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Foraminifera as indicators of marine environments in the present and past

Larger Foraminifera - Microscopical Greenhouses Indicating Shallow-Water Tropical and Subtropical Environments in the Present and Past

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Abstract

Larger Foraminifera with test sizes from 2mm up to 13cm are characteristic organisms inhabiting shallow water subtropical and tropical environments today. They prefer clear, nutrition depleted water as can be found in the surroundings of coral reefs. Two main factors acting as single gradients regulate the distributions of larger foraminifers within coral reef complexes. All living larger Foraminifera house symbiotic microalgae and are thus restricted to the photic zone (down to 150m), getting independence from food resources outside the cell in various degrees. Differences in water movement, mostly correlated with substrate type, and light availability are managed in various ways. Test constructions in combination with attachment mechanisms of the protoplasm combat strong water movement, while light penetration is handled by test ultrastructure. Larger foraminifers inhabiting intertidal and extremely shallow subtidal environments block high irradiation by thicker tests or porcelaineous structures, making the walls impenetrable. In contrast, species living near the base of the photic zone facilitate light penetration by thin transparent test walls facilitating light penetration and by developing light-collecting mechanisms such as nodes and pillars. Water turbulence, often extreme in coral reef environments, is handled in different ways, but tests are restricted to a few paradigmatic forms. Similar tests were developed in various phylogenetic lines at different climatic climaxes during earth history starting from the Late Paleozoic (325,000,000 years ago). This can be interpreted as analogous developments in handling the main environmental gradients light penetration and water energy.

The host-endosymbiotic algal system

Surface waters of tropical seas (NYBAKKEN, 1988 ; including subtropical and tropical seas, SEIBOLD and BERGER, 1993) are poor in nutrients, especially nitrogen (THOMAS, 1969), which is caused by the pronounced stratification of the water mass. This arrangement in layers isolates warm waters of the photic zone from nutrient rich cold deeper water and thus reduces primary production by the pelagic phytoplankton. The low productivity of tropical seas is higher in winter and spring than in summer and fall, which is caused by a small phytoplanktic 'spring' bloom (VALIELA, 1995) as is shown in satellite data measuring the chlorophyll content of the ocean surface (LONGHURST, 1998). Thus, food becomes poor for consumers in the equatorial divergence zone and is extremely rare in the center of subtropical gyres (VALIELA, 1995) resulting in 'blue deserts' with high water transparency. The coastal areas of continents (coastal biomes in the sense of LONGHURST, 1998) in the tropics and subtropics are often distinguished by a higher amount of nutrients. This is

either due to the organic input by rivers in humid areas, or caused by coastal upwelling in arid regions. The shallow water areas surrounding subtropical and tropical islands and barrier reefs that are located far from the coastal regions of continents are as oligotrophic as the open ocean surface waters (trade wind biomes, LONGHURST, 1998) under natural conditions. In contrast to the latter, productivity is high in coral reefs leading to 'oases in ocean deserts'. This is yielded by extreme recycling of nutrients within the coral reef system (EREZ, 1990). Anthropogeneous influence remarkably raises the amount of nutrients by changing these environments from oligotrophic to eutrophic conditions (GENDRE *et al.*, 1995).

Beside nutrients, the carbon dioxide content is also low in the warm and alkaline surface waters of tropical seas and decreases in hypersaline lagoons, where dissolved salts impede the solution of carbon-dioxide (SKIRROW, 1975). This low content impairs photosynthesis of both pelagic primary producers and benthic sea-weeds in the surrounding of small tropical islands and barrier reefs. Depending on raising temperature and alkalinity, the amount of dissociated hydrogen and bicarbonate (HCO_3^-) or carbonate (CO_3^{2-}) ions increases. Combined with the saturation of calcium ions (Ca^{2+}) in the sea, precipitation of calcium carbonate ($CaCO_3$) is relieved in surface waters of tropical and warm temperate seas. Calcium carbonate is largely biologically produced or induced (DICKSON, 1990). Not only invertebrates - like corals, mollusks, echinoderms, bryozoans - and macroalgae (*Halimeda*, *Penicillus*, corallinacean algae), but also protists (*Foraminifera*) intensively produce calcium carbonate skeletons in the shallow tropical seas (LEADBEATER and RIDING, 1986). Against the conventional meaning, that photosynthesis induces calcification by removing carbon dioxide from the following equilibrium (e. g., SIMKISS, 1986 ; Cis-calcification in MCCONNAGHEY and WHELAN, 1997)

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

which tries to explain the production of huge carbonate skeletons in symbiont-bearing heterotrophic organisms like corals (*e. g.*, PEARSE and MUSCATINE, 1971 ; GOREAU, 1977), larger foraminifers (TER KUILE, 1991), and the giant clam *Tridacna*, a controversial hypothesis called 'Trans-calcification' was established by MCCONNAGHEY and WHELAN (1997). According to their theory, the production of calcium carbonate skeletons promotes photosynthesis in carbon dioxide depleted environments. During the mineralization process of the calcium carbonate skeleton, the hydrogen ion is set free (SIMKISS, 1986)

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

and reaction of the free hydrogen with the bicarbonate ions promotes photosynthesis in the following simplified way

$$nH^+ + n(HCO_3^-) \overset{energy(light)}{\Rightarrow} (CHOH)_n + nO_2$$

Thus, symbiosis of microalgae with organisms producing calcium carbonate skeletons is advantageous for the whole ecosystem in shallow tropical environments, where corals become the most effective marine primary producers according to the annual net production rates (VALIELA, 1995, p. 29). The host–microalgae system is advantageous for both partners in different degrees. On the one hand, symbionts are protected against competitive macroalgae by their hosts in the uptake of nutrients, but the supply of nutrients, especially fixed nitrogen as the waste product of the hosts' metabolism, is regulated (FALKOWSKI *et al.*, 1993). Furthermore, symbionts are provided with carbon dioxide during the secretion of large calcium carbonate skeletons by the host (corals, foraminifers, giant clams). The host, on the other hand, profits from the symbionts in various ways. Only a small part of photosynthates is normally used by microalgae, while the main proportion is released to the environment. In the case of symbionts, the host profits in using this 'junk food' (lipids and glycerol; *e. g.*, MUSCATINE, 1990 ; FALKOWSKI *et al.*, 1993) as an energy resource for metabolic processes. Additionally captured food can then be applied to growth and reproduction processes. The symbionts are digested by the host either for regulating their density or in case of starvation (*e. g.*, TITLYANOV *et al.*, 1996 ; SCHMALJOHANN, 1980). In some host-symbiont systems, food uptake from the environment by the host is not necessary as long as the carbon fixed by the symbionts equals or exceeds the combined host-symbiont requirement for respiratory carbon and the uptake of dissolved nutrients (DON and DOP) is possible by the host surface. In that case, the host-symbiont system totally becomes photoautotrophic (MULLER-PARKER and D'ELIA, 1997).

Foraminifers functioning as greenhouses

The unicellular heterotrophic foraminifera depend on food in being either micro-herbivores (littoral benthic and some planktic forms), micro-carnivores (mostly planktics), omnivores, detrivores or suspension feeders (benthic forms; LIPPS, 1983; MURRAY, 1991). Planktic foraminifers that are abundant in temperate zones (westerly wind biomes; LONGHURST, 1998) become less numerous in the nutrient and phytoplankton depleted surface waters of tropical seas, but survive these unfavorable conditions in housing symbiotic microalgae (HEMLEBEN *et al.*, 1989 ; LEE and ANDERSON, 1991). They promote their symbionts with necessary nutrients by gathering food, either feeding the few phytoplankton or capturing planktic metazoans. The food for benthic foraminifers is also restricted by the low content of nutrients in oligotrophic shallow water environments of the tropics and subtropics. Only fine-grained sediments deposited in calm water of lagoons and in deeper fore-reef areas are more or less rich in microbes (DUCKLOW, 1990) and particulate organic substance enabling life of smaller benthic foraminifers. Nutrients result from the decay of epilithic or endolithic algae inhabiting non-tissued hard reef substrates (HATCHER, 1997), or from sea-grass those roots in coarse-grained sediments (HOTTINGER, 1997). Most substrates in high energetic regions on the reef flat and the upper reef slope like coral rubble, coral rocks, and mobile coarse-grained sand are unfavorable habitats for the smaller benthic foraminifers. Only species like

Cymbaloporetta that attaches to various macroalgae, or a few miliolids resisting high illumination and raised salinity are the few representatives of smaller benthic foraminifers in these extreme environments. Corresponding to increasing depth and decreasing grain size in fore-reef areas, the amount of smaller benthics rises until the normal proportion level of smaller benthics on shelf areas is reached below the euphotic zone (MURRAY, 1991 ; see also zonation in HALLOCK and GLENN, 1986).

Housing symbiotic microalgae creates a host-symbiont system as described above that relieves settlement of benthic foraminifers under oligotrophic conditions in shallow tropical environments. The necessity for promoting symbionts with sufficient carbon dioxide might be the cause for intensive growth during the whole life span producing a large amount of calcium carbonate. This necessity for growth leads to tests larger than 1mm surpassing the mean diameter of 'adult' smaller benthic foraminifers (~600μm) by far in getting size of a few centimeters in some species. Extreme size is reached in living *Cycloclypeus* (13cm ; KOBA, 1982) and in the fossil *Lepidocyclina* (15cm), which are the largest single celled organisms known in the living and fossil record. Thus, shallow benthics forms with symbionts are called 'larger foraminifera', but this term characterizes the group inadequately. On the one hand, some species of the *Peneroplidae* and *Amphisteginidae* - both families houses symbionts and belong to this group - get maximum size around 1mm and are thus not significantly larger than the 'normal' small benthic foraminifers. On the other hand, some genera lacking symbionts and living in shallow tropical environments - like the sessile *Homotrematidae* and *Acervulinidae* - surpass the size of 2mm by far. Especially representatives of the latter family covering calcareous cobbles in deeper parts of the euphotic zone (macroids ; HOTTINGER, 1983b), often develop larger tests than the giant symbiont-bearing form *Cycloclypeus*. In that case, gigantism is caused by space competition of these encrusting foraminifers with rapidly growing corallinacean algae, both covering cobbles. Some genera with agglutinated tests living in the deep sea and belonging to the *Komokiacea* (TENDAL and HESSLER, 1977) obtain extreme size also, but lack symbiotic algae. Therefore, the correct name for categorizing the larger forms with symbionts seems to be 'symbiont-bearing benthic foraminifera'.

Longevity of benthic forms is usually more than six months in larger (symbiont-bearing) foraminifers, where several years were supposed for the sexually produced generation (agamonts), which is often distinguished by much larger tests than the asexually produced gamonts and schizonts (KRÜGER *et al.*, 1996). Accelerated growth often starts with a large embryonic apparatus that relieves survival of young individuals (HALLOCK, 1985) and makes carbon dioxide available for photosynthesis of the symbionts by the enormous production of calcium carbonate. Growth is restricted through the limited information transfer between a single nucleus or several nuclei and the cell organelles, and by the regulation capacity of metabolic processes within large protoplamatic bodies. Planktic forms following the same principle of carbon dioxide production by calcification processes cannot grow in the same manner as benthic foraminifers in getting large size, since they lose their floating capacity by heavy tests. These difficulties are avoided through short life spans (normally 1 month ; *e. g.*, BIJMA *et*

al., 1990) and compensated by high reproduction rates.

Wall strucure, light and symbionts

Taking the hypothesis of Trans-calcification as the prominent motor for establishing the foraminiferal-microalgal symbiosis, only benthic forms with 'secreted' calcium-carbonate tests are able to occupy niches in the shallow tropical marine environments and thus developing large tests. Foraminifera are distinguished by different wall structures that evolved during their long geological history. Four wall types are represented : 1. organic walls, 2. agglutinated foreign particles bound by organic cements (BENDER, 1989), 3. agglutinated foreign particles bound by inorganic cements (mainly $CaCO_3$; BENDER, 1989 ; SiO_2 in extremely few cases), and 4. biologically induced mineralized ('secreted') calcium carbonate. Only foraminifers belonging to groups 3 (except SiO_2-cement) and 4 can provide carbon dioxide for symbionts for developing large tests. Living symbiont-bearing benthic foraminifers show 'secreted' tests exclusively (for calcification modes see HEMLEBEN *et al.*, 1986). Some fossil larger forms that obviously lived in shallow environments (*e. g.*, *Orbitopsellidae* of the Jurassic, *Orbitolinacea* of the Cretaceous; systematic position according to LOEBLICH and TAPPAN, 1988) belong to the group with agglutinated particles fixed by calcium carbonate cements, thus could be interpreted as symbiont-bearing benthic foraminifers in meeting the requirements for this ecological group.

Two types of wall structures are represented in living larger foraminifers differing in crystal chemistry and structure of calcium carbonate. The first group (miliolid foraminifers) build their walls with tiny, irregularly oriented calcite needles of 1 to 2 micrometer size, where the mole content of $MgCO_3$ exceeds 10% (high-magnesian calcite; DICKSON, 1990). The extreme disorientation of optical c-axes prevents transparency, since incident light is broken in a thousand ways and even cannot pass through thin walls. Needles are oriented on both the inner and outer wall surfaces in a single layer like a parquet floor resulting in extremely smooth surfaces (*e. g.*, TOWE and CIFELLI, 1967 ; HAAKE, 1971). Therefore, incident light is broken and completely reflected giving those tests a white and porcelaineous appearance. Smaller benthic foraminifers with opaque walls are thus protected against noxious UV-irradiation in shallow surface waters, where they become the dominant foraminifers in normal marine lagoons, hypersaline lagoons, marshes, and moats (MURRAY, 1973). Larger foraminifers with porcelaineous tests must provide their symbionts with light. Thus, different mechanisms of wall thinning enabling light penetration are developed in the miliolid larger foraminifers. Pore-like 'pits' without connections to the chamber lumen (*e. g.*, GUDMUNDSSON, 1994), grooves (*e. g.*, HALLOCK *et al.*, 1991), and large areas of the chambers with extreme thin walls called 'windows' (*e. g.*, GUDMUNDSSON, 1994) are such structures.

The second group of living larger foraminifers build their walls by regularly arranged, small rhomboedric low magnesian calcite crystallites that are united in larger 'crystal' units (*e. g.*, BELLEMO, 1974). Optical axes are oriented either perpendicular or at an angle of 45° to the surface, thus incident light easily penetrates these 'hyaline' or

'glassy' walls. All walls are covered with pores that are closed by organic membranes, which enable gas exchange between the chamber lumen and the cytoplasm outside the test. Smaller hyaline benthic foraminifers avoid high illuminated regions, since the genetic material is not protected against UV-radiation. Larger foraminifers settling in high illuminated shallow regions of tropical seas had to develop special mechanisms like wall thickening that impedes penetration of light. During the construction of a new chamber, the new walls are not restricted to the chamber but completely cover the remaining test leading to lamellar walls. The intensive production of calcium carbonate in the shallow regions results in thick lamellae that weaken light penetration. Additionally, hyaline larger foraminifers hide in shadows of macroalgae and coral rubble or live just below the surface of sandy sediments for weakening the exposure to extreme illumination (*e. g.*, LEE, 1994; HOTTINGER, 1997). The hyaline wall structure is useful to supply symbionts with enough light in regions near the base of the euphotic zone. Similar to the porcelaineous forms, wall thinning relieves light penetration. In contrast to the nonlamellar walls in miliolid foraminifers, where thinning results from restricting the mineralization to thin layers (*e. g.*, HALLOCK and PEEBLES, 1993), the lamellar test structure complicates these processes in hyaline forms (HALLOCK and HANSEN, 1979). Especially species with gigantic tests living in light depleted environments (*Cycloclypeus*) shows incomplete lamellation in peripheral chambers walls (KRÜGER *et al.*, 1996). Again, additional structures are developed by the hyaline foraminifers in these light depleted environments that are interpreted as focusing mechanisms (HOTTINGER, 1997). Imperforate glassy structures sometimes project over the surface (*e. g.*, knobs, papillae, plugs, bosses, interseptal piles, elevated suture ridges) and may work as optical lenses.

Wall structure is thus a prominent mechanism for regulating light in passing through the walls, especially in high illuminated regions and, controversially, the deeper parts of the euphotic zone. Dissimilar to other host-microalgae systems, which mainly have dinoflagellates (*Zooxanthellae*) as the symbiotic part, the larger foraminifers house several microalgae belonging to rodophyceans, chlorophyceans, and diatoms beside *Zooxanthellae* (LEE and ANDERSON, 1991). All these groups are specified to light intensities and wavelengths by their photosynthetic pigments (VALIELA, 1995). Dinoflagellates and diatoms as the main symbionts of larger foraminifers show similar absorption spectra with a broad peak at the violet-blue-green and a smaller one at the red wavelengths (FALKOWSKI *et al.*, 1990 ; VALIELA 1995). This is caused by the content of chlorophyll a and c beside carotenoids in chromatophores of both groups. The photosynthetic pigments of red algae are chlorophyll *a* and phycoerythrin that relieves absorption of blue and green wavelengths. Only plastids of the chlorophycean algae contain chlorophyll b allowing absorption of the colors yellow and red. These wavelengths are normally absorbed in the upper 25m by oceanic waters, but can reach deeper parts in the 'blue deserts' of tropical seas. The normal depth sequence of macrobenthic primary producers in accordance to wavelengths starts with the predominance of green algae in the shallowest regions, followed by dominating brown and red algae in the deeper regions of the euphotic zone. This tendency is upset by the symbionts of larger foraminifers.

The deepest living larger foraminifers house pennate diatoms belonging to the genera *Fragilaria, Navicula, Nitzschia, Amphora, Achnanthes, Cocconeis*, and *Protokeelia* (LEE, 1994). Their photosynthetic pigments are distinguished by an absorption maximum of blue and green wavelengths that penetrate water masses down to 150m in very clear oceans. This could be the reason why the mean maximum of net photosynthesis rate of this algal group is located at low light intensities (RAVEN and RICHARDSON, 1986). Nevertheless, benthic diatoms are also abundant in shallow, high illuminated environments. Thus, tolerance of light intensity and wavelength varies between the different diatom species. Light ranges of larger foraminifers housing diatoms seems to depend on the proportion of symbiont species inhabiting a single host, all distinguished by differing light tolerance (LEE *et al.*, 1989). UV-irradiation is blocked either by the porcelaineous wall structure in *Alveolinidae* or by wall thickening through lamellae and hiding in shadow places, which is exercised by all families with hyaline, transparent tests.

Although the optimum of dinoflagellates according to light intensities and wavelength absorption is similar to the planktic diatoms (RAVEN and RICHARDSON, 1986), all shallow living invertebrates keeping symbionts house *Zooxanthellae*, exclusively the majority of larger foraminifers. Destruction of the symbionts through UV-irradiation is prevented in shallow living corals either by UV-blocking amino acids or pigments transforming the UV-wavelengths into the visible portion of the spectrum (FALKOWSKI *et al.*, 1990). Only larger foraminifers of the family *Soritinae* house *Zooxanthellae*, mainly *Symbiodinium* ssp. and *Amphidinium* sp. (LEE, 1994). This foraminiferal subfamily is characterized by nontransparent porcelaineous tests that easily block irradiation, but enable light penetration through glassy windows. Soritine foraminifers are distributed in regions with extreme irradiation ranging from the shallowest subtidal down to 50m depth (HOHENEGGER *et al.*, 1999). Their depth distribution is thus similar to stony corals. Being attached to smooth surfaces of sea weed or reef rocks, these flat forms expose their tests to solar irradiation (HOHENEGGER *et al.*, 1999). Since the glassy windows neither protects the symbionts nor the numerous nuclei of these foraminifers (LEUTENEGGER, 1977) against UV-radiation, similar mechanisms as in corals must be supposed preventing damaging of the nuclei and the symbionts through irradiation.

Unicellular rhodophyceans belonging to the genus *Porphyridium* are the symbionts in all foraminifers of the family *Peneroplidae* (LEE and ANDERSON, 1991). Rodophyceans seems to be the oldest eucaryotic organisms showing relations to cyanobacteria, but can develop highly organized forms with complex generation cycles (TAPPAN, 1980). Although the absorption optimum of the photosynthetic pigments is located at the blue-green wavelengths, not only the single celled planktic *Porphyridium* but also the complex corallinaceans span a broad tolerance range from the highly illuminated intertidal areas down to the base of the euphotic zone. *Porphyridium* seem not to be endangered by UV-irradiation in the same manner as the zooxanthellae, since the red colored pigments absorb short wavelengths (HAYNES, 1965). This explains the ability for functioning as symbionts in the porcelaineous *Peneroplidae* that inhabit extreme illuminated regions like reef moats, reef flats, and the uppermost reef slope (HOHENEGGER, 1994). Hiding of the

foraminifers between filamentous macroalgal thalli may protect the few nuclei that are sparsely spread in the cytoplasm of peneroplids (LEUTENEGGER, 1977) from extreme irradiation. The walls of the *Peneroplidae* are thicker in the neighborhood of pits in comparison to the windows of the *Soritidae*. This structure additionally blocks irradiation through the opaque walls and thus protects the nuclei. The insufficient thinning of the walls by pit rows in the *Peneroplidae* may restrict the distribution of these foraminifers to the uppermost parts of coral reefs, although rhodophycean symbionts can photosynthesize at extreme low light intensities.

Different chlorophycean species of the genus *Chlamydomonas* act as symbionts in the *Archaiasinae* (LEE and ANDERSON, 1991) and in the genera *Laevipeneroplis* and *Parasorites* (HALLOCK and PEEBLES, 1993), all distinguished by porcelaineous, nonlamellar walls. While members of the subfamily *Archaiasinae* geographically are restricted to the Western Atlantic/Caribbean, both latter genera are also represented in the West Pacific with a single species in each case. According to the absorption spectra of the green photosynthetic pigments with the main peak at the longer wavelengths (VALIELA, 1995), larger foraminifers with green algae inhabit the shallowest regions of coral reefs. Light intensity is regulated by wall thickness, whereby the shallowest living genus *Androsina* is characterized by thick walls. The transition to thinner walls in *Archaias* and to thin walls in *Cyclorbiculina* corresponds to the depth distribution of these three genera (HALLOCK and PEEBLES, 1993). Surprisingly, the deepest living larger foraminifer with opaque tests (*Parasorites*) found at 70m in the West Pacific also house chlorophyceans (HOHENEGGER, 1994). Light is extremely weak at these depths (4.6% surface PAR in very clear tropical water with an attenuation coefficient of 0.04) and mainly belongs to the blue-green wavelengths that seems to complicate photosynthesis in green pigments. But the second peak in the absorption spectra of green algae located at the shorter wavelengths (400 to 480nm ; VALIELA, 1995) in combination with the extreme thin chamber walls in *Parasorites* obviously enables photosynthesis of green algae in deeper parts of the euphotic zone.

Test structure, metabolism and hydrodynamics

Test form is characteristic for benthic symbiont-bearing foraminifers. Except the deep sea *Komokiacea*, all large sizes in foraminifera result from discontinuous growth that is pictured in chambered (polythalamous) tests (for chamber formation see HOTTINGER, 1986). Benthic symbiont-bearing foraminifers were developed during geological time in various, phylogenetically different groups. All mechanisms leading to large tests can be reduced to a few basic constructions relieving an advantageous surface/volume-ratio (BRASIER, 1986). Analogous test architecture iteratively evolved from different groups, where the stem forms are supposed to be multi-chambered planispiral or low-trochospiral tests (Figure 1A). Giant sizes are deduced from these tests following some basic requirements :

1. The information transfer from and to the regulation centers, the nuclei, has to be as short as possible. Since the test opening is important for transportation of food

gathered by pseudopodia into the cell and to extrude waste products, distances between the nuclei and apertures or aperture-like openings (canal openings) have to be minimized. Additionally, movement with the pseudopodia is also regulated by the nuclei. BRASIER (1986) explained the architecture of foraminiferal tests using this shortest line of communication (MinLOC) as the most important factor, also in the small benthic and planktic foraminifers.

2. Regulation of metabolic processes is difficult within large, unstructured protoplasm bodies, especially when a single nucleus located in the initial chamber has to organize metabolism and transportation of synthesized products within large cells (*e. g., Nummulitidae*). Compartments leading to substructures of the protoplasm make regulation and coordination easy. Normally, chambers sufficiently subdivide the protoplasm into compartments, but additional partitioning by septula (*Soritinae, Alveolinidae, Nummulitidae*) or pillars (*Archaiasinae*) is performed in groups with huge tests.
3. Since the endosymbiotic algae attain maximum light just beneath the chamber walls of the test surface, the surface/volume ratio is an important factor of larger foraminifers especially in light depleted environments. This ratio is not important for the shallow living forms, since irradiation penetrates to the inner chambers in globular (*Baculogypsina*) or fusiform tests (*Alveolinella* ; *e. g.*, LEUTENEGGER, 1984).
4. The foraminifers have to release movement of endosymbionts within the cytoplasma. On the one hand, the microalgae have to occupy the best positions near the test surface to get light; on the other hand, they must be protected against harmful disturbance from the test outside by hiding in the central test parts. Microalgae either actively move in a lacunar cytoplasma, which shows ramified branches in the peripheral chambers and becomes a spongy character in central test (*Soritinae* ; LEUTENEGGER, 1977), or they are passively transported by the host cytoplasma (*Amphisteginidae, Nummulitidae*). In any case, larger connections in the septa or septula like foramina and stolons must enable the transport or movement of symbionts between chambers or chamberlets (e. g., HOTTINGER, 1978).

The simplest way to get large size is based on the following two mechanisms: First, the frequencies of chamber construction must become higher in comparison to the normal benthic foraminifers by shortening the time intervals between the construction of two succeeding chambers (RÖTTGER, 1972). Second, the life span has to be longer than in 'normal' benthics for relieving large size. The whorl expansion rate of the logarihmic spiral, which geometrically characterizes the outer margin of a planspirally enrolled test (RAUP, 1966) is low in these cases and approximates a 'spiral of Archimedes' (*Alveolinella, Borelis, Nummulites*). Tests following a 'spiral of Archimedes' are distinguished by whorls with constant height. Since the distances between consecutive septa also keeps constant, the chambers are more or less equally sized during growth, thus completely adhering to the principle of compartments (HOTTINGER, 1978). The disadvantages of these simple mechanisms inducing extreme tests result from the long communication distances

(MinLOC after BRASIER, 1986) between test centers and apertures (Figure 1B). Larger foraminifers with lenticular tests could use these simple mechanisms not until the development of a canal system that shortens distances between the outer margin and the test center (*e. g.*, Hottinger, 1977). Using the canal system, the protoplasm can meet all demands like excretion of waste products, transport of food *etc.*, without disturbing the metabolic processes in the chamber lumina (RÖTTGER *et al.*, 1984) and find direct ways between the regulation center and the ambient seawater.

The second way of getting huge tests is by enlarging the whorl expansion rates of logarithmic spirals (Figure 1C). Following this mechanism, the principle of compartimentation is violated by radial septa that leads to broad and weak chamber parts in peripheral tests (BRASIER, 1986). Constant distances between septa of succeeding chambers from the umbonal part to the periphery are gained by a strong backward bending of chambers thus keeping a mean septal distance (*Peneroplidae, Archaiasinae, Nummulitidae*). Starting at the umbonal part, distances between consecutive radial septa will increase until a specified distance is reached. When this distance is located close to the umbonal part, then a strong backward bend is effected (*Archaiasinae*, some *Nummulitidae*). In nummulitids with high whorl-expansion rates (*Operculina, Operculinella, Planoperculina*) the grade of backward bend is positively correlated with the whorl expansion rate (Figure 1D). While in the first case with radial septa the growth exponent of the chamber volumes is close to the squared whorl expansion rate, both expansion rates (whorl spiral and chamber volume) are rather identical in the second case, where the distances between chamber septa remain constant.

Additional compartments are realized by the division of large chambers into small and equally sized subunits (chamberlets). There are three advantages in this strategy. First, cell regulation is relieved in a subdivided cytoplasm. Second, production of calcium carbonate in building septula generates additional carbon dioxide that is available for the symbiotic algae. The third advantage is test strengthening to resist mechanical stress especially in flat forms that easily break through transportation caused by tropical storms (*e. g.*, SONG *et al.*, 1994) or are damaged by predatory fishes (LIPPS, 1988). From a geometrical point of view, the subdivision of chambers into equally sized chamberlets is easier in forms with backbend chambers (Figure 1F) than in tests with radial septal courses (Figure 1E).

Extreme backbending leads to embracing, circular chambers and annular (cyclic) growth. The advantage of annular growth is the simultaneous production of many chambers (chamberlets) within one growth cycle that induces rapid growth. Furthermore, the ways from the ambient seawater to the test center become short without developing a canal system (Figure 1G). Today, all species of the genera *Cyclorbiculina, Sorites, Amphisorus, Marginopora, Parasorites, Heterocyclina,* and *Cycloclypeus* are distinguished by flat annular tests. The last two genera combine chamber connections by stolons with a canal system that is typical for nummulitids. Flat tests with a large surface/volume-ratio are thus best adapted to light depleted environments under low hydrodynamic conditions. The high drag coefficients of those tests lead to

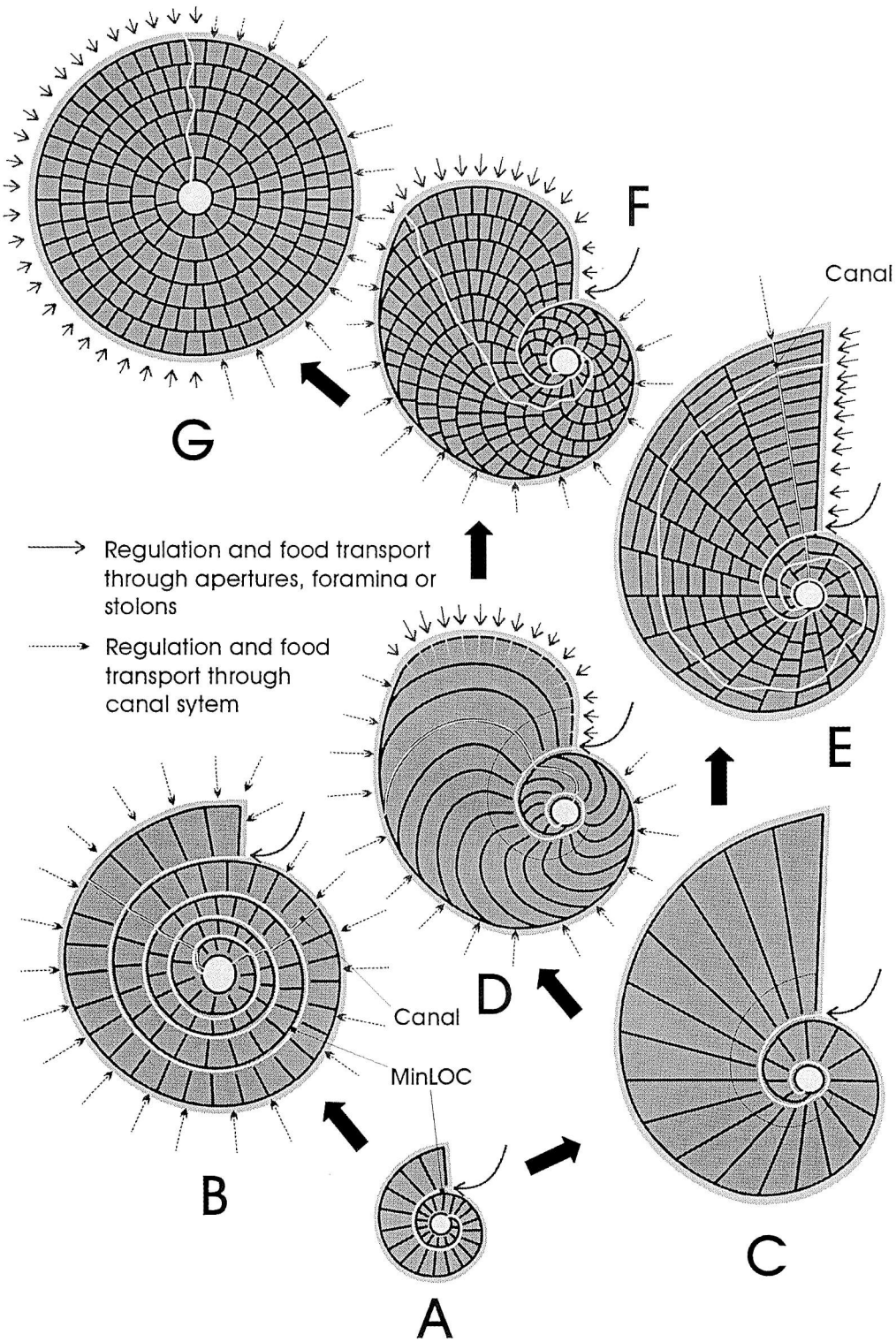


Fig. 1 Test construction trends in larger foraminifera

transportation at low Reynolds numbers (ALEXANDER, 1983), thus they are lifted from a structured bottom surface at laminar flow and low velocities (BOGGS, 1995). Flat plate-like tests are also represented in highly illuminated regions, but require calm water that is found in backreef areas or in protected parts of the uppermost reef slope. Attachment to smooth substrate resists erosion of the tests. Representatives of the porcelaineous genera *Sorites, Amphisorus*, and *Marginopora* either live attached to seagrass (*e. g.*, HOTTINGER 1977) and macroalgae with large, smooth thalli (*Turbinaria* ; HOHENEGGER, 1994), or cling to tiny filamentous macroalgae on smooth coral rock and cobbles (HOHENEGGER, 1994 ; HOHENEGGER *et al.*, 1999).

Strong hydrodynamics in the uppermost reefs are counteracted by test form (WETMORE and PLOTNICK, 1992). The simplest way to resist high water energy in movable substrates like gravel and coarse sand is the development of thick lenticular tests. These tests are found in the porcelaineous genera *Laevipeneroplis, Archaias,* and *Dendritina,* as well as in the hyaline *Amphistegina* and *Nummulites.* The lamellar structure of both latter genera enable the development of extremely thick and large tests, while size is restricted in the former nonlamellar, opaque genera as long as they adhere to lenticular growth in the initial test parts (*Laevipeneroplis, Archaias*). Both latter genera did not live on sandy substrates, but prefer the epiphytic habitat (HALLOCK, 1984 ; HALLOCK and PEEBLES, 1993). They can get larger size by the development of flaring chambers, which are normally broken within intensively moved gravel and coarse sand. The strongly backbend chambers in the peripheral part of *Amphistegina* do not depend on growth strategies as in the flat nummulitids, but seem to strengthen the test periphery against destruction by sediment movement.

Nonlamellar forms developed special growth mechanisms to circumvent the size restriction by long communication ways (MinLOC) in adherence to a planispiral growth. Elongation along the coiling axis creates spindle-formed (fusiform) tests similar to a cigar (*Borelis, Alveolinella*). Again, the elongated chambers have to be subdivided into chamberlets by septula, which makes a complex system of connections between succeeding and neighboring chamberlets necessary. Apertures are located in a single or multitude of rows at the apertural face of the last chamber. While the communication ways remain long through the central apertures and foramina of large tests, they become much shorter at the poles (HOTTINGER, 1978). This explains the numerous apertures located at both poles (*e. g.*, *Alveolinella* ; LIPPS and SEVERIN, 1986), where the one is used for fixation through pseudopods and the other for food gathering (HOHENEGGER, 1994). Sometimes, the central apertures are closed by organic membranes. Two additional advantages explains the construction of fusiform tests by larger foraminifers, which is the oldest strategy attaining large tests first developed in the nonlamellar *Fusulinacea* of the younger Paleozoic. On the one hand, the surface/volume ratio is higher than in smaller lenticular tests (*Peneroplidae*) and, on the other, the drag coefficient (see SEVERIN and LIPPS, 1989) is much lower in comparison to the flat discoid forms possessing comparable volumes (*Soritidae*). Thus, settlement is possible in high energetic environments either protecting in small grooves of coral rocks and rubble or living on sandy bottom in less

turbulent water of the upper reef slope (HOHENEGGER *et al.*, 1999).

Best adaptation to high energetic environments is found in the so-called 'star-sand' foraminifers, the *Calcarinidae*. Their low-trochospiral tests are characterized by long, canaliculate spines (HOTTINGER and LEUTENEGGER, 1980). Additionally to the apertures (*Neorotalia*, most *Calcarina*), protoplasm extruding from the spines serves for food gathering, excretion, and attachment to the substrate (RÖTTGER and KRÜGER, 1990). In a single species of *Calcarina* (*C. gaudichaudii*) and in the genera *Baculogypsinoides, Baculogypsina,* and *Schlumbergerella* the canaliculate spines completely take on the function of apertures. The thick, semiglobular tests hinder penetration of the harmful UV-irradiation in very shallow environments of the reef crest and upper reef slope, where the calcarinids live. Here, the spines act as anchors for fixation on algal thalli or hooking the specimens together.

Test thickness is achieved in the *Calcarinidae* not only by thick lamellae, but also by the production of lateral chamberlets (*Baculogypsina, Schlumbergerella*). This method of test thickening was the primary method developed in hyaline cyclic foraminifers to enable settlement in higher energetic environments of the inner and mid-ramp (TUCKER and WRIGHT, 1990). The orbitoidal 'bauplan' with an equatorial layer of annular arranged chambers and lateral layers of chamberlets is distinguished by large, lenticular tests. Genera with an orbitoidal test construction root in different stem-groups of hyaline foraminifers and became dominant in tropical shallow water environments of the Upper Cretaceous (*Orbitoididae, Lepidorbitoididae*). They got minor importance in the Paleogene (*Orthophragmiidae*) by competition with the Nummulitidae and disappeared in the Middle Miocene (*Miogypsinidae, Lepidocyclinidae*).

Distributions of larger foraminifers

Temperature as the main factor influencing the distribution of larger foraminifers does not show extreme seasonal change in tropical seas. Food availability is also unimportant for most benthic symbiont-bearing foraminifers. Therefore, the main factors influencing the distribution of larger foraminifers remain light intensity, water energy, and substrate. The first two factors are nonlinearly correlated with water depth. Not only light intensity, but also oscillatory water movement through wind induced waves follow an exponential decrease (DREW, 1983 ; HISCOCK, 1983). The sea floor topography leads to directional water movement by tidal- and beach-currents that affect the sea bottom down to 100m, much deeper than the fair weather wave-base (~15m). Breaking waves create different substrates (from coral rubble to macroids and sand) where larger foraminifers live. Thus, water depth as a typical complex environmental gradient combines the single factors light intensity and hydrodynamics in a complex manner. The depth dependency of larger foraminifers is pictured in occupying different niches (=intervals) along the gradient. Species living near the water surface have to protect the cytoplasm against UV-irradiation and must resist extreme hydrodynamics, while specimens living near the base of the photic zone have to provide their symbionts with light in obtaining a positive net photosynthetic rate.

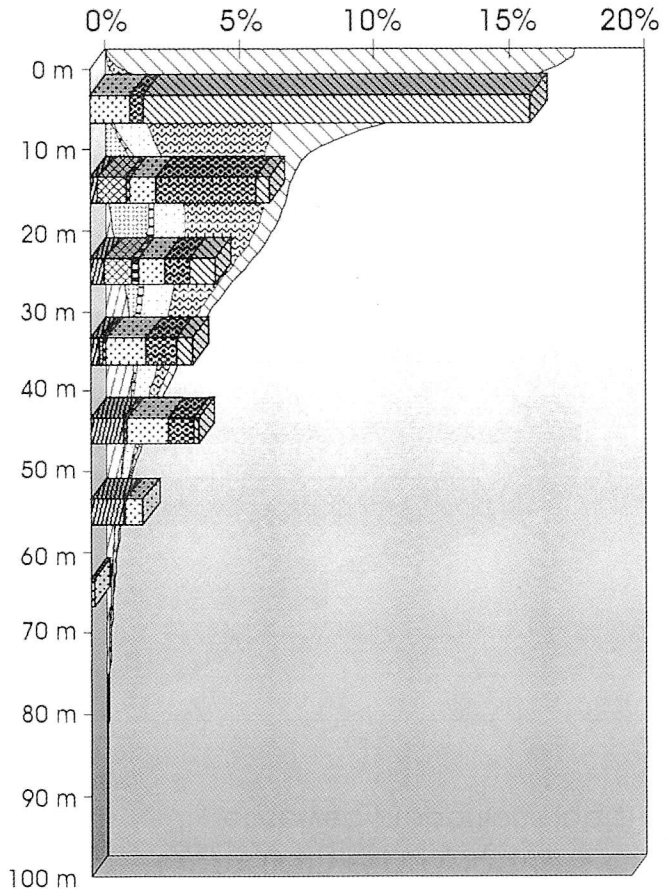
A gradient in species composition is termed 'coenocline', which characterizes the sequence of communities along an environmental gradient (WHITTAKER, 1973). The correlation between a coenocline and the environmental gradient allows determination of gradient values by community composition in case of lacking measurements of the environmental factor (transfer functions, *e.g.*, HOHENEGGER, 1995). Thus, depth determination based on species proportions is useful for ancient environments, where direct gradient measurements are impossible. Depth approximation by species proportion of larger foraminifers is restricted to the younger Neogene through the taxonomic uniformitarianism (DODD and STANTON, 1990) due to the high evolutionary rates in larger foraminifers. Analogous wall and test construction in larger foraminifers could be interpreted as an identical response to environmental parameters that iteratively evolved from various stem groups during the Phanerozoic. Thus, a functional morphological approach extends the estimation of paleodepth to the phylogenetic start of 'modern' larger foraminifers in the younger Mesozoic (HOTTINGER, 1978, 1983a, 1997).

Since benthic organisms living in shallow waters show extreme geographical diversity caused by separation, estimation of global coenoclines are impossible. The strong distinction in the distribution of benthic symbiont-bearing foraminifers between the tropical West Atlantic/Caribbean and the tropical Indo-Pacific restricts the determination of coenoclines to marine biomes in both provinces. Beside the *Archaiasinae*, which are represented in the tropical West Atlantic/Caribbean only, all other families belonging to larger foraminifers show highest diversities in the tropical Northwest Pacific (HOHENEGGER, 1994). Coenoclines reflect characteristic depth sequences in the following manner (HOHENEGGER 1994, HOHENEGGER *et al.*, 1999) :

The *Peneroplidae* (Figure 2) housing rhodophyceans only develop small tests with porcelaineous walls. They are extremely abundant in the shallowest part of the slope hiding between small filametous algae and could be found on the reef flat, which is often exposed to air under low tide. The deepest living peneroplid *Dendritina* prefers sandy bottom. The fusiform *Alveolinidae* with porcelaineous tests house diatoms and are represented in the Northwest Pacific by one species, *Alveolinella quoyi*. Its distribution is restricted to the slope, where the upper distribution boundary is located at 5m and the lower limit at 60m. The three species of the porcelaineous *Soritidae* living on the slope (Figure 3) house different algae, but show similar distributions. *Sorites* and *Amphisorus* with zooxanthellae are rare in highest energetic environments of the reef edge. They live attached to hard organic or inorganic substrate and attain their maximum at 30m. The green colored *Parasorites* house chlorophyceans and prefers sandy bottom down to 70m. *Amphisorus* and its close relative *Marginopora* become extremely abundant in less energetic subtidal areas with hard organic or inorganic substrate behind the reef crest, just settling in the reef moat or in shallow areas of lagoons.

All families with hyaline tests house diatoms. The *Amphisteginidae* (Figure 4) represent the best appropriated foraminifers for depth determination by species proportion (HANSEN and BUCHARDT, 1977), since they inhabit the total range of the euphotic zone and are distributed with several species over the whole tropical Indo-Pacific

Fig. 2 Cumulative proportions of *Peneroplidae* on total larger foraminifers
observed proportions (bars) and theoretical proportions (background)



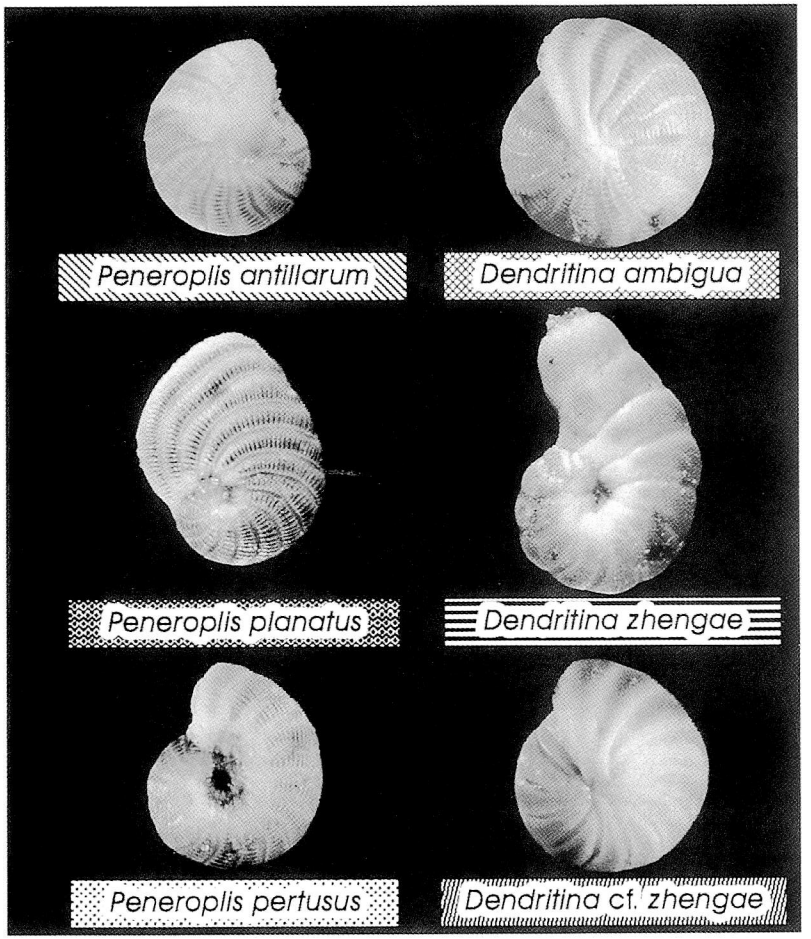
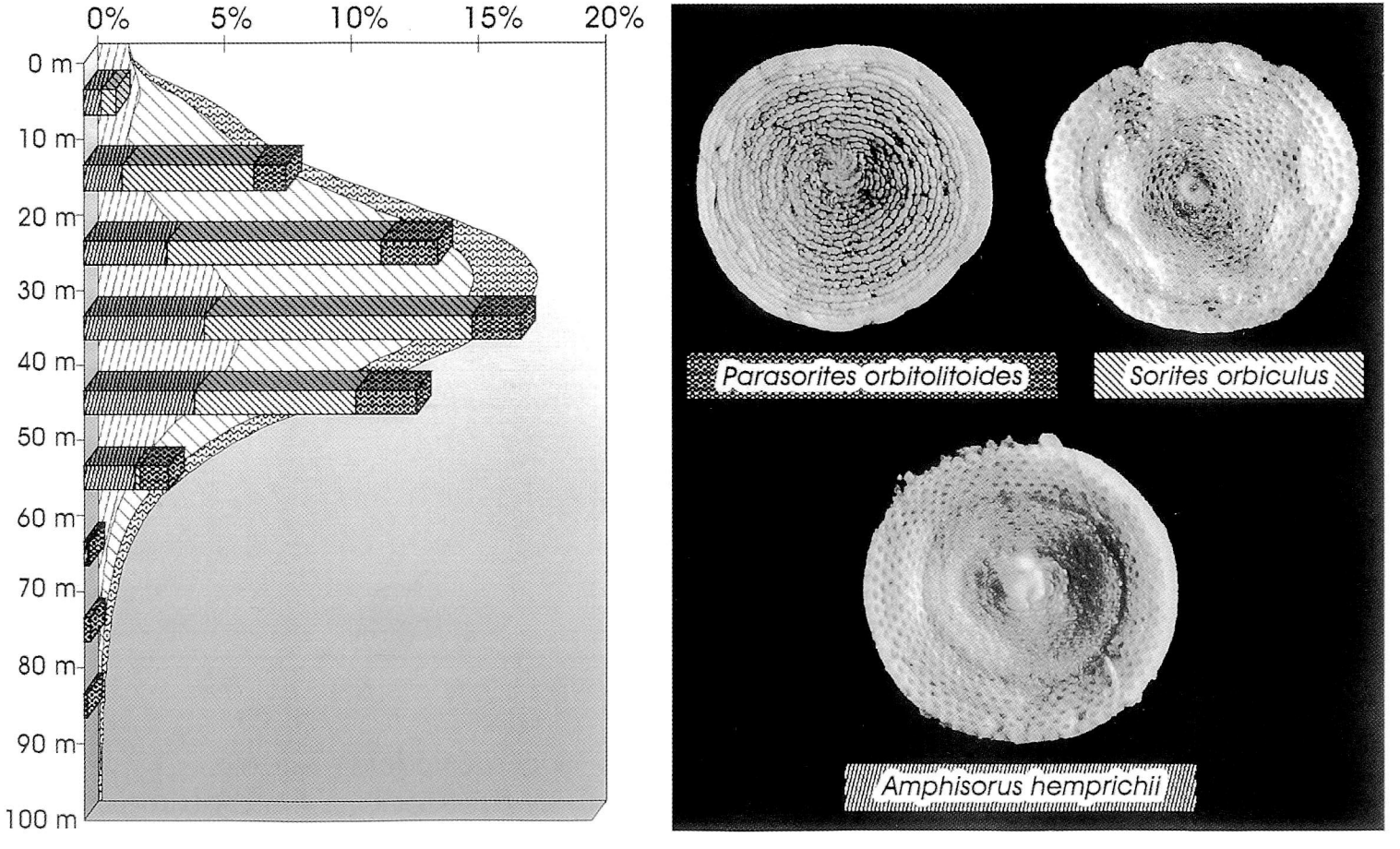


Fig. 3 Cumulative proportions of *Soritidae* on total larger foraminifers
observed proportions (bars) and theoretical proportions (background)



(especially the *Amphistegina lobifera-lessonii-bicirculata*-group; Figure 4). The shallowest living representative (*A. lobifera*) also settles on the reef flat and is represented with lower numbers in the shallowest backreef areas (HOHENEGGER, 1994). Here it protects against UV-irradiation by hiding in shadows of algal thalli or below coral pieces. According to the construction of semi-globular tests with strong spines, the *Calcarinidae* (Figure 5) are best adapted to settle in high-energy regions of the uppermost slope. They become extremely abundant in subtidal pools or macro-algal mats on the reef crest, where they densely cover the bottom giving the impression of 'living sand' (LEE, 1995). Less energetic areas of the backreef are also inhabited by calcarinids, where they cling with the spines to larger macroalgae (*e.g., Sargassum*). The decrease in frequencies with depth is characteristic for the *Calcarinidae*, but *Baculogypsinoides spinosus* can survive at 90m, attaining abundance optimum at 50m (Fig. 5). The opposite trend to the *Calcarinidae* is pronounced in the large-sized *Nummulitidae* (Figure 6). They are extremely rare in high energetic environments (only *Heterostegina depressa* is found in few numbers in subtidal pools of the reef flat), but become the dominant family in deepest parts of the photic zone. This depth trend in frequencies is also coupled with mechanisms that relieve light penetration, such as test flattening, wall thinning, and the development of light focusing structures like papillae or knobs.

Calcium carbonate production and climate, present and past

Coral reefs produce one sixth (900 tons) of the world calcium carbonate per year (MILLIMANN, 1993) that is mainly precipitated by corals, mollusks, benthic foraminifers, echinoids, and rhodophyceans in decreasing order (HOTTINGER, 1997). The proportion of benthic foraminifers is approximately 4.8 percent of the global carbonate reef budget (LANGER *et al.*, 1997). This is low in comparison to the Cretaceous and Paleogene, where calcium carbonate production by larger foraminifers was significantly higher depending on climate and the atmospheric CO_2-content.

High temperatures over geological time induce sea level rising, which results in large, flooded shelf areas. During cold periods (ice ages) the sea level sinks. Flooding caused by rising temperatures is disadvantageous for the development of coral reefs, but advantageous for the settlement of benthic symbiont-bearing foraminifers in shallow areas, which were often developed as huge carbonate ramps (TUCKER and WRIGHT, 1990). Therefore, carbonate sediments produced to the main part of larger foraminifers are common in the Cretaceous and Lower Tertiary (e.g., nummulite-sandstone of the Egyptian pyramids). The rising sea-level in the Upper Cretaceous (SCHLANGER, 1986) apparently correlates with an increase in temperatures (DOUGLAS and WOODRUFF, 1981) that was possibly caused by the 'greenhouse effect' of a high atmospheric carbon dioxide content, several times higher than today (BERNER, 1991). Radiation of benthic symbiont-bearing foraminiferids resulted under these favorable conditions occupying different niches of carbonate ramps. According to the functional-morphologic approach (HOTTINGER, 1983a, 1997), the following subdivision of the ramp is possible in the Upper Cretaceous. Alveolinids (*Subalveolina, Praealveolina, Multispira etc.*) settled in high energy zones of

Fig. 4 Cumulative proportions of *Amphisteginidae* on total larger foraminifers
observed proportions (bars) and theoretical proportions (background)

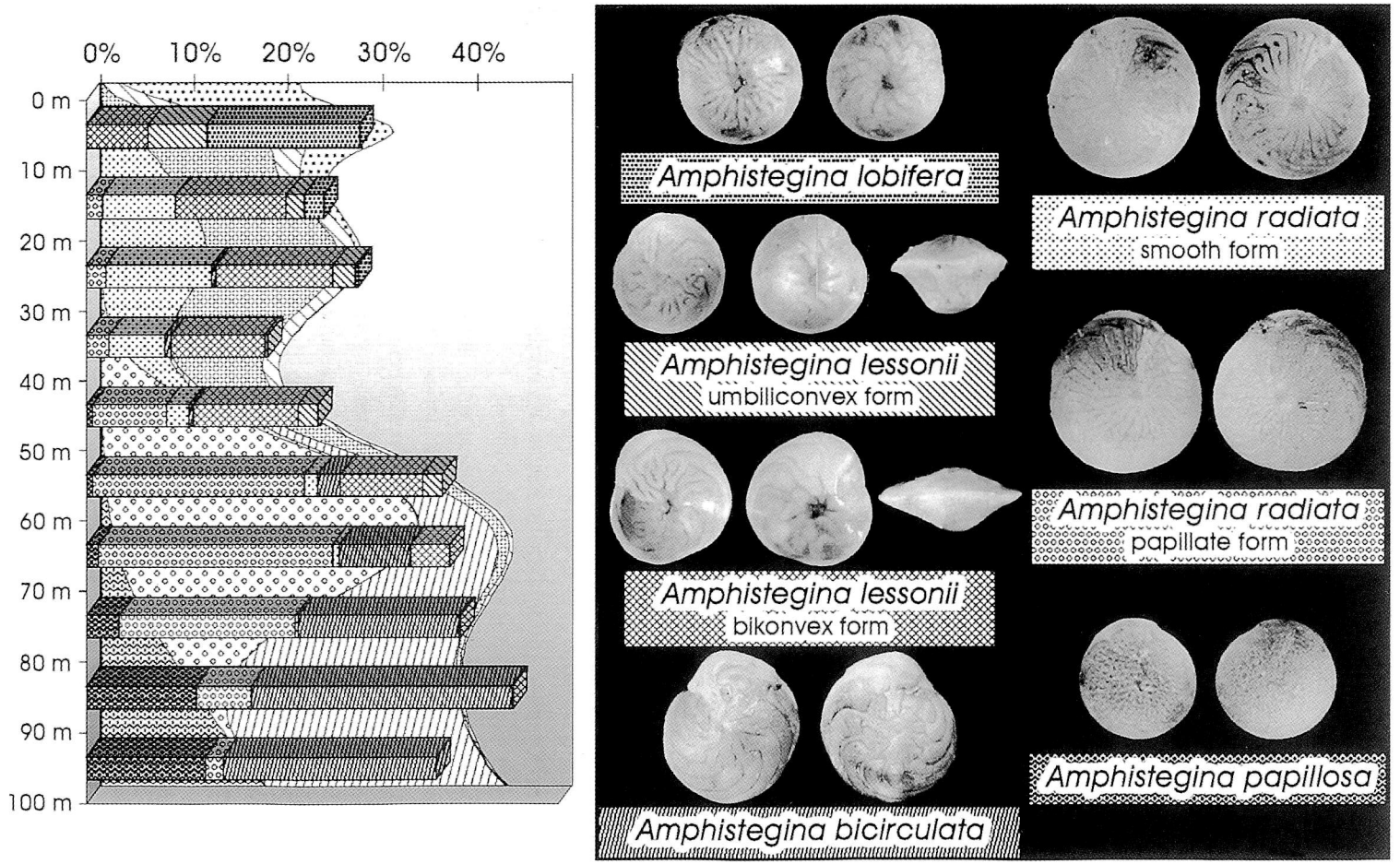


Fig. 5 Cumulative proportions of *Calcarinidae* on total larger foraminifers

observed proportions (bars) and
theoretical proportions (background)

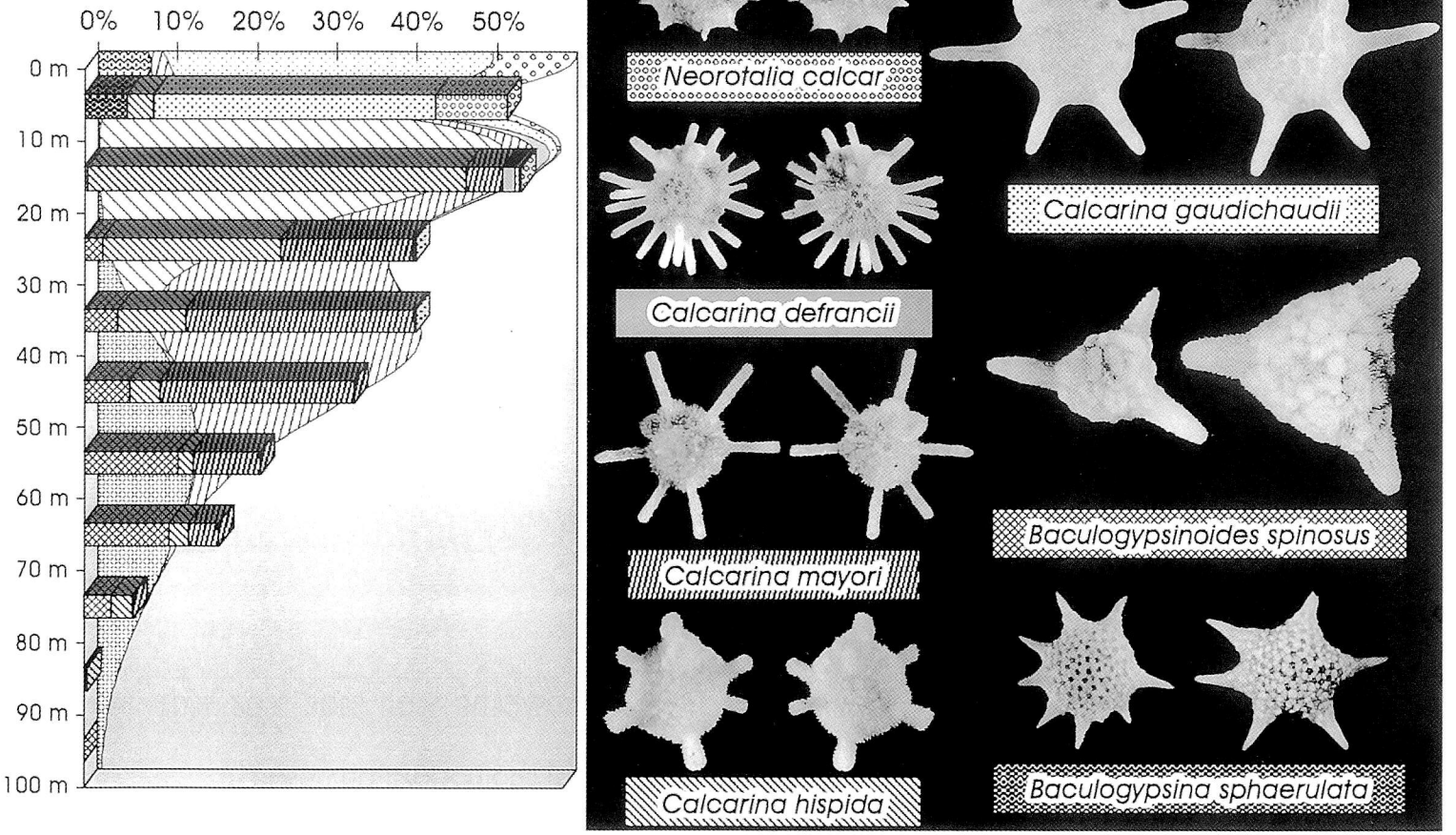
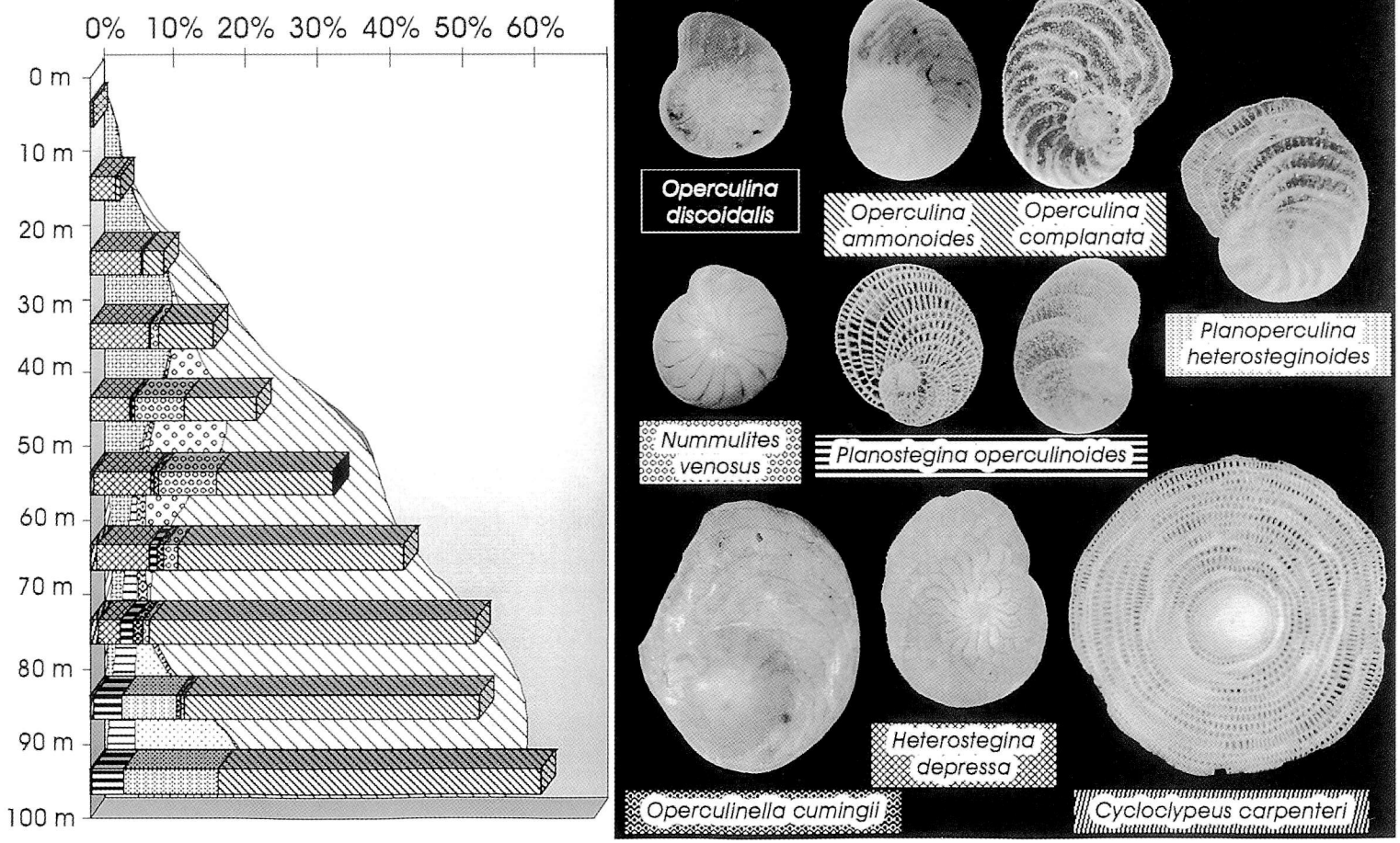


Fig. 6 Cumulative proportions of *Nummulitidae* on total larger foraminifers

observed proportions (bars) and theoretical proportions (background)



the shallow ramp. The 'calcarinid' *Siderolites* possibly lived attached to hard (organic ?) substrates analogous to its recent relatives. Deeper environments were occupied by larger foramifers with annular growth and an orbitoidal test construction, like *Orbitoides, Helenocyclina,* and *Lepidorbitoides.*

The Cretaceous-Tertiary boundary extinction event is not reflected in long-time sea level changes and temperatures. Until the Middle Eocene, temperatures and sea levels were high, but lower than in the Upper Cretaceous. Both are distinguished by a more or less continuous decrease finished at the beginning of the Oligocene (WOLFE and POORE, 1982). The atmospheric carbon dioxide content was 2-3 times higher than today (BERNER, 1991). After the mass extinction at the K/T-boundary and succeeding radiation in the Paleocene, the larger foraminiferids attained their climax in the middle Eocene. While the soritid *Orbitolites* occupied similar niches like its recent relatives, the alveolinids again settled in high energetic parts of the ramp. Thick lenticular nummulitids (*Nummulites*) lived in less energetic environments and were replaced by evolute forms (*Assilina*) in deeper parts. Thin and large orthophragmiids (*Asterocyclina, Discocyclina*) settled near the base of the photic zone (HOTTINGER, 1997). The opening of cold circum-antarctic waters in the Oligocene gave rise to the cooling of oceans. This resulted in the beginning of scleractinian coral reef growth and the disappearance of the cyclic orbitoidal foraminifers (*Lepidocyclina, Miogypsina*).

Since the Mesozoic time, climaxes in larger foraminifers correlate with the atmospheric carbon dioxide-content and temperature. This correlation is invalid for the earliest larger foraminifers in the younger Paleozoic. Spindle-form tests and the shallow environments as inferred by sedimentological investigations can be an argument for algal endosymbionts in Fusulinacea , but the cold temperature and low carbon dioxide level in the Carboniferous and Permian (BERNER, 1991 ; FRAKES *et al.*, 1992) do not correspond to the relations between temperature and larger foraminiferids as obtained in the Mesozoic and Cenozoic. However, cool temperatures are conducive for aragonite precipitation in tropical seas (MORSE and MACKENZIE, 1990), which explains the predominance of scleractinian coral reefs today and this maybe the cause for the large carbonate reef buildups in the Permian. Although the seas were relatively cool in tropical areas of the Carboniferous, the start of algal-host systems in foraminifers can be supposed for the younger Paleozoic.

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