The compound and intermediate wall structures in Cibicidinae (Foraminifera) with remarks on the radial and granular wall structures

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Two wall structure types are described in three species of Cibicidinae: the intermediate type in *Cibicides refulgens* Montfort and *Cibicidella variabilis* (d'Orbigny), and the compound type in *Cibicides lobatulus* (Walker and Jacob).

In the intermediate wall structure type, the *c*-axes incline to the test wall surface at an angle of between 55° and 80°. Under polarized light, the test wall shows characteristics of both radial and granular extinction patterns.

The compound wall structure is here characterized by a two-layered test wall. Each layer has a different orientation of the *c*-axes: the outer layer with the *c*-axes parallel to the test surface, the inner layer with an orientation of the *c*-axes similar to the intermediate type. The extinction pattern in the compound structure type is granular.

These two structural types are compared with the radial and the granular structure types and their taxonomic significance is discussed.

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Introduction

The microstructure in the test wall of calcareous Foraminifera has been studied since the last century. A chronological review of these studies has been given by Stapleton (1973). This review also embraces the ultrastructural studies carried out with the aid of the Transmission Electron Microscope (TEM) and the Scanning Electron Microscope (SEM).

In the classification proposed by Wood (1949), the hyaline Foraminifera were divided into two major groups. In the first group, the calcite crystals were said to be, optically, radially arranged, whereas in the second group, the calcite crystals were said to lack a preferred orientation. Wood termed these two structures the "radiate structure" and the "granulate structure", respectively.

In certain hyaline Foraminifera it has previously been difficult to establish whether the test wall has the granular or the radial wall structure. This has particularly been the case in the members of the Cibicidinae which are to be dealt with here.

Thus, Wood (1949) describes the test wall in *Cibicides refulgens* as granular. In a later paper Wood & Haynes (1957) corrected this previous interpretation saying that *Cibicides refulgens* has a radial structure.

Krasheninnikov (1956) proposed to classify the test wall in the hyaline Foraminifera into six groups, of which three were radial, and three were granular. The groups were distinguished according to different microstructures of the test wall seen in thin section under polarized light. The structure in *Cibicides lobatulus* was described by Krasheninnikov as "lamellar granular" owing to the three different layers he observed in tangential thin sections of the test wall. The layering was said to be caused by the small size of the microcrystals in the central, darker lamella. Krasheninnikov's structural subdivision has not been applied.

Reiss (1959) studied three *Cibicides* species and described their test wall as having a granular-calcareous structure.

Loeblich & Tappan (1964, p. C688) restricted the genus *Cibicides* to "coarsely perforated, plano-convex forms with radial microstructure of the wall". The *Cibicides* species, which were previously described by Wood & Haynes (1957), and Reiss (1959) to have granular wall, were considered by Loeblich and Tappan as "referable to other genera". Loeblich and Tappan's system of classification has been criticized because it splits morphologically united groups (see Discussion).

Hofker (1967) said that in the initial chamber of *Cibicides lobatulus* the test wall consists of a single lamella with granular structure. In the late chambers, this lamella becomes strengthened by an inner lamella and occasionally by an outer lamella, both having radial structure. A similar structure was found by Hofker in *Cibicides refulgens,* except that the outer lamella is thicker than the inner lamella.

The test wall in *Cibicides refulgens* was described as pseudo-trilamellar by Gonzales-Bonoso (1969). According to this author, a microgranular outer lamella covers the bilamellar radial test wall at each chamber.

The concept of radial and granular wall structures became more detailed after the TEM investigation by Towe & Cifelli (1967) on the calcification of foraminiferal tests. These authors stated that the radial and the granular wall structures have a fixed crystal face upon which calcification starts, probably on the (0001) face for the radial type, and on the $(10\bar{1}1)$ rhombohedral face for the granular type. This implies that the optical *c*-axes of the calcite crystals are preferentially oriented in both structural types. *Cibicides refulgens* was studied by Towe and Cifelli under polarized light and with the TEM. Under polarized light, this species showed a structure that had "some optical attributes of both radial and granular character", while TEM studies showed many similarities with the radial structure type. *Cibicides refulgens* was thus classified as indistinctly radial, having a "less regularly constructed radial wall", (Towe & Cifelli 1967, p. 754). The authors stressed that the evaluation of this structure, which is between the radial and the granulate types, implies a subjective interpretation.

Stapleton (1973) described the wall structure in *Gyroidina* sp., and pointed out that it probably closely follows that of the genus *Cibicides.* In both genera, the wall was described as being "of an intermediate type between radial and granular". He termed the latter structural type as the "intermediate type", substituting the "indistinctly radial type" of Towe & Cifelli (1967); this is not identical to the "indistinctly radial type" of Krasheninnikov (1956). The intermediate structure was defined by Stapleton (1973, p. 42) as being "composed of grains in which both orientations (radial and granular) occur".

Haynes (1973) classified the test wall of *Cibicides lobatulus* as "weakly optically radial".

In the present paper, wall structures in *Cibicides refulgens*, *Cibicidella variabilis* and *Cibicides lobatulus* (Cibicidinae) are studied under polarized light and with the SEM. A detailed analysis of the intermediate structure type in *Cibicides refulgens* and *Cibicidella variabilis* is given. In *Cibicides lobatulus* a new type of wall structure, the compound structure type is described and defined. Also, both structure types are compared with here described radial and granular types, and with the species I have described in an earlier paper (Bellemo 1974).

Material and methods

The main stress in the present paper is on the description of the wall ultrastructures in Cibicidinae. The material comprises numerous tests from the following species:

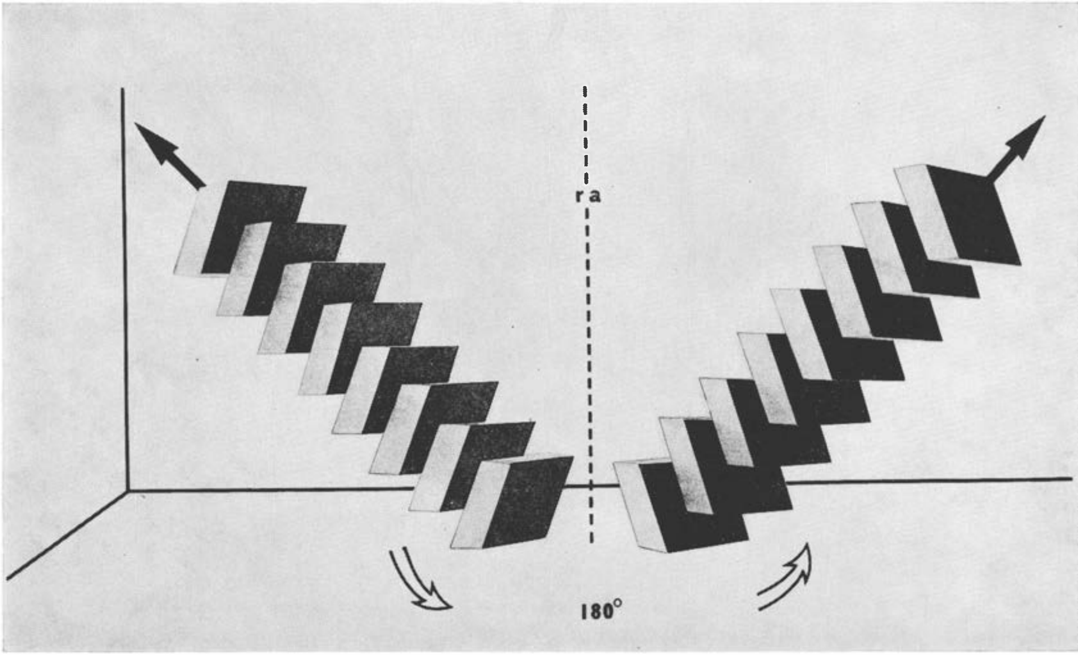
Cibicides refulgens Montfort, Cyprus and Gullmar Fjord.
Cibicides lobatulus (Walker and Jacob), Cyprus and Gullmar Fjord.
Cibicidella variabilis (d'Orbigny), Cyprus and Gullmar Fjord.

These species are compared with the following Foraminifera with radial and granular wall structures:

Radial type:
Bulimina marginata Cushman, Gullmar Fjord.
Globulina sp., Cyprus.
Guttulina sp., Cyprus.
Eponides repandus (Fichtel and Moll), Cyprus.
Granular type:
Melonis zaandamii (van Voorthuysen), Gullmar Fjord.
Nonion labradoricum (Dawson), Gullmar Fjord.
Cassidulina laevigata d'Orbigny, Gullmar Fjord.
Elphidium sp., Ivory Coast.

The material from Cyprus was collected in 1970 from Cape Greco by Dr. T. Alexandersson, Palaeontological Institute, Uppsala. The samples were taken at the sediment-water interface, at a depth of 16 m. The material from Gullmar Fjord was also taken from the sediment-water interface by the author at the Kristineberg Zoological Station at a depth of about 50 m. The specimens from the Ivory Coast were collected in 1966 by Professor R. A. Reyment, Palaeontological Institute, Uppsala, from a depth of 70 m.

The ultrastructure of the test wall was studied on the outer and inner surfaces, as well as in the vertical fracture planes. The crystalline components were etched (1) with a 25 % glutaraldehyde solution at pH 3,5, or (2) with a 2,5 % glutaraldehyde solution at pH 5,5, or (3) with a mixture of glutaraldehyde and acetic acid at pH 2. This etching method is used to study the orientation of the *c*-axes in the test wall. The *c*-axes are parallel to the needle-shaped remnants (crystallites)



Text-fig. 1. Difference in orientation between adjacent crystal units is exemplified by a model from the granular structure type. A crystal column of the test wall undergoes a rotation about 180° around a rotation axis (*ra*) perpendicular to the horizontal plane. After rotation, the inclination of the *c*-axis, about 45° to the horizontal plane, remains constant but the direction of the inclination is different.

of the stacks of calcitic microcrystals (crystal columns).

In order to remove the organic matrix from the calcite crystals, a concentrated solution of sodium hypochlorite was applied. Fragments of the test walls treated in the same way were also used for polarized microscope studies, (Pl. 1). For a detailed description of the methods of preparation the reader is referred to Bellemo (1974) and Mutvei (1974).

The preparations, glued on specimen-holders, were coated with evaporated gold and studied with the Jeolco SEM instrument, ISM-U3, at the Wallenberg Laboratory, Uppsala University, (Pls. 2—9).

Terminology

Most of the following structural terms have been set forth in an earlier paper (Bellemo 1974).

Microcrystals: These are the smallest morphologically distinguishable crystalline elements, usually represented by euhedral, tabular calcite rhomboids.

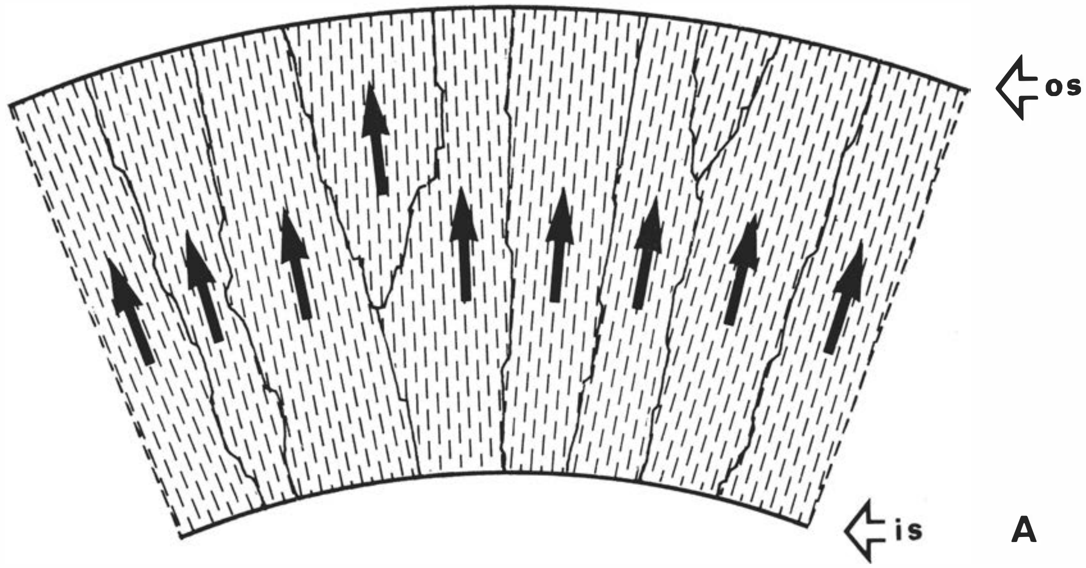
Crystal columns: These are stacks of tabular microcrystals which are characteristic of the radial wall structure. These crystal columns are similar to the arms of dendritic crystals (Text-fig. 2b).

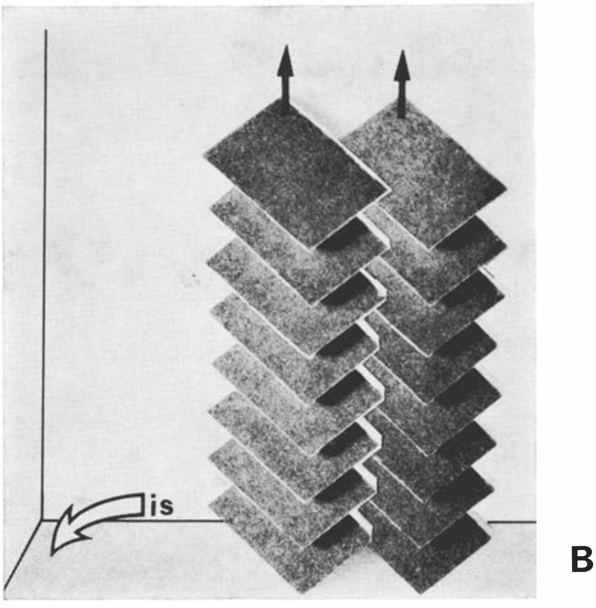
Needle-shaped crystallites: These are remnants of the crystal columns after having been etched. Their orientation is parallel to the *c*-axes.

Crystal units: These are adjacent crystal columns, with the same crystallographic orientation, which form a crystal unit. These crystal units are often separated by organic membranes.

Rotation axis: Difference in orientation between adjacent crystal units, can be described as being caused by rotations of the crystal units in relation to each other. The axis around which the crystal units rotate, is perpendicular to the test surface, and is termed the rotation axis (Text-fig. 1). Only in the radial structure type does this axis coincide with the *c*-axis.

Veneer: This is a layer on the surface of the test





Text-figs. 2 A, B. Radial structure type. A. Orientation of the *c*-axes in adjacent crystal units of the test wall. The *c*-axes, which are perpendicular to the test wall surface, are indicated by arrows. B. Orientation of the crystal columns in the test wall. *is*, inner surface; *os*, outer surface.

wall in which the arrangement, size, or morphology of the microcrystals is modified, but in which the optical orientation usually remains the same.

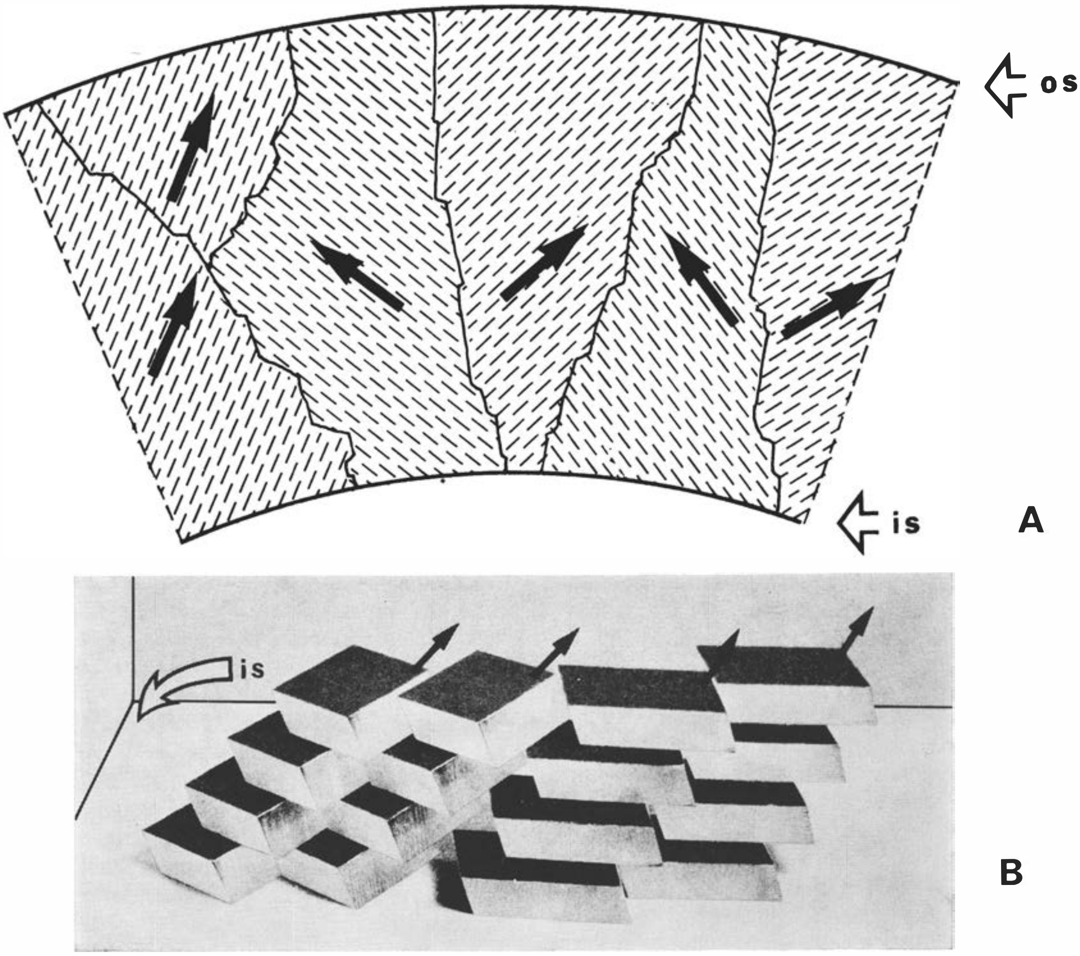
The wall structure types

According to the orientation of the microcrystals in the test wall, four types of wall structures are distinguished here: radial, granular, intermediate, compound.

The radial and the granular types have recently been re-examined (Bellemo 1974).

The radial wall structure type

Definition. — Most of the crystal units extend continuously across the test wall with their *c*-axes



Text-figs. 3 A, B. Granular structure type. A. Orientation of the *c*-axes in adjacent crystal units of the test wall. The *c*-axes, inclined 45° to the test surface, are indicated by arrows. B. Orientation of the crystal columns in the test wall. *is*, inner surface; *os*, outer surface.

perpendicular to the wall surface (Text-figs. 2 A, B). Under polarized light the test wall shows a black cross with concentric colour rings (Pl. 1, Fig. 1). The rotation axis is parallel to the *c*-axis.

Description. — This structure type was examined in *Guttulina* sp. and *Globulina* sp., Nodosariacea, *Bulimina marginata,* Buliminacea, and *Eponides repandus,* Orbitoidacea.

In SEM preparations, treated with sodium hypochlorite, the shape, size and orientation of the microcrystals in the four species largely agree with *Globobulimina turgida*, Buliminacea, *Ammonia beccarii*, Rotaliacea, and *Globorotalia menardii*, Globigerinacea (Bellemo 1974).

In *Guttulina* sp. and *Globulina* sp., it was established that the columns of microcrystals extend continuously across the entire thickness of the test wall (Pl. 2, Fig. 4; Pl. 3, Fig. 1). It is evident from the orientation of the crystal columns that the *c*-axes are perpendicular to the test surface, except for small deviations. The latter condition is clearly indicated in the test wall of *Eponides repandus* etched with glutaraldehyde solution. The needle-shaped crystallites, which are partly dissolved remnants of the crystal columns, are all perpendicular to the spherical surface of the test wall (Pl. 2, Fig. 1).

After treatment with the sodium hypochlorite solution, the inner surface of the test wall in *Guttulina* sp. clearly shows the polygonal outlines of the crystal units (Pl. 3, Figs. 2, 3, 4). The sutures between crystal units are narrow, but in some chambers the sutures widen out towards the surface (Pl. 3, Fig. 2). Their course is considerably less complicated than, for example, that of the radial *Bulimina marginata* (Pl. 3, Fig. 5), or of the granular *Nonion labradoricum* (Pl. 4, Fig. 4), where they are clearly interlocking.

The granular wall structure type

Definition. — Most of the crystal units extend continuously across the test wall (Pl. 4, Fig. 5). The *c*-axes of the crystal units are constantly inclined with an angle of 45° to the surface of the test wall (Text-figs. 3 A, B). This inclination is due to the orientation of one of the rhombohedral faces of the microcrystals always being parallel to the test surface. The crystal units are rotated such that the *c*-axes maintains a 45° angle to the rotation axis (Text-fig. 1). Under polarized light, the test fragments show granular extinction with coloured flecks separated by sutures (Pl. 1, Fig. 2).

Description. — The granular structure type was studied in *Elphidium* sp., Rotaliacea, and compared with that recently rescribed in the following species: *Nonion labradoricum*, *Melonis zaandamii* and *Cassidulina laevigata*, Cassidulidacea (Bellemo 1974).

SEM preparations treated with sodium hypochlorite solution, show that the microcrystals in *Elphidium* sp. are about 1,5 to 2,0 micron in diameter and are thus much larger than the average diameter of about 0,3 to 0,7 micron in the material dealt with earlier. The orientation of the microcrystals can be studied in greater detail than has hitherto been possible in the granular structure type owing to their large size. The outer surface of the test wall shows a veneer of thin microcrystals which are apparently oriented with their tabular faces parallel to the outer test surface (Pl. 4, Figs. 2, 3). A veneer-like arrangement of the microcrystals was also seen on the outer surface of *Melonis zaandamii* and *Cassidulina laevigata* (Pl. 5, Figs. 1 and 3, respectively). However, microcrystals of the latter species are smaller and less tabular than in *Elphidium* sp. Below the veneer, the microcrystals in *Elphidium* sp. are oriented with their tabular faces almost perpendicular to the outer surface (Pl. 4, Fig. 1). Both in the veneer and in the rest of the test wall, the orientation of the *c*-axis is the same.

The microcrystals are distinctly visible in a vertical fracture plane of the test wall. They are arranged in crystal units which are indicated in Pl. 4, Fig. 1 by a broken line. The inclination of the *c*-axis in the crystal units is shown by arrows. The direction of the inclination is different in adjacent crystal units due to the rotation which, in Pl. 4, Fig. 1, amounts to about 180°. This is also illustrated in Text-fig. 1. The rotation of the crystal units does not effect the inclination of the *c*-axis, nor does it effect the orientation of the rhombohedral faces parallel to the test surface.

Following glutaraldehyde etching, the test wall in *Elphidium* sp. became too brittle for SEM studies. However, the etching the outer surface in *Melonis zaandamii* (Pl. 5, Fig. 2) and *Cassidulina laevigata* (Pl. 5, Fig. 4) reveals needle-shaped crystallites which have a constant 45° inclination to the test surface. The crystallites are arranged in groups, each group representing a crystal unit.

The intermediate wall structure type

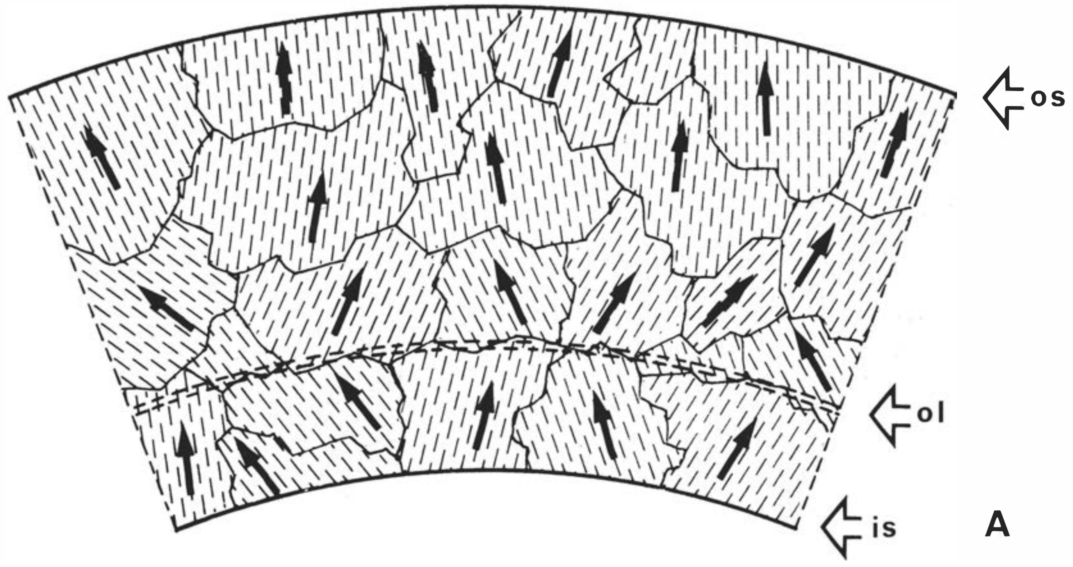
Definition. — The crystal units are comparatively small and do not, therefore, extend continuously through the test wall. Depending on their position in the test wall, the orientation of the crystal units changes as follows: (1) close to the inner and outer wall surface the crystal units are oriented with their *c*-axes almost perpendicular to these surfaces, similar to that of the radial structure type; (2) in the central part of the test wall, the *c*-axes are oblique to the wall surface and are therefore similar to the granular structure type *c*-axes' (Text-figs. 4 A, B). Under polarized light, the test wall shows an extinction pattern characteristic of both the radial and the granular wall structures.

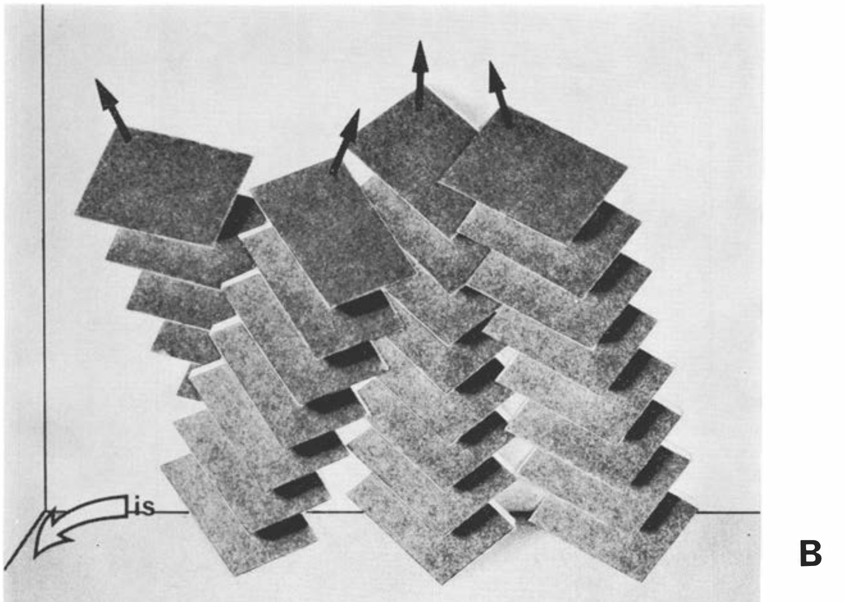
Description. — Towe & Cifelli (1967) described the structure type in *Cibicides refulgens* as "a less regularly constructed radial wall" in which the microcrystals, from some portions of the test wall, have a "good statistical orientation of the *c*-axis, while in other portions they have a heterogeneous orientation".

The term, intermediate structure type, was introduced, for the genus *Gyroidina*, by Stapleton (1973) who briefly noted that it is an intermediate type between the radial and the granular types. The intermediate structure type has, however, not been studied in detail before, and it is still incompletely known.

The intermediate wall structure type described below is from *Cibicides refulgens* and *Cibicidella variabilis,* Orbitoidacea.

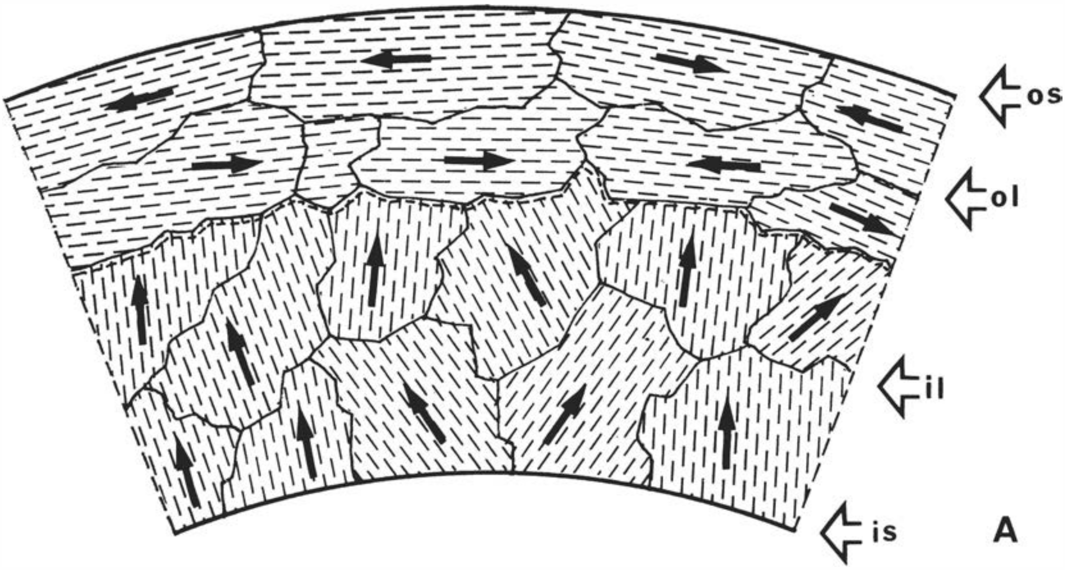
These two species show under polarized light an almost identical extinction pattern, in which the characters of both the radial and the granular wall structures are represented. The two extinction



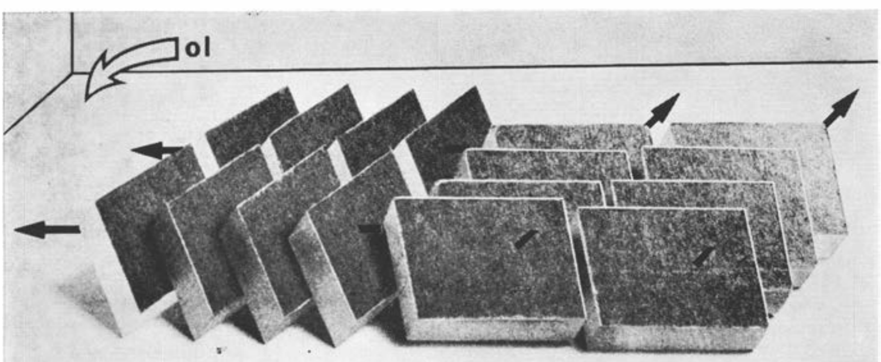


Text-figs. 4 A, B. Intermediate structure type. A. Orientation of the *c*-axes in adjacent crystal units, indicated by arrows. The crystal units are comparatively small and do not extend continuously through the test wall. B. Orientation of the crystal columns in the test wall. *is*, inner layer; *ol*, approximate position of the inner organic lining; *os*, outer surface.

patterns seem to be superimposed, sometimes with a slight preference towards one of the structure types. Usually, the extinction pattern appears as a darker area in the central part of the wall fragments (Pl. 1, Figs. 4, 5, 6), quite dissimilar to the black cross of the radial wall, as for example in *Bulimina marginata* (Pl. 1, Fig. 1). In flat wall fragments, the extinction is extended over the whole area as, for example, in those from the ventrally flattened portions of the chamber in *Cibicidella variabilis* (Pl. 1, Fig. 7). Within the dark extinguished area of both species are unextinguished light patches. These patches are randomly distributed and surrounded by sutures (Pl. 1, Fig. 7), like those in the granular structure type. The interference colours, usually very strong



A



B

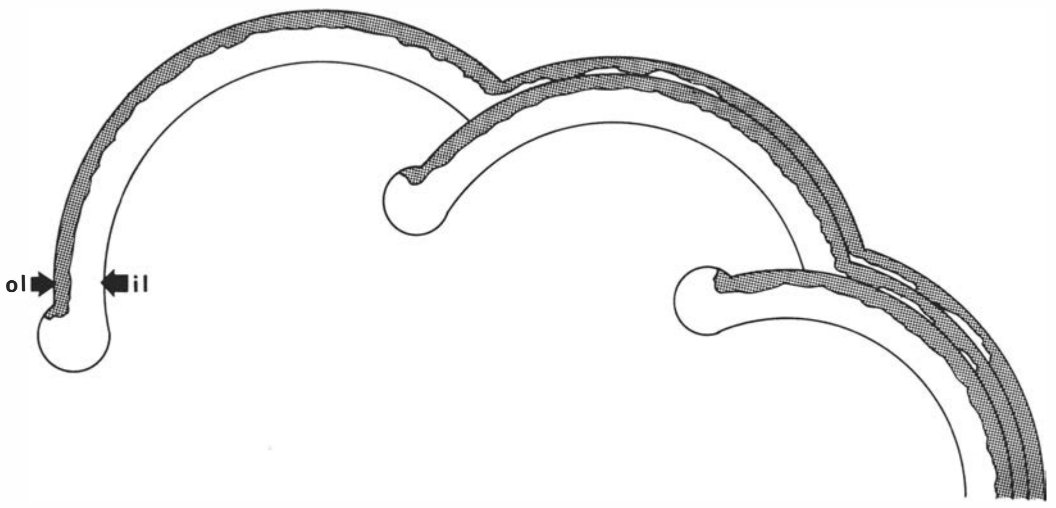
Text-figs. 5 A, B. Compound structures type. A. Orientation of the *c*-axes, indicated by arrows, in the outer and inner layer of the test wall of the last chamber. B. Crystal columns in two adjacent crystal units with surface-parallel orientation in the outer layer of the test wall. *il*, inner layer; *is*, inner surface; *ol*, outer layer; *os*, outer surface.

in the true radial and granular wall structure types, are weaker in this case and more difficult to observe.

As already indicated under polarized light, SEM studies show an unusual crystal arrangement in the test wall. The microcrystals in the two species are euhedral rhomboidal and approximately 0,6 micron in diameter (Pl. 6, Fig. 2; Pl. 7, Figs. 1, 2). They tend to grow in clusters in which the crystal columns cannot always be distinguished (Pl. 6, Fig. 1; Pl. 7, Fig. 1). The clusters of microcrystals have independent crystal orientation, and are therefore considered as separate crystal units. In vertical fracture planes, treated with sodium hypochlorite solution, the crystal units do not show preferred orientation (Pl. 6, Fig. 1; Pl. 7, Fig. 1). On the inner and outer surfaces of the test wall, respectively, the microcrystals are exposed as small three-sided pyramids in both species (Pl. 6, Fig. 2; Pl. 7, Fig. 2). The arrangement of these pyramids indicates a higher degree of orientation than could be observed on the vertical fracture planes.

The orientation of the *c*-axes was best obtained by etching the vertical fracture planes of the test wall with a glutaraldehyde solution. With this etching method the microcrystals are partially dissolved and remain as needle-shaped crystallites oriented parallel to the *c*-axes.

In the outermost and in the innermost portions



Text-fig. 6. Equatorial section of the last three chambers in *Cibicides lobatulus* showing the increase in thickness of the outer layer by the addition of new lamellae on its surface. *il*, inner layer; *ol*, outer layer.

of the test wall, which vary in thickness, the needle-shaped crystallites show an orientation almost perpendicular to the wall surface with a deviation of 10° to 15°. This regularity agrees with the arrangement of microcrystals on the inner and outer wall surfaces mentioned above. In the middle part of the test wall, the orientation of the needle-shaped crystallites becomes more oblique, approximately 20° to 35° from the perpendicular to the test wall surface (Pl. 6, Fig. 4; Pl. 7, Fig. 4). This orientation shows a greater similarity to the granular wall structure than to the radial wall structure.

In *Cibicidella variabilis,* the orientation of the needle-shaped crystallites is influenced by the curved wall surface in the vicinity of the large pores. The crystallites have a fan-like arrangement, which is indicated by arrows in Pl. 7, Fig. 3.

The compound structure type

Definition. — The test wall consists of two or more layers with different structure types. In *Cibicides lobatulus,* it is divided into an inner and an outer layer. In the inner layer the *c*-axes are approximately perpendicular to the test surface, as in the intermediate structure type. In the outer primary layer, the *c*-axes and one edge of each microcrystal, are always parallel to the test wall surface (Text-figs. 5 A, B). The latter structure is termed the surface-parallel structure. Under polarized light, both layers of the test wall, together, show a granular extinction pattern (Pl. 1, Figs. 8, 9, 10).

Description. — This structure type was studied in *Cibicides lobatulus.* SEM preparations of the outer surface of the test wall, treated with sodium hypochlorite solution, show regularly oriented microcrystals. These microcrystals have always one of their edges parallel to the test surface (Pl. 8, Figs. 1, 2). The microcrystals are arranged in parallel rows, and in adjacent crystal units these rows have a different orientation. In places, the crystal units are separated by distinct sutures which were originally occupied by intra-sutural organic membranes (Pl. 8, Fig. 3). This pattern of sutures resembles those seen under polarized light (Pl. 1, Fig. 8).

On the inner surface of the test wall the microcrystals show an entirely different orientation. The rhombohedral faces of the microcrystals appear as three-sided pyramids indicating that the *c*-axes are approximately vertical to the test surface, as in the intermediate structure type (Pl. 8, Fig. 4).

In the vertical fracture planes of the test wall, treated with sodium hypochlorite solution, the euhedral, rhomboidal microcrystals which are approximately 0,5 micron in diameter can be clearly seen (Pl. 8, Fig. 2). The microcrystals are grouped in small clusters. However, by using this method of preparation, the orientation of the microcrystals cannot be established, nor can a layering in fracture plane of the test wall be distinguished.

The composition of the test wall, with two layers each having different optical orientation, is clearly demonstrated after etching with a glutaraldehyde solution. In the inner layer, the needle-shaped crystallites are arranged almost perpendicularly to the wall surface with a deviation of 10° to 15°. Hence, the orientation of the *c*-axes is similar to that which has already been described for the intermediate wall structure type. In the outer layer, the crystallites are parallel to the test surface (Pl. 9, Fig. 6). Adjacent crystal units are clearly distinguished by the crystallites having a different direction and, consequently, of the *c*-axes (Pl. 9, Fig. 6). Between the two layers, the wall structure is often irregular and the crystallites lack any visible orientation (Pl. 9, Fig. 5).

In the test wall of the last chamber, the outer layer is much thinner than the inner layer. As a new chamber is formed, the outer layer grows successively in thickness by the addition of a new lamella on its surface (Pl. 9, Fig. 7; Text-fig. 6).

A similar method by which the wall thickens, occurs in *Bolivina* (Sliter, 1974) in which a thin veneer is added upon the entire wall surface each time a new chamber is formed.

Discussion

The recent SEM and TEM studies have shown that the use of the polarized light to determine the test wall structure is unsatisfactory, owing to extinction patterns which have been the same for different *c*-axis orientation.

The radial extinction pattern occurs when the *c*-axes are perpendicular to the spherical wall surface. This pattern is maintained when the *c*-axes show some small deviations, about 5° to 10° from its perpendicular orientation. If deviation increases, the radial pattern becomes indistinct and it is, at first, substituted by the intermediate extinction pattern. The intermediate pattern, showing characteristics of both the radial and the granular extinction patterns, appears when the orientation of the *c*-axes varies approximately from 55° to 80° to the test wall surface. Finally, the granular extinction pattern appears when the *c*-axes are inclined at an angle of 45° to the test wall surface. In this structural type, a rhombohedral face of the microcrystals is always parallel to the wall surface.

Further complications occur when the test wall is composed of two or more structurally different layers. This is found in the compound structure type of *Cibicides lobatulus* in which the *c*-axes have an entirely different orientation in the two layers (Table 1): (1) the inner layer with intermediate structure, and (2) the outer layer with surface-parallel structure, in which the *c*-axes are oriented parallel to the test wall surface. The latter layer has been said by Hofker (1967) to show granular extinction under polarized light.

Table 1 shows the extinction patterns of the four types of wall structures discussed here. These patterns are compared with the *c*-axes' inclinations to the wall surface observed in SEM preparations.

Table 1

Wall structure type		*Extinction under polarized light*	*Angle between c-axes and wall surface*
Radial		Radial	90°
Intermediate		Intermediate	55°—80°
Granular		Granular	45°
Compound	Inner layer	Granular	75°—80°
	Outer layer		0°

In SEM preparations, untreated or treated with sodium hypochlorite solution, the orientation of the *c*-axes is often difficult to determine from the external morphology of the microcrystals. The size of the microcrystals is, in some species, below the resolution power of the SEM. However, the etching of the test with glutaraldehyde solution has turned out to be a considerably more accurate method than the use of polarized light for determining the orientation of the *c*-axes. Using this method, the orientation can be expressed quantitatively in degrees instead of in extinction patterns only, which can be similar for different structure types. The orientation of the *c*-axes can also be determined in imperfectly preserved tests, and in specimens where the microcrystals are too small for morphological studies.

Good results have been obtained by the author from well preserved Tertiary Foraminifera.

The taxonomic significance of the radial and the granular wall structure types has been discussed by several authors. Wood & Haynes (1957) warned against a classification of the Foraminifera based mainly on the wall structures. However, the current classification, set up by Loeblich & Tappan (1964) uses radial and granular wall structures for erecting the superfamilies.

Towe & Cifelli (1967) agreed with Wood and Haynes in expressing caution with such a taxonomic subdivision above the species level. Different structural types can easily be derived from each other but at which taxonomic level this takes place is still unknown. The latter writers concluded that "only a careful study of the fossil record for the tracing of the phylogenetic patterns can be of help in this regard".

The following observations demonstrate that the radial and granular wall structures types can be used, as taxonomic characteristics, at the specific level only.

Thus, Buzas (1966) found that both radial and granular structure types occur in the genus *Elphidium.*

Hofker (1967) pointed out that Lower Cretaceous representatives of the genus *Bolivina* have a granular structure type, whereas the Early Tertiary species have radial structure type. Thus he noted that "genera may have quite different finer wall structure and yet belong together phylogenetically".

Hansen (1972) described two morphologically indistinguishable species of *Turrilina* with granular and radial wall structures from the Upper Eocene, and from the Middle and Upper Oligocene, respectively.

Also the four structure types, distinguished in the present paper, have their taxonomic application at species level only. Both the intermediate and the compound wall structure types were found to occur in different species of the genus *Cibicides.*

The compound structure type demonstrates that considerable structural changes take place by the ontogenetic growth of the test wall: the outer primary layer in *Cibicides lobatulus* has a surface-parallel structure, while the inner secondary layer has a intermediate structure type.

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PLATES

Plate 1

Fig. 1. *Bulimina marginata* Cushman; fragments of the test wall showing radiate extinction. Crossed nicols, × 80.

Fig. 2. *Elphidium* sp.; fragment of the test wall showing granulate extinction. Crossed nicols, × 400.

Fig. 3. *Cassidulina laevigata* (d'Orbigny); fragment of the test wall showing granulate extinction. Crossed nicols, × 400.

Figs. 4, 5. *Cibicides refulgens* Montfort; fragments of the test wall showing intermediate extinction pattern; note the darker area in the centre of the fragments composed by smaller extinguished and unextinguished grains (compare with the extinction of the granular type in Figs. 2, 3). Crossed nicols, × 400.

Figs. 6, 7. *Cibicidella variabilis* (d'Orbigny).
6. Fragment of the test wall showing intermediate extinction; note the dark extinguished area in the centre of the fragment (compare with fig. 7). Crossed nicols, × 80.
7. Extinguished and unextinguished grains in the darker, central portion of a test wall fragment. Crossed nicols, × 400.

Figs. 8—10. *Cibicides lobatulus* (Walker and Jacob).
8. Fragments of the septal wall with compound structure showing granulate extinction. Crossed nicols, × 400.
9, 10. Fragments of the dorsal and ventral parts of the test wall, respectively, showing the same extinction as in Fig. 8. Crossed nicols, × 200.

Plate 2

Figs. 1, 2. *Eponides repandus* (Fichtel and Moll).
1. Etched vertical fracture plane of the test wall showing the orientation of the needle-shaped crystallites. The crystallites are perpendicular to the spherical surface of the test chambers. Etched with 25 % glutaraldehyde solution at pH 3,5 for 30 minutes, × 1 500.
2. General view of the same specimen showing the location of Fig. 1, × 200.

Fig. 3. *Globulina* sp.; etched vertical fracture plane of the test wall showing the orientation of the needle-shaped crystallites. Etched with 25 % glutaraldehyde solution at pH 3,5 for 30 minutes, × 3 000.

Fig. 4. *Guttulina* sp.; vertical fracture plane of the test wall showing large, euhedral, tabular microcrystals arranged in vertical columns. Treated with sodium hypochlorite solution for 24 hours, × 10 000.

Plate 3

Fig. 1. *Globulina* sp.; vertical fracture plane of the test wall showing vertically continuous columns of microcrystals. Treated with sodium hypochlorite solution for 24 hours, × 10 000.

Figs. 2—4. *Guttulina* sp.; inner surface of the test wall showing crystal units separated by sutures which in Figs. 2 and 3 widen out towards the surface. Pore-openings are placed either along the sutures and in the crystal units (Fig. 4), or along the sutures only (Fig. 2). The preparation was treated as in Fig. 1, × 10 000.

Fig. 5. *Bulimina marginata* Cushman; inner surface of the test wall showing pore-centered crystal units separated by interlocking sutures. Treated as in Fig. 1, × 12 000.

Plate 4

Figs. 1—3. *Elphidium* sp.
1. Vertical fracture plane of the test wall showing the arrangement of the large, tabular microcrystals. The arrows approximate the orientation of the *c*-axes in different crystal units. The boundaries between the crystal units are indicated by broken lines. Treated with sodium hypochlorite solution for 24 hours, × 14 000.
2. Outer surface of the test wall showing microcrystals arranged in a veneer with their tabular faces parallel to the surface. Treated as in Fig. 1, × 15 000.
3. Orientation of the microcrystals on a vertical fracture plane and on the outer surface of the test wall. Treated as in Fig. 1, × 10 000.

Figs. 4, 5. *Nonion labradoricum* (Dawson).
4. Outer surface of the test wall showing interlocking sutures between crystal units. Treated as in Fig. 1, × 10 000.
5. Vertical fracture plane of the test wall showing how the sutures pass through the whole test wall. Treated as in Fig. 1, × 10 000.

Plate 5

Figs. 1, 2. *Melonis zaandamii* (van Voorthuysen).
1. Outer surface of the test wall showing microcrystals arranged in a veneer with their tabular faces parallel to the test wall surface. Treated with sodium hypochlorite solution for 24 hours, × 10 000.

2. Etched outer surface of the test wall showing a constant 45° inclination of the needle-shaped crystallites. The direction of the inclination is different in adjacent crystal units (indicated by broken lines). Etched with 2,5 % glutaraldehyde solution at pH 5,5 for 20 minutes, × 10 000.

Figs. 3, 4. *Cassidulina laevigata* d'Orbigny.
3. Microcrystals on the outer wall surface arranged as in Fig. 1. Treated as in Fig. 1, × 10 000.
4. Etched inner surface of the test wall showing the same orientation of the needle-shaped crystallites as in Fig. 2. Etched with 2,5 % glutaraldehyde solution at pH 5,5 for 20 minutes, × 6 000.

Figs. 5, 6. *Cibicides refulgens* Monfort.
5. Dorsal view, × 160.
6. Ventral view, × 130.

Figs. 7, 8. *Cibicidella variabilis* (d'Orbigny).
7. Dorsal view, × 80.
8. Ventral view, × 130.

Plate 6

Figs. 1—5. *Cibicides refulgens* Montfort.
1. Vertical fracture plane of the septal wall showing the microcrystals arranged in clusters with different orientation. Each cluster represent a crystal unit. Treated with sodium hypochlorites solution for 24 hours, × 10 000.
2. Dorsal outer surface of the test wall with exposed microcrystals. Treated as in Fig. 1, × 10 000.
3. Etched outer surface of the ventral test wall showing needle-shaped crystallites grouped after the crystal units. The orientation of the crystallites is almost perpendicular to the test wall surface with a deviation of about 15°. Etched with 25 % glutaraldehyde solution at pH 3,5 for 25 minutes, × 5 000.
4. Etched cross section of the test wall of the last chamber. As indicated by the needle-shaped crystallites the orientation of the *c*-axes is almost perpendicular near the outer and inner test surfaces but more inclined towards the centre of the test wall. The location of the organic lining is indicated by arrows. Etched with 25 % glutaraldehyde solution at pH 3,5 for 25 minutes, × 5 000.
5. Etched inner surface of the test wall showing needle-shaped crystallites with varying inclination. Etched with a solution of glutaraldehyde and acetic acid at pH 2, × 8 000.

Plate 7

Figs. 1—4. *Cibicidella variabilis* (d'Orbigny).
1. Microcrystal in the vertical fracture plane of the test wall showing indistinct, small clusters of microcrystals, each of which represents a crystal units. Treated with sodium hypochlorite solution for 24 hours, × 7 000.
2. Inner surface of the test wall showing rather well oriented microcrystals around a large pore. Treated as in Fig. 1. × 10 000.
3. Etched vertical fracture plane of the test wall at a pore-opening showing orientation of the needle-shaped crystallites (indicated by arrows). Etched with 25 % glutaraldehyde solution for 20 minutes, × 3 000.
4. Etched vertical fracture plane of the test wall. The small crystal units of Fig. 1 are here represented by bundles of parallel needle-shaped crystallites. The orientation of the crystallites is almost perpendicular near the outer and inner test surfaces, but become more inclined towards the center. The probable position of the inner organic lining is indicated by a broken line. Etched with 25 % glutaraldehyde solution at pH 3,5 for 25 minutes, × 4 500.

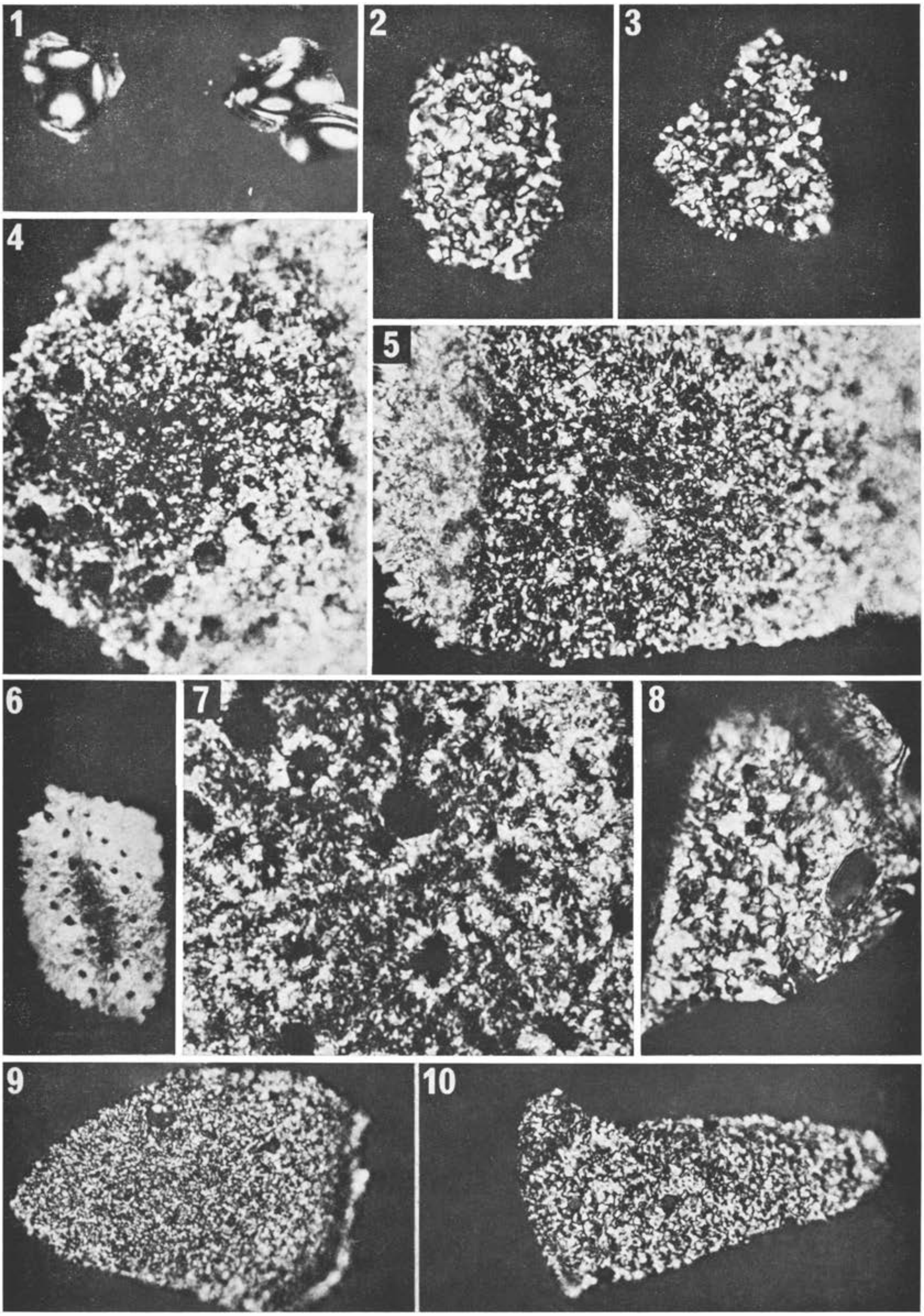
Plate 8

Figs. 1—4. *Cibicides lobatulus* (Walker and Jacob).
1. Outer ventral surface of the test wall showing the surface-parallel orientation of the microcrystals. Adjacent crystal units are distinguishable by the differentially oriented microcrystal groups. Treated with sodium hypochlorite solution for 24 hours, × 10 000.
2. Fragment of the test wall showing both the surface of the outer layer and a fracture plane of the test wall. On the surface the microcrystals show an orientation as in Fig. 1, whereas in the fracture plane they are arranged in differentially oriented clusters; each cluster represent a crystal unit. Treated as in Fig. 1, × 20 000.
3. Outer surface of the test wall showing crystals units separated by interlocking sutures. Treated as in Fig. 1, × 4 500.
4. Inner surface of the test wall showing almost regularly oriented microcrystals. Treated as in Fig. 1, × 15 000.

Plate 9

Figs. 1—7. *Cibicides lobatulus* (Walker and Jacob).
1. Dorsal view, × 160.
2. Ventral view, × 140.
3. Dorsal view, × 120.
4. Ventral view, × 140.
5. Etched vertical fracture plane of the septal wall showing the different orientation of the needle-shaped crystallites (indicated by arrows) in the outer and inner layer. Etched with 25 % glutaraldehyde solution at pH 3,5 for 15 minutes, × 7 000.
6. Etched surface of the outer layer showing the surface-parallel orientation of the needle-shaped crystallites. Adjacent crystal units have different direction of crystallite-bundles. Etched as in Fig. 1, × 7 000.
7. Etched vertical fracture plane of the test wall. In the inner layer the crystallites are almost perpendicular to the test surface, whereas in the outer thickened layer they have surface-parallel orientation. Etched as in Fig. 1, × 5 000.

Plate I



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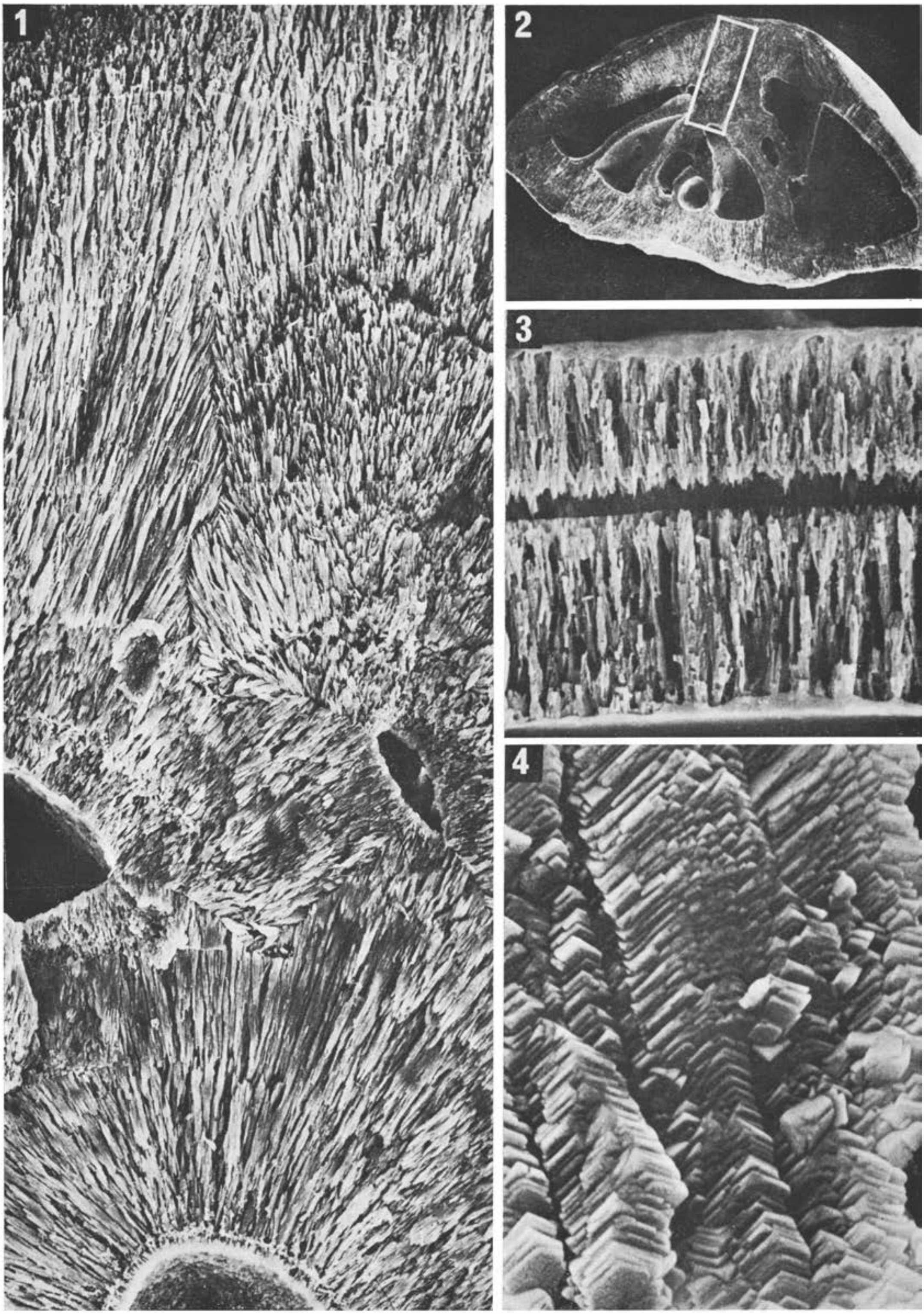

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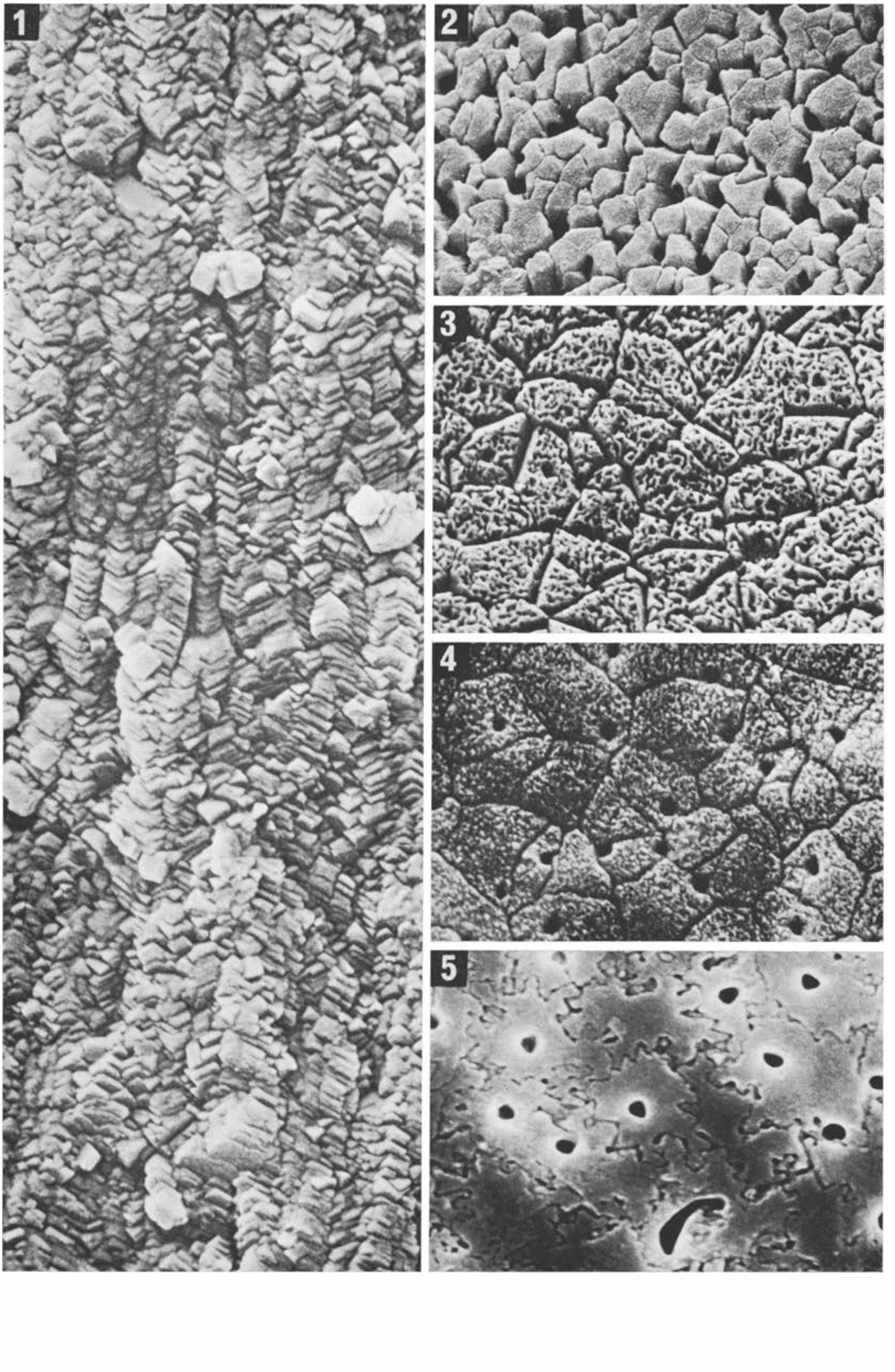

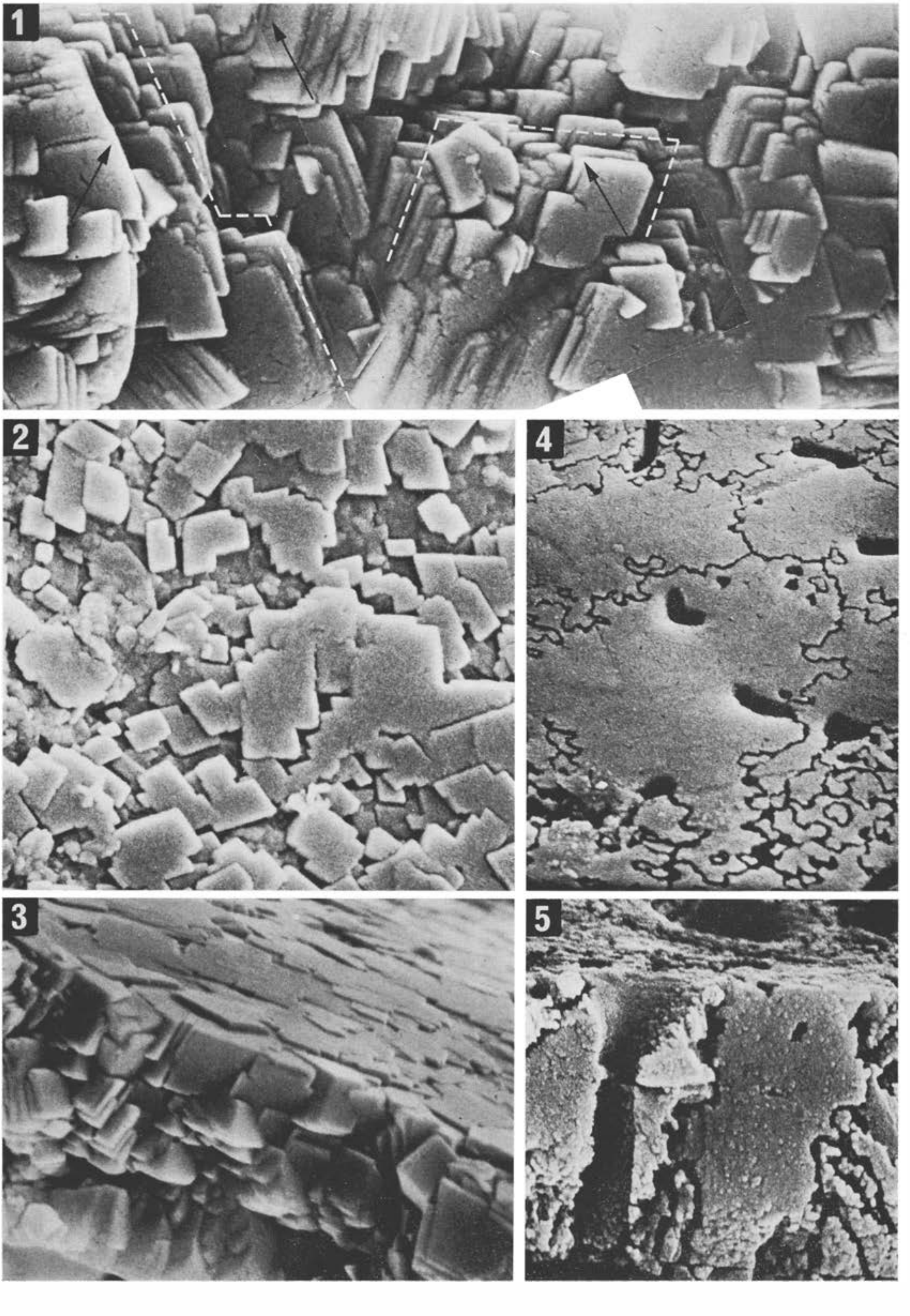
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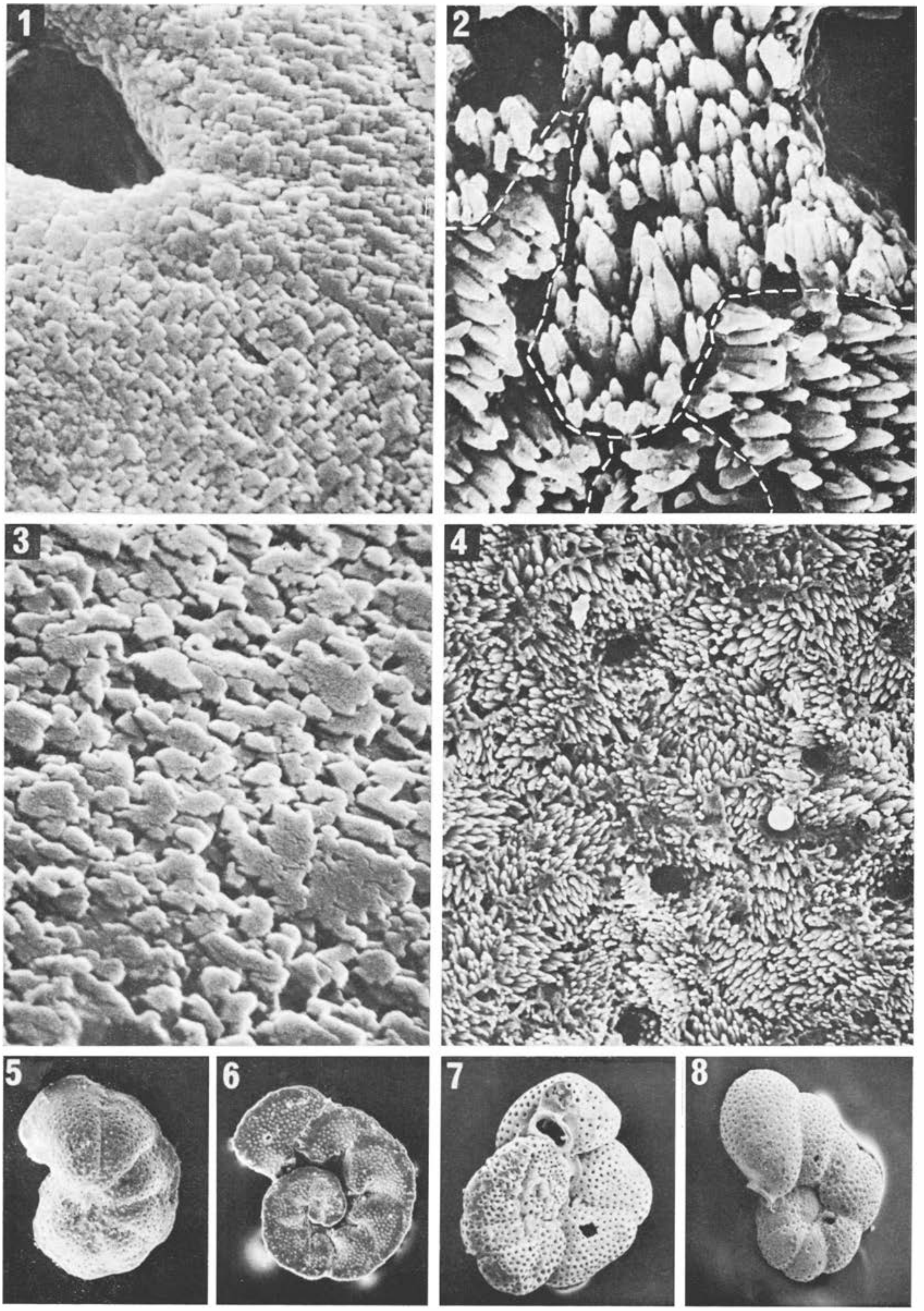
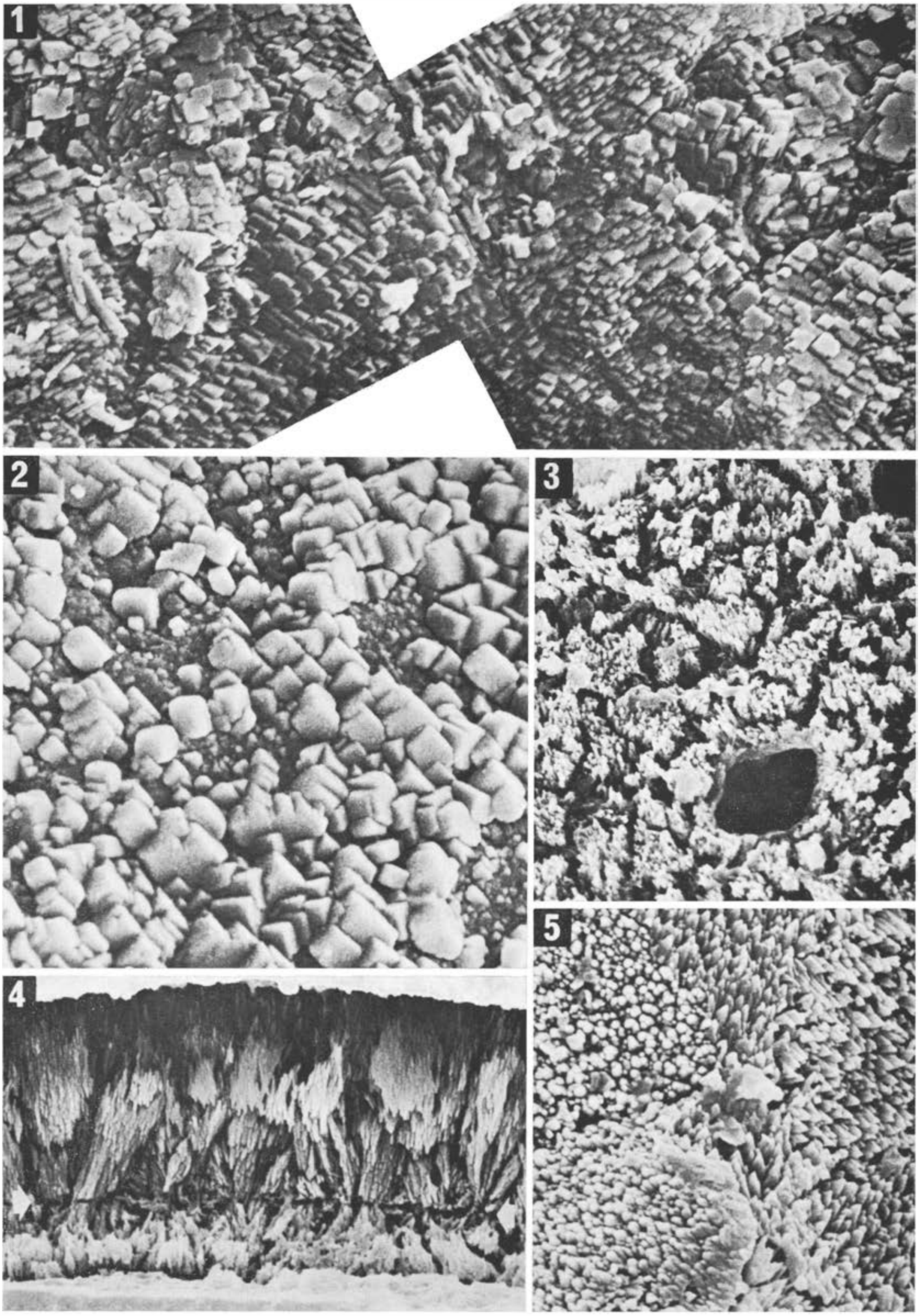
Plate V





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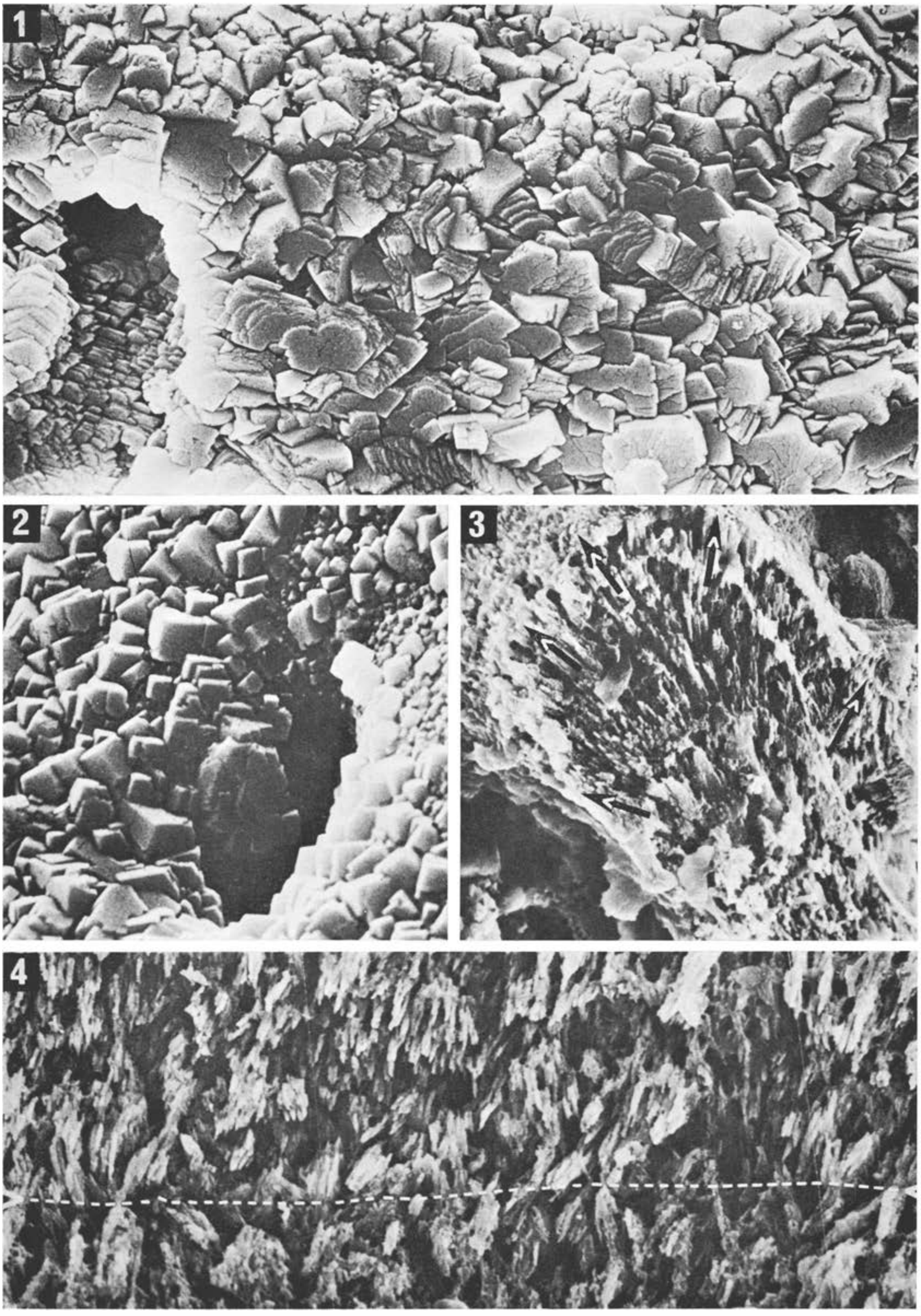

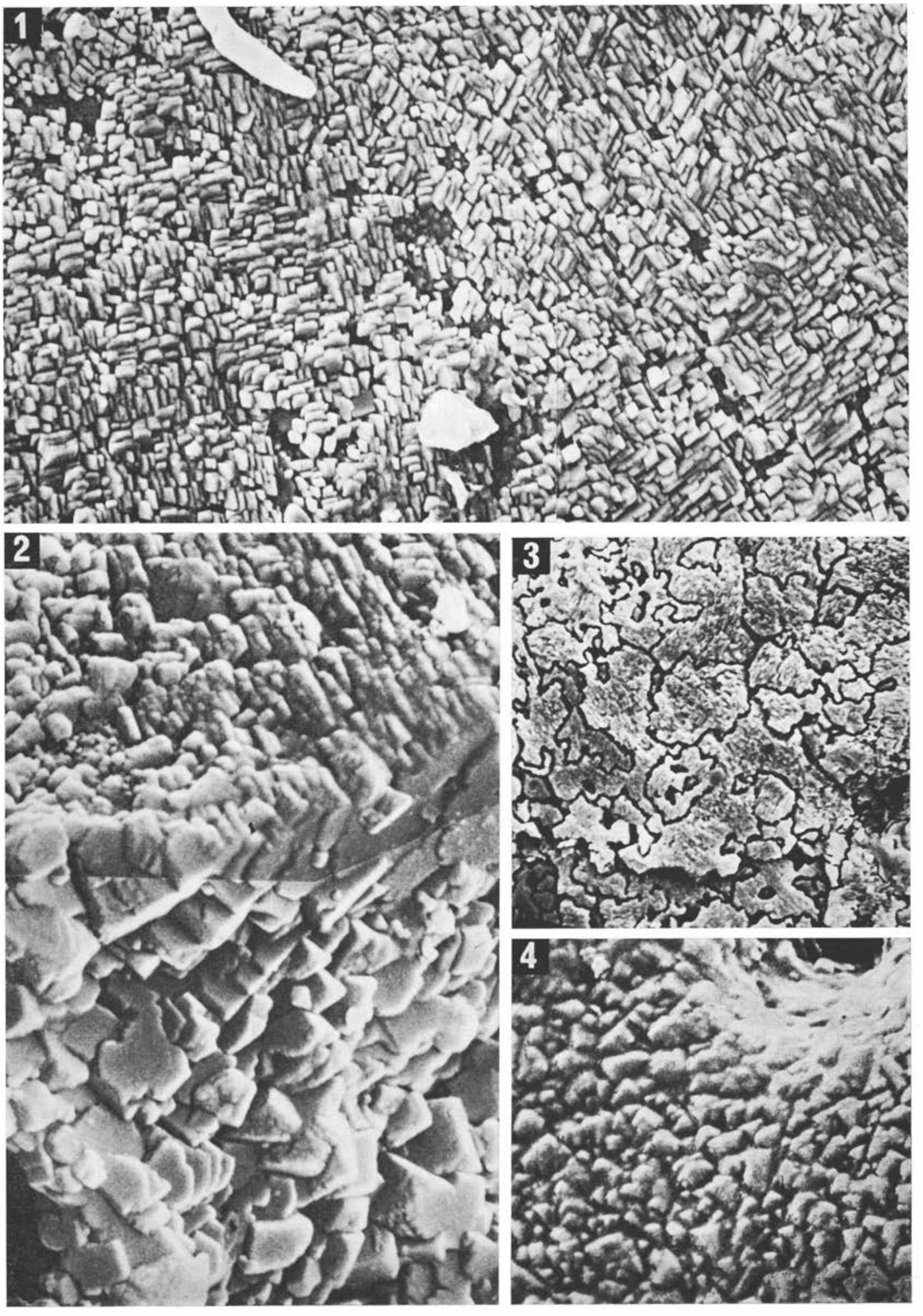
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Plate IX