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ULTRASTRUCTURAL STUDIES ON CEPHALOPOD SHELLS PART II

Orthoconic Cephalopods from the Pennsylvanian Buckhorn Asphalt

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Abstract. Ultrastructures of the shell wall, septa and siphonal tube in some aragonitically preserved orthoconic cephalopods from the Pennsylvanian (Carboniferous) Buckhorn asphalt, USA, are described with the aid of scanning electron microscope studies. The structure of the shell wall and septa essentially agrees with that of the recent *Nautilus* (see Part I), whereas the structure of the siphonal tube shows the following differences: (1) the septal neck is thin and composed of a continuation of the ontogenetically older (dorsal) half of the septal nacreous layer; (2) the outer spherulitic-prismatic layer is absent in the septal neck and connecting ring; (3) the connecting ring is structurally differentiated into an outer conchiolin stratum and an inner prismatic stratum; (4) only a short distal portion of the connecting ring extends upwards into the cavity of the preceding septal neck; (5) there is no auxiliary ridge, but the connecting ring fuses to a prismatic layer on the inner face of the proximal portion of the preceding septal neck.

The following structural details are similar in the orthoconic cephalopods and *Nautilus*: the nacreous layer in the distal end of the septal neck is rich in conchiolin; this layer therefore became modified and acquired a predominantly prismatic structure; the connecting ring originates from this structurally modified, conchiolin-rich nacreous layer.

INTRODUCTION

As shown by Stehli (1956), the shells of the orthoconic cephalopods from the Pennsylvanian Buckhorn asphalt often retain their original aragonitic composition. The cameral deposits in these shells were described by Fischer and Teichert (1969), the early ontogenetic growth stages of the shell wall and septa by Erben *et al.* (1969), and the structure of the siphonal tube by Ristedt (1971). In addition, details of organic and mineral components of the shell were published by Grégoire (1959 *a*, *b*), Grégoire and Teichert (1965), and Mutvei (1969, 1970).

The present paper deals with the ultrastructures of the shell wall, septa and siphonal tube in some orthoconic cephalopods from the Pennsylvanian Buckhorn asphalt. Since the shells in these cephalopods were studied in the same manner as those of the recent *Nautilus* (see Part I), a detailed structural comparison was facilitated. The structure of the siphonal tube in the Pennsylvanian orthoconic cephalopods described here is also compared with that in some Ordovician orthocerids and actinocerids.

MATERIAL AND METHODS

The material available for the present study comprises about twenty fragmentary shells of orthoconic cephalopods from the Pennsylvanian (Carboniferous) Buckhorn asphalt, south of Sulphur, Oklahoma, USA. As pointed out by Fischer and Teichert (1969), the classification of these fragmentary specimens is difficult. They may belong to the genus *Pseudorthoceras* which has been previously identified from this locality. However, all the shells studied by me have a similar ultrastructure of the siphonal tube, which indicates that they are closely related. The diameter of the shell in these fragmentary specimens ranges from 2 to 5 mm.

The shell ultrastructures were mainly studied in vertical polished sections prepared in a similar manner to those of *Nautilus* (see Part I). The shells were embedded in a cold setting plastic, Castolite (manufactured by the Castolite Co., Woodstock, Illinois, USA), and ground vertically through the siphonal tube to a suitable level, using a fine carborundum. The sections were then polished on a polishing machine using diamond pastes of 7 and 0.25 micron grain size, and etched for 60 seconds with chromium sulphate. The etching time needed for the fossil cephalopods under discussion was considerably longer than that for *Nautilus.* The sections were mounted on preparation holders, coated with evaporated gold, and studied with a scanning electron microscope, STEREOSCAN (Cambridge Instruments Ltd.), at the Swedish Museum of Natural History, Stockholm. In addition, thin sections of two well preserved specimens were prepared for light microscope studies.

OBSERVATIONS

The shell wall. As already described by previous writers (Erben *et al.*, 1969; Ristedt, 1971), the shell wall is composed of the following three aragonitic layers: the outer prismatic layer, the nacreous layer, and the inner prismatic layer (*o.pr*, *nac*, *i.pr*, Pl. 1, Fig. 1).

The outer prismatic layer of my specimens comprises about 1/3 of the total thickness of the shell wall (*o.pr*, Pl. 1, Fig. 1). It is considerably more affected by recrystallization than the succeeding nacreous layer. The prisms are oriented roughly vertically to the shell surface (*o.pr*, Pl. 1, Fig. 2), but owing to their recrystallization, further details of their structure could not be observed (see also Ristedt, 1971, p. 172).

On the other hand, the nacreous layer is excellently preserved in several specimens. This is probably due to the occurrence of the inter-lamellar conchiolin membranes in this layer. These membranes have retained much of their original composition and structure (e.g. Mutvei, 1969, Pl. 6; Ristedt, 1971, Pl. 31, Fig. 6) and have protected the crystals against recrystallization. The nacreous crystals are 0.4—0.5 micron thick (*nac*, Pl. 1, Figs. 2, 4; Pl. 2, Fig. 1). They are composed of acicular crystallites which are about 0.1—0.2 micron in diameter and oriented at right angles to the crystal surfaces. Hence, these crystals have an internal structure identical to *Nautilus* (see Part I). At the boundary of the outer and inner prismatic layers, the outermost and innermost inter-lamellar conchiolin membranes extend into the basal parts of the adjacent prisms and then fade away (*nac*, Pl. 1, Fig. 2, 3, 4).

The inner prismatic layer compirses about 1/6 of the total thickness of the shell wall (*i.pr*, Pl. 1, Fig. 1). In most places, the recrystallization has obscured the detailed structure of this layer of the same extent as in the outer prismatic layer (*i.pr*, Pl. 1, Figs. 3, 4). However, this layer is seen to be composed of acicular crystallites in better preserved parts of the shell wall. These crystallites are about 0.2 micron in diameter and seem to consist of fused aragonitic granules (Pl. 3, Fig. 3). A similar size and composition of the acicular crystallites were also noticed in the prisms of the shell septa and septal necks in *Nautilus* (see Part I). The acicular crystallites are oriented at right angles or somewhat obliquely to the inner face of the shell wall (*i.pr*, Pl. 3, Figs. 1, 2).

The shell septum proper. The periphery of the septum is somewhat thinner than the shell wall. It increases gradually in thickness in the central direction and attains about the same thickness as the shell wall at the siphonal tube (Pl. 6, Fig. 1).

The dorsal (convex, adapical) and the ventral (concave, adoral) faces of the septum are each covered by a thin conchiolin layer (see also Erben *et al.*, 1969; Ristedt, 1971). As seen in a vertical section, the dorsal conchiolin layer is about 0.6 micron thick (*d.c.l*, Pl. 8, Fig. 3).

Each septum proper consists of three aragonitic layers which correspond to those in *Nautilus* (see Part I), i.e. the dorsal spherulitic-prismatic layer, the nacreous layer, and the ventral prismatic layer.

The spherulitic-prismatic layer is found only in the peripheral portion of the septum, adjacent to the shell wall, where it is comparatavely thick (*sph.pr*, Pl. 3, Figs. 1, 2; "Zwickelfüllung" in Ristedt, 1971). It consists of small spherulites and prisms, the latter without a preferred orientation. Both the spherulites and prisms are made up of acicular crystallites which have a diameter of 0.1—0.2 micron (*sph.pr*, Pl. 3, Figs. 2, 4). The spherulitic-prismatic layer decreases rapidly in thickness and disappears in the central direction. Consequently, this layer is absent in the rest of the septum and the dorsal conchiolin layer of the septum is immediately succeeded by the nacreous layer. The corresponding layer in *Nautilus* displays a similar development (see Part I).

As in *Nautilus* (Part I), the septal nacreous layer commences with a dorsal, structurally modified stratum in which the inter-lamellar conchiolin membranes are fairly thick and have an undulating course. These membranes therefore coalesce partially with each other, forming a meshwork (*d.nac.h*, Pl. 3, Fig. 4; Pl. 5, Fig. 2; Pl. 8, Fig. 3). In the remaining part of the septal nacreous layer, the inter-lamellar conchiolin membranes are thin and regularly spaced. Most of the nacreous crystals have the same thickness as those in the shell wall (*nac*, Pl. 4, Fig. 3), but in places they are considerably thinner (Pl. 2, Figs. 2, 3). As measured on the horizontal fracture planes, their maximum diameter is about 20 microns (Pl. 2, Fig. 4). The nacreous crystals are composed of typical, vertically oriented, acicular crystallites. Rows of these crystallites form parallel mineral laths (Pl. 2, Fig. 4; see also Mutvei, 1970, 1972).

The prismatic layer is found on the ventral face of the central part of the septum proper, adjacent to the septal neck (*pr,* Fig. 1 *A*; Pl. 7, Fig. 2; Pl. 11, Fig. 1). It decreases in thickness in the peripheral direction and seems to disappear. However, its absence in the peripheral parts of the septum cannot be definitely established by studies of vertical sections, because, as in *Nautilus*, the prisms in this layer might have been separated by wide interspaces. The prismatic layer forms a prominent ridge which encircles the entrance to the septal neck (*pr*, Pl. 4, Fig. 1; Pl. 5, Fig. 1). Most of this ridge is composed of a compact prismatic layer in which the acicular crystallites can be clearly distinguished. These crystallites are about 0.1—0.2 micron in diameter, and they are oriented vertically or somewhat obliquely to the ventral septal face (*pr*, Pl. 4, Figs. 2, 3; Pl. 5, Figs. 1, 2). As those in the inner prismatic layer of the shell wall, the crystallites seem to be composed of fused aragonitic granules (Pl. 4, Fig. 4). In agreement with *Nautilus* (see Part I), the basal portions of the prisms are crossed by numerous, parallel conchiolin membranes which in places fade away (Pl. 4, Figs. 2, 3; Pl. 5, Fig. 2). In vertical sections, these membranes have the same appearence as the inter-lamellar conchiolin membranes in the adjacent nacreous layer. In addition, zones of parallel conchiolin membranes occur in the inner parts of the prismatic ridge (*pr*, Pl. 4, Fig. 1; Pl. 5, Fig. 1). The outer parts of the prismatic ridge are porous. The prisms are here separated by interspaces and composed of bundles of radiating, acicular crystallites (*pr*, Pl. 4, Fig. 1; Pl. 5, Fig. 1).

The septal neck. The septal nacreous layer rapidly decreases in thickness on passing into the septal neck. This is due to the fact that the ontogenetically younger (ventral) half of the septal nacreous layer is wedged out. In addition, the spherulitic-prismatic layer, which in *Nautilus* constitutes a large part of the septal neck (see Part I), is here absent. Consequently, the septal neck consists solely of a continuation of the ontogenetically older (dorsal) half of the septal nacreous layer. The surface of the septal neck is covered by a thin conchiolin layer, homologous to that on the dorsal septal face (*d.c.l*, Fig. 1 *B*, Pl. 8, Fig. 2). The inner face of the most proximal portion of the septal neck is invested by a thin prismatic layer which continues from the prismatic ridge on the ventral septal face (*pr.*, Fig. 1 *A*; Pl. 7, Fig. 2; Pl. 11, Fig. 1).

In the proximal portion of the septal neck, the nacreous layer has the same, typical structure as that in the septum. However, further distally, the typical nacreous layer gradually thins out and is replaced by a structurally modified nacreous layer (*nac*, *m.nac*, Fig. 1 *A*; Pl. 7, Fig. 1; Pl. 11, Fig. 1; "Siphowulst" in Ristedt, 1971). As seen in thin sections, the latter layer is very rich in conchiolin over its entire extension, and the boundary of the typical nacreous layer is therefore distinct (Pl. 6, Figs. 1, 2, 3). A similar sharp boundary between these two layers is also seen in most vertical sections, studied with SEM. The structural relationships between the typical and structurally modified nacreous layers could be studied in detail only

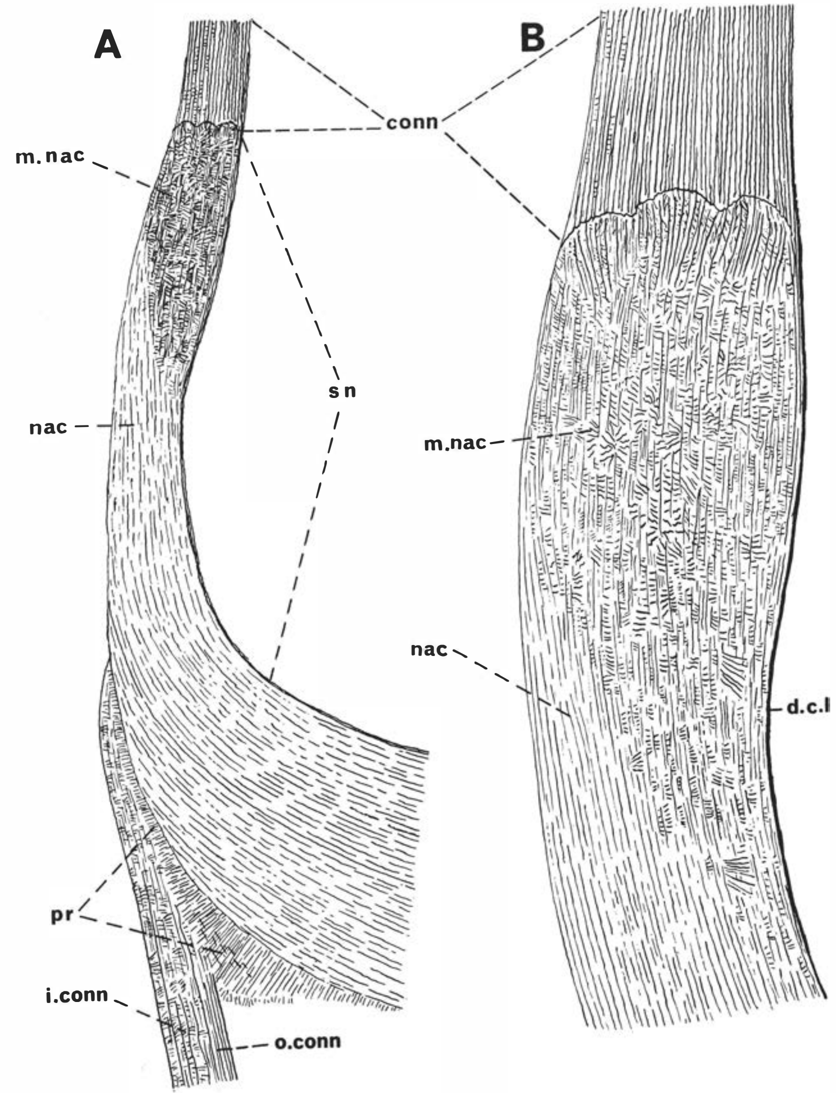

Fig. 1. A, schematic vertical section of a septal neck, parts of septum proper, and parts of the contiguous and succeeding connecting rings. *B*, detail of the distal portion of the same septal neck to show the transformation of the typical nacreous layer into the structurally modified nacreous layer, and its relationship to the contiguous connecting ring. *conn*, connecting rings; *d.c.l*, conchiolin layer on the outer surface of the septal neck; *i.conn*, *o.conn*, inner and outer stratum of the connecting ring, respectively; *m.nac*, structurally modified nacreous layer; *nac*, typical nacreous layer; *pr*, prismatic layer; *s.n*, septal neck.

in one of my vertical sections, in which the shell structure is exceptionally well preserved. The electron micrographs taken of this septal neck are reproduced in the following three plates: the proximal portion in Pl. 8, Fig. 1, the next following distal portion in Pl. 9, Fig. 1, and the most distal portion with the contiguous part of the connecting ring in Pl. 10, Fig. 1. Already in the proximal portion of the septal neck, it may be clearly seen that the nacreous lamellae in the outer part of the typical nacreous layer are replaced by prismatic lamellae (right hand side in Pl. 8, Fig. 1). These prismatic lamellae are separated by conchiolin membranes which are continuations of the inter-lamellar conchiolin membranes in the adjacent, typical nacreous lamellae. Further distally, most of the nacreous layer has acquired a prismatic structure. However, a thin layer of typical nacre remains in the inner part of the septal neck (left hand side in Pl. 9, Fig. 1). Details of the structural transformation from the nacreous lamellae into the prismatic lamellae are shown in the electronmicrograph in Pl. 9, Fig. 3. The acicular crystallites in the prisms have a highly variable, radial arrangement and they are embedded in a rich conchiolin matrix (Pl. 9, Fig. 2). The prisms are crossed by zones of subparallel conchiolin membranes in several places. In the most distal portion of the septal neck the entire nacreous layer has acquired a prismatic structure (*m.nac*, Fig. 1 *A*, *B*; Pl. 10, Fig. 1). In places, even typical spherulites occur (Pl. 10, Fig. 2). Nevertheless, numerous, parallel conchiolin membranes, corresponding to the inter-lamellar conchiolin membranes of the typical nacreous layer still remain.

The distal end of the septal neck forms a distinct boundary with the contiguous connecting ring (*m.nac*, *conn*, Pl. 10, Fig. 1). The distinctness of this boundary seems to have been secondarily accentuated by the fossilization processes. Thus, in the septal neck, which has been non-permeable in life, the conchiolin membranes have been embedded in the mineral substance, and therefore they were less altered than those in the permeable connecting ring. In view of the conditions in *Nautilus* (see Pl. 25 in Part I), it is quite probable that the conchiolin membranes in the septal neck originally continued directly into the connecting ring where they have become uncalcified or only partly calcified (see below).

The transformation of the typical nacreous layer into the structurally modified nacreous layer in the septal neck is also demonstrated in another vertical section (Pl. 10, Fig. 3). The prismatic, and partially spherulitic, structure of the structurally modified nacreous layer in the distal end of the septal neck is illustrated on vertical and horizontal fracture planes in Pl. 11, Figs. 2, 3. As seen on these fracture planes, the prisms are separated by wide interspaces which are occupied by conchiolin.

As described in Part I, the nacreous layer in the distal portion of the septal neck of *Nautilus* is also rich in conchiolin and most of its crystals acquire a prismatic structure comparable to that of the orthoconic cephalopods.

The connecting ring. As far as can be seen, the connecting ring originates from the structurally modified, conchiolin-rich, nacreous layer in the distal portion of the contiguous septal neck (see above). It has about the same thickness as the septal neck. It is composed of two, structurally different strata. The outer stratum, which comprises about half of the total thickness of the connecting ring, consists of uncalcified conchiolin membranes which still can be distinguished, even if somewhat indistinctly, in the vertical sections (*o.conn*, Pl. 12, Fig. 3). The inner stratum of the connecting ring, on the other hand, has a prismatic structure (*i.conn*, Pl. 12, Fig. 3). Nevertheless, the latter stratum has probably been porous, and its calcification has not affected the permeability of the connecting ring. It is composed of prismatic lamellae of varying thickness which consist of acicular crystallites, about 0.2 micron in diameter (Pl. 12, Fig. 4). These crystallites are oriented at right angles or somewhat obliquely to the inner face of the connecting ring. The consecutive prismatic lamellae are separated by thick conchiolin membranes, and thinner, parallel membranes within the prismatic lamellae seem to occur. The boundary between the outer and inner strata of the connecting ring is indistinct (*o.conn*, *i.conn*, Pl. 12, Fig. 3).

In the distal part of the connecting ring, adjacent to the precedent septal neck, the inner prismatic stratum increases in thickness in relation to the outer conchiolin stratum (*i.conn*, *o.conn*, Fig. 1 *A*; Pl. 12, Fig. 1). Therefore, the connecting ring acquires here a predominantly prismatic structure (Pl. 12, Fig. 2).

Only a short distal portion of the connecting ring extends into the cavity of the preceding septal neck. This portion is fused to the prismatic ridge on the ventral septal face and to the thin prismatic layer which invests the inner face of the proximal portion of the septal neck (*conn*, *pr*, Fig. 1 *A*; Pl. 11, Fig. 1). The auxiliary ridge, which in *Nautilus* acts as an intermediary for a firm fusion between the connecting ring and the septal neck (see Part I), is here absent.

DISCUSSION

Comparisons with Nautilus. The ultrastructure of the shell wall in the orthoconic cephalopods, described above, is essentially as in *Nautilus* (see also Erben *et al.*, 1969; Ristedt, 1971). The only difference worth mentioning, is that the outer prismatic layer is composed throughout of prisms, whereas in *Nautilus* it is usually differentiated into an outer spherulitic and an inner prismatic lamella. However, the outer spherulitic lamella is absent in the early growth stages of the shell wall in *Nautilus.*

The ultrastructure of the septum proper in the orthoconic cephalopods shows close agreement with that in *Nautilus.* (1) The peripheral, dorsal part of the septum, adjacent to the shell wall, is composed of a thick spherulitic-prismatic layer which is absent in the remaining dorsal parts of the septum. This layer is only exceptionally found in *Nautilus* in other than peripheral parts of the septum. (2) The septal nacreous layer has a thin, dorsal, structurally modified stratum which is characterized by partially coalesced, thick interlamellar conchiolin membranes. (3) A prismatic layer always occurs on the ventral septal face. In *Nautilus*, this layer usually covers the entire septal face, whereas in the orthoconic cephalopods in question, it was observed only in the central parts of the septum; its actual extension in the latter forms was difficult to establish in the vertical sections here studied.

The ultrastructure of the siphonal tube in the orthoconic cephalopod shows several pronounced differences in comparison with *Nautilus* (see Part I). These differences may be briefly summarized as follows. (1) The septal neck is thin and composed of a continuation of the ontogenetically older (dorsal) half of the septal nacreous layer. The ontogenetically younger (ventral) half of the septal nacreous layer is wedged out and does not take part in the formation of the septal neck. (2) The spherulitic-prismatic layer is absent in the septal neck. (3) The prismatic layer invests the inner face of only the most proximal portion of the septal neck. (4) As in the septal neck, the spherulitic-prismatic layer is absent in the connecting ring. (5) The connecting ring is structurally differentiated into an outer, conchiolin stratum and an inner, prismatic stratum. (6) Only a short distal portion of the connecting ring extends upwards into the cavity of the precedent septal neck, and is fused to the inner prismatic layer of that septal neck. (7) The auxiliary ridge is absent.

The following similarities in the ultrastructural details between the orthoconic cephalopods and *Nautilus* occur. Thus, the conchiolin content in the nacreous layer increases considerably towards the distal end of the septal neck. This brings about structural modifications in the nacreous crystals in that they acquire a more or less prismatic structure. The connecting ring originates from this conchiolin-rich nacreous layer and can therefore be regarded as a modified, uncalcified or partly calcified nacreous layer.

The ontogenetic growth of the siphonal tube. As in *Nautilus* (see Part I), so also in the orthoconic cephalopods, the formation of a new septum commenced with a secretion of a thin conchiolin layer which at the later growth stages covers the surface of the septum, septal neck and connecting ring. Internal to this conchiolin layer, the spherulitic-prismatic layer has been secreted in the peripheral, dorsal portion of the septum proper but not, as in *Nautilus*, in the septal neck and connecting ring.

After this growth stage, the ontogenetically older half of the nacreous layer was secreted in the septum proper, the septal neck and the connecting ring. In the outer stratum of the connecting ring, this layer became entirely uncalcified, whereas in the inner stratum it was partially calcified. Both the septal neck and the connecting ring were completed at the end of this stage. Only the septal nacreous layer continued to grow in thickness during the succeeding secretory phase. Finally, the prismatic layer was deposited on the ventral septal face and on the inner face of the most proximal portion of the septal neck. Thus, in the orthoconic cephalopods, the wall of the siphonal tube in a new chamber reached its full thickness when only half of the total thickness of the adjacent septum proper had been completed. This condition is in agreement with *Nautilus* (see p. 252 in Part I).

The mechanical strength and function of the siphonal tube. The connecting ring in the orthoconic cephalopods is thick and has therefore been strong enough to withstand the same hydrostatic pressures of the sea as *Nautilus* (see p. 253 in Part I). Moreover, it seems to have been as firmly anchored in the conchiolin-rich distal end of the contiguous septal neck as in *Nautilus*. However, its mode of fusion to the preceding septal neck appears to have been less firm than in *Nautilus*. Thus, only a short distal portion of the connecting ring projects into the cavity of the preceding septal neck where it is fused to the inner prismatic layer. The most striking difference is found in the absence of the auxiliary ridge which in *Nautilus* acts as an intermediary for a firm fusion between the connecting ring and the preceding septal neck (see Part I).

The absence of the outer, porous spherulitic-prismatic layer has certainly been of great importance for the hydrostatic function of the siphonal tube in the orthoconic cephalopods. In *Nautilus*, the spherulitic-prismatic layer acts as a wick for "sopping up" of the cameral liquid, and as a reservoir of the liquid adjacent to the epithelium of the siphonal cord. According to Denton and Gilpin-Brown (1966, pp. 741—742), this layer, together with the conchiolin layer on the dorsal septal face, forms the only connexion between the cameral liquid and the siphonal cord as soon as the chamber has been half emptied of its liquid. This "coupling" probably reduced the osmotic stress of the siphonal cord. In the orthoconic cephalopods, the thin conchiolin layer on the surface of the septum, septal neck and connecting ring alone has had the corresponding function. In addition, the occurrence of the prismatic structure of the inner stratum of the connecting ring in the orthoconic cephalopods might have had some unknown relation to the osmotic pump mechanism of the siphonal cord.

Comparisons with other fossil cephalopods. As already pointed out, the taxonomic identification of the Buckhorn asphalt orthoconic cephalopods is difficult. Therefore, it is uncertain whether the orthoconic cephalopods described by Ristedt (1971) from the same formation are identical with my material. However, the schematical illustrations on the structure of the siphonal tube given by Ristedt (1971, Text-fig. 7 *A*, *B*) resemble those in Fig. 1 *A*, *B* of the present paper, although there are several important differences. In Ristedt's figures, the typical nacreous layer decreases distally in thickness in the same manner as in my specimens. The distal end of the septal neck, according to him, is composed of a prismatic layer rich in conchiolin ("Siphowulst"). This layer seems to correspond to the modified nacreous layer with predominantly prismatic structure, described here. In Ristedt's figures, the connecting ring is composed of a thin, outer prismatic layer and a thick, inner conchiolin layer. Moreover, there is a continuous conchiolin lining along the entire inner face of the siphonal tube. In my specimens, the outer prismatic layer of the connecting ring is absent, as well as the inner conchiolin lining of the siphonal tube. The inner stratum of the connecting ring has instead a prismatic structure.

The Pennsylvanian orthoconic cephalopods here described differ considerably from *Orthoceras regulare* Schlotheim and other Ordovician orthocerids. The connecting ring in the latter forms is composed of an outer, porous spherulitic-prismatic layer and probably also of an inner conchiolin layer (unpublished observations), whereas in the Pennsylvanian orthoconic cephalopods, the outer spherulitic-prismatic layer is absent.

On the other hand, the Pennsylvanian orthoconic cephalopods closely resemble the actinocerids in the structure of their siphonal tube in that the latter forms also lack an outer spherulitic-prismatic layer. Moreover, in the Ordovician actinocerid *Adamsoceras* (Mutvei, 1964), and other genera of the family Ormoceratidae, the connecting ring is thick and has a prismatic structure, the prisms being oriented at right angles to the surface of the connecting ring. As described above, the connecting ring in the Pennsylvanian orthoconic cephalopods also has a partly prismatic structure.

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PLATES

All the preparations shown in the following plates were etched for 60 sec. with chromium sulphate.

Plate 1

Fig. 1. Vertical section of a shell wall (× 1120).
Fig. 2. Same section to show the boundary between the outer prismatic and nacreous layers. Note different preservation of these two layers (× 11000).
Fig. 3. Vertical section through the nacreous and inner prismatic layers in the same shell wall, and through the nacreous layer in the mural portion of an adjacent septum (× 2200).
Fig. 4. Detail of *Fig. 3*, showing the boundary between the nacreous and inner prismatic layers of the shell wall (× 5700).
i.pr, inner prismatic layer of the shell wall; *nac*, nacreous layer of the wall; *o.pr*, outer prismatic layer of the shell wall; *sep*, septal nacreous layer.

Plate 2

Figs. 1, 2. Vertical sections of the nacreous layer of a shell wall and a septum, respectively. Note the acicular, vertical crystallites in the nacreous crystals. The nacreous crystals in the shell wall are considerably higher than in the septum (both sections × 10300).
Fig. 3. Vertical fracture plane of the septal nacreous layer (× 6800).
Fig. 4. Horizontal fracture plane of the septal nacreous layer, treated for 6 min. with sodium hypochlorite before etching with chromium sulphate. Note the composition of the nacreous crystals of parallel, narrow, mineral laths (×5100).

Plate 3

Figs. 1, 2. Vertical section through the nacreous and inner prismatic layers of a shell wall, and through the spherulitic-prismatic and nacreous layers of an adjacent septum (× 1100 and × 2200, respectively).
Fig. 3. Detail of the same section to show the acicular crystallites in the inner prismatic layer of the shell wall (× 11000).
Fig. 4. Detail of the same section, showing the boundary between the spherulitic-prismatic and nacreous layers of the septum. Note the structurally modified, dorsal nacreous stratum (× 11000).
d.nac.h, dorsal, structurally modified, stratum of the septal nacreous layer; *i.pr*, inner prismatic layer of the shell wall; *nac*, nacreous layer of the shell wall; *sep*, septal nacreous layer; *sph.pr*, spherulitic-prismatic layer of the septum.

Plate 4

Fig. 1. Vertical section through the central prismatic ridge on the ventral septal face, and through the adjacent septal nacreous layer (× 2200).
Figs. 2, 3. Boundary between the prismatic ridge and the nacreous layer in the same section (× 5500 and × 11000, respectively).
Fig. 4. Detail of the prismatic ridge in the same section to show the granular composition of the acicular crystallites (× 11000).
nac, septal nacreous layer; *pr*, prismatic ridge on the ventral septal face.

Plate 5

Fig. 1. Vertical section through the central prismatic ridge on the ventral septal face and through the septal nacreous layer (× 2200).
Fig. 2. Detail of the same section to show the boundary between the prismatic and nacreous layers. Note the dorsal, structurally modified, nacreous stratum (× 5500).
d.nac.h, dorsal, structurally modified stratum of the septal nacreous layer; *nac*, septal nacreous layer; *pr*, ventral prismatic layer.

Plate 6

Fig. 1. Vertical thin section through a septum, septal neck and parts of the succeeding and contiguous connecting rings (× 40).
Fig. 2. Another vertical thin section through a septal neck and the contiguous connecting ring (× 40).
Fig. 3. Detail of the same thin section (× 110).
conn, connecting rings; *m.nac*, structurally modified nacreous layer; *nac*, nacreous layer; *s.n*, septal neck.

Plate 7

Figs. 1, 2. Vertical section through a septal neck and contiguous parts of a septum. Note the rapid decrease in thickness of the septal nacreous layer at the passage to the septal neck (*Fig. 2*) and the boundary between

the typical and structurally modified nacreous layers in the distal portion of the septal neck (Fig. 1) (× 1400).
m.nac, structurally modified nacreous layer; *nac*, typical nacreous layer; *pr*, prismatic layer on the ventral septal face.

Plate 8

Fig. 1. Vertical section through the proximal portion of a septal neck to show the transformation of the typical nacreous layer into the structurally modified nacreous layer (× 2200).
Fig. 2. Same section, showing the outer (dorsal) conchiolin layer, split up into several sub-layers, and the adjacent nacreous layer (× 2200).
Fig. 3. Vertical section through the dorsal portion of a septum to show the dorsal conchiolin layer, the dorsal, structurally modified nacreous stratum, and the typical septal nacreous layer (× 5000).
d.c.l, dorsal conchiolin layer of the septum and outer conchiolin layer of the septal neck; *d.nac.h*, dorsal, structurally modified stratum of the septal nacreous layer; *m.nac*, strtucturally modified nacreous layer; *nac*, nacreous layer.

Plate 9

Fig. 1. Distal continuation of the section in *Pl. 8*, *Fig. 1*, showing the increase in thickness of the structurally modified nacreous layer (× 2200).
Fig. 2. Detail of the same section, showing the structurally modified nacreous layer. Note the prismatic arrangement of the acicular crystallites and the occurrence of parallel conchiolin membranes (× 5500).
Fig. 3. Detail of the same section to show the transformation of the typical nacreous lamellae into the structurally modified nacreous lamellae (× 5500).
m.nac, structurally modified nacreous layer; *nac*, typical nacreous layer.

Plate 10

Fig. 1. Distal continuation of the section in *Pl. 9*, *Fig. 1*, to show the distal end of the septal neck and a part of the contiguous connecting ring. This part of the septal neck is composed entirely of the structurally modified nacreous layer (× 2200).
Fig. 2. Detail of the same section. Note the prismatic arrangement of the acicular crystallites and the occurrence of numerous, parallel conchiolin membranes (× 5500).
Fig. 3. Vertical section of another septal neck to show the transformation of the typical nacreous layer into the structurally modified nacreous layer (× 6800).
conn, connecting ring; *m.nac*, structurally modified nacreous layer.

Plate 11

Fig. 1. Vertical section through a septal neck and the contiguous part of a septum. The succeeding and contiguous connecting rings are completely recrystallized. Note the extension of the ventral prismatic layer of the septum into the proximal portion of the septal neck (× 550).
Figs. 2, 3. Vertical fracture plane of the structurally modified nacreous layer at the distal end of a septal neck to show the composition of this layer of bundles of prismatic elements which are separated by interspaces, occupied by conchiolin (× 5500 and × 2200, respectively).
conn, connecting ring; *m.nac*, structurally modified nacreous layer; *nac*, typical nacreous layer; *pr*, prismatic layer on the ventral septal face and on the inner face of the septal neck.

Plate 12

Fig. 1. Vertical section through the distal portion of a connecting ring at the preceding septal neck. Note the prismatic structure in the inner stratum of the connecting ring (× 2200).
Fig. 2. Detail of the same section to show the prismatic structure in the inner stratum of the connecting ring (× 5500).
Fig. 3. Vertical section through a connecting ring in the central portion of a shell chamber, showing the composition of the connecting ring of the outer conchiolin stratum and the inner prismatic stratum (× 2200).
Fig. 4. Detail of the same section to show the prismatic structure of the inner stratum of the connecting ring (× 5500).
i.conn, inner prismatic stratum of the connecting ring; *o.conn*, outer conchiolin stratum of the connecting ring.

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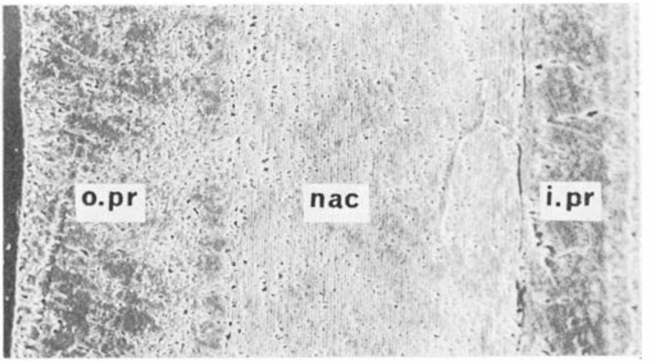

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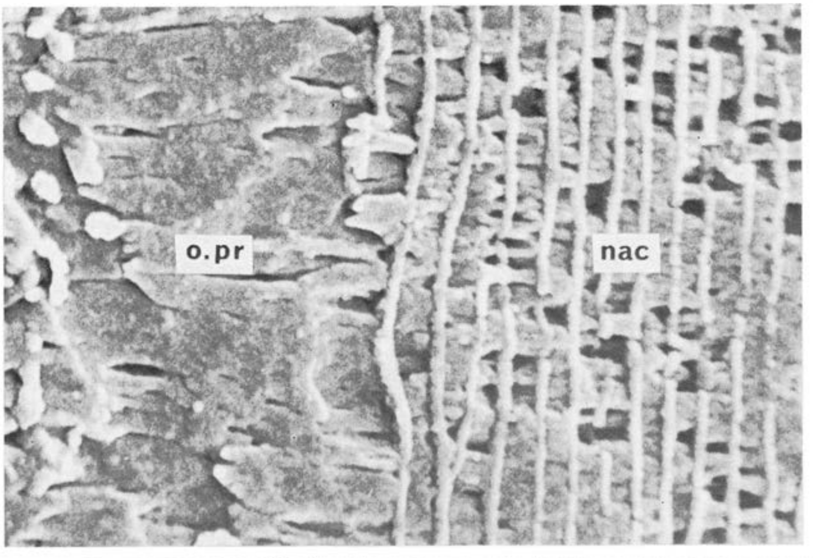

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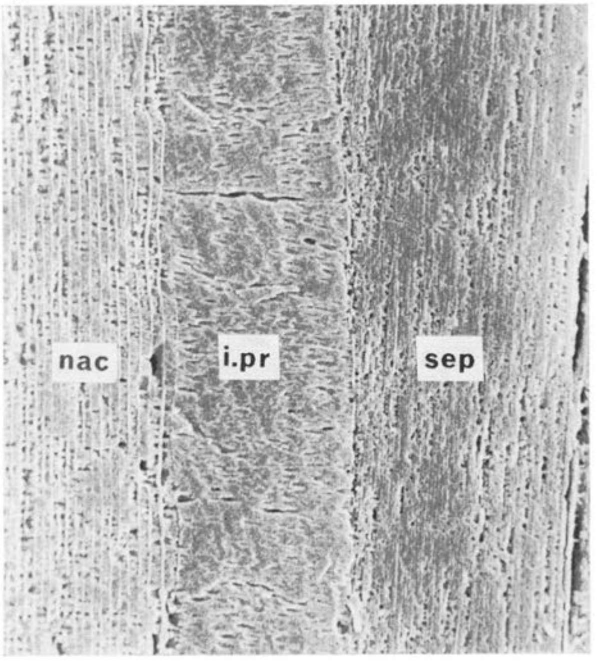

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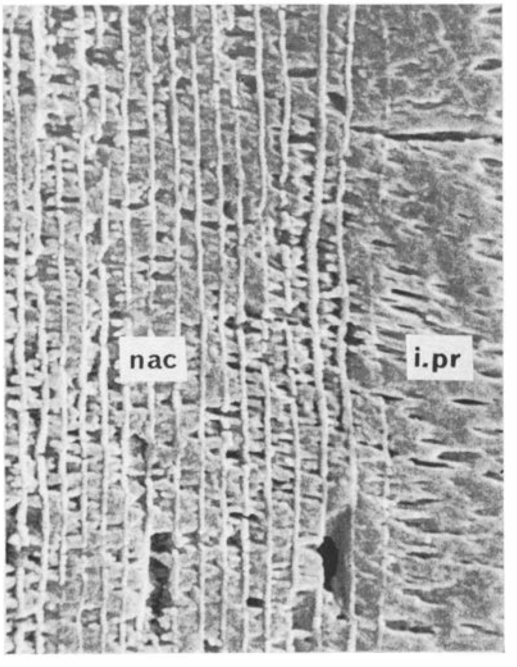

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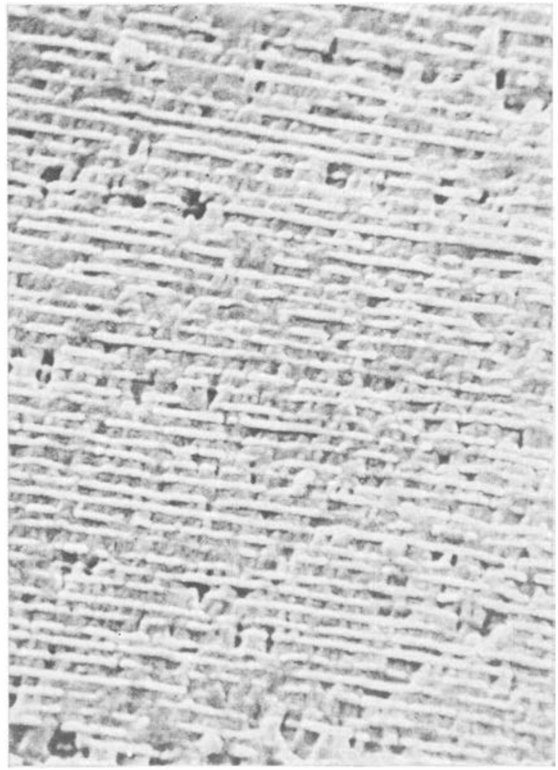

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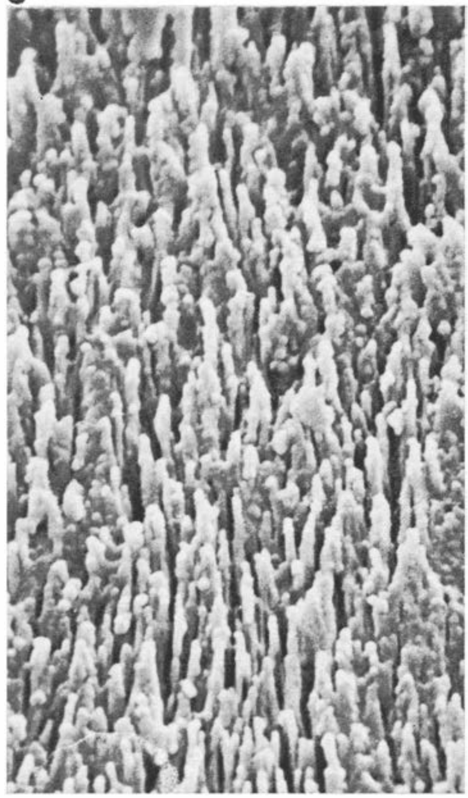

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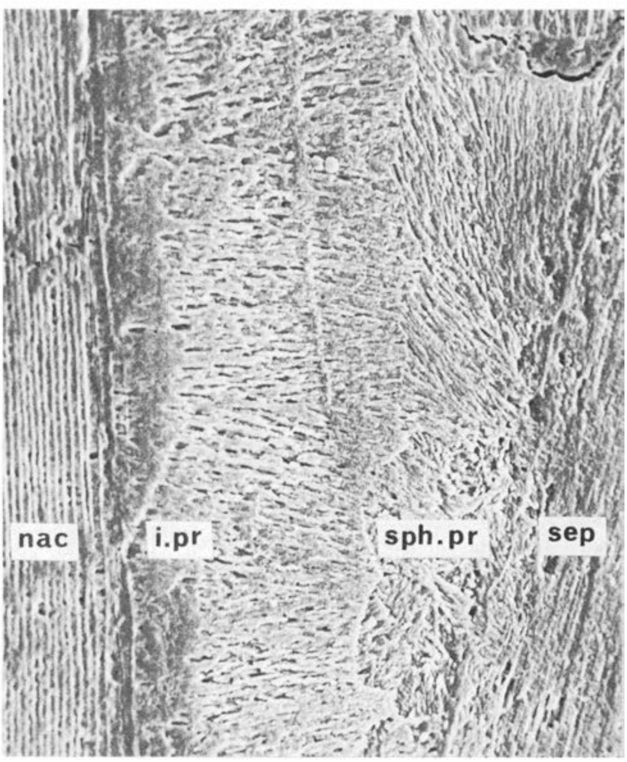

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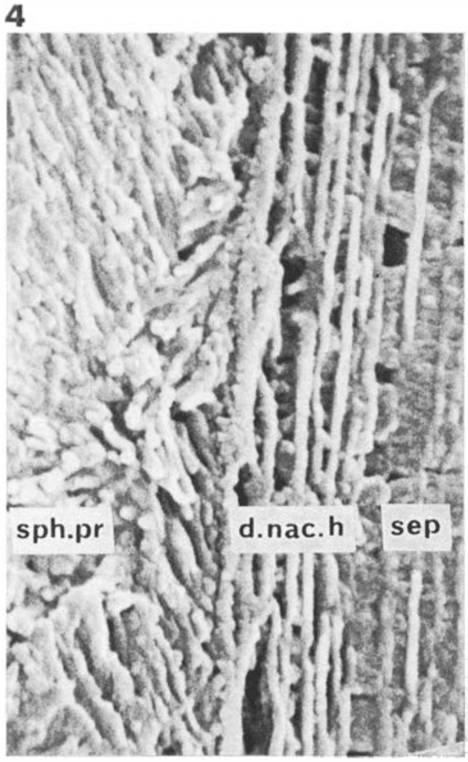

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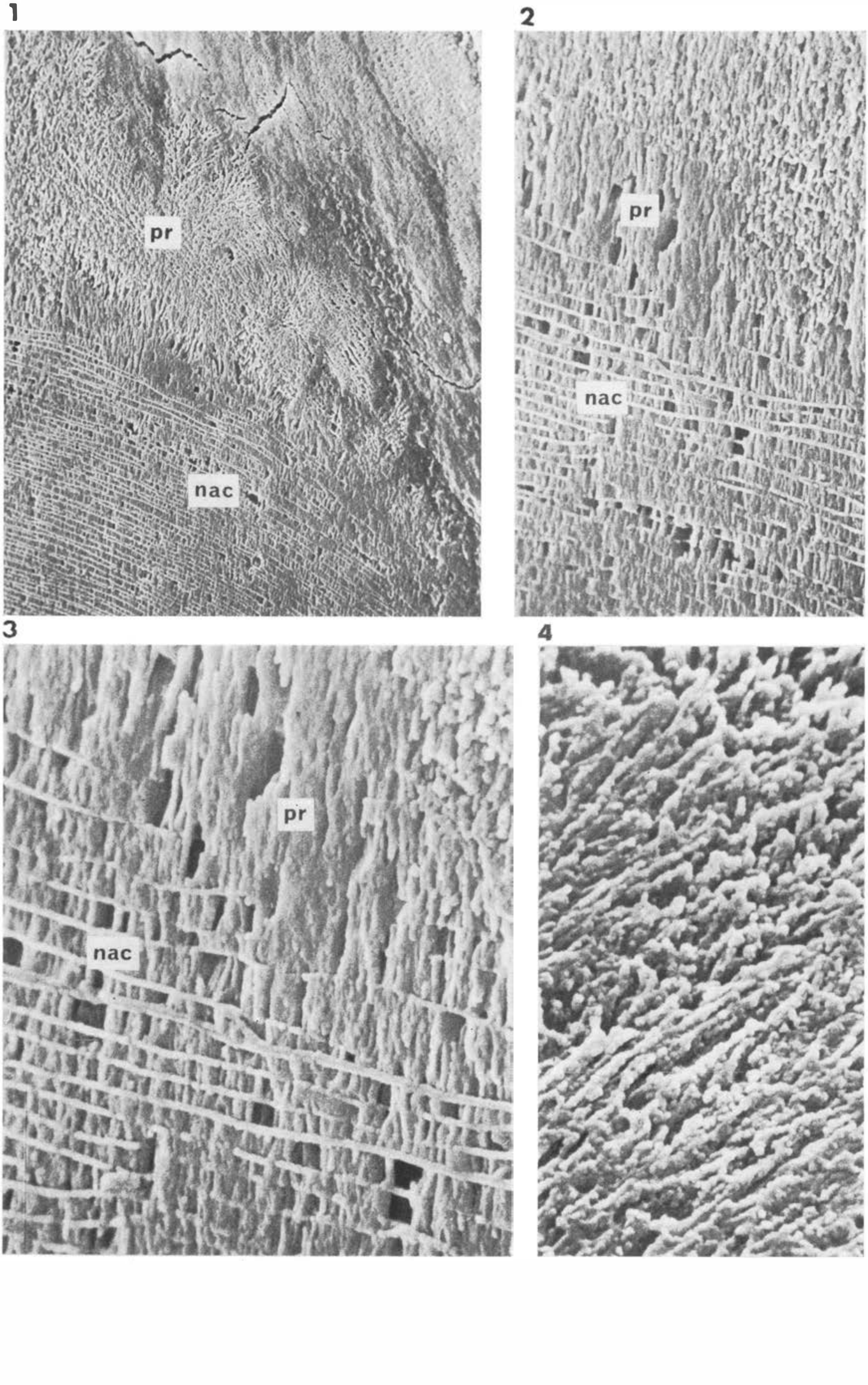

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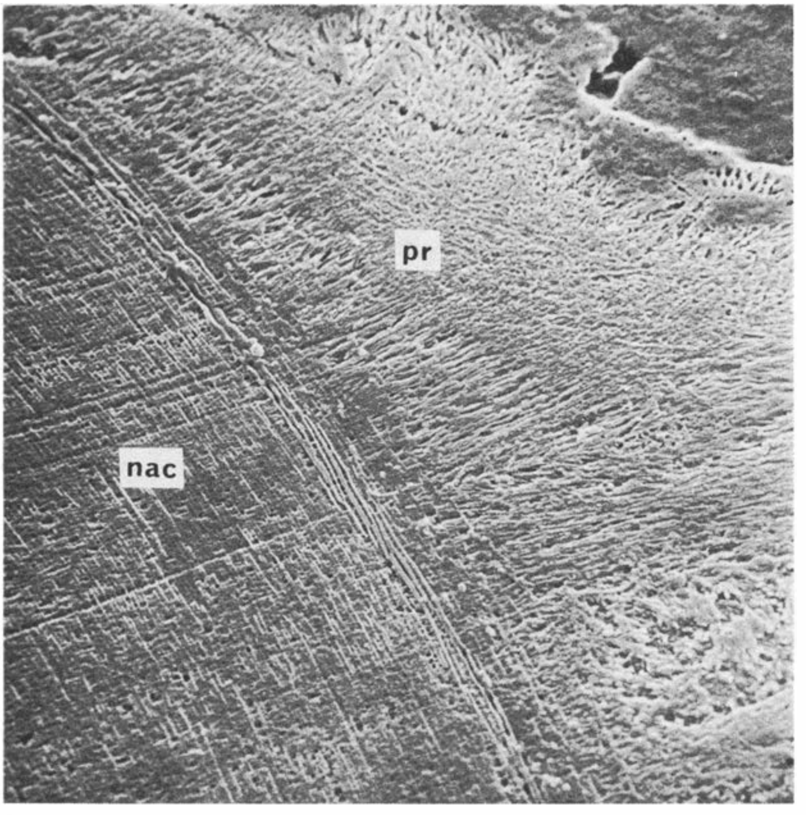

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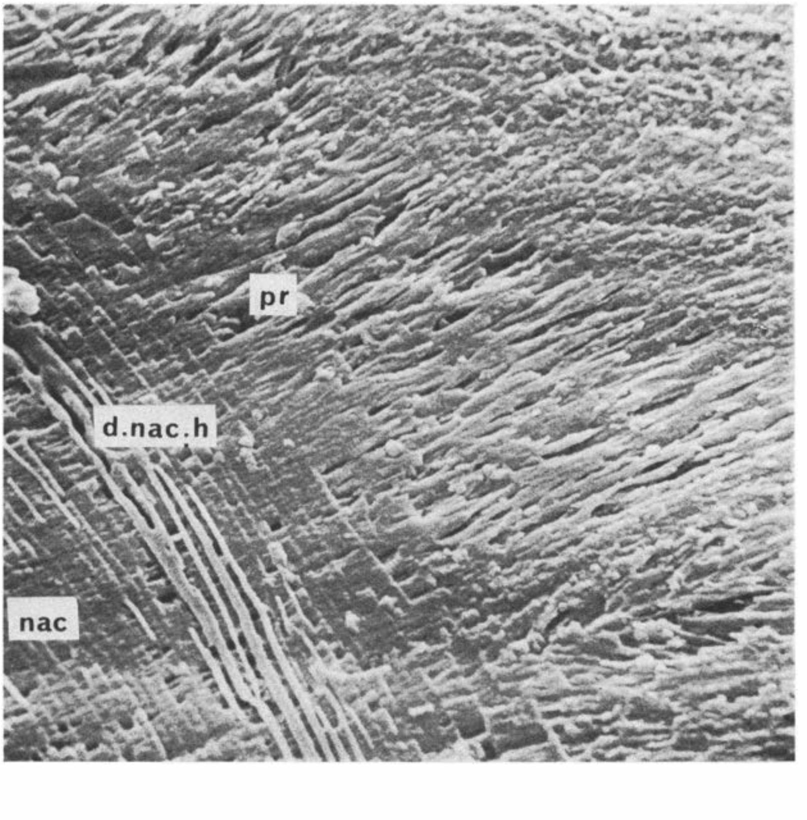

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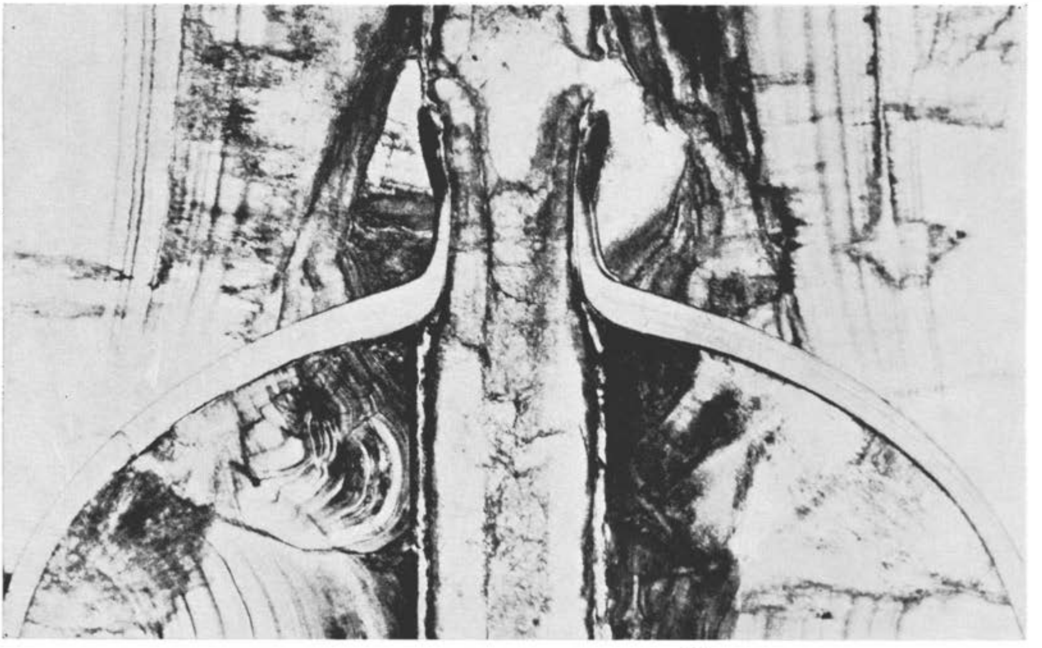

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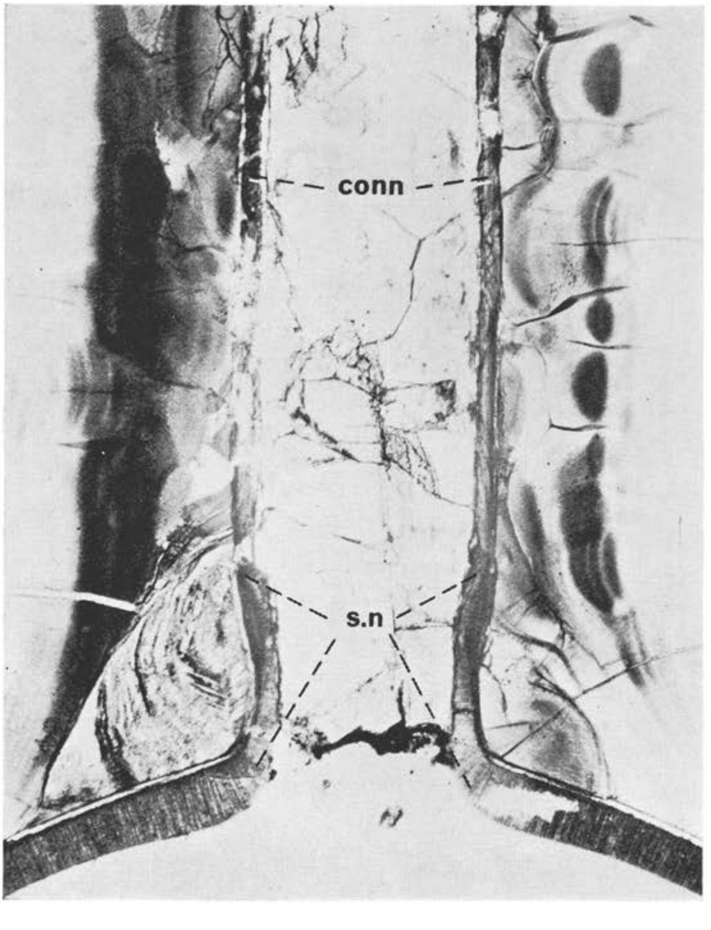

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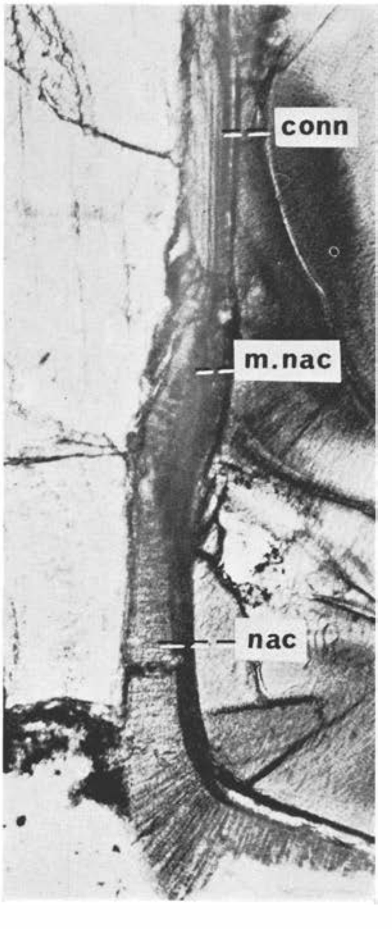

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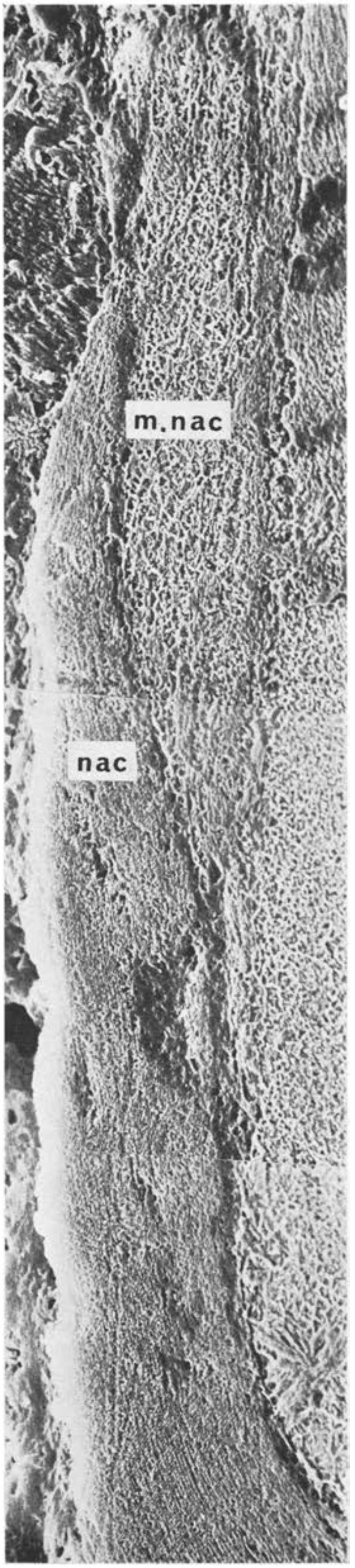

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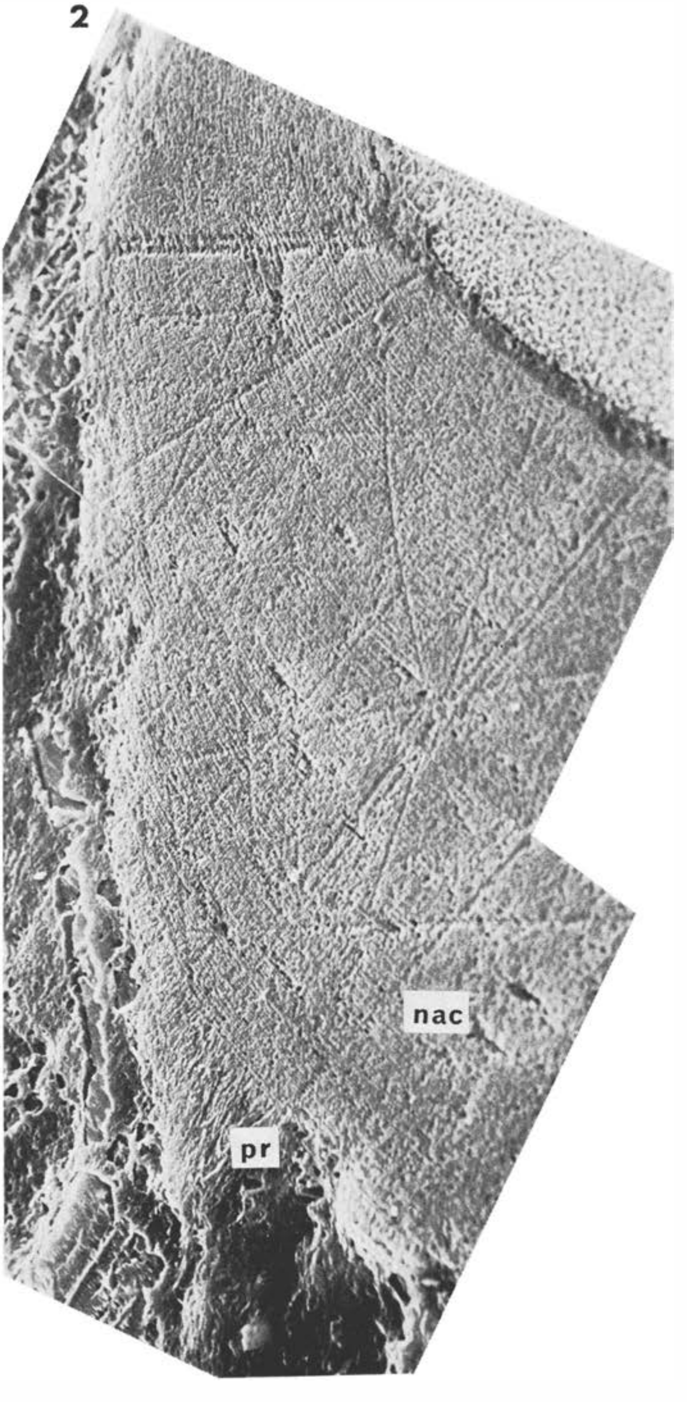

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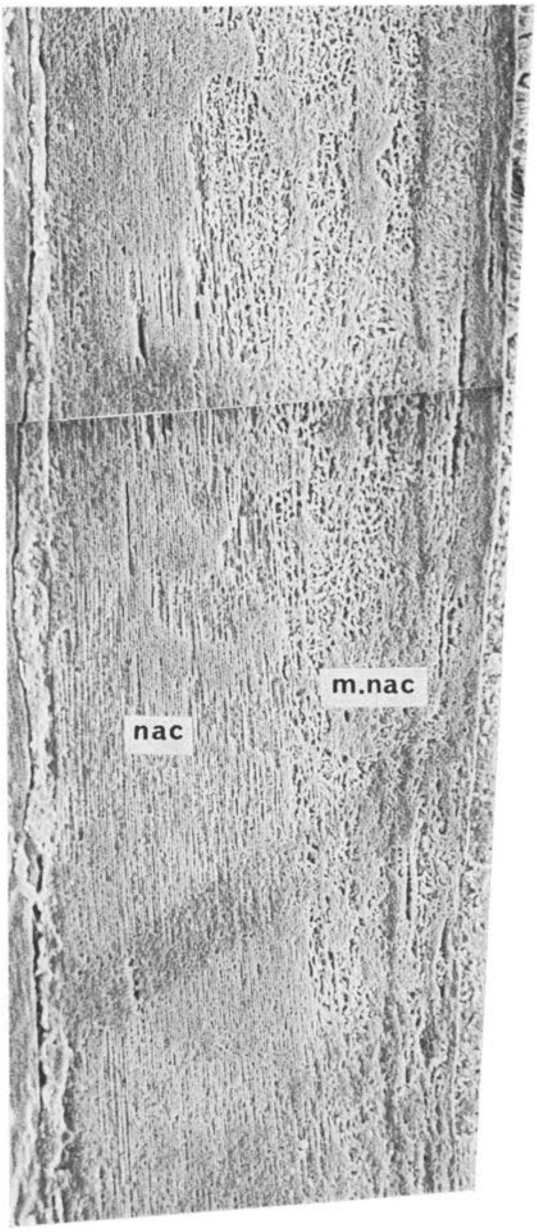

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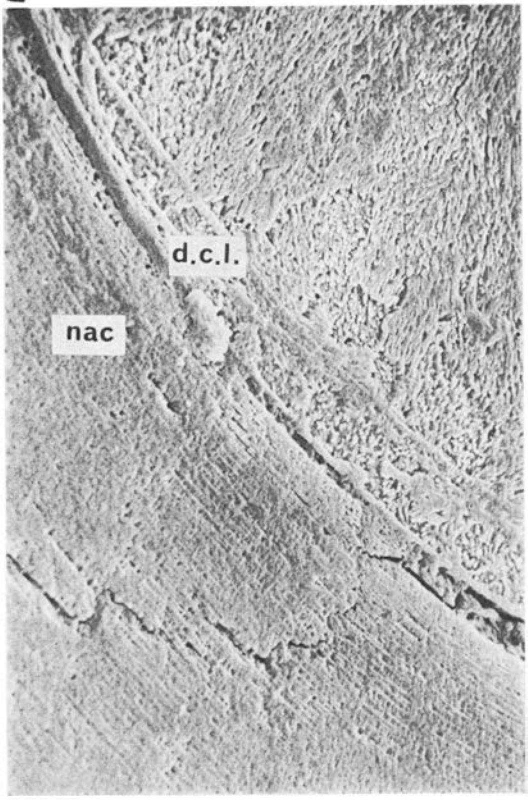

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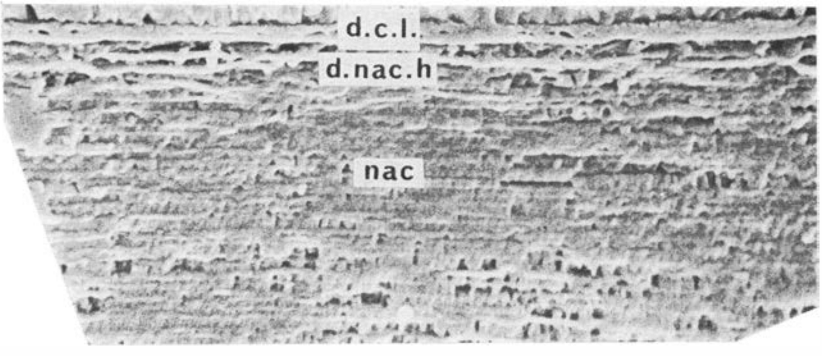

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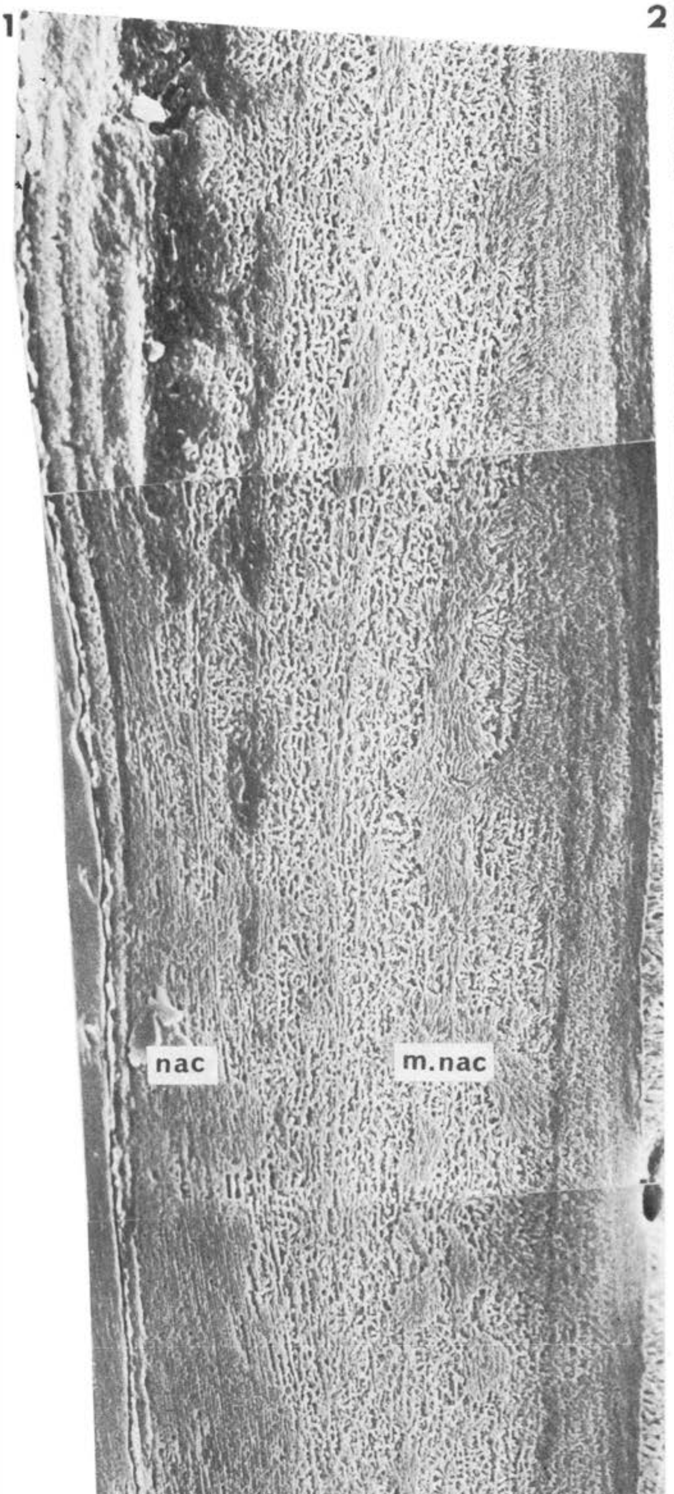

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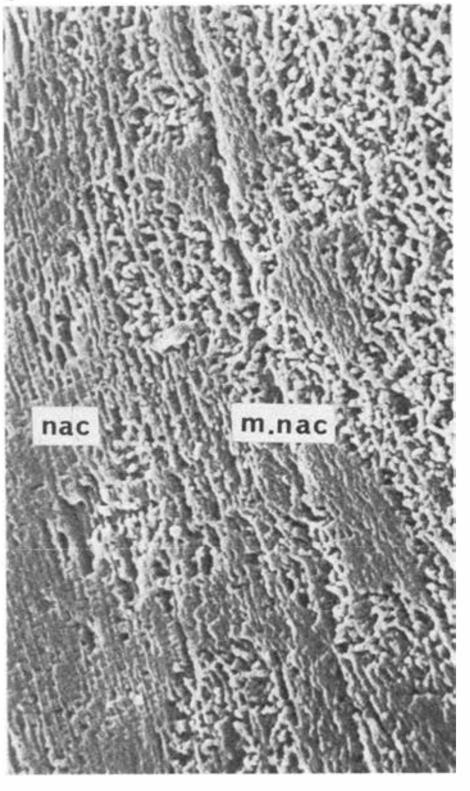

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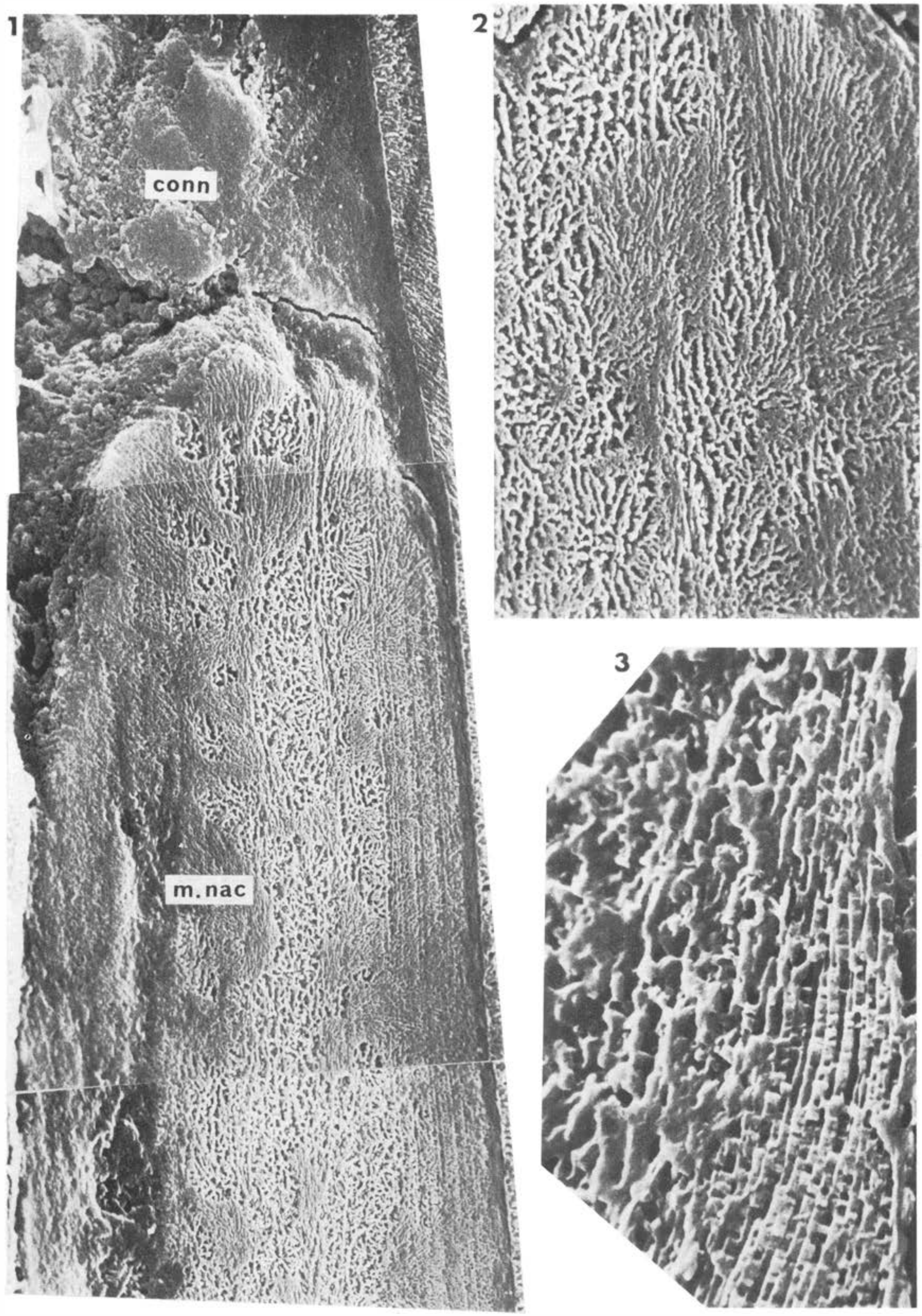

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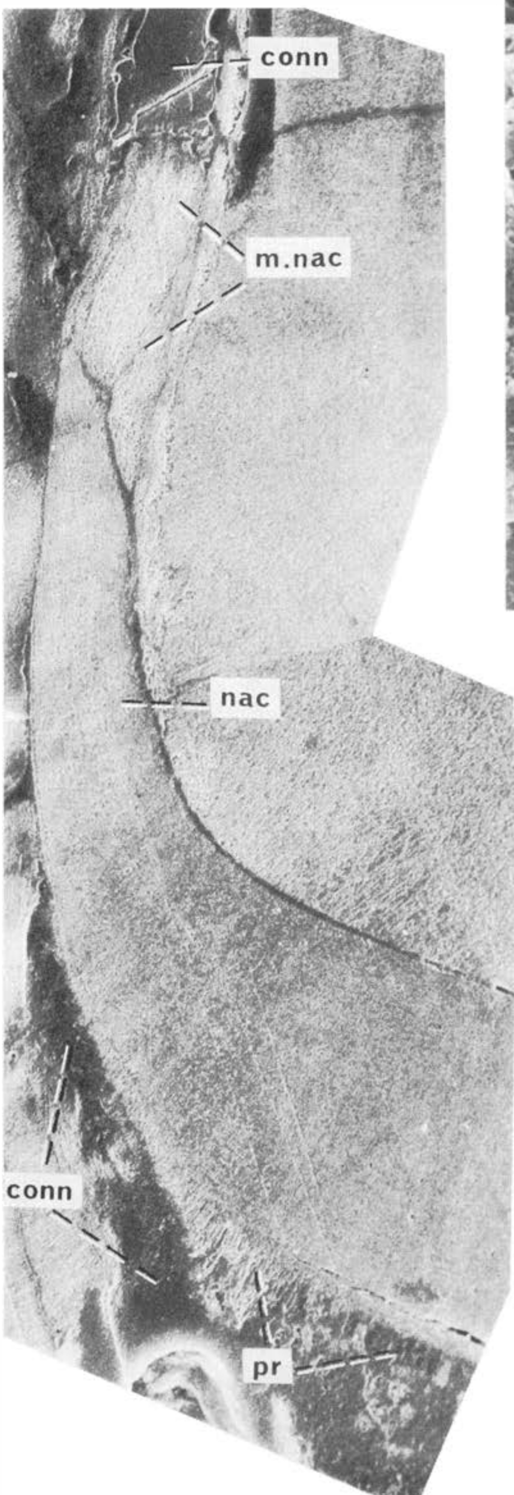

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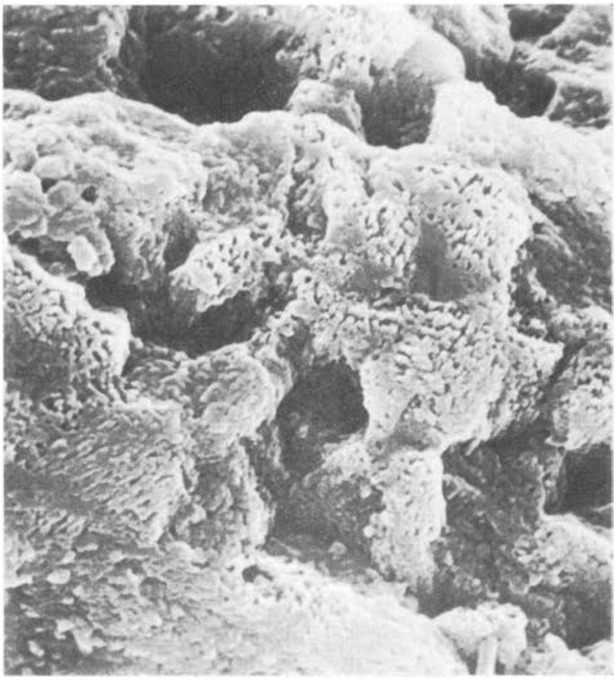

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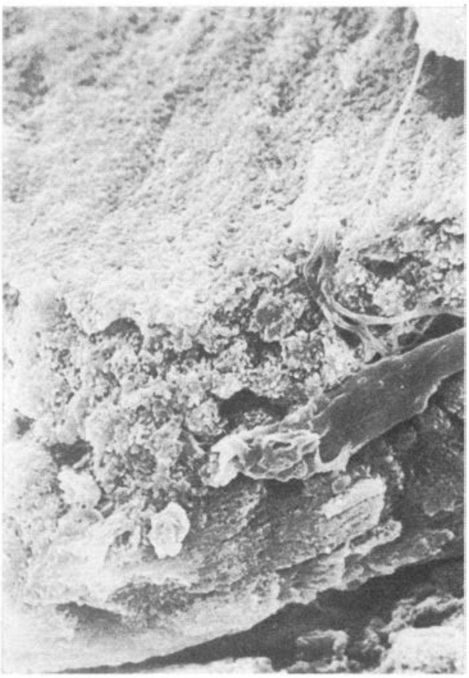

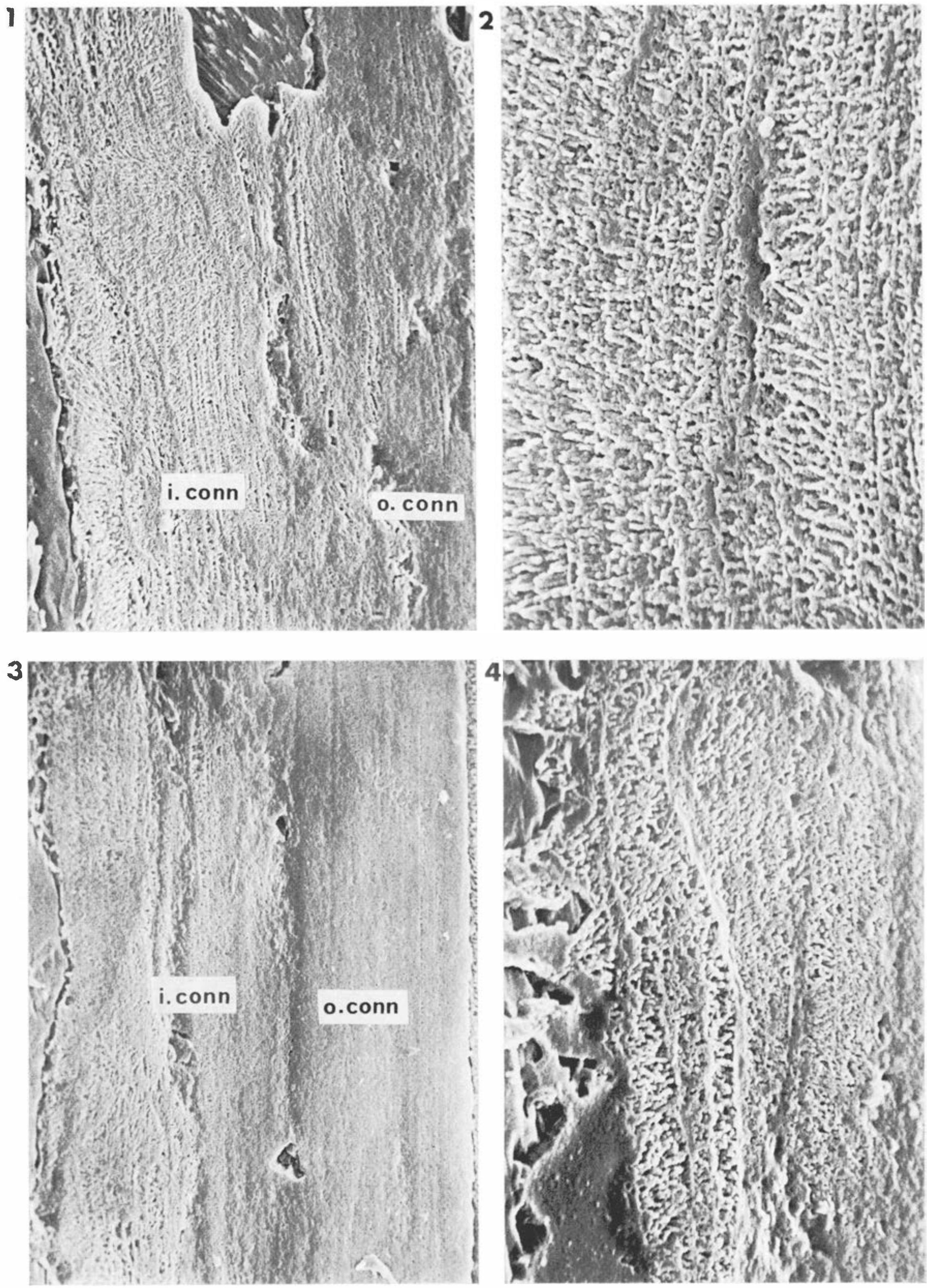
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