Test wall structures in some Spirillinacea (Foraminifera)

SANDRO BELLEMO

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The structure of the test wall in members of the superfamily Spirillinacea is studied with polarized light and by scanning electron microscopy.

In most cases, Spirillinacea show a monocrystalline structure in which the whole test in polarized light behaves as a single calcite crystal. The orientation of the c-axis is either parallel or vertical to the spiral (umbilical) plane of the test. In addition to the monocrystalline structural type, three other structural types are described, these having been found in a few specimens only. These anomalous structural types are here termed: the transitional, the helicoidal, and the oligocrystalline.

Both monocrystalline and anomalous structure types may even occur in one and the same species, as in *Spirillina vivipara.* The presence of different wall structural types in the same species imply that wall structures, at least in some cases, cannot be used as taxonomic criteria at a higher level than the intraspecific.

S. Bellemo, Paleontologiska Institutionen, Uppsala Universitet, Box 558, S-751 22, Uppsala, Sweden, March 1, 1978.

Introduction

In the perforate, hyaline Foraminifera, Rotaliina, the test wall structure has been considered as an important character for their classification at the superfamily and family levels.

Before the introduction of the transmission electron microscopic (TEM) and the scanning electron microscopic (SEM) techniques, the test wall of the Rotaliina could be studied only with light microscope in polarized light. The detailed structure of the test wall was therefore incompletely understood. On the basis of the studies in polarized light, three optically differentiated structural types were usually distinguished in Rotaliina: the radial, the granular, and the monocrystalline.

During the last decade, several authors, using TEM and SEM techniques, were able to describe the ultrastructures of the radial and the granular types in great detail (Towe & Cifelli 1967; Stapleton 1973; Bellemo 1974a, b, 1976) but the monocrystalline type has been largely neglected.

Within the Rotaliina, the forms with the wall structure which "may consist optically of a single crystal of calcite" have been grouped by Loeblich & Tappan (1964, pp. 598—605) in the superfamily Spirillinacea.

In contrast to the comprehensive studies on the biology, life history and test morphology in Spirillinacea, and in particular in *Spirillina* and *Patellina* spp., (Myers 1936, 1939; Berthold 1971, 1976), the ultrastructures of their test wall is still incompletely known.

Although the Spirillinacea are defined as having the test wall composed of a single calcite crystal, several optical structures or structural varieties have been previously described.

Sollas (1921, p. 208) found the following optical structures in *Spirillina* spp. in polarized light: (a) the monocrystalline with the optical axis, the c-axis, interpreted as being parallel, vertical or with any intermediate position to the spiral plane (*Spirillina obconica*, *Spirillina infundibulata*, *Spirillina lucida*, *Spirillina vivipara*), (b) an optical structure showing "a spiral cross in the middle which extends over the first whorl" with an optical axis "making an angle with the spiral of the shell" (*Spirillina vivipara*); (c) an optical structure in which the shell consist of an irregular mosaic of crystals (*Spirillina vivipara*); and (d) an optical structure in which "the shell is more granular rather than fibrous, and remains illuminated, except for some irregular areas, throughout a complete rotation between crossed nicols" (*Spirillina limbata*). His brief description was accompanied by two micrographs.

Wood (1949) regarded the structure of the Spirillinacea as abnormal and mentioned, without illustrating them, three structural types: (a) tests of a single crystal of calcite; (b) occasional tests of several large crystals with irregular boundaries; and (c) occasional irregularly fibrous tests.

Towe *et al.* (1976), with the aid of X-ray diffraction and crystal overgrowth techniques, improved the previous results achieved in polarized light. In *Patellina corrugata*, the c-axis is found to be parallel to the umbilical plane of the test and the a-axis vertical to the same plane. These authors suggested that the a-axis is the axis of preferred orientation.

Hohenegger & Piller (1977) investigated the test ultrastructures in *Patellina*, *Spirillina* and *Planispirillina* sp. In *Spirillina vivipara* and *Patellina corrugata* they confirmed the occurrence of the monocrystalline structure previously described by Sollas (1921), whereas in *Planispirillina*, the test was not found to be monocrystalline but to consist of numerous acicular crystals. Therefore these authors removed Planispirillina sp. from the family Spirillinidae to the Involutinidae.

In the present paper, the morphology of the crystalline ultrastructure is described, based on SEM studies of etched and unetched tests of some Spirillinacea. Complementary studies were made of the optical structures in polarized light.

Material and methods

The material was collected in the summer of 1970 from Cape Greco, Cyprus, by Dr. T. Alexandersson, Palaeontological Institution, Uppsala. The foraminifers lived on an algal mound at the depth of about 18 m. The material was washed in tap water and sieved.

The identification of the genera and species of Spirillinacea was difficult due to the scarcity of modern taxonomical studies. Since the aim of the present paper is to describe the test ultrastructures, a taxonomic revision could not be carried out on the basis of the available material.

The following species were identified and used for ultrastructural studies and studies in polarized light:

Patellina corrugata WILLIAMSON (Pl. 1, Fig. 1)
Sejunctella cf. *lateseptata* (TERQUEM) (Pl. 1, Fig. 3)
Planispirillina cf. *wrightii* (HERON-ALLEN & EARLAND) (Pl. 2, Figs. 1—4)
Spirillina vivipara EHRENBERG (Pl. 1, Figs. 4, 5; Pl. 2, Figs. 5, 6; Pl. 3, Figs. 1—6; Pl. 5, Figs. 5, 6)
Spirillina cf. *lucida* SIDEBOTTOM (Pl. 1, Fig. 6)
Spirillina sp. (Pl. 1, Figs. 2, 7—10; Pl. 4, Figs. 1—4; Pl. 5, Figs. 1—4)
?*Spirillina* sp. (Pl. 1, Figs. 11, 12)

The material comprises about 200 selected tests which were studied in polarized light, immersed either in tap water or in immersion oil. The tests immersed in tap water were used for subsequent SEM studies. For the latter studies, the tests were (1) treated with a concentrated solution of sodium hypochlorite containing 8 % to 12 % active chlorine for 24 to 48 hours, in order to remove the organic matrix from the calcite crystals; or (2) etched with 25 % glutardialdehyde solution at pH 3.5 for 1 to 20 minutes, in order to dissolve partly the carbonate phase. Method (2) facilitates the study of the orientation of the c-axis in the test wall. After being etched, the microcrystals in the test wall became partially dissolved, leaving needle-shaped crystallite remnants oriented parallel to the c-axis.

Before etching, the specimens were mounted on the specimen holders. Considerable variation was observed in the etching results for the same periods of immersion. Because of their fragility and small size, about one fourth of the available specimens were crushed or lost during the preparation procedure for SEM.

The preparation, affixed to specimen holders, were coated with evaporated gold in an ion sputterer and studied with a Jeolco SEM instrument, JSM-U3, at the Wallenberg Laboratory, Uppsala University.

For a detailed description of the methods, the reader is referred to Bellemo (1974) and Mutvei (1977).

Observations

Polarized light studies

Three different wall structural types were recognized in polarized light among the specimens investigated, namely: (1) monocrystalline; (2) transitional; and (3) helicoidal.

(1) *Monocrystalline structural type.* — In this type, two structural varieties can be distinguished on the basis of the orientation of the optical axis, c-axis, relative to the spiral (umbilical) plane of the test:

(a) The c-axis is parallel to the spiral (umbilical) plane of the test. This variety was observed in *Patellina corrugata* (Pl. 1, Fig. 1), *Sejunctella* cf. *lateseptata* (Pl. 1, Fig. 3), *Planispirillina* cf. *wrightii* (Pl. 2, Fig. 2) and *Spirillina* sp. (Pl. 1, Fig. 2).

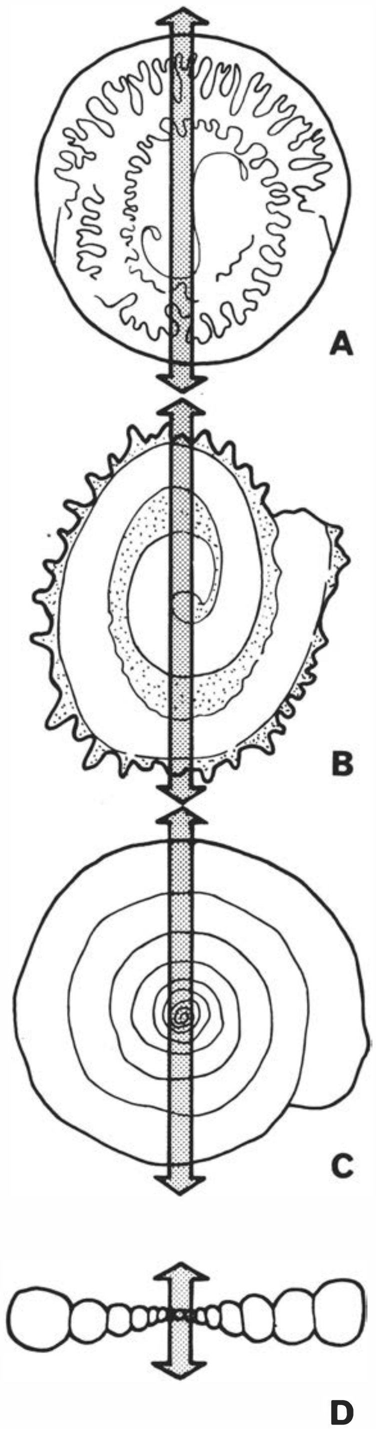
The studied tests, oriented with the spiral (umbilical) side parallel to the stage of the microscope, underwent complete extinction alternating with a maximum of interference colours when the stage was rotated. (Text-figs. 1A—C).

(b) The c-axis is perpendicular to the spiral plane of the test. This variety was observed in the majority of *Spirillina vivipara* (Pl. 1, Fig. 4) and *Planispirillina* cf. *wrightii* (Pl. 2, Fig. 1).

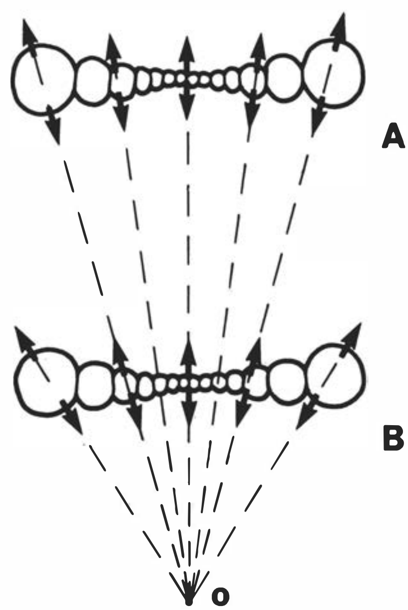
Here, when the tests are oriented with the spiral plane parallel to the stage of the microscope, interference colours are not seen but the tests remain extinguished during the 360° rotation of the stage. The c-axis is therefore perpendicular to the spiral plane of the test (Text-fig. 10).

(2) *Transitional structure type.* — The c-axis are not parallel but radiate from a common point situated on the coiling axis at a variable distance from the test. The inclination of the c-axes increases towards the periphery of the test (Text-figs. 2A, B).

This variety was found in few tests of *Spirillina vivipara* (Pl. 1, Fig. 5) in which a black cross was seen during a 360° rotation of the stage. The black cross seems to be superimposed on an incomplete permanent extinction as in the above mentioned structural variety (b). There is a continuous transition between the tests showing a distinct black cross (Text-fig. 2B) to those in



*Text-figs. 1*A, B, C, D. Monocrystalline structural type. The c-axes, indicated by arrows, are parallel to the umbilical, A, or to the spiral plane of the test, B, C, as in *Patellina corrugata*, *Sejunctella* cf. *lateseptata* and some *Spirillina* sp., respectively. D, the c-axes are perpendicular to the spiral plane of the test as in the majority of *Spirillina* sp.



*Text-figs. 2*A, B. Probable orientation of the c-axes, indicated by arrows, in tests with transitional structural type. The origin, *o*, of the c-axes lies on the coiling axis of the test. This implies that the c-axes of the central part of the test are less oblique than those in the periphery. Tests situated near the origin as in B show, in polarized light, a distinct black cross superimposed an incomplete permanent extinction; in A only a faint black cross on an incomplete permanent extinction is shown. A test situated far from the origin will show complete permanent extinction.

which the black cross is faint (Text-fig. 2A) or scarcely visible.

(3) *Helicoidal structure type.* — The c-axes are here arranged obliquely, about 45°, to the axial intersections on the spiral plane (Text-fig. 3A). This structure was observed in tests of *Spirillina* cf. *lucida* (Pl. 1, Fig. 6), *Spirillina* sp. (Pl. 1, Figs. 7—10), and *?Spirillina* sp. (Pl. 1, Figs. 11—12).

The test, oriented with the spiral side parallel to the stage of the microscope, showed a black cross with curved arms during a 360° rotation of the stage. The monocrystalline and helicoidal structure types were briefly mentioned by Sollas (1921). Hohenegger & Piller (1977) confirmed that *Spirillina vivipara* has a monocrystalline wall structure. However, all their specimens showed permanent extinction in polarized light corresponding to the variety (1b) in the monocrystalline structure type. The variety (1a), and the transitional and helicoidal structure types were not mentioned.

SEM studies

The results obtained with SEM on wall ultrastructures are an important source of information for completing and interpreting the differences in optical patterns seen in polarized light on the same material. Although no direct optical information is available from the SEM studies, the morphology of the crystalline elements is clearly seen in the tests treated with sodium hypochlorite. Here, the orientation of the rhombohedral faces of the microcrystals in the test wall is visible, either on test surfaces or on fracture planes. On the basis of the morphological arrangement of the microcrystals only, the c-axis orientation of the test wall cannot be established for certain.

The morphological arrangement of the c-axis is, on the other hand, indicated in the test wall etched with glutardialdehyde. Here the orientation of the c-axes is parallel to that of the needle-shaped crystallites (Bellemo 1974a, b).

SEM investigations on the tests treated with sodium hypochlorite solution or etched with glutardialdehyde showed three different wall structure types in investigated specimens, namely: (1) monocrystalline; (2) helicoidal; and (3) oligocrystalline.

(1) *Monocrystalline structural type.* — In this type, two structural varieties of the test wall can be distinguished on the basis of the orientation of the microcrystals and their needle-shaped remnants: (a) after etching with glutardialdehyde the needle-shaped crystallites are parallel to each other and to the spiral plane of the test. Consequently, the c-axes are parallel to the same plane and parallel to each other. The latter condition implicates that the test is monocrystalline. This structural variety was observed in *Patellina corrugata* and in some specimen of *Spirillina* sp. (Pl. 3, Figs. 3, 4). (b) After etching with glutardialdehyde, the needle-shaped crystallites are oriented vertically to the spiral plane of the test. Even the c-axes are therefore vertical to the same plane. As the needle-shaped crystallites are parallel to each other, the test is monocrystalline. This variety is observed in the majority of the tests in *Spirillina vivipara* (Pl. 3, Figs. 3, 4).

The above described differences in the orientation of the c-axes, seen under the SEM, correspond to the optical structural varieties (1a) and (1b) distinguished in polarized light.

After treatment with sodium hypochlorite solution, the unetched microcrystals of the monocrystalline structure type could be studied in the tests of *Planispirillina* cf. *wrightii* and *Spirillina vivipara.* On the outer surface of the test of *Planispirillina* the microcrystals were seen with their rhombohedral faces constantly oriented (Pl. 2, Fig. 4). The same constant orientation of the microcrystals was observed both on the outer surfaces and on the fracture planes of the test wall in *Spirillina vivipara* (Pl. 2, Figs. 5, 6).

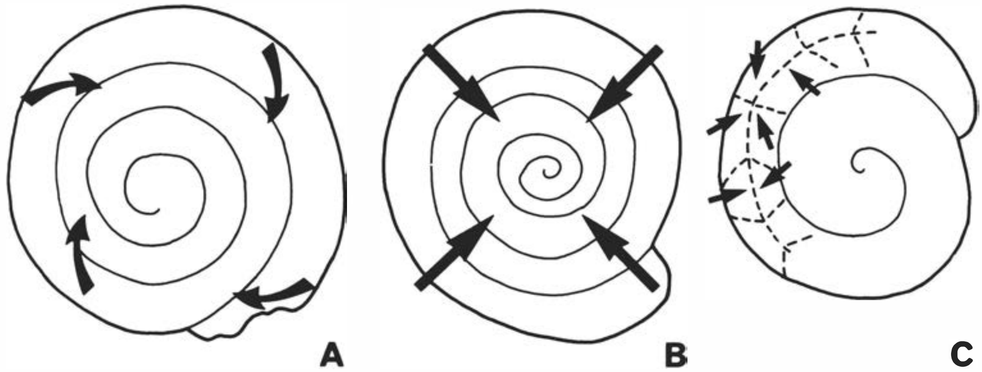
(2) *Helicoidal structural type.* — Among the tests which show a black cross with curved arms in polarized light only two specimens showed this structural type under the SEM (Pl. 4, Figs. 1—4; Text-fig. 3A).

After etching, the needle-shaped crystallites are here oriented along a helicoidal spiral and with an angle of about 45° to the axial intersections of the test. The needle-shaped crystallites are parallel or subparallel to the test surface.

One specimen of *Spirillina* showed a different ultrastructure. After etching with glutardialdehyde, the needle-shaped crystallites are arranged parallel to the spiral plane of the test and they are obliquely oriented, about 20°, to the axial intersections of the test (Text-fig. 3B; Pl. 5, Figs. 1—4).

Thus the orientation of the c-axes in the latter specimen is different from that of the helicoidal type. However, the scarce information provided by only one specimen was not sufficient to establish a new structure type.

(3) *Oligocrystalline structural type.* — One specimen of *Spirillina vivipara* etched with glutardialdehyde (Pl. 5, Figs. 5, 6) showed a particular ultrastructural pattern. The test wall is here subdivided into several crystal units similar to those



*Text-figs. 3*A, B, C. Differences in the orientation of the c-axes, indicated by arrows, in the anomalous structure types. A, the helicoidal type with the c-axes oriented along a helicoidal spiral and therefore oblique to the axial intersections of the test. B, a structure with the c-axes obliquely oriented to the axial intersections but parallel to the spiral plane of the test. C, the oligocrystalline structure type with different orientation of the c-axes in adjacent crystal units. The outlines of the crystal units are indicated by dashed lines.

in the radial and granular tests of Rotaliina (Bellemo 1974a, b). These crystal units are separated by narrow interspaces (Pl. 5, Fig. 6). The needle-shaped crystallites seem to be parallel to the spiral plane of the test but assume different orientation on the same plane in different crystal units. This structure is probably the same as Sollas (1921) described in polarized light as "consisting of an irregular mosaic of crystals". Text-fig. 3C shows the arrangement of the crystal units and their optical orientation.

Summary and conclusions

Four different wall structure types have been found, so far, in the investigated material, namely: (1) the monocrystalline; (2) the transitional; (3) the helicoidal; and (4) the oligocrystalline.

(1) In the monocrystalline structured type, two varieties have been distinguished in which the c-axis is (a) parallel or (b) perpendicular to the spiral (umbilical) plane of the test.

(2) In the transitional structure type, the c-axes are perpendicular to the spiral plane in the central part of the test but they incline increasingly to the spiral plane towards the periphery of the test. The degree of inclination of the c-axes varies from specimen to specimen.

(3) In the helicoidal structural type, the c-axes seem to be "twisted" to an helicoidal spiral along the tubular test chamber.

(4) In the oligocrystalline structure type the orientation of the c-axes varies in different crystal units.

These structure types and occurrence in the species dealt with in the present paper are summarized in the table below.

The results obtained here with polarized light and SEM studies, show the complexity of the wall structures of the Spirillinacea. From the taxonomical point of view, it is important to stress that

Table 1

Structure type —	Pol. light	SEM	— Species
(1) *Monocrystalline*			
(a) c-axis parall. to spiral (umb.) plane.	*	*	*Spirillina* sp., *Planispirillina cf. wrightii*, *Sejunctella* cf. *lateseptata*, *Patellina corrugata.*
(b) c-axis vert. to spiral plane.	*	*	*Spirillina vivipara*, *Planispirillina* cf. *wrightii.*
(2) *Transitional*			
c-axes with radiate incl.	*		*Spirillina vivipara.*
(3) *Helicoidal*			
c-axes "twisted"	*	*	*Spirillina* cf. *lucida*, *Spirillina* sp.
(4) *Polycrystalline*			
c-axes with diff. orient. in diff. crystal units		*	*Spirillina vivipara.*

* structure investigated in this paper in polarized light and, or, SEM.

different structural types occur in the same genus and even in the same species and are therefore of limited value in taxonomy.

The earlier view on the role of the wall structures in foraminiferal classifications has been modified by Loeblich & Tappan (1974). They pointed out that similar structures may be repeatedly derived in various lineages, and that different wall structures could derive from each other at various times.

On the other hand, Hohenegger & Piller (1977) used the differences in the wall structure to remove *Planispirillina* sp. from the Spirillinidae to the Involutinidae. According to these authors, their specimens of *Planispirillina* sp. do not show a monocrystalline structural type.

In my material, *Planispirillina* cf. *wrightii* shows a monocrystalline structure with two different orientation of the c-axis, parallel or vertical, to the spiral plane of the test.

Moreover, the monocrystalline, the helicoidal, the transitional and the oligocrystalline structural types were encountered in the genus *Spirillina.* The dominant species of this genus is *Spirillina vivipara* and in this single species, at least, three different wall types were found. It is probable that most of the specimens here designated as *Spirillina* sp. are in fact *Spirillina vivipara.*

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PLATE 1

Fig. 1. *Patellina corrugata*; spiral view of the test in the position of maximum interference colours. Crossed nicols, × 200.

Fig. 2. *Spirillina* sp.; lateral view view of the test in the same position as in Fig. 1. Crossed nicols, × 200.

Fig. 3. *Sejunctella* cf. *lateseptata*; lateral view of the test the same in position as in Fig. 1. Crossed nicols, × 200.

Fig. 4. *Spirillina vivipara*; lateral view of the test showing permanent extinction. Crossed nicols, × 80.

Fig. 5. *Spirillina vivipara*; lateral view of three tests showing black cross with superimposed permanent extinction. Crossed nicols, × 80.

Fig. 6. *Spirillina* cf. *lucida*; lateral view showing a scattered black cross with curved arms. Crossed nicols, × 80.

Figs. 7—10. *Spirillina* sp.

7. Spiral view of the test showing a black cross with curved arms. Crossed nicols, × 200.
8. The same test as in Fig. 7. Transmitted light, × 200.
9. Spiral view of the test showing a black cross with curved arms. Crossed nicols, × 200.
10. The same test as in Fig. 9. Transmitted light, × 200.

Figs. 11, 12. *?Spirillina* sp.

11. Spiral view of the test showing a black cross with curved arms. Crossed nicols, × 200.
12. The same test as in Fig. 11. Transmitted light, × 200.

PLATE 2

Figs. 1—4. *Planispirillina* cf. *wrightii*

1. Lateral view of the test showing permanent extinction except for the central boss. Crossed nicols, × 200.
2. Lateral view of the test in the position of maximum of interference colours. Crossed nicols, × 200.
3. Lateral view of the test. The lamellar structure of the central boss is distinguishable. SEM micrograph, × 220.
4. Outer surface of the test wall showing the constant orientation of the calcite microcrystals in the monocrystalline structure. Treated with sodium hypochlorite for 48 hours. SEM micrograph, × 4 800.

Figs. 5, 6. *Spirillina vivipara*

5. Constantly orientated microcrystals on the outer surface of the test wall. Treated with sodium hypochlorite for 24 hours. SEM micrograph, × 8 000.
6. Vertical fracture plane of the test wall showing the constant orientation of the microcrystals of the monocrystalline structure. Treated as in Fig. 5. SEM micrograph, × 8 000.

PLATE 3

Figs. 1—6. *Spirillina vivipara*; all figures SEM micrographs.

1. Lateral view of a test without visible pores, × 320.
2. Lateral view of a coarsely perforated test, × 400.
3. Outer surface of the test wall showing needle-shaped crystallites oriented perpendicularly to the spiral plane of the test. Etched wit 25 % glutardialdehyde for 5 minutes, × 2 400.
4. View of the broken end of the tubular chamber; the needle-shaped crystallites are oriented perpendicularly to the spiral plane of the test. Etched as in Fig. 3, × 2 400.
5. Outer surface of the test wall showing needle-shaped crystallites oriented parallel to the spiral plane of the test wall. Etched as in Fig. 3, × 4 800.
6. Vertical fracture plane of the tubular chamber showing needle-shaped crystallites parallel to the spiral plane of the test. Etched as in Fig. 3, × 4 800.

PLATE 4

Figs. 1—4. *Spirillina* sp.; all figures SEM micrographs.

1. Outer surface of the test wall showing the orientation of the needle-shaped crystallites in the helicoidal structure. Etched with 25 % glutardialdehyde for 1½ minutes, × 4 000.
2. General view of the same specimen showing the location of Fig. 1 and distinct perforation; *p*, pores. × 350.
3. General view of the specimen in Fig. 4, × 640.
4. Outer surface of the test showing the orientation of the needle-shaped crystallites in the helicoidal structure. Etched with 25 % glutardialdehyde for 5 minutes, × 2 000.

PLATE 5

Figs. 1—4. *Spirillina* sp.; all figures SEM micrographs.

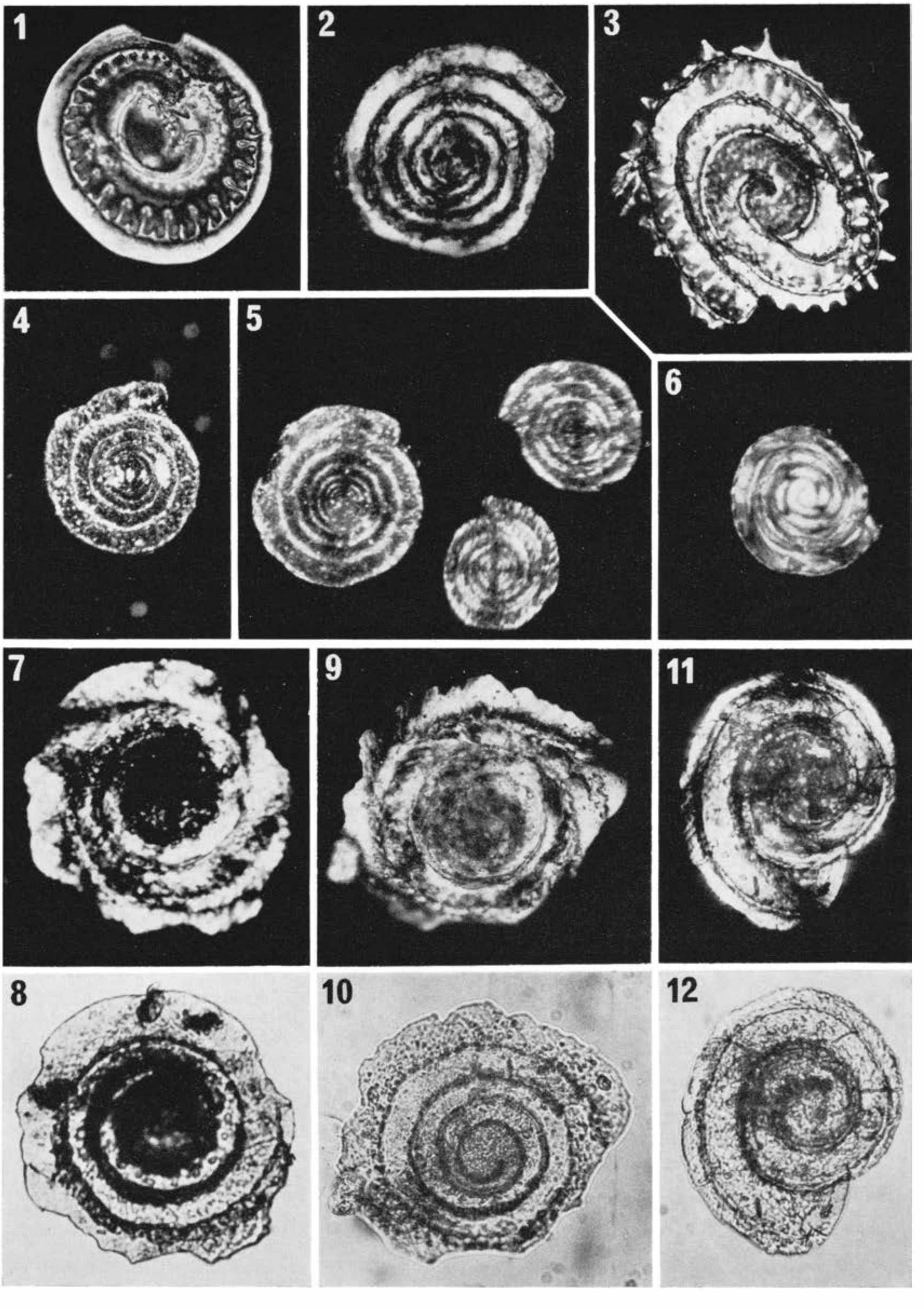
1. General view of the lateral side of an etched test showing the location of the micrographs in Figs. 2—4 indicate by the numbers in boxes, × 600.

2—4. Etched outer surface of the test showing needle-shaped crystallites differently oriented in different parts of the tests but with a constant inclination to the radial intersections of the test. The locations of Figs. 2, 3 and 4 are indicated in Fig. 1 with the same numbers. Etched with 25 % glutardialdehyde for 9 minutes, × 8 000.

Figs. 5, 6. *Spirillina vivipara*; all figures SEM micrographs.

5. General view of the test showing the oligocrystalline structure type. Crystal units are delimited by narrow interspaces. Etched with 25 % glutardialdehyde for 3 minutes, × 480.
6. Outer surface of the test wall with oligocrystalline structure type showing the different orientation of the needle-shaped crystallites in adjacent crystal units. Etched as in Fig. 5, × 4 000.

Plate I



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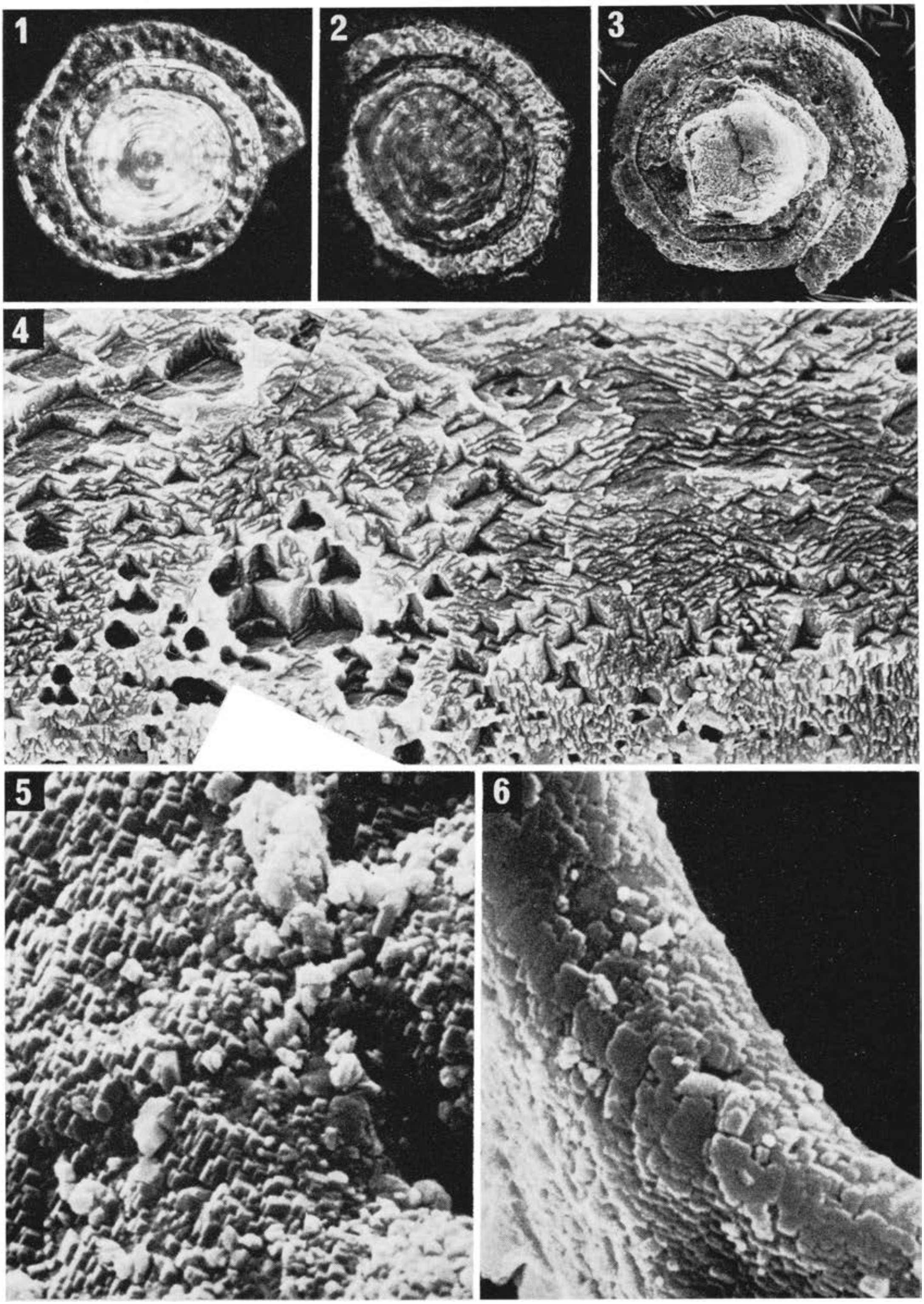

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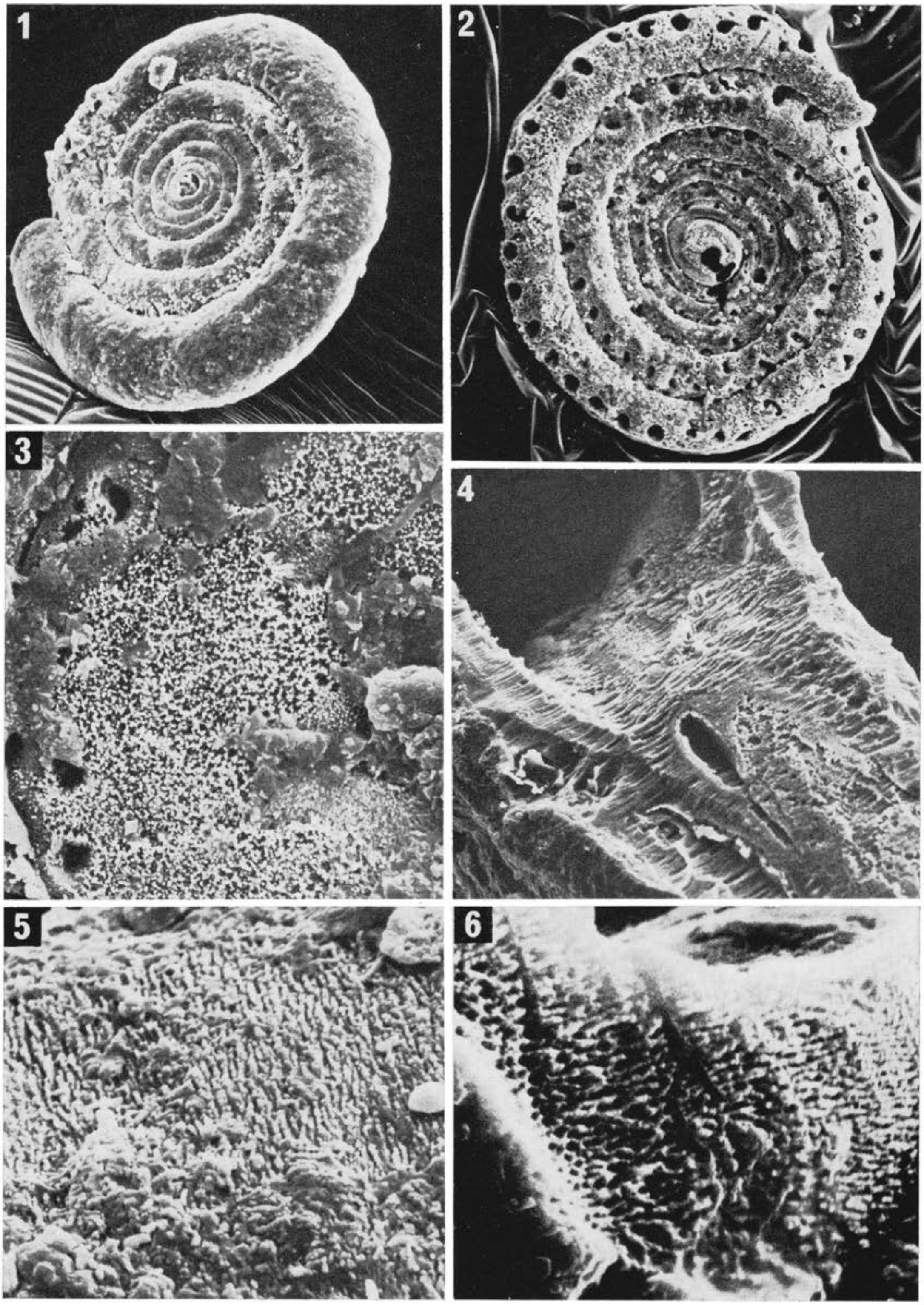

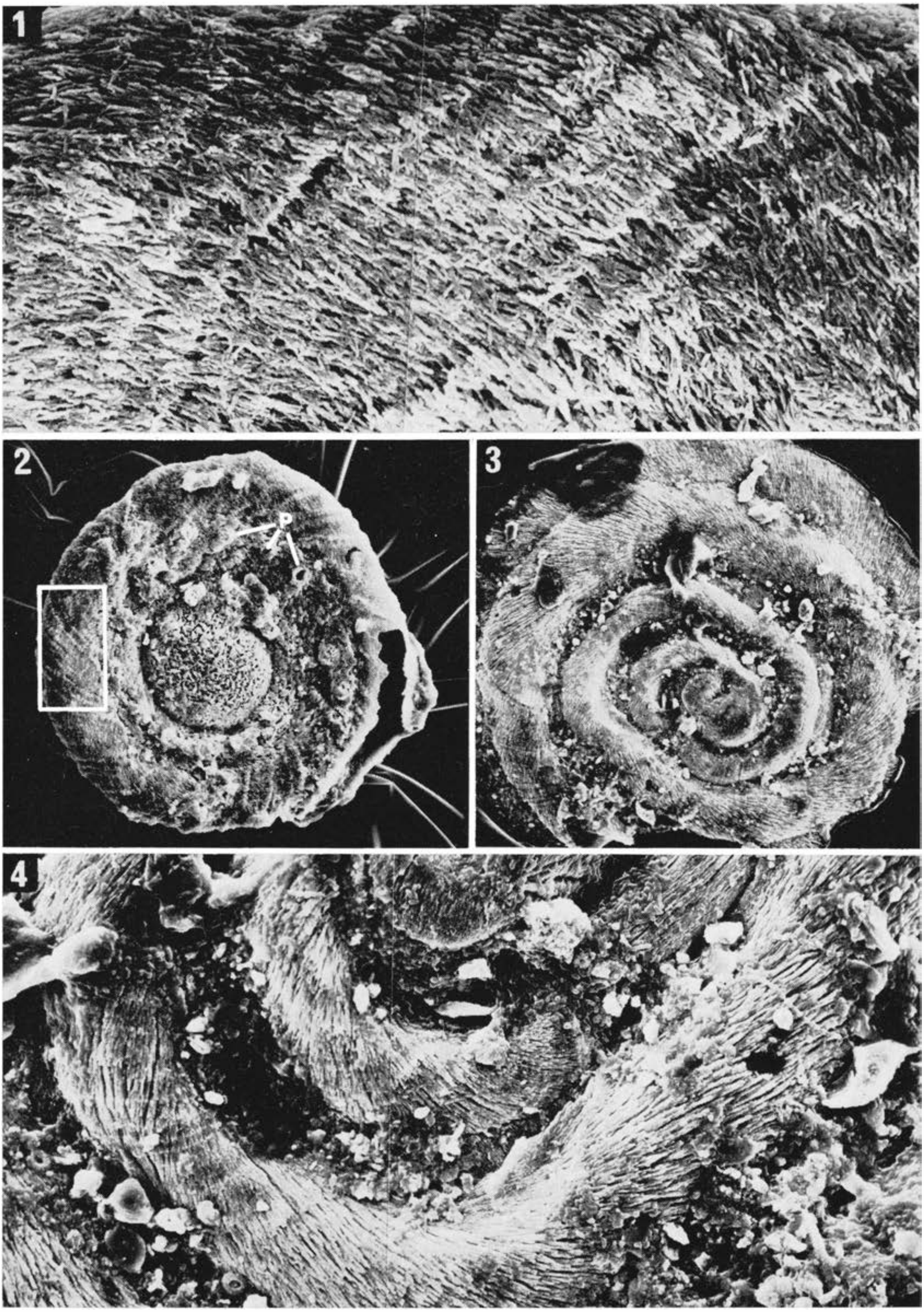
1
2
P
3
4

Plate V