropical sea, where the weak light enables their plants to obtain positive photosynthetic rates. This allows



Living *Baculogypsina sphaerulata* (size = 2.3 mm).



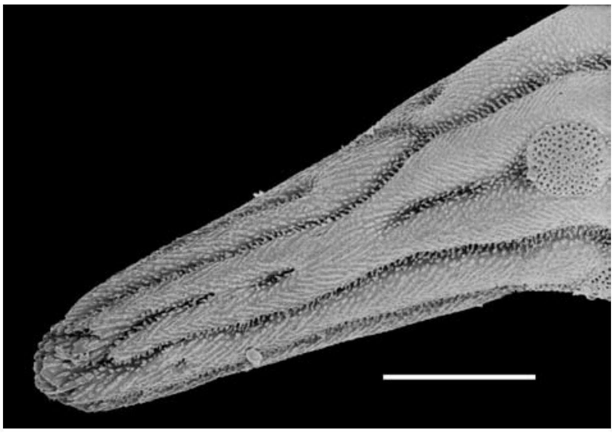
SEM micrograph of *Baculogypsina sphaerulata* (body size without spines = 1.2 mm).



SEM micrograph of the shell surface of *Baculogypsina sphaerulata* (scale bar = 0.01 mm) showing elevated transparent pillars and numerous pores between.

the gardener to profit from the carbohydrates produced by the microalgae. This relationship functions so well for all nummulitids that they do not depend on additional food.

All glasshouse constructions start from an initial plan of spirally arranged chambers within a plane. They possess



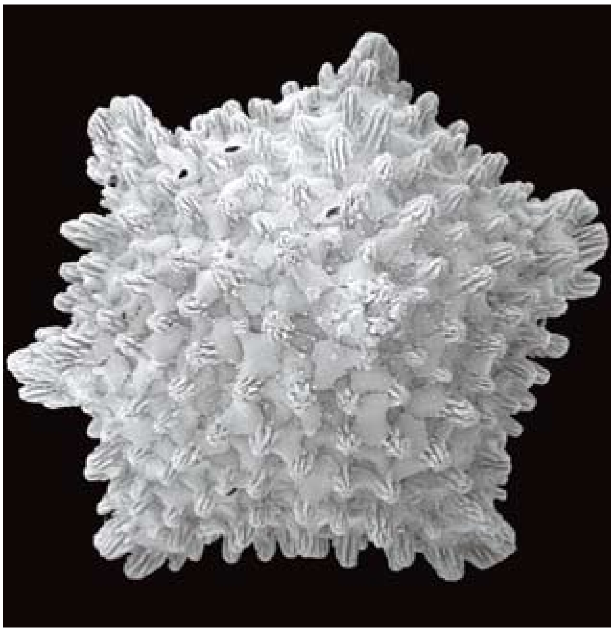
SEM micrograph of a spine of *Baculogypsina sphaerulata* (scale bar = 0.1 mm).

a canal system to shorten the path from the surroundings of the glasshouse to the first chamber, where the regulation center, the cell nucleus, is located.

A single group of clan members keeps the chamber height more or less constant during growth (*Nummulites*).

Living *Schlumbergerella floresina* (scale bar = 1 mm); mark the difference between the dominating sexual generation (gamont) and the single individual in the center belonging to the asexual generation (agamont).

SEM micrograph of a gamont of *Schlumbergerella floresina* (body size = 2.3 mm; photo C. Baal).



SEM micrograph of an agamont of *Schlumbergerella floresina* (body size = 3.1 mm).

Living *Nummulites venosus* (size = 2 mm).

This arrangement is called a 'spiral of Archimedes'. Therefore, all chambers are of similar size. Chambers of the last whorl overlap the former whorls on the lateral side; thus, only the last whorl is visible from outside, which is a growth form known as **involute**.

These thick glasshouses can be found on sandy bottom between 30 and 70 m in clear water of the central Indian Ocean and the northern and central West Pacific.

Another group with similar glasshouse constructions is differentiated from the first group by a stronger increase in chamber height (*Operculinella*). This leads to flat outer chamber parts in large individuals (up to 1 cm). They are restricted to the tropical West Pacific, where they prefer sandy bottom from 50 to 90 m depth.

Similar to the amphisteginids, there are groups with similar glasshouse construction that changes depending on water depth. All are characterized by papillae that are located in rows above the septa which separate the chambers.

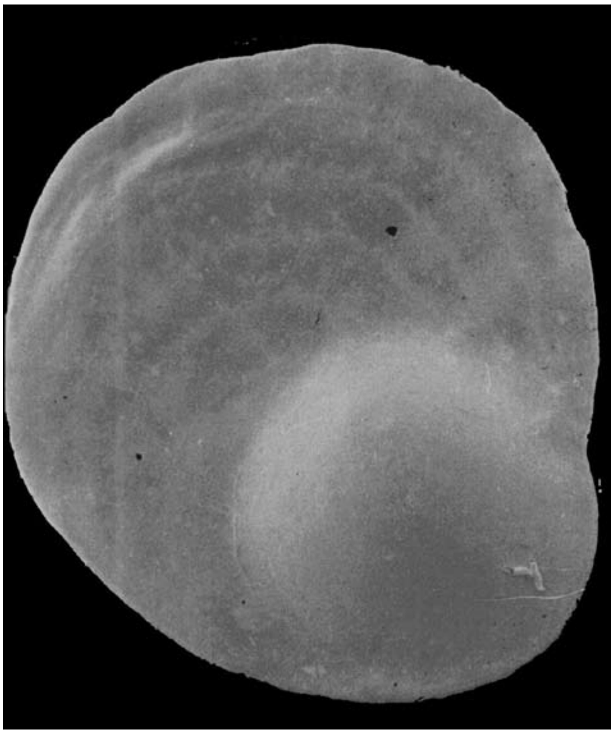
Two groups of gardeners living in shallower tropical water (but always below 20 m) construct thick tests. One group makes discoid glasshouses, where only the last whorl is visible (*Operculina discoidalis*). These gardeners prefer soft bottom such as found in tropical lagoons of the West Pacific or in about 50 m depth in front of coral reefs.

The second group (*Operculina ammonoides*) is distributed from the Red Sea to the West Pacific, starting at 10 m depth. In the Red Sea and Indian Ocean these

SEM micrograph of *Nummulites venosus* (size = 2.2 mm).

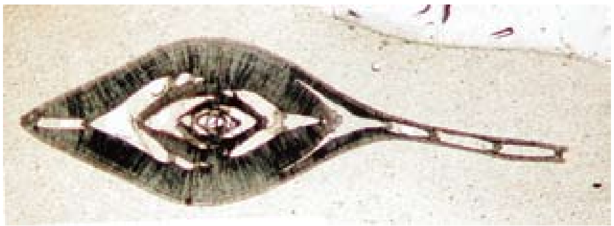
Thin section of *Nummulites venosus* (size = 1.8 mm; photo E. Iordanova).

Living *Operculinella cumingii* (size = 10 mm).



SEM micrograph of *Operculinella cumingii* (size = 6.4 mm).

Light micrograph of *Operculinella cumingii* (size = 4.8 mm).



Thin section of *Operculinella cumingii* (size = 1.3 mm; photo E. Iordanova).

Living *Operculina discoidalis* (size = 2.5 mm).

gardeners can live in deeper clear water down to 100 m, where they construct large and flat glasshouses.

A third group with similar construction but elevated septa is restricted to fine sediments of the warm temperate northwestern Pacific. It prefers 10 to 20 m depth.

Similar forms with larger and flatter greenhouses live in

SEM micrograph of *Operculina discoidalis* (size = 1.8 mm; photo C. Baal).

Living *Operculina ammonoides* (size = 2.2 mm) from 20 m depth.

SEM micrograph of *Operculina ammonoides* (size = 2.1 mm; photo C. Baal).

Living *Operculina ammonoides* (size = 6 mm) from 60 m depth.

deeper regions of the East Indian Ocean and West Pacific (*Operculina complanata*). All chambers are visible from the lateral sides (evolute) and the chamber arrangement follows a 'logarithmic spiral', which means that the chambers increase in height during growth.

From 30 to 50 m depth the glasshouses are thick, becoming extremely thin and flat with increasing depth. The deepest-living gardeners belonging to this group can be found in clear tropical water at 120 m.

In the deepest, light-depleted regions the glasshouses are extremely flat, very glassy and not as large as in shallower regions (*Operculina elegans*). This helps them retain the smaller chamber size necessary for regulating chemical processes.

A further modification to inhabit the deepest, light-depleted regions while keeping the large flat size and having small cytoplasm units to promote regulation and metabolic

Light micrograph of *Operculina ammonoides* from the Northwest Pacific (size = 1.9 mm; photo C. Baal).

SEM micrograph of *Operculina ammonoides* from the Northwest Pacific (size = 2 mm; photo C. Baal).

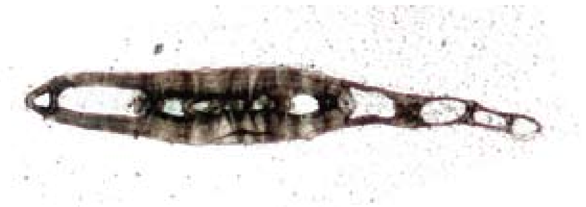
Living *Operculina complanata* (size = 4.8 mm).

SEM micrograph of *Operculina complanata* (size = 4.3 mm).

processes, is to divide the strongly increasing chambers by septula into smaller, equally sized compartments. Two groups can be found, one where the division into chamberlets is incomplete (*Planoperculina*) and another where the division is complete (*Planostegina*).

All these gardeners are restricted to the tropical Indian Ocean and West Pacific.

Similar to the last group, but with much thicker central test parts caused by the involute chamber arrangement, are other gardeners (*Heterostegina*) that show the widest distribution range within the nummulitids, both geographically and according to water depth. These gardeners are the only nummulitids with a worldwide distribution. They are found in the Caribbean and in parts of the Mediterranean, where they intruded from the Red Sea through the Suez Canal as so-called 'Lessepsian migrants'. They are abundant in the whole tropical Indian



Thin section of *Operculina complanata* (size = 2.2 mm; photo E. Iordanova).

Living *Operculina elegans* (size = 2.8 mm) from 100 m depth.

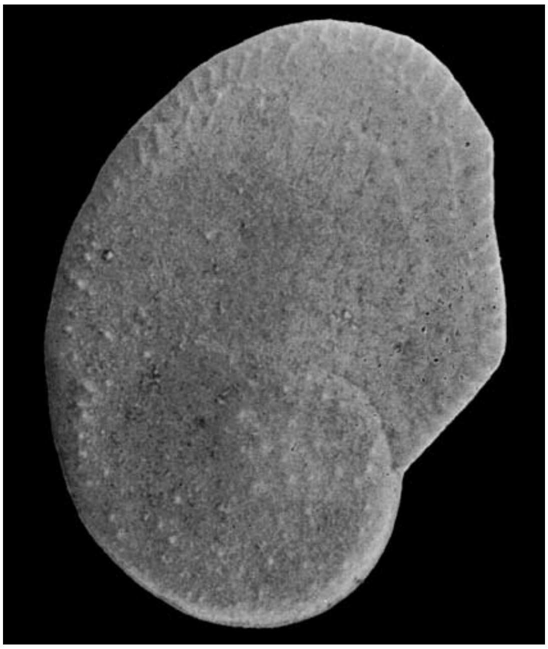
Living *Planoperculina heterosteginoides* (size = 3.5 mm).

Living *Planostegina longisepta* (size = 3.2 mm).

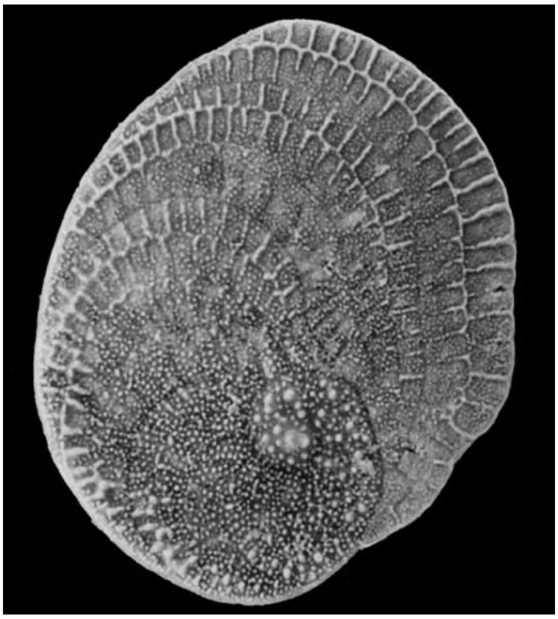
and Pacific Ocean and inhabit high energetic regions near the reef crest, where they protect themselves in holes, down to 70 m depth. At this depth, the glasshouses are flat and differentiated from the former relatives only by their involute coiling in the glasshouse center.

The last two gardeners belonging to this group are distinguished by the construction of large, flat and circular glasshouses. After an embryonic part (which differs in the two gardeners), the following constructions involving a cyclic arrangement of similar-sized chambers are identical. This leads to very large tests up to 13 cm, making them one of the largest single-celled organisms in the world.

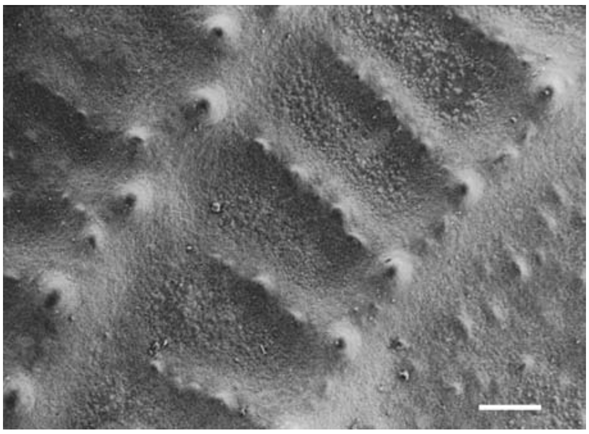
Their habitat depends on light availability and is located between 40 and 100 m depth. Both gardeners differ in their initial part. While the first group – distributed in the Indian Ocean – shows a planspirally enrolled chamber arrangement in the initial part (*Heterocyclina*), the second



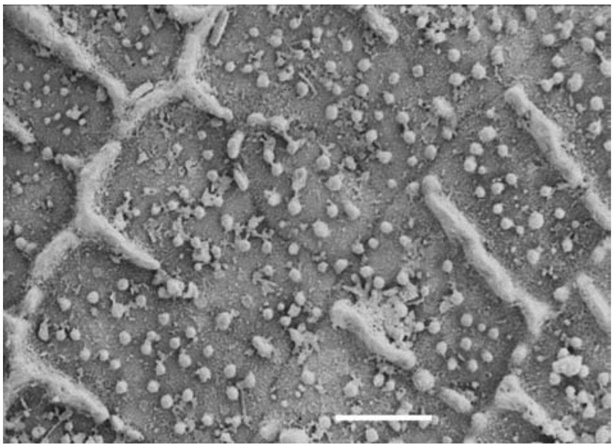
SEM micrograph of *Planostegina longisepta* (size = 5.6 mm).



SEM micrograph of *Planostegina operculinoides* (size = 3.3 mm).



SEM micrograph of the shell surface of *Planostegina longisepta* (scale bar = 0.1 mm).



SEM micrograph of the shell surface of *Planostegina operculinoides* (scale bar = 0.1 mm) with small pustules.

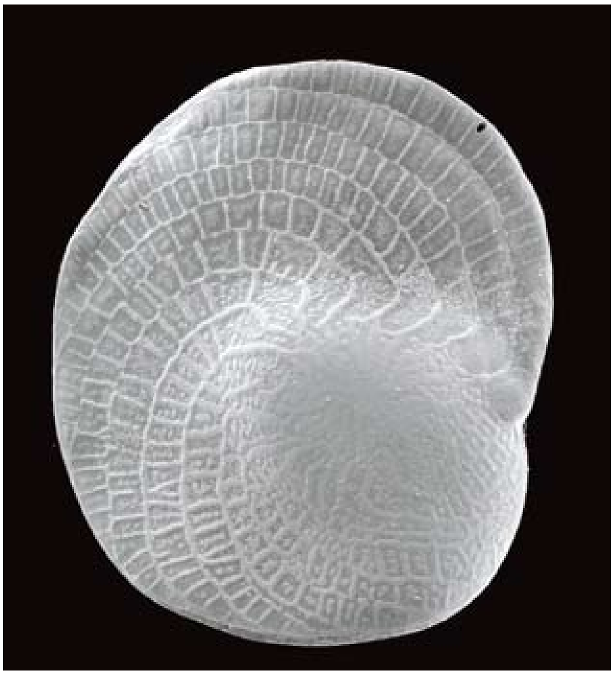
Thin section of *Planostegina longisepta* (size = 1.9 mm; photo E. Iordanova).

Living *Heterostegina depressa* (size = 3.4 mm).

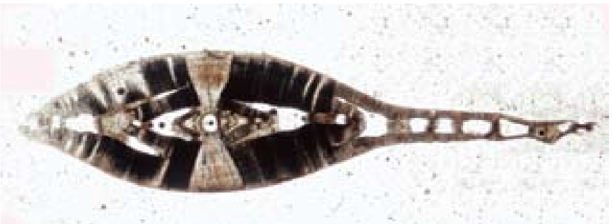
group of gardeners – restricted to the tropical Pacific Ocean – possesses a large embryonic part constituted of a few chambers (*Cycloclypeus*) .

The fate of empty glasshouses

What's the fate of glasshouses when the gardeners leave



SEM micrograph of *Heterostegina depressa* (size = 3.5 mm; photo C. Baal).



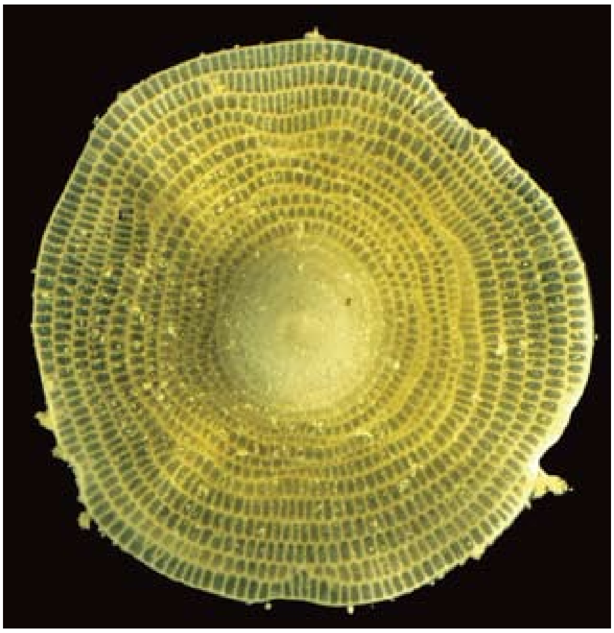
Thin section of *Heterostegina depressa* (size = 3.2 mm; photo E. Iordanova).

Light migrograph of *Heterocyclina tuberculata* (size = 5.8 mm; photo C. Baal).

them either during reproduction or at death?

First, the glasshouses lose their connection to the substrate where they were attached by the gardener's pseudopods. This exposes them to water motion like other sediment grains. Depending on the intensity, form (laminar or turbulent flow) and direction of the water motion, these

SEM micrograph of *Heterocyclina tuberculata* (size = 5.8 mm; photo C. Baal).



Living *Cycloclypeus carpenteri* (size = 7.8 mm).

Thin section of *Cycloclypeus carpenteri* (size = 8.2 mm; photo E. Iordanova).

glasshouses will be transported. As opposed to normal sediment grains that are ellipsoidal or spherical, the form and density of glasshouses determines the transport distance: they are not as heavy as compact grains, and plate-like objects will be transported by fluids further than spherical forms. In analogy, a tree leaf is transported more easily by wind compared to a compact fruit with the same volume and weight as the leaf.

SEM micrograph of *Cycloclypeus carpenteri* (size = 8.5 mm; photo C. Baal).

The empty glasshouses of extremely abundant calcarinid gardeners on the reef crest are transported by waves to the beaches, where they accumulate. This often leads to large dunes consisting of sand with a significant proportion of foraminiferal tests.

The spines of calcarinid tests are abraded, secondarily during transport but primarily at the beach by oscillatory wave action. This yields well-rounded calcite grains of a few mm size. Especially at the beaches of the Indonesian archipelago, when no human influence like pollution by agriculture destroys the ecosystem, the beach sand consists to more than 90% of well-rounded, equally sized calcareous grains originating from gardeners living 100 m in front of the beach. Such beaches are ideal tourist places.

When this beach sand is no longer moved by waves and becomes stabilized, then the evaporation of sea water between the grains leads to the precipitation of calcium carbonate crystals that adheres the loose grains to one another. This phenomenon is called **cementation**. It results in so-called **beachrocks**, which in this case consist mostly of calcarinid glasshouses that can be preserved for further millions of years.

Less stabile plate-like glasshouses from gardeners living in shallow water are also transported to the beach by wave action, where they are fractioned and pulverized.

The less abundant gardeners living in front of the reef are mostly transported downslope, either through currents - very strong during low (ebb) tide - or by tropical storms. Such storms affect the seafloor with oscillatory movement down to 50 m, while additional current flow can influence

Sandy beach west of Okinoerabu Island, Japan.

Beach sand of Sesoko Island, Okinawa, Japan with numerous rounded *Calcarina* shells (scale bar = 10 mm).

Sand of Nusa Dua Beach, Bali, Indonesia consisting of more than 90 % rounded *Schlumbergerella* tests (scale bar = 10 mm).

the waters down to 2000 m. Therefore, depending on slope inclination and the size and form of the glasshouses, they can be transported. Size and shape determine transport distances even if the foraminifera belong to the same clan.

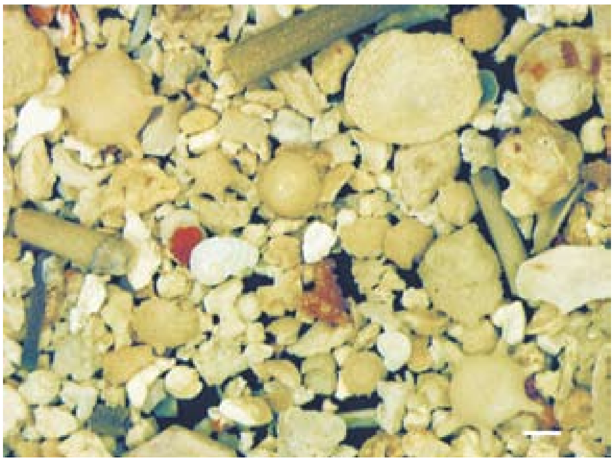
Most of the sand in front of coral reefs down to 200 m is composed in the West Pacific of larger foraminiferal tests. The proportion and composition of glasshouses in

Beach rock at the coast west of Okinoerabu Island, Japan.

Details of the beach rock consisting of abundant *Calcarina* tests.

the sand depends on the depth at which the gardener lived. Therefore, in shallow water down to 50 m, glasshouses of shallow-living species are abundant; here, they have a grain size similar to other components of the sand originating from organisms like corals, bivalves, gastropods and spines of sea urchins.

The grain size becomes finer with increasing depth, making empty glasshouses now much larger compared to 'normal' grains. When storms affect sediments at these depths, then the fine particles could be removed while the larger particles remain and are compacted. This procedure is called **winnowing**. It must be differentiated from **sorting**, where glasshouses of the two generations of the same gardener are unequally widely transported by water motion and deposited at different places due to their differing buoyancies. Winnowing explains the accumulation of a species where glasshouses of both generations are present, like the stones of the Egyptian pyramids. Sorting, on the other hand, is the main mechanism explaining the



Sand from 10 m depth in front of Sesoko Island, Okinawa, Japan with abundant empty shells of larger foraminifera together with sea urchin spines, broken coral peaces and mollusk shells (scale bar = 1mm).

Sand from 50 m depth in front of Sesoko Island, Okinawa, Japan with abundant empty thick shells of larger foraminifera together with broken coral peaces and mollusk shells (scale bar = 1mm).

Sand from 80 m depth in front of Sesoko Island, Okinawa, Japan with abundant empty thin and flat shells of larger foraminifera together with broken coral peaces and mollusk shells (scale bar = 1mm).

accumulation of a single generation − almost of the same size − of gardener's glasshouses.

All empty glasshouses, whether non-transported or transported, can be covered by sediment. When this becomes petrified, they become part of the sedimentary rock. Often they are dissolved in coarse-grained sediments due to the large pore space here: oxygenized pore waters lead to the solution of calcium carbonate. Here, aragonite and high magnesium calcite tests are more affected than those composed of low magnesium calcite. Fine-grained sediment hinders the penetration of pore waters, allowing a better preservation of glasshouses in the fossil record.

Pleistocene outcrop west of Okinoerabu Island, Japan.

Details of the Pleistocene outcrop west of Okinoerabu Island, Japan (scale bar = 10 mm) with densely packed flat *Planostegina* shells together with non rounded gravel of volcanic rocks.

According to these differences the preservation of larger foraminifera from shallow turbulent waters is poor, especially when the test consists of high-magnesium calcite. Preservation is much better in deeper water and very good in fine-grained sediment.

Sediments with larger foraminifera deposited in water depths from 20 to 50 m depth due to winnowing or sorting are excellent reservoirs of hydrocarbons like petrol and petroleum gas based on their large pore space. Thus, most of the petrol reservoirs today are found in such limestone mainly composed of larger foraminifera.

This leads to the question when and why in Earth history such accumulations of microscopic glasshouses were formed.

The history of gardeners (Figure 8)

The foraminifera, the group of organisms to which the gardeners belong, show a long history. These single-celled organisms are first documented with simple tests in the oldest rocks where other remains of organisms also appear in high numbers. This is the **Cambrian** period about 540 million years ago. These oldest foraminifera remained rather conservative with simple, single-chambered tubular or spherical tests until the **Devonian**, where the first chambered tests are reported. The Devonian is the last period of the so-called Early Paleozoic time, ranging from 416 to 359 million years. This period is distinguished by a high proportion of land mass, which was important for the development of land plants. The first fish-like vertebrates left the sea. In the shallow parts of the oceans surrounding the large continents, the foraminifera developed different types of tests. In the latest Devonian, beside agglutinated and secreted walls − the latter made of fine globular microcrystals − the first transparent (hyaline) walls appeared. A bloom of the foraminifera in the following period, the **Carboniferous**, parallels the development of shallow marine organisms as well as plants and terrestrial organisms. In the Late Carboniferous called **Pennsylvanian** and in the following **Permian**, the first gardeners within the foraminifera appeared, showing high evolutionary trends in the Pennsylvanian and the Permian. These trends are used for time determination of the sediments in which the glasshouses are preserved.

The glasshouse construction of these earliest gardeners,

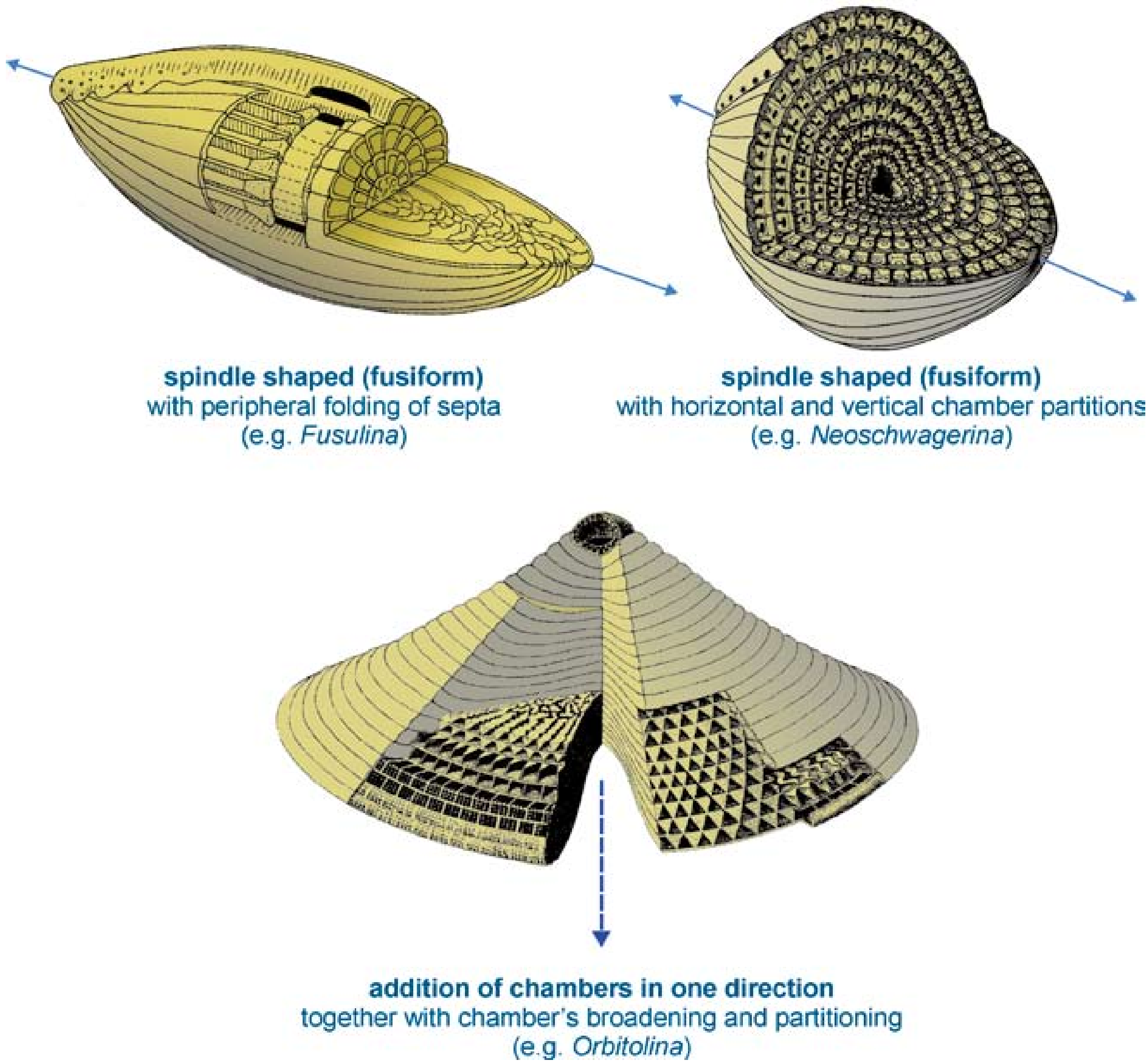


Figure 7. Additional test constructions found in fossil larger foraminifera (*Fusulina* modified after Pokorny 1958, *Neoschwagerina* modified after Dutkevitch 1932, *Orbitolina* modified after Douglass 1960).

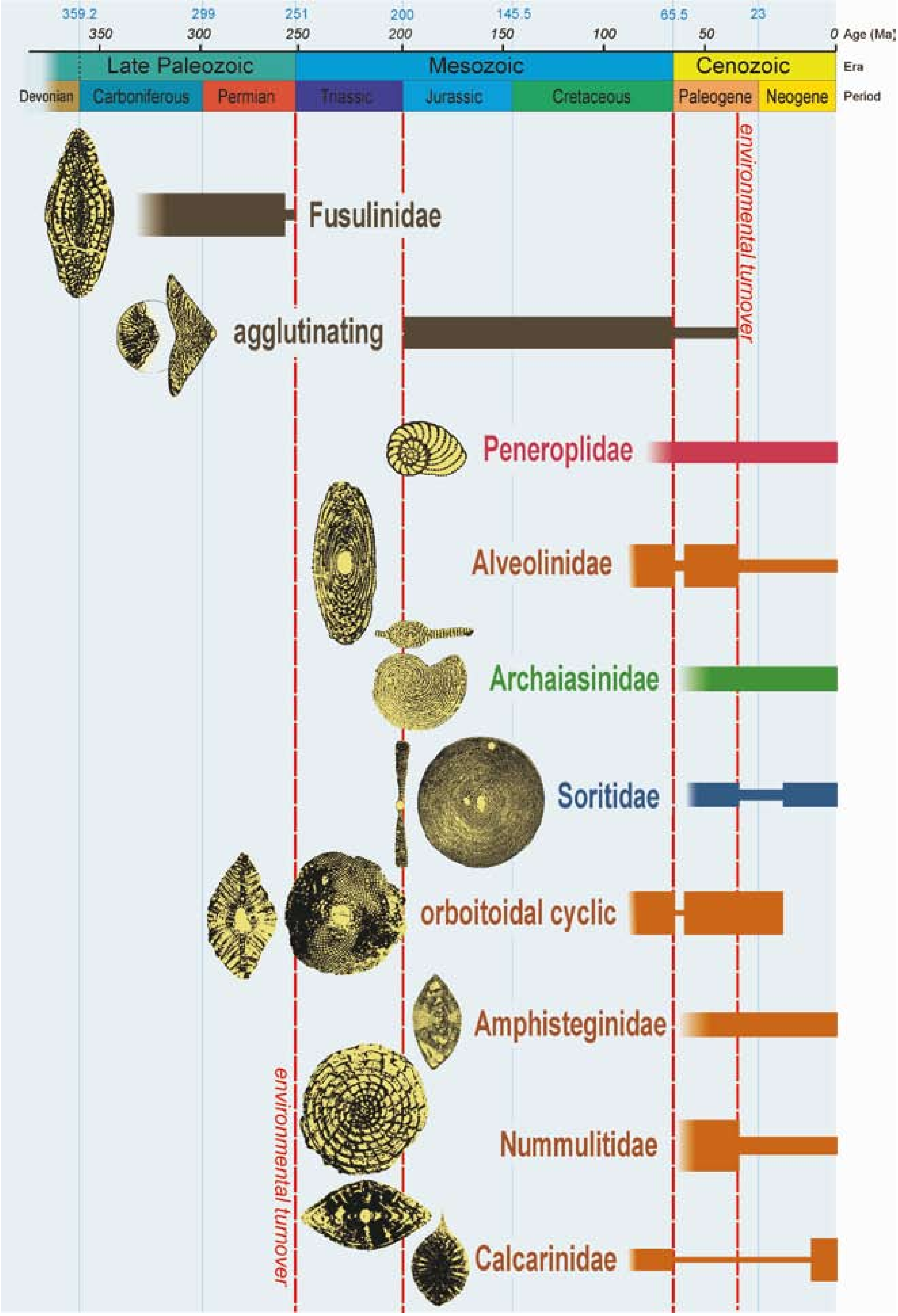
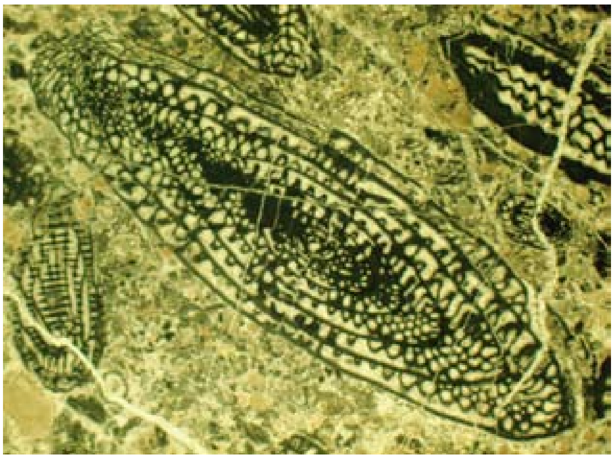


Figure 8. Time distribution of the most important groups of larger symbiont-bearing foraminifera (colors corresponding to the symbiotic microalgae, where symbionts of the extinct Fusulinidae and agglutinating foraminifera are unknown).

known as **fusulinids**, is a spindle, similar to the spindle-shaped alveolinids today.

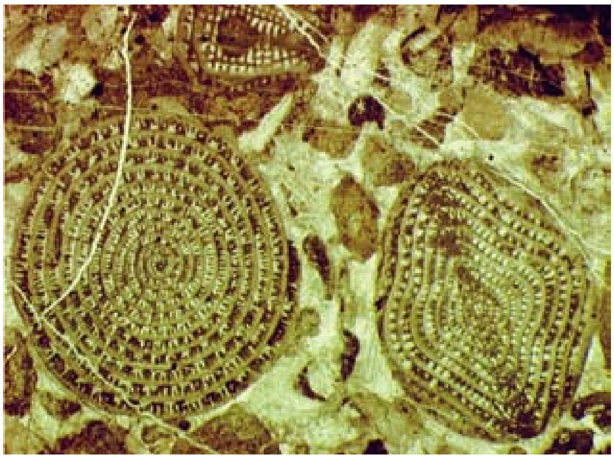
The main characteristic of the glasshouse construction is the division of the axially elongated chambers into smaller compartments, especially when the glasshouse reached a large size. This chamber division was obtained in two ways (Figure 7). The first way was by folding the septum, thus coming in contact with the septum of the former chamber, or by dividing the chamber by horizontal and

The spindle shaped foraminifer *Fusulina* (size = 5.6 mm) from the Late Carboniferous (~ 308 million years ago; photo C. Baal).

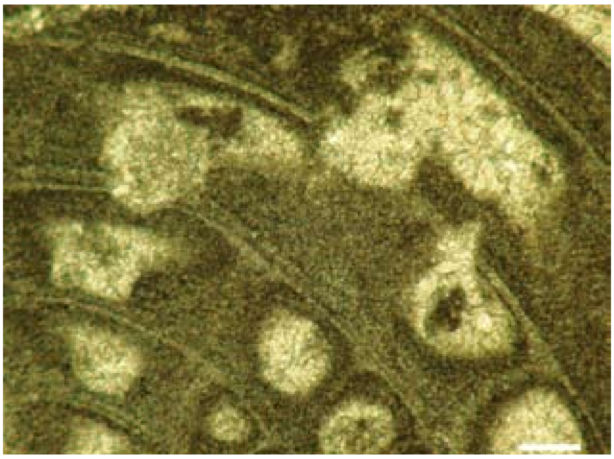


Thin section of an Early Permian limestone (~ 270 million years ago) showing an axial section of *Parafusulina* (size = 13 mm). Mark the septal folding for dividing the large chambers into smaller compartments (photo C. Baal).

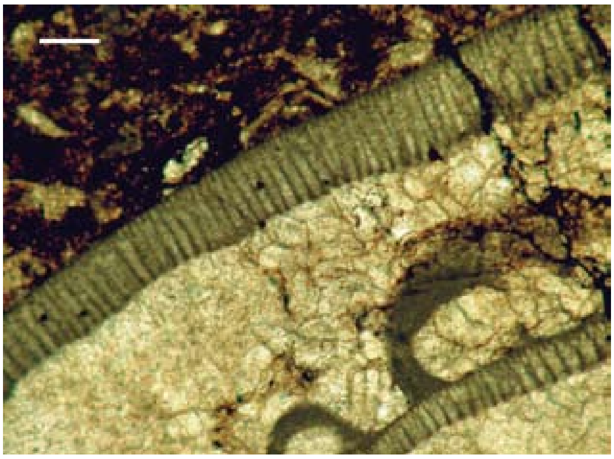
Thin section of a Late Carboniferous limestone (~ 305 million years ago) showing an equatorial section of *Triticites* (size = 3.1 mm; photo C. Baal).



Thin section of an Early Permian limestone (~ 305 Million years ago) showing an equatorial section of *Neoschwagerina* to the left and an axial section to the right (size ~ 5.5 mm; photo C. Baal).



The wall of *Fusulinella* (Late Carboniferous, ~ 310 million years ago) in thin section showing a thick dark wall with an inner thin transparent layer that is called 'Diaphanotheka' (scale bar = 0.1 mm; photo C. Baal).

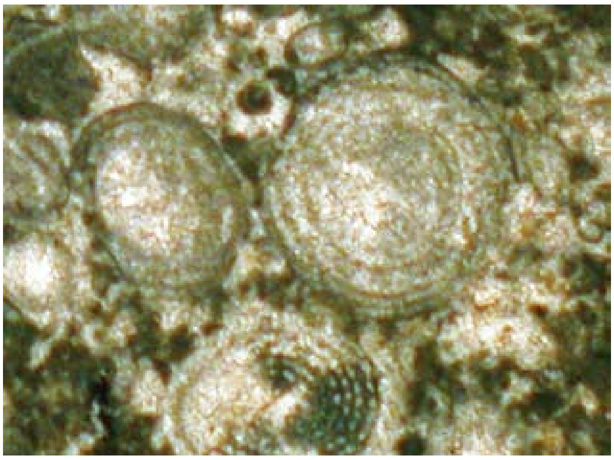


The wall of *Pseudoschwagerina* (Early Permian, ~ 290 million years ago) in thin section showing a thin dark outer layer and a thick inner, still dark but more transparent layer, which is called 'Keriotheka' (scale bar = 0.1 mm; photo C. Baal).

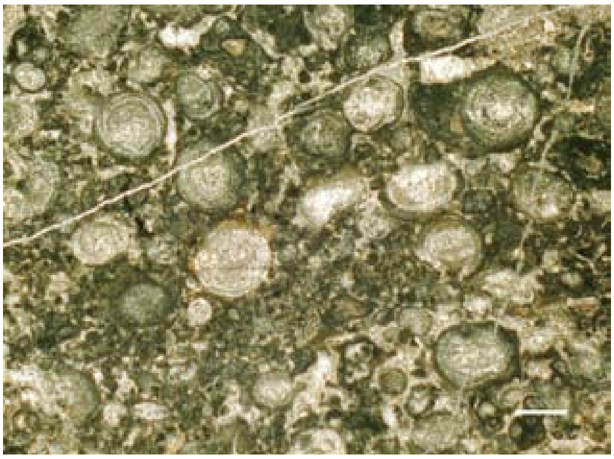
vertical partition panels. Additionally, these gardeners can be differentiated into two groups by their walls structure named ‘diaphanothekal’ and ‘keriothekal’.

The role as gardeners can be proved based on the chemical composition of the walls. This composition deviates from normal foraminiferal tests by a higher content of heavy carbon isotopes (^{13}C) compared with the normal sea water, as can be measured in tests and shells of animals without symbiotic microalgae. This higher content is characteristic for the glasshouses of living gardeners because the cultivated plants inside the glasshouse use the lighter carbon isotope (^{12}C) for photosynthesis. This left only the heavier carbon isotopes in the cytoplasm and for use to construct the glasshouse walls consisting of calcium carbonate ($CaCO_3$). Nothing is yet known about the nature of the microalgae: they could have belonged to the green or red algae, but also ancestors of the dinoflagellates are possible.

An Early Permian (~ 270 Million years ago) fusulinid limestone with numerous specimen of *Pseudoschwagerina* (scale bar = 1 mm; photo C. Baal).

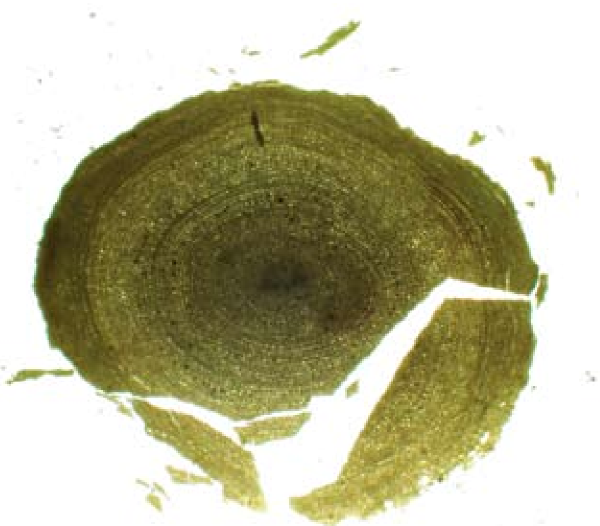


Thin section of a Late Triassic limestone (~ 205 million years ago) showing *Triasina* (diameter of the largest specimen = 1.8 mm; photo C. Baal).

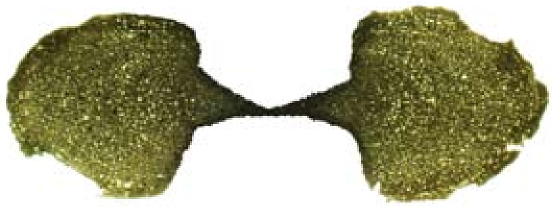


A Late Triassic (~ 205 Million years ago) limestone with numerous *Triasina* specimens (scale bar = 1 mm; photo C. Baal).

The cyclic larger foraminifer *Orbitopsella* (size = 6.6 mm) from the Early Jurassic (~ 170 million years ago) with a test wall consisting of small agglutinated particles (photo C. Baal).



Equatorial section of *Orbitopsella* (diameter = 10 mm) showing the cyclic arrangement of chambers (photo C. Baal).



Axial section of *Orbitopsella* (diameter = 9 mm; photo C. Baal).

Sandstone from the Late Cretaceous (~ 68 million years ago) with the spindle-shaped foraminifer *Loftusia* (scale bar in mm; photo C. Baal).

Axial section of *Loftusia* (length = 2 mm) showing the non transparent walls made of agglutinated foreign particles (photo C. Baal).

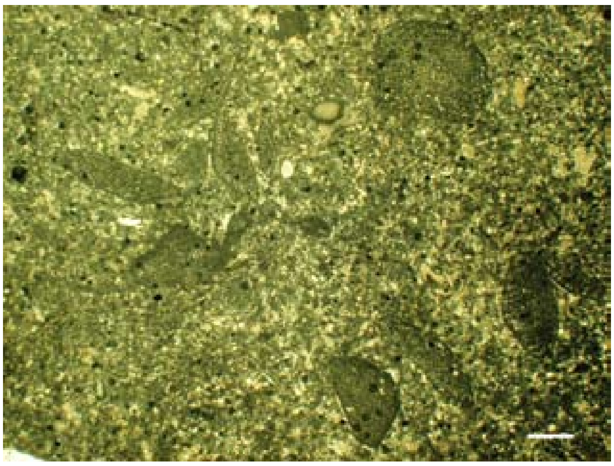
After the catastrophic mass extinction at the end of the Permian 251 million years ago, the foraminifera needed time to resettle the marine environment. They started in the Early **Triassic** with forms similar to the representatives with simple tests of the Early Carboniferous.

The rapid evolution during this period led to tests similar to the type of today's glasshouses that make pillars instead of septula to strengthen the test (*Triasina*). This phase was interrupted at the beginning of the Jurassic, the period in which the largest dinosaurs lived.

In shallow waters of the Early **Jurassic** until the Late **Cretaceous**, some glasshouses with wall structures similar to the Paleozoic forms−meaning composed of small and tiny granular microcrystals or constructed by collected sand particles fixed with calcareous cement – can be found. Their test construction resembles either flat circular (*Orbitopsella*) or spindle-shaped glasshouses (*Loftusia*).

The flat conical, disc-shaped *Orbitolina* (size = 6.8 mm) from the Middle Cretaceous (~ 97 million years ago; photo C. Baal).

Axial section through *Orbitolina* (size = 4.6 mm) showing the non transparent walls made of agglutinated foreign particles (photo C. Baal).



A Middle Cretaceous (~ 100 Million years ago) sandstone with numerous *Orbitolina* specimens (scale bar = 1 mm; photo C. Baal).

During the middle Cretaceous (125 to 93 million years ago), the foraminifers with sandy test walls invented a different way of constructing large-sized tests that cannot be compared with older or younger forms. These ‘architects’ got new ideas. They started with a chambered test, where after an initial and short planispirally coiled part the chambers were arranged in a straight series. By strongly increasing chamber width and reducing the planispiral part to a short embryonic part, these constructions became small cones (Figure 7). The size increase during evolution was obtained by reducing the cone height while at the same time widening the chambers. The result: extremely flat, disc-like, large tests at the end of the Cretaceous (*Orbitolina*). These architects probably also housed symbiotic plants and thus worked as gardeners.

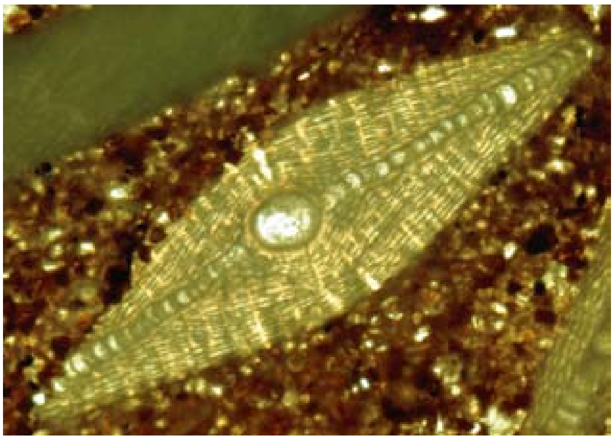
In the Late Cretaceous, ancestors of living gardeners

The cyclic foraminifer *Orbitoides* (size = 3.3 mm) from the Late Cretaceous (~ 67 million years ago; photo C. Baal).

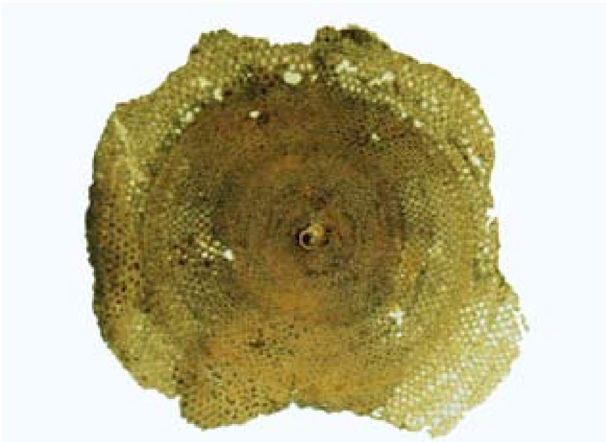
Equatorial section through Orbitoides (size = 4.7 mm) showing a large embryonic apparatus (nepiont) surrounded by an annular arrangement of chambers (photo C. Baal).

(those with spindle-shaped glasshouses and porcellaneous walls) appeared.

They are accompanied by gardeners with circular glasshouses and transparent walls, where the chambers are arranged in cycles, similar to the two largest gardeners living today. In contrast to these forms, these glasshouses are not flat, but lens-shaped. This reflects the addition of



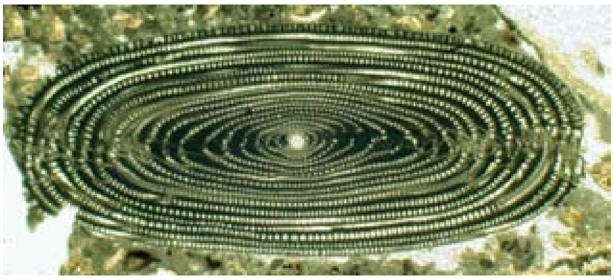
Axial section through *Orbitoides* (size = 5.1 mm) showing the large nepiont, the median layer and lateral chambers between transparent piles (photo C. Baal).



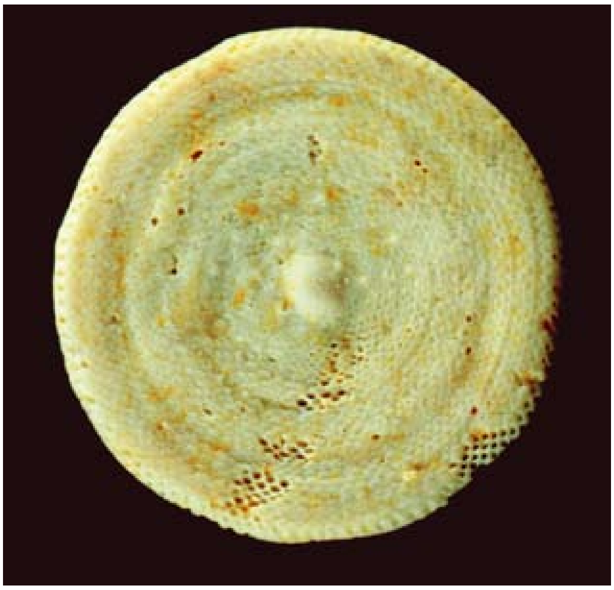
Equatorial section through *Lepidorbitoides* (size = 5.9 mm) from the Late Cretaceous (~ 67 million years ago) showing a large embryonic apparatus (nepiont) surrounded by an annular arrangement of chambers. Mark the difference in the nepionts between *Orbitoides* and *Lepidorbitoides* (photo C. Baal).

Thin section of a Late Cretaceous (~ 67 million years ago) sandstone with numerous axially sectioned *Orbitoides* specimens (scale bar = 1 mm; photo C. Baal).

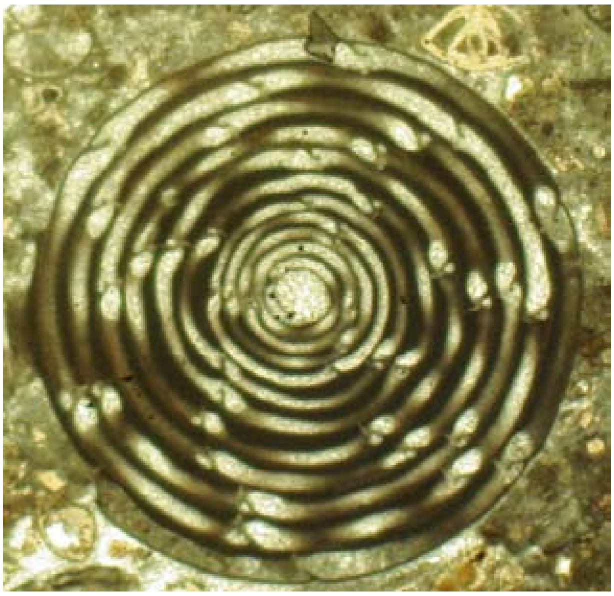
lateral small chambers, similar to the construction of the today's most developed star-sand gardeners. Also similar to the living star-sand, they developed transparent plugs or pillars to promote photosynthesis for algae living in the inner parts of the glasshouses.



Axial section of the spindle shaped *Alveolina* (size = 6.3 mm) from the Middle Eocene (~ 45 million years ago) showing the dark, porcellaneous, non transparent wall (photo C. Baal).

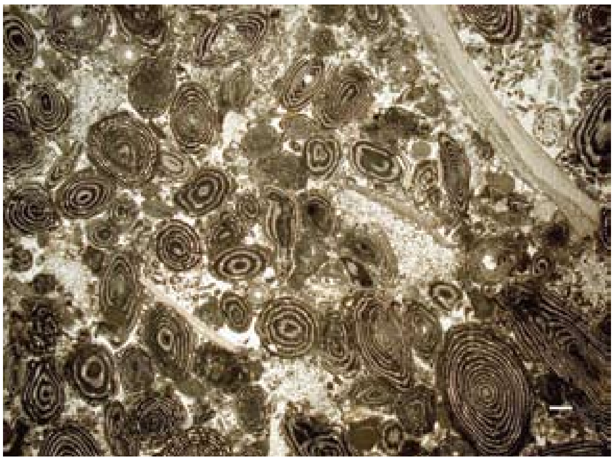


The cyclic foraminifer *Orbitolites* (size = 2.6 mm) from the Middle Eocene (~ 45 million years ago; photo C. Baal).

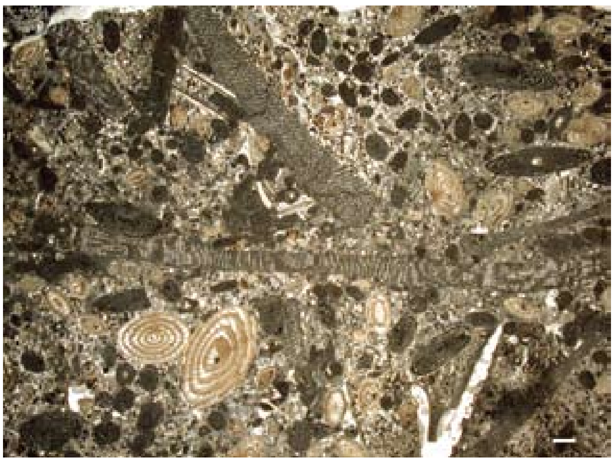


Equatorial section of *Alveolina* (size = 3.2 mm; photo C. Baal).

Equatorial section through *Orbitolites* (size = 7.6 mm) showing the non-transparent porcellaneous wall (photo C. Baal).



Thin section of a Middle Eocene (~ 45 million years ago) limestone with numerous *Alveolina* specimens with dark, non transparent walls (scale bar = 1 mm; photo C. Baal).



Thin section of a Middle Eocene (~ 45 million years ago) limestone with numerous *Orbitolites* and *Alveolina* specimens with dark, non transparent walls and *Nummulites* specimens with bright, transparent walls (scale bar = 1 mm; photo C. Baal).

This glasshouse construction was very successful, allowing the settlement of gardeners in a wide range of habitats, from high energetic zones with intense water motion down to the base of the photic zone with low light intensities. These successful constructions were developed independently by different clans of gardeners. They cannot be differentiated from the outside, where all feature lens-shaped glasshouses, but they differ strongly in their initial part, the embryonic chambers called nepiont (*Orbitoides, Lepidorbitoides*). According to evolutionary tendencies from simple nepionts to complex forms, they can be used to determine the deposition time of the sediments in which these forms are preserved.

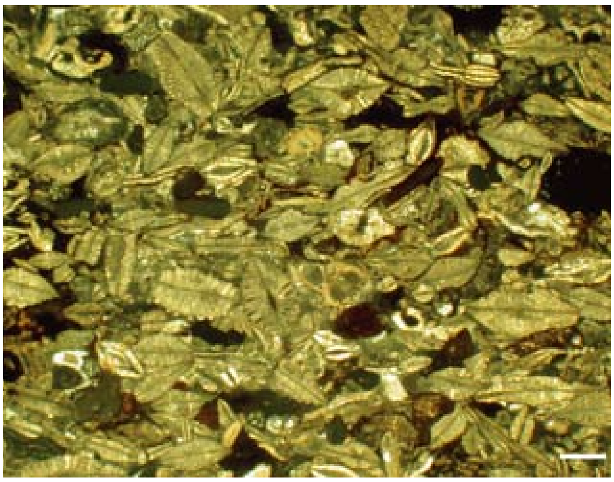
After the second catastrophic mass extinction at the end of the Cretaceous, where the dinosaurs and ammonites disappeared, the development of the foraminifera was quite

Isolated *Nummulites* specimens washed from Middle Eocene marls, showing the difference between sexual (small shells) and asexual (large shell) generations (scale bar = 2 mm; photo C. Baal).

The planispirally coiled foraminifer *Nummulites* (size = 4.7 mm) from the Middle Eocene (~ 45 million years ago; photo C. Baal).

Equatorial section through *Discocyclina* (size = 10.6 mm) from the Middle Eocene (~ 45 million years ago) showing a large embryonic apparatus (nepiont) surrounded by an annular arrangement of chambers. Mark the difference in the nepiont and chamber arrangement to the Cretaceous species *Orbitoides* and *Lepidorbitoides* (photo C. Baal).

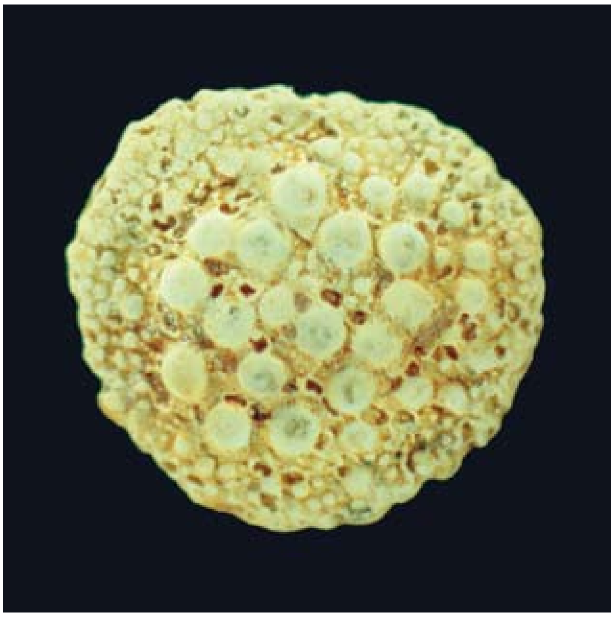
Thin section of a Middle Eocene (~ 45 million years ago) limestone with numerous *Nummulites* specimens with transparent walls (scale bar = 1 mm; photo C. Baal).



Thin section of a Middle Eocene (~ 45 million years ago) limestone with numerous axially sectioned *Discocyclina* specimens (scale bar = 1 mm; photo C. Baal).

similar to their evolution after the first mass extinction. Starting from surviving forms with simple tests, the foraminifera soon developed gardeners in different lines. Precursors and ancestors of all living gardeners started in the **Paleocene**, the first epoch of the **Cenozoic**. Beside the recurrence of spindle shaped glasshouses with porcellaneous walls (alveolinids), a phenomenon known as a **Lazarus** effect, the soritids (*Orbitolites*) and archaiasinids appeared, settling in the shallowest, most light-intensive regions.

The main evolution took place in the newly developed nummulitids. They constructed planispiral glasshouses with transparent walls that reached immense abundances and sizes (up to 17 cm) between 55.8 to 37.2 million years ago, belonging to the **Eocene** epoch. Sediments with enormous



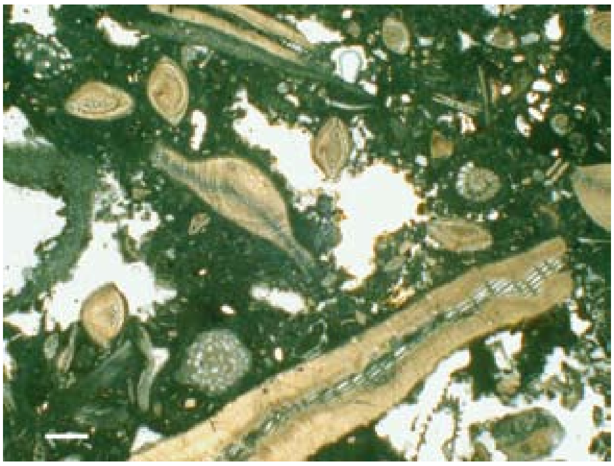
The cyclic foraminifer *Miogypsina* (size = 3 mm) from the Early Miocene (~ 20 million years ago; photo C. Baal).

Equatorial section through *Lepidocyclina* (size = 2 mm) from the Late Oligocene (~ 27 million years ago) showing a large embryonic apparatus (nepiont) surrounded by an annular arrangement of chambers. Mark the difference in the nepiont and chamber arrangement to the Eocene *Discocyclina* (photo C. Baal).

Axial section through *Lepidocyclina* (size = 1 mm; photo C. Baal).

Equatorial sections of *Miogypsina* (scale bar = 1 mm) showing the embryonic apparatus that does not lay in the center. Mark the evolution in the nepiont from a planispiral arrangement to a typical miogypsinid nepiont (photo C. Baal).

Thin section of an Early Miocene (~ 20 million years ago) sandstone with numerous *Miogypsina* specimens (scale bar = 1 mm; photo C. Baal).



Thin section of a Pleistocene (~ 1.5 million years ago) limestone with numerous *Cycloclypeus* specimens together with *Baculogypsinoides* and *Amphistegina* (scale bar = 1 mm; photo C. Baal).

amounts of nummulitids are today's largest oil reservoirs, and the stones of the pyramids also belong to this epoch.

Glasshouses with cyclic chamber arrangement and lateral chambers that were successful in the Late Cretaceous were still constructed in the older Cenozoic period, the **Paleogene**. But they originate from different groups of foraminifera compared to the Cretaceous forms (*Discocyclina*).

There was a strong environmental change at the end of the Eocene epoch, leading to a size decrease in nummulitids. This also corresponds to the development of new cyclic gardeners (*Lepidocyclina, Miogypsina*).

Both groups survived the boundary between the Paleogene and **Neogene** 23.03 million years ago and survived until 15.97 million years ago. Then, glasshouse constructions with lateral chambers disappeared and were replaced by nummulitids dividing their strongly increasing chambers by septula into smaller chamberlets. Circular forms were then developed in the youngest Earth period.

Today, the extreme pollution and destruction of shallow-water environments in the oceans endanger the glasshouse gardeners, which need clear, nutrient-poor sea water and abundant light for survival. Global warming, without pollution, would promote the development of glasshouse gardeners. Huge carbonate buildups could be produced in the future, replacing coral reef growth. The latter do not like higher water temperatures, as is evident in the lack of carbonate buildups made by corals during the high temperatures in the Paleogene, when carbonate buildups by larger foraminifera dominate. Despite this good prognosis for gardeners reacting to global warming, they are endangered by high pollution, the acidification of the oceans and the many forms of habitat destruction caused by human activities.

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italic: in photograph and figure explanation