

# *Carterina*: its morphology, structure and taxonomic position

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Hansen, H. J. & Grønlund, H.: *Carterina*: its morphology, structure and taxonomic position. *Bull. geol. Soc. Denmark*, vol. 26, pp. 147–154, Copenhagen, August 2nd, 1977.  
<https://doi.org/10.37570/bgscd-1977-26-11>

The external and internal morphology of *Carterina spiculotesta* is described and illustrated. Sections and decalcified preparations demonstrate that the spicules composing the wall have a concentric layering. There is, moreover, a 0.1–0.2  $\mu\text{m}$  sub-layering at right angles to the long axis of the spicules. The inner organic chamber lining is different from the organic matrix in being laminated and more compact. There are no pores in the shell. It is concluded that the spicules most likely are secreted by the animal. It is suggested that *Carterina* should be transferred to the Textulariina and that the 'allochthonous' spicules ('allochthonous' relative to their final position in the wall) must be regarded as distinct from the 'autochthonous' material in the walls of Miliolina and Rotaliina.

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Ever since Carter described this species in 1877 its systematic relationships have been somewhat uncertain.

Cushman (1948) placed it in the family Trochamminidae and described its wall as being made of 'cement in which are thin, translucent, fusiform bodies'. In this systematic designation Cushman followed Flint (1899) and Galloway (1933). Loeblich & Tappan (1964, 1974) placed this monotypic genus in a separate superfamily in the suborder Rotaliina.

This position would seem somewhat enigmatic, since the suborder Rotaliina encompasses forms with 'wall calcareous, perforate'. To the knowledge of the present authors no light microscope study has ever demonstrated pores in the shell of *Carterina*. Scanning electron micrographs of the shell surface (Deutsch & Lipps 1976) demonstrated that no external openings for pore tubules were present.

The present investigation is devoted to a closer examination of the characters of the test of *Carterina* and a discussion of its taxonomic position.

## Material and methods

This species appears to be rather rare and despite repeated calls to numerous colleagues in different countries for specimens, none were re-

ceived. During a routine search in one of the samples from the 'Nørvang collection' (now transferred to our laboratory) three specimens were discovered in a sample from a depth of 20 m from the island of Wailing Banda, collected by the late Dr. Th. Mortensen during an expedition to the Kei Islands.

The specimens have undergone different preparational procedures in order to give information regarding morphology, ultrastructure of the wall and optical orientation of the spicules.

Intact specimens were mounted on SEM stubs by the aid of double adhesive tape for examination of the external morphology. Subsequently the test was embedded in Lakeside 70, ground to the desired level, polished, and etched in EDTA (see e. g. Grønlund & Hansen 1976). The ultrastructure of the spicules was studied in this preparation. Finally the embedding medium was dissolved in ethanol in order to reveal the internal morphology. Part of the shell was crushed and placed between crossed nicols under the light microscope.

Half a specimen was decalcified, followed by fixation for one hour in 1%  $\text{OsO}_4$  buffered to pH 7.2. For decalcification an aqueous semisaturated solution of EDTA buffered to pH 7.0 was used. The decalcified residue was dehydrated and embedded in Epon 812 following commonly used techniques. For light microscopy 2  $\mu\text{m}$  sections were cut using glass knives while ultrasections

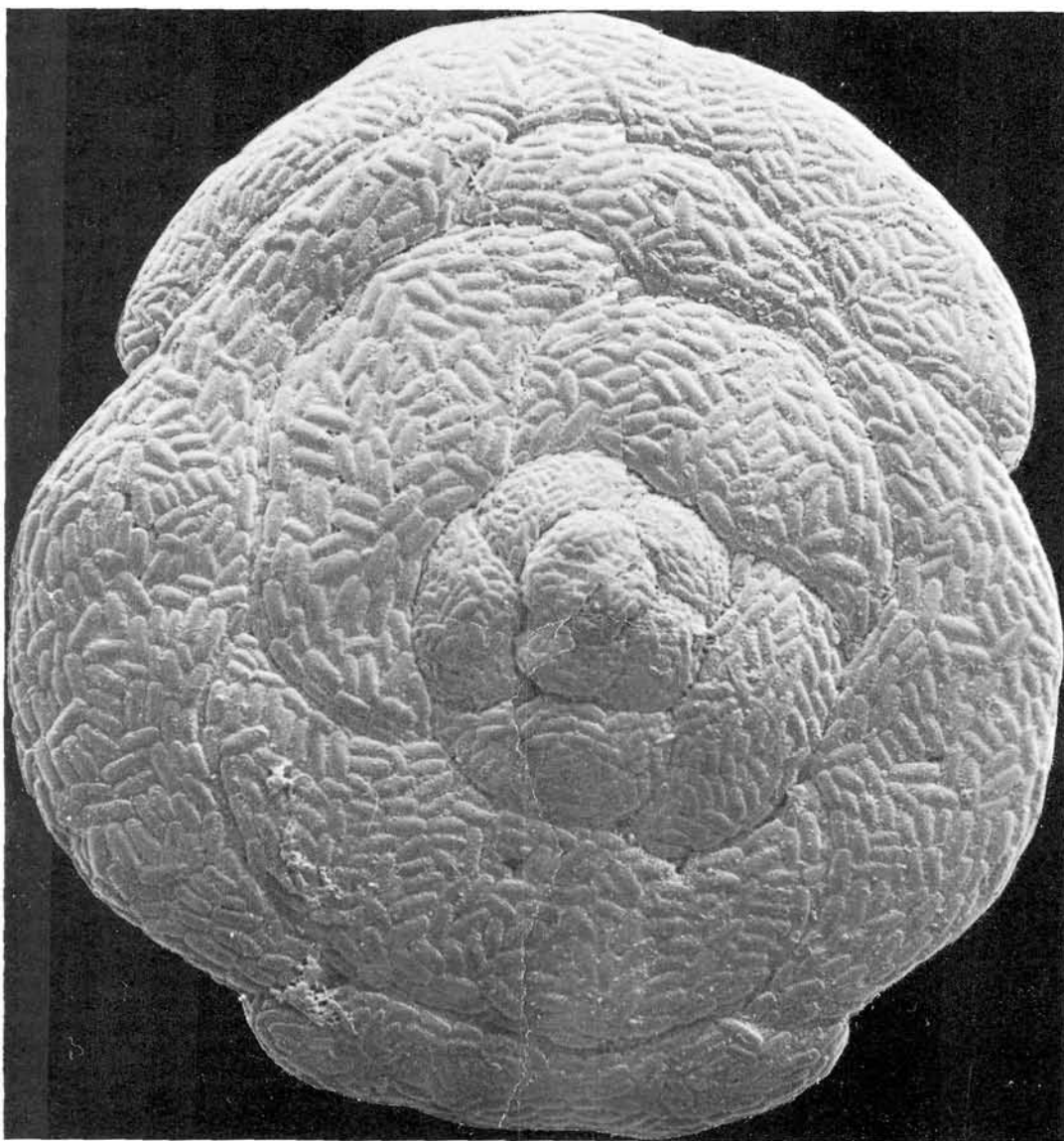


Fig. 1. *Carterina spiculotesta* (Carter, 1877). Spiral view (composite SE micrograph). Note the increase in size of spicules from the earlier to the later chambers;  $\times 300$ .

for study in the TEM were cut using an LKB ultramicrotome III.

The specimens were studied in a Cambridge Stereoscan MK IIa scanning electron microscope and in a Hitachi HU 11 C transmission electron microscope both housed in the Laboratory of Electron Microscopy, Geological Institute, University of Copenhagen.

The shell mineralogy was determined by X-ray diffraction of one specimen mounted on a glass needle by cellulose glue. It was irradiated by Cu  $\alpha$  radiation in a Gandolfi camera for 20 hours.

Species belonging to the genera *Textularia* and *Quinqueloculina* were studied for comparison. *Textularia* sp. was collected in the Gulf of Elat

by the senior author. *Quinqueloculina* sp. originates from Brønlund Fjord, Greenland; collector Jean Just.

The Geological Institute, University of Copenhagen, is thanked for permission to use the facilities of the above mentioned laboratory.

## Observations

The test is a low trochospiral coil in the earlier part, while the later part develops an irregular growth pattern (figs 1 & 2) being slightly reminiscent of an annular growth pattern. After about two coils the chambers are subdivided by secondary septa the number of which increases with chamber size (fig. 3).

The apertures of the final and previous chambers remain open into the umbilical area (fig. 4).

The wall is composed of spicules of calcite (determined by X-ray diffraction). No reflection besides that characteristic of calcite was detected. The spicules are generally rounded rectangular (fig. 5). Passing from the earlier towards the later part of the shell there is a distinct size increase in the surface spicules (namely from about 8  $\mu\text{m}$  to about 22  $\mu\text{m}$  in length; fig. 1). The spaces between these are filled in by still smaller spicules having sizes around 1–2  $\mu\text{m}$ . However, the sizes here reported are characteristic for the surface layer only, since the wall below the surface contains a variety of spicule sizes that are in gen-

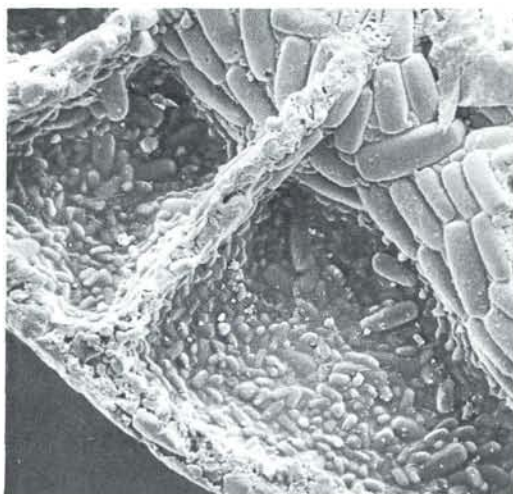


Fig. 3. Detail of 'half section' of specimen shown in fig. 1. Note the difference in size of spicules between outer surface (upper part of the micrograph) and inner surface (lower part of micrograph) as well as presence of two secondary septa;  $\times 615$ .

eral smaller than the surface ones (figs 3 & 6).

The observation by Deutsch & Lipps (1976) that in cross section the spiral wall has two layers of spicules each oriented at different angles was not observed in our specimens.

Polished and etched sections of the spicules demonstrated that they are constructed of concentric layers of calcite (fig. 7). In addition to the

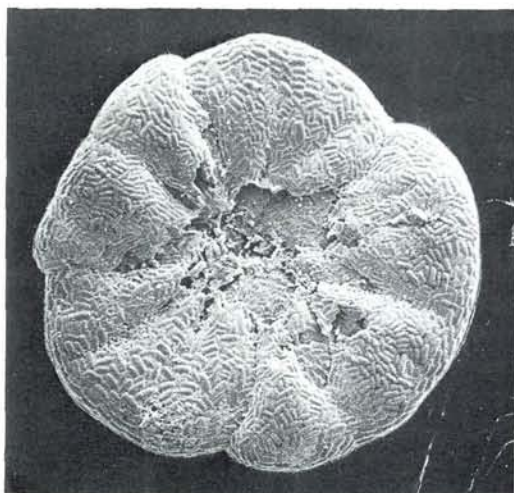


Fig. 2. Umbilical view of specimen shown in fig. 1;  $\times 125$ .

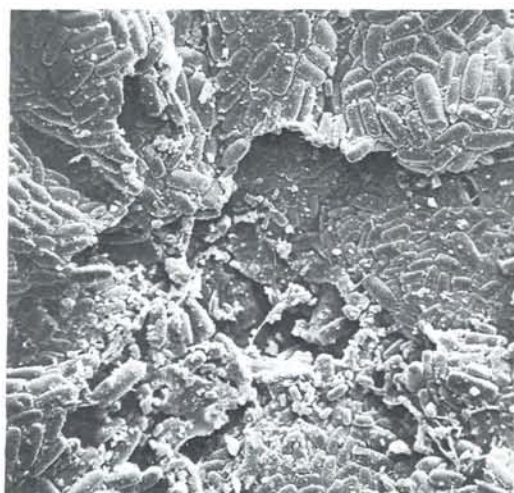


Fig. 4. Detail of fig. 2 showing umbilical apertures;  $\times 410$ .



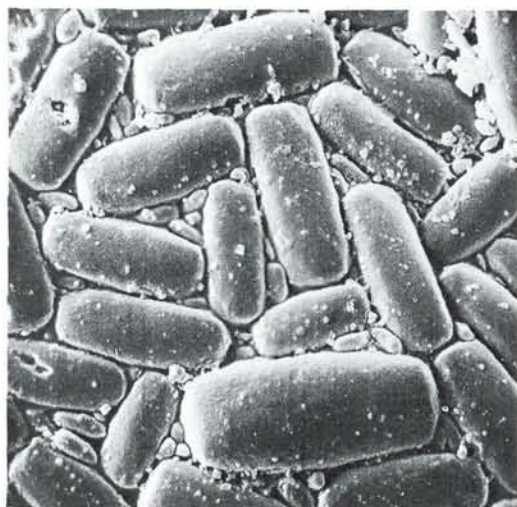


Fig. 5. Detail of fig. 2 showing rounded rectangular spicules and infilling smaller spicules between larger ones;  $\times 1640$ .

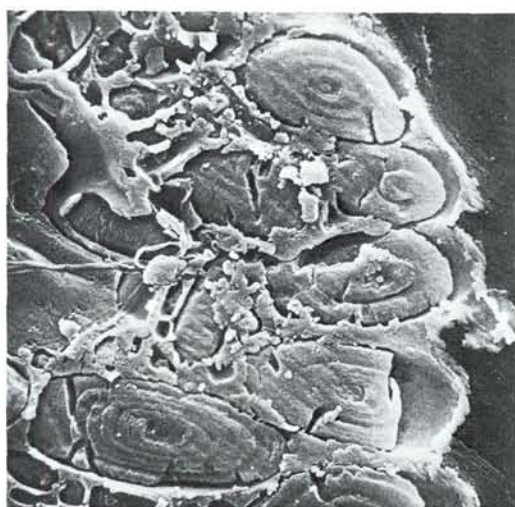


Fig. 7. Detail of polished and etched section through peripheral part of the shell wall of specimen shown in fig. 1. Note the concentric construction of the spicules as well as the prominent organic matrix surrounding the spicules;  $\times 1725$ .

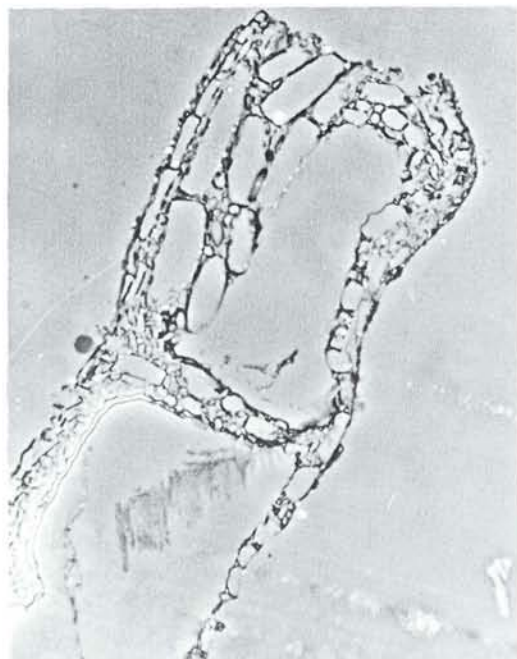


Fig. 6. Light micrograph (phase contrast) of 2  $\mu\text{m}$  vertical tangential section of decalcified specimen. Note the difference in refraction between the organic matrix and the inner organic chamber lining (lower left part of micrograph);  $\times 820$ .



Fig. 8. Detail of polished and etched section showing concentric layering of the spicule as well as transverse plate-like subdivisions. Note laminated inner organic chamber lining;  $\times 4310$ .

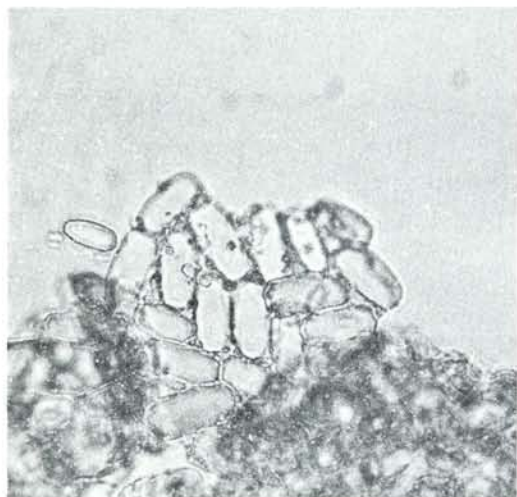


Fig. 9. Light micrograph of shell fragment;  $\times 820$ .

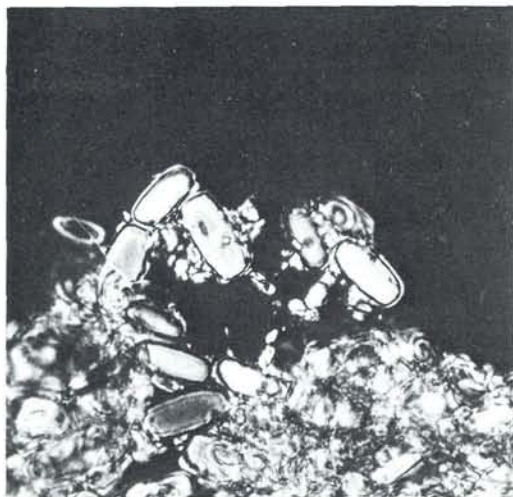


Fig. 10. Same fragment as shown in fig. 9. Crossed nicols. Note extinction of spicules with their long axis N-S and E-W;  $\times 820$ .

concentric structure a substructure marking an incomplete division of the spicules into about  $0.2\ \mu\text{m}$  thick plate-like units was observed (fig. 8). Figures 9 & 10 show that each spicule forms an optically single crystal with the c-axis parallel to the length of the spicule.

The spicules are embedded in an organic matrix (figs 6, 7 & 11). The inner surface of the shell is covered by an apparently laminated organic

layer (figs 8, 11 & 12) increasing in thickness towards the ontogenetically younger chambers (figs 3 & 13). Both in the light microscope (fig. 6) and in the TEM (fig. 11) the inner organic chamber lining and the organic matrix has a different appearance. The inner organic chamber lining in the light microscope has a higher refraction than the organic matrix. In the TEM the organic matrix has a spongy appearance, while the inner

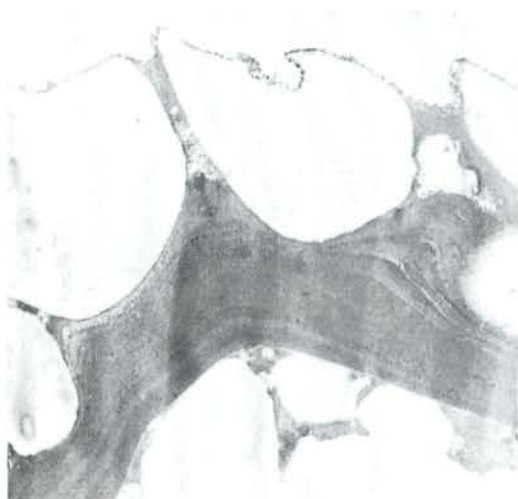


Fig. 11. TE micrograph of section through laminated inner organic chamber lining and organic matrix;  $\times 8150$ .

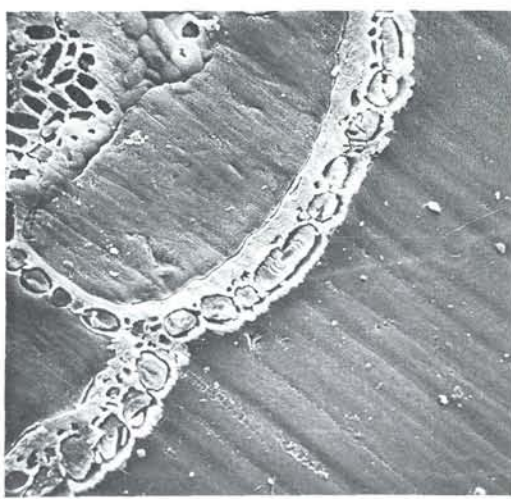


Fig. 12. Detail of polished and etched section showing thick inner organic chamber lining in the earlier part of the shell;  $\times 855$ .



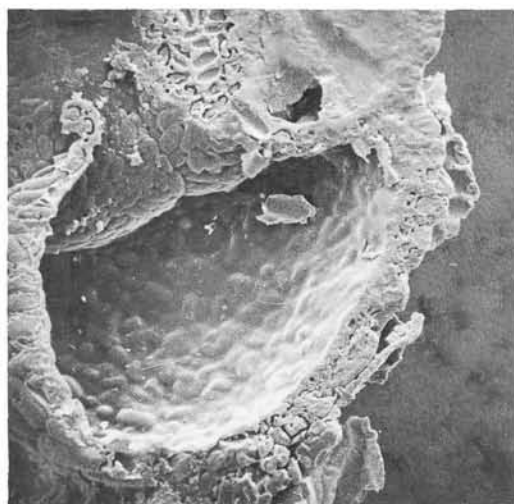


Fig. 13. Chamber shown in fig. 12 after removal of embedding medium showing veiling of spicules of the inner chamber surface due to addition of organic material during ontogeny (compare fig. 3);  $\times 615$ .

organic chamber lining seems more compact and exhibits a slight lamination parallel to the chamber surface.

## Discussion and conclusions

As mentioned by previous authors (opp. cit.) no pores have been observed in the shell of *Carterina*. This lack of pores is further corroborated by the present investigation.

The placement of *Carterina* within the suborder Rotaliina by Loeblich & Tappan (1964, 1974) thus would seem unjustified since they defined the Rotaliina by 'wall calcareous, perforate'. Their reason for placing *Carterina* in the Rotaliina may well be found in the fact that it is generally recognized that the spicules are secreted by the cytoplasm of the animal. The present authors agree with previous authors in supposing that the spicules are secreted by the animal. However, there are no indications that the secreted spicules are secreted 'in situ' in the wall. On the contrary, the perfect shape of the spicules (no spicule has been affected in its shape by neighbouring spicules) strongly indicates that the spicules are not secreted in their position in the wall. Thus they are 'allochthonous' relative to their final placement in the wall.

The only characters in which *Carterina* differs from members of the Textulariina is the origin of the spicules, which most likely are secreted by the foraminifer. That the spicules are not inorganic in their origin is indicated by the discovery by Deutsch & Lipps (1976) of organic inclusions in the single crystal spicules. These inclusions actually mark the concentric construction of the spicules along with a marking of a substructure at right angles to the optical axis ( $\neq$  basal pinacoid). This interpretation is based on the fact that independent of section plane the substructure always runs perpendicular to the longest axis of the sectioned spicule.

Thus any stage in the formation of the spicule in view of the concentric construction will result in a perfectly shaped unit. We did not find any identifiable nuclei in the spicule centers. Our X-ray diffraction experiment did not show reflection of material other than calcite. This, in a way, also supports the hypothesis that the wall material is primarily secreted by the foraminifer. It is our experience that even though some agglutinated foraminifera are highly selective in their choice of material for wall construction they invariably make mistakes and incorporate material of other composition.

It has been argued that the foraminifer having an attached mode of life will be prevented from getting material for shell construction since it cannot move freely. This argument, however, does not hold true since it is our experience from the Gulf of Elat that *Halophila* and other erect standing features of the bottom often are covered by fine sediment particles. Forms like *Trochammina* living an attached mode of life on vertical faces are quite capable of producing an agglutinated shell. We do, however, believe that *Carterina* secretes its own wall material.

We feel convinced that the capability by *Carterina* to secrete carbonate led Loeblich & Tappan to place this form within the Rotaliina and thus disregarding the absence of pores in the shell. We may at the present stage conclude that *Carterina* should be placed within the Textulariina since it lacks pores (i. e. pore tubules with sieveplates) and since it builds a wall of constructional elements that are allochthonous with respect to the wall itself.

Inner organic chamber linings are well known from other species of foraminifera. Thus Angell

(1967) demonstrated that the inner surface of *Rosalina floridana* is covered with a compact, laminated layer of organic material. Such layers were reported from *Operculina* and *Heterostegina* by Hottinger & Dreher (1974) although the lamination is less pronounced. In the *Miliolina* and *Textulariina* inner organic chamber linings are developed as well (figs 14 & 15). Consequently the presence in *Carterina* of an inner organic chamber lining does not point to any particular taxonomic relationship.

There is no doubt, however, that the capability of *Carterina* to secrete  $\text{CaCO}_3$  is something unique within the *Textulariina* and the form may well have to be kept separate on a rather high taxonomic level within the *Textulariina*. In our experience no documented example exists (compare Jørgensen, in press) of a textulariid foraminifer having a secreted carbonate matrix. Numerous examples of textulariid foraminifera have been studied in our laboratory in this respect and all examples turned out after examination in the electron microscope to have an allochthonous carbonate 'matrix' which is definitely not secreted by the animal.

We therefore favour the idea that the main emphasis in the superior classification of the foraminifera ought to be based on a division between, on the one hand, forms with a shell composed of elements that are allochthonous with regard to their placement and, on the other hand, forms that have a shell composed of material that is autochthonous with respect to its placement.

## Dansk sammendrag

*Carterina spiculotesta* danner en skal, der er konstrueret af calcit-spikler indlejret i et organisk materiale (figs 1 & 2). Spiklernes ensartede form (fig. 5) indikerer, at spiklerne ikke dannes i væggen under opbygningen af et nyt kammer. Man kender ikke andre organismer, der danner calcit-spikler af denne type. Den koncentriske opbygning af spiklerne (fig. 7), sammenholdt med oplysninger om, at spiklerne indeholder små indlejringer af organisk materiale (Deutsch & Lipps 1976), udelukker, at spiklerne er en uorganisk dannelselse. Det er derfor rimeligt at tro, at dyret selv danner spiklerne i cytoplasmaet, hvorfra de føres til den endelige plads i væggen.

Hvis denne tolkning er rigtig, skal *Carterina* placeres i underordenen *Textulariina* (de agglutinerende foraminiferer), da *Carterina* blot adskiller sig fra de øvrige arter i denne underorden ved selv at danne de partikler, der er indlejret i den organiske grundmasse.

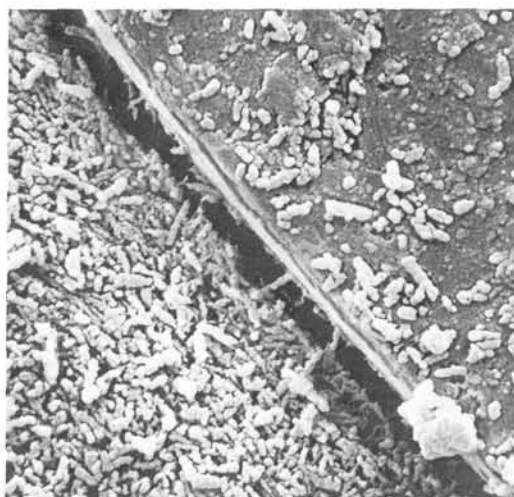


Fig. 14. *Quineloculina* sp., Recent, Brønlunds Fjord, North Greenland. Detail of polished and etched section showing chamber wall (lower left side of micrograph) and the inner organic chamber lining now attached to embedding medium;  $\times 4425$ .

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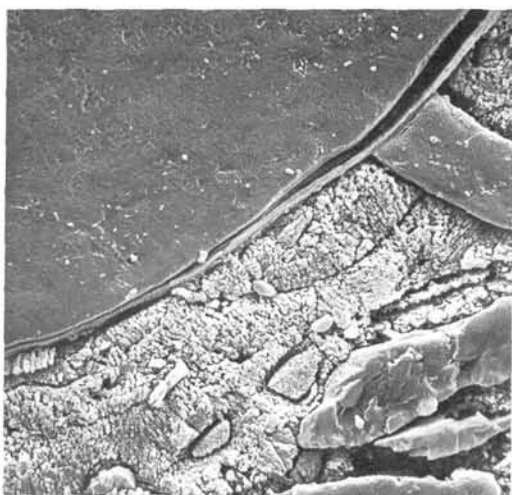


Fig. 15. *Textularia* sp., Recent, Gulf of Elat, Israel. Detail of polished and etched section through chamber wall demonstrating presence of inner organic chamber lining;  $\times 1800$ .

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