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ULTRASTRUCTURAL STUDIES ON CEPHALOPOD SHELLS
PART I
The Septa and Siphonal Tube in *Nautilus*

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Abstract. The structure of the shell septa and wall of the siphonal tube in *Nautilus pompilius* L. is described on the basis of scanning electron microscope studies. Considerable structural variations of the shell layers, above all in the septal neck are recorded. Owing to these variations, it is, in places, difficult to distinguish the nacreous layer from the adjacent prismatic and spherulitic-prismatic layers. In all, eight varieties of the nacreous crystals are described.

It is demonstrated that the inner conchiolin layer of each connecting ring originates from the structurally modified nacreous layer of the contiguous septal neck. This conchiolin layer can therefore be regarded as an uncalcified nacreous layer. The structural relationship between the uncalcified and calcified nacreous layers in the siphonal tube of *Nautilus* is analogous to that between the ligament and calcified valves in lamellibranch shells.

During ontogenetic growth, the distal portion of the septal neck and the connecting ring are completed much earlier than the remaining parts of the septum. The functional advantage of this condition is discussed. A short comparison in the structure of the siphonal tube between *Nautilus* and fossil cephalopods is made.

INTRODUCTION

Nautilus (sub-class Tetrabranchiata) has a limited geographical distribution in the Pacific Ocean. It is the only genus of the living cephalopods which still possesses an unreduced, external shell to support and protect the soft body. The shell also functions as an hydrostatic apparatus by means of which the animal can undertake vertical migrations from the surface of the sea to the depths of probably 500—600 m. (Denton and Gilpin-Brown, 1966). For the latter function, the shell structure is more complex than that in other molluscs. Thus, the shell cavity is divided by calcareous septa into numerous chambers which are traversed by the siphonal tube. This tube is formed by a fusion between funnel shaped prolongations of the successive septa. In each chamber the siphonal tube is composed of the proximal, non-permeable septal neck and the distal, permeable connecting ring. The chambers are initially filled by a liquid which, in order to maintain the buoyancy of the animal, is osmotically pumped out through the permeable connecting rings into the siphonal cord, housed in the cavity of the siphonal tube (Denton and Gilpin-Brown, 1966). Porous layers of calcium carbonate and conchiolin in the septa and wall of the siphonal tube participate in this osmotic mechanism.

Cephalopods with unreduced, external shells were abundant in the Paleozoic and Mesozoic seas, and under long periods they dominate the invertebrate faunas. The structure of the siphonal tube in several of these extinct cephalopods seems to have been similar to that in *Nautilus*, whereas in others it has been somewhat different. A detailed knowledge on the shell structure in *Nautilus* is necessary for the analyses of these differences, and for their bearing on the hydrostatic mechanism.

Light microscopic studies on the structure of the *Nautilus* shell have been summarized in a previous paper (Mutvei, 1964*a*). Transmission electron microscope studies, based mainly on replica techniques, were published by Grégoire (1962). Recently, several structural details in the *Nautilus* shell have been investigated with scanning electron microscope by Erben *et al.* (1969), Wise (1969, 1970) and Mutvei (1970, 1972).

The present paper deals with scanning electron microscope studies on the structure of the septa and wall of the siphonal tube in *Nautilus*. Particular attention is paid to the structural variations of the shell layers, and on the relationship between the septal necks and connecting rings.

MATERIAL AND METHODS

The material investigated comprises several dry shells of *Nautilus pompilius* L., collected on the shores of the Solomon Islands, Pacific Ocean.

Preparations of surfaces and horizontal fracture planes. The surface of the septa, septal necks and connecting rings were cleaned from conchiolin with sodium hypochlorite, usually for about 10—15 minutes. After a thorough washing in tap water, the preparations were dried in air. They were then glued on preparation holders without a further treatment, or etched before the mounting with chromium sulphate in 15—30 seconds (Sundström, 1968; Mutvei, 1970, 1972). The preparations were coated with evaporated gold and studied with a scanning electron microscope STEREOSCAN (Cambridge Instruments Ltd.; abbreviated below to SEM) in the Swedish Museum of Natural History, Stockholm. For studies of horizontal fracture planes, pieces of shell were broken horizontally with a pair of tongs and then treated as the surface preparations. In other cases, pieces of shell were left overnight in sodium hypochlorite. After this treatment the conchiolin between the crystalline layers was dissolved and these layers could be separated from each other for preparations.

Preparations of polished sections. Pieces of shell were embedded in a transparent, cold setting plastic, Castolite (manufactured by the Castolite Co., Woodstock, Illinois, USA). The shell was then ground to a suitable level either vertically or tangentially, using a fine grained carborundum. The polishing of the sections was accomplished on a polishing machine by using diamond pastes of 7 microns and 0.25 micron grain size. The polished sections were etched with chromium sulphate (see above) in 15—30 seconds. After removal from the etching solution, the preparations were drained of excess solution with a filter paper and left to dry in air. The mounting and coating of the preparations were made in the same manner as for the preparations of the surfaces and fracture planes.

Other etching solutions, such as picrinic acid, uranyl acetate, phosphortungic acid, and a mixture of EDTA and 25 % glutaraldehyde, were also attempted on the polished sections, but with results inferior to those obtained with chromium sulphate.

Preparations of demineralized nacreous conchiolin. The inter-lamellar conchiolin membranes of the nacreous layer were demineralized in EDTA (Mutvei, 1970), washed in tap water and mounted on thin glass plates where they were left to dry. The mounting of the glass plates on the preparation holders, and the coating, were then done in the usual manner, as described above.

TERMINOLOGICAL AND STRUCTURAL REMARKS

The shell of *Nautilus* is composed of aragonitic crystals and conchiolin. Three principal aragonitic layers have been previously distinguished by light microscope studies of thin sections (Mutvei, 1964*a*), i.e. the spherulitic-prismatic, the nacreous, and the semi-prismatic layer.

The term 'semi-prismatic' was introduced by me for such layers in which the prisms have retained an uncomplicated structure. However, a detailed classification of the aragonitic prismatic structures has hitherto not been carried out. The term semi-prismatic is therefore here replaced by a more general term, prismatic, as suggested by Erben *et al.* (1969).

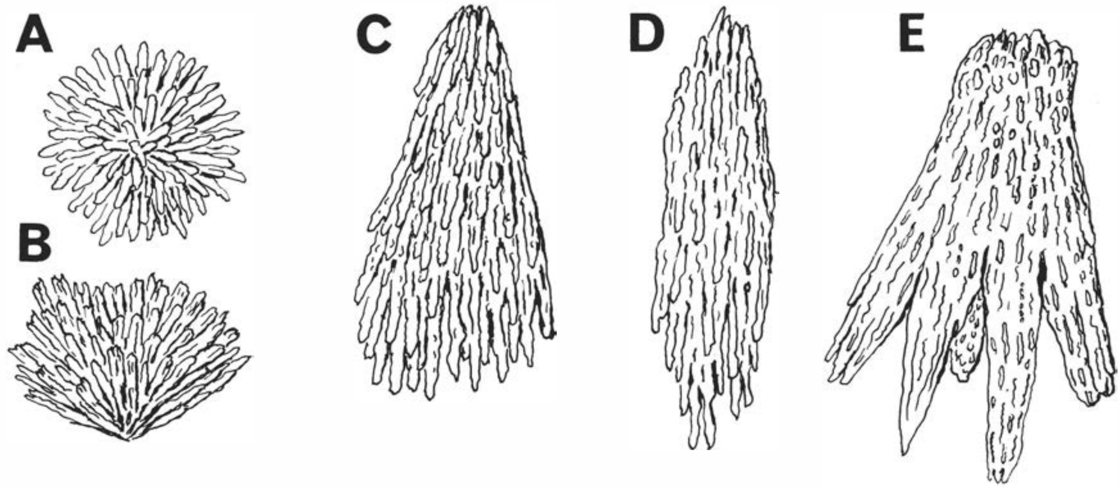

Fig. 1. Structural relationship between spherulites and prisms. *A*, spherulite with regular spherical orientation of the crystallites; *B*, incompelte spherulite with crystallites developed only in the upper half; *C*, prism composed of radiating crystallites; *D*, prism in which crystallites have a parallel arrangement; *E*, complex prism of several, partially fused minor prisms.

The spherulitic-prismatic and prismatic layers in the septa and siphonal tube consist of acicular crystallites. In complete spherulites, the crystallites are arranged spherically, radiating from a centre in all directions (Fig. 1 *A*). However, most spherulites tend to be incomplete (Fig. 1 *B*). Schmidt (1924) pointed out that the prisms can be ranked as incomplete spherulites. Here, only parts of the spherulites continue to grow and form bundles of crystallites (Fig. 1 *C*, *D*, *E*).

The typical nacreous crystals are tabular and often hexagonal in outline (Fig. 11 *A*). They are arranged in horizontal, consecutive mineral lamellae, separated by inter-lamellar conchiolin membranes. As demonstrated below (see also Mutvei, 1972), most nacreous crystals also consist of acicular crystallites which are arranged vertically to the crystal surfaces (Fig. 11 *A*).

Light microscope studies (Mutvei, 1964 *a*) show that boundaries between the spherulitic-prismatic, nacreous and prismatic layers in the septa and septal necks are often indistinct. Moreover, considerable structural variations occur within each of these layers. The nacreous layer may, in places, acquire a structure similar to that of the spherulitic-prismatic and prismatic layers, due to these variations, and *vice versa* (see also Mutvei, 1972).

The previously used terms, the inferior and superior divisions of the siphonal funnel, introduced by me to emphasize the structural continuity between these divisions (Mutvei, 1964 *a*), are now abandoned and replaced by the current terms, the septal neck and the connecting ring, respectively. The anatomical orientation of cephalopod shells has been discussed by me in several papers (e.g. Mutvei, 1964 *a*, 1967, 1971). According to this concept of orientation, which is also used here, the shell aperture is directed downwards and the shell apex upwards. The convex (adapical) face of the septum is therefore dorsal, and the septal necks and the connecting rings are directed upwards.

OBSERVATIONS

The Shell Septum Proper

The entire dorsal (convex, adapical) face of the septum is covered by a conchiolin layer which is about 1 micron thick in the ontogenetically younger septa (*d.c.l*, Fig. 4 *A*; Pl. 4, Figs. 1, 3). The structure of this layer is not dealt with in the present paper, but as shown by transmission electron microscope studies (Grégoire, 1962), it consists of fibrous membranes. The conchiolin

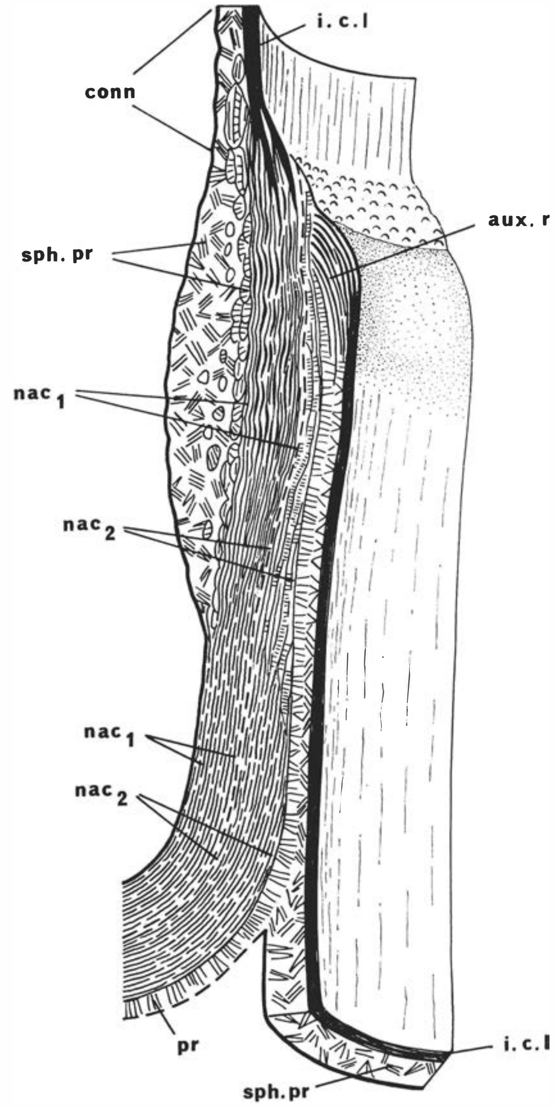

Fig. 2. Septal neck with parts of the contiguous and succeeding connecting rings. *aux.r,* auxiliary ridge; *conn,* connecting ring; *i.c.l,* inner conchiolin layer of the connecting ring; nac_1, nac_2, outer and inner nacreous sublayer of the septal neck, respectively; *pr,* inner prismatic layer of the septal neck; *sph.pr,* spherulitic-prismatic layer of the septal neck and connecting rings.

layer is succeeded by three aragonitic layers (Mutvei, 1964*a*), previously distinguished by light microscope studies of thin sections: (1) a dorsal, thin spherulitic-prismatic layer; (2) a thick nacreous layer; and (3) a ventral, thin prismatic layer. These three aragonitic layers were restudied in SEM preparations. Also the ventral (concave, adoral) face of the septum is covered by a conchiolin layer, but this is considerably thinner than the dorsal layer, and discontinuous in my preparations, covering only the distal ends of the ventral prisms.

The spherulitic-prismatic layer. This layer (*sph.pr,* Fig. 4*A*; Pl. 1, Figs. 1, 2) is always present in the peripheral, dorsal portion of the septum, adjacent to the shell wall. It forms a narrow zone, termed by Grégoire (1962) the sutural cements and infillings, and by Erben *et al.* (1969) the "Zwickelfüllung". It may be as much as 1/10 of the total thickness of the septum. As seen in surface preparations, its major structural elements are aragonitic prisms and spherulites. The prisms vary considerably in diameter and length, and lack a preferred orientation (Fig. 4*A*; Pl. 1, Fig. 1; Pl. 2, Fig. 1; Pl. 3, Figs. 3, 4). They may be partially fused (Pl. 3, Fig. 4), but narrower or wider interspaces remain between them. The prisms are composed of acicular crystallites, often fused with each other to form larger prismatic sub-units (Pl. 2, Fig. 1; Pl. 3, Figs. 3, 4). These crystallites and prismatic sub-units are oriented either parallel to the long axis of the prism (Pl. 3, Figs. 3, 4), or they radiate more or less distinctly towards one or both ends of the prism (Pl. 1, Fig. 1; Pl. 2, Fig. 1).

The spherulitic-prismatic layer rapidly decreases in thickness centrally, towards the siphonal tube (Fig. 4*A*; Pl. 1, Fig. 1). One or several terraces are formed on its centrally facing slope (Fig. 4*A*; Pl. 1, Fig. 2). The horizontal floors of these terraces were originally covered by conchiolin membranes (see below) which were removed by the treatment with sodium hypochlorite. These membranes have hindered the further growth of the prisms. On the floors of the terraces tabular aragonitic crystals were deposited between the conchiolin membranes (Fig. 4*B*; Pl. 2, Figs. 2, 3, 4, 5). These crystals are sparse, and they often occur in small stacks on the truncated ends of the prisms. Some of the tabular crystals show all the features typical for the nacreous crystals on the ventral septal face (compare Pl. 2, Figs. 3, 4 and Pl. 7,

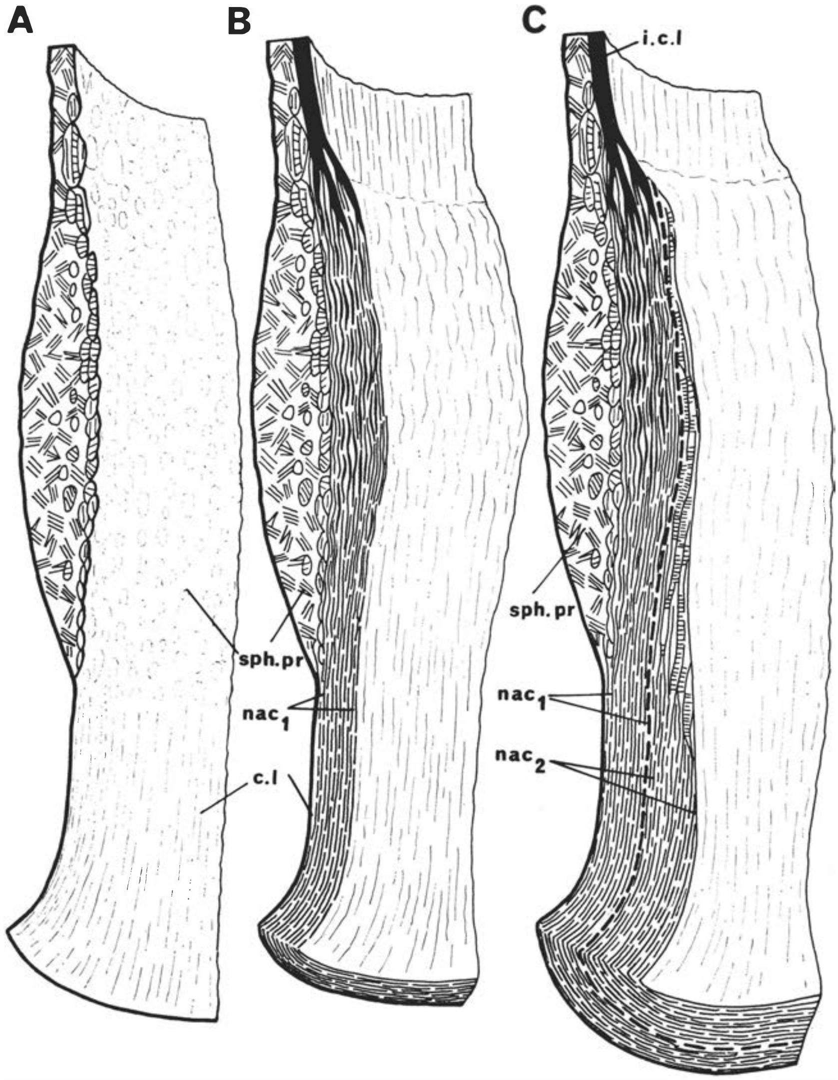

Fig. 3. Three successive growth stages of a septal neck and proximal part of the contiguous connecting ring (compare with *Fig. 2*). *A*, growth stage after the formation of the spherulitic-prismatic layer of the septal neck and connecting ring; *B*, growth stage after the formation of the outer nacreous sub-layer of the septal neck and the inner conchiolin layer of the connecting ring; *C*, growth stage after the formation of the inner nacreous sub-layer of the septal neck. *c.l*, conchiolin layer covering the surface of the septal neck and connecting ring; *i.c.l*, inner conchiolin layer of the connecting ring; nac_1, nac_2, outer and inner nacreous sub-layer of the septal neck, respectively; *sph.pr*, spherulitic prismatic layer of the septal neck and connecting ring.

Fig. 2). Thus, they are hexagonal in outline, and composed of aragonitic granules of about 0.1—0.2 micron in diameter (Figs. 4*B*, 8*B*; Pl. 2, Fig. 4). In addition to the tabular crystals, small accumulations of aragonitic granules occur, scattered over the horizontal floors of the terraces (Pl. 1, Fig. 2). These granular accumulations may be initial growth stages of the granular, tabular crystals already described.

The peripheral, thickened portion of the spherulitic-prismatic layer was also studied in polished vertical sections, etched with chromium sulphate. These preparations show that this layer is traversed by several horizontal conchiolin membranes with

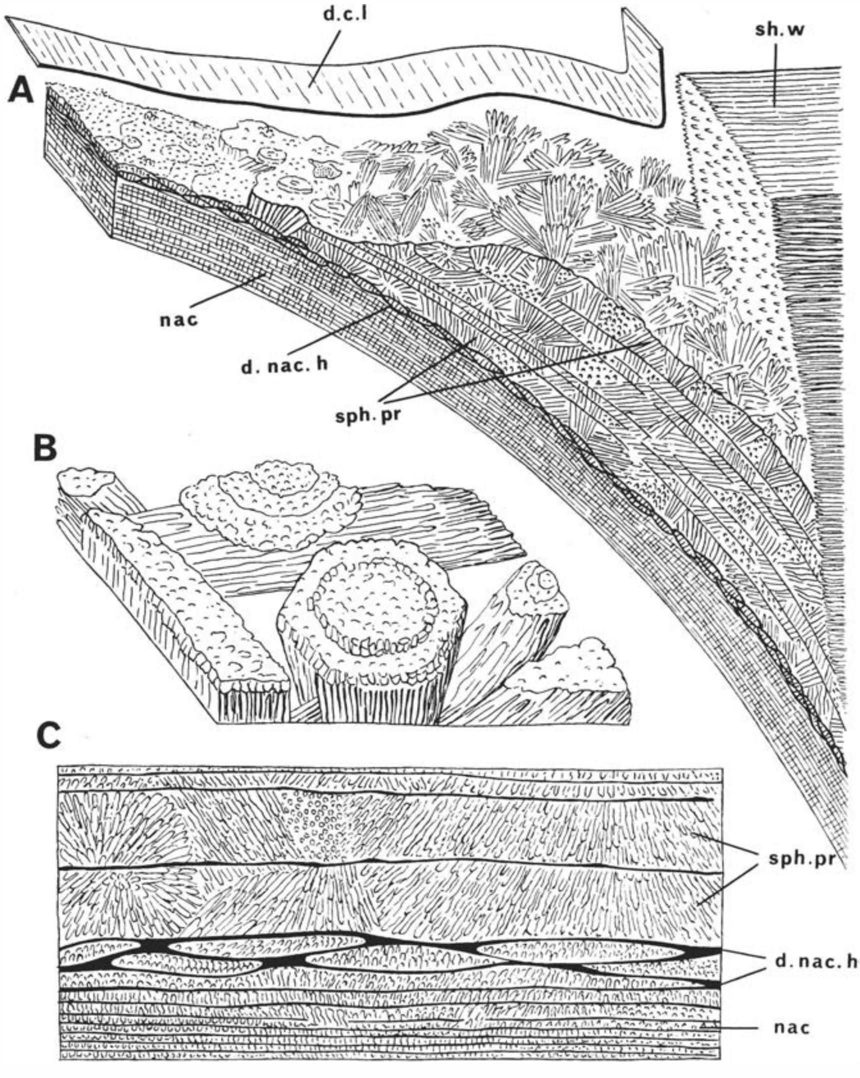

Fig. 4. A, block diagram to show the dorsal conchiolin layer of the septum, the thickened, peripheral portion of the spherulitic-prismatic layer of the septum, and parts of the septal nacreous layer and shell wall (approx. × 700). *B*, detail of *Fig. A*, showing stacks of tabular crystals on truncated ends of prisms (approx. × 10 000); *C*, detail of the vertical section in *Fig. A* to show arrangement of horizontal conchiolin membranes and crystallites in the spherulitic-prismatic layer and in the adjacent nacreous layer (approx. × 8 000).
d.c.l, dorsal conchiolin layer of the septum; *d.nach.h*, dorsal, structurally modified stratum of the septal nacreous layer; *nac*, septal nacreous layer; *sh.w*, shell wall; *sph.pr*, thickened, peripheral portion of the spherulitic-prismatic layer of the septum.

irregular spacing (*sph.pr*, Fig. 4 *A*, *C*; Pl. 5, Figs. 1, 4). These membranes do not interrupt the growth of the prisms and spherulites, except on the centrally facing terraces, described above. The prisms and spherulites are composed of acicular crystallites, about 0.1—0.2 micron in diameter. Apparently, these crystallites have arisen by a fusion of globular aragonitic granules (Fig. 11 *B*; *sph.pr*, Pl. 5, Fig. 4). The layer in question may be predominantly spherulitic in composition in its thinner, central portion (*sph.pr*, Pl. 4, Figs. 1, 2, 4). The spherulites consist of radiating acicular crystallites, and they are traversed by several horizontal conchiolin membranes which do not interrupt their growth. Similar spherulites, composed of acicular crystallites, were described in the corresponding portion of the spherulitic-prismatic layer in a previous paper (Mutvei, 1972, Text-fig. 1 *B*; Pl. 2, Fig. 1).

In the remaining, main portion of the septum, the spherulitic-prismatic layer is often absent, and the dorsal conchiolin layer is immediately succeeded by a dorsal, structurally modified stratum of the nacreous layer (*d.c.l*, *nac*, Fig. 5 *A*; Pl. 4, Fig. 3). However, in one of my preparations, the spherulitic-prismatic layer forms a broad zone which extends from the thickened, peripheral portion in the central direction. This layer is here very thin and composed of groups of spherically arranged acicular crystallites (Pl. 3, Fig. 1). In another preparation, the spherulitic-prismatic layer forms a broad zone in the central portion of the septum. It consists of large, porous prisms, up to 8—10 microns in diameter. The prisms are separated by narrower or wider interspaces, and

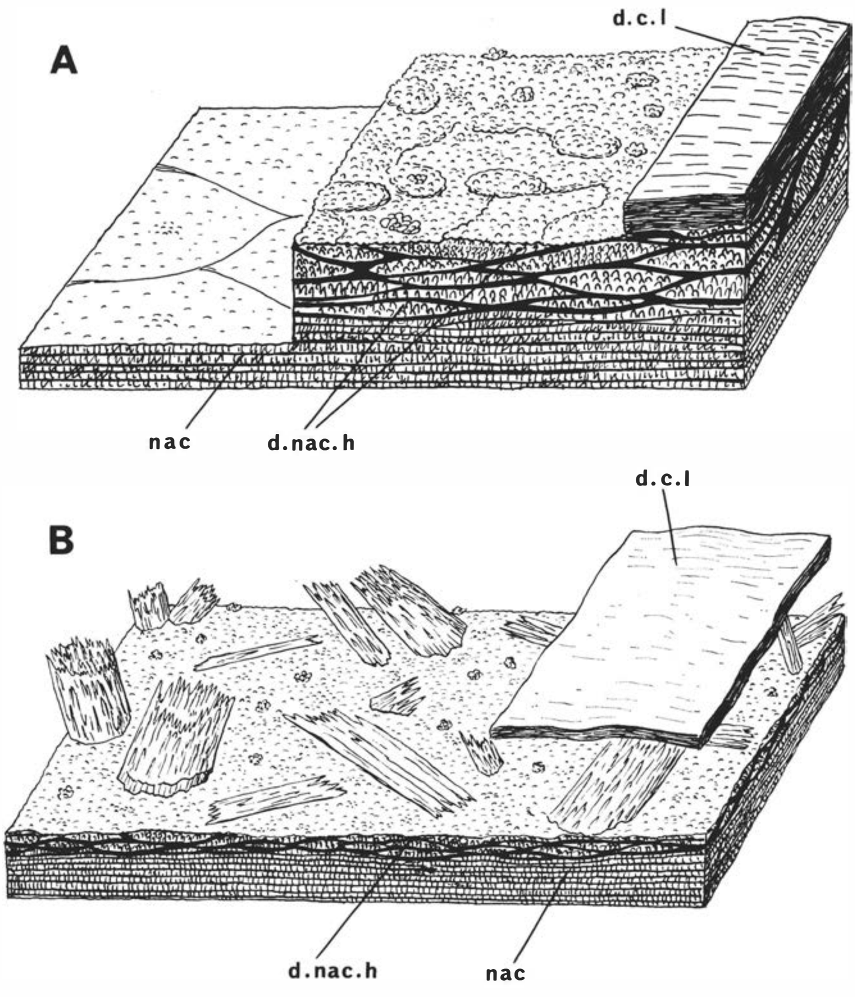

Fig. 5. A, block diagram of the dorsal portion of a septum, showing the dorsal conchiolin layer and the succeeding nacreous layer with its dorsal, structurally modified stratum (approx. × 5000). *B*, similar block diagram as in *Fig. A* to show the spherulitic-prismatic layer which occasionally is developed between the dorsal conchiolin layer and the nacreous layer (approx. × 2000). *d.c.l*, dorsal conchiolin layer of the septum; *d.nac.h*, dorsal, structurally modified nacreous stratum; *nac*, septal nacreous layer.

composed of numerous acicular crystallites (Fig. 5 *B*; Pl. 6, Figs. 5, 6). They have a highly variable orientation in relation to the succeeding nacreous layer.

Erben *et al.* (1969) were not able to find the spherulitic-prismatic layer in the main, dorsal portion of the septum. This can be explained by the fact that in most septa the layer in question is absent, except most peripherally, adjacent to the shell wall.

The nacreous layer. Vertical polished sections show that the dorsal part of the nacreous layer forms a structurally modified stratum which, in the ontogenetically younger septa, is 3—5 microns thick. This stratum is characterized by the occurrence of unusually thick, inter-lamellar conchiolin membranes with an undulating course, and which therefore coalesce in places with each other (*d.nac.h*, Figs. 4 *A*, *C*; 5 *A*, *B*; Pl. 4, Figs. 1, 2, 3; Pl. 5, Figs. 1, 4). The interspaces between the conchiolin membranes are occupied by tabular nacreous crystals, composed of globular aragonitic granules (*d.nac.h*, Pl. 4, Fig. 3). These crystals were also studied in surface preparations, in which both the dorsal conchiolin layer of the septum and the inter-lamellar conchiolin membranes within the stratum in question were removed by a treatment with sodium hypochlorite. After this treatment, the dorsal septal face shows a dull, milkish-white lustre which differs from the bright, iridescent lustre of the typical nacreous layer. The nacreous crystals in the dorsal stratum have a tabular shape (Fig. 8 *C*). The boundaries between the adjacent crystals are irregular and often difficult to distinguish (*d.nac.h*, Fig. 5 *A*; Pl. 3, Figs. 5, 6; Pl. 6, Figs. 3, 4). The crystals are composed of globular aragonitic granules without a preferred arrangement. Most of these granules have a diameter of 0.1—0.2 micron, but both larger and smaller granules occur in places (Pl. 3, Figs. 5, 6; Pl. 6, Fig. 4). The most dorsally situated crystals in this stratum are composed of small accumulations of aragonitic granules (Pl. 6, Fig. 4).

The dorsal, structurally modified stratum is succeeded by the typical nacreous layer in which the inter-lamellar conchiolin membranes become thin and regularly spaced. However, the conchiolin membranes may still have a slightly undulating course at the boundary region, close to the dorsal stratum (*nac*, Pl. 4, Figs. 1, 2, 3; Pl. 5, Fig. 1). Moreover, in peripheral parts of the septum the nacreous structure is in places interrupted by inclusions of prism-like elements, composed of acicular crystallites. These crystallites may be oriented parallel to each other, at right angles to the nacreous lamellation (*pr.i*, Pl. 5, Fig. 2), or they may have a more or less distinct radial arrangement (*nac*, Pl. 5, Fig. 1).

The shape, structure and arrangement of the typical nacreous crystals in the septa have been described in several papers (Grégoire, 1962; Erben *et al.*, 1969; Wise, 1969, 1970; Mutvei, 1970, 1972). These crystals are larger than those in the shell wall. Most crystals are composed of acicular crystallites, oriented parallel to the c-axes, and arranged into rows (laths), parallel to the a-axes. The acicular crystallites seem to consist of fused aragonitic granulates (Fig. 11 *A*).

The nacreous crystals are best exposed on the ventral (adoral) face of the nacreous layer, where they have retained various stages of their growth. As already pointed out by Grégoire (1962, Text-fig. 2), these crystals have regular hexagonal outlines, and they are elongated along their a-axes (Fig. 8 *A*; Pl. 7, Figs. 1, 3). The direction of a-axes are different in adjacent groups of the crystals. Occasionally, the crystals in the same group may change their directions (Pl. 7, Fig. 3). Most of the crystals are composed of globular aragonite granules, about 0.1—0.2 micron in diameter (Pl. 7, Fig. 2). The granular composition is particularly pronounced in the crystals which were etched with chromium sulphate, but it can often be distinctly observed also in the side faces of unetched crystals. These granules seem to lack a preferred orientation in surface views. However, a distinct vertical orientation of the granules is always present in vertical polished sections (*nac*, Pl. 22, Fig. 1). The granules within the crystals appear as tubercles on the crystal faces (Pl. 7, Fig. 3).

The prismatic layer. Ontogenetically, this layer is the last formed of the aragonitic layers, and it coats the ventral (concave, adoral) face of each septum (Fig. 6). It is composed of vertical prisms

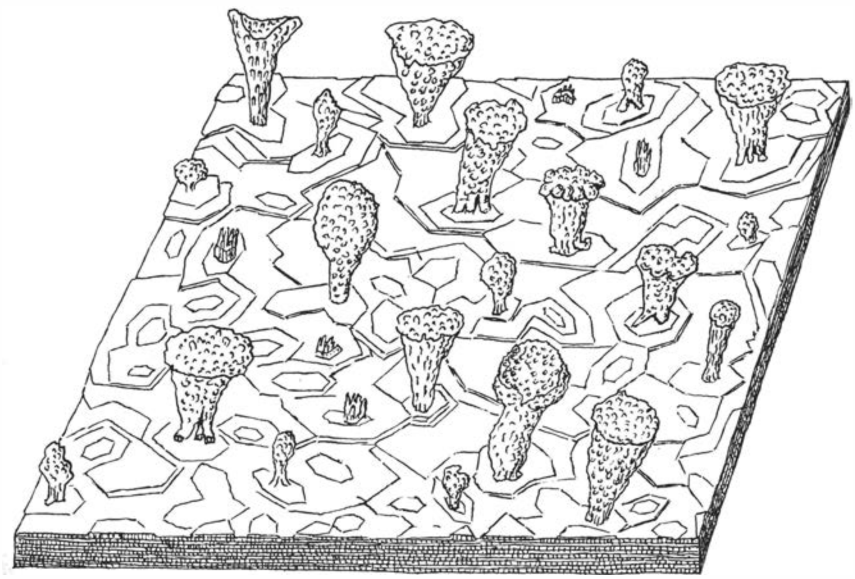

Fig. 6. Block diagram of the ventral face of a septum, showing various shapes of the prisms in the porous, ventral prismatic layer (approx. × 1 000).

which grow on the tabular crystals of the preceding nacreous layer. The prisms are occasionally sufficiently numerous to form a continuous layer. In most cases, they are scattered over the ventral septal face with varying densities, and arranged in rows of varying patterns (Fig. 6; Pl. 8, Fig. 1). The fully developed prisms have highly variable shapes. The may be club-shaped (Erben *et al.*, 1969, Pl. 12, Fig. 2), or conical (Pl. 8, Figs. 3, 6). In several cases they are mushroom-like in having a columnar basal portion and an irregularly expanding distal portion (Pl. 9, Figs. 3, 5). In rare cases they have a thin, stalk-like base and a vase-shaped distal portion (Pl. 8, Fig. 2). The various prisms can be solid, or provided with a wide cavity along their central axes (Pl. 8, Fig. 5; Pl. 9, Fig. 6). The prisms always have uneven surfaces. They show vertical, acicular crystallites (Pl. 8, Fig. 3) or vertical rows of globular and angular granules of various sizes (Pl. 8, Fig. 4).

The prisms have a mineral structure identical to that of the adjacent nacreous crystals in vertical polished sections, etched with chromium sulphate. As in these crystals, the prisms are composed of acicular crystallites which seem to have arisen by a fusion of aragonitic granules (*pr*, Pl. 22, Fig. 1).

Among the fully developed prisms, there are several the growth of which has stopped at various stages (Fig. 6; Pl. 8, Fig. 5; Pl. 9, Figs. 1, 2). At their incipient growth stages, the prisms show certain similarities with the nacreous crystals on which they grow. Like those, they are tabular and sometimes somewhat hexagonal in outline (Pl. 9, Figs. 1, 2, 3). They differ from the nacreous crystals in being considerably higher and having uneven ventral surfaces. During their further growth, the prisms increase in height. This often takes place at different rates in different parts of the prism. As a result, prisms of highly irregular shape are formed. Parts of such prisms may consist of several high peaks, whereas other parts remain at their incipient growth levels (Pl. 9, Fig. 2). The high peaks of two or several of the adjacent prisms may fuse and form the basal portion of the fully developed prism (Pl. 9, Figs. 3, 4, 5).

The Siphonal Tube

Each shell septum forms a narrow, funnel-shaped, central prolongation which extends upwards and consists of a proximal, non-permeable division, and a distal permeable division. These two divisions are currently termed the septal neck and the connecting ring, respectively (Fig. 2). The most distal portion of the connecting ring projects into the septal neck of the preceding septum and is fused to the auxiliary ridge on its inner face (*aux.r*, Fig. 2). In this manner, the successive septa form the continuous siphonal tube which extends from the domiciliary cavity to the shell apex. The cavity of the siphonal tube is occupied by a cord of soft tissue from the body proper.

The septal neck

The septal neck consists of the same three, principal aragonitic layers as the septum proper, *i.e.* the outer spherulitic-prismatic, the nacreous, and the inner prismatic layer (*sph.pr*, *nac*, *pr*, Fig. 2). However, these layers undergo here considerable structural modifications, described in the following

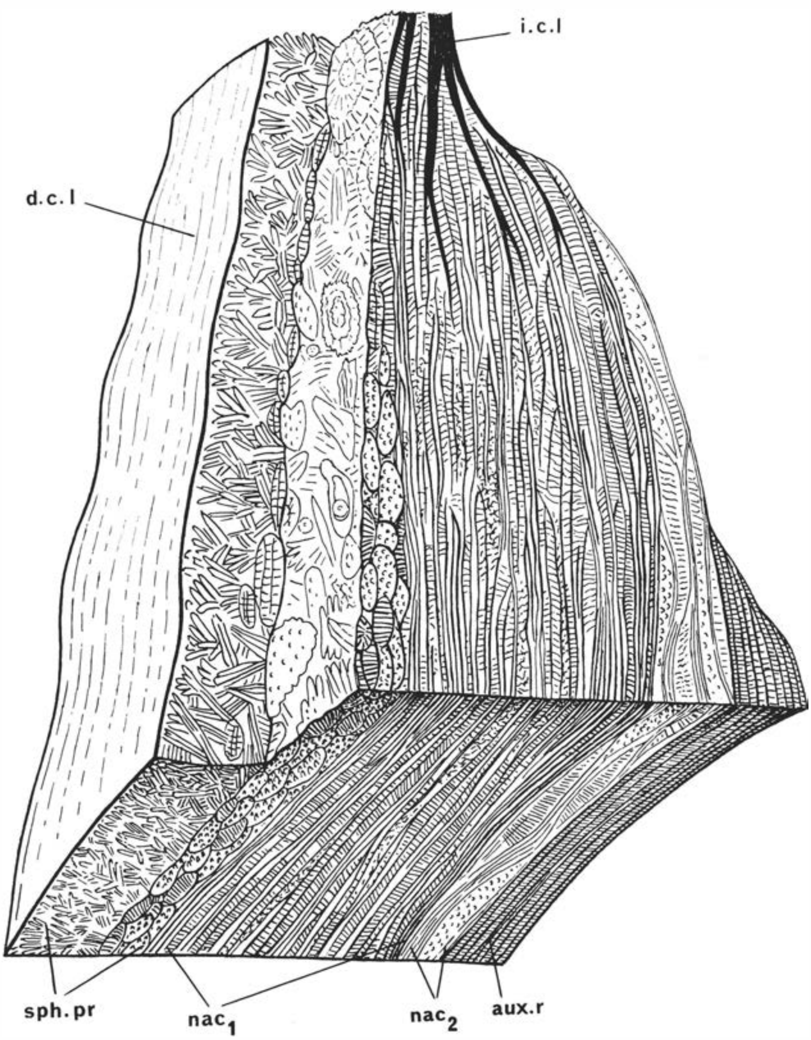

Fig. 7. Block diagram of the distal end of a septal neck and its structural relationship to the contiguous connecting ring (approx. × 800).
aux.r, auxiliary ridge; *d.c.l*, outer conchiolin layer; *i.c.l*, inner conchiolin layer of the connecting ring; *nac_1*, *nac_2*, outer and inner nacreous sub-layers of the septal neck, respectively; *sph.pr*, spherulitic-prismatic layer of the septal neck and connecting ring.

in SEM preparations. Externally the septal neck is covered by a thin conchiolin layer (*d.c.l*, Fig. 7) which is a direct continuation of that layer on the dorsal septal face.

The spherulitic-prismatic layer. With few exceptions, this layer is absent in the proximal portion of the septal neck, but in the distal portion it is always present (*sph.pr*, Fig. 2; Pl. 10, Figs. 1, 2). It increases rapidly in thickness in the distal direction and forms often a ridge with an uneven surface around the septal neck (*sph.pr*, Fig. 2; cf. Mutvei, 1964 *a*, Pl. 12, Fig. 1; Pl. 13, Fig. 1). Its thickness may attain half that of the septal neck in the ontogenetically younger septa, but it is usually thinner in the ontogenetically older septa. In the outer (peripheral) parts of the septal neck, the dominating structural elements of this layer are the long and slender aragonitic prisms (*sph.pr*, Fig. 7). These prisms vary considerably in size, and lack a preferred orientation (Pl. 11, Figs. 1, 3; Pl. 12, Figs. 4, 5). In some strata, the prisms attain a length of 40 microns and a diameter of 5 microns, but in other strata they are smaller. Many of the prisms are partially fused with one or several adjacent prisms (Pl. 12, Fig. 4). However, since numerous interspaces always remain between the prisms, the layer in question is highly porous. In a few places, these interspaces are traversed by conchiolin membranes. Prismatic sub-units, composed of several acicular crystallites, can be clearly distinguished in many prisms (Pl. 11, Figs. 1, 2, 3, 4; Pl. 12, Fig. 5). The diameters of these sub-units vary from 0.3 to 0.8 micron. They can be oriented parallel to the long axes of the prisms (Pl. 11, Figs. 1, 3; Pl. 12, Fig. 5), or they radiate towards one, or both ends of the prisms. The surfaces of the prismatic sub-units form often globular swellings (Pl. 11, Figs. 2, 4).

The prisms acquire a discoidal (Pl. 6, Fig. 1) or irregular (Pl. 6, Fig. 2) shape towards the succeeding nacreous layer. In addition, several of these prisms are larger, and they become fused with the adjacent prisms more extensively than those in the outer parts of the spherulitic-prismatic layer. Moreover, the prisms in question seem to contain much conchiolin matrix, in which the crystalline sub-units are embedded.

The prisms are cut at various angles in vertical polished sections of the septal neck (*sph.pr*, Fig. 7; Pl. 10, Figs. 1, 2; Pl. 13, Figs. 1, 2, 3, 4). From these sections, information was gained on the boundary region between the spherulitic-prismatic and the succeeding nacreous layer. It is clearly seen that the prisms in this region are fused to an almost compact layer (Pl. 13, Figs. 1, 2, 4). Most prisms are encased by conchiolin membranes (Pl. 13, Figs. 1, 2) which become continuous and parallel to each other at the actual boundary (*sph.pr*, *nac*, Pl. 13, Fig. 4). At the distal end of the septal neck, the structure of the inner parts of the spherulitic-prismatic layer resembles in places that of the nacreous layer. Stacks of large, tabular crystals, separated by conchiolin membranes occur (*sph.pr*, Fig. 7; Pl. 14, Figs. 1, 3, 4). Narrower or wider interspaces, which are partly occupied by conchiolin matrix, remain between the adjacent crystal stacks (Pl. 14, Fig. 3). The tabular crystals in a stack consist of acicular crystallites, which usually have a distinct radial arrangement (Pl. 14, Figs. 3, 4). These crystallites have uneven suraces in vertical sections, and seem to be composed of fused aragonitic granules (Pl. 14, Fig. 2).

The proximal nacreous layer. In the proximal portion of the septal neck, the main part of the nacreous layer still has the same structure as that in the adjacent septum proper. However, in the inner stratum of the nacreous layer, close to the succeeding prismatic layer, the nacreous crystals exhibit considerable morphological variation, not observed in the corresponding stratum of the septum. The following five crystal varieties occur here. (1) Large, solid tabular crystals which at their two opposite endes have several distinct spinous projections (Fig. 8 *E*; Pl. 15, Fig. 1). The surfaces of these crystals are parallely striated and there are rows of small, indistinct tubercles. The striation and rows of tubercles have the same orientation as the spinous projections at the crystal ends. Some of the tabular crystals under discussion are stacked upon each other so as to form vertical crystal columns (Pl. 15, Fig. 1), whereas others

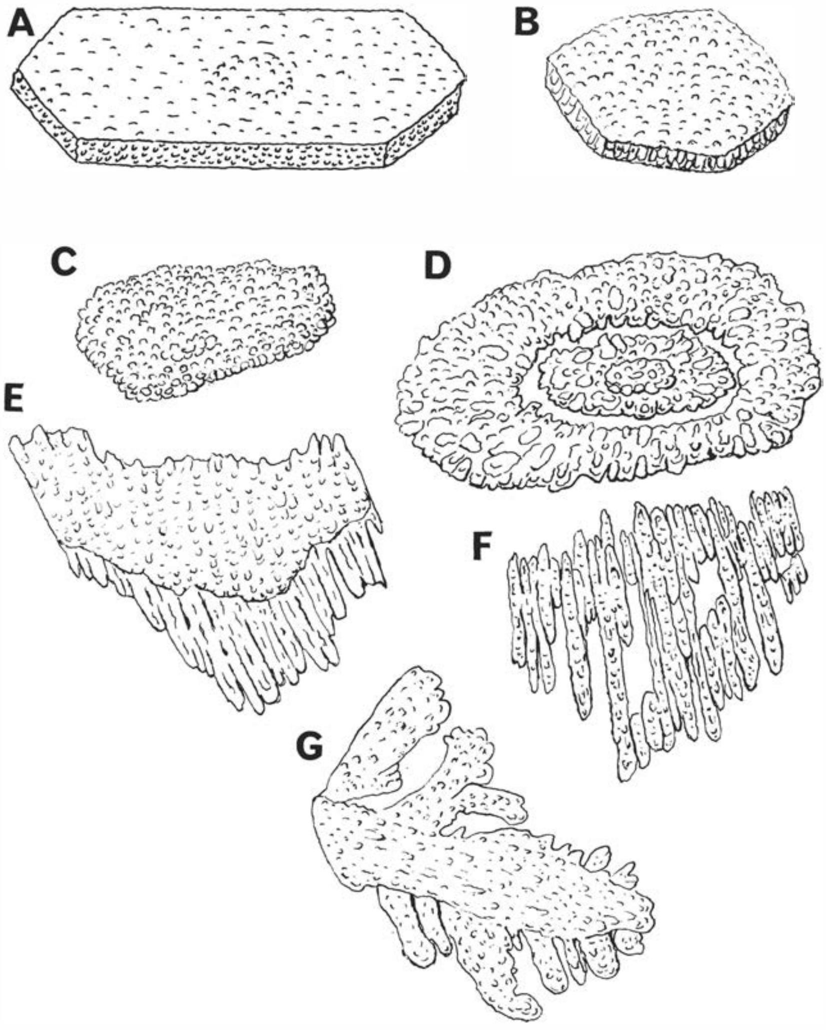

Fig. 8. Morphological variations of the nacreous crystals.

lack such an arrangement and, in addition, lack a preferred orientation with regard to their a-axes. (2) Among the solid, tabular crystals, just described, tabular, somewhat porous crystals are found. The latter crystals are composed of numerous, parallel horizontal laths, about 0.2—0.5 micron in breath (Fig. 8 *F*; Pl. 15, Fig. 3; Pl. 16, Fig. 1). The adjacent laths in a crystal are separated by furrows or narrow interspaces. Since the laths in the crystals are of variable length, the crystal ends are irregular in shape. It is obvious that the laths correspond to the spinous end-projections in the crystals of the first variety. (3) In places, the nacreous crystals are developed as typical dendrites, in that they are composed of a long axial plate and numerous, shorter or longer side branches, arranged in a feather-like manner (Fig. 8 *G*; Pl. 15, Figs. 2, 4; Pl. 16, Figs. 2, 4). Other dendritic crystals have a smaller number of side branches, or consist only of an axial plate. The latter crystals may be deposited irregularly upon each other so as to form a porous meshwork (Pl. 16, Fig. 3). (4) In several places, the nacreous layer is composed of consecutive lamellae of tabular, distinctly granular crystals with irregular outlines (Pl. 15, Fig. 4; Pl. 16, Figs. 2, 4). These crystals resemble those in the dorsal, structurally modified stratum of the septal nacreous layer (cf. Pl. 3, Figs. 5, 6; Pl. 6, Figs. 3, 4). The aragonitic granules within these crystals are mostly globular and about 0.1—0.2 micron in diameter. The boundaries between the adjacent crystals are usually indistinct. The dendritic crystals, already described, are often intercalated between the lamellae of the granular crystals (Pl. 16, Fig. 2). On the inner face of the nacreous layer, adjacent to the succeeding prismatic layer, the granular crystals attain a large diameter. In addition, the central part of most crystals is pronouncely elevated towards the prismatic layer. This elevation appears on the opposite crystal face as a deep concavity (Pl. 17, Figs. 1, 4). (5) Among the granular crystals on the inner face of the nacreous layer, already described, another type of granular crystal occurs. The latter crystals are large, attaining a diameter of 20—30 microns. They are composed of several concentric plates (Fig. 8 *D*; Pl. 17, Fig. 3) consisting of large aragonitic granules, 0.2—0.3 micron in diameter (Pl. 17, Fig. 2).

The variations in the morphology of the nacreous crystals, described above, are closely related to the amount of conchiolin matrix present. Thus, the adjacent crystals of the varieties (1), (2) and (3) are usually separated by wide interspaces, not occupied by conchiolin matrix (Pl. 15, Figs. 1, 2, 3; Pl. 16, Figs. 1, 2, 3). The granular crystals of the varieties (4) and (5), on the other hand, seem to be embedded in conchiolin matrix (Pl. 15, Fig. 4; Pl. 16, Figs. 2, 4; Pl. 17, Figs. 1, 2, 3, 4).

The distal nacreous layer. The nacreous layer in the distal portion of the septal neck can be subdivided into two sub-layers, here termed the outer and the inner sub-layer, on the basis of differences in growth rate and structure (nac_1, nac_2, Fig. 2; Pl. 10, Figs. 1, 2).

The outer sub-layer, which corresponds to only about 1/3 of the total thickness of the septal nacreous layer, gradually increases in thickness upwards and is ultimately the main component of the most distal portion of the septal neck (nac_1, Fig. 2). Its content of conchiolin matrix increases considerably in the same direction. Owing to the latter condition, the nacreous crystals in this sublayer become greatly modified. Three crystal varieties can be distinguished on the fracture planes, partially freed from the conchiolin matrix by a treatment with sodium hypochlorite, although the total number of crystal varieties is probably higher. (1) Granular, tabular crystals of the some appearance as those in the dorsal, structurally modified stratum of the septal nacreous layer (p. 244) and in the inner stratum of the nacreous layer of the proximal portion of the septal neck (p. 248). (2) Large, tabular nacreous crystals, up to 40 microns in diameter, composed of thin, vertical, closely packed lamellae. These lamellae, which seem to be about 0.2 micron thick, radiate from a central elevated area of the crystal (Fig. 10 *B*; Pl. 19, Figs. 3, 4). The boundaries between the crystals are indistinct, and the vertical lamellae from the adjacent crystals seem to interlock. Occasionally, other lamellar crystals occur which are much smaller than the former, and which are intercalated between the granular crystals of the first variety (Pl. 20, Fig. 5). (3) Large crystals, about 20—30 microns in diameter, in which the acicular crystallites and prismatic sub-units show a distinctly radial arrangement (Fig. 10 *A*; Pl. 7, Figs. 4, 5, 6; Pl. 13, Fig. 5; Pl. 19, Figs. 1, 2). The crystallites and prismatic sub-units have a diameter of 0.2—0.4 micron, and they are embedded in conchiolin matrix.

Studies of vertical polished sections, etched with chromium sulphate, supply evidence on the conchiolin matrix around and within the nacreous crystals in the outer nacreous sub-layer (nac_1, Fig. 7; Pl. 21, Fig. 1; Pl. 25, Figs. 1, 2). The conchiolin matrix appears here as a network of mostly thick conchiolin membranes (Pl. 21, Figs. 2, 3, 4; Pl. 22, Fig. 6; Pl. 23, Fig. 3). The crystals and their crystalline components, described above in the fracture planes, originally occupied the interspaces between these membranes, but were dissolved by the etching with chromium sulphate.

The inner sub-layer is a continuation of the ventral part of the nacreous layer in the septum, where it originally comprises about 2/3 of the total thickness of the nacreous layer. This sub-layer decreases gradually in thickness and ultimately wedges out towards the distal end of the septal neck (*nac*$_2$, Fig. 2; Pl. 10, Figs. 1, 2). The tub-layer in question becomes more and more prismatic as it decreases in thickness. This transformation takes place in such a way that the inter-lamellar conchiolin membranes in several strata disappear and are replaced by thinner or thicker prismatic strata, composed of acicular crystallites (Pl. 3, Fig. 2). Thus the inner nacreous sub-layer is composed of alternating prismatic and nacreous strata in the distal portion of the septal neck (*nac*$_2$, Figs. 7, 9; Pl. 18, Fig. 4). The acicular crystallites within the prismatic strata are about 0.1—0.2 micron in diameter: they show a highly variable orientation (Pl. 18, Figs. 4, 5).

The prismatic layer. Ontogenetically, this is the last-formed layer of the septal neck, and it coats the inner face thereof (*pr*, Figs. 2, 9; Pl. 10, Fig. 2). It is a direct continuation of that layer on the ventral septal face. It consists of aragonitic prisms which usually are more numerous and have a less complicated shape than those on the ventral septal face. Most prisms are oriented about vertically to the surface of the preceding nacreous layer (*pr*, Pl. 22, Figs. 3, 4), but some may have an oblique orientation (*pr*, Fig. 9; Pl. 22, Fig. 2; Pl. 23, Fig. 1). The prisms are composed of acicular crystallites which are about 0.2 micron in diameter (Pl. 22, Figs. 2, 5). The basal portions of the prisms are traversed by a varying number of parallel, irregularly spaced conchiolin membranes which in vertical sections have the same appearance as the inter-lamellar conchiolin membranes in the adjacent nacreous layer (*pr*, *nac*, Pl. 22, Figs. 2, 4, 5). Distally, the prismatic layer is fused to the auxiliary ridge, dealt with below (*pr*, *aux.r*, Fig. 9; Pl. 23, Fig. 1).

The connecting ring

The connecting ring is structurally the most modified part of the septum, being permeable for gas and liquid (*conn*, Fig. 2). It is composed of two layers: the outer spherulitic-prismatic layer (*sph.pr*, Figs. 2, 7; Pl. 10, Fig. 1; Pl. 25, Fig. 2), and the inner conchiolin layer (*i.c.l*, Figs. 2, 7; Pl. 10, Fig. 1; Pl. 25, Figs. 1, 2). The surface of the connecting ring is covered by a thin conchiolin layer, corresponding to that layer on the dorsal septa face (*d.c.l*, Fig. 7).

The outer spherulitic-prismatic layer. The spherulitic-prismatic layers of the septal neck and connecting ring are directly continuous (*sph.pr*, Figs. 2, 7; Pl. 10, Fig. 1). In the connecting ring, this layer retains its porous structure, but decreases in thickness. It is mainly composed of slender aragonitic prisms which may be partially fused and lack a preferred orientation (Pl. 12, Figs. 1, 2). In the innermost part of the layer, adjacent to the inner conchiolin layer, the prisms are traversed by numerous, irregularly spaced conchiolin membranes (Pl. 12, Fig. 2). The latter prisms often consist of outer walls only, leaving the interior empty (Pl. 18, Figs. 1, 2, 3). These walls therefore resemble palisades, composed of acicular prismatic sub-units.

Distally, the connecting ring projects into the septal neck of the preceding septum (Fig. 2; Pl. 18, Fig. 1). The inner face of the septal neck is therefore invested by the spherulitic-prismatic layer of the succeeding connecting ring. In most cases, these two layers can be easily distinguished by the fact that in the prismatic layer most prisms are oriented vertically, whereas in the spherulitic-prismatic layer, they lack a preferred orientation (*pr*, *sph.pr*, Pl. 22, Fig. 3). Before its fusion to the auxiliary ridge (see below), the structure of the spherulitic-prismatic layer becomes modified. It consists here of stacks of large tabular crystals (*sph.pr*, Fig. 9; Pl. 23, Fig. 1; Pl. 24, Fig. 1). These stacks are separated by narrower or wider interspaces. In each stack, the consecutive tabular crystals are separated by thin, parallel conchiolin membranes which also seem to extend from one stack to another through the interspaces between the stacks (*sph.pr*, Fig. 9; Pl. 23, Fig. 1). The tabular crystals in the stacks are composed either of radially arranged, thin and rather broad crystalline plates, or radially or spherically oriented acicular crystallites (Pl. 24, Fig. 1). These crystalline components are embedded in an abundant conchiolin matrix.

The inner conchiolin layer. This layer consists of numerous conchiolin membranes which are arranged concentrically to the height axis of the siphonal tube (*i.c.l*, Figs. 2, 7; Pl. 10, Fig. 1; Pl. 25, Figs. 1, 2). Each membrane is composed of comparatively coarse fibres (Grégoire, 1967; Mutvei, 1970). This layer is often parted from the septal neck in the dry shells available for the present study. However, the contact between the septal neck and connecting ring is well preserved in some preparations, which were carefully embedded into the plastic. In these, it is clearly seen that the inner conchiolin layer originates deep within the outer nacreous sub-layer of the septal neck (*i.c.l*, nac_1, Figs. 2, 7; Pl. 25, Figs. 1, 2). This layer is here represented by several membranous

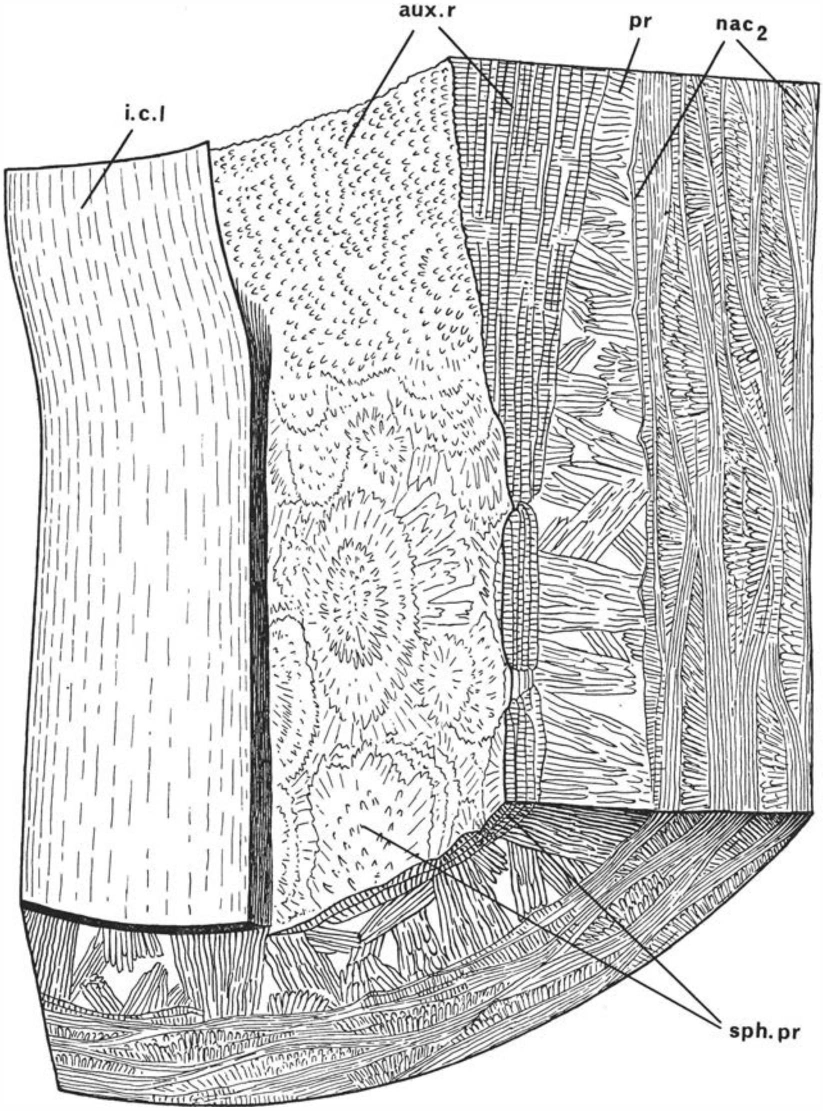

Fig. 9. Block diagram to show the fusion of the distal end of the connecting ring into the auxiliary ridge of the preceding septal neck (approx. × 1000). *i.c.l*, inner conchiolin layer of the connecting ring; nac_2, inner nacreous sub-layer of the septal neck; *pr*, inner prismatic layer of the septal neck; *sph.pr*, spherulitic prismatic layer of the connecting ring.

strata which increase in thickness in the distal direction and coalesce with each other. These membranous strata form together a continuous conchiolin layer immediately distal to the septal neck (*i.c.l*, Fig. 7; Pl. 25, Figs. 1, 2). The inner conchiolin layer fuses to the auxiliary ridge of the preceding septal neck at its distal end (see below).

Demineralized nacreous conchiolin. The nacreous layer of the septal neck was completely demineralized in EDTA. In the proximal portion of the septal neck, the inter-lamellar conchiolin membranes still have the pattern typical for the nacreous layer (Pl. 20, Fig. 2; see also Mutvei, 1970, Pl. 5 *a*, *b*, *c*). Thus, in these membranes, one can distinguish the crystal scars, separated by numerous, ridge-like, vertical conchiolin membranes, and the trabeculae. At the distal end of the septal neck, the membranes form a zone, composed of large, rounded elevations which may have pitted surfaces (Pl. 20, Figs. 1, 3). The crystal scars, vertical conchiolin membranes and trabecular pattern have disappeared in this zone. Instead, the membranes are composed of rather coarse fibres .The rounded elevations also disappear further distally, but the fibrous composition of the membranes is retained (Pl. 20, Fig. 4).

The auxiliary ridge. This ridge is an annular, calcified thickening on the inner face of the distal portion of the septal neck (*aux.r*, Figs. 2, 7, 9; Pl. 10, Figs. 1, 2; Pl. 23, Fig. 1). It is formed by a fusion of the distal end of the succeeding connecting ring to the septal neck. How this fusion takes place is illustrated in Fig. 9 and Pl. 23, Fig. 1. The auxiliary ridge is composed of acicular crystallites, about 0.2—0.4 micron in diameter. The crystallites are arranged in rows and small groups, separated by interspaces (Fig. 9; Pl. 23, Fig. 2; Pl. 24, Fig. 2). These interspaces are occupied by abundant conchiolin matrix (Pl. 24, Fig. 2). Moreover, as seen in vertical polished sections, the auxiliary ridge is traversed by numerous, irregularly spaced, parallel conchiolin membranes (*aux.r*, Fig. 9; Pl. 23, Fig. 1). These membranes form a direct continuation of those in the outer spherulitic-prismatic layer of the preceeding connecting ring (Pl. 23, Fig. 1) and also of those in the inner conchiolin layer.

DISCUSSION

The ontogenetic growth of the septum. As pointed out above, the septal neck and connecting ring are structurally modified parts of the septum. The septum proper is secreted by the epithelium which covers the dorsal end of the body, whereas both the septal neck and the connecting ring are formed by the epithelium on the proximal portion of the siphonal cord (see Mutvei, 1964 *a*).

The formation of a new septum commences with the secretion of the continuous, thin conchiolin layer which at the later growth stages covers the surface of the septum, septal neck and connecting ring. During the succeeding secretory phase, the spherulitic-prismatic layer is deposited internally to the conchiolin layer. More precisely, this layer is formed in the peripheral region of the septum proper, adjacent to the shell wall, and in the outer parts of the septal neck and connecting ring (*sph.pr*, Fig. 3 *A*). The layer in question has a similar, porous structure in all these places (pp. 240, 247). Moreover, the course of the growth lamellae in the succeeding nacreous layer clearly demonstrates that the spherulitic-prismatic layer in the septal periphery and siphonal tube is formed during the same secretory phase. The latter conclusion is supported by the fact that in some septa, the spherulitic-prismatic layer also occurs in the main, central part of the septum (see p. 243). Next in the secretory sequence comes the formation of the thick nacreous layer. The two nacreous sub-layers, distinguished above (p. 249), have the same type of nacreous structure in the septum proper and proximal portion of the septal neck. In the distal portion of the septal neck, however, the ontogenetically older, outer sub-layer increases in thickness and constitutes, alone, the distal end of the septal neck (*nac*$_1$, Fig. 3 *B*). It is here rich in conchiolin and its mineral structure is therefore highly modified (see p. 249). Further distally it becomes completely uncalcified and continues upwards as the inner conchiolin layer of the connecting ring (*i.c.l*, Fig. 3 *B*). The sub-layer under discussion corresponds to only about 1/3 of the total thickness of the septal nacreous layer. The ontogenetically younger, inner nacreous sub-layer, on the other hand, decreases in thickness and is wedged out in the distal end of the septal neck (*nac*$_2$, Fig. 3 *C*). The latter sub-layer corresponds to the remaining, approximately 2/3 of the total thickness of the septal nacreous layer. These conditions show that the distal portion of the septal neck and the connecting ring grow considerably faster in thickness, and are completed earlier, than the rest of the septum. During the final secretory phase, the porous prismatic layer is secreted on the ventral septal face and on the corresponding, inner face of the septal neck. Most distally, this layer is transformed into a solid calcareous formation which constitutes the basal portion of the future auxiliary ridge. The prismatic layer is absent in the connecting ring (*conn*, Fig. 2).

The modifications in the ontogenetic growth of the septum proper, septal neck and connecting ring, discussed above, can be functionally interpreted in the following way. Denton and Gilpin-Brown (1966) pointed out that the new chamber is always completely filled by liquid when formed. For *Nautilus*, with its heavy shell, it is necessary to "pump out" the liquid by the osmotic mechanism at the fastest possible rate in order to maintain the buoyancy of the animal. However, the "pumping out" of the liquid cannot take place before the permeable connecting ring in the new chamber has reached its full thickness and acquired the strength to withstand the hydrostatic pressure of the sea. For this reason, the distal portion of the septal neck and the connecting ring attain their maximum thickness when only one third of the total thickness of the rest of the septum has been formed. This condition has been directly observed by Denton and Gilpin-Brown (1966) in an animal where the last septum was still incompletely developed.

The mechanical strength of the siphonal tube. Experimental tests have shown that the shell of *Nautilus* is sufficiently strong to withstand hydrostatic pressures of 50—60 atm. of the sea, corresponding to the depths of 500—600 m. (Denton and Gilpin-Brown, 1966; Collins and Minton, 1967). In the connecting rings, the inner conchiolin layer alone must withstand these pressures, because the outer spherulitic-prismatic layer is porous and acts mainly as a wick for "sopping up" the cameral liquid. To achieve this strength, the inner conchiolin layer is composed of numerous fibrous membranes. However, equally important for the mechanical strength of the connecting ring is the mode of fusion of its inner conchiolin layer to the contiguous and preceeding septal necks.

It is shown in the present paper that the content of the conchiolin matrix in the outer nacreous sub-layer increases considerably towards the distal end of the septal neck. The inner conchiolin layer of the connecting ring originates from this conchiolin-rich sub-layer. It appears first as several separate, thin, membraneous strata, embedded deep into the nacre. In the distal direction, these strata increase in thickness and coalesce with each other so as to form a continuous conchiolin layer immediately distal to the septal neck (Pl. 25, Figs. 1, 2). In this manner, the inner conchiolin layer is firmly anchored in the contiguous septal neck.

At its distal end, the inner conchiolin layer of the connecting ring is fused to the auxiliary ridge of the precedent septal neck. This fusion seems to take place in such a way that the membranes of the inner conchiolin layer pass into the auxiliary ridge and become calcified. This ridge itself is rich in conchiolin matrix which probably acts as a "glue" for a firm attachment.

The structure of the nacreous layer. The intracrystalline mineral structure and its variations in the nacreous crystals have been particularly emphasized in the present paper. The typical nacreous crystals are tabular with hexagonal outlines (Fig. 11 *A*). Such crystals build up the main part of the nacreous layer in the septum proper and the proximal portion of the septal neck. In a previous paper (Mutvei, 1970), these crystals were described as consisting of numerous, narrow, mineral laths, oriented parallel to the a-axes. In a more recent paper (Mutvei, 1972), the mineral laths were shown to consist of rows of vertical, acicular crystallites.

The intra-crystalline aragonitic components are granular in a new variety of the nacreous crystals, described above (Pl. 7, Fig. 2). In some of these crystals, the granules seem to be arranged into vertical rows, whereas in others they lack a preferred orientation. It was noticed that the acicular crystallites in the majority of the nacreous crystals also have a granular structure in that they seem to be composed of fused aragonitic granules (Fig. 11 *A*). On the basis of these observations, we may conclude that the basic mineral components in the nacreous crystals are the aragonitic granules; these are in most cases fused into vertical acicular crystallites. The diameters of the aragonitic granules and acicular crystallites are mostly 0.1—0.2 micron. Moreover, as demonstrated above (pp. 240, 250), the aragonitic prisms and spherulites are composed of the same mineral components as the nacreous crystals (see also Mutvei, 1972).

Bevelander and Nakahara (1969) showed that the initiation and growth of the nacreous crystals take place within interspaces between pre-formed inter-lamellar conchiolin membranes. These interspaces enclose a modified pallial fluid. The observations now presented demonstrate that there are considerable variations in the conchiolin content within the nacreous crystals. These variations have a pronounced influence on the intracrystalline structure. In other words, the crystals which grow in a medium rich in conchiolin acquire a different structure from those growing in a medium deficient in conchiolin. The crystals of the following three categories were chosen to exemplify these conditions. (1) The nacreous crystals which, in all certainly grew in a medium deficient in conchiolin, are either typically dendritic, or tend to be porous (Fig. 8 *E*, *F*, *G*). The interspaces between the adjacent crystals are wide and not filled by conchiolin. (2) The crystals which grew in a medium rich in conchiolin often have a granular structure (Fig. 8 *B*, *C*, *D*). In most cases, the boundaries between the adjacent crystals are indistinct, and the consecutive crystals are separated by thick inter-lamellar conchiolin membranes (*d.nac.h*, Pl. 4, Fig. 3). (3) The nacreous crystals in the distal portion of the septal neck (outer nacreous sub-layer) grew in a medium extremely rich in conchiolin. They are characterized by

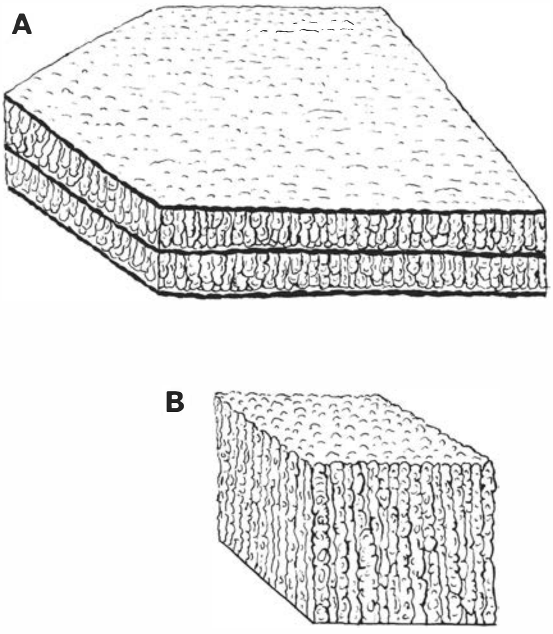

Fig. 11. A, block diagram of two successive nacreous crystals, showing the shape of their acicular crystallites; *B*, a section of a prism to show the shape of the acicular crystallites. Both figures approximately × 30 000.

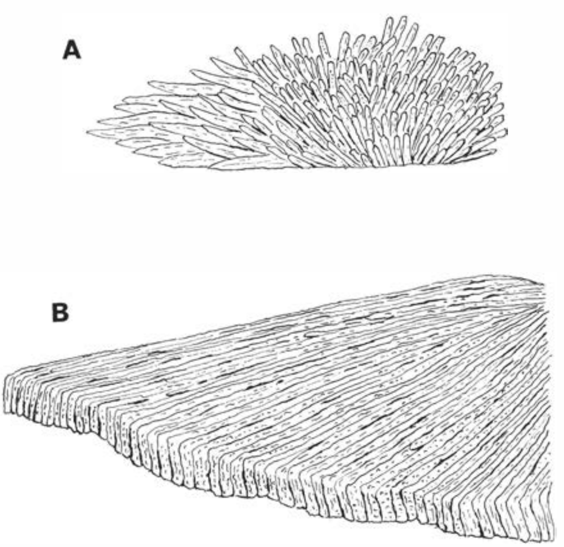

Fig. 10. A, B, modified crystals in the outer nacreous sub-layer of the distal portion of a septal neck (approx. × 10 000).

aberrant structural modifications in being composed of thin mineral plates (Fig. 10 *B*) or radiating acicular crystallites (Fig. 10 *A*). In fact, the crystals in question show a closer structural agreement with the modified prisms in the spherulitic-prismatic and prismatic layers (e.g. see Pl. 14; Pl. 24, Fig. 1) than with the typical nacreous crystals. Moreover, the inter-lamellar conchiolin membranes, between which these modified crystals grew, have lost their typical structure, and are composed of fibres (Pl. 20, Figs. 3, 4).

The inner conchiolin layer of the connecting ring. It is demonstrated in the present study (see also Mutvei, 1964 *a*) that the inner conchiolin layer of the connecting ring originates from the outer nacreous sub-layer of the septal neck which is unusually rich in conchiolin. The inner conchiolin layer can therefore be regarded as an uncalcified, structurally modified, nacreous layer. It is composed of numerous conchiolin membranes. These membranes have a coarse, fibrous structure which differs considerably from the trabecular structure in the inter-lamellar conchiolin membranes of the typical nacreous layer. However, as shown above (p. 252, Pl. 20, Figs. 1, 2, 3, 4), this trabecular structure is, in the most distal portion of the septal neck, gradually replaced by a coarsely fibrous structure. Consequently, there is a gradual transformation of the trabecular inter-lamellar conchiolin membranes into the coarse-fibrous conchiolin membranes of the inner conchiolin layer of the connecting ring.

Structural conditions analogous to these in the siphonal tube of *Nautilus* are encountered in the shells of lamellibranchs. Beedham (1958, p. 553) pointed out that "the corresponding layers of the valves and ligament are basically identical and are, in fact, locally modified regions of the same layers of the shell". In particular, the entirely uncalcified, outer ligamental layer shows great similarities to the calcified outer layer of the valves. The structural relationship between these two layers seems to be principally in accordance with that between the outer nacreous sub-layer of the septal neck and the inner conchiolin layer of the connecting ring in *Nautilus.*

The structure of the prismatic and spherulitic-prismatic layers. Previous workers have not reported any practical difficulties in distinguishing the nacreous layer from the spherulitic-prismatic and prismatic layers. This can probably be explained by the fact that, up to now, only the most typical parts of these layers have been described, disregarding the variations.

Schmidt (1924) pointed out that the aragonitic prisms and spherulites are composed of acicular crystallites (see also Mutvei, 1972). As measured in polished sections, etched with chromium sulphate, these acicular crystallites have a diameter of 0.1—0.2 micron, which corresponds to that of the acicular crystallites in the nacreous crystals. As in the nacreous crystals, the crystallites seem to be composed of fused aragonitic granules (Fig. 11 *B*; Pl. 5, Figs. 3, 4; Pl. 14, Fig. 2).

The typical nacreous layer is traversed by numerous, parallel, regularly spaced inter-lamellar conchiolin membranes which are absent in the prismatic and spherulitic-prismatic layers usually. However, the prisms and spherulites are in places also traversed by parallel conchiolin membranes. In polished vertical sections, the latter membranes have the same appearance as the inter-lamellar conchiolin membranes. In the prisms and spherulites, the membranes often do not interrupt the growth direction of the acicular crystallites (*sph.pr*, Pl. 4, Figs. 1, 2, 4; Pl. 5, Figs. 1, 4; Pl. 14, Fig. 2; *pr*, Pl. 22, Figs. 2, 4, 5). The parallel conchiolin membranes may even become exceedingly numerous in certain parts of the spherulitic-prismatic layer, i.e. at the distal end of the septal neck and the connecting ring, respectively (Pl. 14, Fig. 1; Pl. 23, Fig. 1). These parts resemble the structurally modified outer nacreous sub-layer of the septal neck, not only in the occurrence of the numerous conchiolin membranes, but also in the arrangement of the acicular crystallites.

It must also be stressed that the prisms and nacreous crystals may in places co-exist. Thus, typical nacreous crystals are deposited on the truncated ends of the prisms in the spherulitic-prismatic layer of the peripheral portion of the septum (Fig. 4 *B*; Pl. 2, Figs. 2, 3, 4, 5).

As we have seen, definite structural differences between the nacreous crystals, prisms and spherulites do not exist (see also Mutvei, 1972). In places, a gradual transition from one layer to another takes place.

Comparisons with fossil cephalopods. During fossilization, the aragonite in the shells of the majority of the Paleozoic "nautiloids" has been replaced by calcite. This replacement has destroyed most of the original shell structures. I have made several attempts to study these heavily recrystallized cephalopods with SEM, but without success. However, in some cases, remains of the original shell structure can still be seen in thin sections. These structural remains indicate that in most Paleozoic "nautiloids", the wall of the siphonal tube had a similar composition to that of *Nautilus.* For example, as far as can be seen, the Ordovician *Pictetoceras* (Ellesmerocerida) differs from *Nautilus* mainly in it considerably more thickened spherulitic-prismatic layer in the siphonal tube (Mutvei and Stumbur, 1971). This layer is also thick in Tarphycerida, but thin in Orthocerida, Barrandeocerida and Nautilida. On the other hand, the spherulitic-prismatic layer seems to be absent in the siphonal tube of Actinocerida. The connecting ring of certain actinocerids (*Adamsoceras* and other ormoceratids, Mutvei, 1964*a*), has a porous prismatic structure.

The Late Paleozoic (Pennsylvanian) Buckhorn asphalt, USA, has yielded aragonitically preserved orthoconic cephalopods. The shell structure in these cephalopods is described in Part II of the present paper. It is pointed out in this second Part, that the structure of the siphonal tube in these cephalopods differs in several features from that in *Nautilus.* Differences in the structure of the siphonal tube were also described in Mesozoic aulacocerids and belemnitids (Mutvei, 1971), and in Mesozoic ammonoids (Mutvei, 1967).

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PLATES

Plate 1

Fig. 1. Dorsal surface of the thickened, peripheral portion of the spherulitic-prismatic layer in a septum (× 500).
Fig. 2. Centrally facing terraces of the same portion of the spherulitic-prismatic layer (× 1 100).
Both preparations were treated for 7 min. with sodium hypochlorite.

Plate 2

Fig. 1. Detail of the preparation in *Pl. 1, Fig. 1,* showing prisms and spherulites (× 2 000).
Figs. 2, 5. Details of the same preparation to show small stacks of tabular crystals with irregular outlines on the truncated ends of partially fused prisms (× 5 800 and × 2 100, respectively).
Figs. 3, 4. Similar preparation, showing small stacks of nacreous crystals with hexagonal outlines and granular structure deposited on the truncated ends of the prisms (× 5 000 and × 20 000, respectively).
The preparation figured in *Figs. 3* and *4* was treated for 10 min. with sodium hypochlorite and then etched 10 sec. with chromium sulphate.

Plate 3

Fig. 1. Dorsal surface of a septum showing the thin spherulitic-prismatic layer, partly covered by the dorsal conchiolin layer (× 2 200).
Fig. 2. Vertical polished section of the inner nacreous sub-layer in the distal portion of a septal neck to show transformations of the nacreous strata into the prismatic strata (× 5 000).
Fig. 3. Prisms on the dorsal surface of the peripheral, thickened portion of the spherulitic-prismatic layer in a septum (× 5 000).
Fig. 4. Similar preparation as in *Fig. 3*; note the fusion between several adjacent prisms (× 10 000).
Figs. 5, 6. Tabular, granular nacreous crystals with indistinct, irregular outlines in the structurally modified, dorsal nacreous stratum of a septum (× 10 000 and × 11 000, respectively).
Preparation in *Fig. 1* untreated; in *Fig. 2* etched for 30 sec. with chromium sulphate; in *Fig.* 3 treated 7 min. with sodium hypochlorite; and in *Figs. 4, 5* and 6 treated for 10 min. with sodium hypochlorine and then etched for 10 sec. with chromium sulphate.

Plate 4

Fig. 1. Vertical polished section of the dorsal conchiolin layer, and the succeeding spherulitic-prismatic and nacreous layers in the peripheral part of a septum (× 2 600).
Fig. 2. Continuation of the same section in the peripheral direction towards the shell wall, showing the increase in thickness of the spherulitic-prismatic layer and the spherulitic structure of this layer (× 2 600).
Fig. 3. Vertical polished section of the dorsal conchiolin layer and the succeeding nacreous layer in a septum; note the thick inter-lamellar conchiolin membranes and their undulating course in the dorsal nacreous stratum; the spherulitic-prismatic layer is here absent (× 6 500).
Fig. 4. Detail of *Fig. 2*, showing a spherulite, traversed by three, horizontal conchiolin membranes, and composed of radiating crystallites (× 13 000).
All preparations figured in this plate were etched for 30 sec. with chromium sulphate.
d.c.l, dorsal conchiolin layer of the septum; *d.nac.h*, dorsal, structurally modified nacreous stratum; *nac*, nacreous layer of the septum; *sph.pr*, spherulitic-prismatic layer of the septum.

Plate 5

Fig. 1. Vertical polished section of the peripheral, thickened portion of the spherulitic-prismatic layer and the succeeding nacreous layer. The spherulitic-prismatic layer is traversed by four, irregularly spaced, conchiolin membranes which do not interrupt the growth of the prisms and spherulites. The nacreous layer internal to the structurally modified, dorsal stratum has a predominantly prismatic structure (× 6 500).
Fig. 2. Dorsal portion of the nacreous layer in the same preparation, showing several prismatic inclusions (× 13 000).
Fig. 3. Vertical polished section of the inner prismatic and the nacreous layer in the proximal portion of the septal neck. Note the agreement in the shape and orientation of the acicular crystallites in both layers (× 13 000).
Fig. 4. Detail of the section in *Fig. 1*, showing the shape and orientation of the acicular crystallites in the spherulitic-prismatic layer, and their relationship to the horizontal conchiolin membranes (× 13 000).
All preparations in this plate were etched for 30 sec. with chromium sulphate.

d.nac.h, dorsal, structurally modified nacreous stratum; *nac*, nacreous layer; *pr*, inner prismatic layer of the septal neck; *pr.i*, prismatic inclusions within the nacreous layer; *sph.pr*, spherulitic-prismatic layer of the septum.

Plate 6

Fig. 1. Discoidal prisms in the spherulitic-prismatic layer of the distal portion of a septal neck (× 1100).
Fig. 2. Irregularly shaped prisms in the same layer (× 2300).
Figs. 3, 4. Tabular, granular crystals in the structurally modified, dorsal nacreous stratum of a septum (×2200 and 12000, respectively).
Fig. 5, 6. Spherulitic-prismatic layer in the dorsal, central part of a septum (× 230 and × 2400, respectively).
All preparations shown in this plate were treated for 6 min. with sodium hypochlorite.

Plate 7

Fig. 1. Ventral face of the septal nacreous layer, showing the shape and orientation of the crystals (× 2100).
Fig. 2. Detail of the same preparation, showing the granular composition of the nacreous crystals (× 24000).
Fig. 3. Similar preparation to show consecutive nacreous crystals with different orientations, and the tuberculated crystal surfaces (× 11000).
Figs. 4, 5. Modified crystals in the outer nacreous sub-layer of the distal portion of a septal neck. The crystals are composed of radially oriented acicular crystallites (× 2100 and × 5300, respectively).
Fig. 6. Modified nacreous crystals in the same preparation (× 5000).
The preparation shown in *Figs. 1* and *2* was treated for 10 min. with sodium hypochlorite and then etched 10 sec. with chromium sulphate; the remaining preparations were treated for 5 min. with sodium hypochlorite.

Plate 8

Fig. 1. Ventral face of a septum, covered by rows of prisms (× 115).
Fig. 2. Vase-shaped prism with a thin base on the ventral septal face (× 1150).
Fig. 3. Conical prisms with expanded distal ends on the ventral septal face. The prisms loosened from the underlying nacreous layer during the preparation (× 2100).
Fig. 4. Detail of surface of a conical prism, showing vertical rows of granules (× 10800).
Fig. 5. Large, fused prisms, each with a central cavity, which are surrounded by smaller prisms with pointed distal ends on the ventral septal face (× 600).
Fig. 6. Group of conical prisms attached on the underlying nacreous crystals (× 2000).
The preparations shown in *Figs. 1, 2* and *5* were treated for 6 min. with sodium hypochlorite; the preparations in *Figs. 3* and *4* were treated for 10 min. with sodium hypochlorite and then etched for 10 sec. with chromium sulphate; the preparation in *Fig. 6* was left untreated.

Plate 9

Fig. 1. Initial growth stage of a prism on the surface of a nacreous crystal on the ventral septal face (× 5500).
Fig. 2. A prism at a somewhat more advanced growth stage than that in *Fig. 1* (× 5800).
Fig. 3. Fully grown prism with columnar base and expanded distal end on the ventral septal face (× 2000).
Fig. 4. Detail of the same prism to show that it is formed by a fusion of several, initially separate prisms (× 5000).
Fig. 5. Fully grown prism with expanded distal end, in which the basal portion is formed by a fusion of several, initially separate prisms (× 2000).
Fig. 6. Distal end of a fully grown prism with a central cavity (× 2200).
All preparations shown in this plate were treated for 6 min. with sodium hypochlorite.

Plate 10

Fig. 1. Vertical polished section of the distal portion of a septal neck with contiguous proximal portion of a connecting ring. Note the direct continuation of the spherulitic-prismatic layer between the septal neck and the connecting ring, and the relationship between the inner conchiolin layer of the connecting ring and the outer nacreous sub-layer of the septal neck (×620).
Fig. 2. Same preparation showing the proximal portion of the septal neck. Note the upward increase in thickness of the outer nacreous sub-layer (×620).
The preparation figured in this plate was etched for 30 sec. with chromium sulphate.
aux.r, auxiliary ridge of the septal neck; *con.i*, inner conchiolin layer of the connecting ring; nac_1, nac_2, outer and inner nacreous sub-layers, respectively; *pr*, inner prismatic layer of the septal neck; *sph.pr*, spherulitic-prismatic layer of the septal neck and connecting ring.

Plate 11

Fig. 1. Porous prisms in the spherulitic-prismatic layer of the septal neck (× 2200).
Fig. 2. Detail of the surface in one of these prisms (× 5500).
Fig. 3. Solid prisms with pointed ends in the same preparation (× 2200).
Fig. 4. Detail of the surface in one of these prisms (× 5500).
The preparation figured in this plate was treated for 6 min. with sodium hypochlorite.

Plate 12

Fig. 1. Distal end of the septal neck with parts of the contiguous connecting ring (× 55).
Fig. 2. Detail of the same preparation, showing numerous, parallel conchiolin membranes in the inner portion of the spherulitic-prismatic layer of the connecting ring (× 250).
Fig. 3. Same preparation to show partially fused prisms in the spherulitic-prismatic layer of the septal neck (× 1 100).
Fig. 4. Solid prisms on the surface of the spherulitic-prismatic layer of a septal neck (× 2 250).
Fig. 5. Porous prisms in the same preparation (× 2 300).
All preparations figured in this plate were treated for 6 min. with sodium hypochlorite.

Plate 13

Figs. 1, 2. Vertical polished section of the inner parts of the spherulitic-prismatic layer, adjacent to the succeeding nacreous layer, of a septal neck. The prisms are extensively fused and surrounded by conchiolin membranes (× 2 000 and × 10 500, respectively).
Fig. 3. Vertical polished section of the spherulitic-prismatic layer of a septal neck. Note the shape and orientation of the acicular crystallites in the prisms and spherulites (× 6 000).
Fig. 4. Vertical polished section of the spherulitic-prismatic layer and the succeeding nacreous layer. At the boundary region between these two layers the spherulitic-prismatic layer is traversed by several, horizontally continuous conchiolin membranes (× 2 500).
Fig. 5. A modified crystal, composed of acicular crystallites, in the outer nacreous sub-layer of a septal neck (× 5 300).
The preparations in *Figs. 1—4* were etched for 15—30 sec. with chromium sulphate; the preparation in *Fig. 5* was treated for 7 min. with sodium hypochlorite.
nac, nacreous layer of septal neck; *sph.pr*, spherulitic-prismatic layer of septal neck.

Plate 14

Fig. 1. Vertical polished section of the spherulitic-prismatic layer at the distal end of the septal neck. The layer is traversed by numerous, parallel conchiolin membranes which subdivide it into stacks of tabular crystals (× 1 200).
Fig. 2. Detail of the same layer, showing the acicular crystallites in the tabular crystals and the conchiolin membranes (× 12 500).
Figs. 3,4. Stacks of tabular crystals in the same layer seen in surface preparation. The crystals are composed of radiating, acicular crystallites (× 1 100 and × 2 200, respectively).
The preparation shown in *Figs. 1* and *2* was etched for 30 sec. with chromium sulphate; that in *Figs. 3* and *4* was treated for 10 min. with sodium hypochlorite.

Plate 15

Fig. 1. Solid nacreous crystals in the proximal portion of a septal neck. The crystal ends show spinous extensions, and there are large, empty interspaces between the adjacent crystals (11 000).
Fig. 2. Dendritic nacreous crystal in the same preparation (× 11 000).
Fig. 3. Nacreous crystals composed of parallel crystalline laths in the same preparation (× 6 200).
Fig. 4. Dendritic and granular nacreous crystals in the same preparation (× 11 000).
The preparation shown in this plate was treated for 5 min. with sodium hypochlorite.

Plate 16

Fig. 1. Highly porous nacreous crystal, composed of parallel crystalline laths, in the same preparation as in *Pl. 15* (× 11 000).
Fig. 2. Layer of dendritic nacreous crystals, intercalated between lamellae of granular nacreous crystals in the same preparation (× 11 000).
Fig. 3. Porous, partly dendritic nacreous crystals in the same preparation (× 11 000).
Fig. 4. Dendritic and granular nacreous crystals in the same preparation (× 5 600).

Plate 17

Fig. 1. Fine-granular nacreous crystals with indistinct outlines at the boundary to the inner prismatic layer of the septal neck, seen from outside. The outer crystal faces bear deep depressions which appear as elevations on the inner faces (× 200).
Fig. 2. Nacreous crystal, composed of coarse-granular, concentric plates in the same preparation (× 10 000).
Fig. 3. Similar crystals (× 2 000).
Fig. 4. Detail of *Fig. 1* (× 1 000).
The preparation figured in this plate was treated for 2 hours with sodium hypochlorite.

Plate 18

Fig. 1. Distal portion of a connecting ring and parts of the preceding septal neck, showing hallow, palisade-like prisms in the innermost part of the spherulitic-prismatic layer of the connecting ring (× 55).
Figs. 2, 3. Details of the same preparation, showing the

hollow, palisade-like prisms (× 230 and × 2300, respectively).
Fig. 4. Vertical polished section of the inner nacreous sub-layer in the distal portion of a septal neck. Note the alternation of nacreous and prismatic strata (× 2400).
Fig. 5. Detail of a similar preparation to that of *Fig. 4* (× 12000).
The preparation figured in *Figs. 1—3* was studied in untreated condition; the sections in *Figs. 4* and *5* were etched for 30 sec. with chromium sulphate.

Plate 19

Figs. 1, 2. Modified nacreous crystals of the outer nacreous sub-layer in the distal end of a septal neck, intercalated between lamellae of inner conchiolin layer of the connecting ring (× 2200 and × 11000, respectively).
Figs. 3, 4. Modified crystals, composed of thin, vertical, crystalline lamellae in the outer nacerous sub-layer of the distal portion of a septal neck (× 2100 and × 5000, respectively).
The both preparations figured in this plate were treated for 7 min. with sodium hypochlorite.

Plate 20

Fig. 1. Surface of an inter-lamellar conchiolin membrane, demineralized in EDTA, in the outer nacreous sub-layer of the distal portion of a septal neck, showing large elevations with pitted surfaces (× 1350).
Fig. 2. Similar inter-lamellar conchiolin membrane in the proximal portion of a septal neck. Note the typically developed crystals scars and the inter-crystalline membranes separating these scars (× 2100).
Fig. 3. Surface of an inter-lamellar conchiolin membrane immediately distal to that in *Fig. 1.* The large elevation of the membrane lacks the pitted surface. The membrane has a fibrous composition (× 5600).
Fig. 4. The same conchiolin membrane as in *Fig. 3*, but more distally. The elevations are absent, and the membrane has a coarse-fibrous structure (× 5500).
Fig. 5. Lamellar crystals in the outer nacreous sub-layer of the distal portion of a septal neck, treated for 2 hours with sodium hypochlorite (× 20000).

Plate 21

Fig. 1. Vertical polished section of the outer nacreous sub-layer at the distal end of a septal neck, etched for 30 sec. with chromium sulphate (× 2400).
Figs. 2, 3, 4. Details of the same layer. Note the distribution of the abundant conchiolin matrix in this layer. The modified nacreous crystals are partly dissolved and their position is indicated by impressions (× 6000, × 10500 and × 13000, respectively).

Plate 22

Fig. 1. Vertical polished section of the ventral part of a septum, showing a prism and the underlying nacreous layer (cf. *Pls. 8, 9*). Note the similarity in composition of the prism and the nacreous crystals (× 10500).
Fig. 2. Vertical polished section of the inner prismatic layer and the adjacent nacreous layer in a septal neck. The prisms show a variable orientation, they are composed of acicular crystallites, and their basal portions are traversed by numerous parallel, conchiolin membranes (× 6300).
Fig. 3. Vertical fracture plane of a septal neck, showing the nacreous and inner prismatic layers, and the spherulitic-prismatic layer of the succeeding connecting ring (× 550).
Fig. 4. Similar vertical section as in *Fig. 2.* The prisms show here a more regular, vertical orientation (× 2600).
Fig. 5. Detail of the same section, showing the basal portion of a prism traversed by conchiolin membranes (× 13000).
Fig. 6. Vertical polished section of the outer nacreous sub-layer in the distal portion of a septal neck. Note the variations in the amount and distribution of the conchiolin matrix (× 6000).
The polished sections depicted in *Figs. 1, 2, 4, 5, 6* were etched for 30 sec. with chromium sulphate; the fracture plane in *Fig. 3* was treated for 5 min. with sodium hypochlorite.
nac, nacreous layer; *pr*, inner prismatic layer; *sph.pr*, spherulitic-prismatic layer of the connecting ring.

Plate 23

Fig. 1. Vertical polished section of the auxiliary ridge, the inner prismatic layer and the nacreous layer of a septal neck, and the spherulitic-prismatic layer of the succeeding connectiong ring. Note the mode of fusion of the spherulitic-prismatic and prismatic layers to the auxiliary ridge (× 550).
Fig. 2. Vertical fracture plane of an auxiliary ridge, showing the prismatic elements in this ridge (× 5700).
Fig. 3. Vertical polished section of the outer nacreous sub-layer in the distal portion of a septal neck, showing the distribution of the conchiolin matrix (× 6200).
All preparations figured in this plate were etched for 30—40 sec. with chromium sulphate.
aux.r, auxiliary ridge; *nac*, nacreous layer; *pr*, inner prismatic layer of the septal neck; *sph.pr*, spherulitic-prismatic layer of the connecting ring.

Plate 24

Fig. 1. Inner face of the spherulitic-prismatic layer in the most distal portion of a connecting ring (cf. *sph.pr*, *Pl. 23*, *Fig. 1*). Note the stacks of tabular crystals, composed of radiating acicular crystallites and crystalline plates (× 1 000).

Fig. 2. Inner face of the auxiliary ridge of the same preparation to show the prismatic composition of the ridge (× 5 000).

The preparation figured in this plate was treated for 7 min. with sodium hypochlorite.

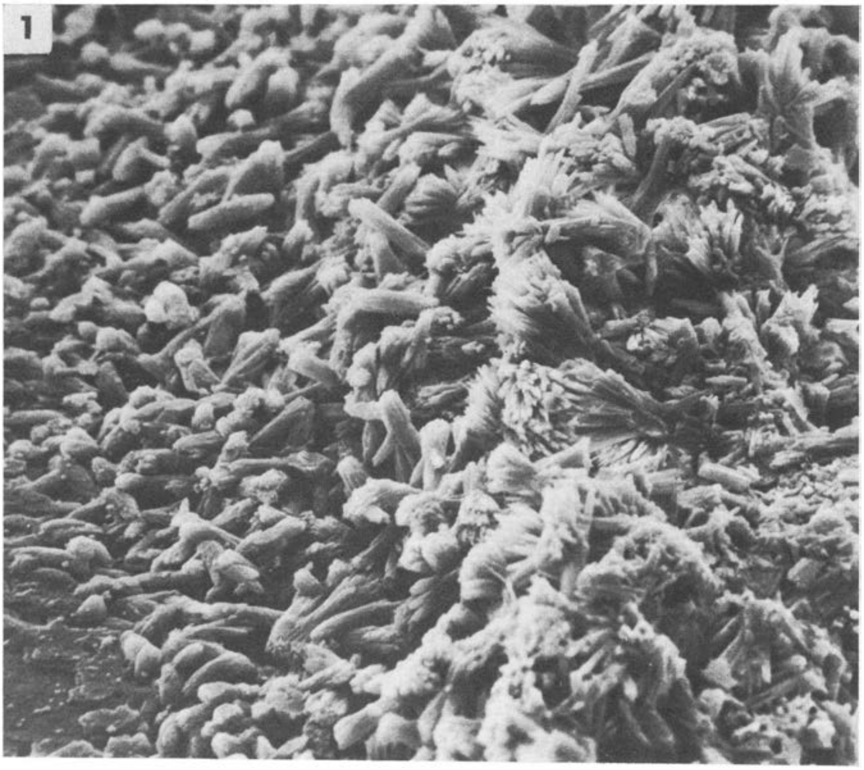
Plate 25

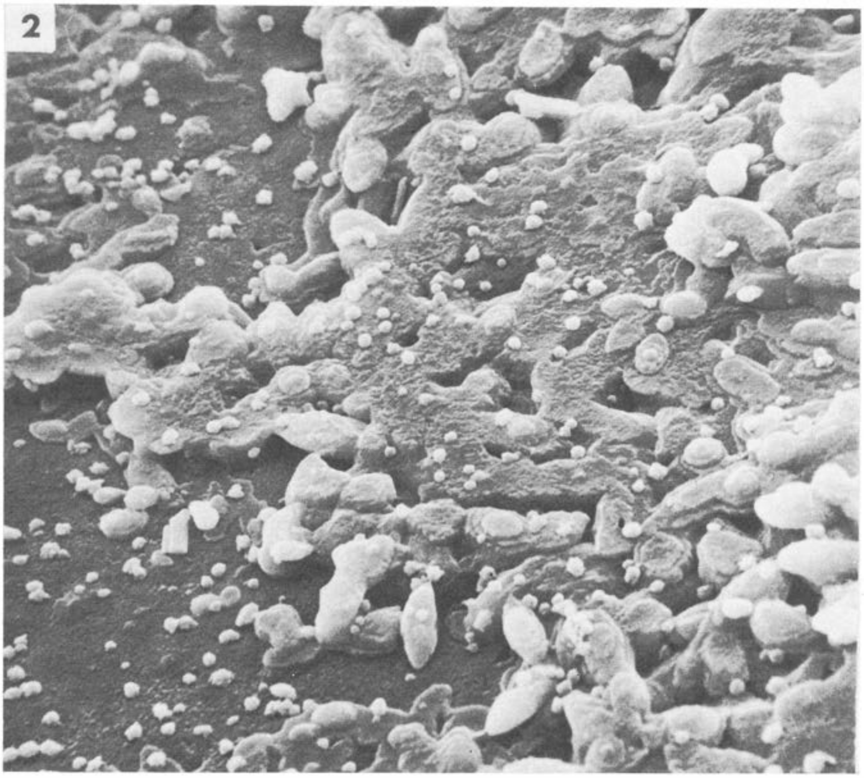
Fig. 1. Vertical polished section through the distal end of a septal neck and the inner conchiolin layer of the contiguous connecting ring. The inner conchiolin layer originates deep in the outer nacreous sub-layer of the septal neck (× 2 400).

Fig. 2. Same preparation, showing also the spherulitic-prismatic layer (× 600).

The preparation figured in this plates was etched for 30 sec. with chromium sulphate.

Plate I





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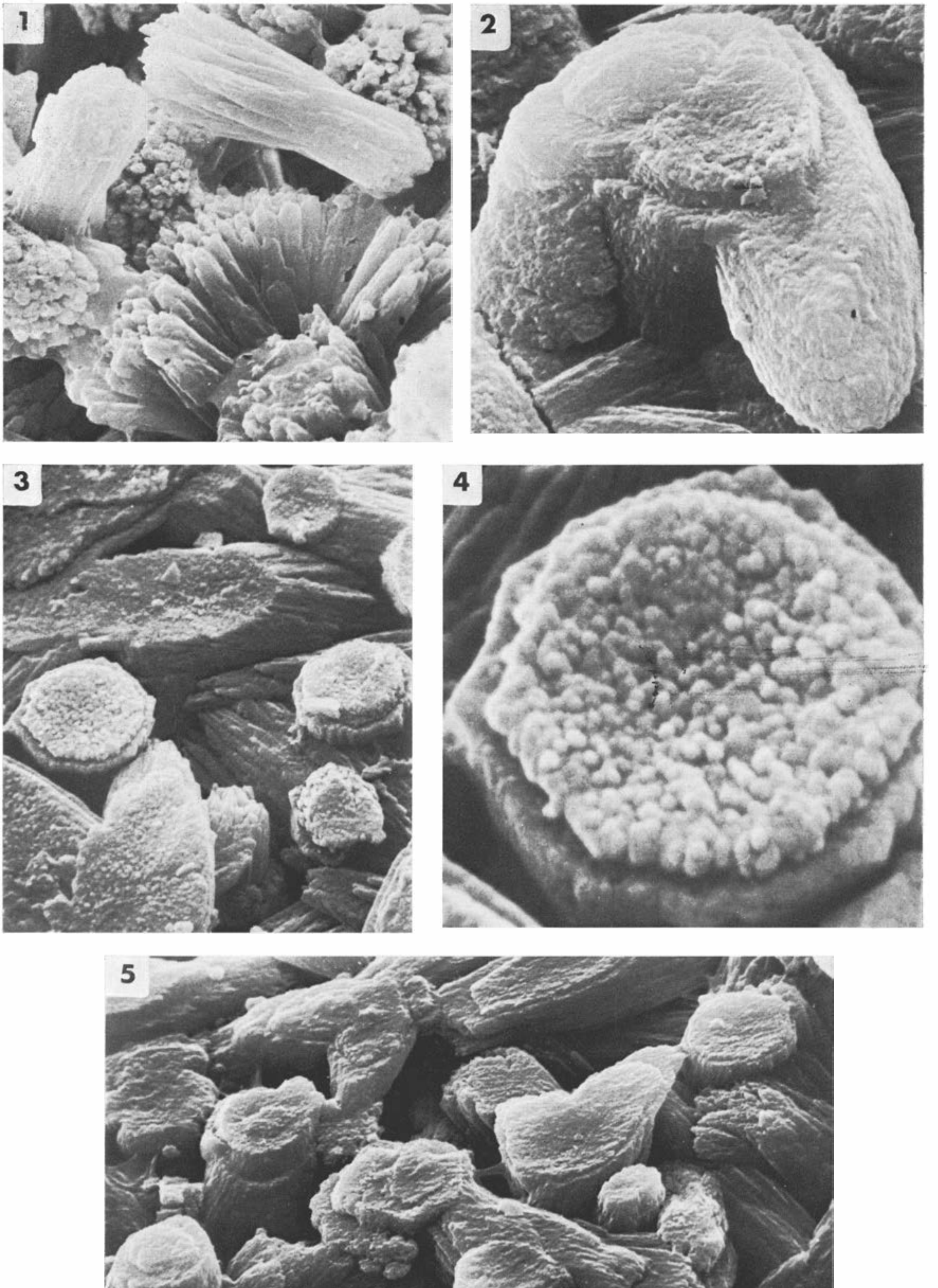

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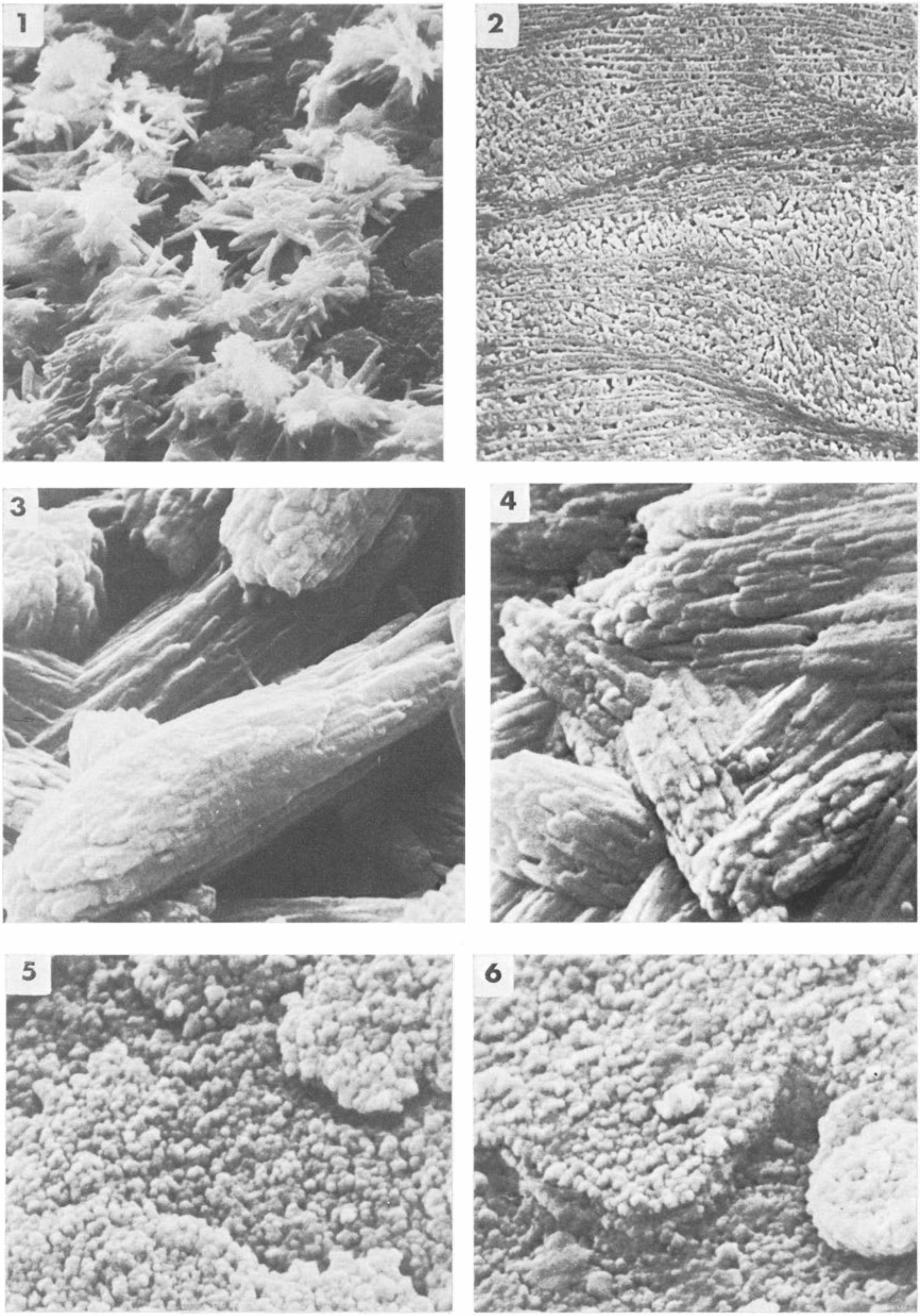

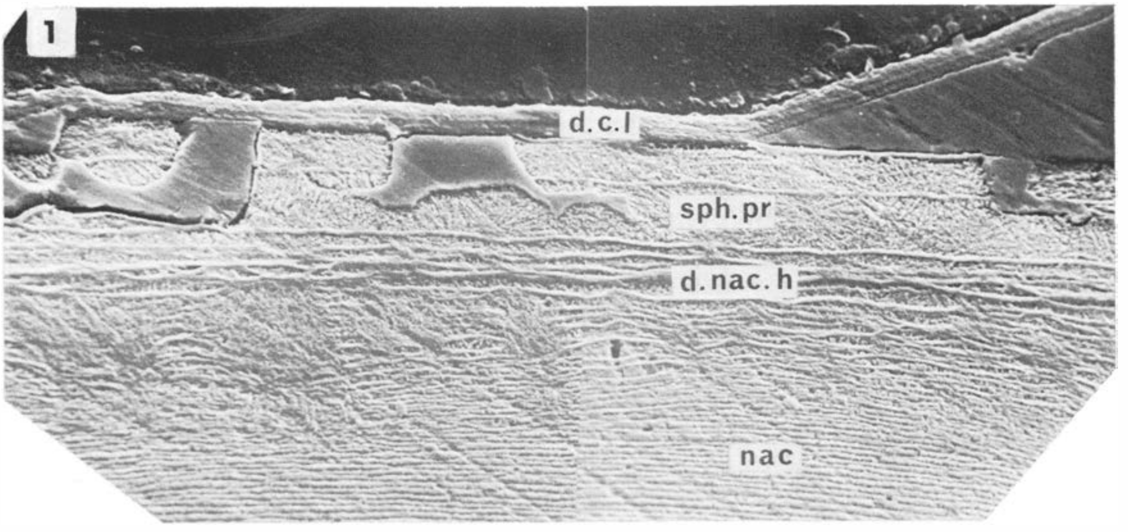
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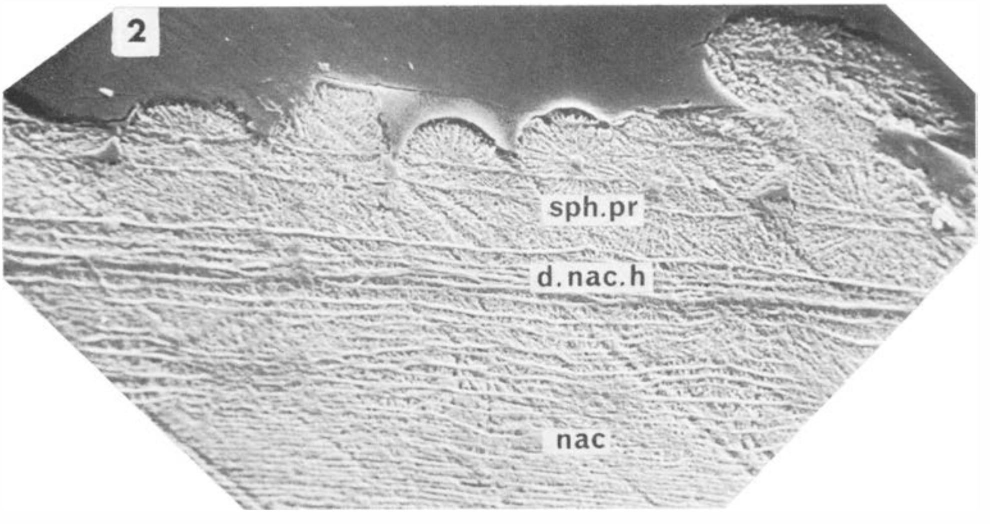
nac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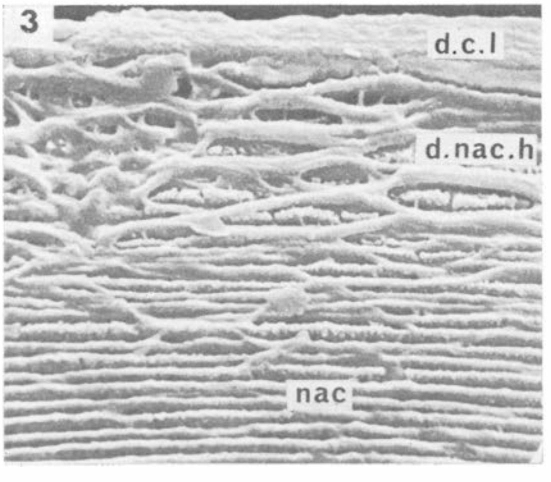
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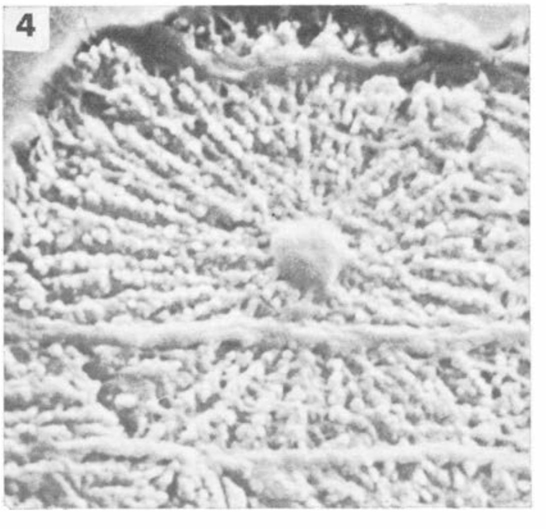
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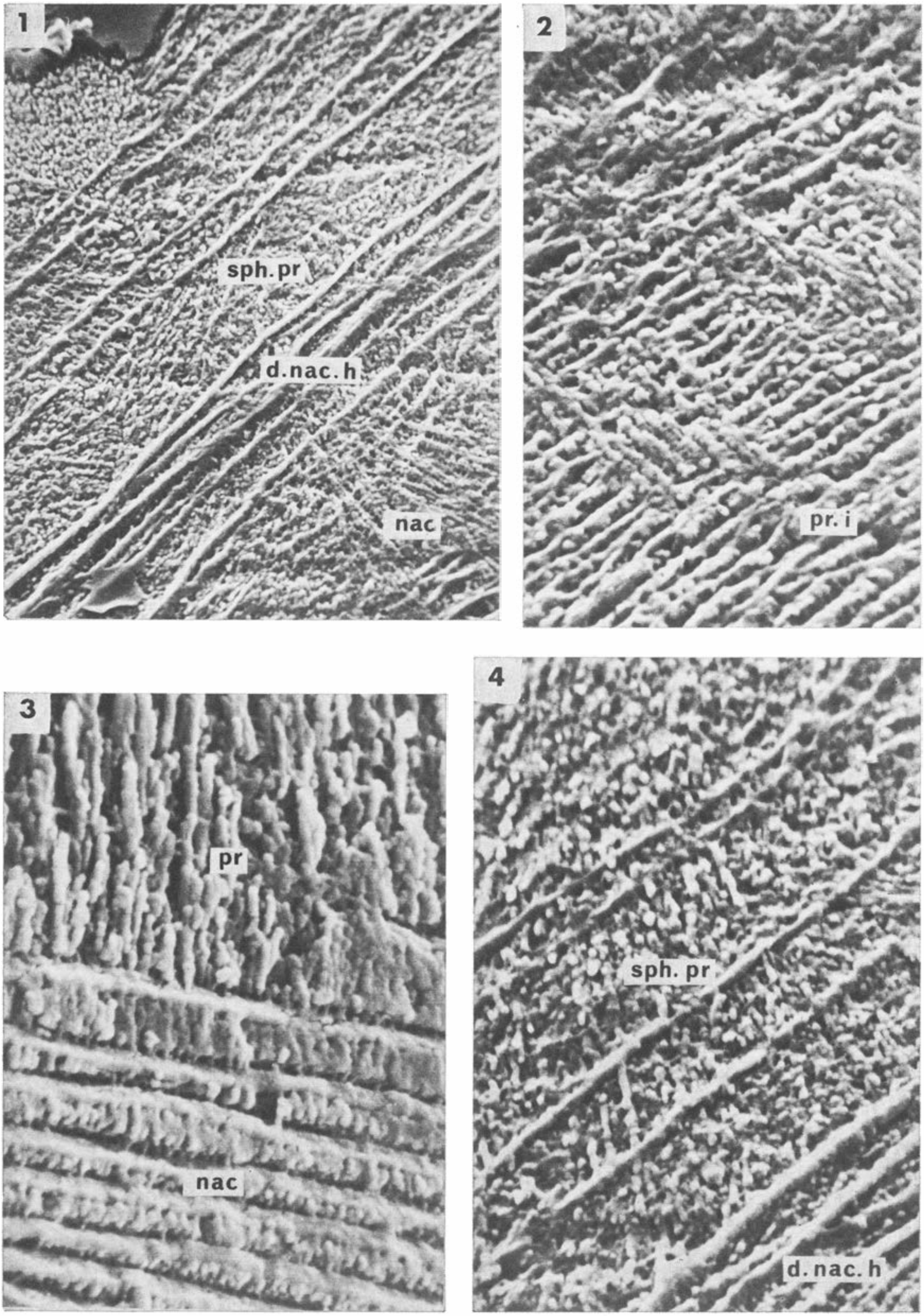
Plate V



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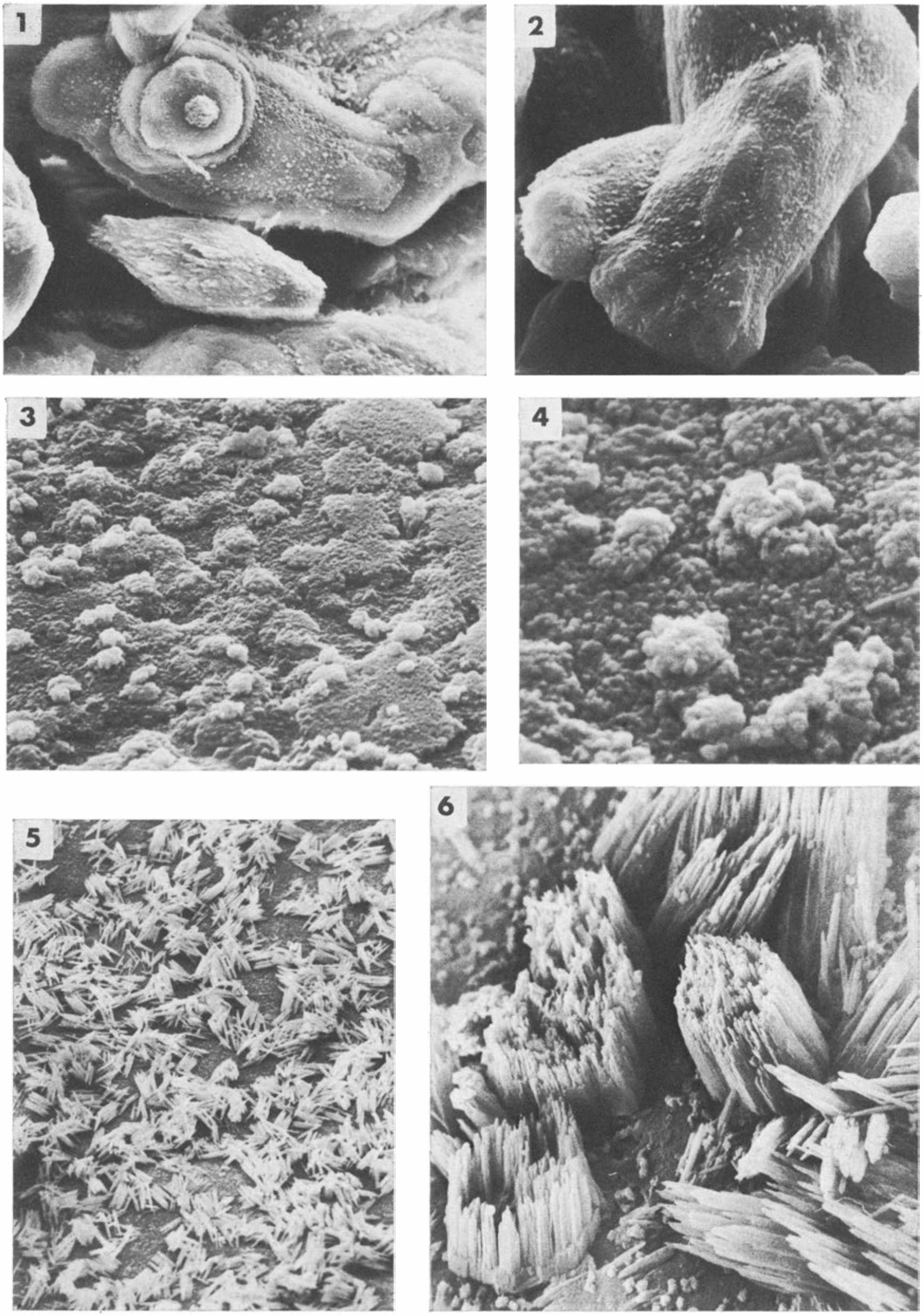

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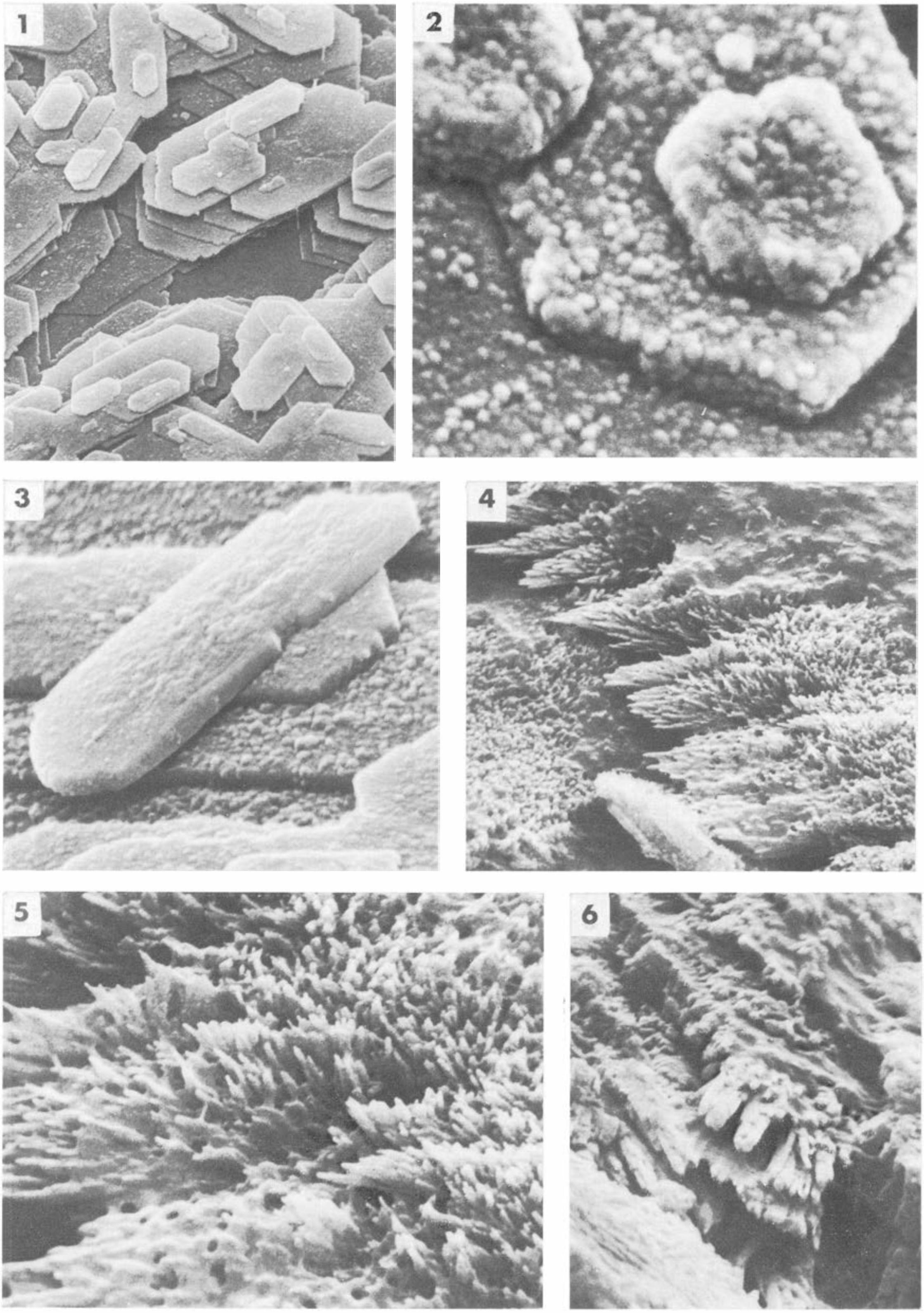

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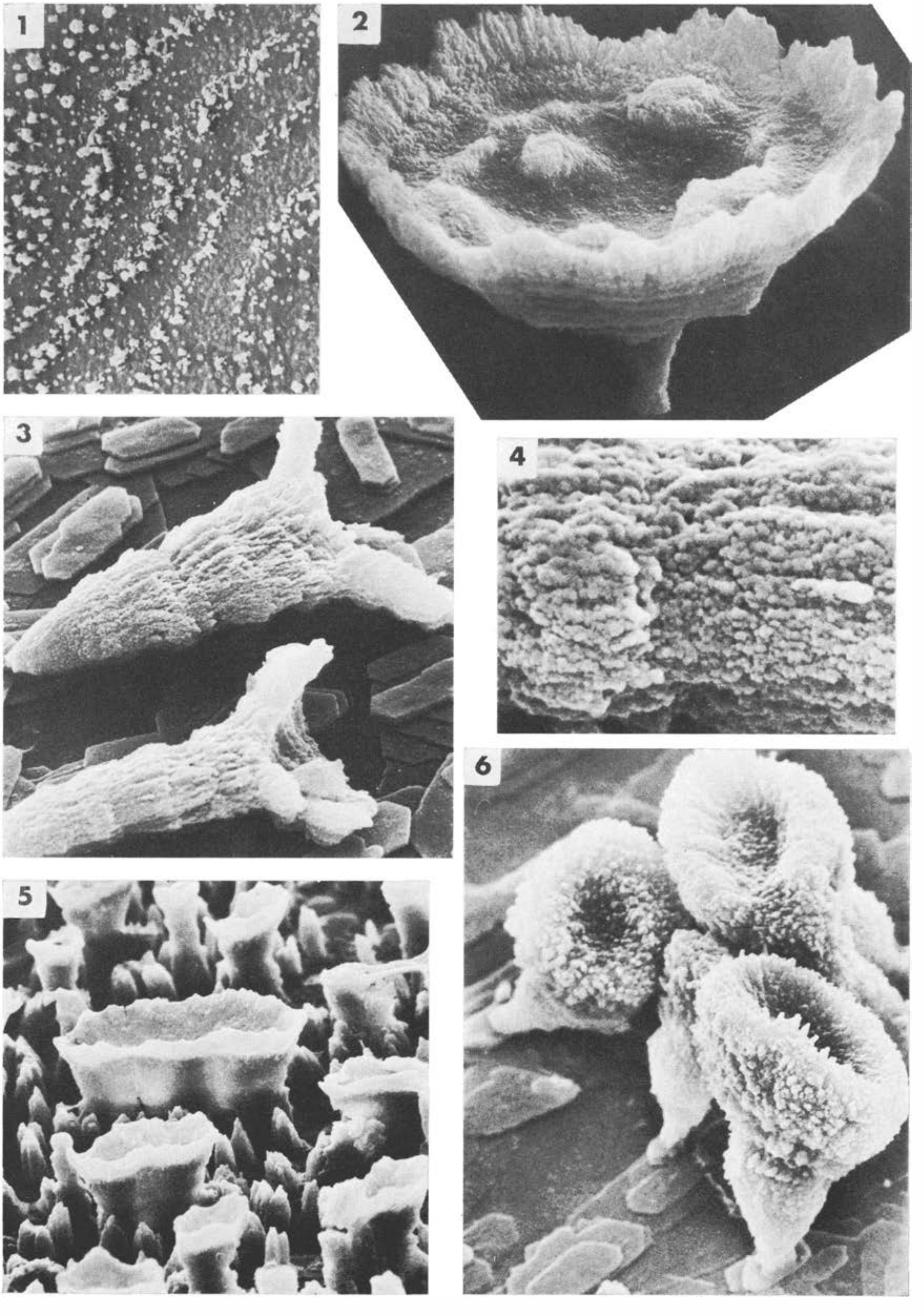

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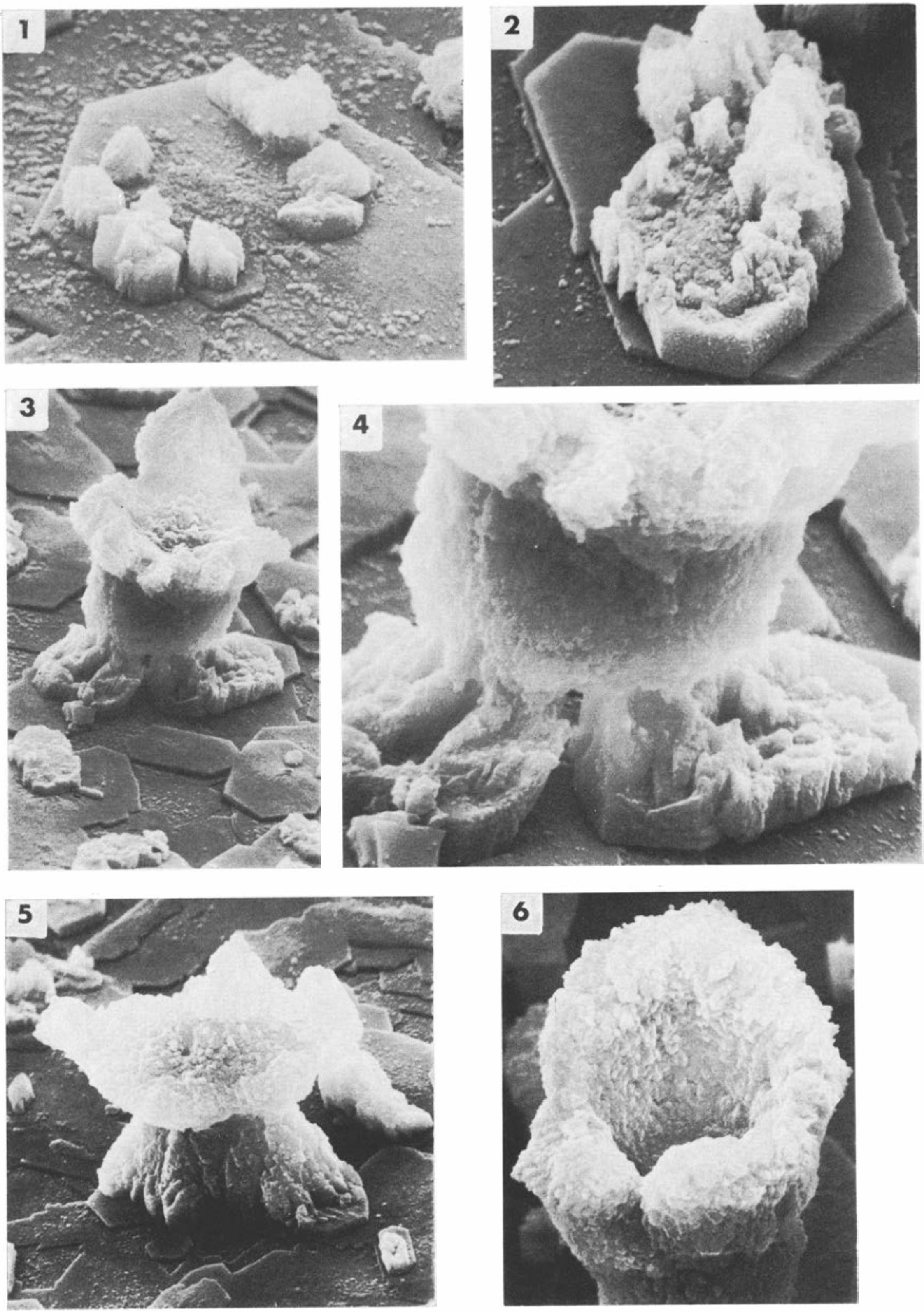


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i.c.l
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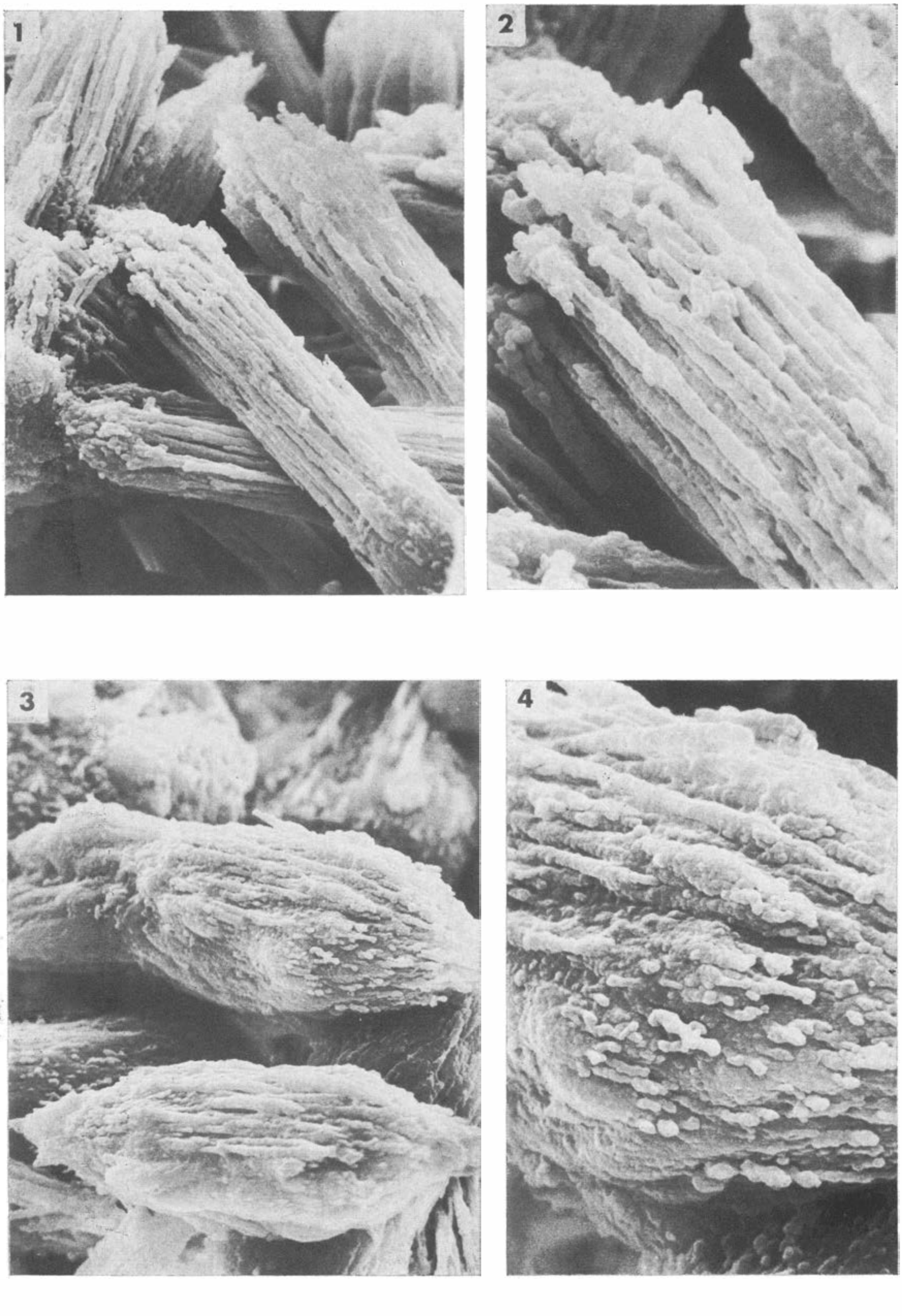
nac 2
aux.r


2
sph. pr
nac 1
nac 2
aux.r
pr

Plate XI



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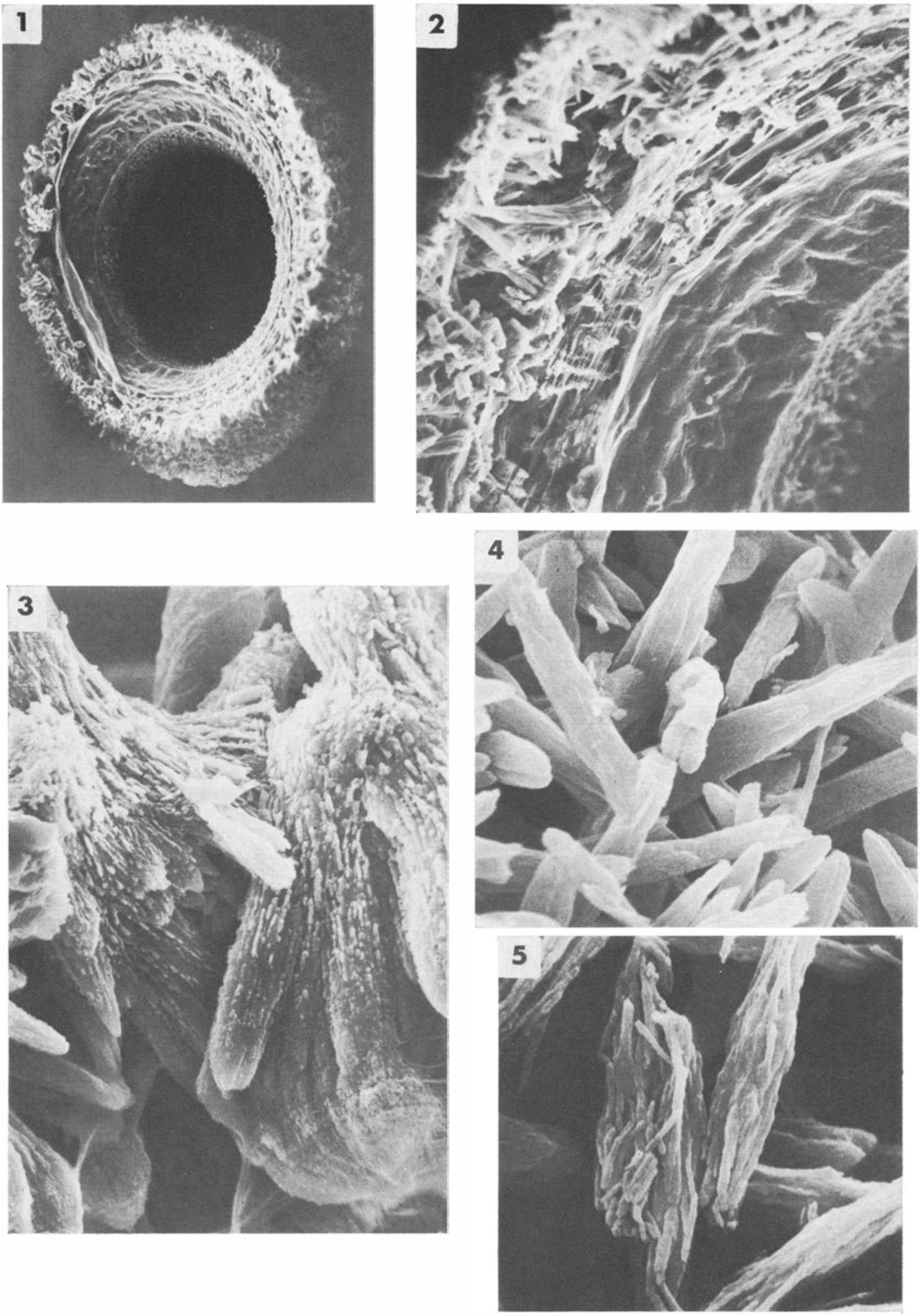

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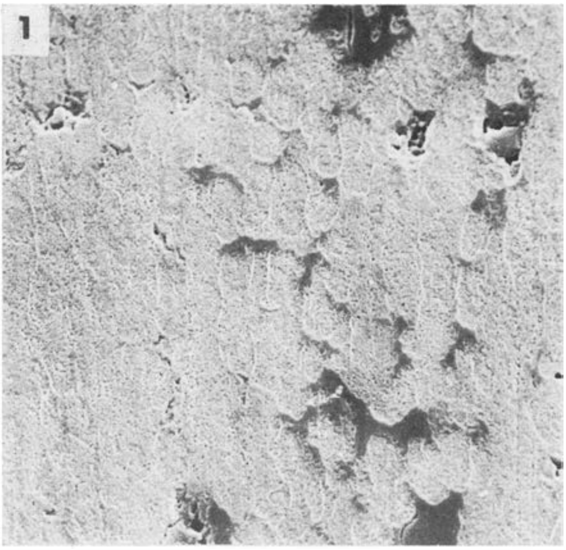
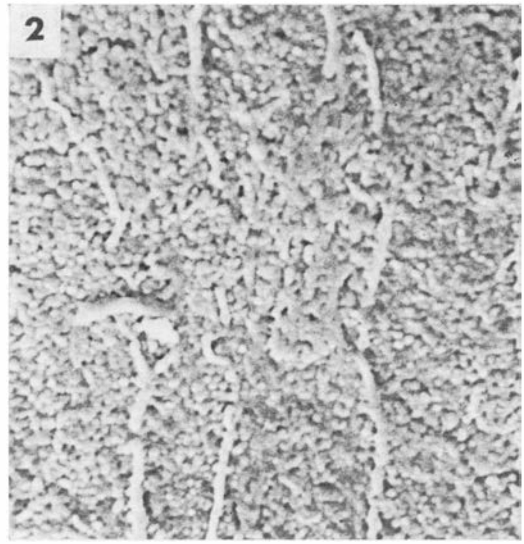
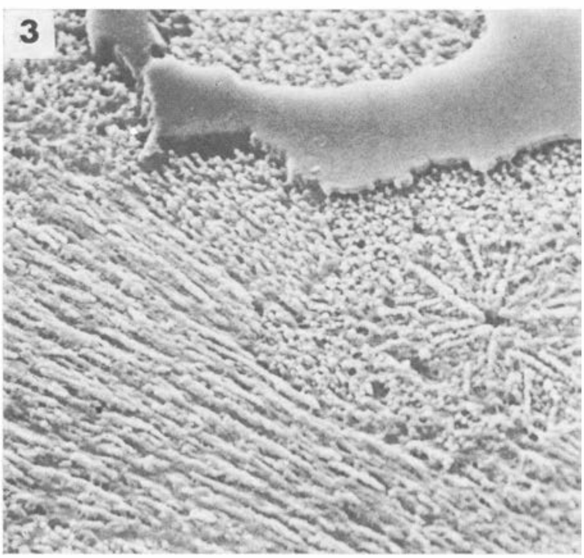
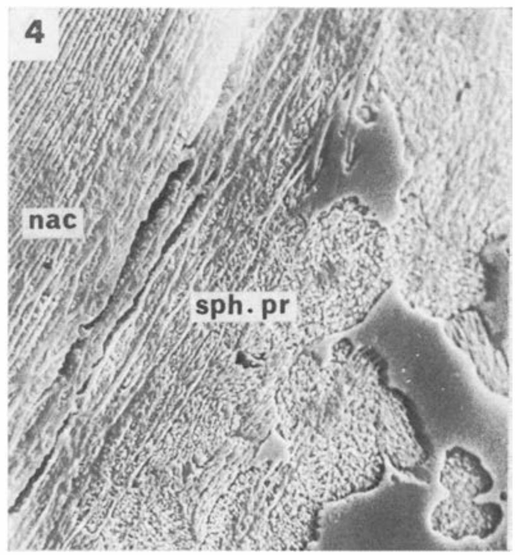








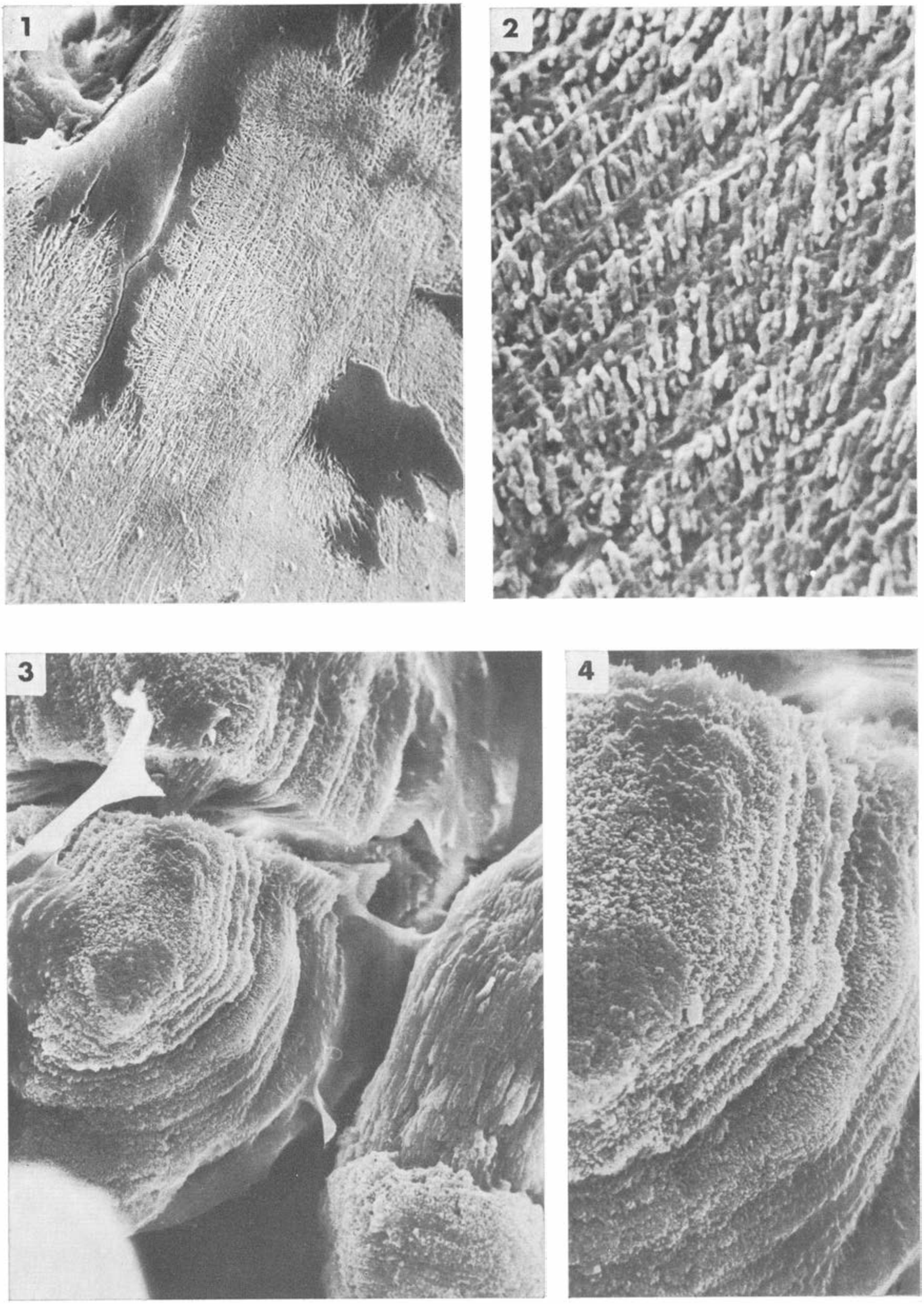
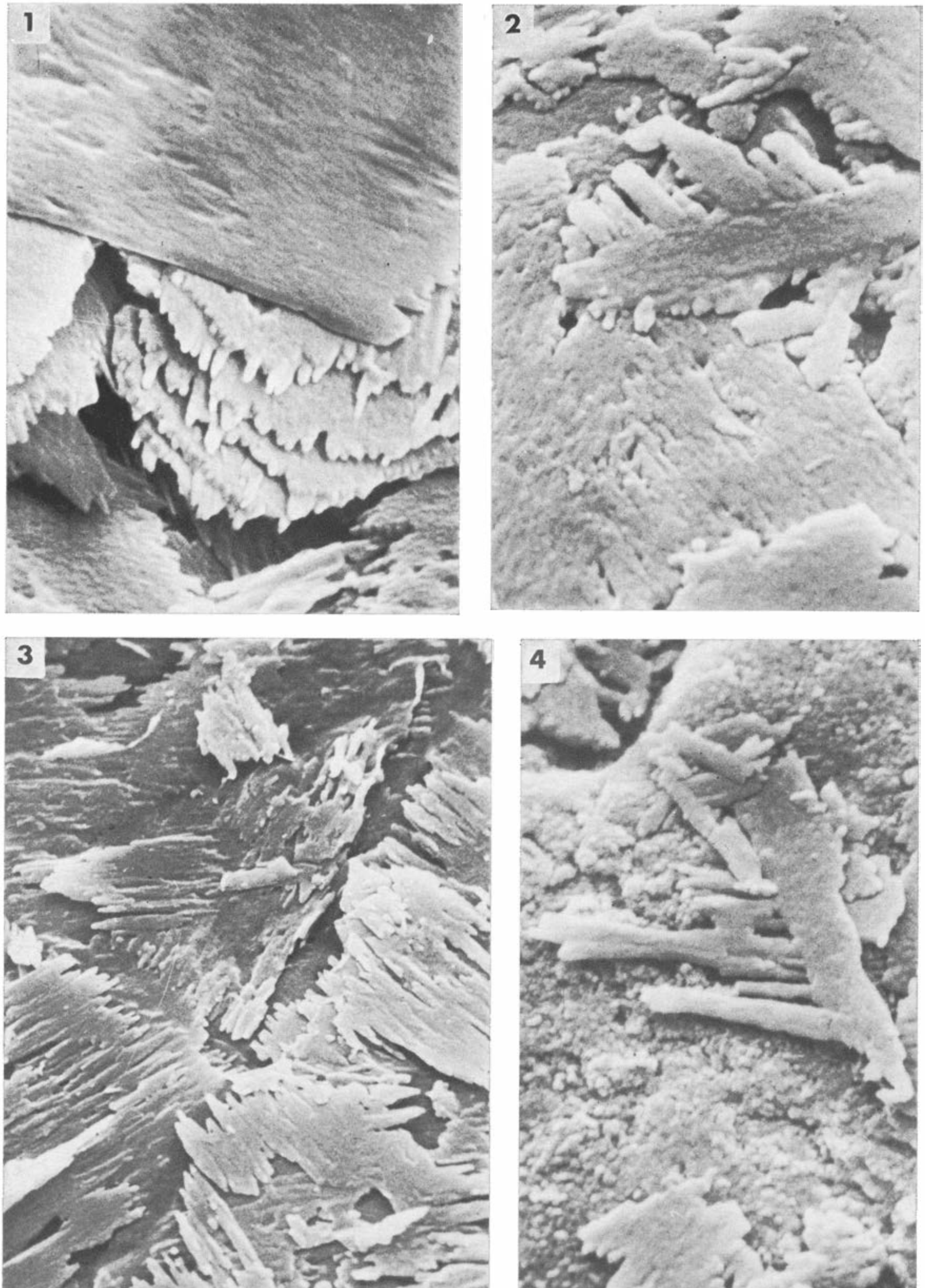

1
2
3
4

Plate XV



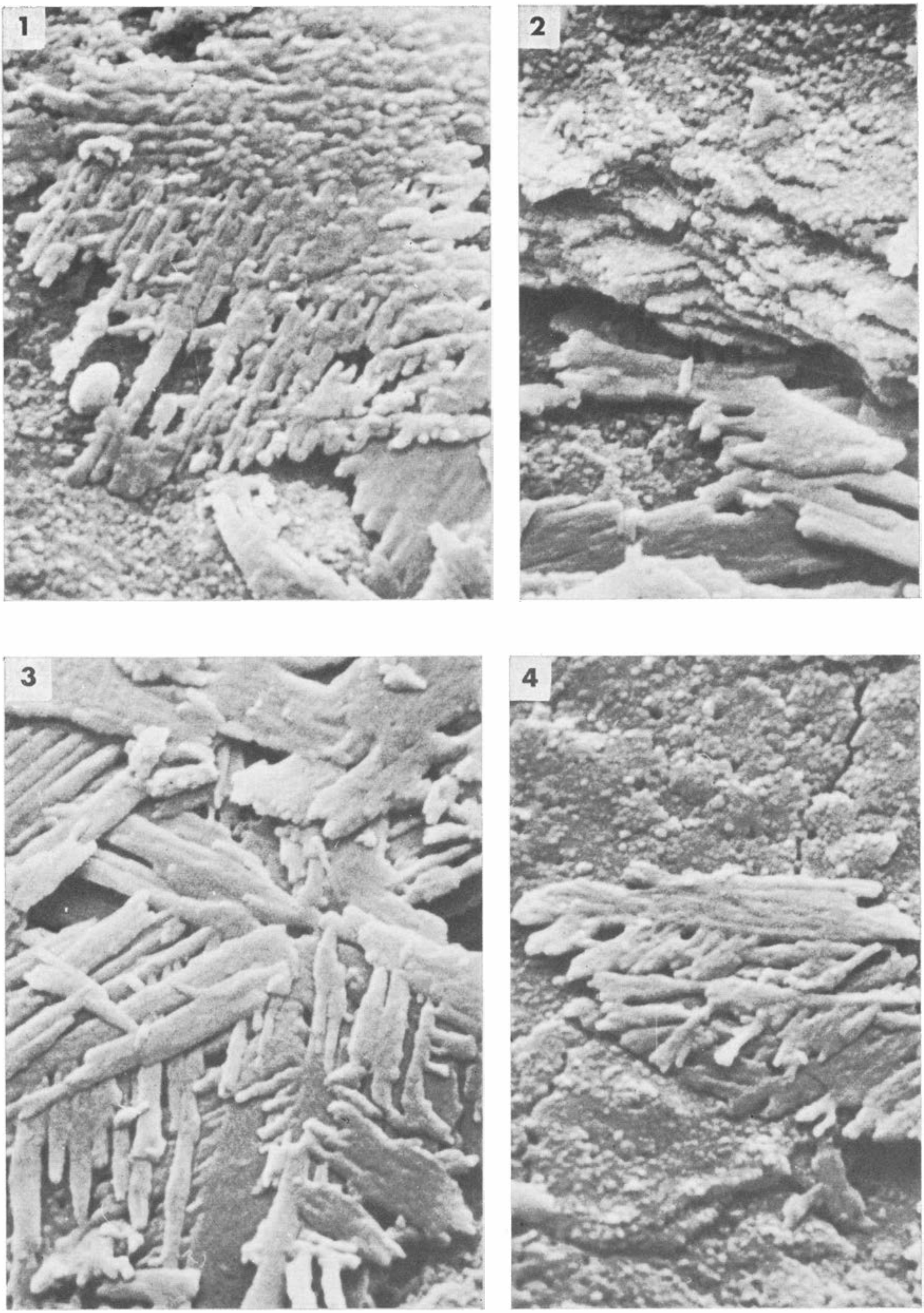

1
2
3
4

Plate XVII

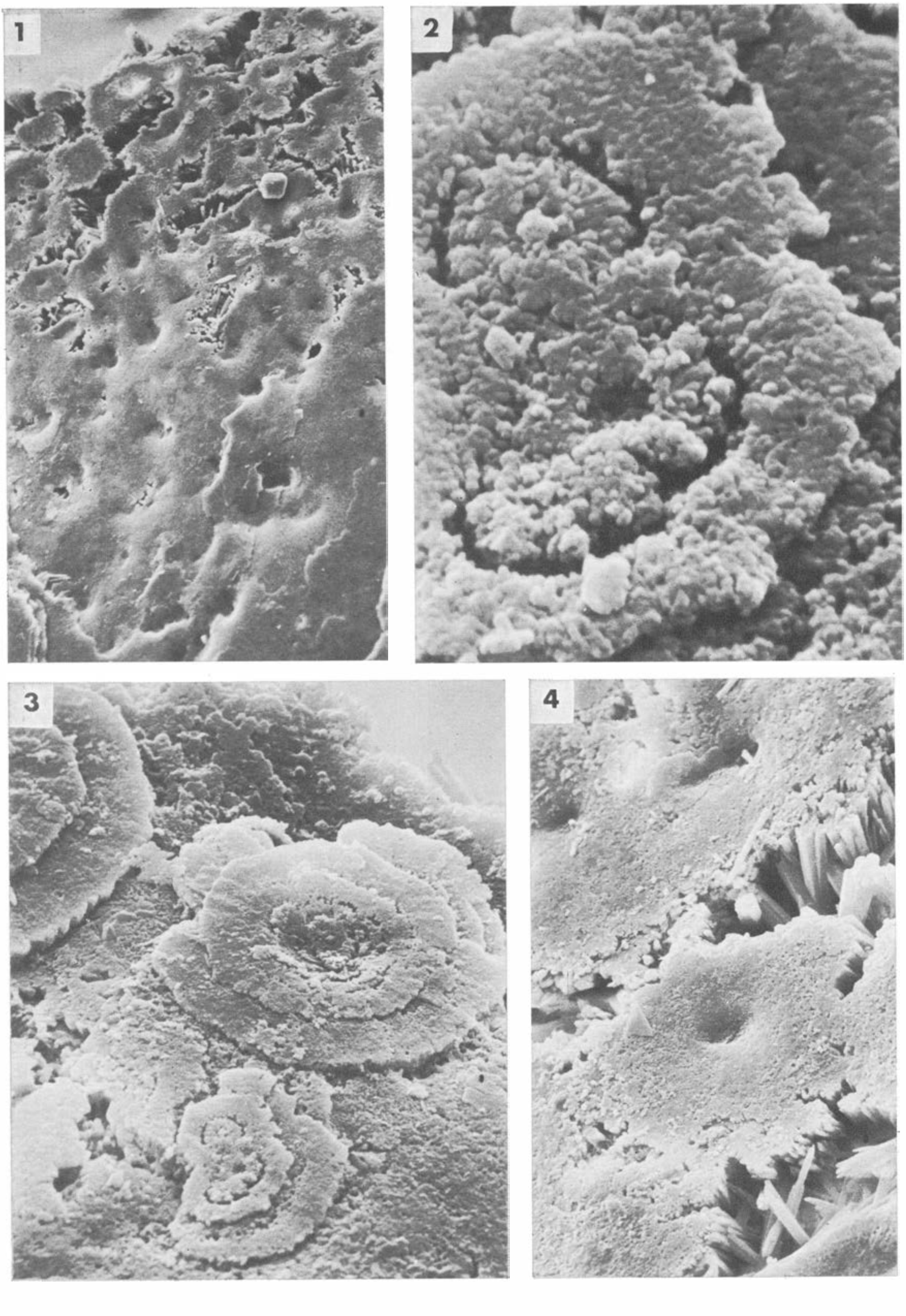


Plate XVIII

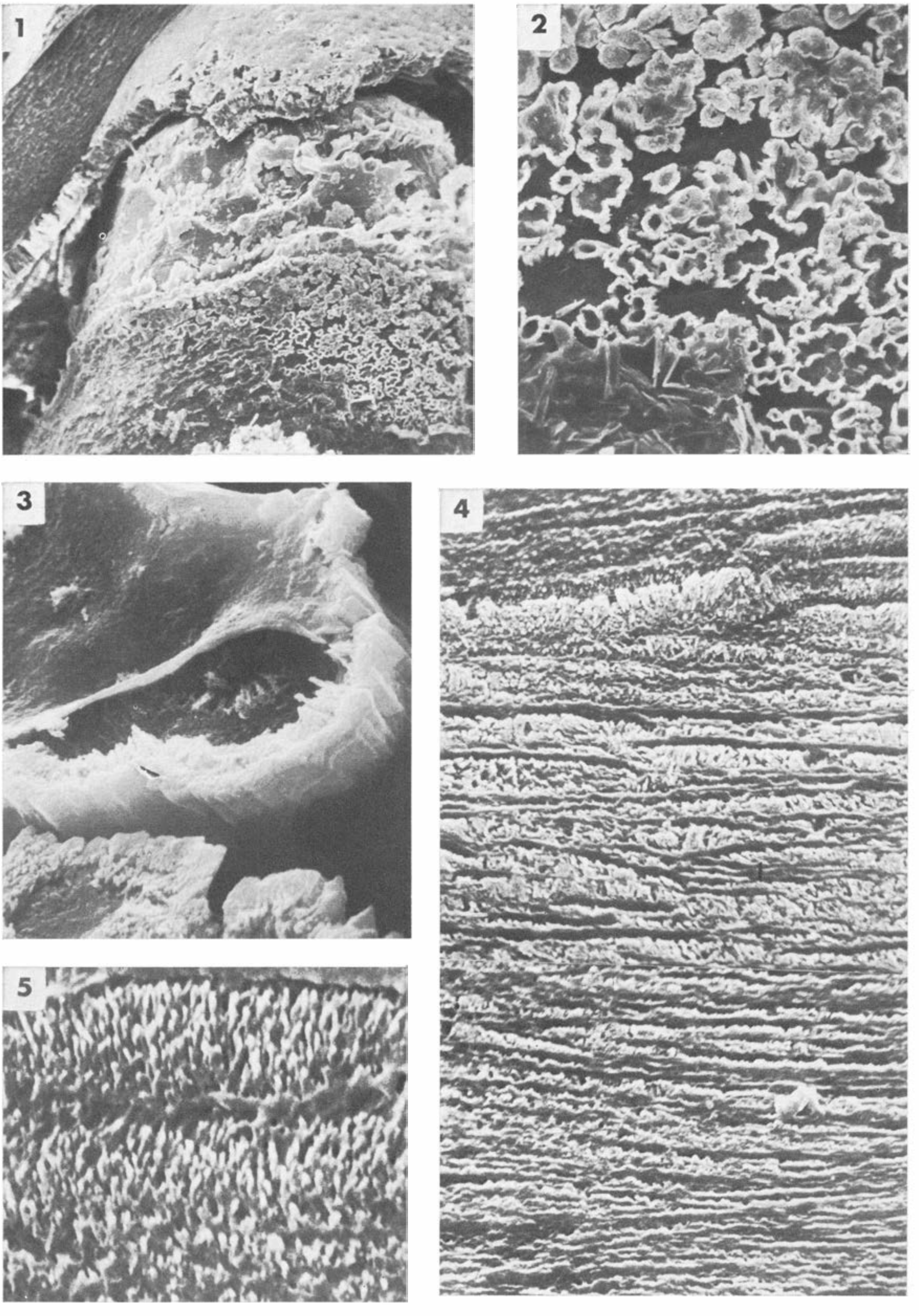


Plate XIX

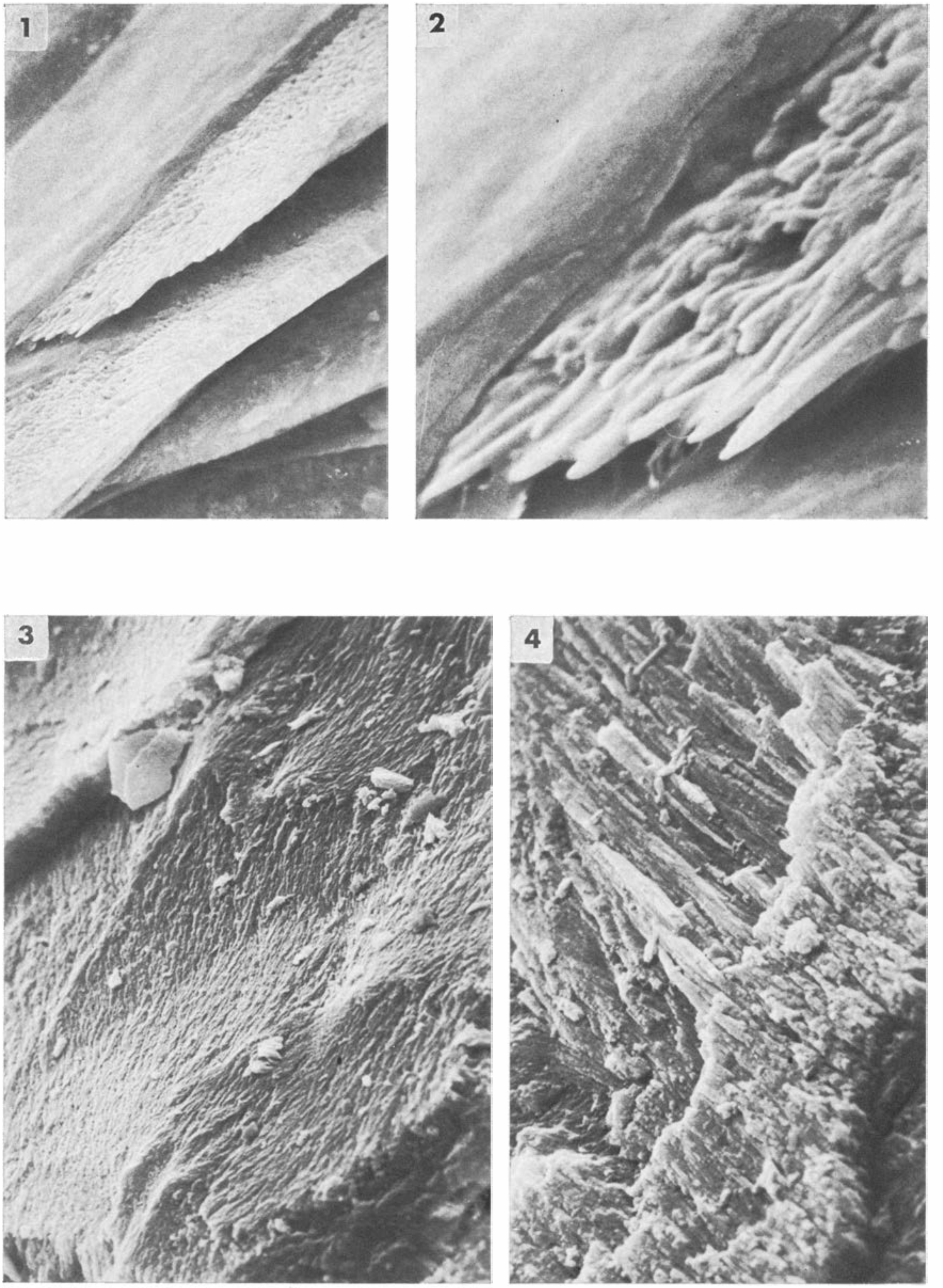


Plate XX

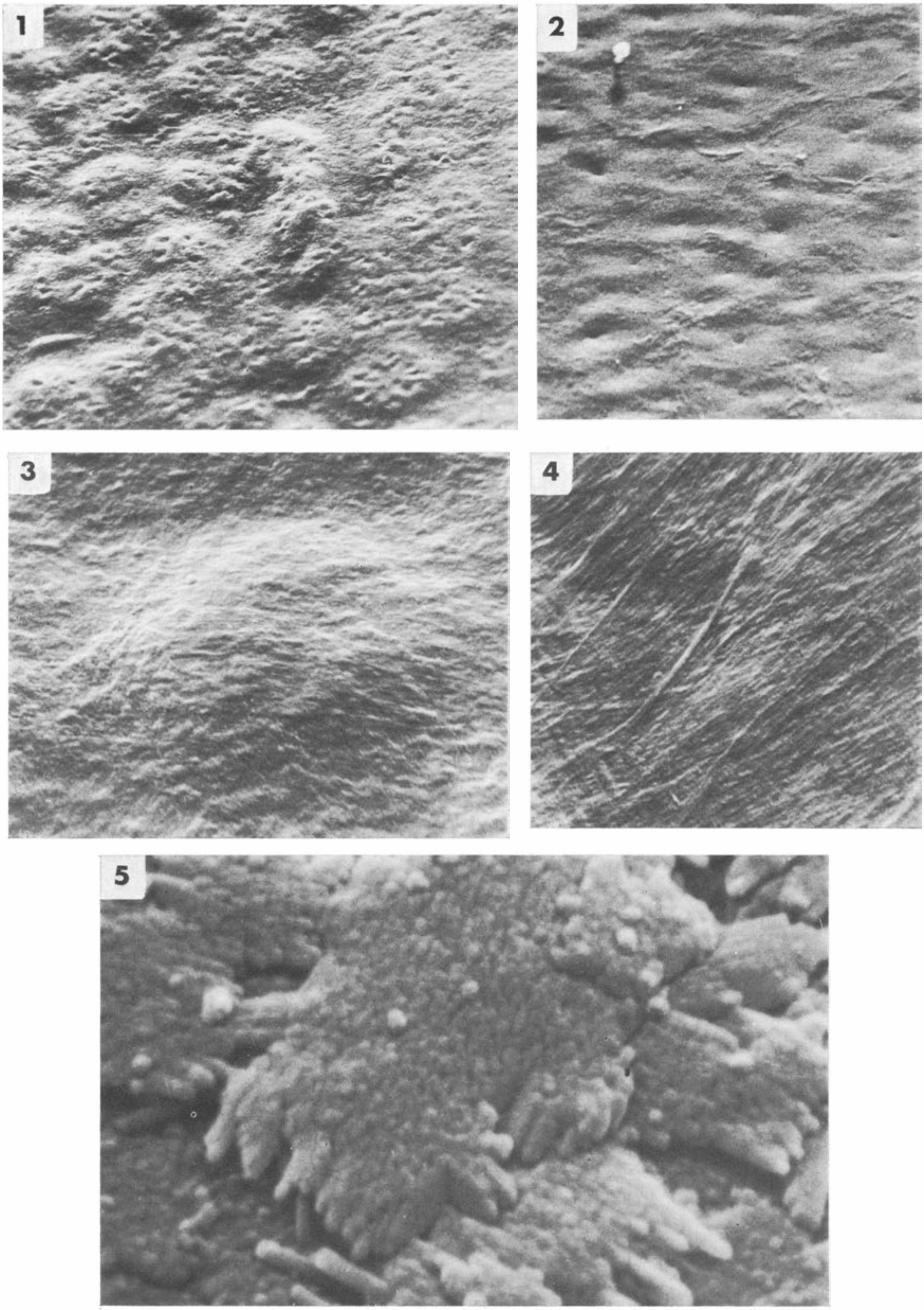


Plate XXI

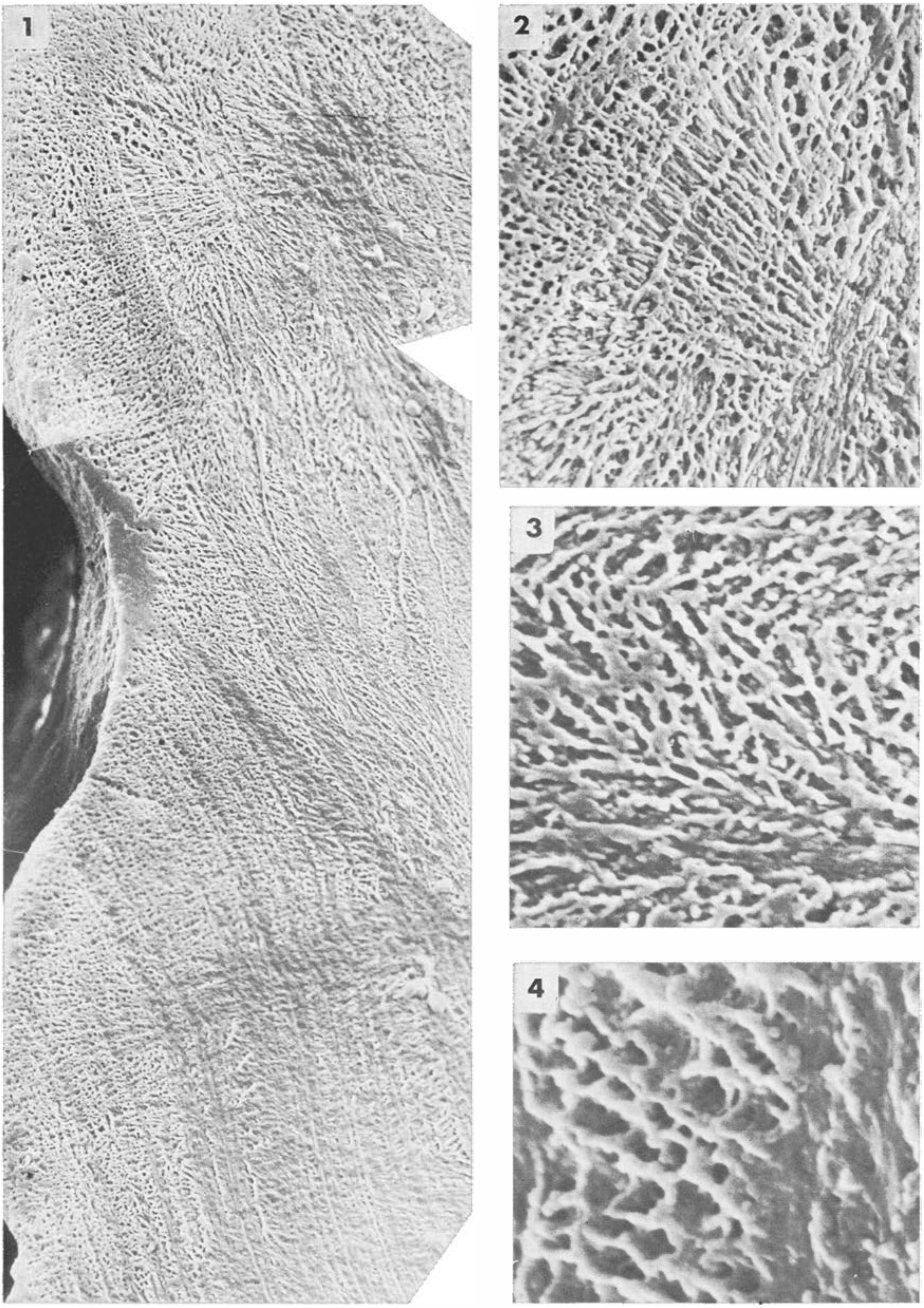
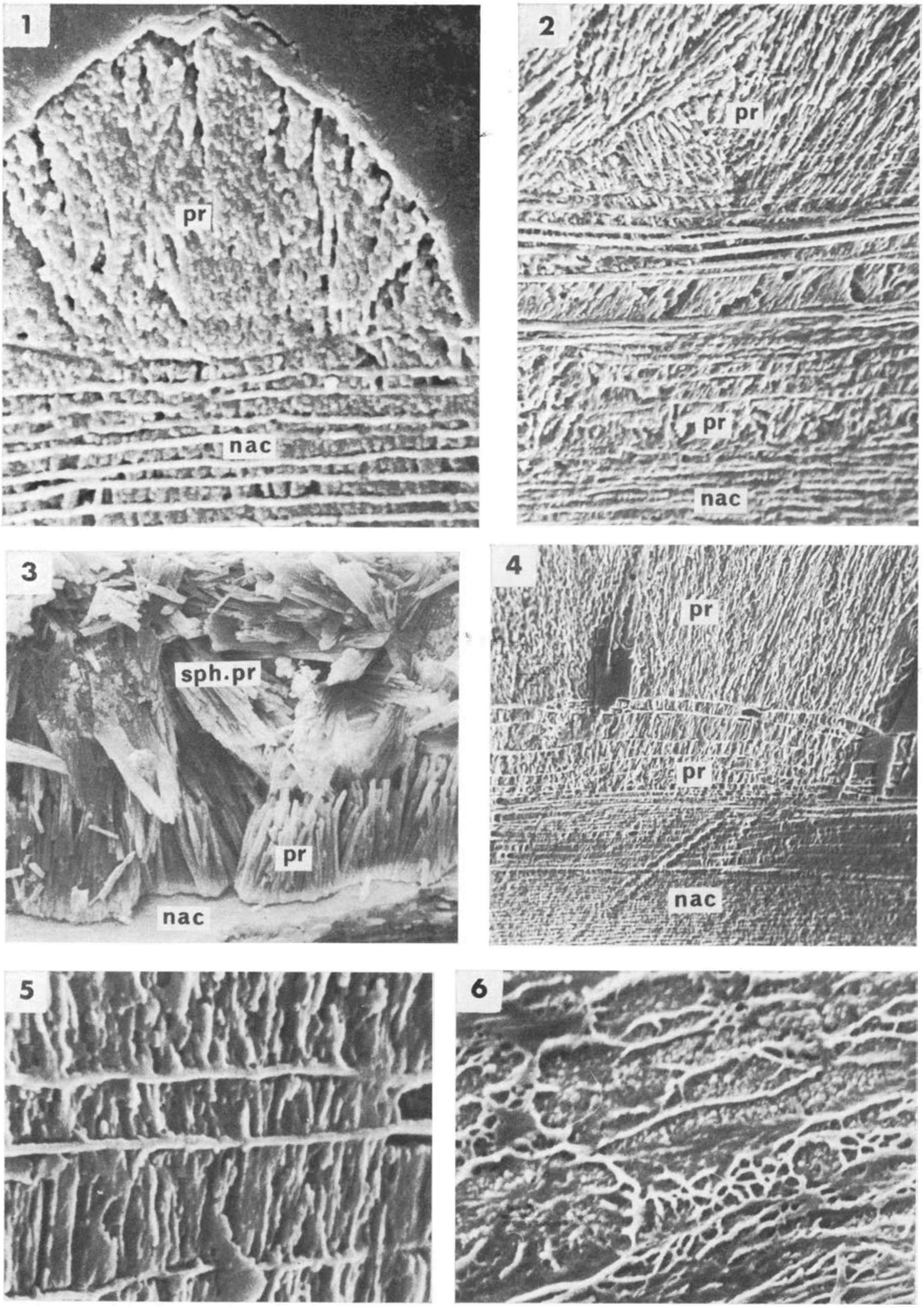
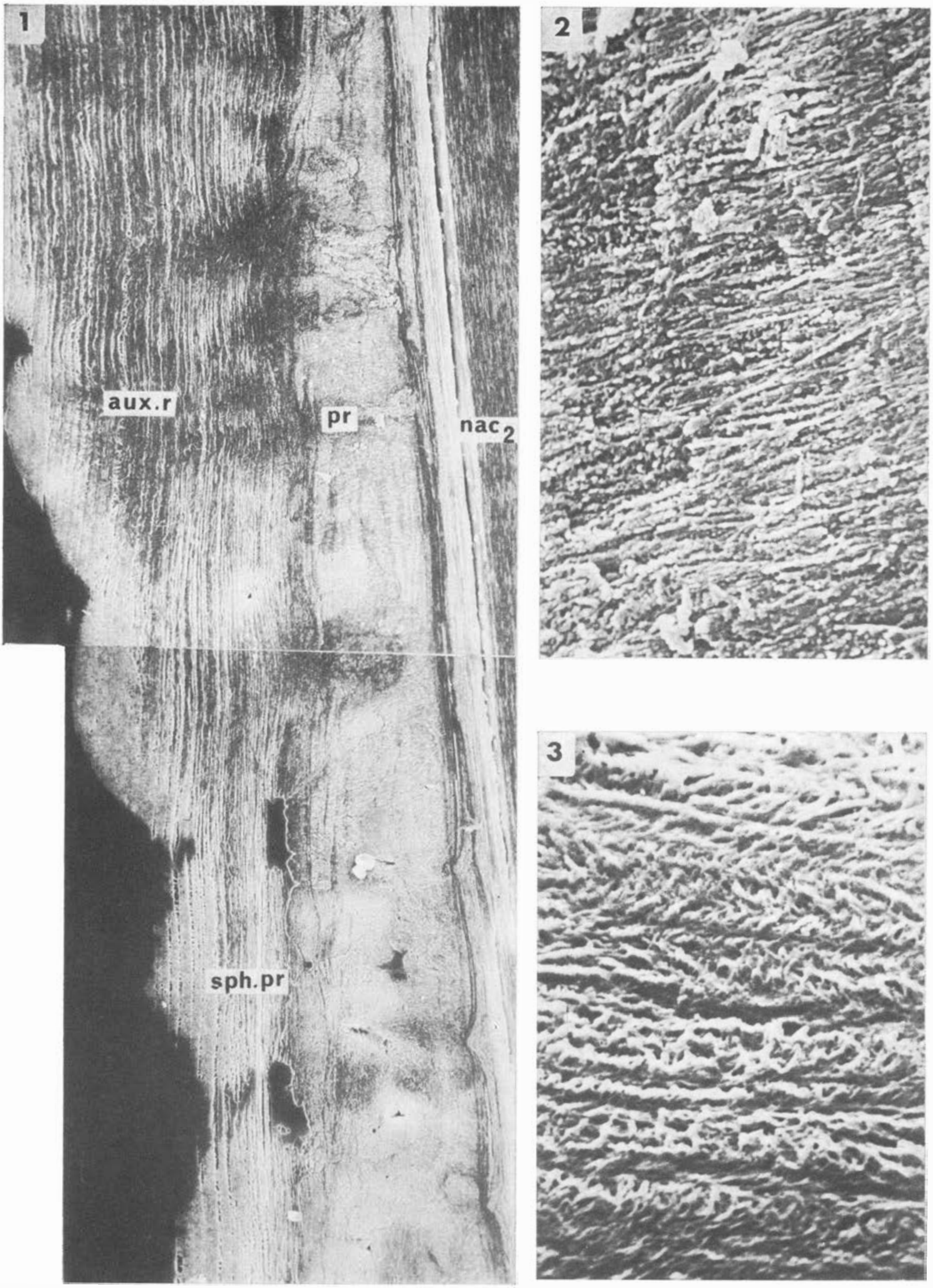


Plate XXII




1
aux.r
pr
nac2
sph.pr
2
3


1

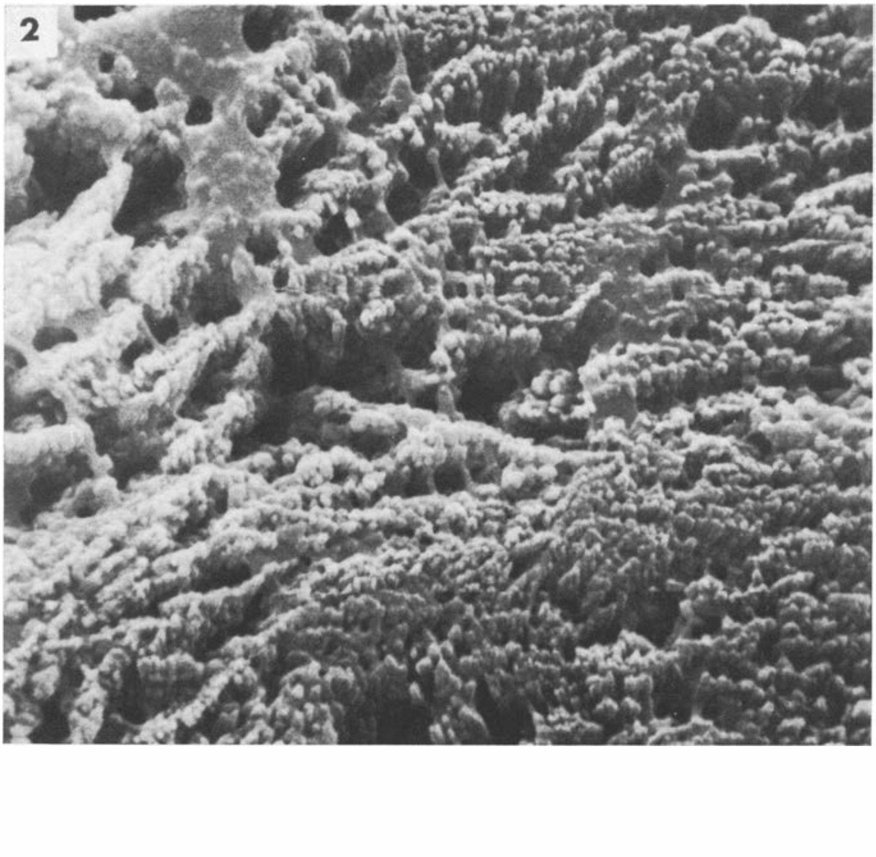

2

Plate XXV

2