The depth-depending ornamentation of some lamellar-perforate foraminifera

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Abstract
The rising ornamental relief on perforate-lamellar, lateral chamber walls progressing with increasing water depth of the symbiont-bearing foraminifera's habitat suggests a functional connection between relief height and irradiation intensity needed by the symbionts for their photosynthesis. Three kinds of ornamental elements have to be distinguished: papillae on perforate lateral walls, beads on sutures and piles built up by subsequent outer lamellae over consecutive whorls or layers of lateral chamberlets by blueprinting processes. The three elements are all connected to a circular – or at sutures linear – spreading process of the pores which might be responsible for the local thickening of the lamellae. The indices of refraction of the media involved, seawater and calcite, indicate total reflection to take place over an arc of 26° arising from the shell surface. Total reflection is estimated at near to 50% of the total incident light on a smooth shell surface. A rising relief on the shell surface reduces the totally reflected light to considerable extent by recapturing the reflected rays and may thus contribute – not as light lense but as light trap – to enhance irradiation of the symbionts. This warrants the design of optical experiments with shells in seawater and further studies of pore distribution in smooth shells.

Keywords: Lamellar-perforate foraminifera, inflational ornamentation, papillae, beads, piles, light lenses, light traps, habitat depth gradient

1. Introduction

With increasing depth of habitat, an increase of relief height has been reported in the ornamental sculptures on perforate lateral chamber walls in many nummulitid and amphisteginid recent species. In the same time, wall thickness and involuteness were reported to decrease in greater depths. The general flattening of the shells with increasing depth seems to affect not only lamellar-perforate but also porcelaneous discoidal shells in species belonging to *Amphisorus* and *Marginopora*. In this contribution, only the meaning of sculptures and their increase in height in the depth gradient will be discussed. A possible connection between relief height and the progressive light absorption in the water column characterizing the depth gradient may be given by the optical properties of the foraminiferan shell and the need of light of the symbionts to fulfill their function in the host.

There are two main kinds of endosymbioses in larger foraminiferans: dinophycean symbionts in porcelaneous hosts such as *Amphisorus* spp. which are living in the lacunar system of the protoplast and may move actively, with short flagellas, within their host (Leutenegger, 1977a). This system represents a device for regulating the irradiance during the daily cycle in order to avoid photoinhibition during high stand of the sun. Bacillariophycean (diatom) symbionts live and reproduce in closed vacuoles of a lamellar-perforate host such as amphisteginids or nummulitids. These symbionts have no flagella and can not move (Leutenegger, 1977b). The host houses them below inner pore mouths coated by an organic lining in so-called eggholders. Their position below pores enhances the exchange of small molecules, in particular O_2 and CO_2, as suggested by a similar position of mitochondria below pore mouths in smaller lamellar species living without symbionts in oxygen-deficient environments (Leutenegger and Hansen, 1979).

Amphisteginid species inhabit with overlapping ranges the entire photic zone (Hansen and Buchardt, 1977; Larsen and Drooger, 1977; Leutenegger, 1984). The shallower

species, *A. lobifera* and *A. lessonii*, exhibit thick shells and heavily spiked faces hinting to active movement of the host in its environment. This coincides with *in situ* observation of their negative phototropy. The deeper species of the Western Indian Ocean including the Red Sea, *A. bicirculata*, *A. papillosa* and *A.* aff. *radiata*, have flattened shells. This flattening of the test is related to the thinning of the outer lamellae with depth linked to decreasing water turbulence with depth and thus reducing the rate of calcification (ter Kuile,1991).

In the Western Indian Ocean, the nummulitid species are less numerous: each genus is represented by only one species or by two species replacing each other in the depth gradient. Their respective depth range is comparatively long and their intraspecific variation is clearly linked to the depth of their recovery. In the Red Sea, *Assilina* (ex *Operculina*) *ammonoides* is distributed over almost the complete photic zone. Their more or less lenticular shells from shallow water are involute and have thick walls. The shells from the lower part of the photic zone are much flatter, more evolute and exhibit thin walls. *Heterostegina depressa* presents the same range of variation in the depth gradient and is replaced in depth by the totally evolute species *H.(Planostegina) operculinoides*, which has plan-parallel, thin lateral shell walls. *Heterocyclina tuberculata* is present only in the deeper parts of the photic zone, below 60 m, and represents a vicariant substitute of *Cycloclypeus carpenteri* in the Central Indopacific with similar ornamentation. In the Far Eastern Pacific, the nummulitid species richness is reported to be higher (Hohenegger, 2000) but the morphological trends in the coenoclines are similar.

All nummulitids exhibit in their lateral chamber or chamberlet walls so-called papillae (Fig. 1). The papillae
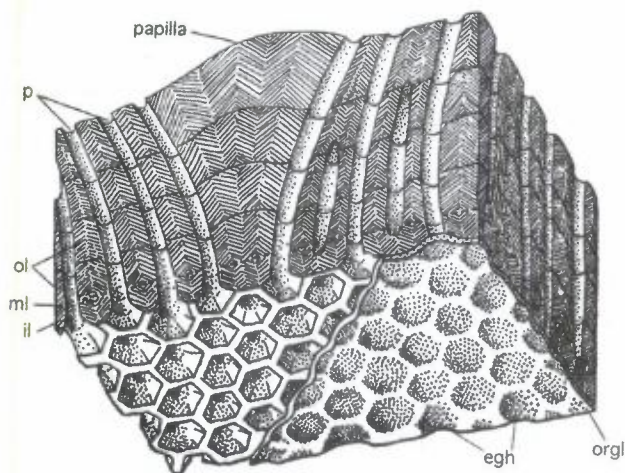

Figure 1. Perforate-lamellar chamber wall with papilla. Schematic, not to scale. egh: eggholder housing the symbionts; il: inner lamella; ml: median layer; ol: outer lamellae; orgl: organic lining of host protoplast; p: pore. (After Hottinger, 1977b).

are imperforate parts of conical outline within the wall. The base of the papillar cone forming the surface of the lateral chamber wall is flat in nummulitids from shallow water, not forming any relief on the wall. In deeper water, the papillae start to form reliefs, reaching the shape of hemispherical protuberances in the lower part of the photic zone (60–140 m in blue deserts). In *Assilina* species, the number of papillae is high, in *Heterostegina*, the number is much lower, often reduced to two per chamberlet, in *Heterocyclina*, there may be only a single one (Figs. 4–6). Accordingly, their diameter is very different. Their increasing height with progressing depth of their habitat however is similar in all three genera.

The rising relief of papillae with inceasing depth of their habitat have been interpreted as light lenses for collecting light at the lower end of the photic zone. This is suggested by the transparent, clear aspect of the papillae in the light microscope. The following report discusses in some detail the nature of papillae and similar ornamental shell textures as well as some aspects and approaches to the interpretation of the papillae as light lenses.

The names of the taxa mentionened in this paper refer to Hottinger et al. (1993). They will not be discussed here in spite of various open questions. The material investigated was collected by the author in the Gulf of Aqaba (see Reiss and Hottinger, 1984) or on various other expeditions to New Caledonia or Mauritius in later years. The latter will have to be described elsewhere.

2. Symbiont Bearing Larger Foraminifera in their Natural Environment

In shallow water, the symbiont bearing porcelaneous larger foraminifera produce either discoidal (*Sorites, Amphisorus, Marginopora*) or spherical to fusiform shells (alveolinids: *Borelis* and *Alveolinella*). The former expose a large surface to light, the latter a relatively small one. Under the large lateral surface of the soritid discs, the symbionts are exposed to the irradiation of sunlight. Their ability to move in the lacunar system of the host protoplasm with their short flagella provides them the possibility to regulate irradiation intensity by displacement from the exposed to the unexposed side of their host. This device, however, is working only if 1. the architecture of the shell permits short paths of displacement from one side of the other in the disc (Hottinger, 1997) and if 2. the host is placed on a dark background avoiding the up to 50% backscattering of sunlight by the carbonate sands in their ambient environment. The dark surface is provided by the plants of the vegetation cover and therefore the larger discoidal porcelaneous foraminifera exhibit an epiphytic behaviour (Fig. 2A). In the field, we observe the olive-brown coloration of the porcelaneous discs produced by the dinophycean symbionts under the lateral surface of the host

to fade during the daily highstand of the sun, in order to avoid photoinhibition. So far, there is no evidence of species-specific relations between taxa of foraminifera and their vegetal substrates. As epiphytes, the discs are oriented in space according to their substrate, the leaves of seagrasses or other vegetal surfaces of all kinds. This means, that the inclination of the discs in relation to the angle of incident sunlight is unspecific (Fig. 2A).

The spherical to fusiform alveolinids are not epiphytic. They live on the bottom, on sandy or solid carbonate substrates (Reiss and Hottinger, 1984). Fusiform shells are positioned with their coiling axis parallel to their substrate and move in polar direction. They are exposed to light with

a hemicylindrical to hemispherical surface. Their bacillarian symbionts have no flagella and must be moved passively towards the inner shell whorls in order to regulate irradiation intensity. The details of this mechanism have still to be worked out, in particular to understand the meaning of the multistorey chamber architecture in *Alveolinella* and the striking morphological diversity including flosculinisation of the Eocene alveolinids.

The trochospiral-involute amphisteginids house their bacillarian symbionts in the eggholders below the inner pore mouths in more than the last whorl. Symbionts in penultimate whorls therefore are in the shade of the ultimate whorl. The curvature of the shell's outer shape and

Figure 2. Symbiont bearing foraminifera in their habitat: A: shallow environment with *Amphisorus hemprichii* (arrows) epiphytic on *Halophila* leaves as dark background. Note inclination of discoidal shells in respect to light source. B: Deeper, softbottom environment covered by *Assilina ammonoides*. Note inclined position of larger microspheric form (arrow). Gulf of Aqaba, Red Sea. The larger foraminiferal shells have a diameter of about 6–8 mm.

its flattening with depth are therefore irrelevant for the intensity of irradiation of the symbionts. This is in good agreement with the observation in the field of their negative phototropy supported by the fact of their intensive spiking of their face indicating high motility in shallow environments (Hottinger, 2006, in press).

The nummulitids, defined by having as face a marginal cord providing multiple canal orifices all around the periphery of the shell (Hottinger, 2000), are living either on hard substrates (*Heterostegina depressa*) or on soft substrate (*Assilina ammonoides*) (Reiss and Hottinger, 1984). In the deeper parts of the photic zone, the nature of the substrate seems to be of secondary importance for the distribution of the deeper species, but the number and quality of direct visual observations in these depths is restricted due to the difficulties of scuba diving with compressed air to depths below 60 m. Whereas the position of *Heterostegina* shells on hard substrate is very variable in respect to the incident light due to the irregular, rubble bottom "micro"-topography, the assilinas tend to take a 30–45 degree inclination of their flattened-lenticular to discoidal shells on the much more even, fine-grained substrate (Fig. 2B). In the lower part of the photic zone, below 60–80 m, the planparallel, discoidal shells of *Heterostegina operculinoides* and *Heterocyclina tuberculata* seem to keep their shell axis perpendicular to their substrate in agreement with the reduced tickness of their marginal cord. Thus, we may restrict our considerations about the functionality of papillae and/or beads as light lenses to more or less flat, discoidal shell surfaces with an inclination between 0 and 45 degrees to the horizon.

3. The Distribution of Light in the Photic Zone of the Sea

Scuba divers are familiar with the observation, that shadows disappear almost totally below 10–20 m depth. This means that in the lower part of the photic zone, the irradiation is diffused, poorly directed or entirely undirected. Direct observations *in situ* indicate that the most intensive illumination comes from vertically overhead, the darkest sector being in the horizontal direction and intermediate illumination comes from the sea bottom as backscatter from carbonate sands or rubble. This is to be seen best during descent in open water, when bottoms below 40 m depth begin to emerge from murk. Dense vegetation covers may reduce the reflection from the overhead light source almost completely.

Schematising illumination intensity in the lower part of the photic zone (see Jerlov, 1968) might be depicted as ellipsoid where the distance between a point within the ellipsoid to its periphery may represent the relative quantity of light irradiating a minute object from that direction. A

sphere with the irradiated object in its center would mean equal irradiation from all sides. On a dark substrate, where the reflection is very low or nil, we can describe the situation with a hemisphere.

The deeper we submerge our irradiated object in the water column, the fatter the irradiation ellipsoid will be (Fig. 3). In the same time, the irradiation by backscattered rays from the substrate will be reduced; the position of the irradiated object will sink in respect to the center of the ellipsoid. Moreover, we have to take into account, between 80 and 120 m depth, the daily migration of the plankton in the water column, producing during the highstand of the sun clearly visible clouds at these depths which considerably increase the scattering of the light coming from above. This was observed during the dives with the submarine GEO in Elat and illustrates the difficulties of quantitative approaches to light measurements (review in Reiss and Hottinger, 1984: p. 83–87).

Where irradiation intensity from diffuse light sources is equal from all sides, corresponding to a hemisphere, the inclination of a discoidal shell in respect to its horizon has no effect what so ever on the intensity of its irradiation. The inclination of the disc therfore must have other biological meanings.

Taking into account the above considerations, our question may be focussed on asking, whether a more or less hemispherical protuberance on the surface of a mineralized shell may help to collect light from an extremely undirected source by suppressing the total reflexion of incident light at low angles to the shell surface.
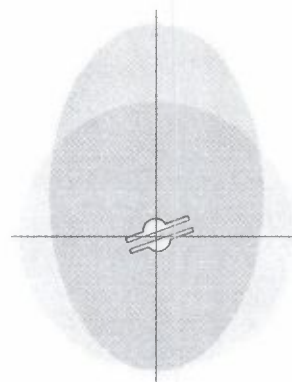

Figure 3. Irradiation of a symbiont bearing foraminifer by diffused light prevailing in marine environments. The quantity of light irradiating an object from a particular direction is indicated by the distance between this object and the surface of the ellipsoid in that direction. The shallower the habitat, the slimmer the ellipsoid (darker stippled) and the nearer the object's position to the center of the ellipsoid, where backscattering from the substrate would be almost equal to half of the irradiation from the sea surface above. With increasing depth, the ellipsoid grades into a hemisphere (lighter stippled), where the inclination of a discoidal shell in respect to the horizon looses any significance as to the amount of irradiation.

4. The Nature of Papillae, Beads and Piles

Many if not most lamellar perforate shells of symbiont bearing foraminifera exhibit surface "ornaments", sculptures of more or less circular outline producing a rounded protrusion. The relief is pruduced by an "organised" local thickening of subseqent lamellae described by Smout (1954) as "inflational" ornaments. The "organisation", i.e. the continuity of such inflational structures through many stages of growth, are due to blueprinting the circular contours of thickening from one outer lamella to the next one along increased rates of lamellar bending.

We distinguish three kinds of such protrusions according to their relation to other elements of the shell's architecture: 1. protrusions positioned on the perforate lateral wall called papillae (Figs. 1, 4–6), 2. protrusions positioned along spiral, septal, septular or hemiseptular sutures called beads, usually forming a line of elements, the beading, along the corresponding suture (Fig. 7) and 3. protrusions rooted on privileged sites in inner whorls and persisting through several volutions of a spiral shell or through several layers of lateral chamberlets in the case of cyclical growth. These are called piles of lamellae and appear often in the axis of coiled shells. Ferrandez (1999) calls them "cristalline cones" in foraminifera exhibiting an
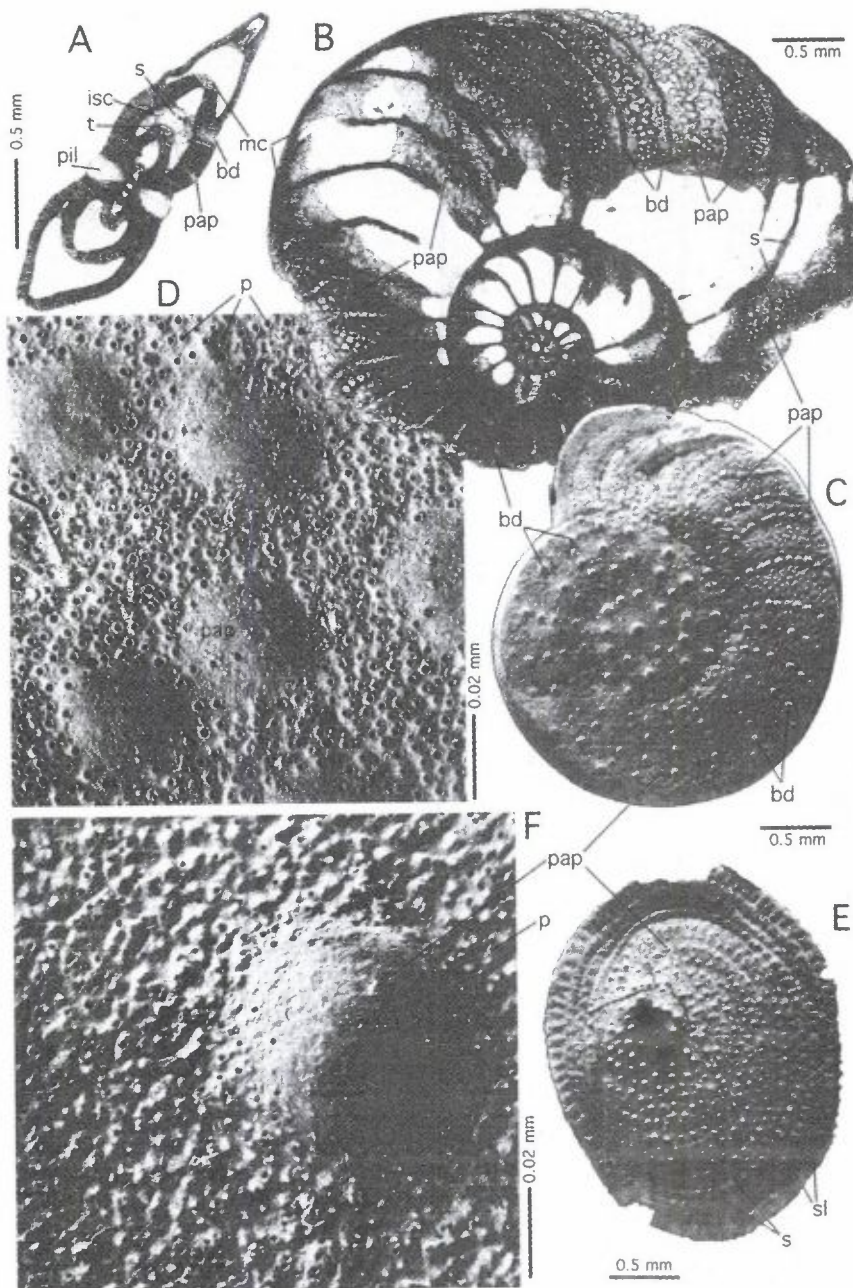

Figure 4. Papillae on perforate lateral chamber walls in *Assilina ammonoides* (A–D) and *Heterocyclina tuberculata* (E, F). Gulf of Aqaba, Red Sea. Recent. A: axial section of megalosperic specimen from shallow habitats, transmitted light micrograph. B: tangential section of megalospheric specimen from comparatively deep habitats, transmitted light micrograph. C: External, lateral view of megalospheric specimen showing distribution of beads and papillae. Scanning Electron Microscopy (SEM) graph. D: detail of C, showing distribution of pores and papillae, SEM image. E: External, lateral view of the paper-thin test of megalospheric *H. tuberculata*, showing a single papilla per chamberlet. SEM image. F: detail of E showing distribution of pores around a papilla. SEM image. bd: bead; isc: intraseptal canal system; mc: marginal cord; p: pore; pap: papilla; pil: pile (of lamellae); s: septum, septal suture; sl: septulum, septular suture; t: tunnel.

orthophragminid architecture in order to stress the fact that the piles have no mechanical function to support the lateral chamberlets.

In *Amphistegina papillosa*, many beads are to be observed on the lateral wall in between the beaded septal sutures. They are not papillae because they are positioned over walls subdividing as hemiseptula the chamber lumen (Fig. 7). Thus, beads are always supported by underlying walls perpendicular to the shell surface, irrespective of their position over or between chamber septa. Papillae are not supported by any structure below the lateral perforate wall. The relief is produced in both cases by a coordinated thickening of the subsequent outer lamellae over a restricted area.

Early, involute parts of the shell (assilinids) or lenticular shells remaining involute throughout their ontogeny (amphisteginids) produce imperforate or poorly perforate piles of thickened lamellae over their proloculus in the
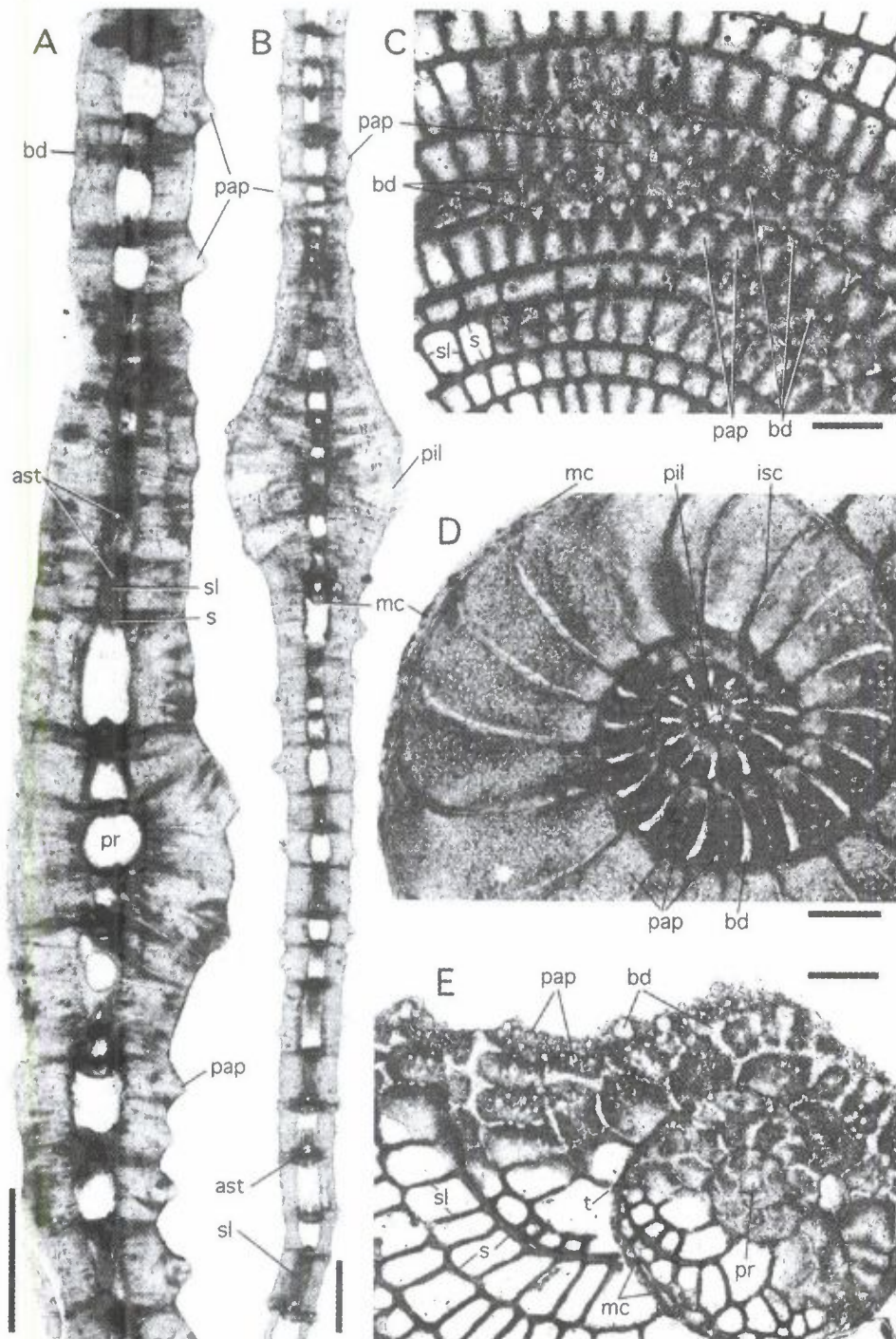

Figure 5. Papillae and beading in *Heterocyclina tuberculata* (A–C), *Assilina madagascariensis* (D) and *Heterostegina operculiniformis* (E) from the lower limit of the photic zone. Mauritius, Indian Ocean. Recent. Transmitted light micrographs. Scale bars 0.1 mm. A: axial section of shell center showing position of single papilla per chamberlet. B: axial section of megalosperic specimen. C: section tangential to lateral shell wall. D: section parallel to equator of semiinvolute shell. Compare Fig. 6. E: section traversing the lateral wall of discoidal shell at a very low angle. ast: annular stolon; bd: beads; isc: intraseptal canal system; mc: marginal cord; pap: papillae; pr: proloculus; s: septum; sl: septulum; t: tunnel.

coiling axis (Figs. 4A, 6B, 7A). Built in continuation in subsequent whorls or, in the case of cyclical growth, through subsequent lateral chamberlet layers (orbitoidiform architecture), the question arises, whether beads and piles also may have functions related to the irradiation of the greenhouse by conducting light to the deeper part of the shell.

There is a relation between pore distribution in the wall and the local thickening of the outer lamellas. In most cases, the raised ornaments in lamellar-perforate shells are imperforate or present a very low number of pores per unit area of the shell's surface (Hottinger, 1977a). The inner surface of the wall supporting papillae is evenly covered by pore mouths and the corresponding eggholders housing the symbionts. Towards the outer wall surface, groups of parallel pores are deviated from their perpendicularly to the wall directed path and spread out leaving between them a conical, imperforate space where the subsequent lamellae are thickened (Figs. 4D, 6C and D). The distribution of the pores, their diameter and their density per unit area of the
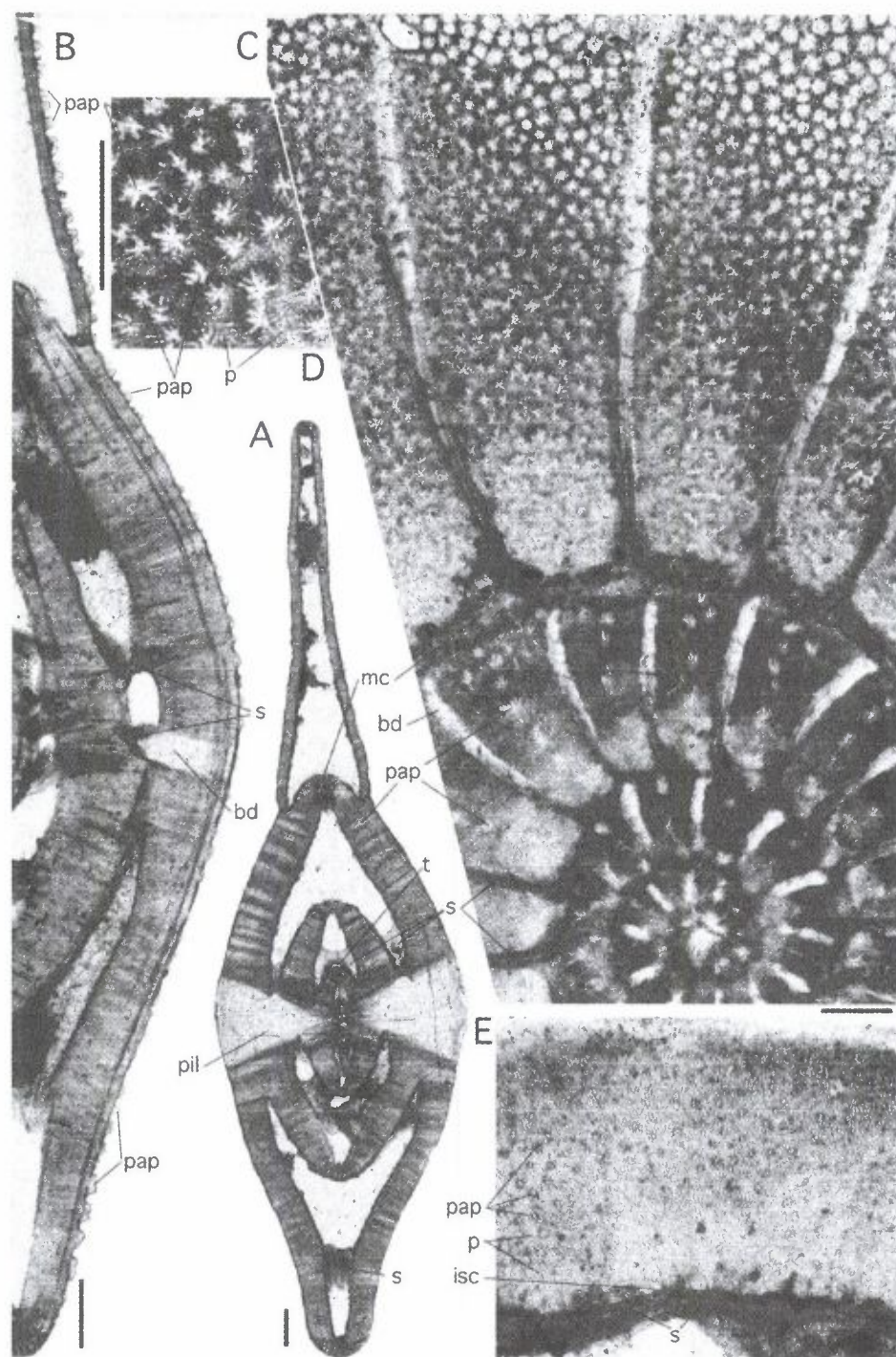

Figure 6. Small, dense papillae on lateral shell walls of *Assilina madagascariensis* from the lower end of the photic zone. Mauritius, Indian Ocean. Recent. transmitted light micrographs. Scale bars 0.05 mm. A: axial section. B: detail of axial section showing minute papillae on perforate chamber walls. C: tangential section running within perforate lateral chamber walls. D: detail of C showing stellar pattern of outspread pores below papilla. E: tangential section through inner part of perforate wall where spreading of pores start. At this level the papillae appear indistinctly. bd: beads; isc: intrasetal canal system; mc: marginal cord; p: pore; pap: papilla; pil: pile (of lamellae); s: septum.

wall is determined by the properties of the organic template, the median layer in bilamellar shells, governing the biomineralisation process. From the organic template, cylindrical organic sheets rise in proximal and distal directions and delimit the mineralisation process suppressing any growth of crystals in the pore tube. From the original outer lamella to the subsequent ones, the diameter of the pore is blueprinted by the organic pore coat with considerable precision, creating at each boundary beween successive outer lamellas a so-called interlamellar disc (Leutenegger, 1977b). A deviation from the parallel path perpendicular to the wall surface must be due to a gradual displacement of successive interlamellar discs with respect to the pore axis. This displacement is organized and forms patterns. The bending of pore axes may produce an inclination of the originally parallel planes in successive interlamellar discs which, in their turn, might generate and/or govern the local thickening of the lamellas to form papillae. The patterns produced by the distribution of pores obviously are fixed by the genome of the foraminifer because they are part of the taxonomic diagnoses at least on the specific if not on higher levels. The quantitative aspect however, i.e. the diameter and/or height of the papillae for instance, may be influenced by ecological factors. For this reason, some new investigations on the taxonomy of recent *Assilina* for instance are urgent.
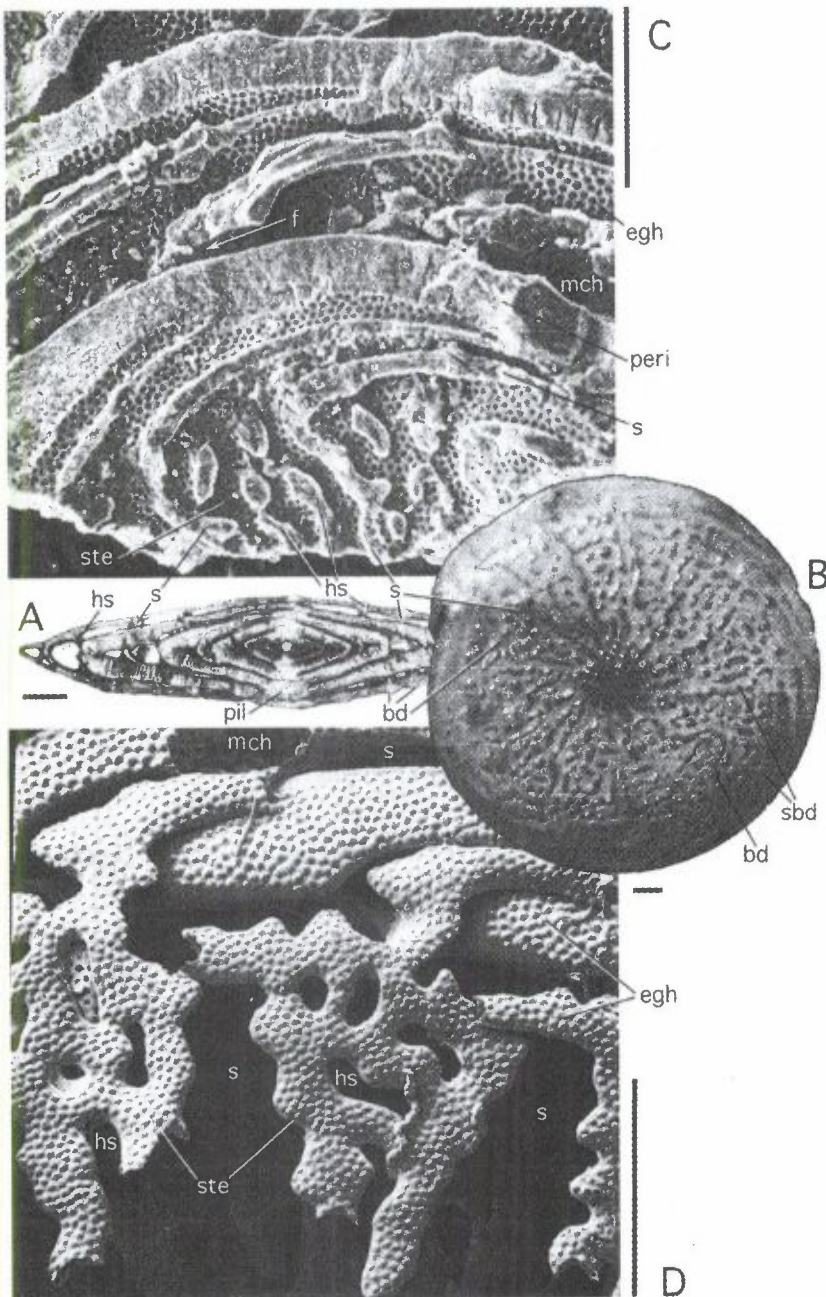

Figure 7. Beading in *Amphistegina papillosa* from the lower photic zone in the Gulf of Aqaba, Red Sea. Recent. Scale bars 0.1 mm. A: Axial section, transmitted light micrograph. B: Lateral ventral view of shell surface showing beads in between septa and revealing the position of short hemiseptula partially subdividing the stellar chamberlets. Note also the small aperture in almost peripheral position. Incident light micrograph. C: Shell fragment showing internal surface covered by eggholders of the stellar chamberlets and their subdivision by hemiseptula. SEM image. D: epoxy resin cast of a stellar chamberlet's cavity partially subdivided by short hemiseptula supporting interseptal beads. SEM image. bd: interseptal beading; egh: eggholders housing the symbionts; f: foramen; mch: main chamber lumen; hs: hemiseptulum; peri: periphery of whorl; pil: pile of lamellae; s: septum; sbd: septal beading; ste: stellar chamberlet.

The beads are located at the boundary between the perforate, lateral and the imperforate, septal walls, usually linked to a sharp bending of the wall. No details are known about the distribution of pores along imperforate sutures and their relation to beading or continuous imperforate bands along the suture (raised sutures as in *Challengerella bradyi* for instance). However, their position over sharp bends of the wall suggests there also a spreading of the pores along the margin of the lateral chamber wall to be connected with a thickening of the outer lamellas. Their position at the chamber margin in evolute shells of *Assilina* (Fig. 4A) or *Heterocyclina tuberculata* (Fig. 5A) hints that the beads are probably unrelated to light collecting because there are no chamber cavities bearing symbionts below them.

The piles are rooted on surfaces of the shell with scarce or no perforation, such as proloculus walls, umbilical chamber tips (folia for instance) or imperforate margins of early whorls (marginal cords in nummulitids or peripheral walls in orbitoid foraminifera). In orthophragminids, the piles may take their origin on top of regular papillae or of beads by blueprinting the thickening over several successive layers of lateral chamberlets.

The lamellar perforate shell consists of low-magnesium-calcite crystals forming uniform stacks of twinned platelets. Their C-axis is radial, perpendicular in respect to the shell surface, as revealed by the cross of interference seen in sections of papillae perpendicular to the papillar axis (Towe and Cifelli, 1967; Ferrandez, 1999). Thus, papillae, beads and piles behave like glass, where the index of refraction and the shape of the glass lens determine the path of light through the crystalline shell. However, neither the impact of the numerous pore tubes surrounding the imperforate cones nor the orientation of the small crystals in between pores on the path of light through the biomineralized wall has ever been studied yet. The inclination of the polygonal eggholder walls may also play a role in directing light on the symbiont in the eggholder. The pores of living foraminifera are filled with a structureless gel very rich in water.

The organic structures seen in TEM graphs filling the pores most probably are an artefact of the fixation process denaturing the proteins in the gel (Leutenegger, 1977b). We may consider the refraction index between the calcite crystals and the pore tubes to have approximately the same value as between the calcite and the seawater of the ambient environment of the shell. Therefore, the geometry of the paths of light through the shell get so complicated that a theoretical approach seems to be difficult and might be better replaced by direct optical experiments on shell fragments immerged in seawater and exposed to to light that is scattered or tangentially directed to the wall surface.

5. Estimation of Loss of Light by Total Reflection

Under the conditions of totally scattered light in the foraminiferan's environment (and neglecting backscattering from the substrate), we may consider the relative sum of light irradiating a single point on a plane surface as the surface of a hemisphere. As the refractive index between the two media involved, seawater and calcite, is <1, total reflection takes place for all incident rays irradiating that point between the critical angle of 64° and 90°in respect to the axis of the hemisphere. Therefore, we estimate the loss of light by total reflection at a single point relative to the total amount of irradiation at this point as follows. The relative amount of light that would be reflected is equivalent to the surface area ΔA relative to the total surface area of the hemisphere (Fig. 8A). The surface area of a hemisphere with a radius r = 1 is $2\pi r^2 = 2\pi = 6.28$ (since r = 1).

The surface area of a dome with the height h cut off from this hemisphere is $2\pi rh$, where r = 1 and $h = 1 - \sin26° = 1 - 0.438 = 0.562$. The surface area of the dome is therefore $2\pi \cdot 0.562 = 3.53$.

ΔA, the difference between the surface area of the hemisphere and the one of its calotte is therfore $6.28 - 3.53 = 2.75$. This is 43.8% of the hemisphere surface area. Thus, almost half of the incident diffused light is reflected at each point of a plane surface of the shell.
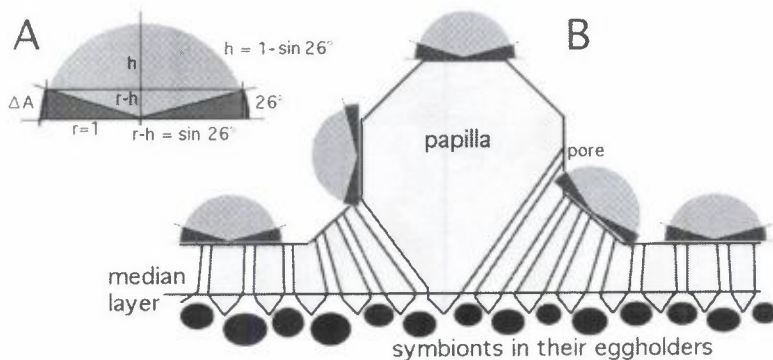

Figure 8. A: Hemisphere symbolizing the amount of totally diffuse light incident from all directions on a single point with equal intensity. The surface ΔA, delimited by the critical angle of total reflection, indicates the relative quantity of loss of light at a particular point of the irradiated surface. B: Basic geometry of shell surface sculptured by papillae and relative position of symbionts in their eggholders below the inner surface of the perforate chamber wall. Two-dimensional cartoon simplifying a three-dimensional problem, not to scale.

In Fig. 8B the geometrical relationships between different points in a sculptured shell surface are schematically sketched out: on the top of a papilla, the amount of reflected light would be totally lost. On a surface perpendicular to the chamber wall, more than half of the reflected light would be lost but a still sizable amount of reflected light is recaptured by the shell. In the depressions between the papillae, the total amount of reflected light is recaptured. The sum of losses by total reflection over the entire lateral chamber surface depends on number, sizes and shapes of the papillae and can't be calculated here in detail. However, the considerations developed here seem to indicate that the sculpture on the chamber surface appearing in deeper habitats reduces total reflection to considerable amounts and therefore may help to collect light at the lower limits of the photic zone.

The pathways of the light rays within the calcite crystals of the wall are too complicated to calculate because they are refracted at the numerous tubular pore walls in complicated ways. Interpreting the papillae as lenses concentrating the light on restricted areas of the inner surface of the shell wall wouldn't make much sense any way, since the symbionts are distributed evenly in their eggholders over the whole inner surface of the perforate lateral chamber wall.

6. Conclusions

- Considering the high degree of scattering characterizing the diffuse light irradiating a discoidal or lenticular shell in lower parts of the photic zone of the sea, the inclination of a disc towards the horizon of its substrate can not have sizeable effects on the quantity of light irradiating its exposed surface.
- Three kinds of sculptured elements are to be distinguished: papillae on lateral walls, beads on septa, septular or hemiseptular sutures, and piles of lamellae accumulated during consecutive whorls or lateral chamberlet layers by a blueprinting process.
- The three kinds of ornamentation are linked to a corresponding local spreading of the pores in the subsequent outer lamellas, whereas on the inner surface of the wall the eggholders housing the symbionts are evenly distributed over the whole surface.
- Only the papillae are positioned over the symbionts in their eggholders. Their interpretation as light lenses concentrating irradiation in points below them does not make much sense since the symbionts are distributed evenly over the total inner surface of the lateral chamber wall.
- According to the indices of refraction of the media involved, seawater and calcite, all rays incident on the seawater-calcite interface at angles between the critical angle of 64° and the horizon, i.e. over an arc of 26°, are totally reflected, a loss for the symbionts.

- The relative amount of totally reflected light is calculated as the difference in surface between a hemisphere and a dome delimited by the track on the hemisphere's surface by a radius rotating around the hemisphere's axis under an angle of 64°. The amount of this difference is 43.7%, almost half of the hemisphere's total surface.
- The relief on the wall surface reduces the amount of total reflection to considerable amounts. A calculation of these reductions has not been attempted yet because many quantitative data on number, shape and densities of papillae are missing.
- The observations and considerations resumed above indicate a function of at least the papillae as reducers of total reflection, thus not as light lenses but as light trap. They warrant the design of optical experiments with shells in seawater combined with additional investigations of pore distribution in shells with smooth surfaces from shallow water.

Acknowledgements

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