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On the taxonomic value of the wall structure of *Quinqueloculina*

ABSTRACT

Scanning electron microscope investigation of the walls of different species of the foraminiferal genus *Quinqueloculina* revealed in all cases a three-layered internal structure with a thick central layer consisting of a three-dimensional random array of calcite needles that has a high permeability. The different patterns of crystal arrangement in the thin inner and outer layers are regarded as important for the taxonomy of this genus.

INTRODUCTION

The surface of the porcellaneous wall of *Quinqueloculina*, as described by early students of foraminifera (e. g., d'Orbigny, 1826–1846), shows differences which were used for the first time by Wiesner (1912, 1920) for the classification of this genus. Inspired by this last author, Cherif (1973) divided Recent quinqueloculines into groups of species where each group is considered to be a natural taxon. The surface lustre of the test is one of the most important taxonomic characters for the definition of these groups. Two main types of tests are recognisable, 1) smooth and highly brilliant tests and 2) rough and partly agglutinated tests with a greasy lustre.

The advent of electron microscopy, especially scanning electron microscopy, allows the recognition of three layers in the walls of quinqueloculines (Hemleben, 1969; Haake, 1971). The middle one, constituting the bulk of the test material, is a three-dimensional random array of calcite needles. The outer layer is a smooth, thin veneer of oriented, more or less elongate crystals covering the highly brilliant forms.

In the case of non-brilliant, partly agglutinated tests, this layer is, according to Haake (1971), replaced by a veneer showing a "cobble" pattern. The species observed here, however, possess a roughly wrinkled, unevenly developed outer layer. There seems to be no pattern of crystal arrangement.

Generally, the inner wall of the chambers is coated with a two-dimensional random array of calcite needles.

This paper presents further details on the wall structure of the genus *Quinqueloculina* with an attempt to evaluate the observed features for taxonomy.

TAXONOMIC UNITS STUDIED

The fauna studied was obtained from the samples of Cherif (1973), who divided 62 species of Recent *Quinqueloculina* from the west coast of the Aegean island of Naxos (Greece) into 9 groups of species. In addition to the external appearance of the wall, morphological aspects of the aperture and of the tooth were used for differentiation.

The examined species, regarded as representative of the groups of species to which they belong, and these groups themselves are as follows:

1. Group of *Quinqueloculina triangularis* d'Orbigny: *Q. triangularis* d'Orbigny (= *Q. seminulum* (Linné) of various authors).
2. Group of *Quinqueloculina bicornis* (Walker and Jacob): *Q. planciana* d'Orbigny, *Q. angusteoralis* (Wiesner).
3. Group of *Quinqueloculina rotunda* (d'Orbigny): *Q. inflata* (d'Orbigny).
4. Group of *Quinqueloculina laevigata* (d'Orbigny): *Q. laevigata* (d'Orbigny).
5. Group of *Quinqueloculina disparilis* d'Orbigny: *Q. ludwigi* Reuss.
6. Group of *Quinqueloculina schreibersii* d'Orbigny: *Q. schreibersii* d'Orbigny.
7. Group of *Quinqueloculina flavescens* d'Orbigny: *Q. auberiana* d'Orbigny.
8. Group of *Quinqueloculina aspera* d'Orbigny: *Q. aspera* d'Orbigny; *Q. irregularis* d'Orbigny; *Q. lapidea* Cherif.
9. Group of *Quinqueloculina costata* d'Orbigny: *Q. anguina* Terquem; *Q. costata* d'Orbigny.

The material of this study is deposited in the "Stereoscan Collection" of the Department of Geology at Göttingen University, West Germany (No. Cl₁, 712, 715, 716, 717).

PREPARATION OF SAMPLES

Fresh specimens were chosen for observation. For each species, we tried to obtain an equatorial section by using a normal razor blade to cut the tests. Most of the species gave good results, and well-oriented equatorial sections could be prepared, but individuals belonging to the groups of *Q. rotunda*, *Q. laevigata* and *Q. disparilis* were relatively difficult to cut properly because of their thin walls. Conversely, specimens belonging to the group of *Q. flavescens* gave bad results due to their strong, thick walls.

The foraminifera were mounted on specimen holders using double adhesive tape or electrically conductive glues. Certain tests were slightly etched with dilute acetic acid to show the relation between the outer and inner layers. All specimens were coated with gold-palladium alloy.

WALL STRUCTURES

The groups of *Quinqueloculina triangularis* and *Q. rotunda* have a thin veneer with a wrinkled surface covering the three-dimensional random array of calcite needles (plate 1, figures 2, 9). A detailed observation of the outer surface shows occasionally a "brick" pattern (plate 1, figure 3), but generally only tiny wrinkles parallel to the longitudinal axis of the test are observed.

The group of *Quinqueloculina bicornis* (Walker and Jacob) has a strongly developed outer layer displaying a "tile roof" pattern, giving the impression of wrinkles parallel to the longitudinal axis of the test (plate 1, figures 11–12). The single plates of these wrinkles are, however, characteristically imbricated and more strongly developed than in *Q. triangularis*. In case of extreme development of these wrinkles, the species may appear longitudinally striate (plate 1, figure 13). Pores are often observed between the different plates of the outer structure of the test (plate 1, figure 14). Reticulate species of this group show a thick compact outer surface (plate 1, figures 5–7) without recognisable pattern, even under high magnifications.

The group of *Quinqueloculina laevigata* (d'Orbigny) shows a smooth surface. In the observed specimens the outer layer is thin, covers the test incompletely (plate 2, figure 2), and consists of rather quadratic calcite crystals (plate 2, figure 3). It shows a structure similar to that of the "mosaic" pattern described by Haake (1971). The wrinkled, rather smooth internal layer of the chamber could be well observed in this group (plate 2, figures 4–5).

The group of *Quinqueloculina disparilis* d'Orbigny has a thin, particularly smooth outer veneer consisting of crystals showing a "parquet" pattern in some places (plate 2, figure 11).

The group of *Quinqueloculina schreibersii* d'Orbigny has a particularly thick layer of calcite plates on the costae (thick striations), with a regular arrangement. Between these costae, however, the three-dimensional random array of calcite needles appears gradually and remains mainly uncovered (plate 2, figure 7).

The group of *Quinqueloculina flavescens* d'Orbigny shows a thin outer veneer with a very finely wrinkled surface, where the crystalline plates are arranged in a rather flush "tile roof" pattern (plate 2, figure 9).

The group of *Quinqueloculina aspera* d'Orbigny has a rugged surface consisting of a discontinuous outer layer with relatively large and thick irregular crystal plates (plate 3, figure 3). This rather thick layer overlies incompletely the three-dimensional array of calcite needles. It has been noticed in this case that the wall of the proloculum of *Q. aspera* is composed of a three-dimensional array of calcite needles (plate 3, figure 5). This suggests that the structure is present throughout the whole ontogeny of the quinqueloculines.

Quinqueloculina lapidea agglutinates relatively thick sand grains in an outer layer otherwise similar to that of *Q. aspera* (plate 3, figures 10–11).

In the whole group of *Q. aspera* the interior of the chamber wall is formed by a two-dimensional array of calcite needles (plate 3, figure 7).

The group of *Quinqueloculina costata* d'Orbigny has a thick surficial layer. In *Q. anguina*, it shows an irregular surface (plate 3, figure 13). In *Q. costata*, this layer is only developed on the costae. Between the costae, the three-dimensional array of calcite needles is apparent on the surface (plate 3, figure 15). The surface of the tests in this group differs from that of the individuals of the group of *Q. schreibersii* through the mode of structural arrangement of the outer layer, which is relatively compact as in all species with rough surfaces and greasy lustre.

CALCIFICATION PROCESS IN FORAMINIFERA

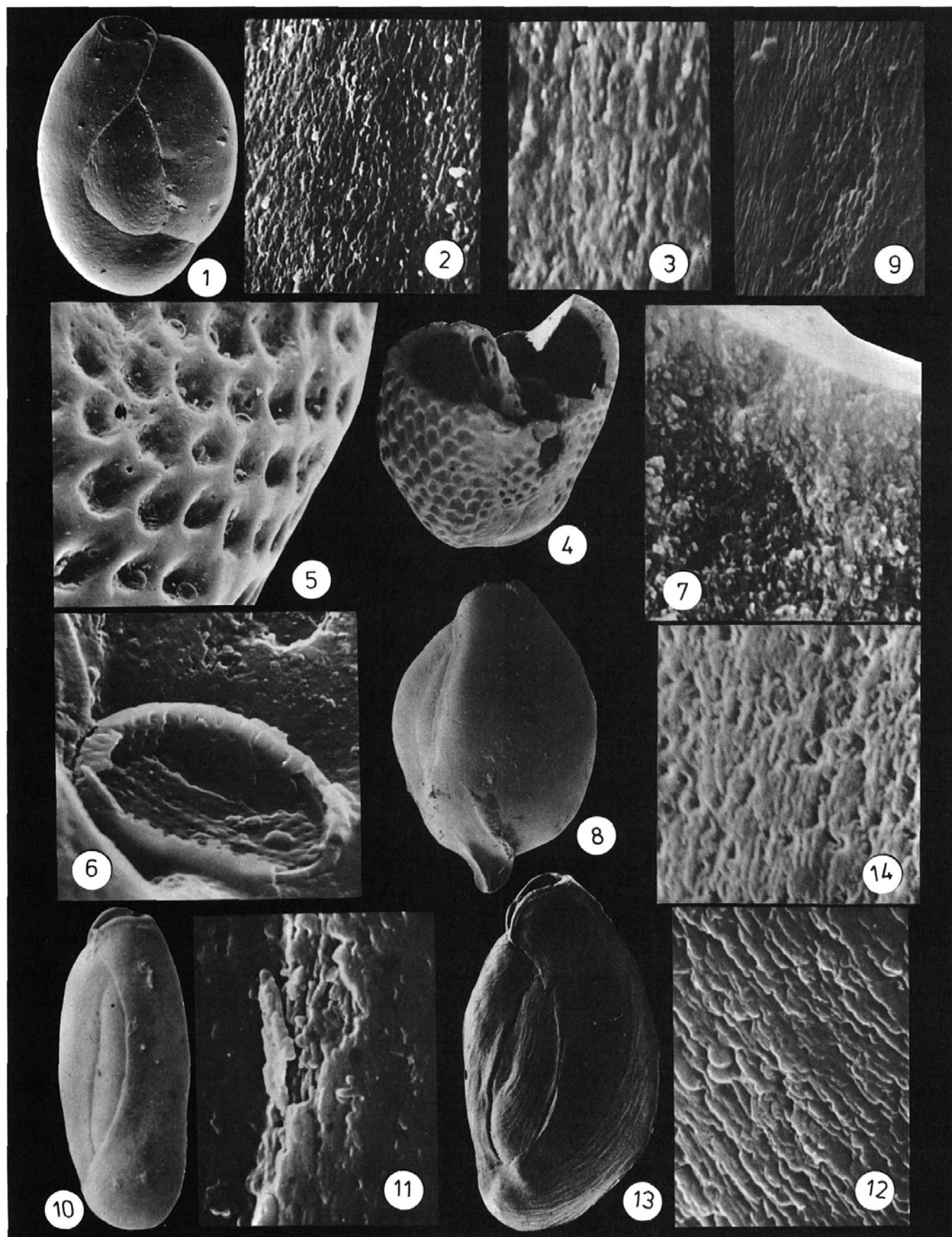
The three-dimensional disorder of the calcite needles in the walls of the Miliolidae is an exceptional structure in organisms, inasmuch as in normal biological calcification the calcite grains or crystals are usually in some degree oriented (Towe and Cifelli, 1967). This may be seen in the normal hyaline foraminiferal wall, where the individual crystals show a uniform crystallographic orientation, in spite of their anhedral shape in many cases. Usually, shell growth in organisms occurs through epitaxial calcification on an organic matrix. In foraminifera, this organic matrix is secreted by uniquely functioning organelles and consists of two different materials, one active and the

other passive (Towe and Cifelli, 1967). The first one is probably a protein, a polypeptide, and the second a polysaccharide (Moss, 1964). The particular steric configuration of the active polypeptide chain is such that it is related to the crystal structure of calcite. This type of growth leads normally to the formation of a relatively compact, impermeable wall. The distribution of the active substance in the organic matrix must allow for the formation of numerous pores in the secreted inorganic wall, to permit metabolic exchanges with the exterior.

In the case of the Miliolidae, the formation of these pores is not necessary because of the highly permeable nature of the secreted wall. This unusual structure became apparent when etching some tests with dilute acetic acid. The acid drop was rapidly absorbed in the interior of the test. The random array of the calcite needles constituting the bulk of the miliolid wall is probably responsible for the high permeability. The secretion of the miliolid wall can not be explained by epitaxial mineralisation on a spatially regular organic template, but instead is thought to be possibly caused by heterogeneous nucleation of calcite induced by the presence of an active but structurally incoherent or colloid organic material (Towe and Cifelli, 1967). Here it is to be noticed that the molecules of the active organic substance must attain a certain degree of organised distribution, in order to produce a wall possessing the needed permeability. Absolute disorganisation, or perhaps greater concentration of molecules of the active organic substance could be only assumed in cases where the outer layer of the miliolid wall shows a very

PLATE 1

- 1–3 *Quinqueloculina triangularis* d'Orbigny
Hypotype (no. 712); 1, general view, x 90; 2, surface with wrinkles, x 7200; 3, surface detail showing "brick" pattern, x 12600.
- 4–7 *Quinqueloculina reticulata* (d'Orbigny)
Hypotype (no. 712); 4, general view of a cut test, x 90; 5, reticulation with diatoms, x 360; 6, diatom lying in a mesh of the reticulation, x 4950; 7, section of the wall showing the upper middle layer, x 1440.
- 8–9 *Quinqueloculina inflata* (d'Orbigny)
Hypotype (no. 712); 8, general view, x 90; 9, surface showing wrinkles, x 6750.
- 10–12 *Quinqueloculina angusteoralis* (Wiesner)
Hypotype (no. 716); 10, general view, x 90; 11, detail of surface, x 6750; 12, surface showing "tile roof" pattern, x 6750.
- 13–14 *Quinqueloculina planciana* d'Orbigny
Hypotype (no. Cl₁); 13, general view, x 126; 14, surface with "tile roof" pattern and pores, x 36000.



fine or complete lack of crystalline structure, as in the outer layer of *Q. reticulata* (plate 1, figure 7) or of different rough, partly agglutinated species (plate 3, figures 3, 11, 13, 15). The outer layer of the highly brilliant miliolid wall attains, as already mentioned, some degree of preferred crystallographic orientation. This layer could be formed by epitaxial mineralisation induced by the existence of specially arranged active organic molecules. These molecules should be only present in the outer organic membrane covering the normal wall of the animal. Evidence on the existence of such a membrane is given by Haake (1971) and in the present work (plate 2, figure 12).

In the group of *Q. bicornis*, the upper lamellar (or crystallographically oriented) layer is too thick to allow metabolic exchanges with the exterior. In some specimens of *Q. planiciana*, additional pores must be developed in this layer to increase the permeability of the wall (plate 1, figure 14). In other species, the tile roof arrangement of the crystals of the outer layer may also increase porosity and facilitate metabolic exchange, as in *Q. angusteoralis* (plate 1, figure 12).

The compact outer surface of the reticulate species of this group attains the needed permeability through development of reticulation. The depressed zones of the reticulation system display high permeability, probably because of the very thin outer veneer in these regions, in which the pseudopodia seem to arise. This is strongly suggested by the accumulation of diatom debris in these places (plate 1, figures 5–6). The diatoms are the remains of food material captured by the pseudopodia and carried near the cell surface of the organism for digestion in the depressed zones.

CONCLUSIONS

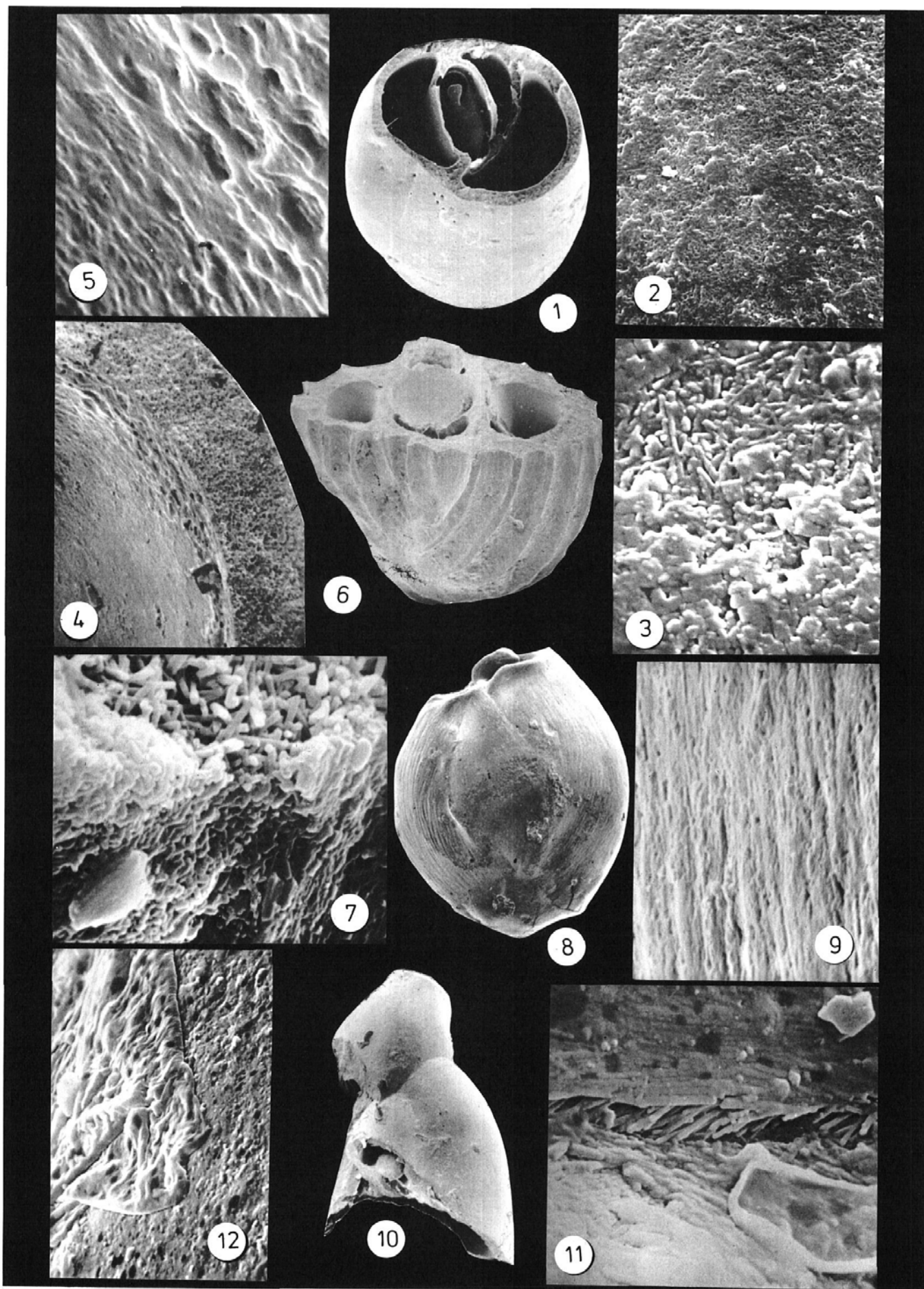
This study shows that the wall of the miliolid *Quinqueloculina* possesses a constant structural character in all species and groups of species, namely, a random, three-dimensional array of calcite needles having a very high permeability (plate 1, figure 7; plate 2, figures 3, 7; plate 3, figures 1, 5, 7, 9, 14). Differences are observed only in the outer and inner surfaces of the chambers, these differences characterising major groups of species. Smooth and brilliant tests have a well-developed outer layer of lamellar crystals, probably the last crystals to be formed (Lynts and Pfister, 1967). These crystals may exhibit different patterns, for which the terms "brick" (plate 1, figure 3), "tile roof" (plate 1, figures 12, 14), "mosaic" (plate 2, figure 3) and "parquet" (plate 2, figure 11) are currently used. According to the present observations, each type of pattern characterises a given group of species. Different patterns were never seen in a single group. This suggests that the crystal arrangement of the outer veneer in the miliolid wall has a genetic origin. Lynts and Pfister (1967) attempted to differentiate several miliolid tests on the basis of the length/width ratio of the calcite rhombs.

The physiological aspects of calcification in foraminifera, including the Miliolidae, as conceived by Towe and Cifelli (1967) indicate that the mode of crystal arrangement depends on the existence of a given type of organisation (or disorganisation) of organic molecules secreted by the protoplasm. It seems very improbable that such a process could be influenced by external, ecologic factors.

Rough tests with greasy lustre also possess an outer layer. They have, however, no recognisable crystal-

PLATE 2

- 1–5 *Quinqueloculina laevigata* (d'Orbigny)
Hypotype (no. 716); 1, general view of a cut test, x 144; 2, surface showing irregular distribution of the outer veneer, x 1260; 3, detail of surface with "mosaic" pattern covering the three-dimensional array of calcite needles, x 6750; 4, section of the wall showing the internal layer, x 1080; 5, detail of the surface of the internal layer, x 6750.
- 6–7 *Quinqueloculina schreibersii* d'Orbigny
Hypotypes (nos. 715, 716); 6, general view of cut specimen, x 144; 7, detail of wall surface also showing in section the three-dimensional random array of calcite needles, x 7200.
- 8–9 *Quinqueloculina auberiana* d'Orbigny
Hypotype (no. 716); 8, general view, x 54; 9, detail of the surface showing wrinkles, x 6300.
- 10–12 *Quinqueloculina ludwigi* Reuss
Hypotype (no. 716); 10, general view of cut specimen, x 117; 11, detail of the surface showing "parquet" pattern, x 6300; 12, detail of the surface showing an outer organic? membrane, x 3420.



line pattern arrangement and show relatively coarse calcite crystals (plate 3, figure 3). This outer layer is often interrupted by irregularly distributed patches showing the underlying three-dimensional random array of calcite needles (plate 3, figures 3, 13). Whether quinqueloculine tests have a brilliant or greasy lustre may be due to the mode of calcification of their outer walls. Brilliant tests have an outer veneer of oriented calcite crystals, which are probably formed through epitaxial calcification. Rough forms belonging to the category of brilliant tests (mainly identified after outer morphologic characters; see Cherif, 1973) show an incomplete covering of such oriented calcite crystals, which may be the result of abrasion. In some cases, this outer covering may be completely lacking, and these forms will then exhibit a more or less "dull" or "resinous" lustre. Rough and partly agglutinated forms have an outer layer deposited through the action of structurally incoherent or colloidal organic material.

The inner wall of the chambers of brilliant forms is covered in most observed cases by a thin layer of lamellar calcite (plate 2, figure 4). Rough tests, on the other hand, have shown an inner chamber wall covered by a two-dimensional array of calcite needles (plate 3, figure 7).

The classification introduced by Cherif (1973) is supported by the present examination of the wall structures of *Quinqueloculina*.

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PLATE 3

- 1 *Quinqueloculina ludwigi* Reuss
Hypotype (no. 716); 1, section in the wall showing the upper and middle layer, x 6300.
- 2–5 *Quinqueloculina aspera* d'Orbigny
Hypotype (no. 715); 2, general view, x 63; 3, surface showing interrupted outer layer, x 720; 4, equatorial section, x 108; 5, section in wall of proloculum showing a three-dimensional random array of calcite needles, x 6750.
- 6–7 *Quinqueloculina irregularis* d'Orbigny
Hypotype (no. 717); 6, general view of a cut test, x 103.5; 7, surface showing the inner wall surface with two-dimensional array of calcite needles, x 6660.
- 8–11 *Quinqueloculina lapidea* Cherif
Hypotype (no. 715); 8, general view, x 67.5; 9, equatorial section, x 108; 10, detail of outer surface showing agglutinated grains, x 324; 11, detail of section in the wall showing the thick outer layer, x 1350.
- 12–13 *Quinqueloculina anguina* Terquem
Hypotype (no. Cl₁); 2, general view, x 765.9; 13, detail of the surface, x 648.
- 14–15 *Quinqueloculina costata* d'Orbigny
Hypotype (nos. 717, Cl₁); 14, general view, x 72; 15, detail of the surface, x 1890.

