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THE AMMONITE SHELL: ITS STRUCTURE, DEVELOPMENT AND BIOLOGICAL SIGNIFICANCE

Abstract. — The author's studies on the development of the siphon and related structures in Triassic and post-Triassic ammonites reveal that, contrary to the views of MUTVEI (1967) and MUTVEI and REYMENT (1973) the siphonal tube in the prochoanitic stage of development is homologous to the organic layer of the siphonal tube of Recent *Nautilus*. During the transition from retrochoanitic to prochoanitic septal necks, a deep furrow encircling the siphonal soft tissue developed within the posterior epithelium of ammonites. It divided the initially synchronous zones secreting the nacreous tissue of the septum and siphonal tube into zones which could secrete asynchronously. Such asynchronous secretional activity was associated with the different organization of the soft tissues in the posterior part of the body, and enabled the animal to both accelerate and retard siphonal tube formation on either the internal or the external side, and also allowed the possibility of connections between the siphon and various auxiliary structures (e.g. siphonal membranes). Auxiliary deposits in prochoanitic ammonites are always bipartite. Posterior auxiliary deposits are homologous with the distal end of the retrochoanitic septal neck, whereas the anterior auxiliary deposits correspond to the auxiliary ridge of Recent *Nautilus*. The results of the author's studies on the early developmental stages of the ammonite shell differ from those of BIRKELUND (1967), BIRKELUND and HANSEN (1968, 1974) and ERBEN *et al.* (1968, 1969). The wall proper of the initial chamber is shown to pass continuously into the external prismatic layer of the first whorl, and is a counterpart of the external prismatic layer of the succeeding whorls. When a complete initial chamber is developed behind the zone secreting the wall proper of the initial chamber and the external prismatic layer of the first whorl, a broad zone appeared secreting prismatic and subprismatic tissue. This tissue builds the internal component of the ventral wall of the initial chamber and, at the same time, the main wall component of the first whorl and proseptum. The proseptum originated in a deep furrow encircling the posterior part of the body as a continuation of the internal prismatic layer of the initial chamber and the first whorl. During later development, the posterior secreting zone was divided into the zone secreting the subprismatic tissue of the first whorl wall, the external component of the dorsal wall, and the zone secreting septa and the internal prismatic layer. In longitudinal sections the external layer of the initial chamber wall is equivalent to the dorsal wall of the first whorl; the thickness decreases considerably at the boundary between the initial chamber and the first whorl. This microstructure reflects a change in the secretory pattern on the nepionic constriction. The change involved only the subzone controlling the secretion of the subprismatic layer of the first whorl. This layer corresponds to the nacreous layer of the following whorls. Observations on shell embryogeny provided new evidence supporting the idea of a direct embryonic development of ammonites against the hypothesis of larval development and metamorphosis of ERBEN *et al.* (1968, 1969). As a result of the present author's experiments with the gradual filling of empty *Quenstedtoceras* shells with water it has been demonstrated that the fluid distributes equally in numerous reservoirs on the margin of septa near the shell wall and adheres there through surface tension. Such a distribution of the fluid assures an invariable degree of decoupling of the main fluid volume from the fluid encircling the siphon. This makes the hydrostatic apparatus of the animal functional in various shell positions and ensures static equilibrium in a turbulent environment.

CONTENTS

INTRODUCTION

The use of the scanning electron microscope (SEM) made possible a marked increase in the accuracy of studies of the microstructure and early development of the ammonite shell. SEM studies on the early development of ammonites were carried out by BIRKELUND (1967), BIRKELUND and HANSEN (1968, 1974), ERBEN, FLAJS and SIEHL (1968, 1969), DRUZCZIC and KHIAMI (1970), DRUZCZIC and DOGUZHAEVA (1974), KULICKI (1974, 1975) and DAUPHIN (1975). The material covered by these studies was of widely differing ages and modes of preservation, and interpretations of structural details and early growth in these papers varies widely, although there is general agreement in respect of other features.

The studies carried out by the present author deal with well-preserved specimens of *Quenstedtoceras*, *Kosmoceras* and other Callovian (Jurassic) ammonite genera from well-known locality at Łuków, eastern Poland. The work permitted a revision of current views on the nature of the early ontogenic growth stages of ammonites.

A detailed anatomical study of the early growth stages allows reconstruction of ontogenic development of zones of secretion and casts some light on the embryogenesis of the group. Numerous specimens of *Quenstedtoceras* with unmineralized interiors were used in experiments which involved infilling of phragmocone chambers with water. This gave information on the function of folded septa from both physiological and mechanical points of view.

The characteristics of the periostracum and some other organic films not related to the siphuncle are omitted below because of their variability throughout the shell. There is some evidence for diagenesis and secondary mineralization of the organic films which is reflected by differences in thickness, resistance to etching by various chemical reagents, as well as their absence in some parts of shell. Thus the question of organic films is considered as requiring separate treatment.

The terminology widely used in the literature is accepted here except for following new terms:

nepionic swelling — for shell thickenings on the nepionic constriction;
tissue — for mineral and organic matter forming separate shell layers;
posterior auxiliary deposits — for auxiliary deposits forming the anterior end of the connecting ring; the name is chosen because of the posterior position of these deposits in relation to the septal neck, and it is equivalent of the term „manzheta" used by DRUZCZIC *et al.* (1974, 1976);
anterior auxiliary deposits — for auxiliary deposits forming the posterior end of the connecting ring; the name is chosen because their position is opposite to that of the posterior deposits;
angular deposits — for mineral deposits occurring between proximal part of a prochoanitic neck and the posterior auxiliary deposits;
wall proper of the initial chamber — for the original wall of the *initial* chamber.

The specimens covered by these studies are housed in the Institute of Paleobiology of the Polish Academy of Sciences abbreviated as ZPAL. SEM micrographs were made using the microscope J.S.M.-1 in the Laboratory of Electron Microscopy, Nencki Institute of Experimental Biology, Polish Academy of Sciences in Warsaw.

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MATERIAL AND METHODS

The studies covered the following specimens:
(1) *Nathorstites gibbosus* STOLLEY; Carnian (Upper Triassic), Odgeöya Island (E Svalbard); two specimens, one of which was infilled with calcite and very well preserved, were studied using the SEM;

(2) *Holcophylloceras zignodianum* (d'ORBIGNY); Callovian (Middle Jurassic), Ratscha village in the Setsiskvile valley, Georgian SSR; two specimens, one with well preserved siphuncular tube in the body chamber.
(3) *Quenstedtoceras* sp.; Callovian (Middle Jurassic), Łuków, Poland; numerous specimens were used for making 100 polished sections; SEM studies covered 27 polished sections and 23 fractured specimens.
(4) *Cadoceras* sp.; Callovian (Middle Jurassic). Anabar valley, Siberia, USSR; 3 polished sections.
(5) *Kosmoceras* sp.; age and occurrence as (3); 10 polished sections (4 used in SEM studies) and 8 fractured surfaces.
(6) *Perisphinctes* sp.; the age occurrence as (3); 8 fractured surfaces.
(7) *Polyptychites* sp.; Lower Valanginian (Lower Cretaceous), mouth of the Anabar, Siberia, USSR; one polished section.
(8) *Dichotomites* sp.; Upper Valanginian (Lower Cretaceous), Bajarka Valley, Siberia, USSR; one polished section.
(9) *Surites subanalogus* SCHULGINA; Berriasian (Lower Cretaceous), Bajarka Valley, Siberia, USSR; one polished section.
(10) *Aconeceras trautscholdi* SINZOV; Aptian (Lower Cretaceous), Ulianovsk, right bank of Volga, USSR; three polished sections.

The specimens used for SEM investigation were prepared as follows: (a) the fractured samples were attached directly to the sample holder using electro-conductive glue and subsequently coated with evaporated carbon and gold; (b) polished sections were etched for 2–5 minutes in 2% EDTA and subsequently attached and coated as (a); (c) acetate peels of large polished fragments were taken and pieces stuck to the sample holder and similarly coated.

The analysis of mineral composition (STAHL and JORDAN, 1969) has shown that the shell of *Quenstedtoceras* from Łuków consists primarily of aragonite and that only 2–4% calcite is present. This indicates that recrystallization was slight, and that the structure observed are largely original.

SIPHONAL DEPOSITS

OBSERVATIONS

Septal necks and other siphonal elements in *Nathorstites gibbosus* Stolley

Description. — The position of the siphon is at the ventral margin from the proseptum onwards in *Nathorstites gibbosus*. Medial sections show that the ventral part of septal necks is closely adjoined to the internal surface of the wall, where its thickness is reduced in relation to the dorsal part. This reduction in thickness results in the fact that particular elements of necks are less clear in the ventral part and the description of necks is therefore mainly based on sections through the dorsal part.

In *N. gibbosus* the first two septa are situated one above the another in the dorsal part. They bifurcate as they approach the caecum organic cover of the siphuncle (pl. 24: 5). Any more detailed determination of the characteristics of the siphonal deposits and septal necks based on these septa is not possible. Well-developed retrochoanitic septal necks proper are well displayed on successive septa. From the morphological point of view the retrochoanitic neck represents an extension of the septum directed towards the apical part of the shell (pl. 24: 1–3; figs. 1 A–G, 2). From the forty second septum (or 3·75 of whorl onwards) a sharp margin appears in the ventral part of the anterior part of the septal neck, gradually disappearing somewhat below the mid-height of the neck (fig. 1 E). This sharp margin from the anterior

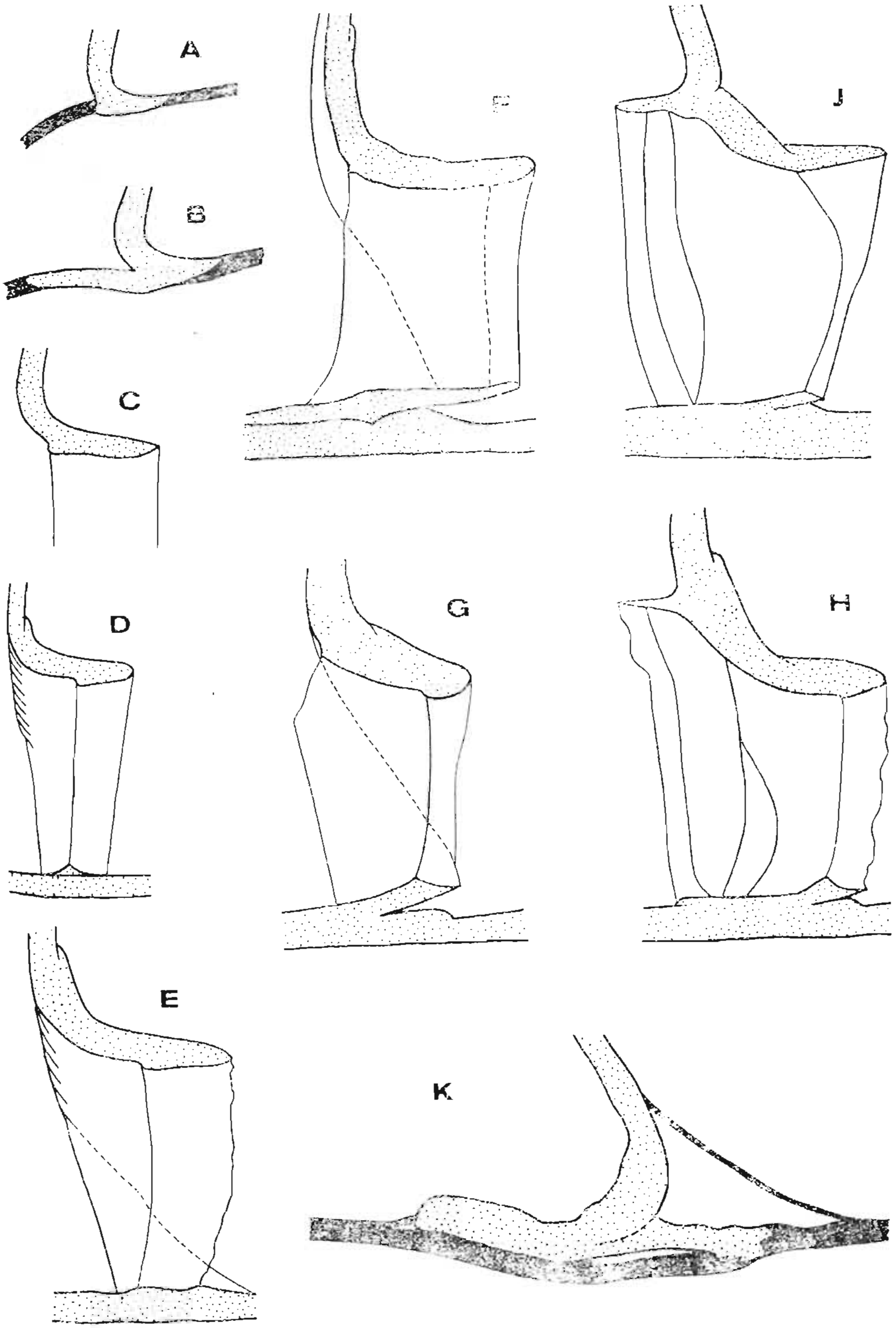

Fig. 1

Scheme of the sections of septal necks in *Nathorstites gibbosus*, ZPAL Am III/3. *A* -- 18th septum, retrochoanitic septal neck. *B* — 20th septum, retrochoanitic septal neck; an exceptionally well developed anterior auxiliary siphonal deposit is visible. *C* — 32nd septum, a retrochoanitic septal neck. *D* — 39th septum, a sharp ridge pointing anteriorly occurs in the ventral part of the neck; it disappears at the mid-point of the neck. *E* — 42nd septum, the ridge disappears a little higher than in D. *F* — 45th septum, a sharp edge extends to the entire perimeter of the neck, at the dorsal side it is in the form of a slight appendix. *G* — 49th septum. *H* — 50th septum, the sharp ridge is at a height sufficient to form a distinct prochoanitic element of the septal neck. *I* — 55th septum, the prochoanitic element of the septal neck is better developed than in the earlier septa. *K* — 89th septum, a typical prochoanitic septal neck part of the neck is marked along the whole periphery of the neck, including its dorsal part, at septum 45 (end of the fourth whorl). The margin is marked as a small projection towards the anterior in medial section through the dorsal part (fig. 1F). It increases in height on successive septa and finally becomes similar to the ending typical of prochoanitic septal necks (fig. 1H, J).

Further growth leads to the development of a prominent prochoanitic neck at the expense of the equivalent of the retrochoanitic neck. As a result of proportional reduction the latter becomes modified into a typical posterior auxiliary deposit (pl. 25: 1; fig. 1K).

The relation of connecting ring to septal neck and septum. — The ending of the retrochoanitic septal neck extends and passes into the posterior section of connecting ring (pl. 24: 1; fig. 1A, B). The anterior section of the connecting ring is attached to the inner surface of the anterior part of the septal neck (pl. 24: 1, 2; figs. 1A–E). A small projection is visible at the place where the anterior section of the connecting ring is attached (pl. 24: 1, 2, 3, 6, 7; fig. 1).

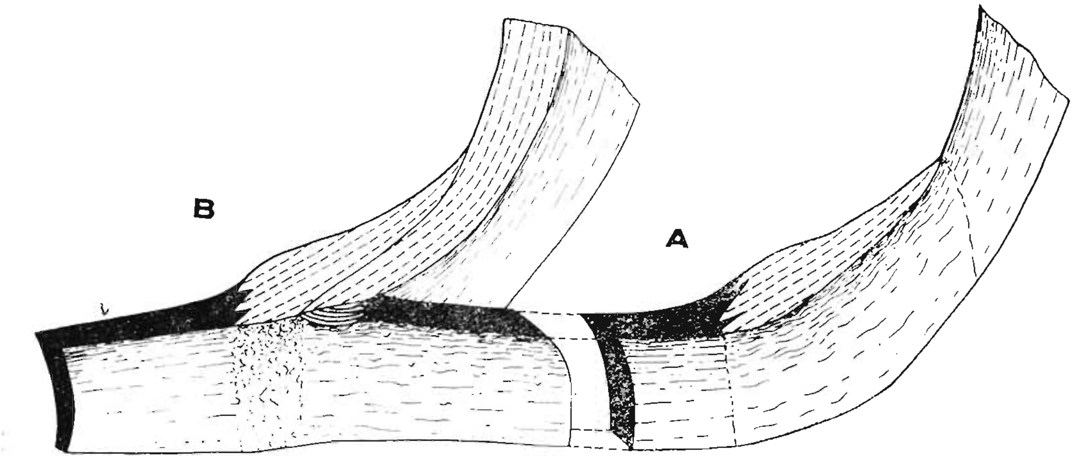

Fig. 2

Diagrammatic drawing of the last two septa in *Nathorstites gibbosus*, at the stage of retrochoanitic septal necks. *A* — The last septum under formation. *B* — The last but one septum completely formed

The anterior ending of the posterior part of the connecting ring and the posterior ending of the next following connecting ring are distant from one another on the earlier septa, but the distance decreases with further growth. When prochoanitic septal necks are formed the siphuncle gains additional connections to the neck and septum as:

(1) the distal end of the prochoanitic septal neck is connected with the connecting ring by a short section of organic membrane (pl. 24: 4; pl. 25: 1, 2a; fig. 1K).

(2) the connecting ring is fused with the organic cover of the internal surface of the septal neck in its mid-length (pl. 25: 2a, b; fig. 3D–G); this connection may widen towards either the back of the neck (pl. 25: 1) or its front (fig. 1K) with further growth.

(3) the adapical septal surface becomes fused with the connecting ring via the so-called siphonal membrane. This connection is more or less regular in character (pl. 25: 1; fig. 1K).

Discontinuities observable in sections of septal necks or in their proximity. — The mineral tissues of the specimen studied are almost completely recrystallized, which precludes any analysis of the mutual arrangement of mineral components and their accurate identification. It should be noted, however, that there are regularly repeated discontinuities on successive septa. Taking into account hypotheses previously put forward, these boundaries may be considered not as diagenetic but rather primary in origin. The boundaries are visible under both optical and scanning electron microscope.

Sections of the dorsal part of the septal neck from the stage of occurrence of retrochoanitic necks display a single discontinuity extending from the apical surface of the septum to the inner side of the neck (pl. 24:, 1, 2, 3, 6, 7). The discontinuity separates the apical part of the retrochoanitic neck from the septum and its proximal part, which is marked as a minor elevation above the adapical surface of septum.

In the transitional zone where the prochoanitic septal necks originate, the discontinuity divides the auxiliary deposits formed from the retrochoanitic part of the septal neck into two parts: the posterior, giving rise to the posterior section of the connecting ring, and the anterior. With further growth, the discontinuity becomes less and less clear, and finally disappears completely, giving an apparently homogeneous appearance to the auxiliary deposits originating from the distal part of retrochoanitic septal neck. Discontinuities running from the apical septum surface still occur repeatedly in the transitional zone (pl. 24: 4; fig. 1H, J); they continue from the angle formed by the auxiliary deposit and the proximal part of the septal neck towards its distal part in the prochoanitic stage, becoming subsequently obliterated (pl. 25: 1; fig. 1K). The discontinuities separate the auxiliary deposit from the prochoanitic septal neck.

Septal necks and deposits in *Quenstedtoceras* and *Kosmoceras*

Description. — In *Quenstedtoceras* the relationship between the first two septa differs from that between the subsequent ones, because of the reduced distance between them and the distinctive curvature of the first septum. The central part of the dorsal side of the second septum grows into the proseptum at 50–60% of its height (pl. 27: 4) and not directly to the wall of the initial chamber. For this reason all sections parallel to the medial plane passing through siphon and caecum display only the ventral part of the second septum and the ventral wall of the first segment of the connecting ring, together with the siphonal deposits. The siphonal portion connecting the proseptum and second septum represents an oblique segment of the tube.

In medial sections, the caecum is connected with the ventral wall of the initial chamber along a short section of variable width (pl. 28: 2; pl. 44: 1). In these sections, the ventral part of the proseptum is generally so short that it is difficult to separate it from the shell wall. In places where the caecum grows into the ventral wall and proseptum, the organic wall of the caecum may thin (pl. 28: 2) or thicken (pl. 44: 1), but there are no mineral deposits connecting the caecal wall and the mineral tissues of the proseptum or the wall of the initial chamber. The dorsal part of the circum-siphonal proseptum is represented by a plate somewhat bent in the direction of apex or aperture (pl. 29: 1, 3; pl. 36: 1; pl. 36: 3). A posterior auxiliary deposit occurs between the organic caecum wall and the mineral tissue of the proseptum (pl. 29: 3; pl. 30: 1; pl. 31: 2; pl. 36: 1, 3; fig. 6, 7E, F). The mineral tissue of the posterior auxiliary deposit is visible on cross-sections as a finely granulate mass of randomly arranged elements. It resembles the mineral tissue separating the subprismatic and prismatic layers of the initial chamber, and that separating the first whorl from the basal and middle parts of proseptum.

The wall of the connecting ring visible in the ventral part of the medial section connects the first and second septa. The anterior auxiliary deposit of the proseptum is relatively well developed between the wall of the connecting ring and the proseptum. It is variable, usually irregular in shape and more or less antero-posteriorly elongated. The mineral tissue of the anterior auxiliary deposit of the proseptum is more regular in texture, somewhat resembling nacreous tissue, with interlamellar spaces oriented concordantly with the walls of the connecting ring, or prismatic tissue with the longer axes of mineral components lying parallel to one another and the wall of the connecting ring (pl. 28: 2; pl. 30: 2; pl. 38: 1a: pl. 39: 1; pl 44: 3).

In medial section the ventral wall of the connecting ring of the first segment is connected by its anterior ending with the posterior auxiliary deposit of the second septum. In that section the posterior auxiliary deposit of the second septum has the outline of acute-angled triangle; the anterior margin of the connecting ring is adjacent to the shorter arm of the triangle and the internal side of the ventral wall to one of the longer arms (pl. 38: 1b; pl. 39: 1; pl. 44: 3). The mineral tissue of the posterior auxiliary deposit of the second septum does not differ from that of the anterior auxiliary deposit of the proseptum. The sections shown here (pl. 28: 2; pl. 39: 2; pl. 30: 2) display marked shortening or absence of a segment of the connecting ring. In the second or third case the anterior auxiliary deposit of the proseptum passes smoothly into the posterior deposit of the second septum.

The anterior auxiliary deposits of the second septum are triangular in outline in medial section. They are partly developed on the posterior auxiliary deposits and partly on the ventral shell wall. The structure and texture of these deposits remain poorly known, but seem somewhat different to that of the mineral tissue of the auxiliary deposits described above (pl. 38: 1b; pl. 39: 1).

The dorsal section of the connecting ring connects the anterior auxiliary deposit of the proseptum and the posterior auxiliary deposit of the third septum in medial section. The mineral tissue of the anterior deposit of the proseptum is the same here as in other parts of the section, although its shape and place of attachment to the proseptum are somewhat variable. The dorsal part of the anterior auxiliary deposit is situated either below the free proseptum margin (pl. 28: 3; pl. 29: 1, 3; pl. 30: 1; pl. 31: 2) or represents an extension of the forwards bend of the proseptum which produces the apparently prochoanitic septal neck of this part of the proseptum (pl. 36: 3).

The subdivision of the auxiliary deposits into anterior and posterior parts is marked throughout the ontogeny in *Quenstedtoceras* and *Kosmoceras*, as it is during the prochoanitic necks stage in all representatives of *Ammonitina*, *Lytoceratina* and *Phylloceratina* studied by the present author.

On some ventral sections of the first half of the first whorl of *Quenstedtoceras* and *Kosmoceras* the anterior and posterior auxiliary deposits are of identical development relative to the septal neck (pl. 32: 1; pl. 34: 1, 2; pl. 35: 4) although differences in size develop subsequently. This reflects a more extensive development of anterior than posterior auxiliary deposits (pl. 33: 1; pl. 32: 2a; pl. 35: 2; pl. 37: 1, 2), and is seen already in the dorsal part of sections of the third septum (pl. 35: 3).

The posterior auxiliary deposits are usually covered, to a minor degree by the anterior early in development (see e.g. pl. 32: 1); subsequently, the anterior deposits meet the posterior along their whole length (pl. 32: 2a; pl. 33: 1; pl. 35: 2; pl. 37: 1, 2).

The mineral tissues of auxiliary deposits from middle and late ontogenetical stages are still poorly known. The genus *Kosmoceras* (pl. 41: 1–3) is an exception, however, for on septa of the sixth whorl the posterior auxiliary deposits are markedly larger than the anterior. The boundary between the posterior and anterior deposits is very sharp, and angular deposits are well developed within the angle between the posterior auxiliary deposits and the proximal part of the septal neck.

The mineral tissues of the posterior auxiliary deposits closely resemble the modified nacreous layer of the distal part of the septal neck of ?*Pseudorthoceras* illustrated by MUTVEI (1972*b;* pl. 7: 1) as well as the nacreous layer of distal end of a septal neck of *Nautilus pompilius* L. also figured by that author (MUTVEI, 1972*a;* pl. 21: 1–2; pl. 25; 1).

In the case of *Kosmoceras*, the posterior auxiliary deposit differs from those figured by MUTVEI in having a more homogeneous structure throughout the section as well as in having fewer organic membranes (corresponding to interlamellar membranes). The mineral tissue of the posterior auxiliary deposits of the specimen of *Kosmoceras* studied are best termed spherulitic-prismatic (pl. 41: 3). The anterior auxiliary deposits (pl. 41: 2) are also uniformly developed throughout the section and are structurally closest to the deposits of the auxiliary ridge of Recent *Nautilus pompilius* L. figured by MUTVEI (1972*a*, pl. 24: 2). The structure is prismatic, without noticeable spherulites and rudimentary transverse membranes such as occur in posterior auxiliary deposits.

The tissues of the posterior and anterior auxiliary deposits from early stages of ontogenetic development of *Quenstedtoceras* and *Kosmoceras* display more features transitional towards prismatic and nacreous tissues than those from the lates stages (pl. 32: 2b, 2a; pl. 35: 1–4; pl. 37: 1a–1b; 2a–2b). It is often possible to note a structural difference between the anterior and posterior auxiliary deposits of a single septum (pl. 35: 1–2; pl. 37: 1–2); the difference is usually small, with the anterior deposits showing more strongly marked prismatic features.

The angular deposits also show a prismatic structure, characterized by a fan-like orientation of the crystalline components in cross-section (pl. 32: 2; pl. 36: 2; pl. 41: 1). Studies of *Quenstedtoceras* and *Kosmoceras* at various growth stages show a marked variability in the degree of development of angular deposits, characterized by prismatic structure independent of ontogenetic stage, mode of development and preservation.

Specimens with body chambers preserved never display a connecting ring in the last chambers of the phragmocone, although they almost always show auxiliary deposits preserved on the last septum. The development of auxiliary deposits is relatively weakest here and the posterior deposits are always stronger than the anterior.

Ontogenetic development of septal necks in Quenstedtoceras and Kosmoceras. — The first septum (proseptum) of representatives of these two genera shows a free circumsiphonal margin around the connecting ring, straight or bent slightly backwards or forwards. A septal neck is not, therefore, developed.

The second septum of *Quenstedtoceras* also lacks a septal neck (pl. 29: 2; pl. 38: 1b; pl. 39: 1), but additional deposits in the anterior part, above the anterior auxiliary deposits (pl. 28: 2; pl. 30: 2). The latter are built of prismatic tissue similar to but not passing into that of the septum. The deposits are found only in paramedial sections, and may be homologous with the distal ending of a prochoanitic septal neck.

The third septum may have a typical prochoanitic septal neck with an elevated distal margin in the ventral part (pl. 30: 3).

Subsequent septa display normal prochoanitic septal necks in their ventral parts (pl. 30: 4; pl. 37: 1a–2a). The middle growth stages are very often characterized by the distal ending of the septal neck rising above the surface of the siphonal tube (pl. 30: 4; pl. 31: 1). The formation of prochoanitic septal necks is retarded in the dorsal part in relation to the ventral part. The third septum (and sometimes subsequent septa) of *Quenstedtoceras* are characterized by a continuous transition from the nacreous tissue of the septum into the prismatic tissue of the siphon edge. It does not form a septal neck but only a slight swelling (pl. 35: 3). Septal necks gradually appear in dorsal part on subsequent septa.

Fully developed prochoanitic septal necks are built of nacreous tissue similar to that of the remaining part of the septum. The arrangement of laminae of nacreous tissue is highly distinctive (pl. 36: 2; pl. 37: 1a, 2a–b): adapertural laminae of the septum continue throughtout the external surface of the neck, up to its distal end, whilst adapical septum laminae wedge out on the inner surface of the neck base.

The dorsal part of the second septum of *Kosmoceras* is not located on the proseptum as in *Quenstedtoceras*, but directly on wall of the initial chamber, the siphonal opening being situated at mid-whorl. Because of this the medial section displays the ventral part of the septum, and the relationship between septum and auxiliary deposits are clearly displayed (pl. 39: 2).

The second septum of *Kosmoceras* has no septal neck. That part of the septum directly surrounding the siphon is club-shaped (pl. 34: 1–2). The anterior and posterior auxiliary deposits connect with the septum at a right angle in the dorsal region (pl. 34: 2); in the ventral part the septum meets anterior and posterior auxiliary deposits at an acute angle (pl. 34: 1).

Angular deposits are visible in the dorsal part of the section. The mineral tissues of the second septum are essentially nacreous; only in the club-shaped widening mentioned above is there a transitional, mainly prismatic structure.

The circumsiphonal part of the third septum of *Kosmoceras* is bent forwards in the form of a prochoanitic septal neck (pl. 35: 1–2) and the distal part of the neck also displays a transitional, nacreous-prismatic structure. Further development of septal necks and auxiliary deposits is the same as in *Quenstedtoceras*.

Caecum and its attachments to the shell. — The spherical, somewhat dorso-ventrally flattened caecum and prosiphon are enclosed in a chamber formed by the walls of the initial chamber and proseptum in the proximity of the external saddle (s) (see pl. 26: 1, 3a, 4; pl. 27: 2). In addition to the connections with proseptum and initial chamber wall already noted, the caecum is connected with the initial chamber wall via the so-called prosiphon. A typical *Quenstedtoceras* prosiphon resembles a three-walled tent, and the oblique wall connects the adapical part of the caecum with the inner surface of the ventral wall of the initial chamber. The two vertical, parallel or slightly convergent walls connect the caecum with the oblique wall and the inner surface of the initial chamber (pl. 26: 2; pl. 27: 1, 2). In the case of the specimen illustrated here (pl. 27: 1) the oblique wall of the prosiphon together with the wall of the initial chamber form a complex suture; in others, the connection between the walls of the prosiphon, caecum and surface of the initial chamber is continuous (pl. 26: 2, 3a, 3b). The cross-section (pl. 44: 3) displays a free space at the connection of caecum and oblique wall. An abnormally developed prosiphon is shown here on pl. 26: 1, 1a; even in this case, however, it is possible to distinguish the oblique wall and a single vertical wall.

The majority of prosiphons are characterized by longitudinal wrinkles, and similar but much finer wrinkles may be also noted on the surface of the caecum (pl. 26: 1a, 3a, 3b).

Several specimens show the surface of the caecum connected with the distal end of the flange by an organic film. The caecum is connected in several places with the ventral wall close to the area of ventral attachment; similar connections are much scarcer in the dorsal part (pl. 26: 3a; pl. 28: 3; pl. 29: 1; pl. 30: 1; pl. 44: 3; pl. 29: 3).

Supplementary attachments between connecting ring and the shell. — Besides the above mentioned attachments between connecting ring and septum via auxiliary deposits, there are several other attachments, by means of so-called siphonal membranes. In *Quenstedtoceras* the connecting ring is attached with the ventral wall by an organic membrane located in the plane of symmetry from the third septum onwards. The membrane frequently fails to reach the ends of septa meeting only their adapical or adapertural parts (pl. 27: 5). An additional, and more complex connection between the siphon, ventral wall and septum appears at the third whorl (pl. 27: 3a, 3b). Such connections are not found on subsequent whorls whereas connections by transverse, somewhat oblique organic membranes becomes more common. Short and narrow organic membranes connecting the surface of the siphon with both adapical and adapertural surface of the septum are relatively rare in *Quenstedtoceras* (see e.g. pl. 27: 6).

A siphon from the body chamber of *Holcophylloceras zignodianum* (d'ORBIGNY)

The specimen studied, 105 mm in diameter, has about a third of a whorl of body chamber, filled with dark greenish limestone, whilst the phragmocone and the last section of the connecting ring are infilled with calcite (pl. 40: 1). The section of the siphon in the body chamber is 16·5 mm long. The sections of siphon from the two preceding chambers of the phragmocone, measured in the same way, are 19·5 and 19·0 mm long respectively. The siphon wall is 35 μm thick at its ending in the body chamber, 121 μm tick in its middle part and 173 μm thick close to the anterior auxiliary deposits. The thickness of the siphonal wall from the last chamber of the phragmocone is 69 μm close to the end of the anterior auxiliary deposits of the last septum. The external diameter of the connecting ring from the body chamber is 1575 μm and 1400 μm close to its termination and to the septal neck respectively, and 1140 μm in the proximity of the posterior auxiliary deposits of the last chamber of the phragmocone. The internal diameter of the connecting ring from the body chamber is 1495 μm at the distal end, 1275 μm in the middle and 1190 μm in the proximity of septal neck, whereas the internal diameter of siphonal tube of the anterior section of the siphon equals 1000 μm in the proximity of the posterior auxiliary deposits.

The last section of the siphonal tube situated in the body chamber is not of uniform colour. Light-brown or yellowish at the distal end, it changes gradually to a dark-brown at the end of septal neck. In all the remaining chambers of the phragmocone the connecting ring is uniformely dark-brown in colour, darker coloured than anywhere in its final section.

Growth lines are visible on the dorsal part of the section of the connecting ring situated in the body chamber: they begin at the inner surface and run towards its external surface in distal direction.

DISCUSSION AND INTERPRETATION

Studies on the internal structure of ammonites, including their septal necks, were carried out by HYATT (1872), BRANCO (1880), GRANDJEAN (1910), SCHINDEWOLF (1931), BÖHMERS (1936), MILLER and UNKLESBAY (1943) and others.

The majority of these authors discovered transition from retrochoanitic septal necks in early stages to prochoanitic necks during later growth. DRUZCZIC, BARSKOV and KHIAMI (1968) proposed a new term "amphichoanitic septal neck" for the transitional stage between the two types of necks: the amphichoanitic septal neck was said to be characterized by two projections directed towards the posterior and anterior of the shell respectively, serving as the place of attachment for the organic wall of the siphon.

Taking into account the types of septal necks present, ammonites may be divided into 3 groups: (a) those with retrochoanitic necks only, (b) those with retro- and prochoanitic necks, and (c) ammonites with prochoanitic necks only. The first group comprises mainly Paleozoic ammonites, the second — Late Paleozoic and Early Mesozoic ammonites, and the third — only some representatives of the suborder Ammonitina, for example the genera *Quenstedtoceras* and *Kosmoceras* covered by the present studies.

Previous descriptions of the ontogenetic development of septal necks (HYATT, 1872; BRANCO, 1880; GRANDJEAN, 1910; SCHINDEWOLF, 1931; BÖHMERS, 1936; VOORTHUYSEN, 1940; MILLER and UNKLESBAY, 1943) were often fairly extensive but, however, the changes found were not compared with those known from Recent *Nautilus*.

MUTVEI (1967: 163) has given two possible interpretations to ammonites with retrochoanitic septal necks.

(1) The connecting ring is homologous with the conchiolin layer of the connecting ring of *Nautilus*, or

(2) the connecting ring is secondary and, therefore, not homologous with that layer in *Nautilus*.

According to MUTVEI (1967) and MUTVEI and REYMENT (1973) only a secondary connecting ring is typical of ammonites with prochoanitic septal necks. DOGUZHAEVA (1973) reported a transition from retro- and prochoanitic septal necks during the ontogeny of Triassic Megaphyllites and stated that "the calcareous circumsiphonal tube is attached to the connecting ring from the back is formed at the expense of the retrochoanitic septal neck. It is not excluded that similar tubes of early Cretaceous phylloceratides also represent a homologue of retrochoanitic septal necks. If this is supported by SEM studies the similarity in structure of the siphon of ammonites and nautiloids will appear much more important than MUTVEI (1967) assumed" (DOGUZHAEVA, 1973).

A transition from typical retrochoanitic septal necks to prochoanitic necks via a transitional stage was traced in the ontogeny of *Nathorstites gibbosus* STOLLEY.

Comparison of retrochoanitic septal necks of *Nathorstites, Nautilus* and other nautiloids

The retrochoanitic septal neck of *Nathorstites*, characterized by a distal part separated from the remaining parts by a discontinuity (pl. 24: 2, 3, 6, 7) and passing into the wall of the connecting ring towards the posterior, may be compared with the retrochoanitic septal neck of *Nautilus* described by MUTVEI (1972*a*) as well as those of fossil orthocone nautiloids from the Pensylvanian Buckhorn asphalt described by MUTVEI (1972*b*) and RISTEDT (1971).

The distal part of the retrochoanitic septal neck of *Nathorstites* may be compared with the "Siphowulst" of RISTEDT (1971, pl. 37: 5; pl. 38: 1–2, 7), the modified nacreous layer of MUTVEI (1972*b*, pl. 6: 1–3; pl. 7: 1; pl. 11: 1; fig. 1A, B) and the distal modified nacreous layer of Recent *Nautilus pompilius* described by MUTVEI (1972*a*, pl. 10: 1; figs. 2–3).

Projections and thickenings of mineral tissue found at the place of attachment of the adapical endings of connecting ring in *Nathorstites* are interpreted here as poorly developed auxiliary deposits corresponding to those of Recent *Nautilus*. The auxiliary deposits of *Nathorstites gibbosus* appear to be less developed in relation to the Recent *Nautilus* figured by MUTVEI (1972*a*, fig. 2).

Ontogenetic development of the septal neck of *Nathorstites*

MUTVEI (1964, 1972*a*, *b*) assumed synchronous development of the laminae of the nacreous layer in the zone of secretion of septa. Studies on the shell wall, of gastropods and bivalves carried out by WISE and HAY (1968) and ERBEN (1972), have shown that synchroneous growth planes are oblique in relation to laminae of nacreous layer. The septa secreting zones of cephalopods were not covered by such studies, but nevertheless, it may be taken that this is also the case here. Following the views of MUTVEI, the secretory zone was of rapidly fluctuating extent. For example, the whole adapical surface of the mantle, including the last section of siphon, participates in the formation of the adapical organic membrane (MUTVEI, 1964, 1972*a*, *b*) whilst, according to MUTVEI (1972*a*: 252), during the next secretory phase, 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 form during the same secretory phase. In consequence, the subsequent secretory phase would be characterized by a great reduction of secreting area, and the subsequent phase of secretion of the nacreous layer would involve, as during the initial phases, the whole adapical surface of the mantle. The oblique course of synchronous growth planes in relation to laminae of the nacreous layer, as is the case in the shell wall, suggests that the structurally modified nacreous layer shown by MUTVEI (1972*b*) was secreted simultaneously with the connecting ring. The oblique boundary (MUTVEI, 1972*b*, pl. 7: 1; pl. 11: 1; fig. 1A, B) is synchroneous and marks the end of the phase of secretion of connecting ring and the distal end of the septal neck. If the secretion of the distal part of the retrochoanitic neck did not end with either a longer break or other additional changes, we are dealing here with a phenomenon of continuation of laminae of the nacreous layer between structurally modified nacreous layer and typical nacreous layer as emphasized by MUTVEI (1972*b*, fig. 1B) or, as in the first case, as it was emphasized by RISTEDT (1971: 182) "besteht der Siphowulst aus prismatischen Schichten ... und wird von einer Vielzahl von relative dicken Membranen durchzogen die, wie aus Fig. 7 auf Taf. 38 zu ersehen ist, oral wärts in der Apikalen Membran des Septums zusammenlaufen".

If follows that in ontogenetic development of the retrochoanitic septal neck of *Nathorstites* two phases of secretion may be distinguished.

(1) The first phase of secretion, ending with formation of distal part of the retrochoanitic neck, begins with formation of auxiliary deposits on the inner surface of the preceding neck and the adapical part of the connecting ring. The wall of the connecting ring, the distal part of the septal neck and some section of the adapical organic membrane covering the septum (fig. 2A) are formed at the end of this phase of secretion. At that time the secretory zone is presumably not much wider than the distal ending of the retrochoanitic septal neck, and is separated from the rest of the neck by a discontinuity. The secretory zone is differentiated into three subzones during the formation of the adapical part of the septal neck: (a) that secreting the organic cover of the siphon; (b) that secreting the mineral tissue of the distal ending of the neck and (c) that secreting the adapical organic membrane of the septum.

(2) In the second phase of secretion the remaining part of the neck and septum are formed (fig. 2B). In the middle of that phase the secretory zone reaches its maximum extend, close to that assumed by MUTVEI (1964, 1972*a*, *b*), i.e. parallel to the laminae of the nacreous tissue. During this phase, secretion is differentiated into two subzones at the most: (a) a subzone secreting nacreous tissue and (b) a subzone secreting the organic adapertural membrane.

Formation of prochoanitic septal necks in ammonites

BRANCO (1880), BÖHMERS (1936), VOORTHUYSEN (1940), MILLER and UNKLESBAY (1943) and others found that the formation of a prochoanitic septal neck always starts at the ventral side, extending subsequently to cover the whole periphery of the retrochoanitic septal neck. This often results in the fact that prochoanitic septal neck is already developed in the ventral part when a retrochoanitic septal neck is still present in the dorsal part of the medial section (BRANCO, 1880, pl. 9: 9; pl. 11: 9; VOORTHUYSEN, 1940, figs. 3, 6). The phylogenetically earliest ammonites with prochoanitic septal necks are represented by some Late Carboniferous Agathiceratidae displaying the transition from retro- to prochoanitic septal necks on the sixth and seventh whorls (DRUZCZIC *et al.*, 1976). This transition is marked at the fifth, fourth and third whorls in Permian Goniatitina, as in Triassic representatives of the Order Phylloceratida proposed by SCHINDEWOLF (1968) and on the second and first whorls of Jurassic and Cretaceous representatives of *Phylloceras* (see DRUZCZIC *et al.*, 1976). Similar examples of an accelerated transition between the two types of septal necks in phylogeny are known in the Lytoceratina and Ammonitina.

Ontogenetic growth of the connecting ring in the transitional phase in *Nathorstites*

In the transitional stage in *Nathorstites* four phases may be distinguished:

(1) A phase corresponding precisely to the first phase of formation of a retrochoanitic septal neck, in which the wall of the connecting ring and distal part of the equivalent of the retrochoanitic septal neck are formed (figs. 3A, 4A). Differentiation of the secretory zone is as discussed above in the first stage of formation of the retrochoanitic septal neck.

(2) In the second phase the subsequent part of the equivalent of the retrochoanitic septal neck forms. In this phase the secretory zone is also narrow, and differentiated into two subzones: (a) the subzone secreting the nacreous tissue and (b) the subzone secreting the conchiolin membrane covering the adapical surface of the septum (figs. 3B, 4B).

(3) In the third phase the adapical part of the nacreous layer of the septum forms. The adapical boundary is represented by a discontinuity, whilst the adapertural boundary is hypothetical. and unmarked in the specimens studied. It is assumed that at this stage it is represented by a synchroneous boundary in relation to which the laminae of the nacreous layer

are arranged adaperturally, following the pattern typical of the prochoanitic septal neck. The zone of secretion is presumably very wide at this stage, and is initially differentiated into two subzones, followed by uniform secretion of the nacreous tissue of the septum (figs. 4C, 3C).

(4) In the fourth and final phase, the remaining part of the septum is formed, as well as the prochoanitic neck proper. A strong forwards twist of the laminae of the nacreous tissue, without a return towards the adapical part indicates formation of a deep furrow surrounding the extension of soft siphonal tissues in body chamber during this phase. Moreover, secretion of the anterior auxiliary deposits and the conchiolin cover of the siphon is initiated. At the end of this phase the distal ending of the prochoanitic part of the septal neck becomes con-

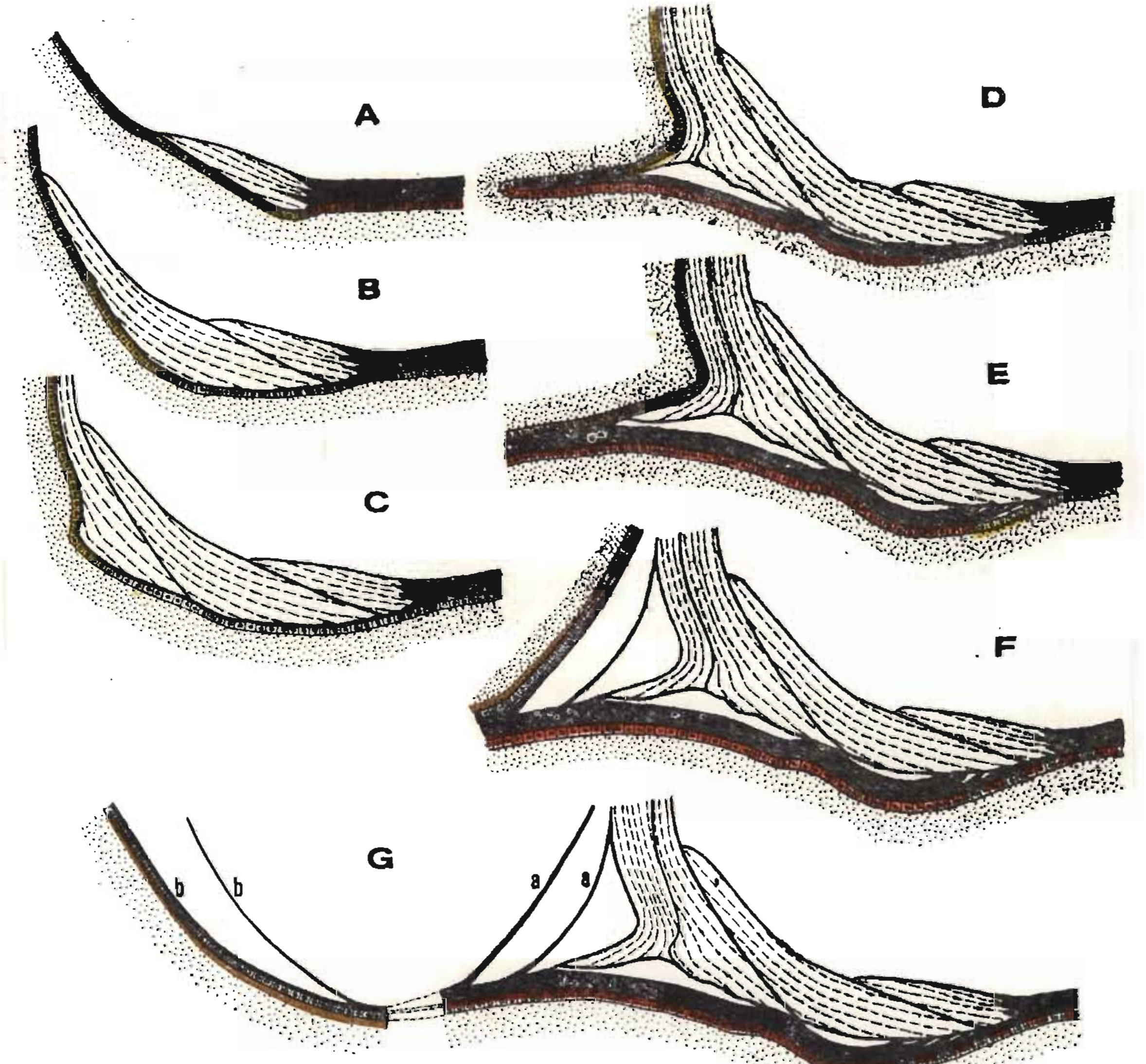

Fig. 3

Development of secretion zones at various stages of formation of the septal neck and connecting ring at the transitory stage in *Nathorstites gibbosus*. *A–G* — Successive developmental stages. *a* — Siphonal membranes formed after formation of an adequate section of connecting ring; their organic tissue is discordant relative to the organic tissue of the connecting ring, or is adaperturally extended into the external layer of connecting ring. *b* — Siphonal membranes in the form of a continuation of the external organic layer of the connecting ring; they are extended adapically. *Yellow* — zone of secretion of nacreous tissue. *Red* — zone of secretion of conchiolin of connecting ring from the interior. *Brown* — zone of secretion of adapertural and adapical septum membranes; siphonal membranes, and conchiolin of connecting ring from the exterior nected with the connecting ring. An initially uniform secretory zone finally differentiates into two subzones: the one secreting nacreous tissue, the other the conchiolin membrane of the adapertural surface of the septum (figs. 3DE, 4D).

A reconstruction of secretory zones makes it necessary to discuss the relationship of growth surfaces to laminae and rods of nacreous tissue. Taylor *et al.* (1969) and Erben (1972) have shown that there are two types of nacreous tissue, differing in their mutual arrangement of platelets: one, typical of gastropods, has platelets arranged in so-called stacks, and laminae are difficult to trace; in the other, platelets do not form stacks, and are arranged in distinct laminae. In both cases synchronous planes are set somewhat oblique to the laminae of nacreous tissue.

The bulk of ammonites studied have nacreous tissue of the first type. Some specimens, and especially those representing early ontogenetic stages display parts of the nacreous layer with poorly developed stacks. Longitudinal sections of the shell wall show that laminae of nacreous tissue are nor parallel to the external periostracal surface but diverge at a small angle to the outside in relation to the whorl axis and direction of growth. In some very rare cases, when the course of growth surfaces is visible (pl. 47: 7), the surfaces are deflected from the whorl axis in the same direction but at a somewhat greater angle.

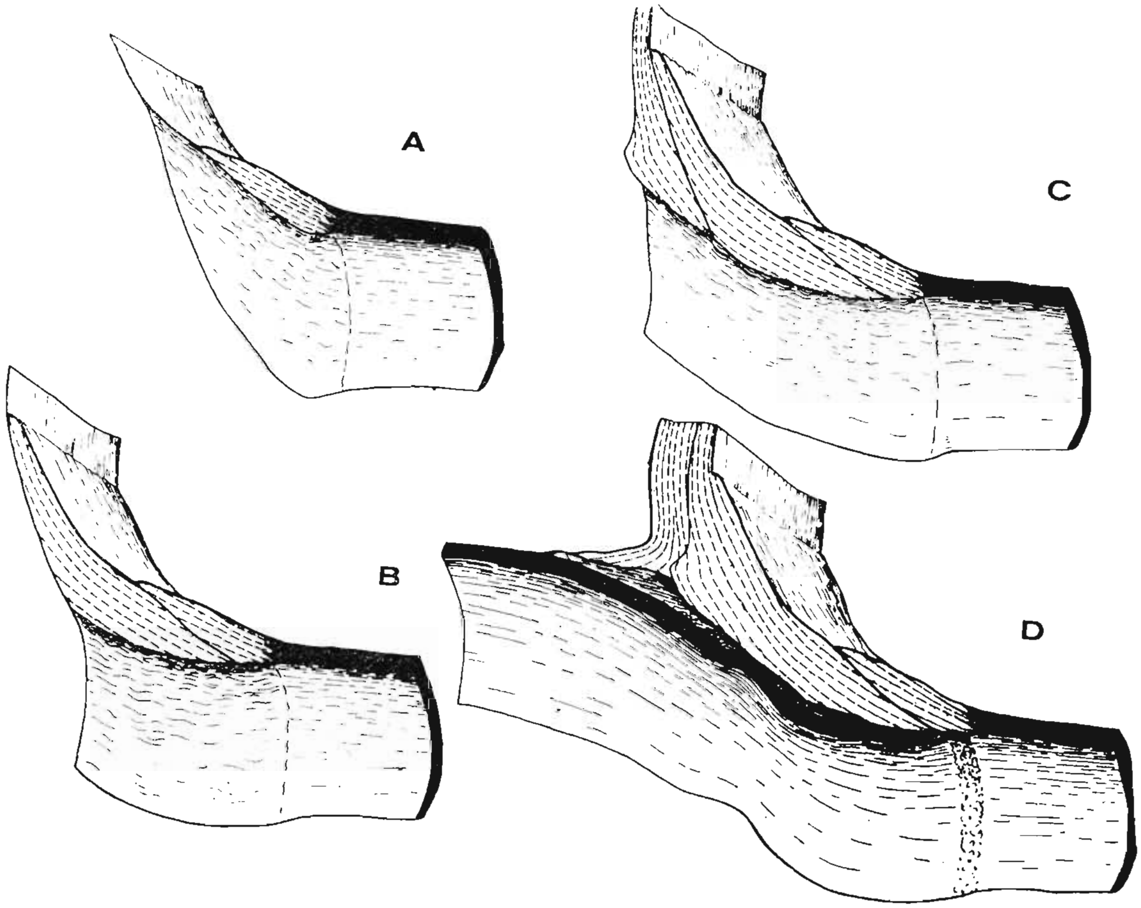

Fig. 4
Diagrammatic drawing of the developmental stages of the septal neck at the transitory stage in *Nathorstites gibbosus*. *A–D*: The latest developmental stages

The reconstruction of secretory zones based on either the course of growth lines or the assumption that growth planes are parallel to laminae of the nacreous layer (Mutvei 1964, 1972*a*), is somewhat erroneous.

Laminae of the nacreous layer are not inclined to the adapical surface of the septum in the case of ammonites studied here. Growth planes are not visible on the surface of the septum, nor in cross-sections. So-called discontinuities, visible on direct replicas of *Nathorstites gibbosus* as depressions, and thus similar to the remaining organic membranes or organic rich areas, seem to be the exception here. Discontinuities are also marked by a break on the adapical surface of the septum in *Nathorstites*. It seems, therefore, that discontinuities displayed by *Nathorstites* do not represent boundaries between laminae of nacreous tissue, but rather synchronous growth planes separating successive phases of secretion. In the case of septa growth planes may be parallel to laminae of nacreous tissue as shown in drawings and descriptions given by MUTVEI (1964, 1972*a*).

On the section through septum, septal neck and siphon of *Eleganticeras elegantulum* given by MUTVEI (1975, fig. 2), we note a dark boundary passing through the middle and approaching adapical surface of the septum in the proximal part of the neck. This boundary corresponds to the discontinuities seen in *Nathorstites*, separating the older part of the septum from the younger part and the septal neck.

The development of secretory zones during the transition from retro- to prochoanitic stages is illustrated in fig. 3A–G. Three types of secretion are distinguished:
(1) secretion of nacreous tissue (yellow), (2) secretion of the conchiolin of the connecting ring from within (red), and (3) secretion of the adapical and adapertural septal membranes, siphonal membranes and the conchiolin of the connecting ring from the outside (brown).

Ontogeny of the prochoanitic septal neck of *Nathorstites*

Some laminae of the posterior auxiliary deposits may originate asynchronously to those of the septal neck and septum. They do not represent a morphological extension of neck and septum as was the case in the retrochoanitic septal neck (see fig. 5). Analysis of the transitional stage of growth of *Nathorstites* has shown a retardation in the final formation of the prochoanitic part of the neck in relation to the posterior auxiliary deposits. Similar retardation may be inferred in the case of the early stages of occurrence of prochoanitic septal necks. In later growth stages it is equally probable that there is both retardation and acceleration in formation of septal neck and septum in relation to the posterior auxiliary deposits and the siphon.

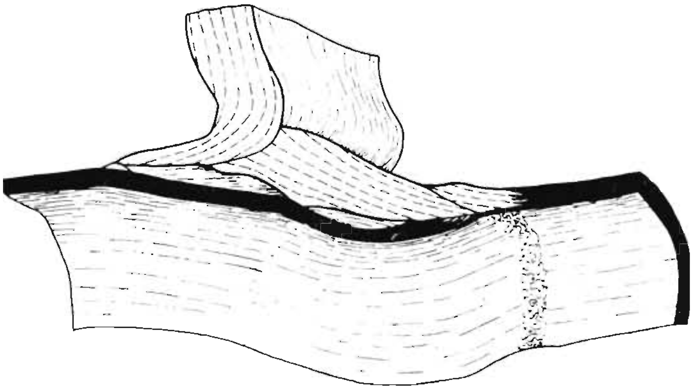

Fig. 5
Diagrammatic drawing of a prochoanitic septal neck in *Nathorstites gibbosus*

Ontogeny of septal necks and auxiliary deposits in *Quenstedtoceras* and *Kosmoceras*

The main difference in the ontogeny of *Quenstedtoceras* and *Kosmoceras* is in the position of the siphon in the second septum: in *Kosmoceras* it occupies a central position and in *Quenstedtoceras* it lies at the ventral margin. The ontogenetic development of septal necks and auxiliary deposits is the same in both genera.

The first one, two, or even three septa are achoanitic, that is without a septal neck; a prochoanitic septal neck first appears on subsequent septa. As a rule, it is initially better developed on the ventral side, but this difference in development soon disappears. In some specimens of *Quenstedtoceras* the deposits occurring between the adapertural surface and the wall of the connecting ring of the second septum may be treated as the distal part of a prochoanitic septal neck. The transitional stage from achoanitic necks to one of a marked difference in development of ventral and dorsal parts of septal necks comprises from one to more than three whorls, and the fully developed prochoanitic septal necks which appear subsequently are retained to maturity.

Posterior and anterior auxiliary deposits are well developed throughout the ontogeny of both *Quenstedtoceras* and *Kosmoceras*, but the latter are usually not developed on the ventral part of the proseptum.

ERBEN *et al.* (1969, pl. 16: 4) misinterpreted anterior auxiliary deposits from the dorsal part of the proseptum of *Quenstedtoceras* as a second septum. Commonly with the second septum in *Kosmoceras* and the third in *Quenstedtoceras*, anterior and posterior auxiliary deposits occur regularly, the latter usually being the better developed.

Juvenile and mature specimens of *Quenstedtoceras* with body chamber preserved display posterior auxiliary deposits and, sometimes, anterior auxiliary deposits, although poorly developed on the last septum. Posterior auxiliary deposits from the last septum are also known from several other ammonite genera including *Cadoceras*, *Polyptychites*, *Craspedites*, *Aconeceras*, *Saynoceras*, *Kosmoceras* and *Holcophylloceras* and anterior ones from the genera *Holcophylloceras* and *Craspedites*.

The last formed section of the siphon

The studies carried out by TRUEMAN (1920) and WESTERMANN (1971) have shown that the siphon is not usually present in the chambers of the last whorl of phragmocone. It is visible in the last chamber of the phragmocone only in the case of exceptionally well-preserved material (verbal communications by REYMENT, HÖLDER and WIEDMANN in: WESTERMANN, 1971). This is explained by MUTVEI (1967, 1973) and WESTERMANN (1971) as a result of retardation in development of the connecting rings in comparison to septa and septal necks.

DRUZCZIC and DOGUZHAEVA (1974) first described and figured a siphon developed in the last chambers of the phragmocone and body chamber of *Phyllopachyceras* sp.; the siphon section from the body chamber of that specimen is twice the length of that in the last chamber of the phragmocone. The specimen of *Holcophylloceras* sp. described above (see p. 14) is the second known with siphuncle preserved in the body chamber, although in this case the siphon section from the body chamber is shorter than that from the last chamber of phragmocone. Both these specimens are members of the Phylloceratina, a group characterized by a siphuncular tube with a much higher strength index than that found in the Ammonitina, and closer to that of *Nautilus* (see WESTERMANN, 1971: 25). The specimens of *Kosmoceras* and *Quenstedtoceras* from Łuków do not have the siphuncle preserved in either the last chambers of the phragmocone or in the body chamber. Nevertheless, the presence of posterior auxiliary deposits and, sometimes, anterior ones indicate its former presence in these last chambers and even in the body chamber.

The last septal neck of a juvenile *Quenstedtoceras* is illustrated in plate 33: 2. A zone of channels, made by boring organisms and subsequently infilled with pyrite, is found in parts of the septum where anterior and posterior auxiliary deposits should occur. The substratum in which the boring organism lived was either removed during preparation by decalcification in EDTA or by diagenetic processes. The thickness of the zone with borings implies a remarkable thickness of the substratum. The zone of infilled borgins is limited and posterior auxiliary deposits are partly calcified on the penultimate septum (pl. 34: 4). The septum third from the rear has calcified auxiliary deposits with no traces of borings on them (pl. 34: 3).

The last three septa of other juvenile representatives of *Quenstedtoceras henrici* (see pl. 32: 3; pl. 33: 1, 3, 4) display fully developed auxiliary deposits without any traces of boring organisms. The last septum shows fully developed posterior auxiliary deposits extending from the distal end of the septal neck and protruding some distance backwards. The auxiliary deposit is here strongly calcified, except for that part adjoining the siphonal opening, which is characterized by free spaces indicating that they were originally infilled with somewhat different material (pl. 32: 3). The penultimate septum has calcified posterior auxiliary deposits and poorly developed, partly calcified anterior auxiliary deposits with free spaces in their frontal part (pl. 33: 3). Normally developed and calcified posterior and anterior auxiliary deposits do not appear before the septum third from the rear of the body chamber (pl. 33: 1, 4).

Interpretation and conclusions

In *Quenstedtoceras* and other ammonite genera the posterior auxiliary deposits, representing the adapertural ending of the connecting ring, are as a rule better developed than the anterior deposits of the same connecting ring, although the anterior auxiliary deposits originate earlier than the posterior of the same connecting ring. The presence of posterior auxiliary deposits on the last septum separating the body chamber and phragmocone, indicates the presence of a connecting ring in the last chamber of the phragmocone. The presence of free spaces in the zone of growth of the auxiliary deposits of the last two septa, resulting from either post-diagenetic processes or etching in EDTA, indicate the presence of mineral or organic tissues in these places which differed from both normal calcified posterior and anterior auxiliary deposits and the organic tissue of the connecting ring. This is further supported by a series of micrographs of the last two septa, which reveal that only certain parts of the auxiliary deposits from the penultimate septum were exposed to the action of boring organisms. A fairly wide zone of borings from the ultimate septum indicates that the substratum was originally very thick. Posterior and anterior auxiliary deposits of the third or fourth septum counting from the body chamber in *Quenstedtoceras* are fully developed whilst the connecting ring is often not preserved for a greater distance.

It follows from the above data, as well as those given by Trueman (1920) and Westermann (1971), that the last section of siphon is usually not preserved for a distance of about one whorl. This implies that the last section of siphon of the Ammonitina is lacking because of both a reduction in thickness of the connecting ring (Mutvei, 1967, 1973) and post-secretory processes (maturation) affecting the organic matter of the tube. Dark matter resembling that forming the connecting ring is visible under the light microscope on the septal neck of the last septum of *Kosmoceras* and *Quenstedtoceras* with preserved body chamber in the position where auxiliary deposits should occur.

The post-secretory changes (maturation) seem also to be indicated by differences in colour and distribution of growth lines on the section of siphonal tube described from the body chamber of *Holcophylloceras zignodianum*.

The post-secretory changes in the organic matter of the connecting ring proceed at a distance of about a whorl or more in immature *Quenstedtoceras*, and about a half of whorl in adult ones.

The connecting ring and auxiliary deposits appear independently of the prochoanitic neck, and it is possible that the connecting ring is formed earlier than the successive septum and its prochoanitic septal neck, as is the case in *H. zignodianum* figured here and in the *Phyllopachyceras* sp. described by Druzczic and Doguzhaeva (1974).

The analysis of the development of posterior and anterior auxiliary deposits from the last septum of specimens of *Quenstedtoceras* made it possible to assume that a siphonal tube was present in the body chamber of these representatives of the Ammonitina as it was in the Phylloceratina.

According to Mutvei (1972*a, b*) the conchiolin layer of the connecting ring of Recent *Nautilus* represents a direct continuation of the nacreous layer of the septal neck, from which it differs in being uncalcified. These two zones of secretion were in action synchroneously during the formation of the septum and the connecting ring. The action of these secretory zones gradually became asynchronous during the formation of prochoanitic septal neck. From a theoretical viewpoint, asynchronous secretion of septal neck and connecting ring may result in:

(1) acceleration or retardation in the formation of the siphonal wall to the last septum;

(2) the possibility of formation of the wall of the connecting ring from both inside and outside, when a deep furrow is produced in the posterior part of the body, i.e. in the case when formation of the connecting ring is accelerated;

(3) the possibility of connection of the external surface of the connecting ring to the surfaces of both the septum and the ventral wall of the shell via auxiliary structures such as siphonal membranes;

(4) the possibility of stepwise movement of the posterior part of the body to the site of formation of successive septa, preceded by the formation of the soft tissues of the siphon. The furrow from the posterior part of the body was deepest before translocation and shallowest after translocation, as a result of partial or complete inversion of the secreting tissue.

With reference to point (1). Mutvei (1973: 629) assumed that the formation of the siphonal tube was somewhat accelerated in relation to the formation of the last septum. The "primary membrane" is the first element originating of the siphonal tube, and it represents a direct extension of the membrane covering the external surface of the neck, being connected with the adapical conchiolin membrane of the following septum (Mutvei, 1973: 29).

With reference to point (2), the following data contradict Mutvei's (1973) concept of a primary membrane: the section of the siphon originating in the body chamber is longer than the inter-septal distance (see Druzczic and Doguzhaeva, 1974, fig. 2) and the septal necks have distal ends rising above the siphonal surface and not connected with it by organic membranes (pl. 30: 4; pl. 32: 1). Membranes connecting the distal ends of prochoanitic necks with the surface of the connecting ring correspond in character to the siphonal membranes connecting the adapertural septal surface and connecting ring.

Growth lines from the walls of the siphonal tube of *Holcophylloceras* described here (p. 14) indicate secretion of the tube from within, whilst illustrations of the siphon of *Lytoceras jurense*, given by Grandjean (1910, figs. 4–5) indicate at least partial secretion from the outside. In all probability secretion from both within and without were involved in the formation of the connecting ring.

With reference to point (3). Ammonites are characterized by the presence of so-called siphonal membranes, viz. organic structures connecting the siphonal surface to other elements of the shell. No such organic films have been found in representatives of the *Nautiloidea*, but organic films in ammonoids were described or illustrated by several authors including Grandjean (1910), Shulga-Nesterenko (1926), Miller and Unklesbay (1943), Hölder (1954), Schindewolf (1967), Westermann (1971), and Erben and Reid (1971). Well-developed membranes from the stage of retrochoanitic septal necks of *Agathiceras uralicum* were described by Shulga-Nesterenko (1926) only, whilst Miller and Unklesbay (1943) described poorly developed siphonal membranes from both the retro- and prochoanitic septal neck stages in Late Paleozoic ammonoids. Other authors described siphonal membranes of ammonites at the stage of prochoanitic septal necks.

The studies carried out by the present author on Permian and Devonian ammonites from his own collections and those of Shulga-Nesterenko and Bogoslovskaya show that siphonal membranes are very rare in Paleozoic ammonites, becoming common and variously developed in Mesozoic forms. Fig. 3G shows the scheme of formation of siphonal membranes postulated for the stage of transitional septal necks. It follows that two types of siphonal membranes may be distinguished, taking into account their relation to the connecting ring: (a) siphonal membranes formed after the formation of the appropriate section of connecting ring, with organic tissue located discordantly in relation to that of the connecting ring, or extending into the external layer of the connecting ring in an adapertural direction (fig. 3Ga); (b) siphonal membranes representing an extension of the external organic layer of the connecting ring in an adapical direction (fig. 3Gb).

From a theoretical standpoint, the connecting ring equivalents in length to the distance to the next septum may originate in the body chamber of both retro- and prochoanitic forms, which permits formation of siphonal membranes as noted above. In the case of *Phyllopachyceras* sp. (see DRUZCZIC and DOGUZHAEVA, 1974) in which the section of the siphonal tube from the body chamber was longer than the distance between successive septa, only prochoanitic septal necks may develop whilst siphonal membranes may originate only when the condition (b) is fulfilled.

Siphonal membranes are common in all but the first or first and second whorls of the Ammonitina (WESTERMANN, 1971), implying that case (b) is more favourable for formation of these membranes, as well as their connections with connecting ring.

With reference to point (4). The relationship between movement of the body inside the body chamber of Recent *Nautilus* and selection of the place of formation of a new septum and formation of new section of soft siphonal tissues remain unknown.

From the theoretical point of view two extreme situations may be expected: (a) when the body moves relatively slowly towards the place of formation of a new septum, and an increase of siphonal length takes place in the growth zone, and (b) when the body moves relatively quickly towards the place of formation of a new septum and there is distension of both the siphon and the posterior part of the body, which is compensated subsequently during the following pause.

The formation of a siphonal tube in the body chamber of an ammonite, presumably before movement of the body to the place of formation of a subsequent septum, may serve as an adaptation to the "stepwise" nature of the movement. This concept seems supported by the fact that "Siphostruktur" and "Muskelansatz-Strukturen" interpreted as muscle scars by JORDAN (1968) are metameric, and correlated with the septal rhythm. It would indicate that they reflect periods of stationary muscles attachment whilst a dark band connecting them would mark the track of the muscles between such pauses.

DRUZCZIC *et al.* (1976, fig. 6) presented a scheme of transition from retrochoanitic septal necks in the ontogeny of *Megaphyllites prometeus*, a representative of the same superfamily as the *Nathorstites gibbosus* studied here, the Arcestaceae MOJSISOVICS, 1875 in which the intermediate stage is the retrochoanitic septal neck. The proximal part of this neck is strongly bent adaperturally along with the septum, which is visible as a fold on the cross-section (*ibidem*, fig. 6b). Studies on the transition from retrochoanitic to prochoanitic septal necks in *Nathorstites gibbosus* failed to confirm the necessity of occurrence of such a stage. The development of an adapertural bend in the proximal part of septal neck and septum is only slightly related to the most important processes active in the secretory zones during the transitional stages.

EMBRYONIC SHELL

OBSERVATIONS

The structure of the initial chamber and the first whorl up to the end of nepionic swelling in *Kosmoceras* and *Quenstedtoceras*

Initial chamber. — The wall between the initial chamber and the first whorl is built of several layers, including organic films. Its apical and dorsal parts are two-layered and the central part four-layered. The increase in number of layers to four is achieved by addition of two layers from within (pl. 44: 3; figs. 6, 7). The total thickness of the wall of the initial chamber is variable, being the greatest in the proximity of the attachment of the ventral part of the proseptum (9–16 μm, on the average 12 μm) and the least in apical and dorsal parts (4–5 μm).

The inner layer present in apical and dorsal parts of the initial chamber represents the wall proper and is built of regular prisms of prismatic tissue (pl. 44: 3–1c; pl. 38: 1b–1a).

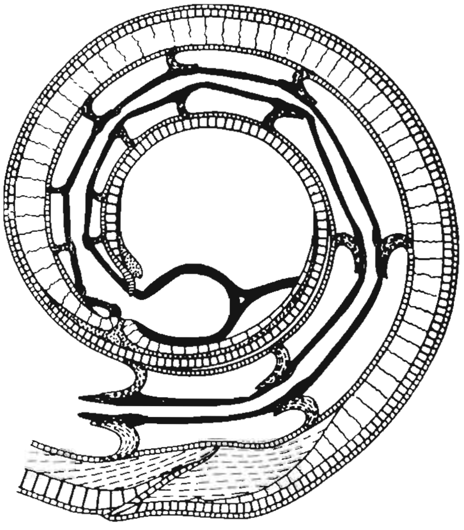

Fig. 6
Median section through the initial chamber and first whorl of *Quenstedtoceras* (diagrammatic drawing of a large phragmocone)

It is 2–2·5 μm thick in these parts of the initial chamber. Small tubercles, directed to the outside, and formed by extensions of prisms (pl. 38: 1b–1a) are visible in cross-sections in the proximity of the attachment site of the proseptum and the second septum. The tubercles are sometimes characterized by a spherulitic structure.

The inner layer, that is the wall proper of the initial chamber, is thickest 3·4–3·6 μm thick) in the proximity of the caecum and prosiphon, in the ventral part of the chamber. The wall proper of the initial chamber is markedly reduced in thickness, wedging out completely. The layer extends continuously as the external layer of the first whorl, being covered only by dorsal wall of the next whorl.

The external layer of the initial chamber represents the dorsal wall of the first whorl and is, therefore, discussed with it. In the ventral part of the first whorl there are also two other layers: an internal layer with obvious prismatic structure (pl. 44: 3), a medial, very thin and also prismatic layer which is always much more markedly effected by etching than other layers, and is built of much thinner prisms.

The prismatic microstructure of this layer becomes obliterated, sometimes completely, and becomes more random in places where it is situated at the base of the proseptum near the ventral wall and the swelling of medial layer (pl. 38: 1a; pl. 28: 1, 2; pl. 31: 1).

The initial chamber is separated from the first whorl by the proseptum, i.e. the first septum.

The relations between the proseptum, the walls and the initial chamber and the first whorl have been discussed elsewhere (KULICKI, 1975). It was found that, depending on orientation of the two cross-sections, the prismatic layer of the proseptum passed smoothly into the prismatic tissue of either the prismatic layer of the initial chamber of ventral part of the first whorl (pl. 29: 1, 2; pl. 30: 2; pl. 31: 1; pl. 38: 1a; pl. 42: 3; pl. 44: 3). Some sections passing through the lateral part of the initial chamber display a discordant arrangement of prismatic proseptum tissue in relation to that of the initial chamber and whorl (pl. 42: 2).

The medial layer forms a swelling anterior to the base of the proseptum in medial and paramedial sections on the ventral side. Sections passing through the lateral part of the initial chamber and proseptum display a medial layer of normal thickness (pl. 42: 3, 4) or none (pl. 42: 2).

The wall of the initial chamber ends with a flange in the dorsal part in medial and paramedial sections (pls. 28: 3; pl. 30: 1; pl. 31: 2; pl. 39: 3; fig. 6). The flange is separated from

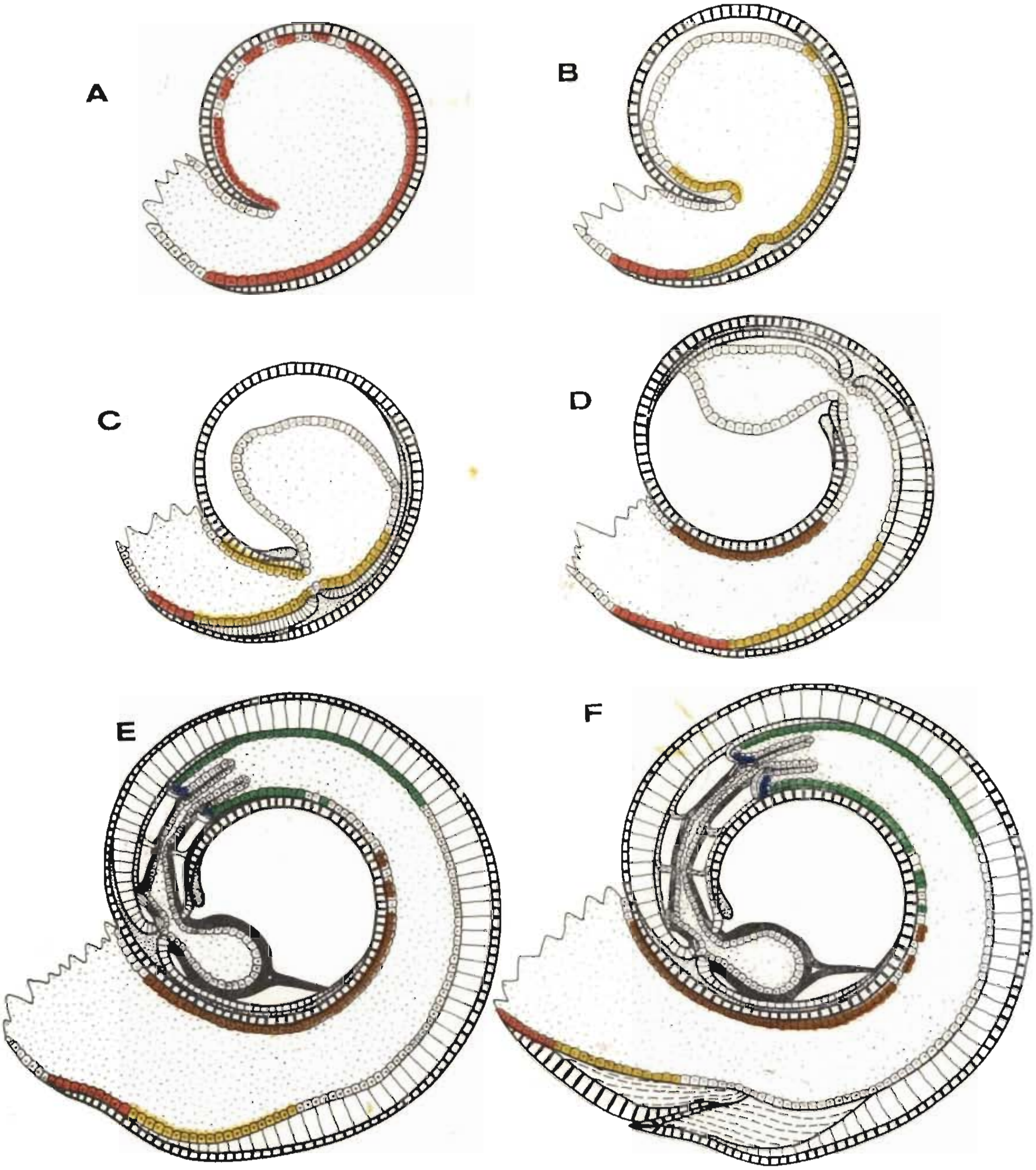

Fig. 7

Ontogenetic development of the initial chamber and first whorl as illustrated by *Quenstedtoceras*. *Red* — secretion of the wall proper of the initial chamber, external prismatic layer of first whorl, and the outer prismatic layer of the postembryonic shell; *yellow* — secretion of the mid-layer of initial chamber and flange; inner prismatic layer of initial chamber and first whorl; prismatic-subprismatic mid-layer of first whorl; and nacreous layer of nepionic swelling and postembryonic shell; *brown* — secretion of outer component of dorsal wall; *green* — secretion of inner prismatic layer; *blue* — secretion of nacreous tissue of septa. *A–E* — Successive phases of the shell formation at embryonic stage. *F* — Early postembryonic stage the wall of the initial chamber by a discontinuity (fig. 6). Its mineral tissue is usually less regular and several times thicker than that of the wall proper of the initial chamber. The flange does not occur in sections passing through the lateral part of the initial chamber, as it is separated from its wall by a discontinuity (pl. 29: 3; pl. 42: 1). In such cases it is possible to detect swelling on the distal end of the wall of the initial chamber. The flange and the end of dorsal wall of the initial chamber appear to have an uneven, hummocky margin when seen from the inside of the chamber (pl. 26: 1, 3a). The relationship between the proseptum and the wall of the initial chamber were discussed in part in an earlier publication by the author (Kulicki, 1975). In that part of the proseptum which shows a well-developed mural section saparated from the wall of the initial chamber by a discontinuity which gradually disappears in the adapertural direction (pl. 28: 3; pl. 30: 1; pl. 36: 3; pl. 39: 3).

The first whorl. — The wall between the first and the second whorl consists of 4 main layers:
(1) the most external, dorsal wall of the subsequent whorl;
(2) the external prismatic layer of the first whorl, representing a direct extension of the wall proper of the initial chamber underlying the dorsal wall of the subsequent whorl. After a reduction of thickness from the transition from the wall of the initial chamber to the wall of the first whorl the wall is 1·3–2 μm thick (1·65 μm thick on the average). The thickness of that layer equals 1–2 μm (1·46 μm on the average) in the proximity of the nepionic swelling. The mineral tissue and ornamentation of that layer were described above along with the initial chamber;
(3) the medial prismatic layer of the first whorl, occurring beneath the external prismatic layer, is characterized by a marked thickening in the proximity of the second septum, being 4·2–7 μm in thickness (6·1 μm on the average) in the proximity of the second septum and 6·5–9·7 μm (7·8 μm on the average) close to the nepionic swelling. The mineral tissue of this layer is characterized by a prismatic structure which usually is, however, less regular than that of the layer (2) and is termed subprismatic. Its structure is differentiated into an external part which is usually less regular, and built of more regular prisms than the internal part (pl. 38: 1b, 1a);
(4) the internal prismatic layer, representing the most internal mineral component of the ventral wall of the first whorl (fig. 6). The internal prismatic layer is clearly separated from the medial prismatic layer of the first whorl, and first appears between the fourth and fifth septa (pl. 43: 1b). Analysis of the boundary between the second septum and ventral wall has shown that it is sharp only in the posterior part. It disappears towards the anterior but its extension is marked as a constriction on etched prisms of the prismatic layer (pl. 28: 2; pl. 38: 1b; pl. 39: 1; fig. 8). The further extension of the boundary cuts normal-size prisms without any traces of growth discontinuities, and it appears that the growth of prisms took place after movement of the body forwards, whilst movement was not connected with any break in growth of prisms.

Taking into account the relationship between the second septum and the ventral wall, it is necessary to assume that the internal prismatic layer continues on the ventral side from

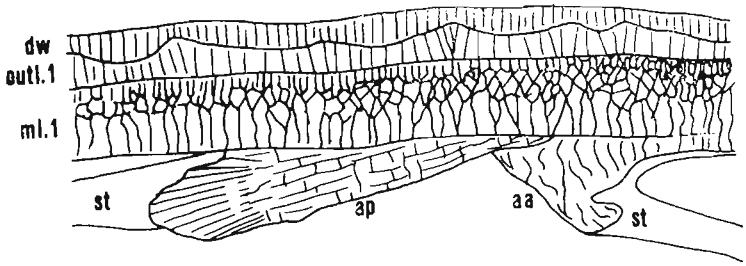

Fig. 8
Median section through the ventral wall in the proximity of the attachment of the second septum

the second septum onwards. It is 1·2 to 2 μm thick (1·63 μm thick on the average) on the first whorl. The tissue of the internal prismatic layer of the first whorl is regularly prismatic.

The dorsal wall of the first whorl represents the most external component of the wall of the initial chamber. A well-developed mural part of the proseptum (pl. 28: 3; pl. 29: 3; pl. 30: 1; pl. 31: 2; pl. 36: 1, 3; pl. 39: 3; pl. 42: 1) originates as a first element of this wall. A boundary separating the mural part of the proseptum from the wall proper of the initial chamber gradually disappears towards the aperture under the mural part of the successive septum (the third septum in *Quenstedtoceras* and second septum in *Kosmoceras*). A similar situation is found in the case of subsequent septa. Except for the apical part of the initial chamber, the subprismatic tissue of the external component of the dorsal wall of the first whorl appears between the mural parts of the septa and the wall proper of the initial chamber, and disappears in the proximity of the prosiphon and caecum (pl. 42: 4; pl. 43: 1a; pl. 44: 3).

The dorsal wall of the first whorl is 2·2–3·0 μm thick (2·7 μm thick on the average) in the apical-ventral part of the initial chamber. The boundary between the dorsal wall of the first whorl and the external wall proper of the initial chamber is not sharp.

The thickness of the dorsal wall decreases to 1·3–1·5 μm in the proximity of the attachment of prosiphon and caecum. The prismatic structure of wall is well-marked here, and the wall is separated from the shell by a clearly marked discontinuity (pl. 28: 1; pl. 30: 2; pl. 44: 3; pl. 38: 1b, 1a: pl. 42: 3, 4; pl. 43: 1a). A change in dorsal wall thickness in the proximity of the attachment of the prosiphon and caecum corresponds to changes in shell structure which originate at the nepionic swelling. The section transverse to the body chamber and the first whorl shows that the most external layer of the dorsal wall in relation to the first whorl (the external component of the dorsal wall) passes on the external side of the whorl beneath the suture, and merges there with the wall proper of the initial chamber and the external layers of the first whorl (pl. 44: 1).

The structure of the shell from the nepionic swelling has been discussed elsewhere (KULICKI, 1974). Further specimens of *Quenstedtoceras* and *Kosmoceras* with thickened shell at the nepionic constriction show the same structure as that previously illustrated (KULICKI, *l. c.*, fig. 1; see pl. 45: 1, 2, 4 herein). The specimen illustrated in pl. 45: 3, is an exception, as it differs from the above cited structural plan in the abnormal growth of a backwardly curved section of prismatic layer, connected with formation of an additional, earlier section of prismatic layer. Disturbances of this type confirm, however, the mode of origin of shell swellings previously suggested by the author (KULICKI, 1974, fig. 3). This specimen also shows a break in secretion of the initial section of the post-embryonic shell, related to retreat of the mantle. The prismatic layer formed after the break also occurs beneath the previously formed nacreous layer.

The structure of the shell after the nepionic swelling in *Kosmoceras* and *Quenstedtoceras*

Ventral wall. — The ventral wall generally consists of 3 mineral layers: external prismatic, median nacreous and internal prismatic. The typical development of these layers has been described by several authors, including BIRKELUND (1967), BIRKELUND and HANSEN (1968, 1974) and ERBEN *et al.* (1968, 1969). The nacreous layer of *Kosmoceras* and *Quenstedtoceras* is built of stacks of tablets as is typical of most gastropod nacre and as is in the lenticular nacre of many bivalves (TAYLOR *et al.* 1969). The stacks are clearly to poorly marked on cross-sections (pl. 35: 6). The internal prismatic layer as typically developed displays a regular arrangement of prisms. It is thickest close to the umbilical suture, thinning out and sometimes completely disappearing on the whorl sides (pl. 48: 1). The layered structures of the internal prismatic layer, observed under the optical microscope by BLIND (1975) is also visible on SEM micrographs of etched longitudinal (pl. 46: 6) and transverse (pl. 48: 2; pl. 44: 2) cross-sections.

Longitudinal sections through ventral wall display discontinuities resulting from breaks in secretion. The discontinuities vary in length and are sometimes confined to the external prismatic layer (pl. 47: 4, 6) or cut both the external prismatic and nacreous layers (pl. 47: 7). No similar discontinuities were found in the internal prismatic layer. The beginning of a new phase of secretion does not require retreat of the mantle margin. The course of discontinuities in particular layers reflects the course of the secretory zone in particular sections.

Dorsal wall. — The dorsal wall from the post-embryonal stage, as seen in medial and paramedial sections, begins at a sharp boundary between the internal prismatic layer of the second whorl and the wall proper of the initial chamber, and the external prismatic layer of the first whorl (pl. 44: 3; pl. 42: 3, 4; pl. 43: 1a). This sharp boundary presumably results from a change in secretion preceding the deposition of the internal prismatic layer, i.e. the section secreting the external component of the dorsal wall in the dorsal zone forming the later wrinkle layer. Sections through the lateral part of the initial chamber show that the dorsal wall consists of the nepionic swelling of the shell with all the elements well-developed (pl. 45: 5). It follows from that illustration that the nepionic swelling, along with all the components, passes towards the posterior into the dorsal wall of the first whorl, i.e. the external layer of the initial chamber. It should be assumed, therefore, that equivalents of all the components distinguished in the ventral wall of the first whorl are involved in the construction of the dorsal wall as far as the stage of formation of the nepionic swelling; and that the inner prismatic layer does not become the main component of the dorsal wall before the nepionic swelling (pl. 46: 4, 5, 6; pl. 47: 1).

The dorsal wall of the second whorl (pl. 48: 3, 5) accurately duplicates the microstructure of the first whorl. A micrograph of a section of the dorsal wall between the second and third whorl (pl. 48: 4) shows that the ornamented inner prismatic layer, representing the dorsal wall of the succeeding whorl, rests on a relatively even external surface of the ventral wall of the preceding whorl. When the two walls are broken, conellae-like prisms are left on the ventral wall. The prisms are uniformly distributed as are knobs from the dorsal wall. They represent torn-out fragments of the inner prismatic layer, and mark places where the dorsal wall (i.e. inner prismatic layer) was more closely adjoining the ventral wall of the preceding whorl. The structure of the dorsal wall becomes much more complex from the end of second whorl in both *Quenstedtoceras* and *Kosmoceras*.

Longitudinal sections (pl. 46: 1–6; pl. 47: 1–8) show that the external prismatic layer of the preceding whorl is overlaind by structured quite different from the normally developed inner prismatic layer, in the form of a layer variable in tickness (see fig. 9). Triangles linked to one another by peeks on the sections represent the basic components of this layer; they are overlain by normally developed inner prismatic layer. Longitudinal sections of specimens of *Quenstedtoceras* at various developmental stages with body chamber preserved allow the distinction of several main stages in the development of the dorsal wall:

Stage (1). Triangular structures with one longer side adjoining the ventral wall and other longer side adapically oriented, appear on the ventral side of the preceding whorl close to the aperture. The somewhat concave shorter side of the triangular structures display a short, also adaperturally oriented projection at the base (pl. 47: 2–4, 6–7; pl. 46: 1, 2; fig. 9A).

Stage (2). Elongation of the long sides of these structures in an adapical direction results in the merging of their bases (pl. 46: 3; pl. 47: 5; fig. 9B).

Stage (3). Infilling of depressions between peaks of the triangles (pl. 46: 3; pl. 47: 8; fig. 9C).

Stage (4). Covering of these structures by a prismatic layer (pl. 46: 4–6; fig. 9D). The position in relation to the aperture, and the mode of development of the elements (1 and 2) discussed above indicates that they represent components of the so-called wrinkle-layer, whilst the other elements (3 and 4) represent parts of the inner prismatic layer. The microstructure of the elements appearing in stage (1) is still poorly known. It may be stated, however, that it differs markedly from that of the prismatic and nacreous tissues. Extensive studies have shown that the arrangement of mineral and organic components is fairly homogeneous, becoming regular only towards the short side of the triangle. Parallel elements are also visible arranged one above another, and somewhat resembling a single "stack" of nacre. It is still an open question whether this microstructure is original or a result of diagenetic changes.

The microstructure of the remaining elements of the dorsal wall mentioned under (2)-(4) above is prismatic and spherulitic-prismatic. The degree of ordering changes from layer to layer, which results in some very sharp boundaries between layers (pl. 46: 4-6; pl. 47: 1).

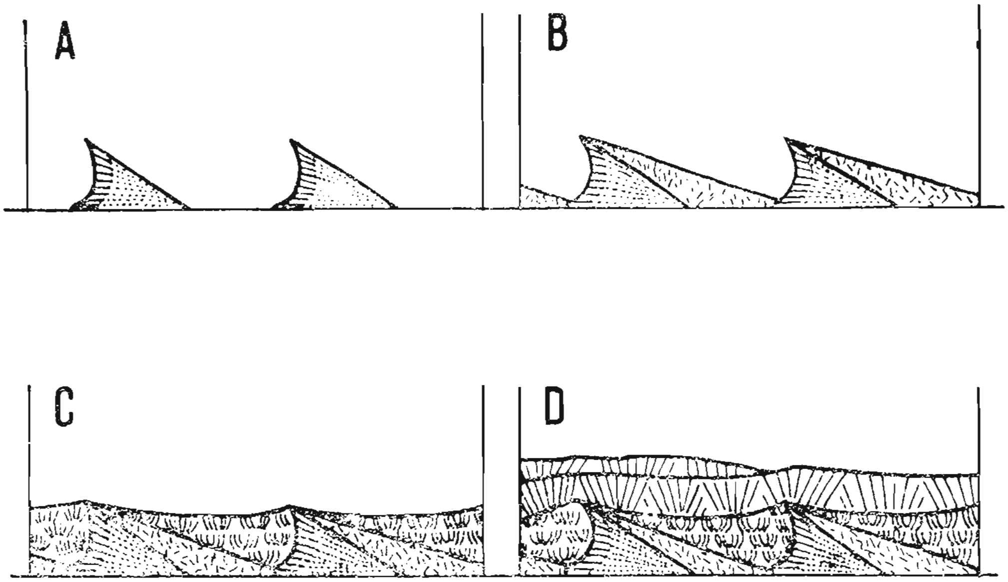

Fig. 9

Successive stages in the formation of the dorsal wall. *A-B* — the outer component of the dorsal wall, in the form of a wrinkle-layer visible in the anterior parts of body chambers. *C-D* — the inner component of the dorsal wall, covering the wrinkle-layer visible in the posterior parts of body chambers and phragmocones

The dorsal wall is connected with the lateral wall of the shell at the umbilical suture. As was previously stated by ERBEN *et al.* (1969), BIRKELUND and HANSEN (1968, 1974), TOZER (1972) and others, the two external layers (the external prismatic and nacreous) wedge out at the umbilical suture (pl. 44: 1; pl. 48: 1), whilst the inner prismatic layer still continues on the dorsal side, although usually thinning out in comparison to its development at the umbilical bend (pl. 48: 1).

Plate 44: 1 represents a transverse section through the initial chamber, the end of the first whorl (nepionic swelling) and a half of the second whorl. In the case of the umbilical suture from the half of the second whorl, it is clearly visible that a layer of prismatic character underlies the inner prismatic layer, and penetrates deeply beneath the layers wedgeing out at the suture. The former layer may be interpreted as an equivalent of the wrinkle-layer; a wrinkle-layer occurring in the same position was described and illustrated by TOZER (1972, fig. 3). In the case of the ending of the first whorl illustrated here (pl. 44: 1) it may be noted that the prismatic layer passing beneath the umbilical suture extends into the external prismatic layer of the first whorl on the one hand, and passes smoothly into the thickened wall proper on the sides of the initial chamber on the other.

Septa. — The mineral tissue and the relation to the walls of the shell of the first septum (proseptum) are described above. The mineral tissue of the second septum is differentiated, however, being characterized by a prismatic structure in medial and paramedial sections (pl. 28: 2; pl. 30; 2) and a nacreous structure in lateral sections (pl. 42: 3; pl. 48: 6). In *Kosmo-*

ceras, in which the siphon penetrates the second septum centrally, it is possible to trace a continuous transition from the prismatic tissue from the surrounding of the connecting ring to the nacreous layer of the remaining part of the septum (pl. 34: 2).

Nacreous tissue is the main component of all the remaining septa in both genera. The exception is that in *Quenstedtoceras*, a spherulitic-prismatic layer is relatively well developed as a second component of the septum on the ventral part of the adapical surface close to the siphon (pl. 33: 4). In the dorsal part, spherulitic-prismatic tissue occurs as a ledge from the adapical side of the septum covering the suture between the septum and the dorsal wall (pl. 46: 4, 6).

In the stages following the first two whorls in *Kosmoceras* the spherulitic and prismatic components of the septum are better developed than in *Quenstedtoceras*. The adapical surface of the septum is covered with by spherulitic-prismatic tissue in the ventral part (pl. 35: 5–6). Similarly developed spherulitic-prismatic tissue is found on the adapertural surface of the septum which is, however, situated on the dorsal side in relation to the septal neck (pl. 41: 1). Prismatic tissue, characterized by irregular development of prisms, is found on the adapertural surface of the septum on the ventral side in relation to the septal neck.

The relation of septum to shell walls is found to be the same as was described by BLIND (1975) on the basis of Callovian material mainly derived from Łuków. A continuous transition from nacreous septum to prismatic dorsal wall in an adapertural direction is clearly visible (pl. 44: 2). So-called sutural infilling is here less obvious than in BLIND'S samples. The sutural infilling is sometimes lacking, as is the case in early growth stages, or is very poorly developed (pl. 46: 5). The best developed sutural infillings were found on the fourth whorl of *Kosmoceras* (pl. 35: 5, 6).

DISCUSSION AND INTERPRETATION

Initial chamber. — ERBEN *et al.* (1969) interpreted the wall of the initial chamber of ammonites as a structure built of layers which wedged out successively towards the exterior. The first of these layers were said to be subprismatic in structure, and the later layers fully prismatic. BIRKELUND (1967) and BIRKELUND and HANSEN (1968, 1974) distinguished two main layers in the wall of the initial chamber: internal prismatic, and external, built of irregular crystals. The results of the author's studies confirm the bipartite nature of the wall of the initial chamber, showing at the same time that the internal prismatic layer represents the external wall proper of the initial chamber, and that the external layer with less regularly distributed mineral components represents the dorsal wall of the next (first) whorl. This is indicated by:
(1) longitudinal sections which show that septa are characterized by adaperturally oriented mural parts so strongly developed that they sometimes penetrate deeply beneath younger septa, and (2) transverse sections of the first whorl and the initial chamber which show that all of the layer of the first whorl participating in the formation of the dorsal wall occur directly on the external wall proper of the initial chamber. According to ERBEN *et al.* (1968, 1969), BIRKELUND (1967), BIRKELUND and HANSEN (1968, 1974) the wall of the initial chamber wedges out close to the first septum. The author's studies do not confirm this, indicating rather the opposite; they show that the external prismatic layer of the first whorl represents a continuous extension of the external wall proper of the initial chamber, and only a thickness decrease of the wall proper of the initial chamber is observed along the transition between the ventral wall of the initial chamber and the first whorl (see p. 34). The above mentioned authors did not give any illustrations which showed unequivocally the wedging out of the wall of the initial chamber. ERBEN *et al.* (1969, pl. 3: 2) illustrated only a decrease in thickness of the wall of the initial chamber, and the illustration given by BIRKELUND and HANSEN (1968, pl. 2) is not convincing. The specimens from the Maestrichtian of western Greenland studied by BIR-

KELUND and HANSEN are diagenetically altered, as was also emphasized by ERBEN *et al.* (1969: 44).

A review and comments on views on the structure of the dorsal end of the wall of the initial chamber and its relation to the proseptum were given elsewhere (KULICKI, 1975).

The flange is here interpreted as the dorsal end of the wall of the initial chamber, separated from it by a discontinuity. This term was used in the same sense in an earlier paper of the present author (KULICKI, 1975). The end of the dorsal wall of the initial chamber illustrated there (*l. c.*, figs 1 and 2) with the proseptum was misinterpreted, as there is no flange here that would match the above definition, and the discontinuity shown in these figures separates the mural part of the proseptum from the external wall proper of the initial chamber.

Dorsal wall. — It follows from the above observations that the dorsal wall of the ammonites studied is built of two main components:
(1) an internal component lining the inside of the shell sides and corresponding fully to the inner prismatic layer, and (2) an external component, resting directly on the preceding whorl and sometimes penetrating beneath the umbilical suture.

With respect to point (1): the inner prismatic layer passes without any break onto the lateral wall of the shell. Its secretion was related to an epithelium developed beneath the muscle attachments of ammonites — it corresponds to the myostracum or myostracal layers of workers on bivalves and gastropods (e.g. TAYLOR *et al.* (1969)). Various sectors of mantle surface, connected with different muscle groups, were presumably responsible for the multilayered nature of the inner prismatic layer of the dorsal wall. Attachment fields of muscles of Recent *Nautilus* are situated in the posterior part of the body. The appearance of the first elements of the inner prismatic layer in the interior of the body chamber of ammonites indicates that the main attachments of muscles were similarly located. BLIND (1975) has shown that the most internal components of inner prismatic layer (fig. 9D) are connected with subepithelial musculature.

With respect to point (2): The external component of the dorsal wall first appears outside the apical part of the initial chamber as a subprismatic layer on the wall proper of the initial chamber. The subprismatic layer is covered with very thin, sometimes poorly visible laminae of prismatic material, identifiable with the mural parts of septa. In the early ontogeny of the dorsal wall, in which apical and dorsal parts of the initial chamber are formed, the whole dorsal wall is limited to the laminae of the mural parts of septa. No elements corresponding to the external component of the dorsal wall were found between the mural laminae and the wall proper of the initial chamber. The external component of the dorsal wall is developed as a prismatic layer in the middle of the second whorl, and is already the typical wrinkle layer on the third whorl.

The zone secreting the external component of dorsal wall. — It is beyond any doubt that both the mantle subzones secreting the external wall of the first whorl were involved in the secretion of the external component of the dorsal wall prior to the end of formation of the nepionic selling. This is indicated by the clearly continuous transition between the nacreous tissue of the nepionic swelling and the subprismatic tissue of the external component of the dorsal wall, clearly visible in transverse sections through the umbilical suture between the initial chamber and first whorl. The transition from the external prismatic layer to the subprismatic tissue continuing above the umbilical suture and connected with dorsal wall, is also clearly discernible. The external prismatic layer connected with the dorsal wall beneath the umbilical suture on the other side produces a projection directed to the outside of the shell. Such development of the external prismatic layer is possible only when a secretory projection directed to the outside of the umbilical suture is developed at the mantle margin on the ventral wall close to the umbilical suture, and in front of the aperture.

In the middle of the second whorl the external component of the dorsal wall penetrates deeply beneath the umbilical suture, being separated from the nacreous and external prismatic tissues by a distinct discontinuity. This indicates that the prismatic tissue of the external component of the dorsal wall was secreted in front of the apertural margin, despite the fact that not only a mantle margin but a broad secretory zone could have been responsible for its formation.

Wrinkle-layer. — This layer occurs in post-Triassic ammonites of the family Graphoceratidae (Ammonitina), a few Middle Jurassic perisphinctids (SENIOR 1971: 113) and in Sonniniidae and Liparoceratidae (BAYER 1974). It is also fairly common in Paleozoic and Triassic ammonites (WALLISER, 1970; HOUSE, 1971; TOZER, 1972 and others).

In the *Quenstedtoceras* studied the first elements of the wrinkle-layer are found close to the aperture, enlarging somewhat towards the interior of the body chamber (figs. 9A, B). The wrinkle-layer was never found outside the umbilical suture in transverse sections of the specimens studied. According to WALLISER (1970), SENIOR (1971) and HOUSE (1971), similarly developed structures on shell flanks belong to the same category and are also described as "wrinkle-layers". According to TOZER (1972), however, they are of a different origin, and he suggests that layers from shell sides and venter should be termed "Ritzstreifen". BAYER (1974) has identified the wrinkle-layer of ammonites with a corrugated inner prismatic layer.

The gradual development of individual wrinkles in *Quenstedtoceras* indicates that they were secreted in a relatively wide zone. The viewpoint of TOZER (1972: 651) is just the opposite; on the basis of data presented by STENZEL (*in:* MOORE, 1964: K 72), TOZER assumes that the black film of *Nautilus* is presumably not secreted by the mantle surface, but rather its margin. This mode of secretion is also suggested by TOZER for the wrinkle-layer of ammonites, which he suggests is comparable with the black film of *Nautilus* in both distribution and ornamentation (SENIOR, 1971; TOZER, 1972). In *Nautilus* this organic layer is covered by nacreous material secreted by a relatively wide zone. Nacreous tissue does not occur on the dorsal wall of ammonites, so it may be stated that the wrinkle-layer of ammonites is the same as the black film of Recent *Nautilus* in development. The former, however, is secreted by a larger part of mantle surface, as is the nacreous layer of the dorsal wall of *Nautilus.* Only primary elements may be secreted by the mantle margin (fig. 9A).

Septa. — The proseptum originates in a furrow surrounding the posterior part of the body, which gradually increases in depth during secretion (comp. KULICKI 1975). There are some premises that the furrow did not originate simultaneously along its whole length, but first in ventral region, close to the center, and subsequently in other parts of the body. Paramedial sections of the ventral area show a swelling of the medial layer which is involved in the formation of the basal part of the proseptum. This indicates that the furrow originates here earlier than the medial layer (fig. 10A). In longitudinal sections passing through the lateral parts of the initial chamber, the medial layer is reduced in thickness, and is not involved in the formation of the basal parts of the proseptum. Moreover, the eldest elements of the prisms are not disturbed here. A disturbed packet of prisms is situated at the middle of thick inner layer and acts as a support for the proseptum (fig. 10B). This indicates a retardation in formation of furrow and proseptum in relation to both the medial layer and the first phase of secretion of the inner layer. There is no reason to assume a synchroneous origin for the remaining septa throughout the surface. In the case of the second septum, the prismatic and nacreous tissues are secreted at the same time. Most probably the zone of secretion of the second septum was mosaic in character.

The mode of formation of the initial chamber and first whorl, and the development of secretory zones

The wall proper of the initial chamber was the first element to be secreted. It was formed initially by a cap-like secretory zone, which widens gradually in time. The apical part of the zone gradually lost its ability to secretion, and become tubular (fig. 7A). This secretory zone was uniform and physiologically undifferentiated, as is indicated by the uniformity of secretory products.

The flange from the dorsal part of the initial chamber does not extend across the whole width of the initial chamber, and it is separated from the wall proper by a discontinuity, indicating that it was formed during secretory phase which followed that responsible for the formation of the dorsal part of the wall proper. The end of the flange, or lateral parts of the dorsal wall of the initial chamber, reflect a break in secretion, as the next material deposited in this part of the initial chamber was the dorsal part of the proseptum (fig. 7C).

The medial layer occurs throughout a large part of the interior of the ventral region beneath the wall proper of the initial chamber, wedging out in where this wall is connected with the first whorl. The wall proper of the initial chamber does not wedge out to the outside as was suggested by Erben *et al.* (1968, 1969), Birkelund (1967), Birkelund and Hansen (1968, 1964) and Kulicki (1975), but continues, without any breaks, in the form of the external layer of the first whorl. It thus appears that the median layer was formed by a very wide secretory zone situated directely behind the zone secreting the wall proper of the initial chamber. At this stage, the originally uniform secretory zone became differentiated into two subzones (fig. 7B). In the dorsal part, the secretion of the medial layer may correspond to the secretion of the flange but there is no evidence for their synchronism. The appearance of a swelling of the medial layer at the site of future formation of the base of the proseptum in the medial and paramedial sections indicates an early phase of formation for the circular furrow.

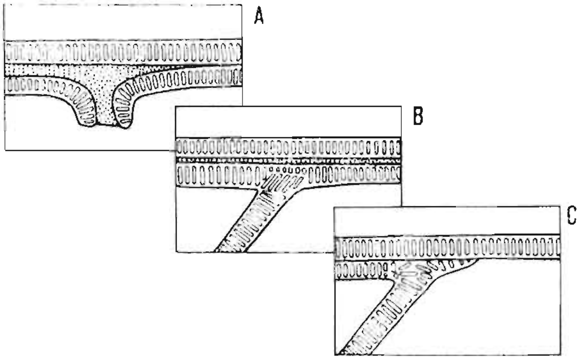

Fig. 10
Schematic sections through the ventral wall of the initial chamber and proseptum. *A* — median section. *B* — lateral section, *C* — extreme lateral section

The next stage involved the secretion of the proseptum together with the inner prismatic layer of the initial chamber, the ventral part of the first whorl and the elongate mural part of the proseptum in the dorsal region. At this stage the secretory zone was tubular and clearly differentiated in ventral, lateral, and part of dorsal region into two subzones: a narrower one, secreting the external prismatic layer of the first whorl and a wider one, situated behind the former, and secreting the inner prismatic layer of the initial chamber, proseptum and medial layer of the first whorl (fig. 7C). This stage was characterized by the progressive development of the furrow, in which the proseptum originated (compare Kulicki 1975).

Following the formation of the flange, but before the formation of the dorsal part of the proseptum, the dorsal part of the body was bent strongly. This is reflected by the way in which the dorsal part of tube of the first whorl formed at the contact with the wall of the initial chamber. A change in direction of growth resulted from continuous, rather than interrupted secretion in the ventral part and the termination of secretion in the dorsal part.

The formation of the proseptum was accompanied by a withdrawal of the soft tissues from the initial chamber. Associated with a slowing of the formation of the lateral parts of the proseptum, the process of retreat of soft tissues from the initial chamber was advanced so that the proseptum extended only into the medial prismatic layer of the first whorl in these regions (fig. 9C; see also Birkelund and Hansen, 1974, fig. 2). When the proseptum was completed a significant portion of wall of the first whorl was also finished. The wall was secreted in the ventral and lateral regions of the first whorl by a secretory zone that was subdivided into two subzones, and corresponded to the zone secreting dorsal wall of the first whorl. In the proximity of the flange, the dorsal wall was initially limited to the mural parts of the proseptum and the first septa, and had an essentially prismatic structure. This indicates that the secretory zone was not differentiated into subzones in the dorsal region. The differentiation is reflected in the appearance of an external component of the dorsal wall in the form of subprismatic tissue in the dorsal wall, outside the apical part of the initial chamber. This differentiation indicates that the zone of secretion of the mural parts of septa separated from the zone secreting the external component of dorsal wall. The external component of dorsal wall shows no differentiated microstructure, which indicates that the secretory zone was also undifferentiated. This undifferentiated zone was connected, without any break, to the zone which secreted the ventral and lateral walls of the first whorl; this, however, was differentiated into two subzones. In the ventral region, the zone of secretion of the mural parts of the septa were clearly differentiated into subzones, as is indicated by the appearance of a discontinuity between the inner prismatic and medial subprismatic layer of the first whorl. In the case of septa built of nacreous tissue, the secretory zone of the free septal wall was directly connected with the mural secretory zone.

Suitably differentiated secretory zones were probably associated with the formation of the angular deposits of septal necks, and the prismatic and spherulitic-prismatic components of septa. One cannot dismiss, however, the possibility that these deposits are the products of some inorganic (diagenetic) deposition: an inorganic growth of some calcium carbonate elements was demonstrated by BANDEL and HEMLEBEN (1975).

The mode of formation of the nepionic swelling of the ammonite shell is described elsewhere (KULICKI, 1974).

This comparison of the secretion zones and their products formed before and after the nepionic swelling demonstrates that:

— Before the formation of the nepionic swelling the zone secreting the wall was subdivided into two subzones: (a) a subzone secreting the external prismatic layer of the first whorl, and (b) a subzone secreting the medial subprismatic or prismatic layer of the first whorl situated behind the nepionic constriction.

— After the nepionic swelling (e.g. in the postembryonic shell) the zone secreting the shell wall was also subdivided into two subzones: (a) a subzone secreting the external prismatic layer and (b) a subzone secreting the nacreous layer.

ERBEN *et al.* (1969: 26) and KULICKI (1974) noted that the external prismatic layer preceding the end of the nepionic swelling, that occurring at the backwards curving section, and the external prismatic layer of the postembryonic shell were structurally identical. It is therefore highly probable that they were formed by the same secretory zone.

THE QUESTION OF EARLY DEVELOPMENT IN AMMONITES

Two main points of view on the embryogenesis of ammonites can be distinguished:

(1) The assumption that there are three stages: (a) embryonic, limited to the initial chamber, (b) larval, of the trochophore or veliger type, and equivalent to that part of the shell as far as to the nepionic swelling, and (c) postlarval, corresponding to the remainder of the shell (ERBEN 1962, 1964, 1966; ERBEN *et al.*, 1968, 1969; LEHMANN 1976; SHULGA-NESTERENKO 1926; ARKEL 1957; MAKOWSKI 1971),

(2) The assumption that development was simple, comprising only two stages: embryonic, comprising the shell as far as the nepionic swelling, and post-embryonic comprising the remainder of the shell (SHIMANSKY 1954; RUZHENCEV and SHIMANSKY 1954; DRUZCZIC 1956;

DRUZCZIC and KHIAMI, 1970; RUZHENCEV 1962; BOGOSLOVSKY 1969; BIRKELUND and HANSEN 1974; KULICKI 1974).

RUZHENCEV and SHIMANSKY (1954: 41) applied the term "larva" in relation to ammonites neither to a veliger nor a trochophore but rather simply to an underdeveloped young individual, as do teuthologists in relation to underdeveloped individuals just after hatching. This concept was subsequently used in the same way by RUZHENCEV 1962; SHIMANSKY 1954; and BOGOSLOVSKY 1969. In his earlier paper and here, the present author (KULICKI 1974) termed this stage "pseudolarval".

The supporters of the first viewpoint assume that the constriction at the front of the initial chamber was the boundary between embryonic and larval stages. According to ERBEN *et al.* (1968, 1969), BIRKELUND (1967) and BIRKELUND and HANSEN (1968, 1974) the subprismatic tissues of the first whorl disappear and the prismatic tissue of the first whorl appears in the proximity of the whorl constriction. A shallow ventral sinus there also appears in growth lines (ERBEN 1962, 1966). The data previously published (KULICKI, 1974) and recently assembled show that there are no changes in microornamentation between the two parts of the shell in Mesozoic ammonites. There is also no discontinuity, represented by either a line on the shell surface or a secretory break in cross-section. The wall proper of the initial chamber always passes, without any break, into the external prismatic layer of the first whorl. The appearance of a shallow sinus in the growth lines, noted by ERBEN *(l. c.)* and interpreted as indicating the position of a locomotive organ such as a velum may also be interpreted as related to the development of the funnel in the embryonic stage, as was emphasized by BOGOSLOVSKY (1969: 66). In Recent mesogastropods, in which larvae with a protoconch hatch from the egg envelope, the point of hatching is marked by a change in surface ornament or the appearance of growth lines (ROBERTSON 1972).

Comparison with Recent *Nautilus* is hindered by our lack of direct observations of this animal. The concepts explaining maximum size of embryonal shell of *Nautilus* assume that hatching is marked by a discontinuity (WILLEY 1896; BLIND 1976) or a change in ornamentation (EICHLER and RISTEDT 1966). The point of hatching is not marked in this way in ammonites; changes concern shape only. The hypothesis that "I Wachstumsänderung" of ERBEN is connected with hatching from the egg envelope cannot be maintained.

Supporters of a simple development of ammonites assume that the nepionic swelling represents the boundary between embryonal and postembryonal stages. According to ERBEN *et al.* (1968) the nepionic swelling reflects metamorphosis which resulted in the changes in the posterior part of the body, which are indicated by changes in the suture line between prosuture and second suture. Thus so far there were no data which indicated that the nepionic swelling originated simultaneously with the change in shape of the posterior part of the body between the first and second septa. The data showing the concentration of septa and length of body chamber make it possible to assume that there were already some septa when the formation of nepionic swelling terminated (KULICKI 1974). A change in shape of the posterior part of the body between the first and second septum may result from difference in formation of the two elements. When the first septum remains in the furrow surrounding the posterior part of the body the second septum represents the product of the posterior part of the body.

A difference in structure of the first whorl before and after the nepionic swelling reflects only the secretion products of the posterior subzone which was secreting the subprismatic and/or prismatic tissues of the medial layer of the first whorl before the nepionic swelling, and the nacreous tissue following nepionic swelling. The swelling formed during a phase when the margin of the mantle halted or even retreated, together with a change in the secretions of the posterior subzone of the mantle margin (comp. KULICKI 1974). Differentiation in secretion of the mantle margin into two subzones is visible before and after formation of the nepionic swelling. The differences in secretory products of the posterior subzone may result, and be correlable with, processes acting just before hatching.

The adaptive significance of the nepionic constriction may have been as follows:
(1) it served to strenghten a wide zone at the margin of the first whorl during hatching from the egg envelopes;
(2) it acted as ballast to the apertural margin during the first phase of development after hatching, helped the animal to maintain the appropriate flotation position (KULICKI, 1974: 213).

The function of the nepionic swelling as a supporting for the apertural margin during hatching may be explained by the steadily increasing mechanical pressure of the embryo on both the egg envelope and the apertural margin closely adjoining the envelope (comp. KULICKI, 1974). The weighing of the apertural margin in the first post-hatching phase may be explained by the fact that a significant part of the first whorl preceding the nepionic swelling (more than a half whorl) displays reduced growth indices (growth of whorl height, width and spiral radius; KULICKI, 1974). This produces a shape close to spherical, with the initial chamber close to the centre. In this situation the centre of gravity of the shell and the centre of buoyancy of the initial chamber are situated close together (soft tissues may be neglected in this analysis as their density was close to that of sea water, which results in the loss of static equilibrium). The formation of the nepionic swelling results in the shifting of the centre of gravity towards the aperture, and compensates the lack of growth in width, height and spiral radius.

DRUZCZIC and KHIAMI (1970) interpreted the nepionic swelling as a structure formed in a result of a growth pause in the first post-hatching stage. In turn, following KULICKI (1974: 213) the fact that the egg envelopes are attached to the shell during the growth of the first whorl may explain:
(1) The ornamentation such as ribs and spines that is typical of postembryonic forms, but is lacking in embryonic shells.
(2) The ephemeral (transitory) occurrence of growth lines on the embryonic shell. This phenomenon may be partly explained by a more stable physico-chemical condition and food supply within the egg envelope.
(3) The presence of long final section of the embryonic shell, without any increase of parameters of the spire, which results in a subspherical shell shape.

The gelatinous egg envelopes of recent Decapoda grow during embryogeny (ZUEV and NESIS 1971), as in the case in some marine gastropods (ROGINSKAYA 1962; SHUTO 1974).

The egg envelopes of ammonites, described by LEHMANN (1966) and MÜLLER (1969) are similar in size to the initial chamber. Because of their small size they may be interpreted as egg envelopes in the earliest phase of development.

The present author investigated a series of minute ammonites with fully developed nepionic swellings and more than one septum from Oxfordian limestones of the Jagua Formation in western Cuba. The mass occurrence of the ammonites (2 to 4 at the average in thin section 3 to 4 cm^2 in surface), the lack of earlier stages and scarcity of somewhat older forms suggest rapid and simultaneous death of these animals, connected, perhaps, with some critical event such as hatching.

BOGOSLOVSKY (1969: 4) discussed the main direction of evolutionary changes of the embryonic shells of ammonites ranging from primitive Lower Devonian to Mesozoic forms. From the oldest forms onwards there is a steady reduction in size of the initial chamber and tubular section of whorl, and the degree of coiling. The maximum degree of coiling is reached in the Middle Devonian. Close coiling of embryonic shell is irreversible in ammonites. The uncoiling seen in heteromorphs, does not affect the embryonic shell. The absolute size of the embryonic shell may increase or decrease with time. For example, embryonic shells equal in size or even smaller than those seen in Cretaceous forms, appear as early as the Late Devonian and Permian (Dr. V. I. BOGOSLOVSKY, pers. inf., and author's observations).

It is obvious that ammonites with large embryonic shells must have hatched from eggs richer in yolk and with a larger initial diameter than those of ammonites with small embryonic shells. As far as the size of ammonite eggs is concerned it may be stated that there was a marked trend towards decrease in size, and that the main changes took place between the Lower and Upper Devonian.

The small size of ammonite eggs could have been of some adaptive value:

(1) Eggs could have been produced in larger quantities, as in the case of some recent Prosobranchia, in which maximalization of survivors is achieved by large numbers of eggs rather than their protection (SHUTO 1974).

(2) The specific character of growth of the ammonite body inside the shell does not allow for extensive development of reproductory organs without distinct increase in body chamber volume (in females of recent squids the reproductory organs may equal up to 35% of weight of body — see ZUEV and NESIS, 1971).

Some light is cast on the size of reproductory organs by the analysis of shortening of the body chamber of fully mature and fully grown ammonites (comp. KULICKI 1974) and finds of egg masses inside the body chamber (LEHMANN 1966; MÜLLER 1969). The size is considerable, and a reduction in the size of eggs results therefore in an increase in their number without the necessity of increase the size of the reproductory organs.

In accordance with data for squids (AKIMUSKIN 1963; ZUEV 1971; ZUEV and NESIS 1971) and prosobranchs (SHUTO 1974) hatching of individuals from small eggs takes place sooner than from large, as the time from fertilization to hatching is shorter in the case of small eggs. Moreover, the pseudolarval stage lasts longer in the case of squids hatching from smaller eggs (ZUEV and NESIS, 1971).

The occurrence of a pseudolarval stage in ammonites was demonstrated by KULICKI (1974) on the basis of shell geometry and an analysis of the relative density of septa.

The spherical initial chamber of ammonites, bactritids and nautiloids with caecum may be interpreted as an especially well developed hydrostatic organ, well-adapted to the planktonic life of the pseudolarval stage of these forms. A similar interpretation of the role of the initial chamber was given by ZAKHAROV (1972) and KULICKI (1974).

MUTVEI and REYMENT (1973), on the basis of anatomical-functional comparisons of Recent *Nautilus* with a relatively short and wide body chamber and ammonites with their typically narrow tubular body chamber, questioned the view that ammonites were capable of efficient swimming by "jet-propulsion" and even questioned whether or not they had a funnel. The body chamber of ammonites from the stage of formation of the nepionic swelling onwards is poorly adapted for the use of a funnel as a locomotive organ according to these authors. In that situation, the role of a spherical initial chamber as an efficient only well-developed hydrostatic organ, by which the ammonite, during very early growth stages, could move vertically, is clear.

THE FUNCTIONAL IMPORTANCE OF FOLDED SEPTA

Previous concepts concerning the functional importance of folded ammonite septa may be divided into two groups:

(1) Those inferring a physiological significance for folded septa (NEWELL 1949; MUTVEI 1967), and

(2) Those suggesting a mechanical significance for folded septa (PFAFF 1911; SPATH 1919; REYMENT 1958; RUZHENCEV 1962; TEICHERT 1967; WESTERMANN 1956, 1958, 1971, 1975*a, b;* SEILACHER 1975; BLIND 1975; MUTVEI 1975).

Recent studies carried out with models by SEILACHER (1975) and WESTERMANN (1975*a, b*) clearly demonstrate a significant physico-mechanical control on the formation of complex septal shapes, as well as the mechanical contribution of the shape of septa to the function of the shell as a hydrostatic organ.

The physiological concept of NEWELL (1949), emphasizing the significance of folding of septa for increased efficiency in some physiological function as, for example, respiration, is not supported by subsequent studies. MUTVEI'S (1967) concept that the folding of septa increased the wettable conchiolin surface in the chambers for faster liquid transport to the siphuncle is also not convincing as, was stated by WESTERMANN (1971: 19–20): "the corrugations (lobe and saddle axes) run more or less perpendicularly to the assumed directions of fluid transport... Therefore the path of transport would not be widened by the corrugations but much extended and corrugated septa would be less efficient". Experiments involving the filling of empty *Quenstedtoceras* shells with water, carried out by the author, show that:
(1) When the chambers are gradually infilled with water, the water flows uniformly and accumulates in the depressed elements on the margins of septa between septum and shell wall. Depressed elements are represented by saddles for the adapical surface and lobes for the adapertural. The first elements infilled are these of the highest order, that is the smallest, and larger elements, of lower order, are infilled later. Water infilling lobes or saddles displays surface tension effects with a concave meniscus. When the amount of water in a chamber is sufficiently small, there develop a series of isolated reservoirs, isolated from one another by convex elements of septa. At the stage when the siphon is in the ventral position, some water is concentrated in the space between it and ventral wall and in space formerly occupied by siphonal membranes. The shortest way through which these isolated reservoirs may communicate is the central surface of septum. When the water is removed from one of the elements, as e.g. from the external lobe, it returns subsequently.
(2) Infilling of subsequent chambers with larger diameters (1·5–2 cm high) leads to their complete flooding and, therefore, to formation of connections between particular "reservoirs", and a weakening of surface tension so part of the water may overflow, with consequent changes in the orientation of the shell. The overflowing water represents only a part of that infilling a chamber, depending on the degree of infilling, size of chamber and degree of folding of the marginal parts of the septum.
(3) When a small amount of water is introduced into the initial chamber, three water reservoirs develop: two symmetrical, situated on the two sides of the chamber, and a third in the middle saddle, around caecum and prosiphon.

Interpretation of functional significance of septal corrugation

According to DENTON and GILPIN-BROWN (1966), MUTVEI (1967) and the present author, the organic conchiolin membranes covering the surface of septa probably participated in liquid transport. A drop of water placed on the adapical surface of the septum of Recent *Nautilus* rapidly spreads and covers a large part of the adapical film. The experiments with *Quenstedtoceras* have shown that the preserved conchiolin films are characterized by the same property, which may be attributed to their granular surface texture (pl. 39: 4). It cannot be excluded, however, that the nature of this surface may be of diagenetic origin since a dried organic film from the adapical surface of *Nautilus* has similar but scarcer and finer granules (pl. 39: 5).

In *Spirula*, as in *Nautilus*, a marked decrease in concentration of salt takes place before the appearance of first gas bubble in the newly formed chamber, which is completely infilled with liquid (DENTON and GILPIN-BROWN 1966; DENTON 1973). In *Nautilus*, after the pumping out of liquid below the siphonal tube level, the contact of the liquid with the conchiolin surface of the siphonal tube takes place via conductive organic membranes and the porous external spherulitic-prismatic siphon layer, which also acts as a reservoir for a small amount of liquid (DENTON and GILPIN-BROWN 1966; DENTON 1973). According to DENTON (1973) "decoupling" of the bulk of the liquid is important as a change in osmotic concentration in the zone surrounding the siphon is sufficient for the pumping out of the chamber or the pumping in of a certain amount of liquid (in *Nautilus* this is the liquid occurring in the pores of the external spherulitic-prismatic siphon layer). It follows that very little osmotic work will have to be done to prevent liquid moving either into or out of the chambers (DENTON 1973: 289).

"Decoupling" of the bulk of liquid from the siphonal surface does not take place in *Sepia*. This is because the very narrow chambers are also separated by dissepiments, as a result of which increase or decrease in concentration of salt in the proximity of the siphonal surface is transmitted to the most distant parts of the chambers after only a few days (DENTON 1973: 290).

When the chambers of an ammonite are appropriately infilled the ratio of the bulk of liquid concentrated in isolated reservoirs from the periphery of septum to the liquid surrounding siphon and concentrated in elements of the external lobe is comparable with the "decoupling" effect in *Nautilus* and *Sepia*. In order to pump liquid in, or out of a chamber it is sufficient to merely change the concentration of salt in the liquid directly in contact with the siphonal tube.

As ammonites are characterized by lower indices of shell growth and a relatively longer body chamber than *Nautilus*, the centre of gravity must have been situated closer to the centre of buoyancy (in adult *Nautilus macromphalus* the distance between the two centres equals 6 mm according to DENTON and GILPIN-BROWN 1966). Regular distribution of liquid in chambers and limited possibilities of overflow thus increase the stability of ammonites.

The data presented by HEPTONSTALL (1970), REYMENT (1973), MUTVEI and REYMENT (1973) indicate that ammonites required much more liquid in the chambers of the phragmocone than the Recent *Nautilus* in order to maintain neutral buoyancy. Therefore the folding of septal margins, which resulted in the retention of liquid in place by the action of surface tension forces, and prevented the overflow of liquid under turbulent environmental conditions and improved the liquid exchange in chambers enabling vertical movements in the water. They should be therefore treated as adaptive features. The folding also increased strength of shell against implosion. It should be stressed that the above mentioned functions are positively correlated; the stronger the folding of septal margin the stronger is the shell and the more numerous are the "reservoirs" holding liquid.

When phragmocone chambers are relatively large (over a dozen cm in diameter), the elements classified in the nomenclature of the suture line as of the lower order are most important for strengthening of shell, whilst the liquid is mainly kept in the elements of the highest order.

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EXPLANATION OF THE PLATES

Abbreviations used:

aa — anterior auxiliary deposits
ap — posterior auxiliary deposits
ad — angular deposits
bch — body chamber
c — caecum
d — discontinuity
dsn — distal part of the septal neck
dw — dorsal wall
dw 1 — dorsal wall of the first whorl
dw 2 — dorsal wall of the second whorl
f — flange
ich — initial chamber
il — inner layer of the initial chamber
ipr — inner prismatic layer
ml — middle layer of the initial chamber
mp — mural part of the proseptum
exc — external component of the dorsal wall
exp l — external prismatic layer of the first whorl
ps — proseptum
si — sutural infillings
sm — siphonal membrane
wcr — wall of the connecting ring
wpich — wall proper of the initial chamber
2s — second septum
3s — third septum

PLATE 24

Nathorstites gibbosus Stolley

1. Dorsal part of the septal neck of the 19th septum; × 2500.
2. Dorsal part of the septal neck of the 46th septum; × 600.
3. Dorsal part of the septal neck of the 43rd septum; × 600.

4. Section through the dorsal part of the septal neck at a transitory stage; the 54th septum; × 400.
5. Section through the caecum and first two septa; × 1000.
6. Section through the distal part of the septal neck of the 49th septum; × 600.
7. Section through the septal neck of the 38th septum; × 1000.
8. Section through the distal part of the auxiliary deposits, with the walls of the connecting ring partly visible; the 65th septum; × 750.

Triassic, Carnian, Odgeöya (E. Svalbard), ZPAL Am. III/3

PLATE 25

Nathorstites gibbosus STOLLEY

1. Section through the dorsal part of the septal neck of the 94th septum; × 300.
2. Section through the dorsal part of the septal neck of the 61st septum; × 1000.
   a — Prochoanitic part of the septal neck
   b — Retrochoanitic part of the septal neck

Triassic, Carnian, Odgeöya (E. Svalbard), ZPAL Am III/3

PLATE 26

1. *Quenstedtoceras* sp. juv., ZPAL Am II/244,
   a — caecum and prosiphon, × 450,
   b — section through a broken part of the prosiphon, × 6000.
2. *Quenstedtoceras henrici* R. DOUVILLÉ, ZPAL Am II/251, caecum and prosiphon, × 450.
3. *Quenstedtoceras* sp. juv., ZPAL Am II/243,
   a — caecum and prosiphon, × 450,
   b — prosiphon; × 1000.
4. *Quenstedtoceras* sp. juv., ZPAL Am II/312,
   caecum with prosiphon broken off; × 300.

Łuków, Poland, Jurassic, Callovian

PLATE 27

1. *Quenstedtoceras* sp. juv., ZPAL Am II/102,
   caecum and prosiphon; × 360.
2. *Quenstedtoceras henrici* R. DOUVILLÉ, ZPAL Am II/252,
   caecum and prosiphon; × 450.
3. *Quenstedtoceras henrici* R. DOUVILLÉ, ZPAL Am II/252,
   connecting ring with siphonal membranes at the ventral side,
   a — × 200,
   b — × 600.
4. *Quenstedtoceras* sp., ZPAL Am II/272,
   interior view of the caecum and siphon; × 600.
5. *Quenstedtoceras henrici* R. DOUVILLÉ, ZPAL Am II/251,
   connecting ring with a single siphonal membrane; × 300.
6. *Quenstedtoceras* sp. juv., ZPAL Am I/30, siphonal membrane linking the adapertural surface of a septum with the siphonal surface; × 450.

Łuków, Poland, Jurassic, Callovian

PLATE 28

1. *Quenstedtoceras* sp. juv., ZPAL Am II/170,
   median section through the ventral wall in the proximity of the attachment of the proseptum and second septum; × 2000.
2. *Quenstedtoceras* sp. juv., ZPAL Am II/160,
   paramedian section through the ventral wall in the proximity of the attachment of the caecum, prosiphon, and first 2 septa; × 1000.
3. The same specimen,
   median section through the dorsal wall of the initial chamber in the proximity of the attachment of the caecum and first and third septa; × 1000.

Łuków, Poland, Jurassic, Callovian

PLATE 29

1. *Quenstedtoceras* sp. juv., ZPAL Am II/160,
   paramedian section through the dorsal wall of the initial chamber in proximity of the attachment of the caecum and first and third septa; × 2000.
2. The same specimen,
   section through the ventral wall in the proximity of the attachment of the first 2 septa; × 2000.
3. *Quenstedtoceras* sp. juv., ZPAL Am II/170,
   section through the dorsal wall and proseptum in the proximity of the attachment of the caecum and siphon; × 2000.

Łuków, Poland, Jurassic, Callovian

PLATE 30

1. *Quenstedtoceras* sp. juv., ZPAL Am I/29,
   section through the dorsal wall, proseptum and third septum in the proximity of the attachment of the caecum and siphon; × 1500.
2. The same specimen,
   paramedian section through the ventral wall in the proximity of the attachment of the first and second septa; × 1500.
3. *Quenstedtoceras henrici* R. Douvillé, ZPAL Am I/21,
   section through the ventral part of the third septum; × 1800.
4. The same specimen,
   section through the ventral part of the 7th septum; × 1800.

Łuków, Poland, Jurassic, Callovian

PLATE 31

1. *Kosmoceras* sp., ZPAL Am II/360,
   median section through the ventral wall in the proximity of the attachment of the proseptum; × 1500.
2. The same specimen,
   dorsal part of the same section; × 1500.

Łuków, Poland, Jurassic, Callovian

PLATE 32

1. *Quenstedtoceras henrici* R. DOUVILLÉ, ZPAL Am I/21,
   section through the ventral part of the septal neck of the fifth septum; × 3600.
2. *Quenstedtoceras* sp., ZPAL Am I/28,
   a — section through the dorsal part of the septal neck at the end of third whorl; × 1200;
   b — portion of the auxiliary deposits; × 3900.
3. *Quenstedtoceras henrici* R. DOUVILLÉ, ZPAL Am II/350,
   section through the dorsal part of the septal neck of the last septum preceding the body chamber; × 1000.

Łuków, Poland, Jurassic, Callovian

PLATE 33

1. *Quenstedtoceras henrici* R. DOUVILLÉ, ZPAL Am II/350,
   section through the dorsal part of the septal neck of the third septum preceding the body chamber; × 1000.
2. *Quenstedtoceras* sp., ZPAL Am II/20,
   section through the dorsal part of the septal neck of the last septum separating the body chamber from the phragmocone; × 600.
3. *Quenstedtoceras henrici* R. DOUVILLÉ, ZPAL Am II/350,
   section through the dorsal part of the septal neck of the second septum preceding the body chamber; × 1000.
4. The same specimen,
   section through the ventral part of the septal neck of the second septum preceding the body chamber; × 1000.

Łuków, Poland, Jurassic, Callovian

PLATE 34

1. *Kosmoceras* sp., ZPAL Am II/360,
   section through the ventral part of the septal neck of the second septum; × 3000.
2. The same specimen,
   section through the dorsal part of the septal neck of the second septum; × 3000.
3. *Quenstedtoceras* sp., ZPAL Am II/20,
   section through the dorsal part of the septal neck of the third septum preceding the body chamber; × 600.
4. The same specimen,
   section through the dorsal part of the septal neck of the second septum preceding the body chamber; × 600.

Łuków. Poland, Jurassic, Callovian

PLATE 35

1. *Kosmoceras* sp., ZPAL Am II/360,
   section through the ventral part of the septal neck of the third septum; × 3000.
2. The same specimen,
   section through the dorsal part of the septal neck of the third septum; × 3000.
3. *Quenstedtoceras* sp. juv., ZPAL Am I/30,
   section through the dorsal part of the septal neck of the third septum; × 4500.

4. The same specimen,
   section through the ventral part of the septal neck of the third septum; × 4500.
5. *Kosmoceras* sp., ZPAL Am II/360,
   section through the septum and ventral wall of the fourth whorl; × 3000.
6. Portion of figure 5; × 1000.

Łuków, Poland, Jurassic, Callovian

PLATE 36

1. *Quenstedtoceras* sp., ZPAL Am I/30,
   median section through the dorsal wall and proseptum; × 1200.
2. The same specimen,
   section through the dorsal part of the septal neck in the middle of the fourth whorl; × 1200.
3. *Quenstedtoceras henrici* R. Douvillé, ZPAL Am I/27,
   section through the dorsal wall of the initial chamber and proseptum, and the attachment of the siphon and caecum; × 1800.

Łuków, Poland, Jurassic, Callovian

PLATE 37

1. *Kosmoceras* sp., ZPAL Am I/28,
   a — section through the dorsal part of the septal neck of a septum of the the second whorl; × 2000;
   b — the relationship between the distal part of the septal neck and to the anterior auxiliary deposits; × 6000;
   c — posterior auxiliary deposits; × 6000.
2. The same specimen,
   a — section through the ventral part of the septal neck of a septum of the second whorl; × 2000;
   b — proximal part of a septal neck, and the relationship of anterior and posterior auxiliary deposits; × 6000;
   c — posterior auxiliary deposits; × 6000.

Łuków, Poland, Jurassic, Callovian

PLATE 38

1. *Quenstedtoceras* sp. juv., ZPAL Am I/30,
   a — median section through the ventral wall in the proximity of the atachment of the proseptum; × 4000.
   b — median section through the ventral wall in proximity of attachment of the second septum (continuation of figure 1a); × 4500.

Łuków, Poland, Jurassic, Callovian

PLATE 39

1. *Quenstedtoceras* sp. juv., ZPAL Am II/170,
   median section through the ventral wall in the proximity of the attachment of the proseptum and second septum; × 1500.

2. *Kosmoceras* sp., ZPAL Am II/360,
   median section through the initial chamber and the proseptum in the proximity of the first 2 septa; × 450.
3. *Quenstedtoceras henrici* R. Douvillé, ZPAL Am I/21,
   median section through the dorsal wall of the initial chamber and proseptum; × 2400.
4. *Kosmoceras duncani* (J. Sowerby), ZPAL Am II/101,
   adapical surface of a septum, with organic membrane preserved; × 1800.
   Łuków, Poland, Jurassic, Callovian
5. *Nautilus pompilius* L., ZPAL Am II/70, loc. indet.,
   adapical surface of a septum, with organic membrane preserved; × 1800.

PLATE 40

1. *Holcophylloceras zignodianum* (d'Orbigny), ZPAL Am III/1,
   portion of the median section, the last part of the siphon remaining in the body chamber; × 3.2.
   Satsiskvile river valley, Ratsha, Georgia, USSR, Jurassic, Callovian
2. *Cadoceras* sp., ZPAL Am III/7,
   septal neck of the last septum separating body chamber from phragmocone; × 100.
   Anabar river valley, Siberia, USSR, Jurassic, Callovian
3. The same specimen,
   septal neck of the last but one septum, with both anterior and posterior auxiliary deposits well developed; × 100.
4. *Surites subanalogus* Schulgina, ZPAL Am III/5,
   septal neck with connecting ring, siphonal membrane and both anterior and posterior auxiliary deposits; × 70.
   Bajarka river valley, Siberia, USSR, Cretaceous, Berriasian
5. The same specimen,
   another septal neck; × 100.

PLATE 41

1. *Kosmoceras* sp., ZAPL Am II/360,
   section through the dorsal part of the septal neck of a septum in the middle of the sixth whorl; × 1500.
2. The same specimen,
   the same septal neck showing the structure of anterior auxiliary deposits; × 6000.
3. The same specimen,
   the same septal neck showing the structure of posterior auxiliary deposits; × 6000.
   Łuków, Poland, Jurassic, Callovian

PLATE 42

1. *Kosmoceras* sp., ZPAL Am I/28,
   section parallel to the median one; relation of the dorsal wall of initial chamber to the first 2 septa; × 3000.
2. The same specimen and sections, showing the relationship of the proseptum to the ventral wall of the initial chamber; × 2000.
3. *Quenstedtoceras henrici* R. Douvillé, ZPAL Am II/180,
   section parallel to the median one showing the relation of the proseptum to the ventral wall of the initial chamber; the nacreous structure of the second septum is visible; × 1000.

4. *Quenstedtoceras* sp. juv., ZPAL Am II/170,
   section parallel to the median one showing the relationship of the proseptum to the ventral wall of initial chamber; × 1000.

Łuków, Poland, Jurassic, Callovian

PLATE 43

1. *Quenstedtoceras* sp. juv., ZPAL Am I/31,
   a-d — section parallel to the medial one, through the ventral wall of the initial chamber and first whorl; × 600.

Łuków, Poland, Jurassic, Callovian

PLATE 44

1. *Quenstedtoceras* sp. juv., ZPAL Am II/311,
   transverse section through the initial chamber and the umbilical seam of the first whorl; at the left side, the section cuts the nepionic swelling of the first whorl; at the right side, it cuts the middle of the second whorl; × 1000.
2. The same specimen,
   transverse section through the ventral wall of the second whorl and the dorsal wall of the third whorl showing the relationship of the nacreous tissue of septum to the prismatic dorsal wall; × 1000.
3. *Quenstedtoceras* sp. juv., ZPAL Am I/30,
   median section through the ventral wall of the initial chamber; × 750.

Łuków, Poland, Jurassic, Callovian

PLATE 45

1. *Quenstedtoceras* sp. juv., ZPAL Am I/31,
   nepionic swelling of the ventral wall of the shell; × 600.
2. *Kosmoceras* sp., ZPAL Am I/28,
   nepionic swelling of the ventral wall of the shell; × 1500.
3. *Quenstedtoceras* sp. juv., ZPAL Am II/160,
   nepionic swelling of the ventral wall of the shell; × 1000.
4. *Quenstedtoceras* sp. juv., ZPAL Am II/170,
   nepionic swelling of the ventral wall of the shell; × 1000.
5. *Quenstedtoceras henrici* R. DOUVILLÉ, ZPAL Am II/50,
   section parallel to the median one, through the wall portion of the initial chamber and the first whorl, and through the nepionic swelling of the dorsal wall; × 600.

Łuków, Poland, Jurassic, Callovian

PLATE 46

1. *Quenstedtoceras henrici* R. DOUVILLÉ, ZPAL Am II/300,
   longitudinal section through the ventral wall; at the wall the outer component of the dorsal wall is visible in the form of prominent wrinkles situated in proximity of the aperture; × 1000.
2. Continuation of figure 1; × 1000.

3. Continuation of figure 2; portion within body chamber; at the left side, the outer component of the dorsal wall is visible in the form of an inner prismatic layer covering the wrinkles; × 1000.
4. Continuation of figure 3; section in the proximity of the septum separating the body chamber from the phragmocone; both components of the dorsal wall are clearly visible; × 1000.
5. Longitudinal section through the ventral wall and also through the dorsal wall of the next whorl, in the proximity of the penultimate septum; × 1000.
6. Longitudinal section through the ventral wall and also through the dorsal wall of the next whorl, in the proximity of the third septum preceding the body chamber; × 1000.

Łuków, Poland, Jurassic, Callovian

PLATE 47

1. *Quenstedtoceras henrici* R. Douvillé, ZPAL Am II/300,
   enlarged portion of the dorsal wall shown in Plate 24: 4; × 3000.
2. *Quenstedtoceras* sp. juv., ZPAL Am II/160,
   longitudinal section through the ventral wall; at the wall the outer component of the dorsal wall is visible in the form of distinctive wrinkles situated in proximity of the aperture; × 1000.
3. The same specimen,
   section situated a little further within the body chamber than figure 2; × 1000.
4. The same specimen,
   section situated a little further within the body chamber than figure 3; in the outer prismatic layer of ventral wall a discontinuity is visible; × 1000.
5. The same specimen,
   section situated a little further within the body chamber than in figure 4; the wrinkles are linked at the base; × 1000
6. The same specimen,
   section situated a little further within the body chamber than in figure 5; in the outer prismatic layer of ventral wall a discontinuity is visible which does not continue into the nacreous layer; × 1000.
7. The same specimen,
   section situated a little further within the body chamber than in figure 6; the discontinuity is marked in both the outer prismatic and nacreous layers; × 1000.
8. The same specimen,
   section situated just anteriory to the last septum; spaces among the interconnected wrinkle tops are filled by inner prismatic tissue; × 1000.

Łuków, Poland, Jurassic, Callovian

PLATE 48

1. *Quenstedtoceras* sp. juv., ZPAL Am II/312,
   transverse section through the ventrolateral wall at the boundary between the end of second whorl and the beginning of third whorl; and through the lateral wall of the next whorl at the umbilical seam; × 600.
2. *Quenstedtoceras* sp. juv., ZPAL Am II/311,
   umbilical seam between the second and third whorls; × 1500.
3. *Kosmoceras duncani* (J. Sow.), ZPAL Am II/101,
   ventral wall of the first whorl, covered by the dorsal wall of the next whorl; × 360.
4. The same specimen,
   ventral wall of the second whorl, visible when the dorsal wall of the next whorl is partly removed; × 360.
5. The same specimen,
   dorsal view of the second whorl in the proximity of the umbilical seam; × 1800.
6. *Quenstedtoceras henrici* R. Douvillé, ZPAL Am II/252,
   the relationship between the nacreous tissue of second septum and the ventral wall; × 4500.

Łuków, Poland, Jurassic, Callovian


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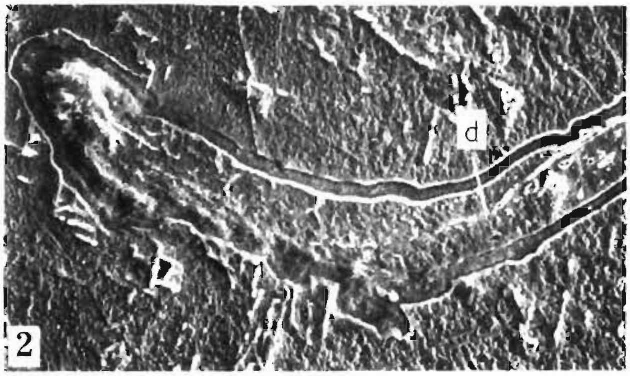
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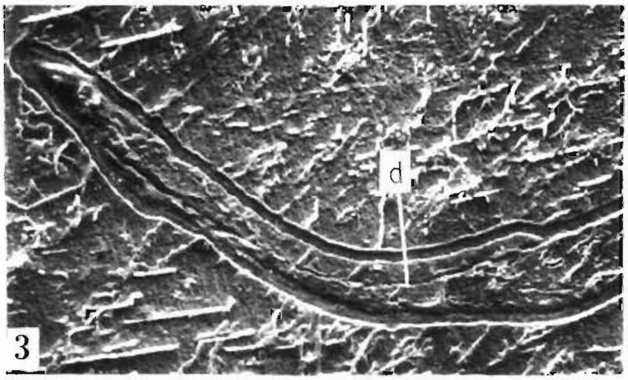
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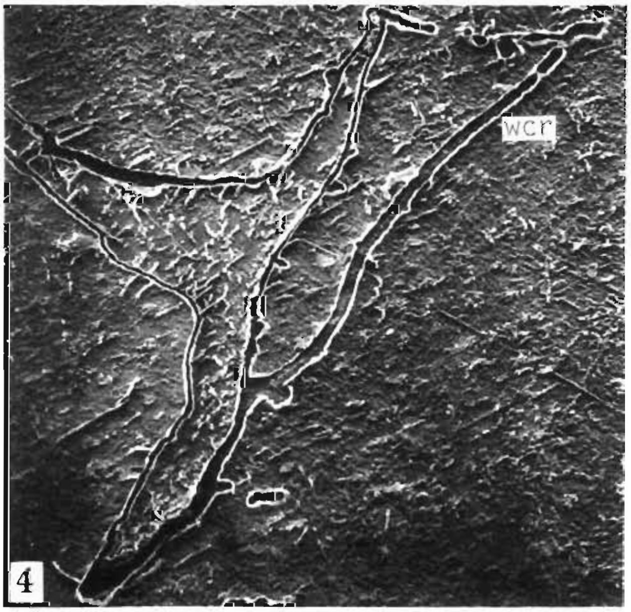
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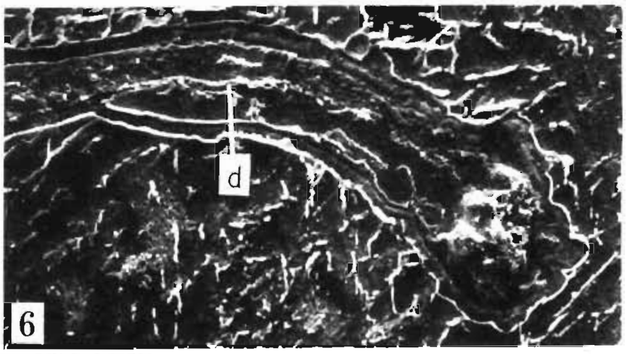
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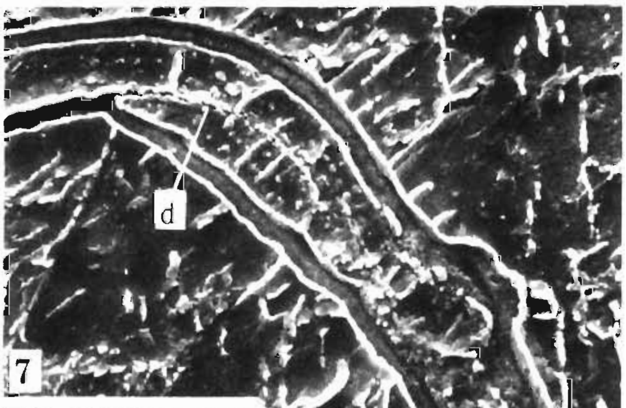
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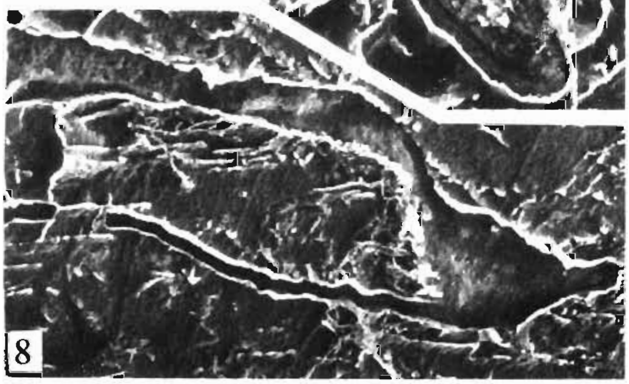
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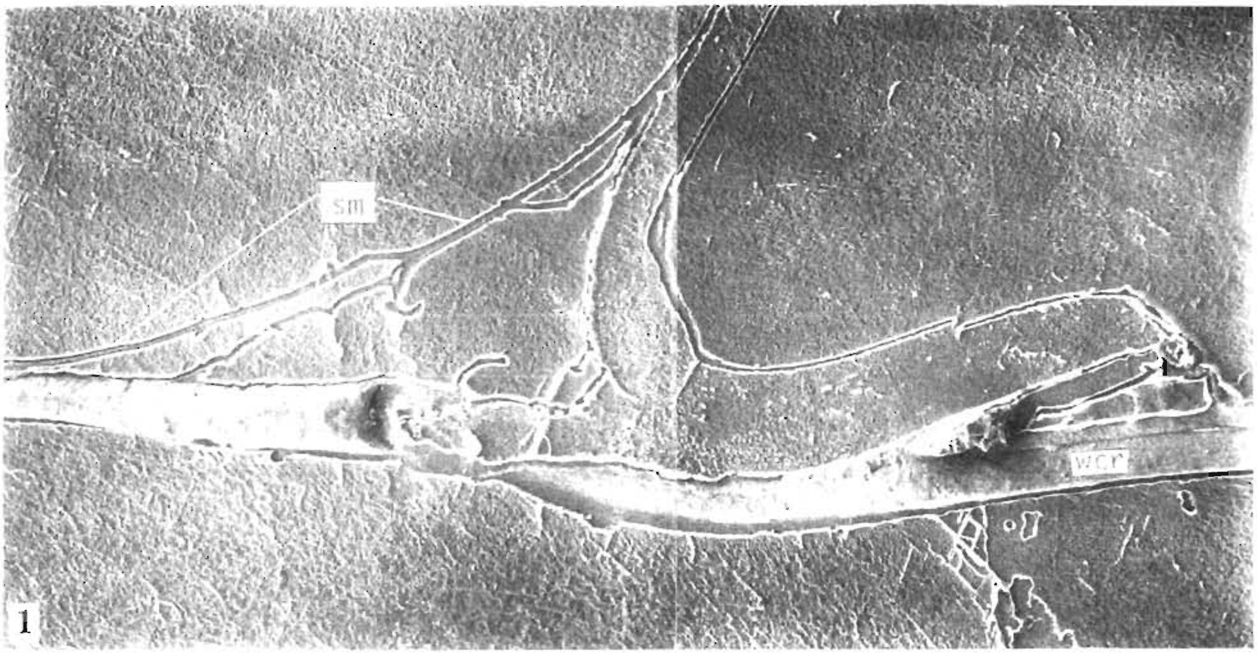
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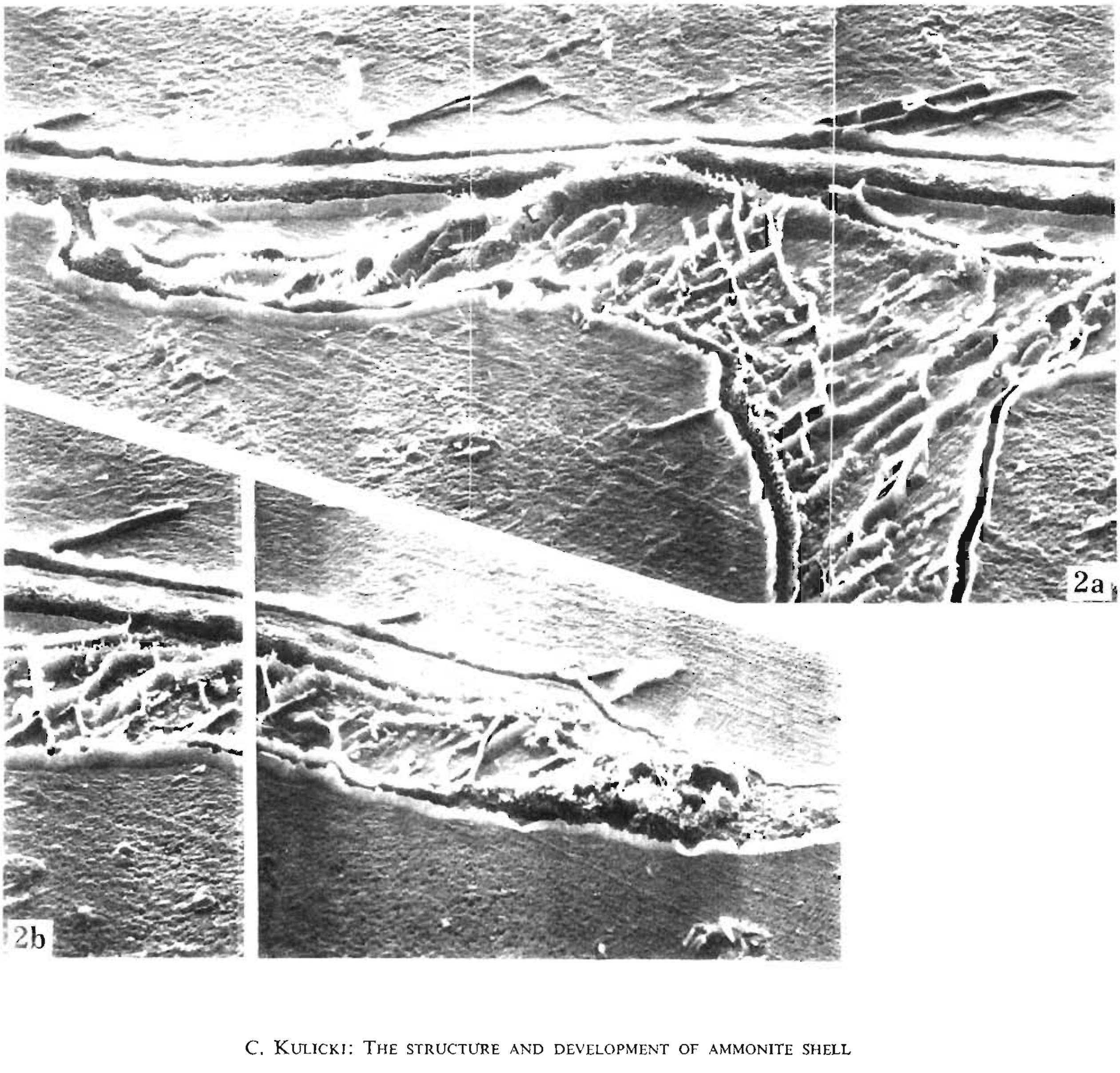

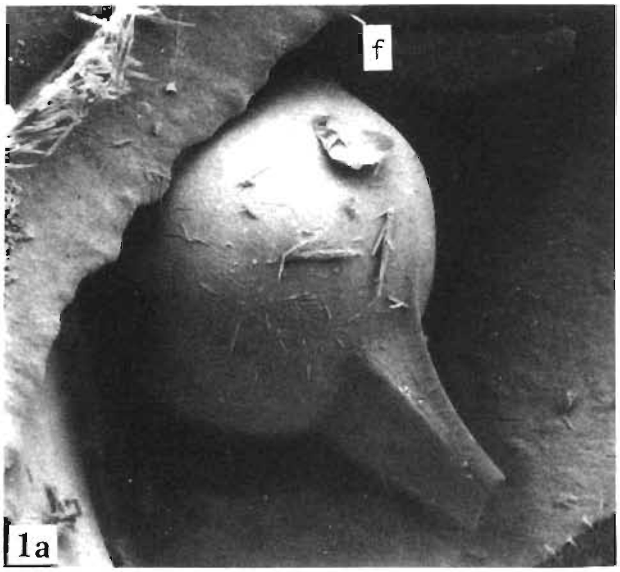

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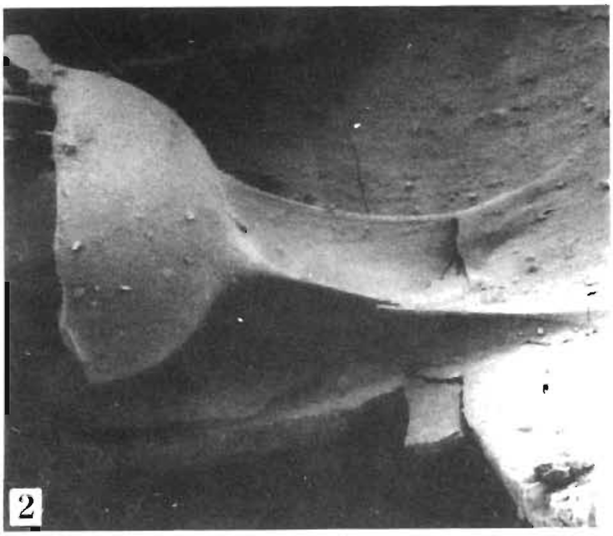

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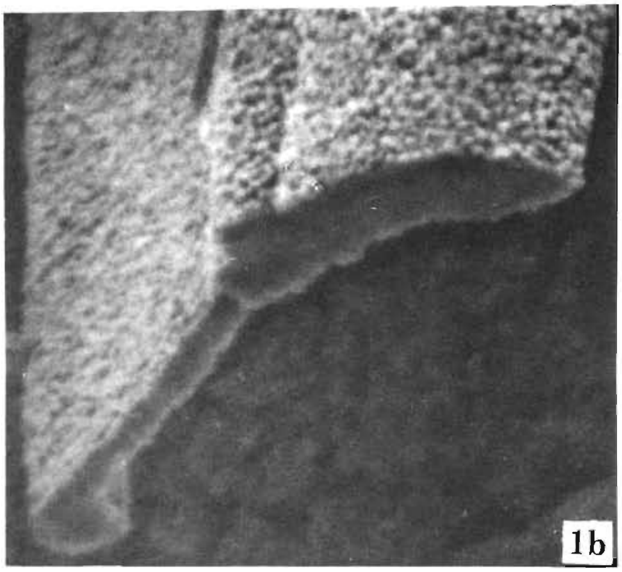

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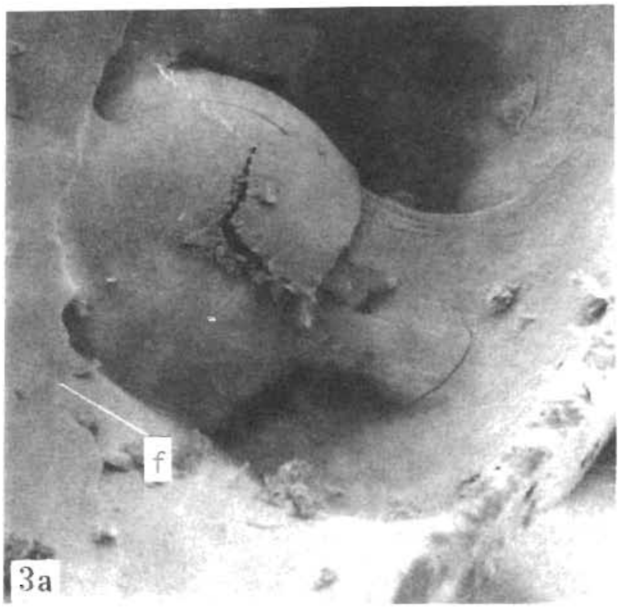

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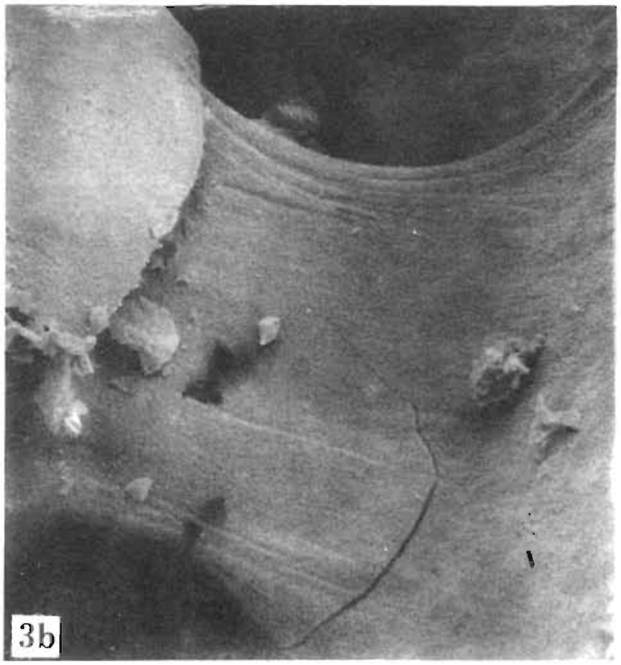

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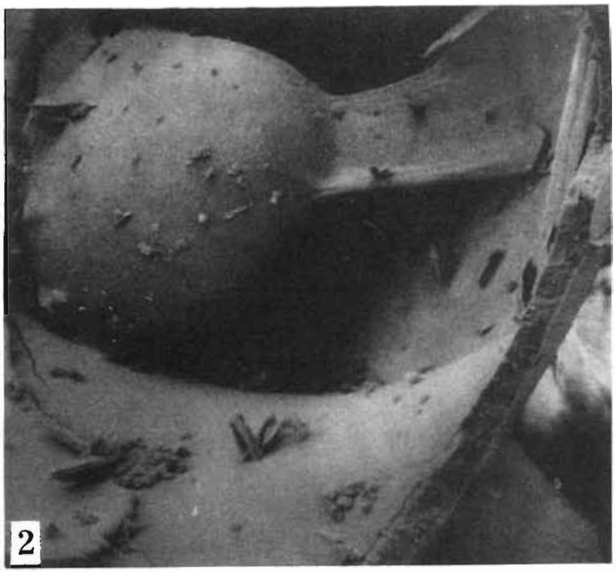
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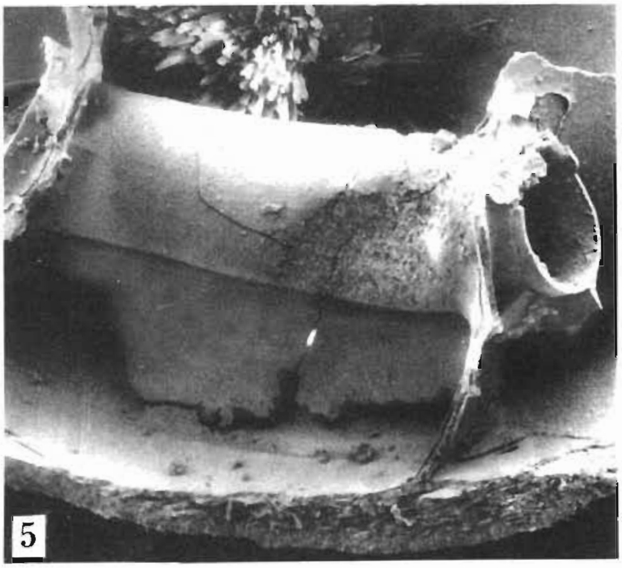
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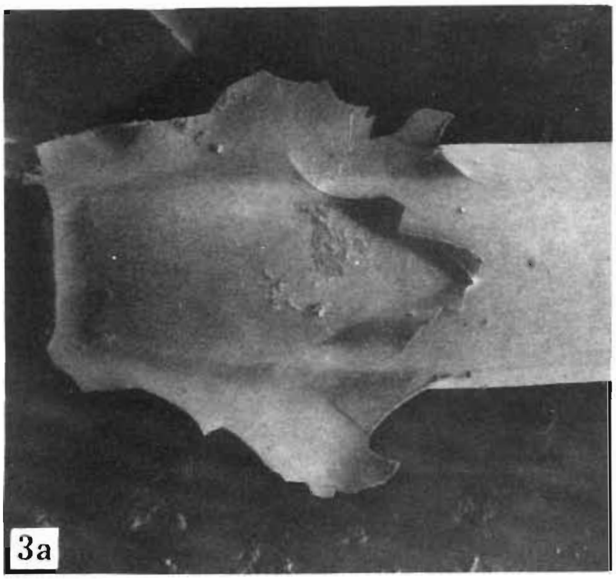
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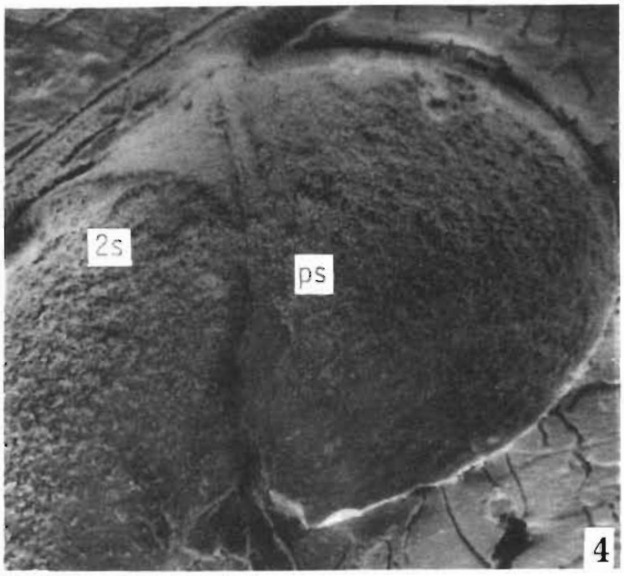

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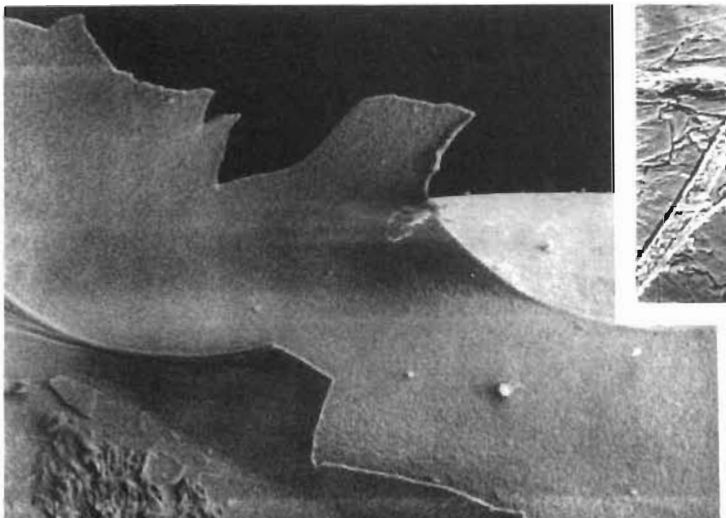
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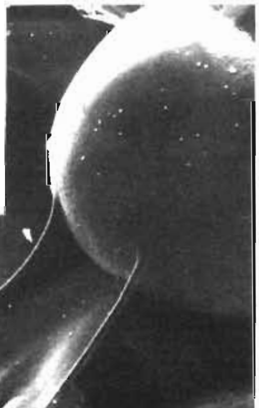
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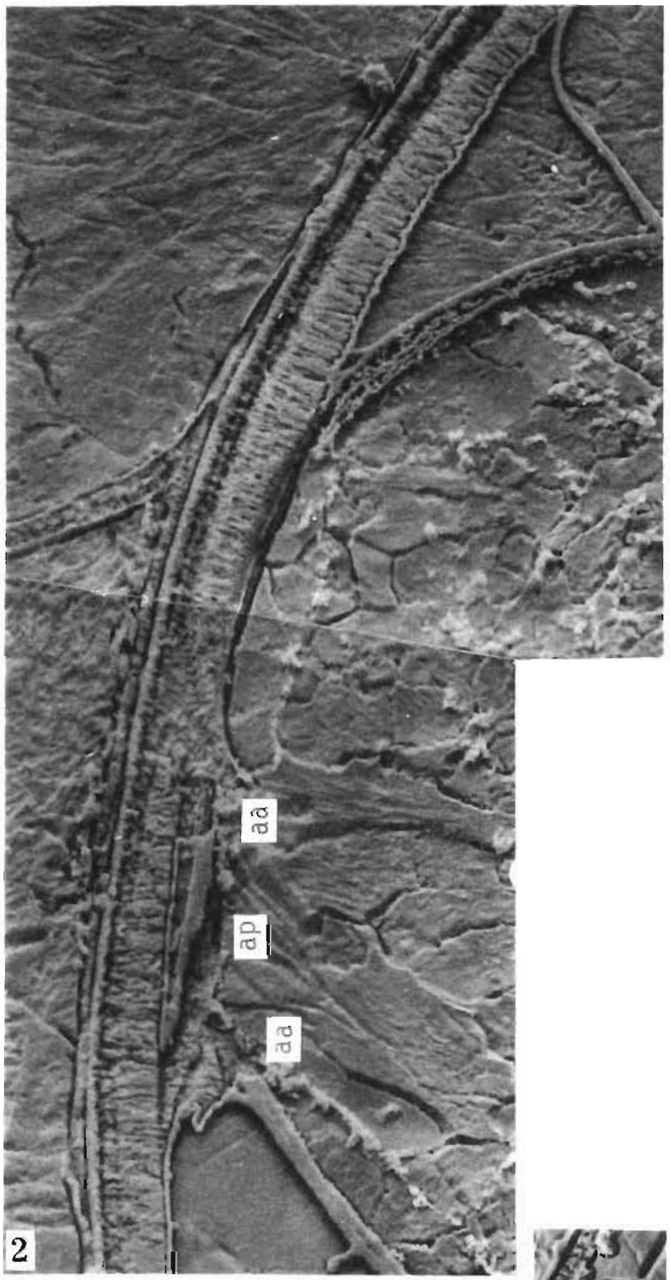

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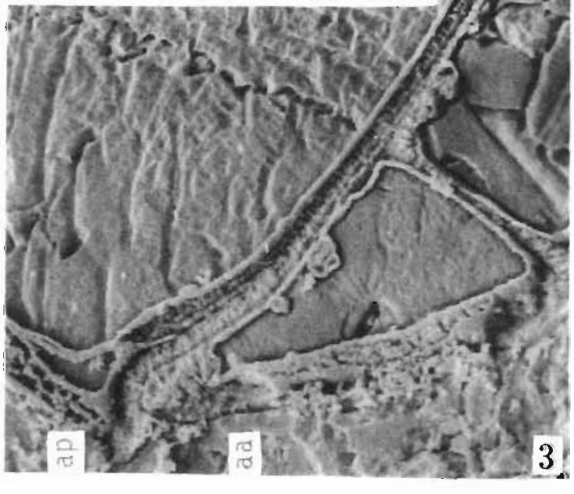

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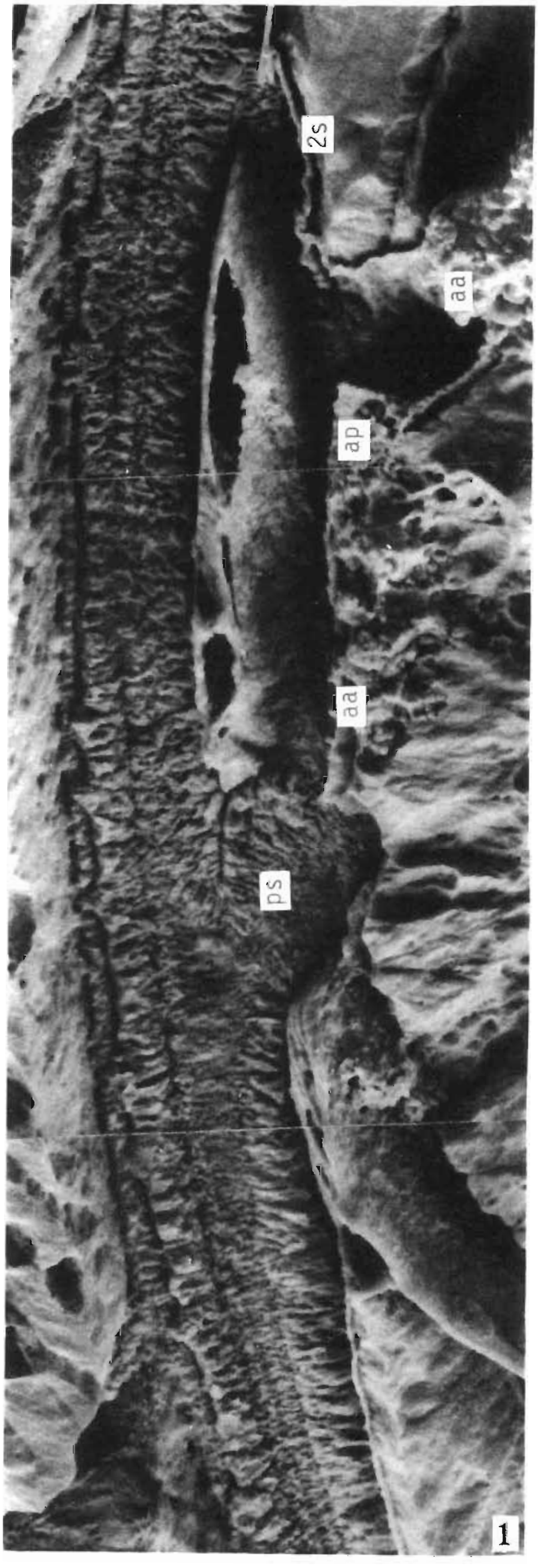

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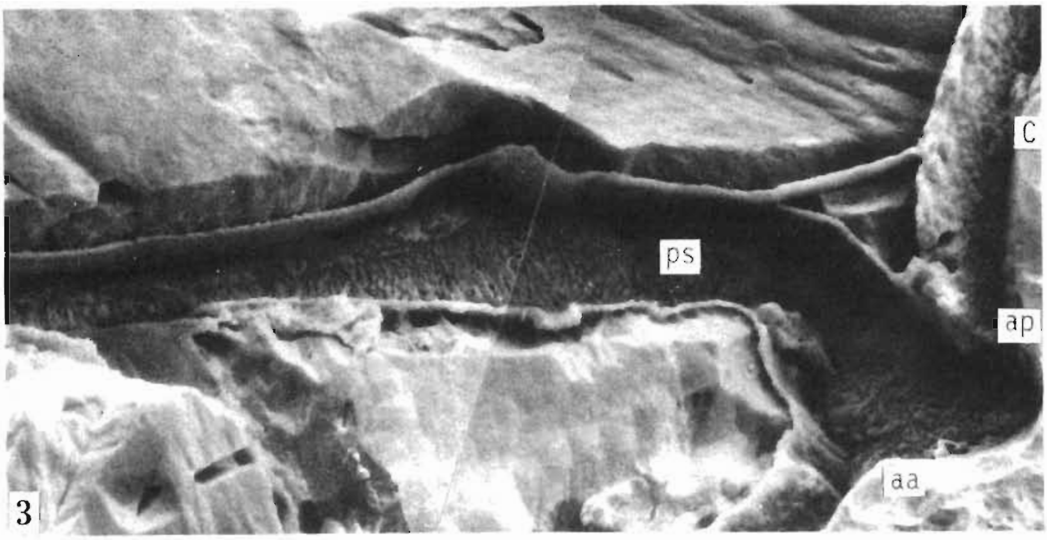
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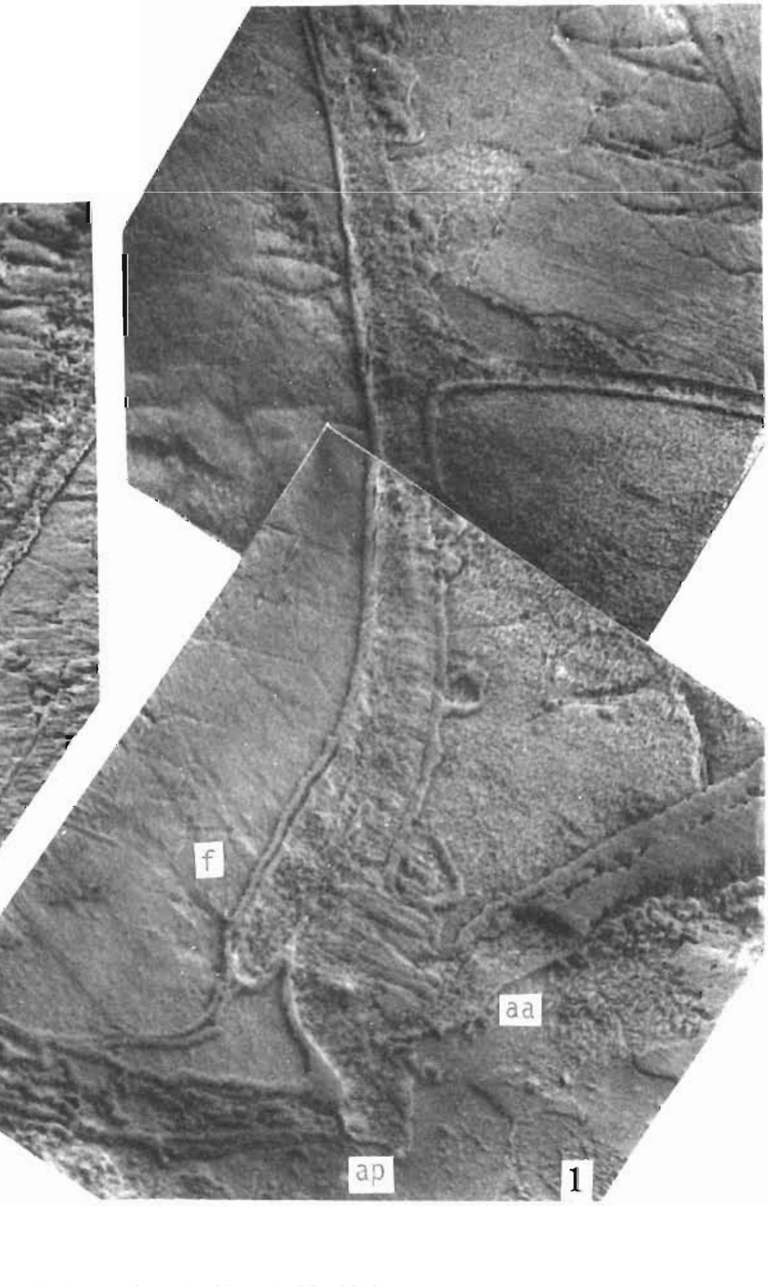
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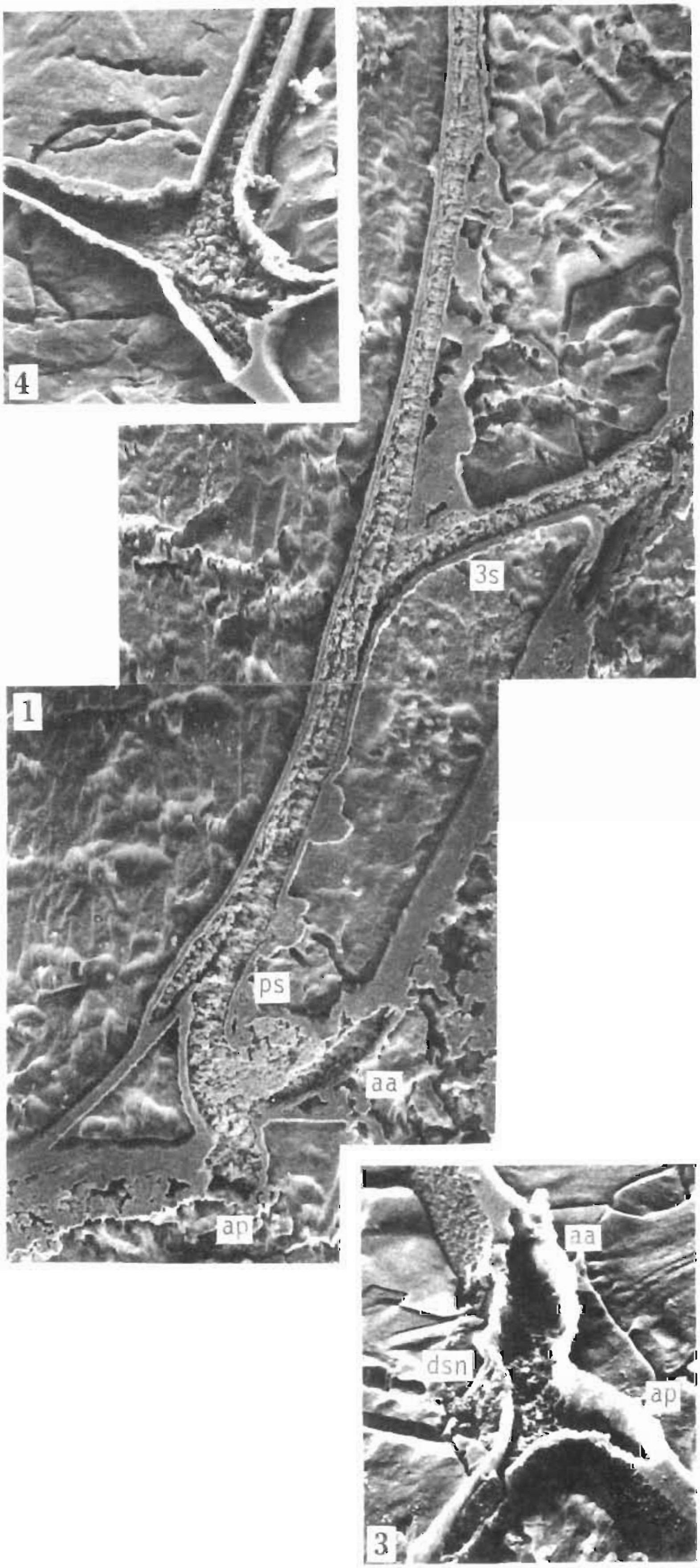
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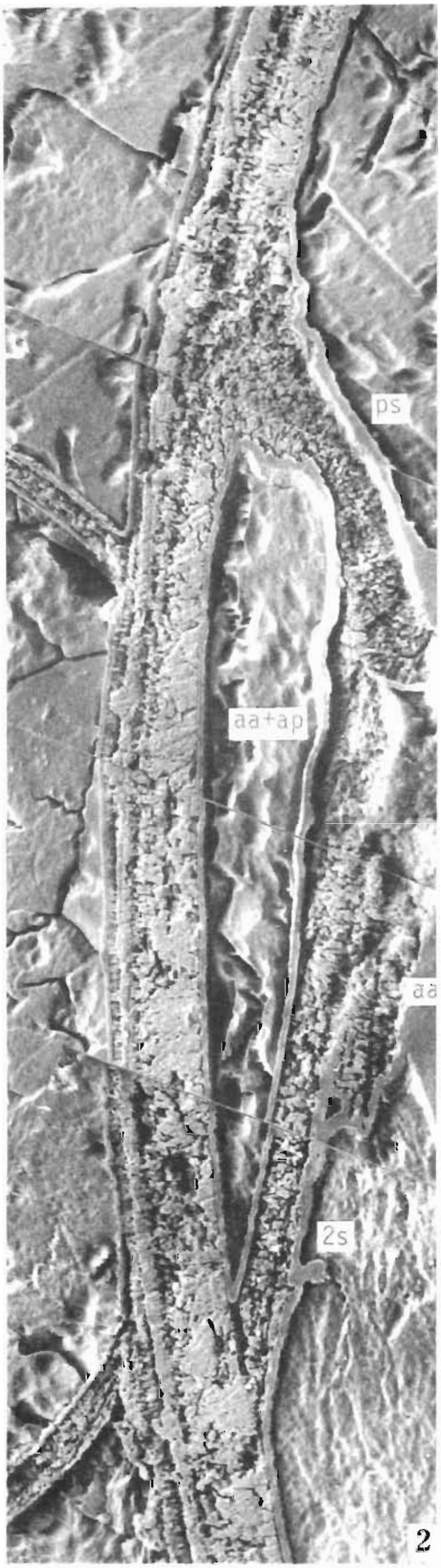
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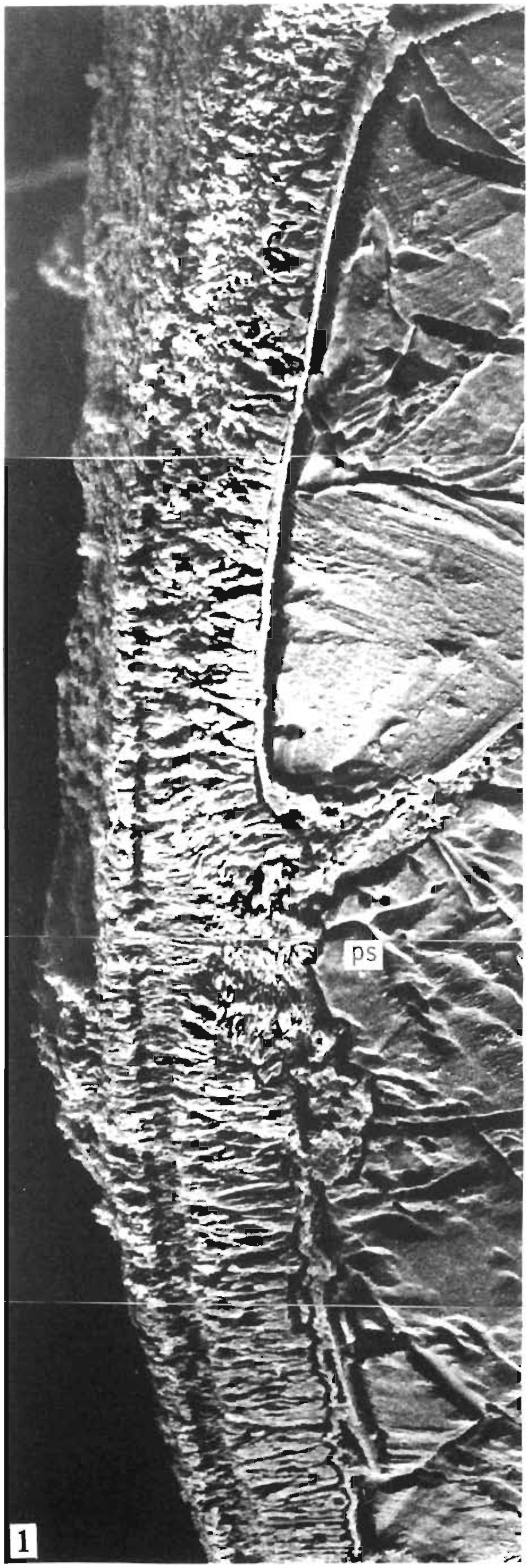

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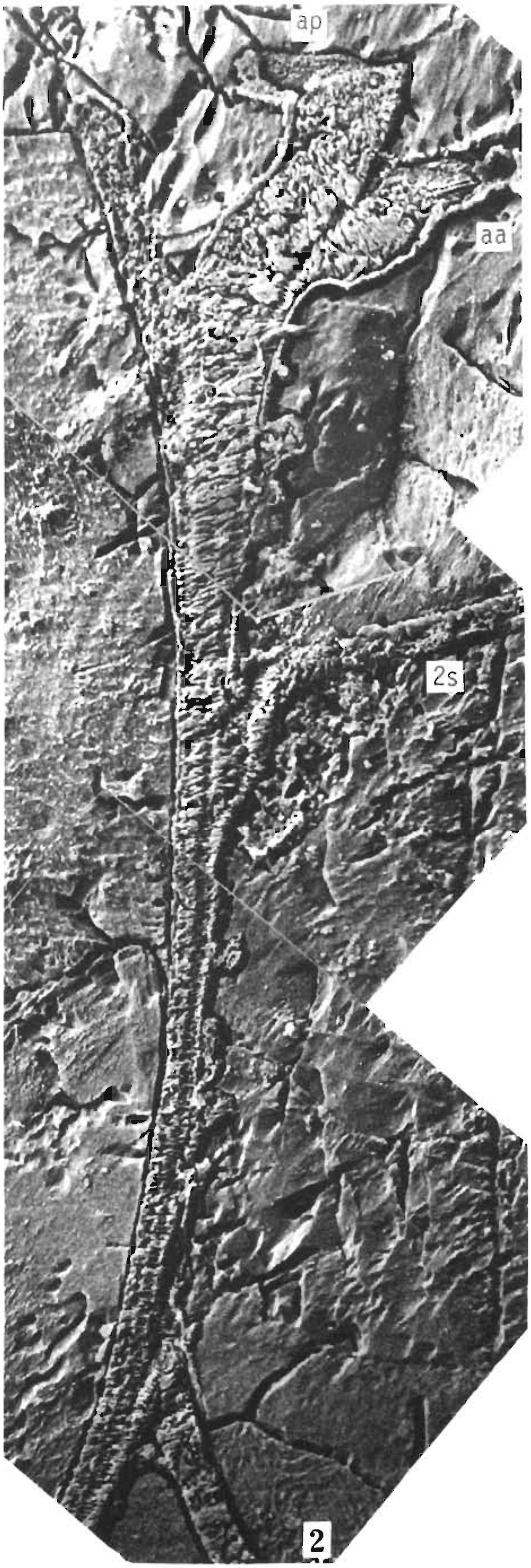

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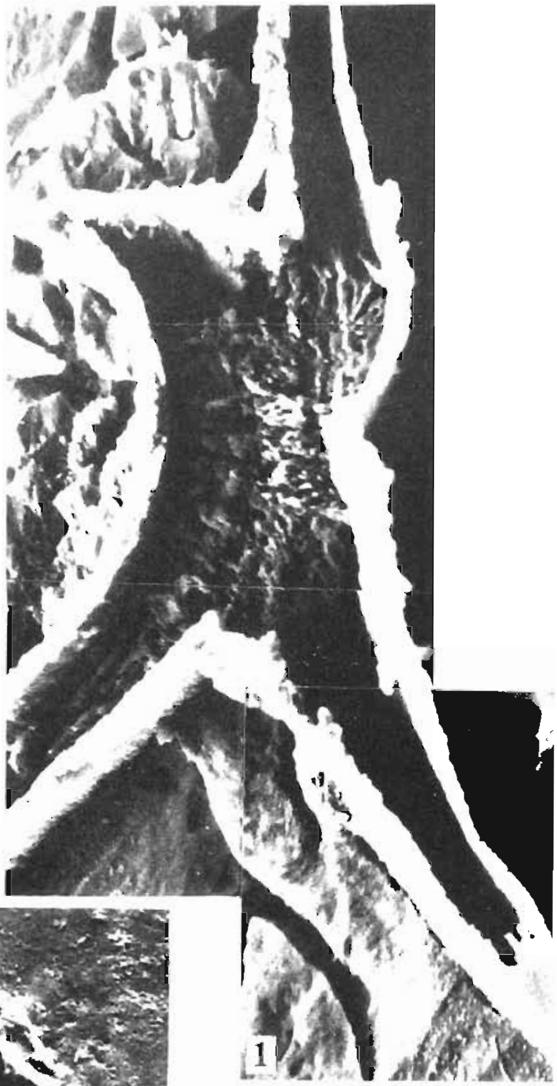
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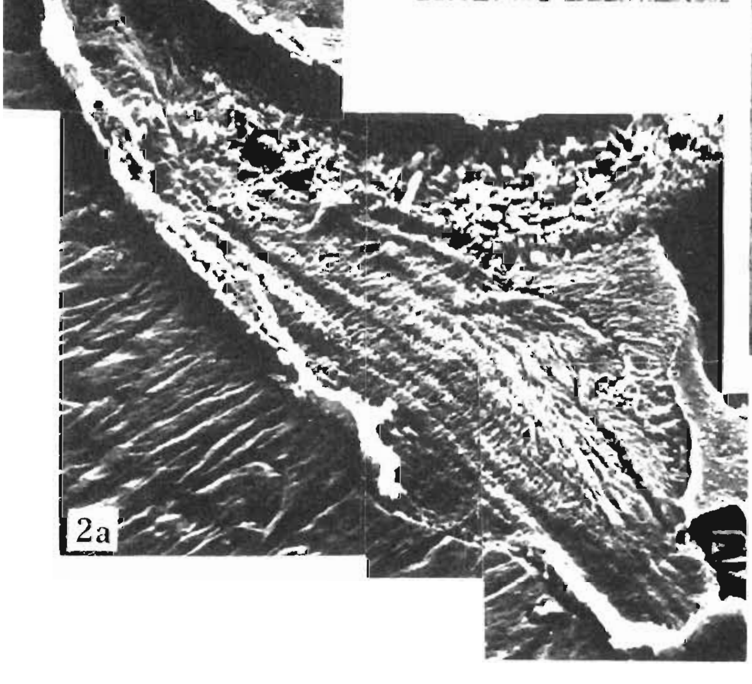
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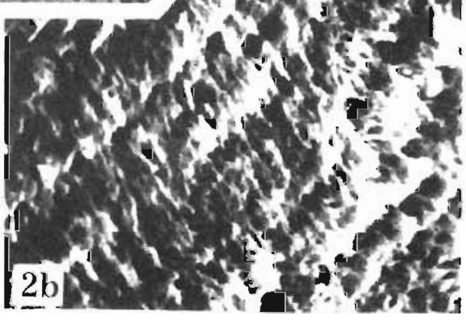
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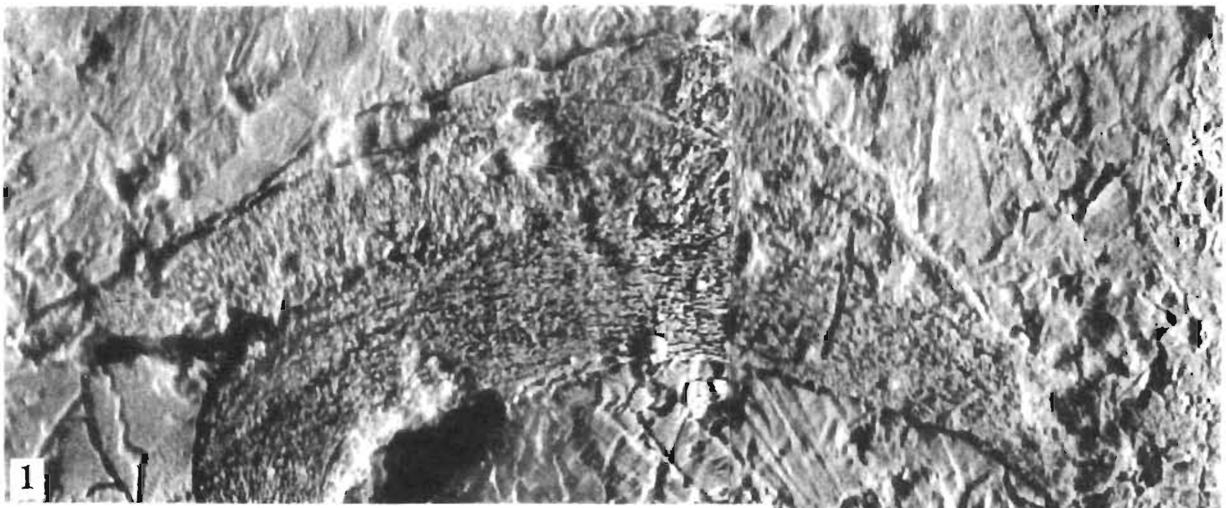

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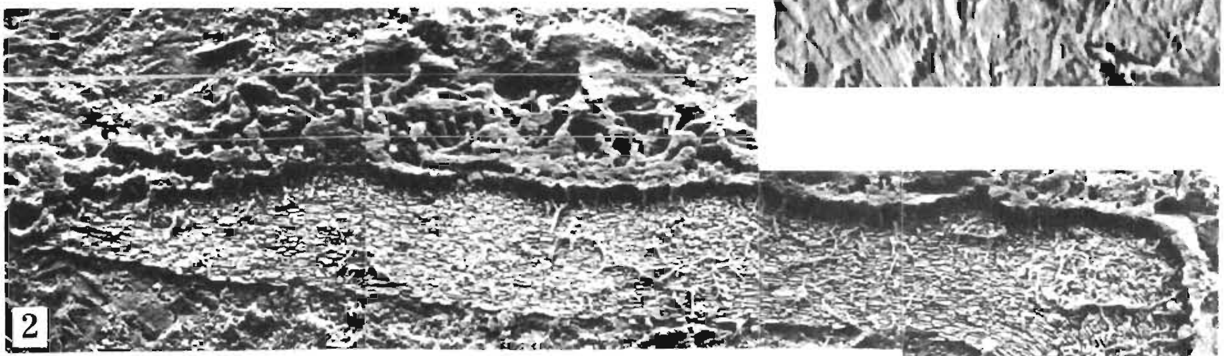

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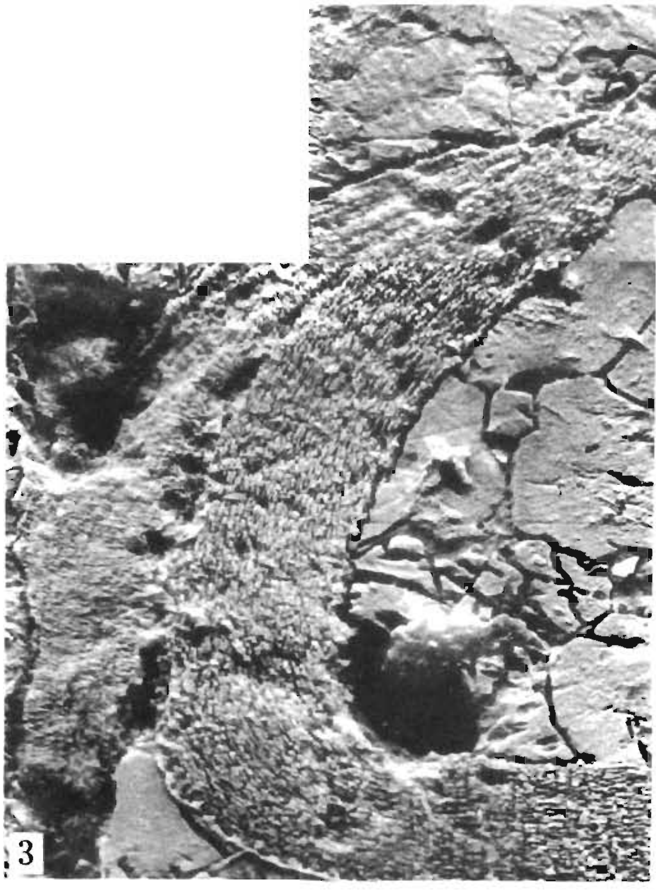

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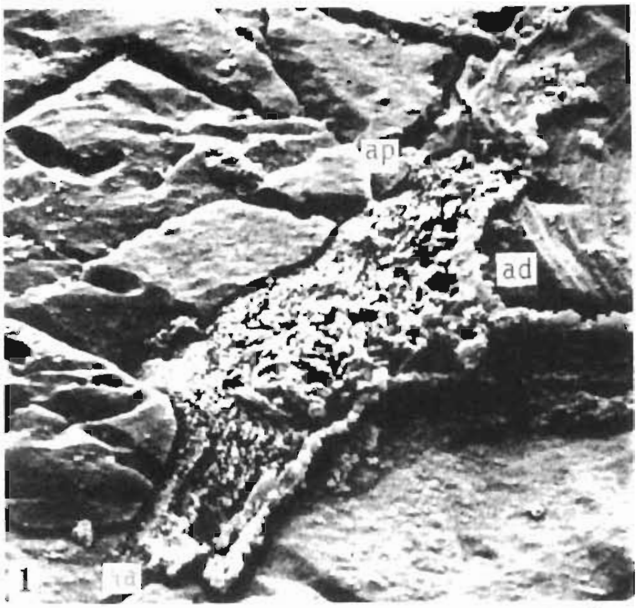
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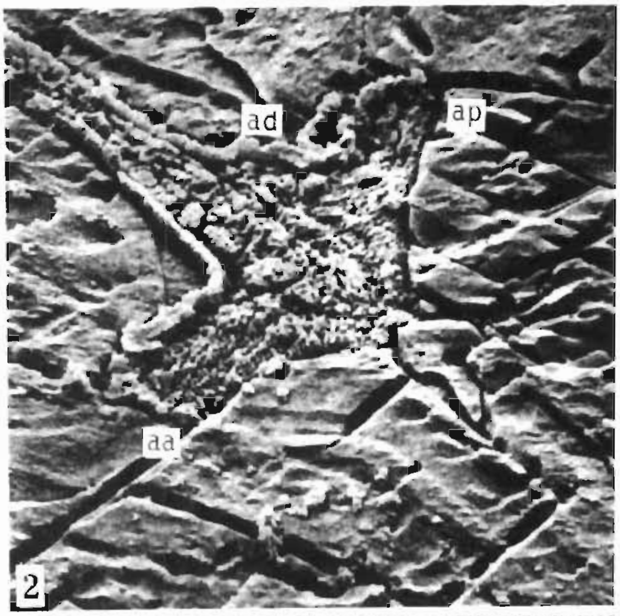
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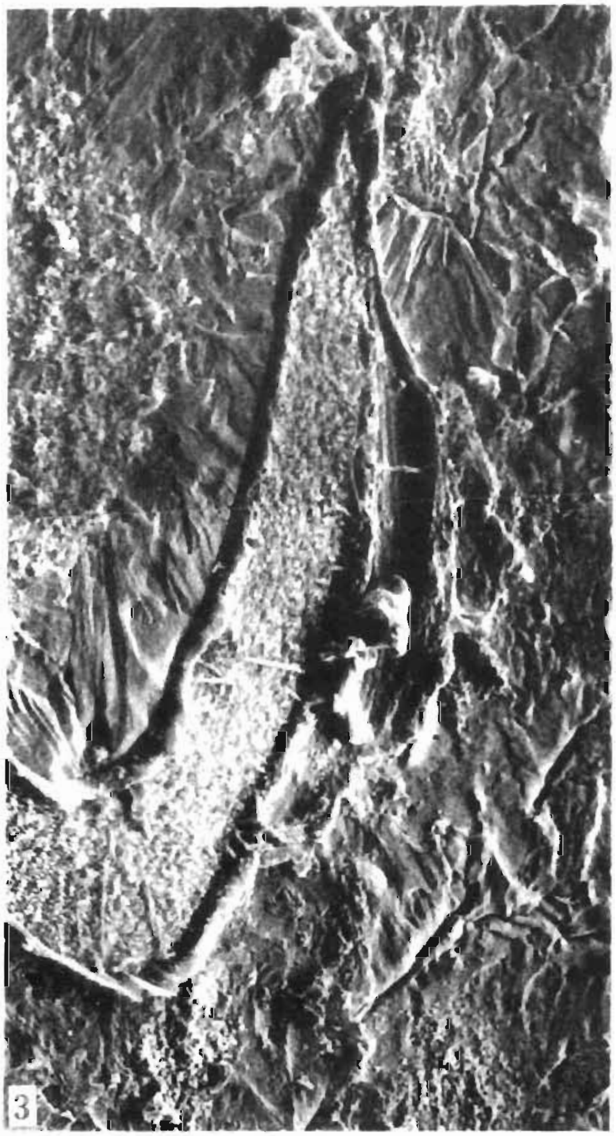
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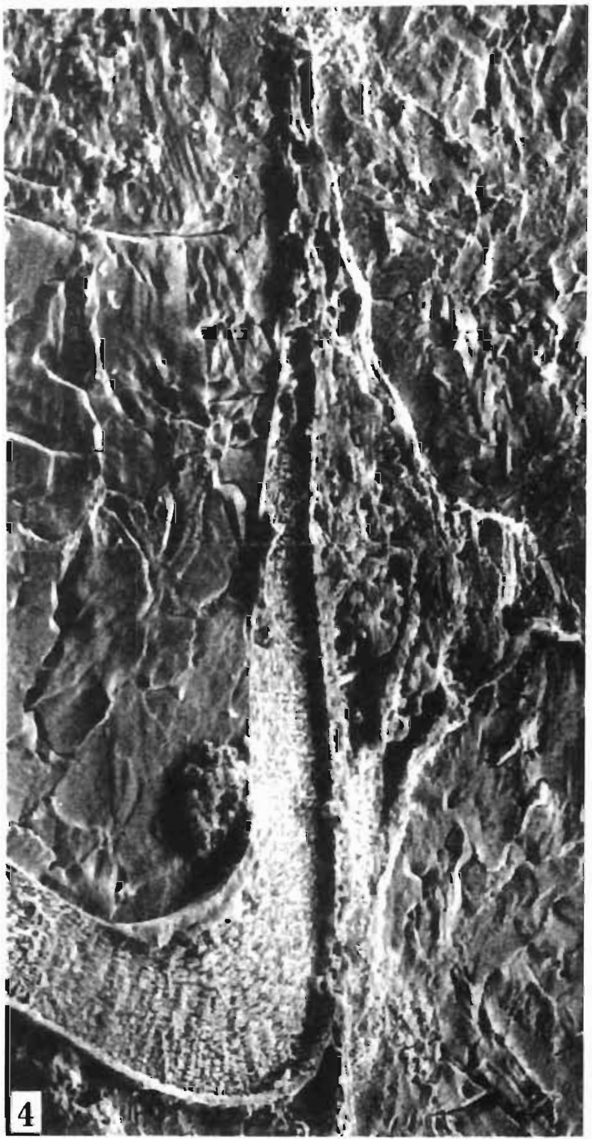
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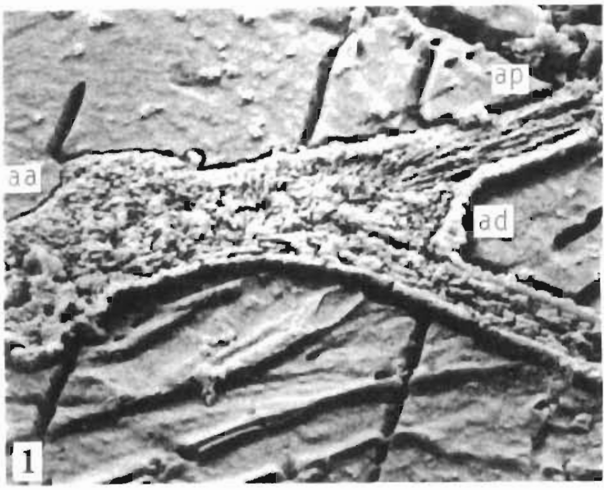

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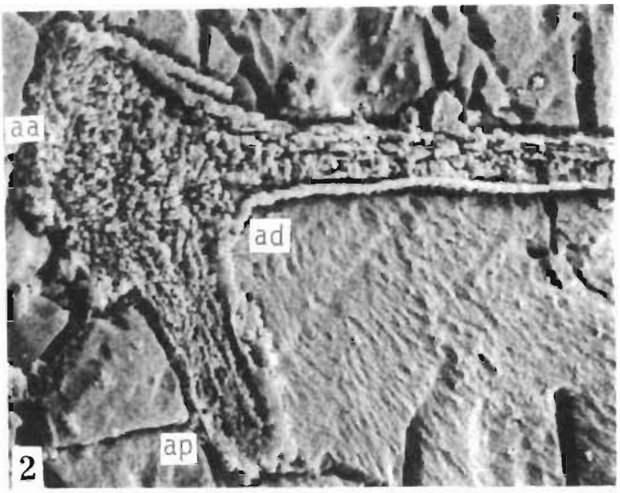

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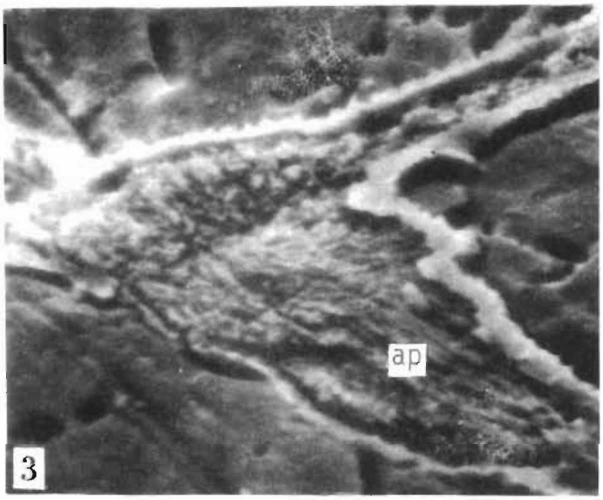

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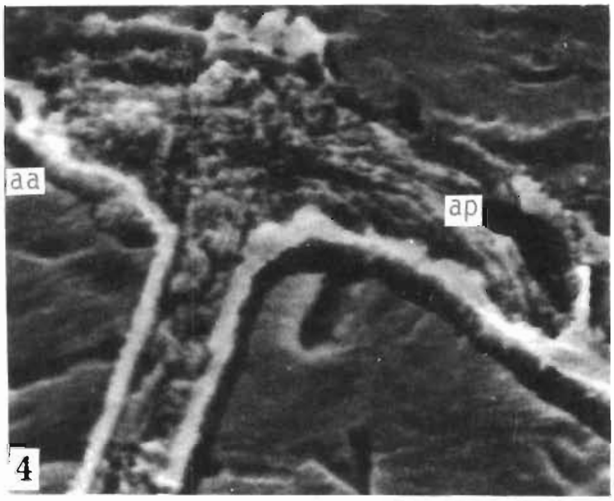

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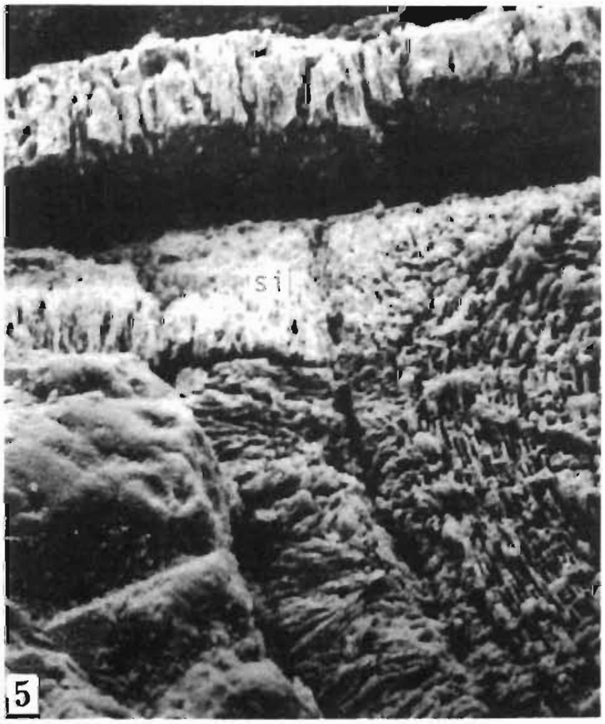

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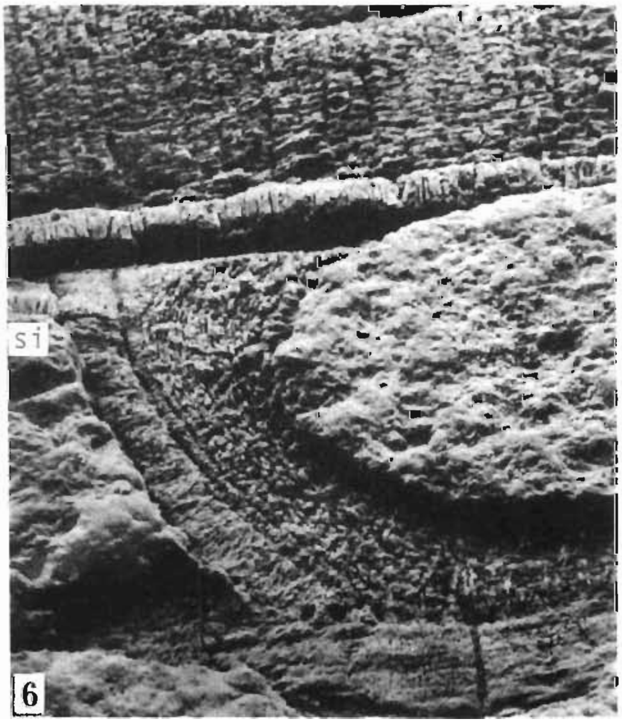

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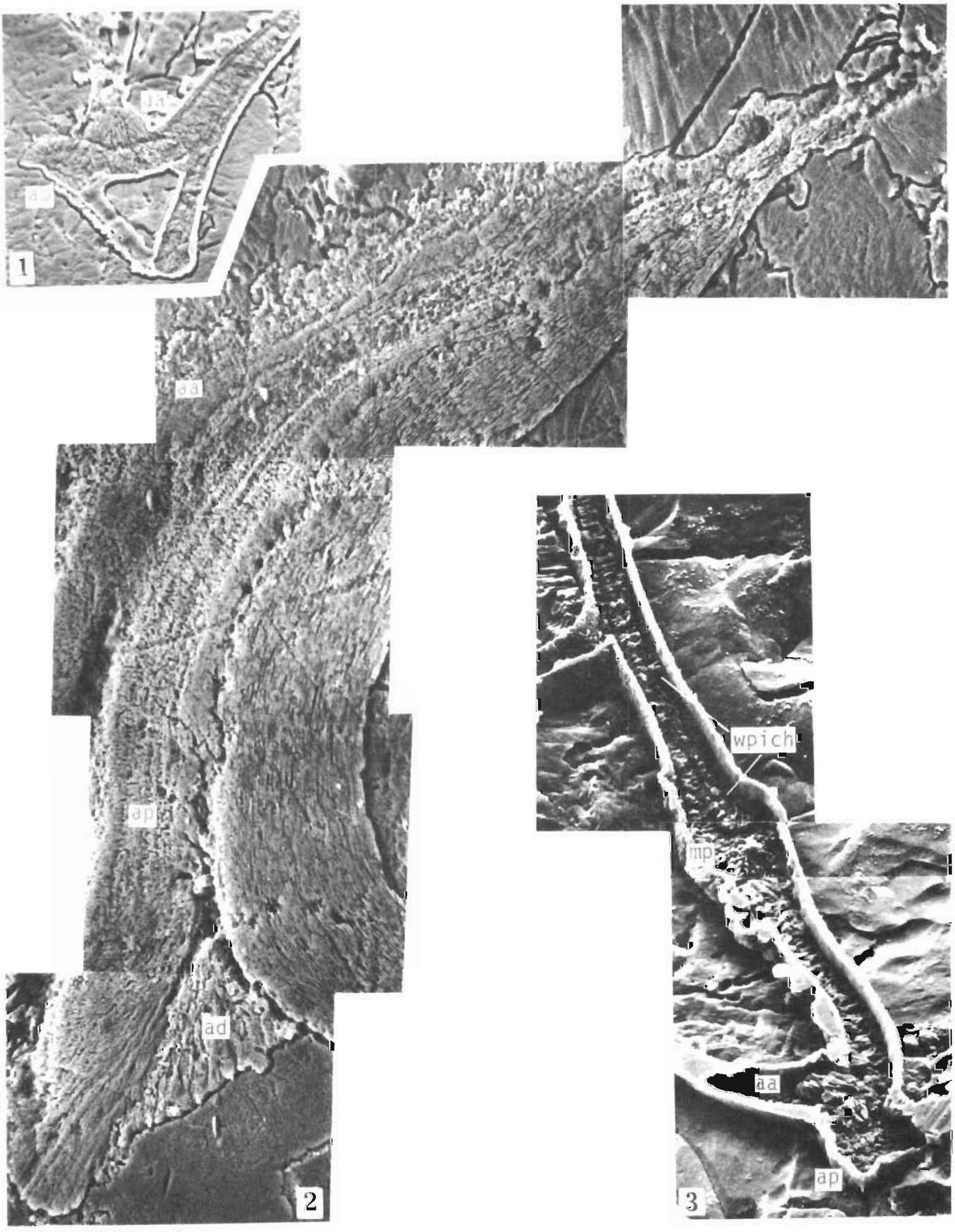
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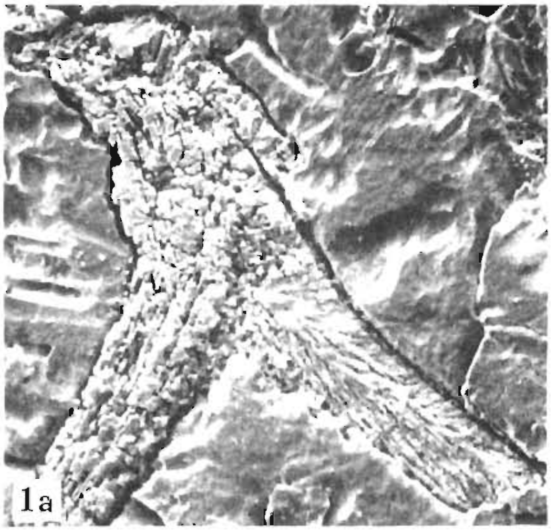
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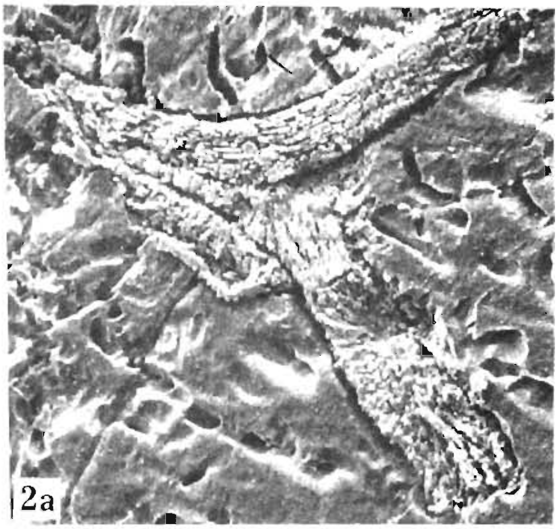
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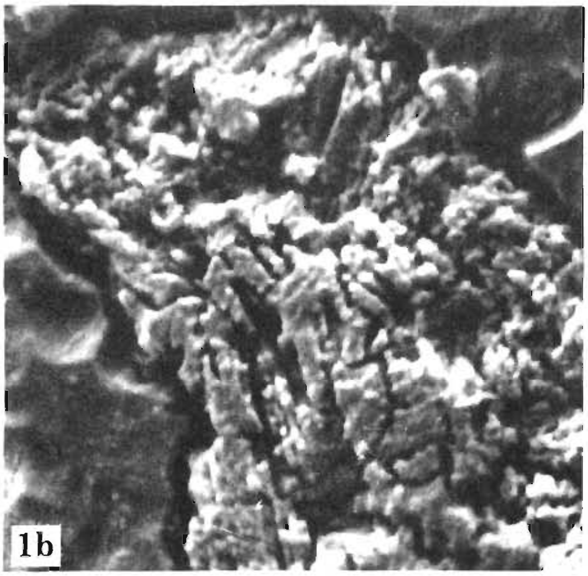
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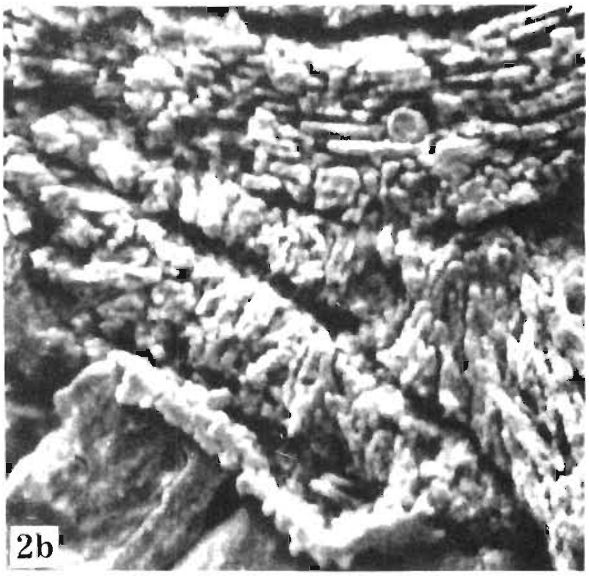
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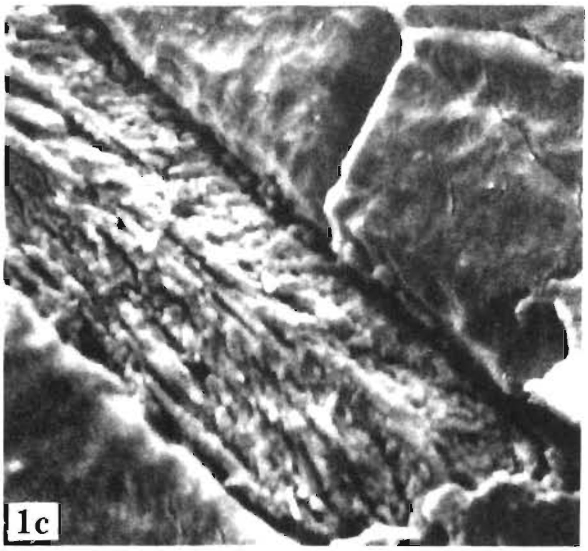
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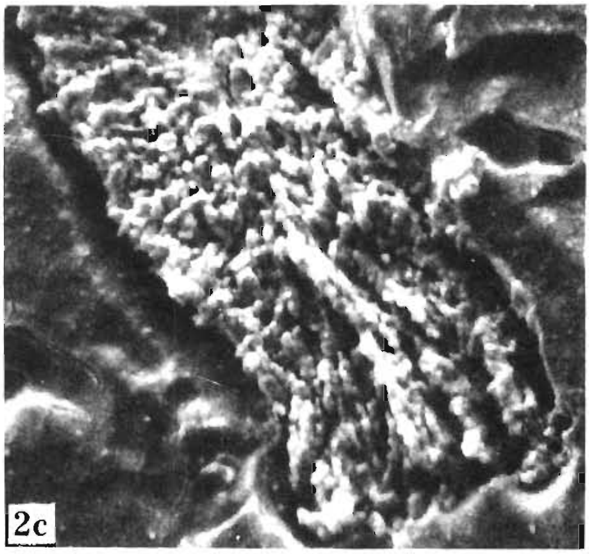
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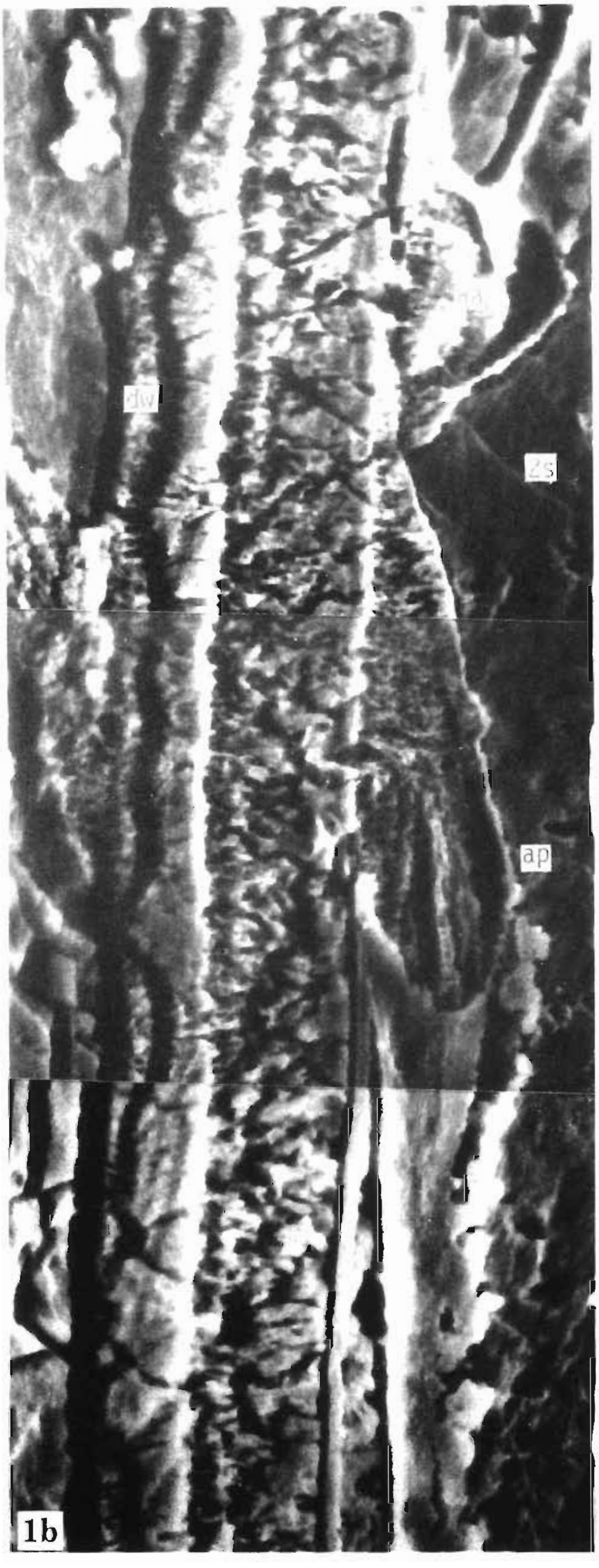
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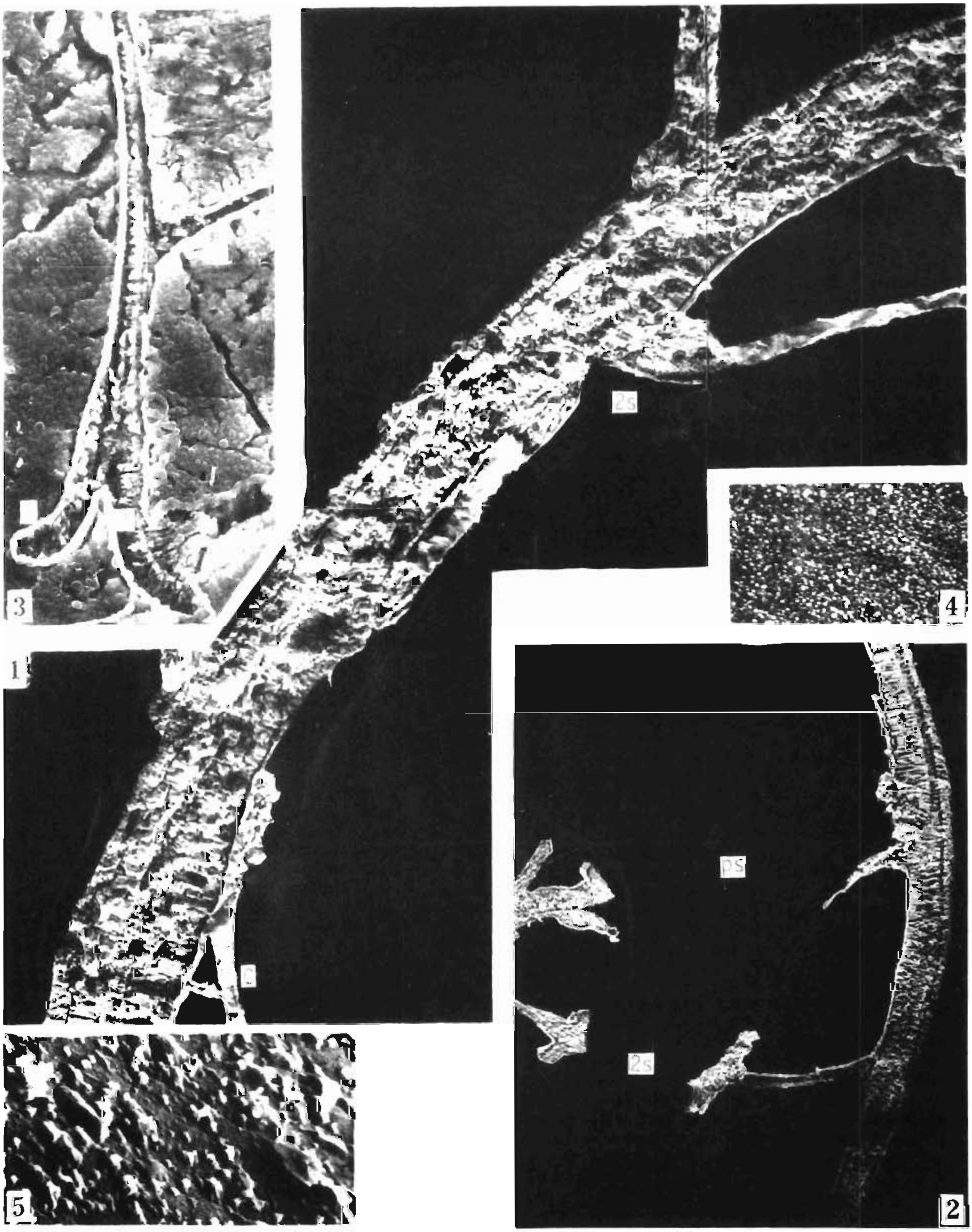
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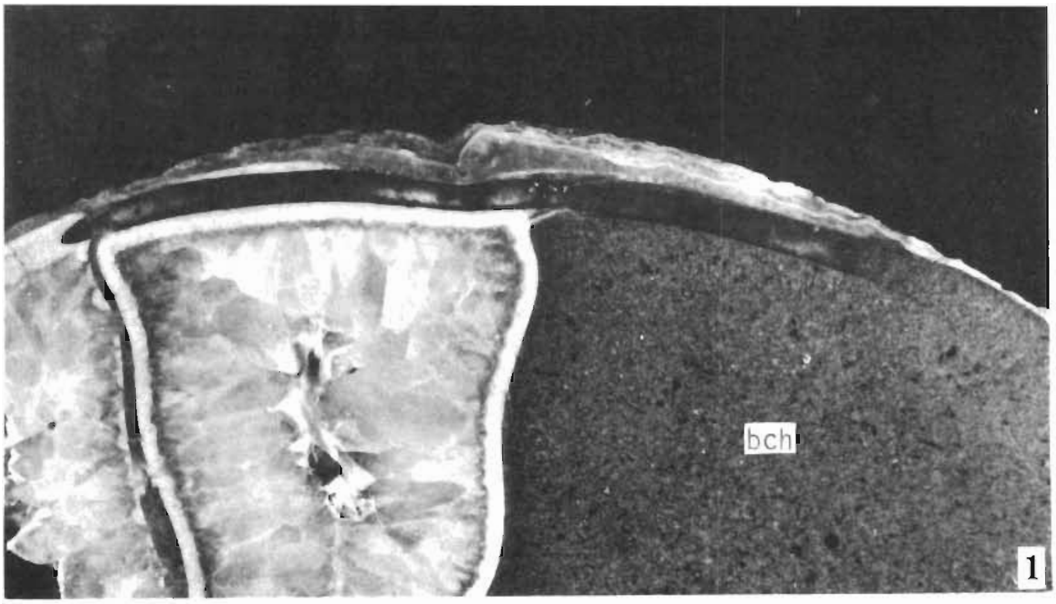
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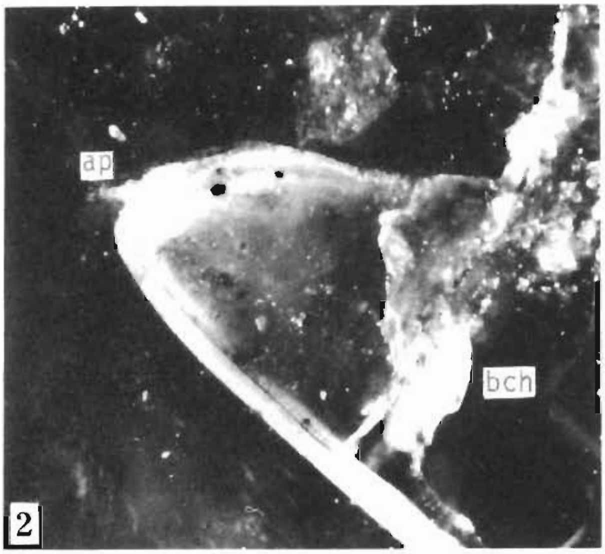
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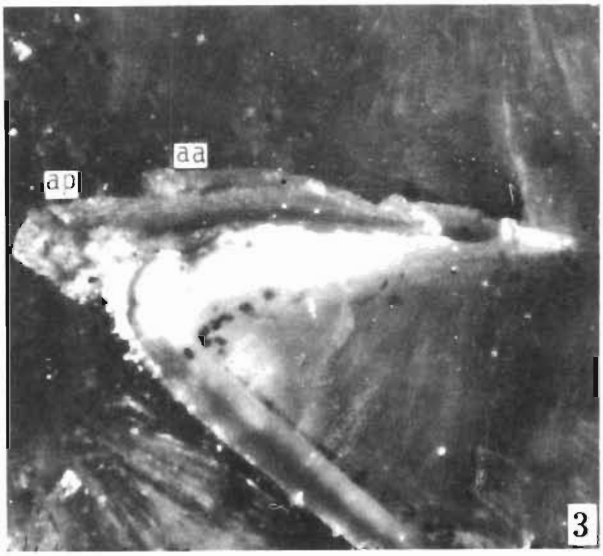
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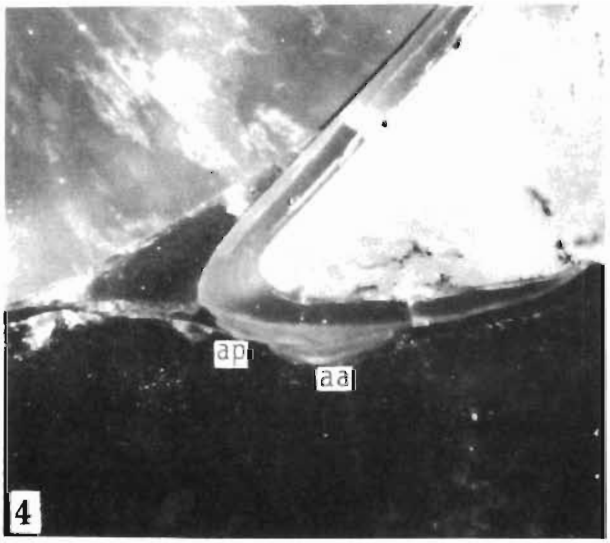
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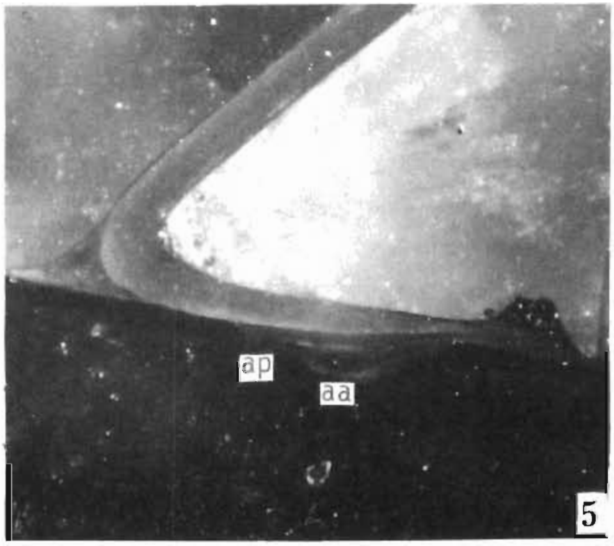
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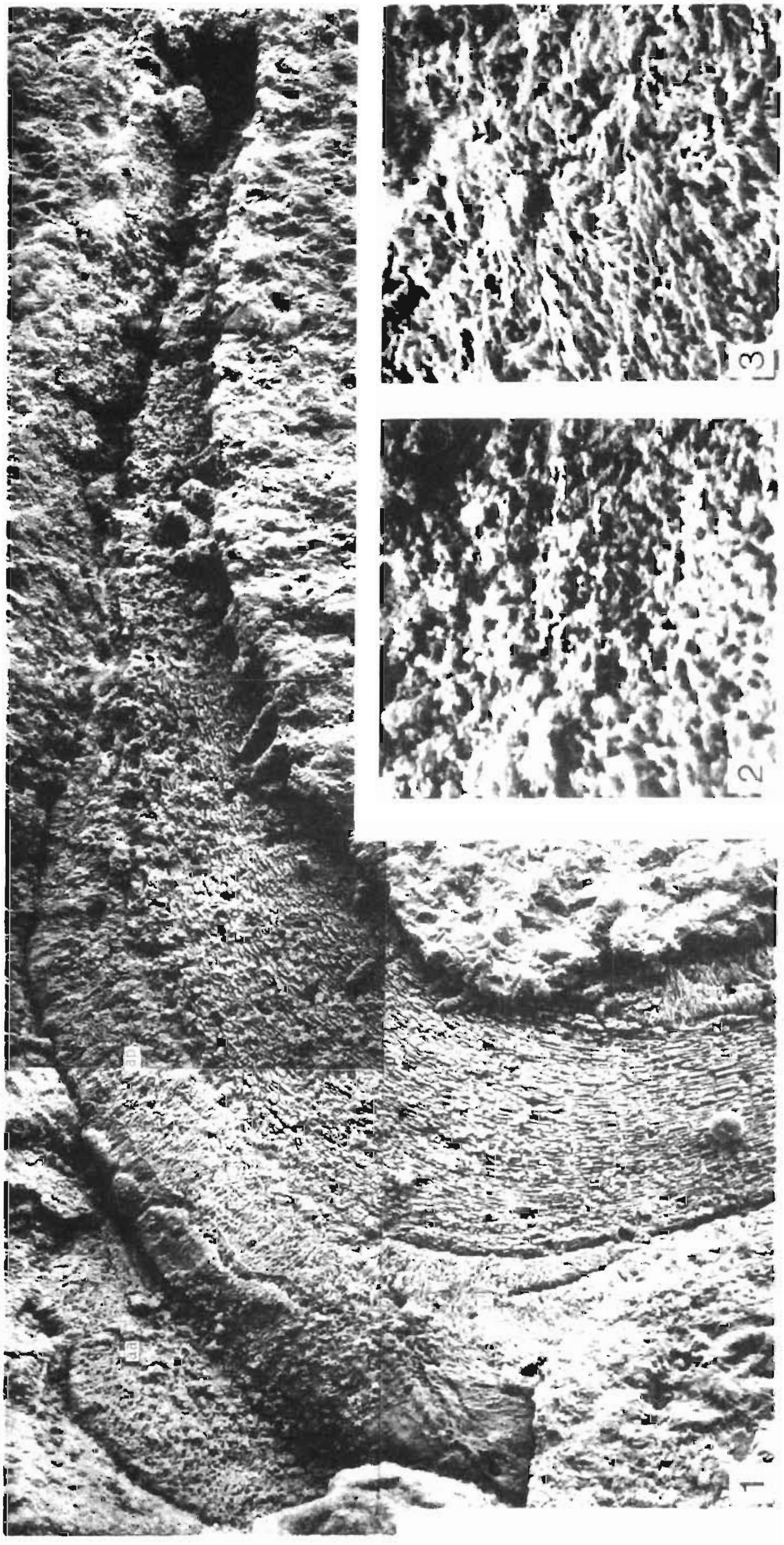
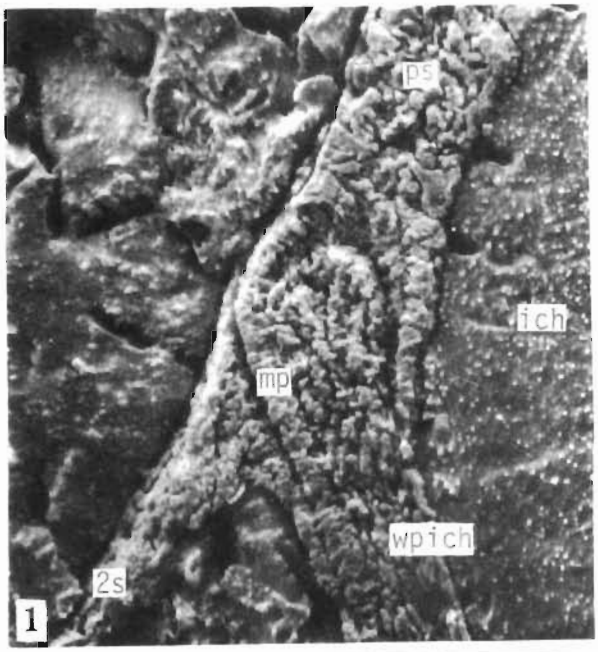


C. Kulicki: The structure and development of ammonite shell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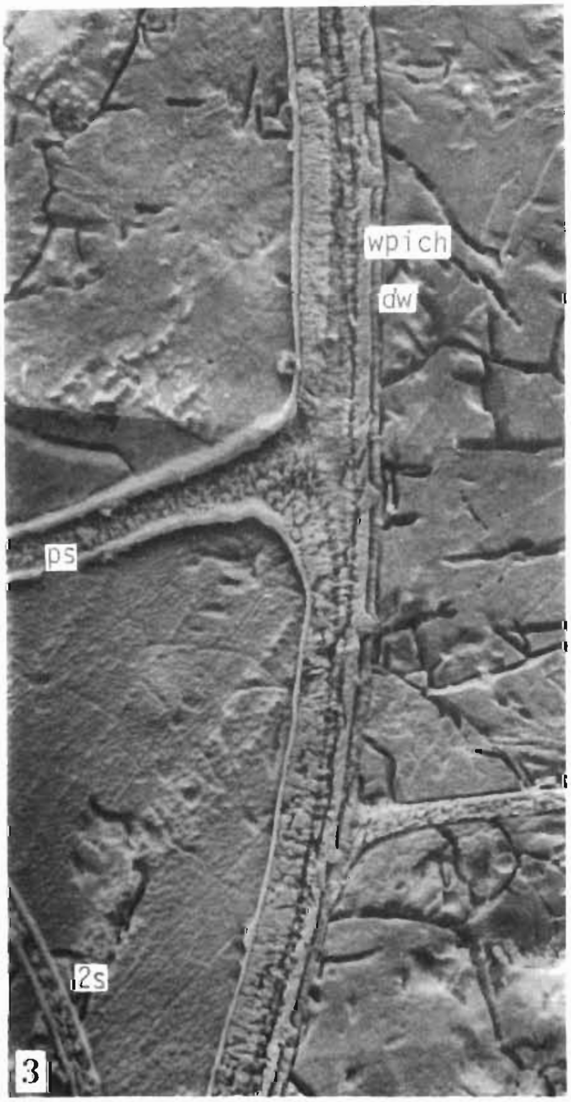
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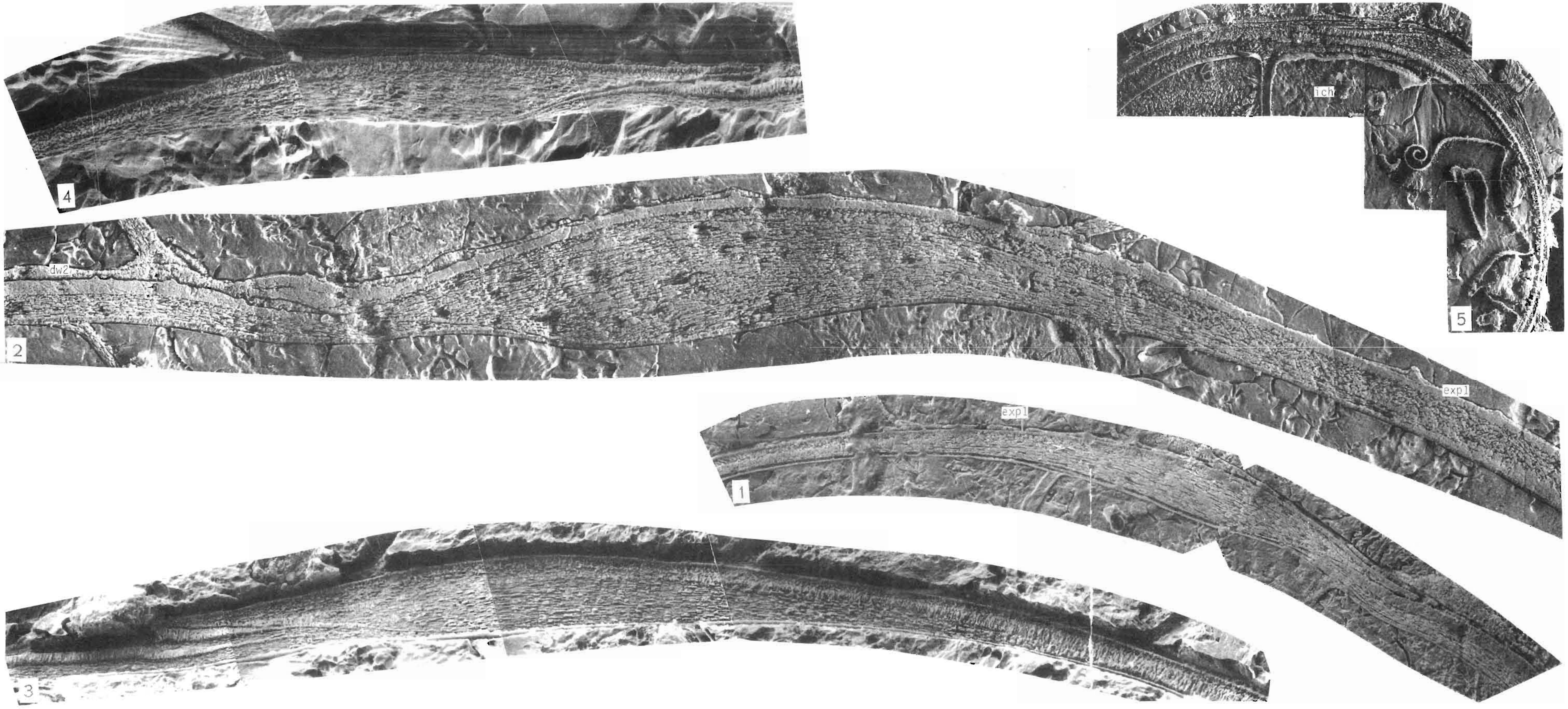
C. KULICKI: THE STRUCTURE AND DEVELOPMENT OF AMMONITE SHELL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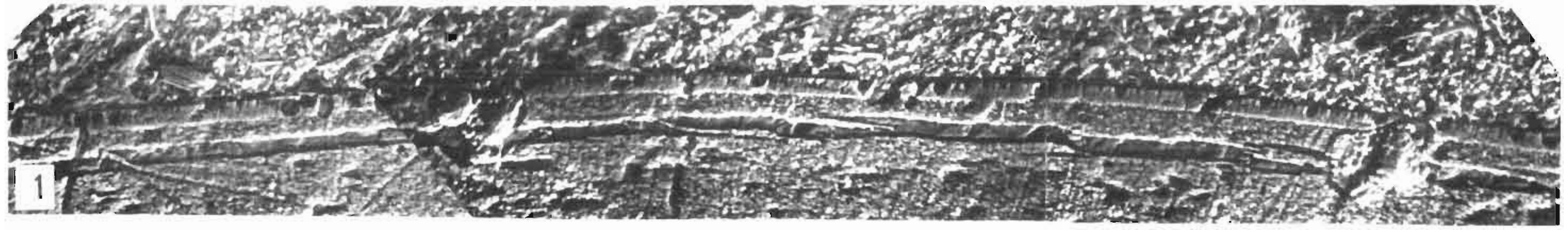
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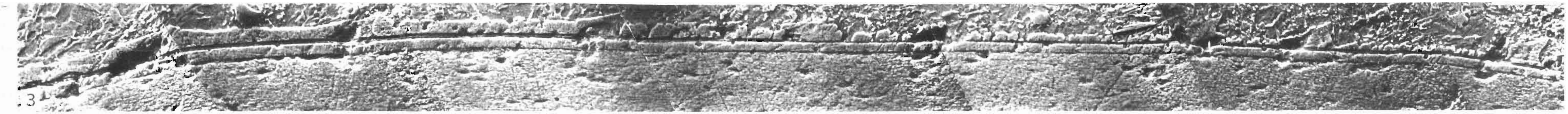
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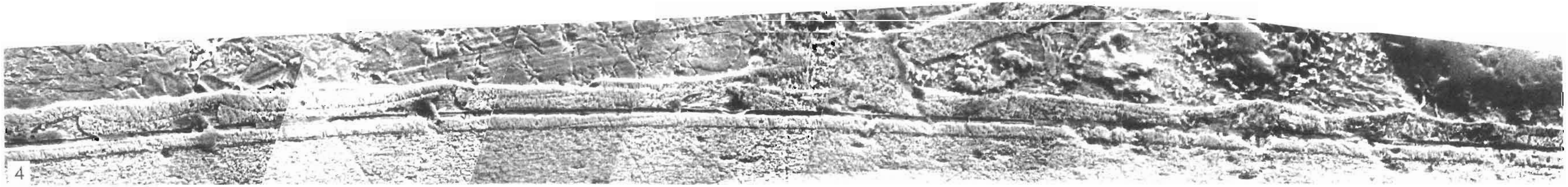
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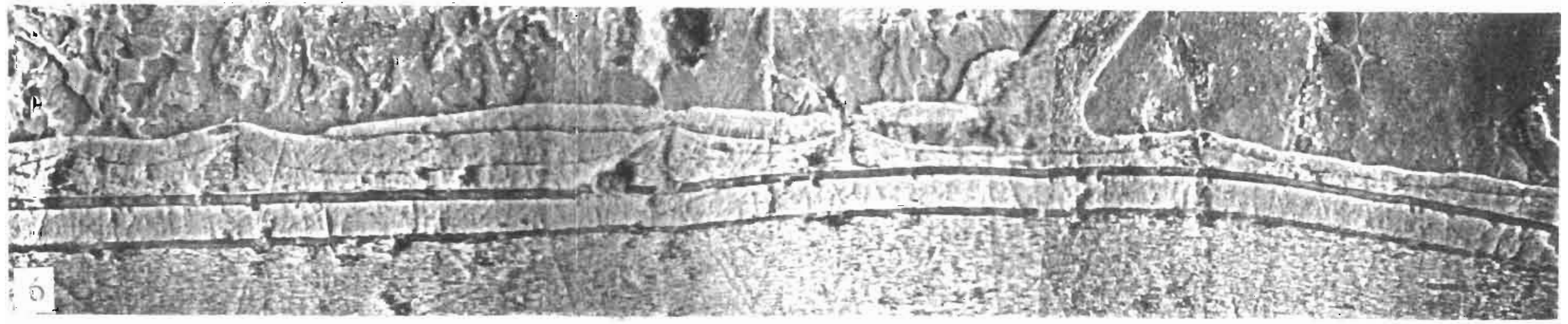
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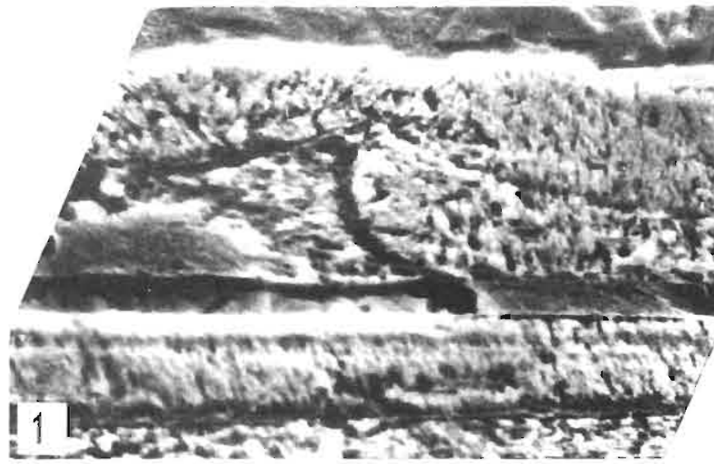
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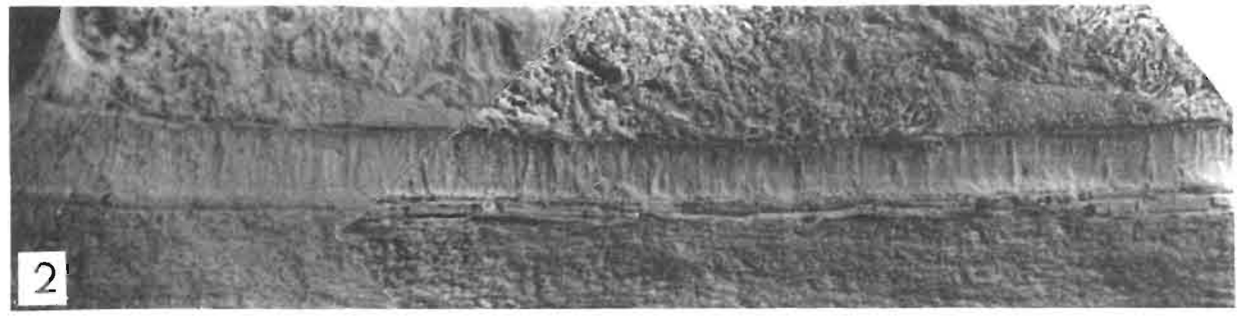
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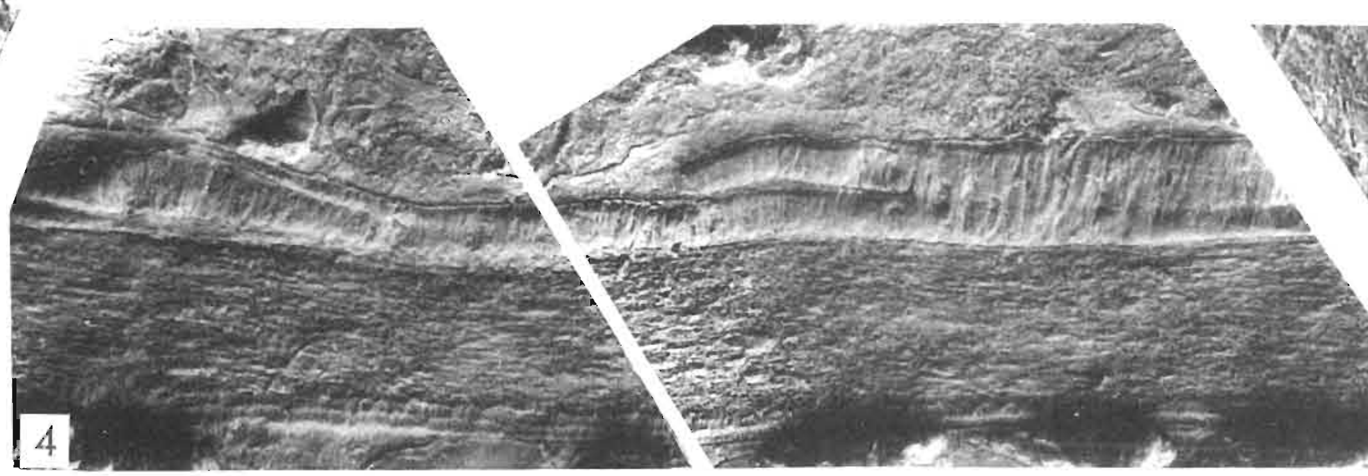
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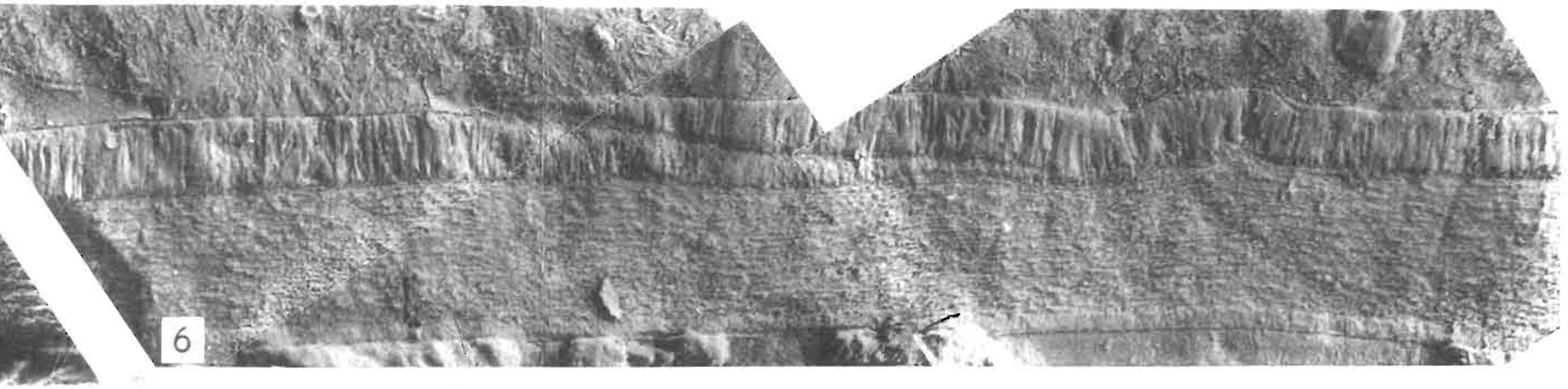
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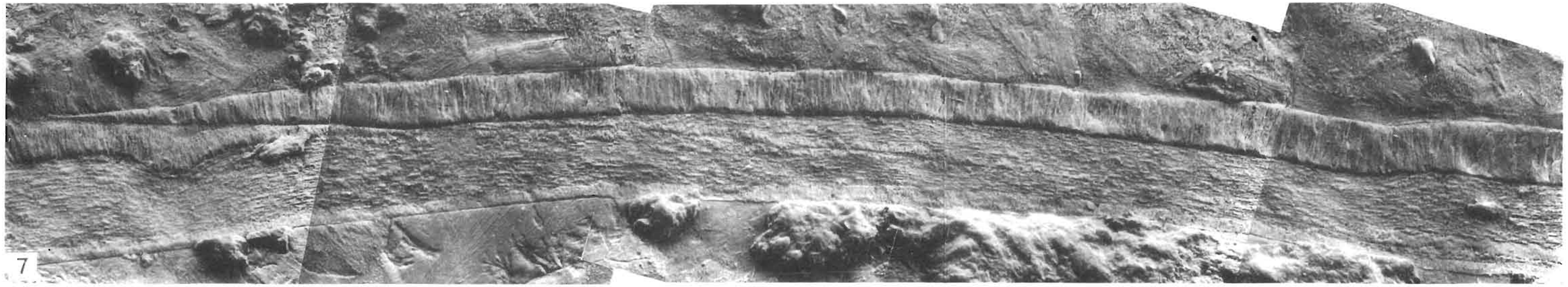
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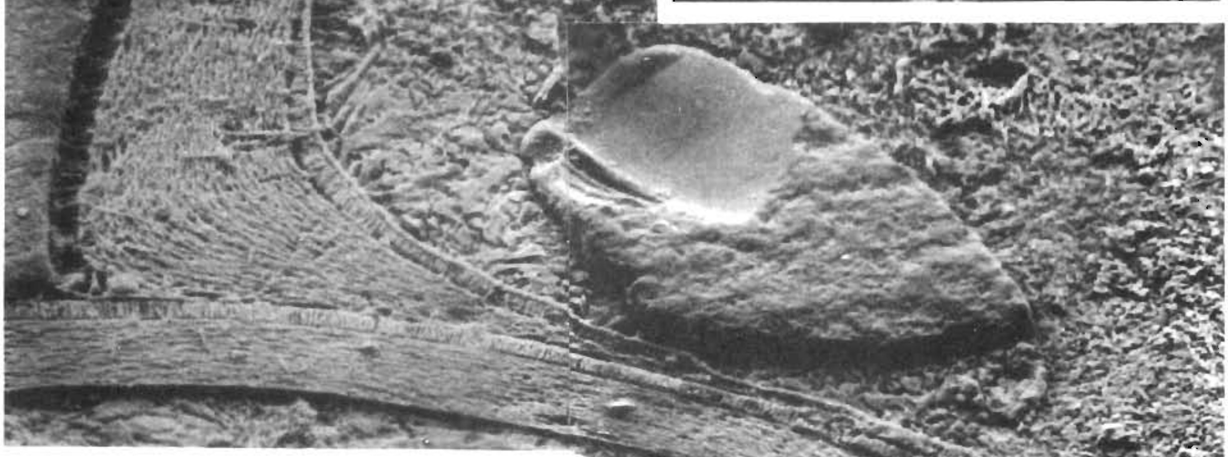
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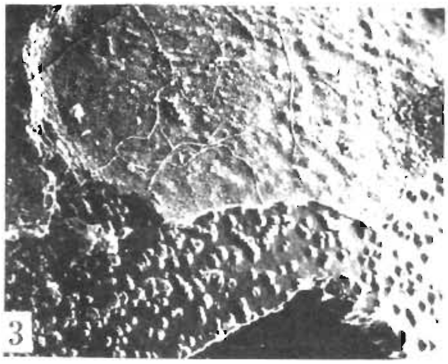
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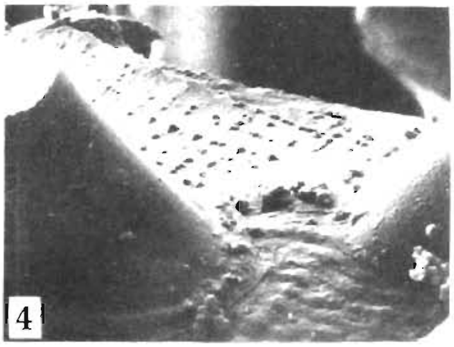
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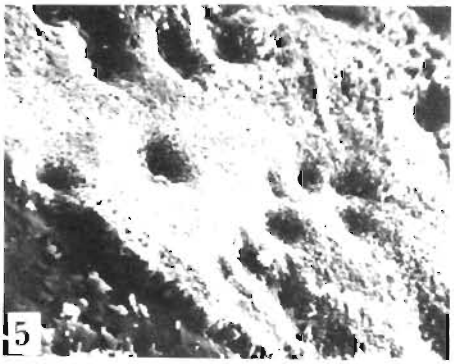
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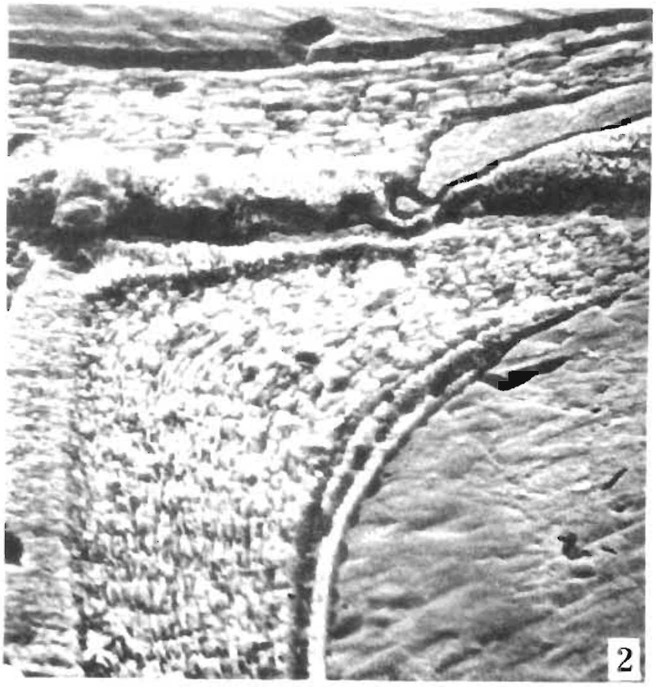
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